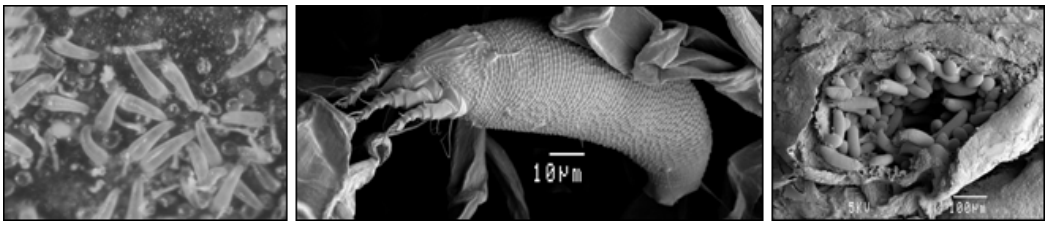
A systematic appraisal of the Eriophyoidea (Acari: Prostigmata)

by

Charnie Craemer



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Philosophiae Doctor in Zoology

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South Africa

Supervisors: Profs. Clarke H. Scholtz and Christian T. Chimimba

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Declaration

I, Charnie Craemer, declare that the thesis/dissertation, which I hereby submit for the degree Philosophiae Doctor in Zoology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE……

DATE……...

Abstract

The diversity of the Eriophyoidea is largely unknown and their systematic study mostly entails alpha-taxonomy which is critically important for these mites. Eriophyoid morphology is almost exclusively studied on slide-mounted specimens, and truly permanent specimen slides cannot be prepared and are eventually lost. Shortcomings in taxon descriptions are persistent, and too few morphological characters are available for systematic use, particularly for phylogenetic studies. The fragile, simplified and minute eriophyoid bodies, and the inadequacy of study methods and technology, including preparation and light microscopy, contribute to these problems. The present eriophyoid classification is widely accepted, relatively stable and useful. The major part of the classification, however, is probably artificial, and some taxon delimitations and identifications are becoming increasingly difficult.

Scanning electron microscopy (SEM) is only sporadically used to supplement conventional descriptions of eriophyoid mites, and their phylogeny has hardly been studied. In the present study some aspects of eriophyoid systematics and its improvements by incorporating SEM for morphological study and phylogenetic analyses for testing and improving the naturalness of the present eriophyoid classification, are used and appraised.

The morphology of about 64 species, mostly from South Africa, was studied with low-temperature (cryo) SEM. The specimens remained turgid and the shape of the mites largely unaltered. A general overview of the contribution of the SEM study towards systematic morphology of the Eriophyoidea is presented. Discrepancies between species descriptions from slide-mounted specimens and the SEM images were found. These include body form, interpretation of structures, resolution and information on minute morphology, and the presence of secretions. Some of these differences were caused by artefacts introduced with slide-mounting of specimens. The SEM study includes a comparative morphological study of the gnathosoma, including a review and appraisal of characters presently used in eriophyoid systematics. New morphological information was found, including new characters that may be of systematic use. Morphology studied with SEM should be routinely incorporated into eriophyoid descriptions, which is not presently the case.

The phylogeny of the Eriophyoidea was studied at genus level, using morphological data, to test the monophyly of the present suprageneric taxa. Three data matrices with 66, 60 and 27 informative characters of 316 (including most *Diptilomiopus* spp.), 64 and 17 eriophyoid ingroup species respectively were analyzed with parsimony analyses, and trees were searched under different parameters. This was done to find different hypotheses regarding the taxon relationships, to roughly assess the robustness of the tree groups, and to use different approaches: a very comprehensive taxon sample, but with low ratio of characters to taxa; an exemplar species sample

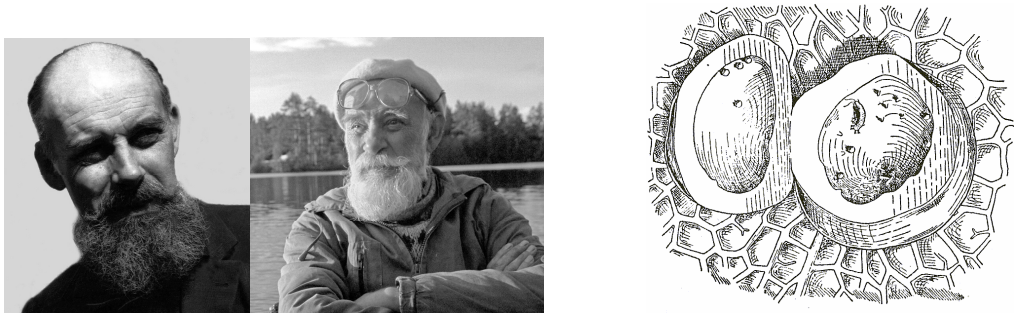
to improve the ratio between characters to taxa; and a very small taxon sample with a good ratio between characters and taxa, but very little inclusion of variation found in the Eriophyoidea. Most groups found were supported only by homoplasy, but many made biological sense and various potentially monophyletic groups, additional to taxa in the present classification, are proposed for further study. The robustness and convergence of these groups on monophyly are discussed. The Phytoptidae was found to be polyphyletic. Part of the Nalepellinae is probably positioned outside the remainder of the Eriophyoidea, while the rest of the Phytoptidae were positioned in smaller subgroups among the Eriophyidae. The Phytoptinae and Sierraphytoptinae, including *Pentasetacus*, may group together. The Eriophyidae never grouped together with much support, and the family is both polyphyletic and paraphyletic. The Diptilomiopidae was largely found to be monophyletic, with a relatively strong phylogenetic structure. The Rhyncaphytoptinae is mainly paraphyletic, and the Diptilomiopinae polyphyletic, but part of the Diptilomiopinae may be monophyletic.

Three new *Diptilomiopus* spp. from South Africa are described as part of the study: *D. faurius* sp. nov. from *Faurea rochetiana* (A. Rich.) Pic. Serm. (Proteaceae); D. *apobrevus* sp. nov. and *D. apolongus* sp. nov. from *Apodytes dimidiata* E. Mey. ex Arn. (Icacinaceae). They were leaf vagrants not causing any observable symptoms.

Key words: Acari, Eriophyoidea, Eriophyidae, Phytoptidae, Diptilomiopidae, systematics, mites, eriophyoid mites, taxonomy, classification, phylogeny, morphology, gnathosoma, worldwide, scanning electron microscopy, SEM, *Diptilomiopus*, new combinations, new species, South Africa

DEDICATION

This dissertation is dedicated to Professor Valeriy Shevchenko (1929 – 2010)[1]

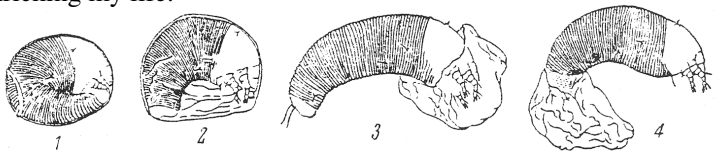


Prof. Valeriy Shevchenko (two photos on left), and a line drawing of an *Eriophyes laevis* colony inside a gall (right), and the "birth" of *E. laevis* (below) (from Shevchenko, 1961). The drawings were scanned from badly photocopied drawings, and the reproductions are not good, but they illustrate Shevchenko's attention to detail.

Valeriy Shevchenko was born on 3 October 1929, in Vladivostok, in the Far East of Russia, but grew up in Leningrad (today St. Petersburg), where he essentially spent his whole life. During his university studies, he chose as his research subject, the then largely unexplored Eriophyoidea (his "Tetrapodili"), and presented the morphology of alder gall mite, *Eriophyes laevis*, for a PhD-degree. Thus began his life-long dedication to the study of these mites at Leningrad State University. He is regarded as the founder of the Russian school of Eriophyoidology.

His research largely concentrated on mite pests of junipers. Early in his career he undertook an expedition into the mountain districts of the Kyrgyz Republic in order to advise the forestry specialists on methods of controlling eriophyoid injury to cultivated juniper trees. He subsequently spent many seasons in these regions, studying the biology and morphology of eriophyoid mites and methods of controlling them. He fell in love with the picturesque nature of central Asia, especially with the mountain forests which are now threatened, exploring it up to the end of his life. He studied different aspects of the evolution of the Eriophyoidea, and his favorite subjects of inquiry remained the Nalepellinae, which live on coniferous trees, and which he believed are the key to understanding eriophyoid evolution. He insisted Eriophyoidea evolution should be examined alongside the evolution of their host-plants. His publications are frequently referred to in the chapter on phylogeny in the present dissertation.

His research on, and his insight in the evolution and phylogeny of the Eriophyoidea prompted me to contact him several years ago. During our ongoing e-mail communication I learned to love and respect him. I found him a fascinating and kind person. Although he dedicated his life to the study of his beloved "four-legged mites", his talents and interests included drawing, public speaking and writing poetry and novels. He also wrote a novel about his famous grandfather "Viktor Vologdin, the welder", and he had a keen interest in Russian politics, and the decline of the Asian forests. We unfortunately seldom discussed the phylogeny of the Eriophyoidea, though, because we planned for me to visit him. Due to my workload and the necessity to first finish my PhD studies, the visit never realized. It was with shock that I learned of his death, at the age of 80, on 22 March 2010, with the sickening realization that I will never have the privilege to meet him in person and discuss the phylogeny of the Eriophyoidea with him. I dedicate this dissertation to him and thank him for his contribution to enriching my life.



[1] Some information in this dedication is from Sukhareva & Chetverikov (2010).

ACKNOWLEDGEMENTS

First, I thank my promoters, **Profs. Clarke Scholtz** and **Chris Chimimba**, for accommodating me as their student, and their support and patience even when the study became long overdue. Thanks also for their noteworthy improvements of the final versions of the dissertation. Sincere thanks to **Prof. Ansie Dippenaar-Schoeman** for her endless encouragement and support. She helped me to commence the study, and finish it, and improved some parts of the dissertation. Without her back up at work and during difficult periods, and moments of crises, it would not have been possible. I cannot have a better role model to follow for becoming an outstanding and productive scientist. *Dankie, Ansie*! Thanks to **Prof. Eddie Ueckermann**, my mite colleague, who is the kindest person I know, and who took over the responsibility for some of the plant-feeding mite groups, to allow me to concentrate on the Eriophyoidea. He also assisted me in choosing the outgroup species and naming their structures.

Thanks to **Prof. Stefan Neser**, an amazing scientist and naturalist, who put me on the path of studying the Eriophyoidea. Without him, any significant biosystematic research on the Eriophyoidea in South Africa probably would not have commenced, and most of the research on these mites in this country is based on material he collected, including most of the specimens used in the present study.

Special thanks to **Alan Hall** who assisted me throughout the SEM study, and who prepared and set up the microscope and specimens for each session. Without him, the results of the SEM study would not have attained the quality it did. He improved some of the procedures, and went to utmost trouble to ensure that we got the best from each session, despite the antics of the microscope. He took real interest in the study, and went far beyond his duty, sometimes with personal sacrifices, in keeping the facility working and to my disposal even to late in the evenings. It was a pleasure to work with him. He also improved the Materials and Methods concerning the SEM study in this dissertation.

My gratitude to **Dr. Pablo Goloboff** for the workshop he presented in South Africa on using TNT, and the insight I gained from his lectures in several aspects of phylogeny. The phylogenetic analyses in the present study were not possible in any other program, and without TNT, this part of the study would not have had usable results. Thanks also to Dr. Goloboff for assistance with some problems I encountered in the program. Thanks to **Prof. Tim Crowe** who initiated and organized this workshop, and to the South African Biosystematics Initiative of the National Research Foundation of South Africa who funded it. Thanks also to **Dr. Steve Farris**, one of the "fathers" of cladistics who co-presented the workshop. Meeting him will always remain an inspiration.

Professional and personal thanks to **Dawid Swart**, my husband. It is well known that one's close family sacrifices much during a doctorate study. Dawid did not just endure this with staying power and with nonstop support; he gives me extraordinary space to lead my own life and follow

my career and enabled my finishing this study. He also spent many hours in editing and improving this dissertation, and checking endless details. *Baie dankie, Dawid*!

I thank the **University of Pretoria** for financial assistance with some of my registration and course fees, and for the use of their infrastructure, in particular the SEM facilities; the **Department of Zoology and Entomology** of this university for allowing me to register for the degree; and the **Agricultural Research Council – Plant Protection Research Institute** (ARC–PPRI) who allowed me to combine some of the research at work with the research towards partial fulfilment of this degree.

My sincere gratitude to my overseas colleagues for their support and assistance, and for their friendship:

- **Prof. Jim W. Amrine jr**, of the University of West Virginia, USA, who, despite his overwhelming work load always answered my questions, of which the *personal communications* attributed to him in this dissertation attest.
- The late **Prof. Valeryi Shevchenko** for continuous e-mail communication (also see dedication above).
- **Prof. Enrico de Lillo** of the University of Bari, Italy, who evaluated an early draft of Chapter 3 (the SEM study) and gave me invaluable advise about my reasoning and interpretation of results, and for his special friendship.
- **Dr. Ron Ochoa** of the USDA, Beltsville, USA, for inviting me to visit him during the study, during which he, among other guidance, exposed me to his phylogenetic research on mites, including his preliminary analyses of the Phytoptidae (see Chapter 4). He also edited an early draft of the phylogenetic results regarding the Phytoptidae. His enthusiasm and love for mites, and nonstop energy, is an inspiration.
- **Prof. Angie Chandrapatya** who edited an early draft of an annotated species list of *Diptilomiopus* who never made it into the final dissertation, and for lending me specimens of *Diptilomiopus* spp. she described, and also thanks to **Dr. K.-W Huang** for the *Diptilomiopus* specimens I borrowed from him.
- **Dr. Mariam Lekveishvili** for giving me information about her molecular study on the Eriophyoidea.
- **Dr. Evert Lindquist** for warning me about testing for birefringence before a structure can be considered a seta.
- Also thanks to **Drs. Sebahat Ozman Sullivan, C.H.W. Flechtmann, Denise Navia, Anna Skoracka, Brian Fenton, Carl Childers, Danuta Knihinicki, Eric Palevsky, Tom Morley**, in no order of importance.

My sincere thanks to my colleagues particularly at ARC-PPRI, and elsewhere in South Africa, for their support and interest in the study, and for their friendship:

- **Riaan Stals** for his valuable discussions on systematics and particularly phylogeny and for his advise which always taught me something. He also provided me with some core cladistic articles. He is a never-ending source of knowledge, and his enthusiasm for science is an inspiration.
- **Beatrix Sunkel**, **Lindie Steynberg** and **Tshidi Makutoane** for general assistance throughout the years.
- **Johan Coetzer** who assisted me in getting the best computer facilities he could, got an extra computer for me to ran the analyses, and who always goes out of his way to help with any computer problems, far beyond his duty.
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- **Elsa van Niekerk** for the design of the dissertation cover, and assistance with printing the dissertation.
- **Dr. Antoinette Swart** for reviewing the "alpha and omega" (the first drafts of the Introduction and General Conclusions).
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On a personal note, I thank my mother, **Henriëtte Craemer**, who is a constant source of support and love in my life. She frequently asked whether it is worthwhile to continue with something that is causing me so much stress, which actually helped to strengthen my resolve to finish it. Also thanks to my aunt, Sallaum, for her interest, and particularly in when I am going to finish. Special thanks to Drs. Engela Young, Adéle Potgieter, and to Isabel Botha, and two horses, Mona and Wyn.

Finally yet importantly, thanks to all the researchers who spent endless hours in describing these smallest of mites. Without their data, this study would not have been possible.

DISSERTATION OUTLINE AND CONTENT

Prologue: A brief introduction to the Acari including classification of the Acari, and biology and ecology of the Eriophyoidea.

Chapter 1: Aims, scope and approaches of this study, followed by a brief review of the evolution, diversity and systematics of the Eriophyoidea.

Chapter 2: General material and methods. A relational database with descriptive data captured from published descriptions, including 304 species records and 400 descriptive fields each, has been prepared to provide data for the present study. In particular, electronic procedures, formats and programs for capturing and structuring descriptive data are proposed and discussed.

Chapter 3: A systematic morphological study of the Eriophyoidea utilizing low-temperature scanning electron microscopy (LT-SEM). It includes an appraisal of some of the characters and character states used in eriophyoid systematics, with emphasis on artefacts caused by slide-mounting; and additional information from SEM studies. The morphology of *ca.* 64 species from South Africa was studied, and includes a comparative morphological study of the gnathosoma based on SEM study. Characters which have not previously been used for eriophyoid systematics are described and their potential systematic usefulness is appraised.

Chapter 4: Phylogenetic parsimony analyses of the Eriophyoidea under different parameters to study relationships between mostly type species of genera worldwide, and to test monophyly of suprageneric groups. Monophyly of suprageneric groupings are appraised and hypothetically monophyletic groups within the Eriophyoidea are identified and proposed for further study.

Chapter 5: General conclusions.

Apart from other Appendices: An article describing three new *Diptilomiopus* spp. from South Africa, which will be submitted to *Systematics and Biodiversity*, is included (Appendix M).

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CHAPTER 3: MORPHOLOGY AND SYSTEMATICS

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Appendix B. Characters coded for phylogenetic analyses: definition, description and discussion.

Appendix C. Character numbers of characters in all analyses.

Appendix D. Data matrix for 318-taxon analyses.

Appendix E. Abbreviated character definition for 66-taxon analyses.

Appendix F. Data matrix for 66-taxon analyses.

Appendix G. **G.1.** Character definition for 18-taxon original and corrected analyses.

G.2. Character definition for 18-taxon modified analyses.

Appendix H. **H.1.** Original data matrix (Hong & Zhang, 1996a) for 18-taxon analyses.

H.2. Corrected data matrix for 18-taxon analyses.

H.3. Modified data matrix for 18-taxon analyses.

Appendix I. Glossary.

Appendix J. Published abstracts 1 & 2.

J.1. Craemer, C. & Hall, A.N. 2003. The use of low-temperature scanning electron microscopy for studying eriophyoid mites (Acari: Eriophyoidea). p. 76 In: *Proceedings of the Microscopy Society of Southern Africa* 33.

J.2. Craemer, C. 2006. Morphology of eriophyoid mites (Eriophyoidea) as elucidated by scanning electron microscopy: trivial pursuit or valuable systematic contribution? p. 45 In: Bruin, J. (Ed.). *Abstract Book.* 12th International Congress of Acarology, 21-26 August 2006, Amsterdam, The Netherlands.

Appendix K. Published article 3.

Craemer, C.; Amrine, J.W. Jr.; De Lillo, E. & Stasny, T.A. 2005. Nomenclatural changes and new synonymy in the genus *Diptilomiopus* Nalepa, 1916 (Acari: Eriophyoidea: Diptilomiopidae). *International Journal of Acarology* 31: 133–136.

Appendix L. Published article 4.

De Lillo, E.; Craemer, C.; Amrine, J.W. Jr. & Nuzzaci, G. 2010. Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). *Experimental and Applied Acarology* 51: 283–307. DOI 10.1007/s10493-009-9311-x

Appendix M. Submitted article 5.

Craemer, C. 2010. Description of three new *Diptilomiopus* spp. (Eriophyoidea: Diptilomiopidae) from South Africa. (will be submitted to *Systematics and Biodiversity*)

LIST OF FIGURES

PROLOGUE

CHAPTER 3

Except where otherwise indicated, all figures in chapter 3 are SEM images.

Trisetacus cupressi Keifer, 1944, drawings by H.H. Keifer, reproduced from Keifer (1944): **h)** internal genitalia (modified from Keifer, 1944), **i)** coxi-genital area. All reproductions with permission where necessary.

Fig. 3.6. Legs and leg structures of adult eriophyoid females. Legs of *Aculops rhodensis* (Keifer, 1957) as drawn by E. de Lillo, from De Lillo (1988): **a)** leg I; **b)** leg II. Different shapes of eriophyoid empodia (featherclaws) of various species: **c)** *Cecidophyes rouhollahi*, drawing by C. Craemer (reproduced from Craemer *et al*., 1999); **d)** *C. rouhollahi*, drawing by H.H. Keifer (reproduced from Craemer *et al*., 1999); **e)** *Dicrothrix anacardii* Keifer, 1966 (reproduced from Keifer, 1966b); **f)** *Dechela epelis* Keifer, 1965 (modified from Keifer, 1965a); **g)** *Acaphyllisa parindiae* Keifer, 1978 (reproduced from Keifer, 1978); **h)** *Diptilomiopus faurius* sp. nov. (Appendix L); **i)** *Acarhis lepisanthis* Keifer, 1975 (reproduced from Keifer, 1975d); **j)** *Acarhynchus filamentus* Keifer, 1959 (reproduced from Keifer, 1959b); **k)** *Diptiloplatus megagrastis* Keifer, 1975 (reproduced from Keifer, 1975c); **l)** *Acritonotus denmarki* Keifer, 1962 (reproduced from Keifer, 1962b); **m)** *Brevulacus reticulatus* Manson, 1984, protogyne female (modified from Manson, 1984a); **n**) *Aberoptus samoae* Keifer, 1951, leg I (modified from Keifer, 1951).

Fig. 3.7. Unmodified SEM images: **a)** Specimens of *Cecidodectes euzonus* Nalepa, 1917 among erineum hairs caused by them on *Trema orientalis*, illustrating the difficulty to sometimes find the mites within complicated plant structures when viewed in a SEM. This and the need to view them from different aspects, creates the need to mount them individually for systematic purposes; **b)** Individual of *Aberoptus*, probably new species, *in situ* on a *Schotia brachypetala* leave - note the good turgor, with no apparent shape distortion, of both plant and mite material, including mite eggs; **c**) *Tergilatus sparsus* Meyer & Ueckermann, 1995 on *Portulacaria afra* – a piece of plant material (leave in this case) with live mites *in situ*, mounted on adhesive carbon tape; **d)** individual mites of *Meyerella bicristatus* (Meyer, 1989) from *Mystroxylon aethiopicum* stuck onto adhesive carbon tape to facilitate observation of different aspects of the mite specimens.

Fig. 3.8. (continued on next page) Dorsal views of legs of: **a)** *Trisetacus* sp. (Phytoptidae: Nalepellinae: Trisetacini), bud mite on *Pinus pinaster*; **b)** *Diptilomiopus faurius* sp. nov. (Diptilomiopidae: Diptilomiopinae), leaf vagrant on *Faurea rochetiana*; **c)** *Cecidophyopsis* sp. (Eriophyidae: Cecidophyinae: Cecidophyini), leaf vagrant on *Yucca guatemalensis*, **d)** *Afromerus* sp. (Eriophyidae: Cecidophyinae: Colomerini), leaf galls on *Psydrax livida*, (the fine cracks are artificial, caused by deterioration of specimen in SEM); **e)** unknown family (Eriophyoidea), vagrant on green fruit of *Anthocleista grandiflora*. Solid white arrows: dorsal completeness of margin between femur and genu on leg I, and presence, position and number of spines on this margin; solid black arrows: ornamentation on femur of leg I; open arrows: shape of tibia of leg I.

Fig. 3.8. (continued from previous page) **f, g)** *Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini), vagrant on *Lantana trifolia*; **h)** leg I and **i)** leg II of *cf. Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini), leaf vagrant on *Psydrax livida*; **j)** *Acalitus mallyi* (Eriophyidae: Eriophyinae: Aceriini), leaf galls on *Vangueria infausta* subsp. *infausta*; **k)** *cf. Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini), leaf galls on *Acacia rehmanniana*; **l)** *Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini), erineum and distortion on *Ipomoea batatas* var. *batatas*. Solid white arrows: dorsal completeness of margin between femur and genu on leg I, and presence, position and number of spines on this margin; solid black arrows: ornamentation on femur of leg I; open arrows: shape of tibia on leg I; white triangles: segment margins on which spicules are present.

Fig. 3.9. *Diptilomiopus faurius* sp. nov. from *Faurea rochetiana* (Appendix L), ventral view of leg I, with a pattern of ridges, **a)** clearly visible in the SEM images, but, **b)** barely visible in the slide-mounted specimens. This descriptive drawing was drawn from the specimen with the most complete visibility of these ridges.

Fig. 3.10. Empodium on tarsus of leg I of *Diptilomiopus faurius* sp. nov. (Appendix L) from *Faurea rochetiana*: **a)** dorsal view depicting shape, **b)** lateral view facilitating count of rays – the empodium of this species has eight rays.

Fig. 3.11. Distal parts of tarsi with focus on the empodia: **a)** *Trisetacus* sp. from *Pinus pinaster*; **b)** *Cecidophyopsis* sp. from *Yucca guatemalensis*; **c)** *Shevtchenkella* sp. from *Psydrax livida*; **d)** unknown species from *Dovyalis*; **e)** unknown species from *Faurea rochetiana*; **f)** *Acalitus mallyi*; **g)** *Aceria* sp. from *Ipomoea batatas*; **h)** unknown species from *Apodytes dimidiata*.

Fig. 3.12. External female genitalia of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995): **a)** slide-mounted specimen (holotype) viewed with phase contrast; **b)** drawing made from slide-mounted specimen; **c)** SEM image of same area in another specimen. Drawing reproduced from the original unpublished drawing with permission from the authors.

Fig. 3.13. Ambulacra with tenent hairs: **a)** leg II of an *Aponychus* sp. (Tetranychidae) from *Solanum mauritianum*; **b)** leg I of a species of the Tenuipalpidae from a *Senecio* sp.; **c)** leg I of a species of the Stigmaeidae from *Apodytes dimidiata*. Empodia with slightly knobbed hairs or rays (*Tydeus*) and "tenent" hairs or rays (*Aberoptus*) of: **d)** leg I of *cf. Tydeus* sp. (Tydeidae) from *Ekebergia capensis* Sparrm.; **e, f)** leg II of an *Aberoptus* sp. (Eriophyidae) from *Schotia brachypetala*; **a, c, f)** scale lines = 10 µm; **b, d, e)** scales line = 1 µm. Arrows pointing towards tips of hairs of rays, with an enlarged drawing of the tip of the ray of the empodium of the *Aberoptus* sp. in image 3.13f.

Fig. 3.14. Microtubercles of *Aceria* sp. nov. from *Ipomoea batatas*: dorsally on first annuli behind the prodorsal shield rear margin - **a, b)** SEM images, **d)** line drawing; dorsally on rear caudal annuli - **c)** SEM image, **f)** line drawing; on ventral annuli about between setae e - **g)** line drawing, **h)** SEM image; on rear, caudal ventral annuli - **e)** line drawing, **i)** SEM image; all scale lines = 10 µm except **h)** scale line = 1 µm.

Fig. 3.15. *Meyerella bicristatus* (Meyer, 1989b), leaf vagrant on *Mystroxylon aethiopicum* subsp. *aethiopicum*: **a)** SEM image of dorso-lateral aspect (scale line = 10 µm); **b)** part of slide-mounted specimens (female) viewed with phase contrast light microscopy in lateral view; **c)** line drawing (reproduced from the original drawing by Meyer with permission) of the specimen digitally imaged in 3.15b. Arrows indicating: ribs or striae on lobes in SEM image; striae very vaguely present in this one slide-mounted specimen of a series of about 100 specimens in which they were invisible (the lines are hardly visible in the printed copy, but when this image is enlarged on screen, the lines are vaguely visible); and the lobes are smooth in the descriptive drawing.

Fig. 3.16. (continued on next page). *Tergilatus sparsus* Meyer & Ueckermann, 1995, leaf vagrant on *Portulacaria afra*: SEM images (a, d, f, h, j), line drawings (c, d, g) [from Meyer & Ueckermann (1995)],and slide mounted specimens viewed with phase contrast (b, i, j, k): **a)** dorsal view; **b, c)** lateral view; **d)** ventral view; **e, f)** enlargement of opisthosomal microtubercles, alternatively lateral and dorsal; **g, h)** dorsal view; **i)** dorsal view of opisthosomal rear end; **j, k, l)** prodorsum (lateral in j, dorsal in k, l) including rear shield margin and first dorsal annuli; **a, d, h, l)** scale lines = 10 µm; **f)** scale line = 1 µm. Open arrows - rear end of opisthosoma; solid black arrows - first annulus behind rear prodorsal shield margin, orange arrow - pointing towards dorsal microtubercles in drawing and SEM image.

Fig. 3.17. *Tetra retusa* Meyer, 1992 from *Bauhinia galpinii* (Meyer, 1992b): **a, c, e)** wax secretions and enlargements thereof on about the entire body, but particularly on the ridges of the opisthosoma and prodorsal shield, all specimens in dorsal view; **b)** descriptive drawing (Meyer, 1992b) in dorsal view, without the wax, which was also not mentioned in the text description. *Calacarus* sp. from *Searsia lancea* (previously *Rhus lancea*): **d)** dorso-lateral aspect of the prodorsum with wax formations, the image of a specimen with some of the wax disturbed and broken off was chosen to be presented, to illustrate the inside and structure of wax cells; **a, d, e)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.18. Spermatophores of *Aculus* sp. from *Lantana trifolia*: **a)** with sperm packet in tact; **b)** without sperm packet. Possibly *Rhynacus* sp. from *Mystroxylon aethiopicum* subsp. *aethiopicum*: c) eggs and immatures.

Fig. 3.19. Eriophyoid gnathosoma: **a)** dorsal view; **b)** line drawing of gnathosoma in image 3.19a; **c)** ventral view; **d)** line drawing of the gnathosoma in image 3.19c. Scale lines = 1 µm.

Fig. 3.20. (continued on next page). Gnathosoma of a *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini): **a)** ventral view; **b)** ventro-lateral view; **c)** line drawing of image 3.20a; **d)** line drawing of image 3.20b; **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm. * These are preliminary new names or terms devised in the present study for these gnathosomal structures on the ventral aspect of eriophyoid mites. ** This structure was named the "basal palp segment" (Keifer, 1975a) or the "oral plate". It is just ahead of the coxal plates of coxae I, and it is situated about on the same vertical level as the pharyngeal pump.

Fig. 3.20. (continued from previous page). Eriophyoid gnathosomas in ventral view. *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from a *Pinus* sp.: **e)** SEM image; **f)** line drawing of image 3.20e. *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Psydrax livida*: **g)** SEM image; **h**) line drawing of image 3.20g; **e, f)** scale lines = 10 µm; **g, h)** scale lines = 1 µm. Key to colours in drawings on previous page.

Fig. 3.21. Eriophyoid gnathosoma: Ventral views of the mostly the infracapitulum and part of the pedipalpi and palpcoxal plate of various species to show the differences in structures. The shape of the ventral part of the stylet sheath is visible between the free palp-segments. Its shape is probably strongly influenced by the angle at which imaged, and the anteriad extension of the gnathosoma at the moment of cryo freezing. However, there are some obvious differences in shape not influenced by these factors, that may be of use in classification and phylogeny. The data was not evaluated and this figure purely demonstrates that there are indeed differences that may be of systematic use. The colours correspond to probably homologous areas between the species, and the key to the colours is given on the first page of Fig. 3.20. The longer scale lines = 10 µm, and the three shortest scale lines = 1 µm.

Fig. 3.22. Eriophyoid gnathosoma. The gnathosoma of all the Eriophyoidea except the Diptilomiopidae has relatively short and straight chelicerae, and the short-form oral stylet: **a)** digital image of slide-mounted specimen viewed with light microscope; **c)** SEM image of lateral view. "Diptilomiopid"-like gnathosoma with large chelicerae sharply bent down at the base and the long-form oral stylet: **b)** digital image of slide-mounted specimen, **d, e)** lateral views of gnathosomas. Scale lines = 10 µm.

Fig. 3.23. Different hypotheses regarding the homology of the pedipalpal segments of the Eriophyoidea with other Acariform pedipalpi: **a, b)** segments according to Lindquist (1996a), *but according to him the first free segment is a fusion of the trochanter, femur and genu, the genu, however, is dorsally fused with the other segments, but ventrally separated from them; **c)** segments according to Keifer (1959a); **d)** segments according to Keifer (1975a).
Scale lines = 10 µm.

Fig. 3.24. Dorsal view of gnathosomas of **a)** *Cecidophyopsis selachodon*; **b)** *C. grossulariae*; **c)** *C. aurea* and **d)** *C. alpina*. cr = cheliceral retainer. Below drawings with species names are the descriptions of the cheliceral retainers from Amrine *et al.* (1994). Cheliceral retainers of *C. ribis* are not depicted in Amrine *et al.* (1994). Drawings were scanned from Amrine *et al.* (1994) (with permission from the author), and were cropped and enlarged or made smaller so that scale lines (10 µm) are all the same length, and thus drawings are at about the same scale.

Fig. 3.25. Gnathosoma of *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from *Pinus pinaster*: **a, b)** dorsal views (probably adults, gender unknown), blue arrows are indicating droplet-like structures that are probably not part of the mite, but artefacts; **c)** line drawing of image 3.25a, red line indicating length of palpcoxal base, blue line indicating distance of seta *ep* from distal margin of palpcoxal base, from base of seta, shortest distance to apical margin; **d)** line drawing of enlargement of "cheliceral lock mechanism" in dorsal view image 3.25b; **e)** dorsolateral view (probably adult, gender unknown); **f)** ventral view (male). Scale lines = 10µm.

Fig. 3.26. Gnathosoma of *Setoptus radiatae* Meyer, 1991 (Phytoptidae: Nalepellinae: Nalepellini) from *Pinus radiata*: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (female); **c)** line drawing of image 3.26a; **d)** lateral view (probably adult, gender unknown). Scale lines = 10µm.

Fig. 3.27. Gnathosoma of *Mackiella* sp. (Phytoptidae: Sierraphytoptinae: Mackiellini) from *Phoenix reclinata*: **a)** dorsal view (probably adult, gender unknown); **b)** line drawing of image 3.27a; **c)** lateral view (male); **d)** ventral view (male); **e)** line drawing of image 3.27d; **a, b)** scale lines = 1 µm; **c, d, e)** scale lines = 10 µm.

Fig. 3.28. Gnathosoma of *Aberoptus* sp. *cf. Aberoptus* sp. nov. (Eriophyidae: Aberoptinae) from *Schotia brachypetala*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female); **c)** line drawing of image 3.28a, red line indicating length of palpcoxal base, blue line indicating distance of seta *ep* from distal margin of palpcoxal base, from base of seta, shortest distance to apical margin; **d)** ventral view (female); **a, c)** scale lines = 1 µm; **b, d)** scale lines = 10 µm.

Fig. 3.29. (continued on next page). Gnathosoma of *Cecidophyopsis* sp. *cf. Cecidophyopsis hendersoni* (Keifer, 1954) (Eriophyidae: Cecidophyinae: Cecidophyini) from *Yucca guatemalensis*: **a)** dorso-lateral view (female); **b)** dorsal view (possibly immature based on gnathosoma morphology); **c)** line drawing of image 3.29a, showing broken off setae which is possibly an artefact caused by cryo-praparation; **d)** enlargement of protuberances basally on the chelicerae; **e)** dorso-lateral view of gnathosoma of just-born larva still emerging from egg; **a, c, e)** scale lines = 10 µm; **d)** scale line = 1 µm.

Fig. 3.29. (continued from previous page). Gnathosoma of *Cecidophyopsis* sp. *cf. Cecidophyopsis hendersoni*: **f)** ventral view (female); **g)** lateral view, gnathosoma with apical palp segments telescoping for feeding (female); **h)** lateral view (female); **i)** line drawing of image 3.29j; **j)** ventro-lateral view of gnathosoma (female); **f, g, h, j)** scale lines = 10 µm; **i)** scale line = 1 µm.

Fig. 3.30. Gnathosoma of *Afromerus lindquisti* Meyer, 1990 (Eriophyidae: Cecidophyinae: Colomerini) from *Psydrax livida*: **a)** dorsal view (female); **b, c)** ventro-lateral views (males); **a, b)** scale lines = 1 µm; **c)** scale line = 10 µm.

Fig. 3.31. Gnathosoma of *Ectomerus* sp. *cf. E. systenus* Meyer, 1990 (Eriophyidae: Cecidophyinae: Colomerini) from *Terminalia sericea*: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (female); **c)** dorso-lateral view (probably adult, gender unknown); **a, c)** scale lines = 1 µm; **b)** scale line = 10 µm.

Fig. 3.32. Gnathosoma of *Neserella* sp. *cf. N. tremae* Meyer & Ueckermann, 1989 (Eriophyidae: Cecidophyinae: Colomerini) from *Trema orientalis*: **a)** dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (immature); **c)** lateral view (probably adult, gender unknown); **d)** line drawing of image 3.32b; **e)** ventral view (female); **a, b, d)** scale lines = 1 µm; **c, e)** scale lines = 10 µm.

Fig. 3.33. (continued on next page). Gnathosoma of *Acalitus mallyi* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Vangueria infausta* subsp. *infausta* leaf galls: **a)** dorsal view (probably adult, gender unknown); **b)** digitally captured image of dorsal view of a slide-mounted female specimen; **c)** line drawing of image 3.33a; **d)** line drawing of part of image 3.33b; **a, c)** scale lines = 1 µm; **b, d)** scale lines = 20 µm.

Fig. 3.33. (continued from previous page). Gnathosoma of *Acalitus mallyi*: **e)** ventral view (female); **f)** ventro-lateral view (female); **g)** lateral view (female); **h)** line drawing of image 3.33f; **i)** line drawing of image 3.33g; **j)** digital image captured of slide-mounted female specimen, outline of flap extension of coxal plate very unclear, traced with a red stipple line; a knob-like structure in a hollow formed by the anterior edge of the ventral coxal base indicated by the green arrows; **e, g, i)** scale lines = 10 µm; **f, h)** scale lines = 1 µm; **j)** scale line = 20 µm.

Fig. 3.34 (continued on next page). Gnathosoma of *Aceria lantanae* (Cook, 1909) (Eriophyidae: Eriophyinae: Aceriini) from *Lantana* x *camara* (hybrid complex) flower galls: **a, b)** dorsal views (probably adults, gender unknown); **c)** line drawing of image 3.34a; **d)** enlargement of cheliceral protuberances in image 3.34b. Scale lines = 1 µm.

Fig. 3.34. (continued from previous page). Gnathosoma of *Aceria lantanae*: **e)** lateral view (female); **f)** line drawing of image 3.34e; **g, h)** ventral views of the same specimen (female); **e, f, g)** scale lines = 1 µm; **h)** scale line = 10 µm.

Fig. 3.35. Gnathosoma of *Aceria ocellatum* Meyer & Ueckermann, 1990 (Eriophyidae: Eriophyinae: Aceriini) from *Searsia lancea* (previously *Rhus lancea*) leaf galls: **a)** dorsal view (probably adult, gender unknown); **b)** dorsal view (immature); **c)** dorso-lateral view (probably adult, gender unknown); **a)** scale line = 1 µm; **b, c)** scale lines = 10 µm.

Fig. 3.36. Gnathosoma of *Aceria* sp. *cf. A. dichrostachyia* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Dichrostachys cinerea* subsp. and var. unknown: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorso-lateral view (larva); **c)** line drawing of image 3.36a; **d, e)** lateral view of the same specimen (female); **f)** ventral view (female); **a, c)** scale lines = 10 µm; **b, d, e, f)** scale lines = 1 µm.

Fig. 3.37. Gnathosoma of *Aceria* sp. *cf. A. giraffae* Meyer, 1990 (Eriophyidae: Eriophyinae: Aceriini) from *Acacia erioloba*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** enlargement of cheliceral protuberances in image 3.37a; **d)** dorso-lateral view (probably adult, gender unknown); **a, b)** scale lines = 10 µm; **d)** scale line = 1 µm.

Fig. 3.38. Gnathosoma of *Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Chrysanthemoides incana*: **a)** dorsal view (probably adult, gender unknown); **b)** line drawing of image 3.38a; **c)** lateral view (female); **d)** ventral view (female); **e)** ventral view (male); **a, b, c, e)** scale lines = 1 µm; **d)** scale line = 10 µm.

Fig. 3.39. Gnathosoma of *Aceria* sp. nov. females (Eriophyidae: Eriophyinae: Aceriini) from *Chrysanthemoides monilifera* subsp. *monilifera*: **a)** dorso-lateral view; **b)** ventro-lateral view; **c)** lateral view; **d)** ventro-lateral view of apical tip of the pedipalpi; **a, b)** scale lines = 10 µm; **c, d)** scale lines = 1 µm.

Fig. 3.40. Gnathosoma of *Aceria* sp. *cf. A. proteae* Meyer, 1981 (Eriophyidae: Eriophyinae: Aceriini) from *Protea caffra* subsp. *caffra*: **a)** dorsal view (probably adult, gender unknown); **b)** dorsal view (larva); **c)** lateral view (female); **d, e)** ventro-lateral views (females); **a, b, e)** scale lines = 1 µm; **c, d)** scale lines = 10 µm.

Fig. 3.41. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Ipomoea batatas* var. *batatas*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably larva); **c)** enlargement of cheliceral protuberances in 3.41a; **d)** line drawing of image 3.41a. Scale lines = 1 µm.

Fig. 3.41. (continued from previous page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **e)** dorso-lateral view (male); **f)** lateral view of basal part of gnathosoma (female); **g)** ventro-lateral view (female); **h)** ventral view (female); **e, h)** scale lines = 10 µm; **f, g)** scale lines = 1 µm.

Fig. 3.42. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Oxalis corniculata*: **a)** dorsal view (probably adult, gender unknown), white arrows indicate seta *ep* (closest to chelicerae), and two protuberances on the side of it; **b)** line drawing of image 3.42a; **c)** enlargement of cheliceral protuberances in image 3.42a; **d)** enlargement of seta ep on the right hand side of the specimen in 3.42a and the first protuberance alongside it; **e)** enlargement of seta *ep* and two protuberances indicated by white arrows in image 3.42a, also here indicated by white arrows; **f)** seta *ep*, and seta (still unnamed, but mentioned in the text description) alongside it on the gnathosomal palpcoxal base of *Acaphyllisa limitata* (redrawn from Flechtmann & Etienne, 2001), which might be homologous with the first protuberance alongside seta *ep* in the *Aceria* sp. from *O. corniculata*; **g)** lateral view (probably adult, gender unknown) with black arrows indicating the first protuberance next to seta *ep*. Scale lines = 1 µm.

Fig. 3.42. (continued from previous page).Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **h)** ventro-lateral view (male), some detail enhanced with black drawing line to make it more visible; **i)** ventro-lateral view (male); **h)** scale line = 10 µm; **i)** scale line = 1 µm.

Fig. 3.43. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Acacia rehmanniana*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorso-lateral view (larva), some lines traced in black to make them more clear; **c)** enlargement of cheliceral protuberances in image 3.43a; **d)** ventral view (female); **e)** ventro-lateral view (female); **f)** lateral view (female); a rounded bump each side laterally on ventral palpcoxal base (indicated by white arrows in images e and f; **a, b, f)** scale lines = 1 µm; **d, e)** scale lines = 10 µm.

Fig. 3.44. (continued on next page). Gnathosoma of unknown genus, nr. *Aceria* (Eriophyidae: Eriophyinae: Aceriini) from *Apodytes dimidiata* subsp. *dimidiata* flower buds: a, **b)** dorsal views (the same specimen, probably adult, gender unknown); **c)** line drawing of image 3.44a; **d)** enlargement of cheliceral protuberances in 3.44b. Scale lines = 1 µm.

Fig. 3.44. (continued from previous page). Gnathosoma of unknown genus, nr. *Aceria*: **e)** ventro-lateral view (male); **f)** dorso-lateral view (probably adult, gender unknown); **g)** line drawing of image 3.44e; **h)** ventro-lateral view (female); **e, g, h)** scale lines = 1 µm; **b)** scale line = 10 µm.

Fig. 3.45. Gnathosoma of *cf. Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini) from *Cineraria* sp. blisters: **a)** lateral view (female); **b, d)** ventral views of the same specimen (female); **c)** dorsal view (probably adult, gender unknown); **a, c)** scale lines = 1 µm; **b, d)** scale lines = 10 µm.

Fig. 3.46. Gnathosoma of *Aceria* sp. (probably a new species) (Eriophyidae: Eriophyinae: Aceriini) from *Xymalos monospora*: **a)** dorsal view (probably adult, gender unknown); **b, c)** ventral views of the same specimen (female); lateral view (female); **a, c)** scale lines = 10 µm; **b, d)** scale lines = 1 µm.

Fig. 3.47. Gnathosoma of *Tumescoptes* sp. *cf. T. dicrus* (Eriophyidae: Phyllocoptinae: Acaricalini) from *Phoenix reclinata*: **a)** ventro-dorsal view (female); **b)** bifurcate setae *d* enlarged to show tiny side branch (probably adult, gender unknown); **c)** enlargement of cheliceral protuberance in image 3.47a; **d)** venro-lateral view (female). Scale lines = 1 µm.

Fig. 3.48. (continued on next page). Gnathosoma of a *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Searsia lancea* (previously *Rhus lancea*): **a)** lateral view (female); **b)** dorso-lateral view (female); **c)** line drawing of image 3.48a. Scale lines = 10 µm.

Fig. 3.48. (continued from previous page). Gnathosoma of a *Calacarus* sp.: **d)** ventral view (female); **e)** ventro-lateral view (female); **f)** line drawing of "oral plate" area of image 3.48d, names for different areas are preliminary. Scale lines = 10 µm.

Fig. 3.49. Gnathosoma of a *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Faurea rochetiana*: **a, b)** lateral view of the same specimen (probably adult, gender unknown). Scale lines = 10 µm.

Fig. 3.50. Gnathosoma of a *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Psydrax livida*: **a)** dorsal view (probably adult, gender unknown), in vagrants, like this *Calacarus* sp., the frontal lobe obscures the gnathosoma which is also usually more hypognathous in these species, in dorsal view; **b)** lateral view (probably adult, gender unknown); **c, d)** ventro-lateral views of the same specimen (female); **a, b, c)** scale lines = 10 µm; **d)** scale line = 1 µm.

Fig. 3.51. Gnathosoma of a *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Psydrax livida*: **a)** gnathosoma obscured by frontal lobe in dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (male); **c)** ventral-dorsal view (female), note extrusion of possibly several gnathosomal stylets closely fitted against each other from the stylet sheath; **d)** ventro-lateral view male; **a, b, d)** scale lines = 10 µm; **c, e)** scale lines = 1 µm.

Fig. 3.52. Gnathosoma of a *Shevtchenkella* sp. *cf. S. rhusi* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Searsia lancea* (previously *Rhus lancea*): **a)** frontal lobe largely obscures gnathosoma in dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (probably adult, gender unknown); **c)** ventro-lateral view (female); **a, c)** scale lines = 10 µm; **b)** scale line = 1 µm.

Fig. 3.53. Gnathosoma of a *Neoshevtchenkella* or *Shevtchenkella* sp. (with wax) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Celtis africana*: **a)** dorso-ventral view (female); **b)** lateral view (female). Scale lines = 10 µm.

Fig. 3.54. Gnathosoma of a genus *cf. Calepitrimerus* (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Celtis africana*: **a, b)** ventral view of the same specimen (female); **c)** dorso-lateral view (female); **d)** enlargement of cheliceral protuberances in image 3.54c; **e)** dorso-lateral view (probably adult, gender unknown); **a, e)** scale lines = 1 µm; **b, c)** scale lines = 10 µm.

Fig. 3.55. Gnathosoma of *Cecidodectes euzonus* Nalepa, 1917 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Trema orientalis*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** lateral view (probably adult, gender unknown); **d)** ventro-lateral view (female); **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm.

Fig. 3.56. Gnathosoma of a *cf. Phyllocoptes* sp. (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Anthocleista grandiflora*: **a)** dorsal view (probably adult, gender unknown); **b)** enlargement of the cheliceral protuberances in 3.56a; **c)** lateral view (female); **d)** line drawing of cheliceral protuberances in 3.56a and enlarged in 3.56b; **e, f)** ventral views (females); **a, c, f)** scale lines = 1 µm; **e)** scale line = 10 µm.

Fig. 3.57. (continued on next page). Gnathosoma of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Portulacaria afra*: **a)** dorsal view (female); **b)** dorso-lateral view (larva); **c)** enlargement of cheliceral protuberances in image 3.57a; **d)** line drawing of image 3.57b; **a)** scale line = 10 µm; **b, d)** scale lines = 1 µm.

Fig. 3.57. (continued from previous page). Gnathosoma of *Tergilatus sparsus*: **e)** ventro-lateral view (male); **f)** ventral view (immature, stage unknown); **g)** ventro-lateral view (female). Scale lines = 10 µm.

Fig. 3.58. Gnathosoma of possibly an *Aculops* or *Metaculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Anthocleista grandiflora*: dorso-lateral view (probably adult, gender unknown). Scale line = 10 µm.

Fig. 3.59. Gnathosoma of an *Aculus* sp. *cf. Aculops lycopersici* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Physalis peruviana*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in image 3.59a; **c)** lateral view (female); **d)** dorso-lateral view (female); ventral view (female); **a, d, e)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.60. Gnathosoma of a *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Acacia burkei*: **a, c, d)** lateral views of different areas and enlargements of the same female specimen; **b)** line drawing of the cheliceral protuberances in image 3.60a (also enlarged in 3.60d); **e)** dorso-lateral view, basal part of gnathosoma obscured by frontal lobe (probably adult, gender unknown). Scale lines = 1 µm.

Fig. 3.61. Gnathosoma of a *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Lantana trifolia*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably adult, gender unknown); **c)** basal part, dorso-lateral view (probably adult, gender unknown); **d)** enlargement of cheliceral protuberances in image 3.61b; **e)** distal part, ventro-lateral view (female); **f)** oral plate region, ventro-lateral view (female, same specimen as 3.61e); **g)** distal part, lateral view (female); **h)** basal part, lateral view (female); **a, b, c, e, h)** scale lines = 1 µm; **f, g)** scale lines = 10 µm.

Fig. 3.62. Gnathosoma of a *cf. Aculus* sp. or possibly an immature of *Quantalitus* (Eriophyidae) from *Rothmannia capensis*: **a)** dorsal view, frontal lobe obscures most of gnathosoma (possibly immature); **b)** lateral view (immature). Scale lines = 10 µm.

Fig. 3.63. Gnathosoma of *Costarectus zeyheri* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Dovyalis zeyheri*: **a)** dorso-lateral view (adult, probably female); **b)** dorso-lateral view (male); **c)** lateral view (female); **d)** ventro-lateral view (female); **a, b, d)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.64. Gnathosoma of *Meyerella bicristatus* (Meyer, 1989) females (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Mystroxylon aethiopicum*: **a, c, f)** ventro-dorsal view of the same specimen, are with cheliceral protuberances in image 3.64a enlarged in c and further enlarged in f; **b)** ventral view; **d)** lateral view; **e)** ventrolateral view; **g)** line drawing of image 3.64e; **a, b, c, e)** scale lines = 1 µm; **d)** scale line = 10 µm.

Fig. 3.65. (continued on next page). Gnathosoma of possibly a new genus (according to traditional taxonomic criteria) nr. *Costarectus* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Mystroxylon aethiopicum*: **a)** dorso-lateral view (probably adult, gender unknown); **b, e)** lateral views of the same specimen (male); **c)** enlargement of cheliceral protuberances in image 3.65a; **d)** dorsal view to show the shape of the dorsal pedipalp genual setae (setae *d*) (probably adult, gender unknown); **a, d, e)** scale lines = 1 µm; **b)** scale line = 10 µm.

Fig. 3.65. (continued from previous page). Gnathosoma of possibly a new genus (according to traditional taxonomic criteria) nr. *Costarectus*: **f)** ventro-lateral view (male); **g)** ventral view (male); **h)** line drawing of image 3.65g. Scale lines = 10 µm.

Fig. 3.66. Gnathosoma of possibly a new genus (according to traditional taxonomic criteria) nr. *Tetra* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Protea caffra* subsp. *caffra*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female). Scale lines = 10 µm.

Fig. 3.67. Gnathosoma of possibly a new genus (according to traditional taxonomic criteria) nr. *Mesalox* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Apodytes dimidiata*: **a)** dorsal view (probably adult, gender uknown); **b)** lateral view (female); **c)** ventro-dorsal view (female); **d)** ventro-lateral view (female); **e)** enlargement of the cheliceral protuberances in image 3.67a; **f)** ventral view (male); **a, c)** scale lines = 1 µm; **b, d, f)** scale line = 10 µm.

Fig. 3.68. Gnathosoma of *Porosus monosporae* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Xymalos monosporae*: **a)** ventro-lateral view (female); **b)** ventral view (female); **c)** ventro-lateral view (male); **a, b)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.69. Gnathosoma of a *Tegolophus* sp. *cf. T. orientalis* Meyer, 1990 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Trema orientalis*: **a)** ventro-lateral view (female); **b)** lateral view (female). Scale lines = 10 µm.

Fig. 3.70. (continued on next page). Gnathosoma of *Tetra retusa* Meyer, 1992 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Bauhinia galpinii*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** enlargement of cheliceral protuberances in image 3.70a; **c)** dorsal view (probably adult, gender unknown). Scale lines = 10 µm.

Fig. 3.70. (continued from previous page). Gnathosoma of *Tetra retusa*: **d)** ventro-lateral view (female); **e)** lateral view (female); **f)** dorso-lateral view (larva); **g)** ventral view (female); **h)** ventral view (male); **d, e, f)** scale lines = 1 µm; **g, h)** scale lines = 10 µm.

Fig. 3.71. Gnathosoma of a *Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Chrysanthemoides monilifera monilifera*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in image 3.71a; **c, d)** lateral views (females); **e)** dorso-lateral view (probably adult, gender unknown); **a, c, d)** scale lines = 10 µm; **e)** scale lines = 1 µm.

Fig. 3.72. Gnathosoma of a *cf. Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Faurea rochetiana*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** lateral view (female); **c)** dorso-ventral view (female); **d)** lateral view (female); **e)** enlargement of cheliceral protuberances; **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm.

Fig. 3.73. (continued on next page). Gnathosoma of a possibly new worm-like genus (according to traditional taxonomic criteria) (Eriophyidae: Eriophyinae?: Aceriini?) from *Faurea rochetiana*: **a)** dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (probably adult, gender unknown); **c)** dorso-lateral view (probably adult, gender unknown); **d)** line drawing of image 3.73a. Scale lines = 1 µm.

Fig. 3.74. Gnathosoma of an unknown genus (could not be identified) (Eriophyidae: Phyllocoptinae?) from *Ekebergia capensis*: ventral view (male). Scale line = 10 µm.

Fig. 3.75. Gnathosoma of a possibly new genus (according to traditional taxonomic criteria) in the Phyllocoptinae or Cecidophyinae (Eriophyidae) from *Acacia burkei*: **a)** lateral view (possibly nymph); **b)** same specimen as 3.75a, enlargement of cheliceral protuberances; **c, f)** ventral view of the same specimen (female); **d)** dorsal view, gnathosoma obscured by frontal lobe (probably adult, gender unknown); **e)** line drawing of image 3.75g; **g)** lateral view (female) with dorso-ventrally flattened and oval shaped setae *v*; **a, d, f)** scale lines = 10 µm; **b, c, g)** scale lines = 1 µm.

Fig. 3.76. Gnathosoma of a *Phyllocoptes* sp. (Phyllocoptinae) or new genus (Cecidophyinae) from *Dovyalis zeyheri*: **a)** dorsal view, basal part of gnathosoma obscured by frontal lobe (probably adult, gender unknown); **b)** ventral view (male); **c)** lateral view of basal part of gnathosoma (female); **d)** ventro-lateral view (female); **e)** lateral view of distal part of gnathosoma (female); **f)** dorso-lateral view (larva); **a, d)** scale lines = 1 µm; **b, c, e, f)** scale lines = 10 µm.

Fig. 3.77. Gnathosoma of a probably new genus (according to traditional taxonomic criteria) (Eriophyidae, subfamily uncertain) from *Cussonia* sp. flowers: **a)** dorso-lateral view (probably adult, gender unknown); **b, d)** ventro-lateral views of the same specimen (female); **c)** enlargement of cheliceral protuberances in image 3.77a; **e)** lateral view (female); **f)** ventral view (male); **a, d, e, f)** scale lines = 10 µm; **b)** scale line = 1 µm.

Fig. 3.78. Gnathosoma of *Diptilomiopus apobrevus* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Apodytes dimidiata*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorso-lateral view (larva); **d)** ventro-lateral view (female); **e)** lateral view, basal part (possibly nymph, or male); **f)** ventro-lateral view, apical part (female); **g)** ventral view (female). Scale lines = 10 µm.

Fig. 3.79. Gnathosoma of *Diptilomiopus faurius* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Faurea rochetiana*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female); **c)** dorso-lateral view, basal part (female); **d, e)** ventro-lateral views of the same specimen (female); lateral view (distal part of gnathosoma); **a, b, d)** scale lines = 10 µm; **c, e, f)** scale lines = 1 µm.

Fig. 3.80. Gnathosoma of an unknown species (species could not be identified) (Diptilomiopidae: Diptilomiopinae) from *Xymalos monospora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** ventral view (male); **d)** lateral view (female); **a, b, d)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.81. Gnathosoma of probably a new genus (according to traditional taxonomic criteria), nr. *Dacundiopus* (Diptilomiopidae: Diptilomiopinae), from *Mystroxylon aethiopicum*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorsal view (immature); **d, e)** lateral views (females); **f)** ventral view (female); ventro-lateral view (female); **a, b, d, e, f, g)** scale lines = 10 µm; **c)** scale line = 1 µm.

Fig. 3.82. Gnathosoma of a probably new *Rhynacus* sp. (Diptilomiopidae: Diptilomiopinae) from *Dovyalis zeyheri*: **a, b)** dorso-lateral view and enlargement of the basal area respectively of the same specimen (probably adult, gender unknown); **c, e)** lateral view and enlargement of the distal part respectively of the same specimen (male); **d)** dorso-lateral view (female); **f)** ventro-lateral view (male); **a, c, d, f)** scale lines = 10 µm; **b, e)** scale lines = 1 µm.

Fig. 3.83. Gnathosoma of probably a new genus (according to traditional taxonomic criteria) (Eriophyidae) from *Searsia lancea* (previously *Rhus lancea*) leaf blisters: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (immature); **c)** preliminary attempt at a line drawing (which is probably still wrong and incomplete, because the SEM images that could be obtained from this species were extremely unclear, probably due to a sticky substance covering the mites) of the dorsal view of the gnathosoma, from image 3.83a; **d)** lateral view (probably adult, gender unknown); **a, c, d)** scale lines = 1 µm; **b)** scale line = 10 µm.

Fig. 3.84. Gnathosoma of unidentified morphospecies two (Eriophyoidae: Eriophyidae or Phytoptidae, but it is probably Eriophyidae) from green fruit of *Anthocleista grandiflora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (larva); **c, f)** lateral views of the same specimen (probably adult, gender unknown); **d)** ventral view (female); **e)** ventral view (male); **a, b, c)** scale lines = 1 µm; **d, e, f)** scale lines = 10 µm.

Fig. 3.85. Gnathosoma of an unknown species (could not be identified) (Eriophyidae) from *Sideroxylon inerme* subsp. *inerme*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorso-lateral view (female); **c)** ventro-lateral view (female); **d)** ventro-lateral view (female); **e)** lateral view (female); **f)** ventro-lateral view (female); **a, b, c)** scale lines = 1 µm; **d, e, f)** scale lines = 10 µm.

Fig. 3.86. Examples of loss of quality of SEM images of species in the current study, in the publishing and photocopying processes, all printed images scanned with the same scanner in Grayscale at a resolution of 200 dpi, and saved as *.tiff: **a)** original printed image Fig. 6, p. 232 in Huang (1992); **b)** photocopy of image received from library, before the original reprint was obtained; **c, d)** photocopies of SEM images (Plate 1 image A and B here c and d alternatively) originally published on p. 441 in Chandrapatya & Boczek (1991b), original article / reprint or original SEM images not yet obtained.

CHAPTER 4

Fig. 4.1. *Orfareptydeus stepheni* Ueckermann & Grout, 2007 (Tydeidae: Tydeinae). Female: **a)** dorsal view; **b)** ventral view; **c)** palp; **d)** leg I; **e)** leg II. Original drawings in Ueckermann & Grout (2007), used with permission.

Fig. 4.2. *Mononychellus yemensis* Meyer, 1996 (Tetranychidae). Female: **a)** dorsal view [setae *h2* not included in original drawing by Meyer (1996)]; **b)** enlargement of lobes on dorsal striae; **c)** ventral view; **d)** apotele of tarsus I. Drawings a, b and d modified from Meyer (1996), drawing c original drawing by author from holotype.

Fig. 4.3. (continued on next page). **a)** Preferred tree of Hong & Zhang (1996a) (redrawn from published tree): strict consensus of 3 equally parsimonious trees found by "branch-and-boud" procedure after the first and second successive reweighting. **b)** Unchanged data of Hong & Zhang (1996a) re-analysed, strict consensus tree (L=80, ci=0.5, ri=0.6) of three shortest trees (each L=77, ci=0.519, ri=0.63) found with implicit enumeration search in TNT under equal weighted characters. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand sides of the trees indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

Fig. 4.3 (continued from previous page). **c)** Unchanged data of Hong & Zhang (1996a) re-analysed, preferred tree, implied weighting with k=999, implicit enumeration search resulted in one tree with L=77, ci=51, ri=63. **d)** Same datamatrix, re-analysed with implied weighting, k=3, one tree found. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand sides of the trees indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

Fig. 4.4. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under equal weighting of characters in TNT: entire tree presented to show topology, and it is a metric tree. Total fit = 57.71; Adjusted homoplasy = 72.29; Total length = 5396; CI = 0.056; RI = 0.086. Uninformative characters included. Resolved part of Eriophyoidea clade enlarged in Fig. 4.5. The key to the classification of the terminal species is also applicable to Fig. 4.5.

Fig. 4.5. Estimated consensus tree found with the analysis of the 318 taxon data matrix under equal weighting of characters in TNT (Fig. 4.4): enlarged resolved part of the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes, and those in red on terminal branches are autapomorphies. Blue numbers underneath the branches close to the nodes are the node numbers from TNT. Key to colours of and corresponding symbols following species names providing taxonomic classification are given in Fig. 4.4. Blue E-numbers on left are reference numbers for groups found in tree, for inclusion with other trees; informal names of groups discussed in text are on the right.

Fig. 4.6. The strict consensus (Total fit = 72.29; Adjusted homoplasy = 57.71; Total length = 2402; CI = 0.125; RI = 0.623; Nodes = 255) of 32 trees (each - Total fit = 72.36; Adjusted homoplasy = 57.64; Total length = 2347; CI = 0.128; RI = 0.633; Nodes = 316) found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, with the best score hit 10 times, under implied weighting of characters with k=10. Uninformative characters were included. Unsupported branches were not collapsed. The entire tree is presented to show topology, and it is a metric tree. The bar on the right hand side indicate families and some notes on broad groups and clades. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between them, it doesn't always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node. The tree is divided into four parts, which are enlarged in Figs 4.7, 4.8, 4.9 and 4.19.

Fig. 4.7. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6): enlarged part of tree including outgroup species and branch of node with the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies or homoplasious characters supporting the nodes, and those on the branch supporting node 346 (Eriophyoidea clade) in bold and dark blue are autapomorphies for the Eriophyoidea. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

Fig. 4.8. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6): enlarged part of tree including Nalepellinae species group at node numbered one in Fig. 4.6. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66 taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.9. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6): enlarged part of tree at node numbered two in Fig. 4.6, which includes the Eriophyidae and part of the Phytoptidae, to largely show topology. The tree is divided into parts 2A-2I which are enlarged in Figs 4.10-4.18.

Fig. 4.10. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.11. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right, and indicated with arrows. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66 taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.12. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2C. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.13. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2D. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66 taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.14. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2E. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of the groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.15. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2F. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.16. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2G. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.17. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2H. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66 taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.18. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2I. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66 taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.19. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6): enlarged part of tree at node numbered three in Fig. 4.6, which consists of the Diptilomiopidae clade, to largely show topology. The tree is divided into four parts 3A-3D which are enlarged in Figs 420-4.23.

Fig. 4.20. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). The grey blocks with a thick light blue margin connecting them, are one larger group in Fig. 4.26 split up in two smaller groups in the tree above. The taxa included in the area margined by the grey stipple line, are positioned close together in the 318 taxon data matrix analysed under implied character weighting with k=20 (Fig. 4.36), excluding Steopa and including Rhinotergum and Hyborhinus. On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.21. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.22. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3C. Black numbers above branches are the character numbers of homoplasies supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.23. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3D. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318 taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66 taxon data matrix.

Fig. 4.24. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 318 taxon data matrix, done in TNT with heuristic ("traditional" in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 50. Values are given above branches. Only those groupings which were not collapsed are presented, the taxa with unresolved relationships and the collapsed groups are substituted by the thick vertical bar.

Fig. 4.25. Symmetric resample group frequency differences (GC) values of symmetric resampling (P=33) of the 318 taxon data matrix done in TNT with heuristic ("traditional" in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 20. Values are given above branches. The resolved part of the tree with groups (supported by GC values of 20 or above) which did not collapse is enlarged on the right hand side.

Fig. 4.26. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 in TNT. Total fit = 94.47; Adjusted homoplasy = 35.53; Total length = 2970; CI = 0.101; RI = 0.521; Nodes = 103. Uninformative characters were included. Unsupported branches were not collapsed. The entire tree is presented to show topology, and it is a metric tree. Tree presented from TNT. Tree name is 318tax-k20 tree. The bars on the right hand side indicate families and some notes on broad groupings and clades. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between them, it doesn't always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

Fig. 4.27. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged part of tree including outgroup species and branch of node with the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies or homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

Fig. 4.28. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): detail of basal part of tree enlarged; the group at node 320 divided into smaller groups (Groups 1-16, and the Diptilomiopidae clade) which are enlarged in Figs 4.29-4.35. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.29. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged view of the polytomy of species with relationships between them unresolved and which are part of the group at node 320 (Fig. 4.28). Black numbers above the branches are the character numbers of the homoplasious characters supporting the terminal taxa.

Fig. 4.30. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 1-5 of Fig. 4.28, and corrected Group 5. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The pink number marked with * on the branch of node 400 of Group 5 is the number of a character in the 318 taxon matrix that were accidentily wrongly coded for *Thamnacus rhamnicola* and *Trimeracarus heptapleuri* as 5 (shape of empodium on leg I divided); it should have been coded as 1 (shape of empodium simple). The data was corrected, and the estimated consensus under implied character weighting with k = 20, here presented, was re-analysed. In the tree with Character 103 coded wrongly, *Thamnacus* groups with *Trimeracarus* and *Diphytoptus*, partly supported by the empodium being divided (Character 103), and *Tegoprionus* and *Monotrymacus* are in the polytomy of this tree, in the tree of the corrected data, *Thamnacus* groups with *Tegoprionus* and *Monotrymacus*, and *Trimeracarus* and *Diphytoptus* are in the polytomy. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

Fig. 4.31. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 6-9 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

Fig. 4.32. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 10-11 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.33. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 13-14 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right, and some indicated with arrows.

Fig. 4.34. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 15-16 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right, and some indicated with arrows.

Fig. 4.35. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Group 17 (Diptilomiopidae clade) of Fig. 4.28. The clade in this figure and at this enlargement is largely presented to show topology and to divide the clade into four separate parts (Diptilomiopidae 17.1-17.4) which are enlarged in Figs 4.36-4.39. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.36. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.1. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.37. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.2. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. The species marked with the blue crosses are part constitute the One-Diptilomiopinae group, and the blue crosses are mapped next to the same species in the 318tax-k10 tree (Figs 4.21-4.22). Informal name of group discussed in the text is on the right.

Fig. 4.38. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.3, which is a polytomy that is part of the group at node 378. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node number from TNT is the green number underneath the branch and close to the node.

Fig. 4.39. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.4. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Figure 4.40. Summary (318-summary tree) of the 318tax-k10 tree (Fig. 4.6), constructed manually to schematically reflect the broad relationships between taxa from the 318 taxon data set which were included in the 66 taxon data set. It is a non-metric tree. It was literally done by eliminating those taxa not included in the 66 taxon analyses from the 318tax-k10 tree (Figs 4.6-4.23). The tree does not portray and should not be interpreted as literally sister group relationships found in the 318tax-k10 tree, but rather relative relationships and a hypothetical topology of what the topology of a 66 taxon tree in this study would be if it fully supported the relative relationships between taxa found in the 318tax-k10 tree. Parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43); parts of the tree blocked in stippled line block occur in the 66tax-k999 tree, but with different topologies.

Fig. 4.41. Strict consensus (Total fit = 38.91; Adjusted homoplasy = 47.09; Total length = 942; CI = 0.201; RI = 0.181) of 768 most parsimonious trees (each - Total fit = 44.20; Adjusted homoplasy = 41.80; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using “traditional searches” in TNT, with the best score hit 207 times out of 7000 (replications overflowed), under equal character weights. Uninformative characters were excluded. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66taxEq tree. The resolved part of the tree is enlarged in Fig. 4.42. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not “homoplasious”). Character numbers above, and character states below circles.

Fig. 4.42. Strict consensus of 768 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under equal character weights (66taxEq tree, Fig. 4.41): enlarged resolved part of the Eriophyoidea clade. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Blue e-numbers on left are reference numbers for groups found in tree, for indication of the groups on other trees. Informal names of groups discussed in text are on the right.

Fig. 4.43. Strict consensus (Total fit = 85.54; Adjusted homoplasy = 0.45; Total length = 649; CI = 0.291; RI = 0.501) of 3 most parsimonious trees (each - Total fit = 85.55; Adjusted homoplasy = 0.45; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 15 times out of 7000, 3 trees swapped with TBR branch-swapping, same 3 trees found, under implied character weighting with k=999, k=500, k=100, k=80, k=50 and k=40. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k999 tree. The bar on the right hand side indicate families and some notes on broad groupings. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between the, it does not always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node do not have "polarity" or "order" and can rotate around the node. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k30 tree (Fig. 4.51) which is one tree found with heuristic searches of the 66 taxon data matrix under implied character weighting with k=30. The tree is divided into six parts, which are enlarged in Figs 4.44-4.48.

Fig. 4.44 Part A. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part A. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes.

Fig. 4.44 Part B. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part B. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weights (Fig. 4.42).

Fig. 4.45. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part C. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weights (Fig. 4.42).

Fig. 4.46. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part D. Unsupported nodes were collapsed. Open circles are homoplasies, black circle an autapomorphy and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weights (Fig. 4.42).

Fig. 4.47. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part E. Unsupported nodes were collapsed. Open circles are homoplasies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weights (Fig. 4.42).

Fig. 4.48. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part F. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66 taxon data matrix under equal character weights (Fig. 4.42).

Figure 4.49. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic ("traditional" in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 50. Values are given above branches.

Figure 4.50. Symmetric resample group frequency difference (GC) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic ("traditional" in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 1. Only values of 20 or above were regarded as significant, and the other nodes were regarded as unsupported. Values are given above branches.

Fig. 4.51. One most parsimonious tree (Total fit = 74.68; Adjusted homoplasy = 11.32; Total length = 651; CI = 0.290; RI = 0.497) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 2 times out of 7000, under implied character weighting with k=30. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k30 tree. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Only the two parts of the tree (Parts A and B) which partly differ in topology are enlarged in Figs 4.52 and 4.53 respectively.

Fig. 4.52. One most parsimonious tree found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied character weighting with k=30 (66tax-k30 tree, Fig. 4.51): enlarged Part A. Unsupported nodes were collapsed. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.53. One most parsimonious tree found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied character weighting with k=30 (66tax-k30 tree, Fig. 4.51): enlarged Part B. Unsupported nodes were collapsed. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.54. One most parsimonious tree (Total fit = 70.86; Adjusted homoplasy = 15.14; Total length = 659; CI = 0.287; RI = 0.489) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 1 time out of 7000, under implied character weighting with k=20. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k20 tree. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. This tree is presented, although it is not the preferred tree, because it has an alternative topology to the other two trees presented, and seems to provide useful alternative hypotheses to be investigated. It provides another parameter "test" for the robustness of groups found in other trees, and gives an indication of the change in topology when weighting against homoplasy is slightly more significant than k=999 and 30 which have topologies very similar to one of the most parsimonious trees found under equal weighting. This tree is not discussed in such detail in the text than the other presented trees.

Fig. 4. 55. Corrected data matrix of Hong & Zhang (1996a) using taxa (but taxa are exemplar species, and not genera) characters and character states as defined by Hong & Zhang (1996a). I.) Preferred tree, implied weighting with k=999, implicit enumeration search resulted in one tree with L=85, ci=0.459, ri=0.483. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. II.) strict consensus (L=118, ci=0.331, ri=0.112) of 141 trees (each L=85, ci=0.459, ri=0.483), same data as for tree I above, analysed with implicit enumeration in TNT under equal weighting of characters. . The bars on the right hand side of the trees indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, the blue bars and text = Diptilomiopidae and the gray bar and text = mixture of Eriophyidae and Phytoptidae species. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

Fig.4.56. Symmetric resampling (P=33) with heuristic (”traditional” in TNT) searches of corrected Hong & Zhang (1996a) data set, 5000 replicates, done under implied weighting of characters with k=999 in TNT: a) group frequencies given above branches, branches with group frequency values of less than 50 are collapsed, average group support of 11; b) frequency differences (GC values) given above branches, branches with group frequency values of less than 1 are collapsed, average group support of 17.3.

Fig. 4.57. Corrected data of Hong & Zhang (1996a) using characters and character states as defined by Hong & Zhang (1996a). Strict consensus (L=87, ci=0.448, ri=0.461) of 2 trees (each L=86, ci=0.453, ri=0.472), analysed with implicit enumeration in TNT under implied weighting of characters with k=3. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

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APPENDIX B

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Table B.3. List of Eriophyoidea species with wax, including their classification and structures from which the wax is probably secreted, or on which it occurs. The data was obtained from the original descriptions of the mites.

A Considerable Speck

A speck that would have been beneath my sight
On any but a paper sheet so white
Set off across what I had written there.
And I had idly poised my pen in air
To stop it with a period of ink
When something strange about it made me think,
This was no dust speck by my breathing blown,
But unmistakably a living mite
With inclinations it could call its own.
It paused as with suspicion of my pen,
And then came racing wildly on again
To where my manuscript was not yet dry;
Then paused again and either drank or smelt--
With loathing, for again it turned to fly.
Plainly with an intelligence I dealt.
It seemed too tiny to have room for feet,
Yet must have had a set of them complete
To express how much it didn't want to die.
It ran with terror and with cunning crept.
It faltered: I could see it hesitate;
Then in the middle of the open sheet
Cower down in desperation to accept
Whatever I accorded it of fate.
I have none of the tenderer-than-thou
Collectivistic regimenting love
With which the modern world is being swept.
But this poor microscopic item now!
Since it was nothing I knew evil of
I let it lie there till I hope it slept.

I have a mind myself and recognize
Mind when I meet with it in any guise
No one can know how glad I am to find
On any sheet the least display of mind.

-- Robert Frost

Man is certainly crazy. He could not make a mite, yet he makes gods by the dozen.
(Michel E. de Montaigne, 1580)

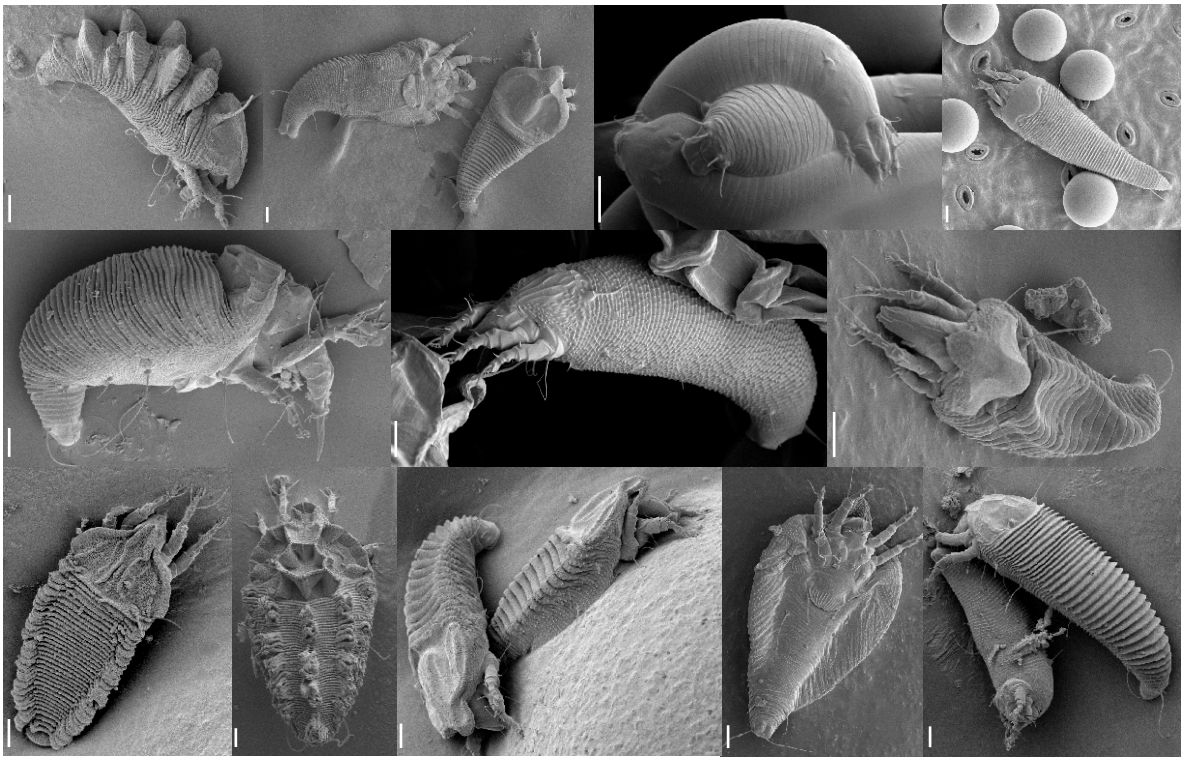


Fig. 0.1. Habitus of mites of the Eriophyoidea: compendium of different genera. Scale bars represent 10μ.

0. PROLOGUE

0.1 ACARI

The Eriophyoidea, which form the subject of this study, are a group of obligatory plant-feeding mites. This superfamily, together with other mites and ticks[1], constitute the subclass Acari (alternative names still in use – Acarina, and in recent years less in use – Acarida). The Acari is one of the largest and most diverse groups of animals (Krantz & Walter, 2009), and rank sixth in animal global diversity after the five largest insect orders (Coleoptera, Hymenoptera, Lepidoptera, Diptera and Hemiptera) (Coddington & Levi, 1991). The word 'mite' originates from Old English and means "a very small creature, beastie or insect", and indeed mites are generally tiny organisms (less than 1 mm long) (Walter & Proctor, 1999). They colonize other living organisms, and virtually every terrestrial, fresh water and marine habitat on earth, including the extreme (Baker & Wharton, 1952; Evans, 1992; Walter & Proctor, 1999; Krantz & Walter, 2009). The omnipresence of mites in the earth's ecosystems is mirrored by the diversity of their habits, including predators, sapro-, phyco- and phytophagous mites, fungivores and parasites of vertebrates and invertebrates (Halliday *et al.*, 1997; Walter & Proctor, 1999; Krantz & Walter, 2009).

Many mites are considered beneficial to humans. Several are predators of undesirable arthropods, some are utilized in controlling weeds (Gerson *et al.*, 2003), while others are major role players in the break-down of soil organic matter (Walter & Proctor, 1999). Mites are also regarded as good indicators of environmental health (Walter & Proctor, 1999).

Mites may also be detrimental to humans. Some species are of medical or veterinary importance, parasitizing either humans directly such as scabies caused by *Sarcoptes scabiei* (Linnaeus, 1758) (Baker, 1999; Walton & Currie, 2007) or their associated animals, such as livestock, pets, poultry, caged birds and honeybees (Baker, 1999). They may infest crops, ornamental plants (Jeppson *et al.*, 1975) as well as cultivated mushrooms (Hughes, 1976; Van der Hoven *et al.*, 1988). These mites can cause severe damage either by their feeding activities or by being vectors of pathogens. Mites can cause hyper-sensitive and allergic reactions by colonizing homes (Hart, 1992), while others tend to infest stored products, and processed foods (Hughes, 1976), and some can interfere with scientific experiments by infesting laboratory insects, plants, animals, or plant cell cultures.

[1] The groups generally known as mites and ticks both belong to the subclass Acari, and ticks can be regarded as "large mites". For convenience, Acari will be generally referred to as "mites" from here on in this dissertation, encompassing the ticks.

The biodiversity of mites is not only varied in habitat, behaviour and life style, but in species richness as well (Krantz & Walter, 2009). In 1997, there were an estimated 48 200 named species of Acari (Halliday *et al.*, 1997), and about 55 000 in 1999 (Walter & Proctor, 1999; Krantz & Walter, 2009), and currently has the largest number of valid described species within the Arachnida (Harvey, 2002). These species are classified into nearly 5 500 genera and 1 200 subgenera representing about 540 families in 124 superfamilies (Krantz & Walter, 2009). The described taxa represent only a scant proportion of mite diversity (Halliday *et al.*, 1997; Walter & Proctor, 1999; Krantz & Walter, 2009), and even those mites living in well-studied biological systems are largely over-looked and unknown (Walter & Proctor, 1999). It is estimated that anywhere between 500 000 to one million mite species may exist, but the total number may be much greater than currently imagined (Krantz, 2009a).

Despite their economic importance and diversity, the study of mites (acarology) remains a largely unexplored discipline (Walter & Proctor, 1999). Historically, the study of mites has for the most part been ignored by zoologists and entomologists alike, probably because mites are not small enough to be handled like protozoans and other pathogens, or soft-bodied enough to be treated as worms, and they are too small to be collected and studied like insects (Baker & Wharton, 1952).

0.2 SYSTEMATICS OF THE ACARI

It is traditionally and generally agreed that terrestrial chelicerate arthropods, including the Acari, are members of the Class Arachnida (Chapter 1, Table 1.1). It is only since the 1990s that cladistic analyses have been utilized to study chelicerate phylogeny (Beall & Labandeira, 1990; Shultz, 1990, 2007; Wheeler & Hayashi, 1998). The systematics of the Chelicerata, and in particular of the Arachnida in the Chelicerata, is still debated and a subject of controversy (Weygoldt, 1998). The Arachnida, however, seems to be a monophyletic taxon, well-supported by morphological characters (Weygoldt, 1998; Shultz, 2007).

The Acari represents one of 11 extant groups (10 orders and one subclass) within the Arachnida (Shultz, 2007). Some of the orders are morphologically easily recognizable, such as the Araneae (spiders), and the Scorpiones (scorpions). Mites, however, are diverse in form and in order to accommodate them in the classification scheme, acarologists treat them as a subclass within the Arachnida (Walter & Proctor, 1999; Krantz & Walter, 2009).

The Acari is among the oldest of all terrestrial animals, with fossils with a moderate level of diversity known from the Early Devonian (about 400 million years ago) (Norton *et al.*, 1988;

Kethley *et al.*, 1989). Krantz (2009b) extrapolated that ancestral mites may have occupied the terrestrial landscape as early as the Late Silurian. Arachnologists and acarologists generally agree that the Acari are a monophyletic group (Lindquist, 1984; Weygoldt, 1998), but some authors (e.g., Van der Hammen, 1977; Alberti, 2000) hypothesized that the group may be diphyletic[2]. Whatever the case, the major lineages within the Acari seem to have originated very early on in the evolution of the Acari and there is substantial morphological divergence within and between them (Lindquist, 1984; Weygoldt, 1998).

It is hypothesized that the Ricinulei is the sister group of the Acari, and they are grouped together as the Acaromorpha (Shultz, 2007). This hypothesis has been tested but is supported by relatively few characters based on cladistic analyses (Weygoldt & Paulus, 1979; Lindquist, 1984; Shultz, 1990, 2007; Evans, 1992).

Leading acarologists divide the Acari either in two (Actinotrichida (Acariformes) and Anactinotrichida (Opilioacarida + Parasitiformes)) (Lindquist, 1984; Evans, 1992), or Acariformes and Parasitiformes at superorder level (Lindquist *et al*., 2009), or three (Acariformes, Opilioacariformes and Parasitiformes) major lineages (Grandjean, 1936; Krantz, 1978; Halliday, 1998; Walter & Proctor, 1999). As exemplified in Table 0.1, the names and taxonomic levels at which these names are used for major groups or lineages within the Acari is widely variable (e.g., Krantz, 1978; Evans, 1992; Walter & Proctor, 1999; Krantz & Walter, 2009) and can be confusing. There has been a remarkable increase in the systematic knowledge on the Acari over the last three decades. Acarine systematics is, however, still based on a fragmentary understanding of the fauna (Krantz & Walter, 2009), and the phylogenies and higher classification within the Acari remains largely unresolved, similar to the situation in the Arthropoda in general (Lindquist *et al*., 2009).

[2] Dunlop & Alberti (2007) reviewed the evidence that supports or contests the monophyly of the Acari.

Table 0.1. The higher classification of the Acari (following Lindquist *et al.*, 2009), with some alternative names and groupings in parentheses, and the taxonomic levels (groups not always used on these levels in the literature) in square brackets. Groups within Acariformes listed to suborder level, Parasitiformes to order level. The groups with phytophagous members are listed (* – some members are phytophagous, ** – all members are obligatory phytophagous) (Lindquist, 1998). It is considered that phytophagy may have developed several times independently in several mite groups (Lindquist, 1998). The Eriophyoidea (subject of this study) and Tetranychoidea (spider mites and their relatives) are the only two groups in which all members and their instars are exclusively and obligatory phytophagous (phytophagous here means to feed on plant sap).

[Superorder] ACARIFORMES (Actinotrichida, Actinochitinosi)

[Orders]

- **Trombidiformes** (Prostigmata)
  [Suborders]
  - **Sphaerolichida**
  - **Prostigmata** (Actinedida + Tarsonemida; Prostigmata suborder (*sensu* Lindquist *et al.*, 2009) or Trombidiformes, + Sphaerolichida). Most diverse mite group in terms of habit, habitat and morphology. Includes free-living predators, fungivores, and parasitic species on plants, vertebrate and invertebrate animals.
    Prostigmatid groups with phytophagous members:

  * Parasitengonina
  * Raphignathoidea
  * Heterostigmatina
  * Eupodoidea
  * Tydeoidea
  ** Tetranychoidea
  ** Eriophyoidea

- **Sarcoptiformes** (Astigmata, Acaridida)
  [Suborders]
  - **Endeostigmata**
  - **Oribatida** (Cryptostigmata, Oribatei). Largely free-living soil inhabiting mites, some live on plants, essentially feeding on dead plant material and fungi, playing an important role in litter-decomposition and soil-formation. Including Cohort **Astigmatina** (Astigmata, Acaridida, Sarcoptiformes) which mostly includes free-living fungivorous and saprophagous mites, often found in large numbers in stored foods and animal nests; also includes the dust mites that are implicated in causing allergies and asthma in humans.
    Only oribatid family with phytophagous species:

  * Galumnidae

[Superorder] PARASITIFORMES
(Anactinotrichida, Parasitiformes + Opilioacariformes, Anactinochitinosi)

[Orders]

- **Holothyrida** (Tetrastigmata). Small group of about 30 relatively large, soil-inhabiting mite species.
- **Ixodida** (Metastigmata). Exclusively blood-feeding ectoparasites of vertebrates (ticks).
- **Mesostigmata** (Gamasida). Typically free-living predators of other small invertebrates in soil, decomposing organic material and on plants, but also include ecto- or endoparasites of vertebrates.
- **Opilioacarida** (Opilioacariformes, Notostigmata). Small group of relatively large mites free-living in dry conditions under stones and in litter.

0.3 ERIOPHYOIDEA

The Eriophyoidea (eriophyoid mites or eriophyoids) are a morphologically distinct group of mites. They are minute (on average 150-250 µm long) with elongated, worm-like and annulated bodies, and are unique in having all instars of both sexes with two pairs of similarly developed legs anteriorly (Fig. 0.1).

0.3.1 Ecology and importance

Eriophyoids generally seek microhabitats on plants in which to live, feed and reproduce. Their mouth-parts are modified to facilitate plant-feeding, and are so small (on average 15-40 µm long) that they can mostly only penetrate epidermal cells, or in the case of some members with slightly longer chelicerae, parenchyma just below the epidermal layer. They feed only on the liquid part of a cell, and cause minimal mechanical damage (Lindquist & Oldfield, 1996; De Lillo & Monfreda, 2004). The feeding of most eriophyoids causes no obvious change in either plant growth or appearance. The feeding of some species, however, may directly induce symptoms, such as a discolouration of tissue (rust), as well as a wide range of growth abnormalities (Fig. 0.2), including gall formation, deformation of growth points, blisters, witches' broom growth and erineum (abnormal plant hair growth) (Jeppson *et al.*, 1975; Westphal & Manson, 1996). These symptoms can occur on all above-ground plant parts, and are probably caused by substances in the mites' saliva being injected into plant cells during feeding (De Lillo & Monfreda, 2004). Symptoms vary in the severity of damage to plants. Based on these symptoms, generally eriophyoid mites are commonly referred to as gall-, rust-, bud-, erineum-, witches' broom- or blister mites, etc. Some eriophyoids are vectors of detrimental plant pathogens, such as viruses and micoplasms (Oldfield & Proeseler, 1996).

Fig. 0.2. Compendium of plant abnormalities caused by feeding of eriophyoid mites. (Photos of symptoms by S. Neser.)

Eriophyoids as a group occur on a vast range of plant families, but the majority of eriophyoid mite species are generally regarded as being very host-specific. Eriophyoidea have a cosmopolitan distribution. They are associated with most groups of land-living multicellular plants.

In southern Africa, 21 eriophyoid species are regarded as economically important agricultural pests (Meyer & Craemer, 1999). The negative economic impact these mites can have on agricultural production, for commercial and subsistence farmers, necessitates a comprehensive knowledge and understanding of their systematics and biology.

The detrimental effect of eriophyoid symptoms can also be useful in agriculture and ecology. Some eriophyoid species are utilised in weed control, especially in classical biological control initiatives, or are investigated as potential weed control agents (Cromroy, 1979; 1984; Craemer, 1993; Gerson *et al.*, 2003; Smith *et al.*, 2010).

Eriophyoid symptoms are easily confused with symptoms from a physiological effect (e.g., dieback of tomato plants caused by the tomato rust mite that may be confused with drought symptoms) or those caused by other organisms, such as pathogens and insects. Thus in many instances the correct control actions for observed damage can not be determined easily. The problem is further exacerbated by the microscopic nature of the mites, and in many cases the lack of knowledge of their presence and on their identity.

Eriophyoids are generally very successful dispersers. They are mainly dispersed by wind (Davis, 1964b; Nault & Styer, 1969; Krantz & Lindquist, 1979; Zhao & Amrine, 1997), but may also be dispersed by insects and other organisms (e.g., Waite & McAlpine, 1992).

0.3.2 Biology

The life cycle of all eriophyoids generally comprises an egg, two nymphal stages, or a larva and nymph, depending on the view of the Acarologist (Shevchenko, 1961; Lindquist, 1996a), and an adult stage (male or female). Sternlicht & Goldenberg (1971) named the stages during the resting period between the first and second nymphs as “nympochrysalis”, and during the period between the second nymph and adult as “imagochrysalis”.

Females are fertilized when they pick up sperm from spermatophores deposited by males (Oldfield *et al.*, 1970; Sternlicht & Goldenberg, 1971). Some eriophyoids were shown to be arrhenotokous (males hatching from haploid or unfertilized eggs, and females from fertilized eggs) (Keifer, 1975a) and this may presumably be true for all eriophyoids.

Some species have an alternation of generations with two different structural types of females, referred to as deuterogyny. The primary female (protogyne) resembles the males and reproduces rapidly during favourable conditions, while the secondary female (deutogyne), with no male counterpart, can carry the species through unfavourable periods (Keifer, 1975a). These alternative forms are of concern to the current classification and identification of eriophyoid mites, and could not be addressed in the present study, but may be of importance to the phylogeny of the group. A more detailed account of deuterogyny in the Eriophyoidea is provided in Chapter 4.

CHAPTER 1

INTRODUCTION

This chapter includes the aim and approaches of this study and an abbreviated literature review of the evolution, diversity and systematics of the Eriophyoidea as background for the research presented in this dissertation.

1.1 AIM AND APPROACHES OF THIS STUDY

1.1.1 Topic

Systematics of the superfamily Eriophyoidea (see classification of the Eriophyoidea in Table 1.1).

1.1.2 Taxa and classification of the Eriophyoidea

The Eriophyoidea are considered to belong to the acariform Prostigmata or Trombidiformes (= Sphaerolichida + Prostigmata *sensu* Lindquist, 1998) (Table 1.1). The Trombidiformes are a large and diverse group of mites, mainly characterized by the lack of character states found in other major groups of acariform mites than by synapomorphies of their own (Lindquist, 1998). Within Trombidiformes, the Prostigmata are united by having the stigmatal openings to the tracheal system located anteriorly (mostly on the prodorsum or near the base of the mouthparts), and this was indicated as a synapomorphy of this group in a cladistic analysis by O'Connor (1984). More recent cladograms of relationships of taxa within Trombidiformes (or Prostigmata) were presented by Norton *et al.* (1993) and Lindquist (1998) but these were based on unpublished analyses. According to Lindquist (1998), Prostigmata constitute a group within Trombidiformes, but confusingly, Prostigmata is frequently used as an alternative name of Trombidiformes and *vice versa* (e.g., Baker, 1999). In this dissertation, I follow the names and groups as shown in a cladogram by Lindquist (1998), but refer to Prostigmata (since this group name is generally used in recent publications) as the major group including Eriophyoidea (also refer to the title of the dissertation). Prostigmata in this dissertation, however, refers to the group within Trombidiformes *sensu* Lindquist (1998), and not as an implied alternative name of Trombidiformes.

The relationship of the Eriophyoidea with other groups of prostigmatid mites will be dealt with in more detail in Chapter 4.

Table 1.1. The classification of Acari and Eriophyoidea within Animalia (including some sister groups) [according to Weygoldt & Paulus (1979) and Lindquist (1984, 1996b)], and the classification of suprageneric groups within Eriophyoidea (following Amrine *et al*., 2003).

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Chelicerata
Class: Arachnida
Subclass: Acari (sister group: Ricinulei)
Order: Acariformes (Actinotrichida)
Suborder: Trombidiformes (= Sphaerolichida + Prostigmata)
Cohort: Prostigmata: Eupodina

Superfamily: **Eriophyoidea** Nalepa, 1898 (sister group: Tydeoidea)

Family: **Phytoptidae** Murray, 1877
- Subfamily: Prothricinae Amrine, 1996
- Subfamily: Novophytoptinae Roivainen, 1953
- Subfamily: Nalepellinae Roivainen, 1953
  - Tribe: Pentasetacini Shevchenko, 1989 (*in* Boczek *et al*., 1989)
  - Tribe: Trisetacini Farkas, 1968
  - Tribe: Nalepellini Roivainen, 1953
- Subfamily: Phytoptinae Murray, 1877
- Subfamily: Sierraphytoptinae Keifer, 1944
  - Tribe: Sierraphytoptini Keifer, 1944
  - Tribe: Mackiellini Newkirk & Keifer, 1971

Family: **Eriophyidae** Nalepa, 1898
- Subfamily: Aberoptinae Keifer, 1966
- Subfamily: Nothopodinae Keifer, 1956
  - Tribe: Colopodacini Mohanasundaram, 1984
  - Tribe: Nothopodini Keifer, 1956
- Subfamily: Ashieldophyinae Mohanasundaram, 1984
- Subfamily: Cecidophyinae Keifer, 1966
  - Tribe: Cecidophyini Keifer, 1966
  - Tribe: Colomerini Newkirk & Keifer, 1975
- Subfamily: Eriophyinae Nalepa, 1898
  - Tribe: Diphytoptini Amrine & Stasny, 1994
  - Tribe: Eriophyini Nalepa, 1898
  - Tribe: Aceriini Amrine & Stasny, 1994
- Subfamily: Phyllocoptinae Nalepa, 1892
  - Tribe: Acaricalini Amrine & Stasny, 1994
  - Tribe: Calacarini Amrine & Stasny, 1994
  - Tribe: Tegonotini Bagdasarian, 1978
  - Tribe: Phyllocoptini Nalepa, 1892
  - Tribe: Anthocoptini Amrine & Stasny, 1994

Family: **Diptilomiopidae** Keifer, 1944
- Subfamily: Diptilomiopinae Keifer, 1944
- Subfamily: Rhyncaphytoptinae Roivainen, 1953

The Eriophyoidea had about 3 500 recognized species of about 300 genera in three families: Phytoptidae, Eriophyidae and Diptilomiopidae (with 21, 227 and 53 genera, respectively) in 2003 (Amrine *et al*., 2003). The suprageneric classification within Eriophyoidea will be treated in more detail in Chapter 4.

1.1.3 Problems with eriophyoid systematics

Many problems are experienced with the systematics of the Eriophyoidea, including:

1) the knowledge on the biodiversity of Eriophyoidea is particularly scant, probably only 1 to 20% or less of extant taxa are known (see later in this chapter);
2) practical difficulties are experienced in the classification and description of eriophyoid taxa, which lead to problems with the identification and differentiation of possibly new taxa, of which some are economically important;
3) few, particularly comprehensive, keys to species are available;
4) relatively little is known about intra-specific variation, and recognition of species is in many regards still uncertain;
5) character, character state and species descriptions are not always adequately precise and thorough, particularly for their utilization in phylogenetic studies;
6) when using phase contrast light microscopy to study slide-mounted specimens, few additional characters, apart from those already used for taxonomy, are available for systematics;
7) the phylogeny of the Eriophyoidea has hardly been studied, especially using new techniques, such as cladistic analyses, and the existing classification seems to be artificial; and
8) there are so many pressing needs, particularly for studying economically important species, and description of new species (alpha taxonomy), that it is difficult to prioritize systematic research for Eriophyoidea.

1.1.4 Primary aim, scope and objectives of this study

The primary aim of this study is to investigate, appraise and propose improvements for some aspects of the systematics of the Eriophyoidea. The study is based on: a) assessing and studying the phylogeny using current systematic techniques and b) improved morphological studies, incorporating scanning electron microscopy (SEM). The study focuses on southern hemisphere taxa in order to provide a systematic framework for future research on the biodiversity of Eriophyoidea in South Africa and beyond. An alpha taxonomic study – description of three new *Diptilomiopus* spp. from South Africa – is included to address the need for the description of unknown taxa.

1.1.5 Relevance of study

Any systematic study on Eriophyoidea will be a valuable contribution to all aspects of research and management of the group. Many eriophyoid species are potential or known economic plant pests, some are important in the quarantine of plant material exported and imported globally, while others are useful as biological control agents of weeds. The current state and lack of knowledge on the systematics of these species, frequently pose major restrictions to their applied research. The Eriophyoidea also constitute a cosmopolitan part of plant ecology and occurs as part of all plant ecosystems, yet less than 1% of this diversity might be known. The taxonomic shortfall for this group is massive. In order to contribute towards improving the systematics of the group, this study includes the evaluation and critical appraisal of some of the techniques and processes used in eriophyoid systematics.

1.1.6 The rationale behind the aim, scope and research order

Lindquist & Amrine (1996) noted that the need for alpha taxonomic research on the Eriophyoidea must be supported and it should not be viewed as a simpler or lesser science. The classification and systematic knowledge (particularly phylogeny) on the Eriophyoidea pose numerous problems, though. This should ideally be addressed simultaneously while documenting the fauna, which will improve the framework for description of yet more new taxa and other alpha taxonomic endeavours.

Some apprehension exists that phylogenetic studies may be premature, seen in the light of the shortfall of basic descriptive data, and urgency to describe existing diversity. It may be detrimental to the future knowledge and further research on the diversity and phylogeny of the Eriophyoidea, however, if taxon descriptions are not improved. Identifying specific improvements needed, can be obtained by formatting and coding descriptive data in comprehensive data matrices, continuously subjecting the data to phylogenetic analyses, and using the data in tools such as multi-access (interactive) keys (see Chapters 2 and 4).

Descriptive data (including definition of characters and character states) has to improve from current norms or at least adhere to an acceptable standard, if it is to be useful or sufficient for analyses (e.g., cladistic analyses) of the group. If this is not done, the description of these taxa will have to be repeated or improved in future. Although re-descriptions will necessarily always remain a part of the systematic study of a group, especially in the Eriophyoidea it should be minimized as far as possible. It is a huge and time-consuming task in this group, because slide-

mounted type material is lost over time and the pressing need for describing new species will remain for a long time to come.

The supraspecific classification of the Eriophyoidea is for now relatively stable and accepted by leading eriophyoidologists globally, but it is most likely artificial (Lindquist & Amrine, 1996), at least in part, and thus has most likely little predictive power and may become unstable and problematic with the addition of new species. To base the classification on natural relationships between taxa is a further reason for continuously analyzing descriptive data, even if the resulting phylogenetic hypotheses may change radically over time. New phylogenetic hypotheses don't necessarily need to be translated into classifications for practical use until they are relatively "stable" and reliable, especially if such new hypotheses may cause confusion in the taxonomy of the Eriophyoidea.

When studying the phylogeny of a group, it can be done from top down or bottom up (of smaller groups). The monophyly of the Eriophyoidea as a group amongst other mites is virtually uncontested (Lindquist, 1996b). However, the monophyly of most supraspecific groups within Eriophyoidea is suspect (Lindquist, 1996b; Lindquist & Amrine, 1996). It was therefore decided to commence this study with preliminary and exploratory analyses of the relationships between type species of selected genera across a large part of the diversity of the superfamily. This analysis will test the monophyly of families, subfamilies and tribes. It also has the purpose to identify smaller hypothetically monophyletic groups for further phylogenetic analyses of relationships between species in these smaller groups. For the current study, the aim was to discover such a small hypothetically monophyletic clade within the Eriophyoidea that contains undescribed species and genera occurring in South Africa that have already been collected, and are ready for description. The aim was to describe these new taxa to include alpha taxonomy as part of the study, and at the same time contribute towards describing new taxa from South Africa. The phylogenetic analysis of the type species of the genera across the Eriophyoidea also tests the results and conclusions of another study (Hong & Zhang, 1996a) published in this regard.

A SEM study of the morphology of selected eriophyoid species was included because it became clear that the characters and character states were not well-defined and described in enough detail to be optimally useful for phylogenetic analyses (see Chapters 3 and 4). Many current descriptions are generally vague and characters carelessly defined in some instances. While capturing data for phylogenetic analyses, it was observed that many of the characteristics of slide-mounted specimens are either obscured and distorted, or not clearly visible using light microscopy. Due to the extremely small size of Eriophyoidea mites and the problems associated with and limitations of

conventional phase contrast light microscopic study of their morphology, an appraisal of the systematics of the group can not be complete without an appraisal of the techniques used to study the group, and an investigation into improved ways of studying these tiny organisms. It was decided to at least investigate and evaluate the potential, usefulness and current use of SEM in the systematics of the Eriophyoidea.

The primary aim of the SEM study was to investigate the morphology in as natural and "true" life state and condition as possible, and also to further investigate the influence and importance of artefacts caused by preparation and slide-mounting on morphological data used for the systematics of the Eriophyoidea. The morphology from SEM images was compared with some slide-mounted specimens and published descriptions to investigate whether more potential systematically informative characters can be identified using SEM studies.

1.1.7 Study material and area

The data sets for the phylogenetic analyses of the Eriophyoidea (including all *Diptilomiopus* spp.) mainly include published descriptive data, and of species worldwide. The study of morphology using SEM, and description of new species, were done on specimens collected in South Africa.

1.1.8 Some published hypotheses and problems regarding the Eriophyoidea prior to and applicable to this study

1) The Eriophyoidea are a natural, morphologically distinct, monophyletic group of phytophagous mites [hypothesized by authors throughout the systematic research history of the group; comprehensively summarized, reviewed and extrapolated on by Lindquist (1996a, b) (see later)].
2) Eriophyoid mites are generally highly host specific or with narrow host ranges (Lindquist & Oldfield, 1996), and it seems that most angiosperm plants will host at least one species (S. Neser, *unpubl. data*, 2003).
3) A tiny proportion of extant eriophyoids are known globally (Farkas, 1969; Amrine *et al*., 2003). In South Africa, and Africa, in particular, the diversity is essentially unknown.
4) General evolution – it is proposed that they originated on gymnosperms, radiated on all plants including angiosperms (Lindquist & Oldfield, 1996).
5) Higher classification is artificial, and not a reflection of phylogenetic relationships (Lindquist & Amrine, 1996).
6) In some groups, problems are experienced with identifying species and assigning species to genera, because generic concepts, diagnoses and delimitations are problematic (Amrine *et al*., 2003). Very few comprehensive species identification keys are available, and some

genera without comprehensive species keys are very large, such as *Aceria* which has more than 900 species worldwide (Amrine *et al*., 2003).

1.1.9 Hypotheses tested and presumptions investigated in this study

1) Study of slide-mounted specimens contributes to errors incorporated in eriophyoid descriptions and classification.
2) Additional useful morphological characters are available for description, classification and study of phylogeny than are currently available or studied.
3) The definition of characters and character states and the description of these for Eriophyoidea are not optimal and should be improved.
4) Families, subfamilies and tribes of the Eriophyoidea are not monophyletic, with the possible exception of the Diptilomiopidae.
5) Phylogenetic analyses of a comprehensive sample of variation at the generic level of the Eriophyoidea will find useful, potentially monophyletic suprageneric groups for further study alternative and additionally to the suprageneric taxa presented in Amrine *et al*. (2003).
6) Phylogenetic studies can be incorporated parallel to pure descriptive work without detriment to the productivity and quality of alpha taxonomy.
7) The more extensive incorporation of new technologies will improve the systematics of the Eriophyoidea.

1.2 EVOLUTION, DIVERSITY AND SYSTEMATICS OF THE ERIOPHYOIDEA

1.2.1 Evolution

- Palaeontology and origin

A fossil rust mite (*Aculops keiferi* Southcott & Lange, 1971) was found in 37 million year old (Lower Middle Eocene) North Maslin Sands in South Australia (Southcott & Lange, 1971). The characteristics of this fossil mite are essentially the same as extant leaf vagrant eriophyoids (Keifer, 1975a) that are hypothetically more derived among Eriophyoidea (Smith, 1984), and it was thus extrapolated that the Eriophyoidea may have originated as long ago as the Early Tertiary, 50 million years ago (Keifer, 1975a), or even earlier (Smith, 1984).

Distribution patterns of species of the Phytoptidae (hypothetically early derived taxa) may indicate an ancestral lineage of eriophyoid mites that arose in association with ancient gymnospermous plants in the Pangaean supercontinent during the Triassic and Jurassic (about 140 - 225 million

years ago) (Lindquist & Oldfield, 1996) when coniferous plants dominated plant diversity due to drier climates. Later, this distribution split into Gondwanian and Laurasian elements during the Early Cretaceous (140 million or fewer years ago) (Lindquist & Oldfield, 1996). Shevchenko *et al.* (1991) proposed that eriophyoids may have originated even earlier based on possible irreversible evolution in setal patterns following the divergence of gymnosperm- and angiosperm plants during the Late Carboniferous (about 270 - 280 million years ago). Care should, however, be taken with evolutionary extrapolations from present, probably artificial classifications of the Eriophyoidea. Be as it may, Eriophyoidea are probably a very old lineage and their biological and morphological homogeneity suggest they originated from a single primordial ancestral lineage (Keifer, 1975a).

- General evolution

General eriophyoid evolutionary trends as first presented by Farkas (1966, 1969) and Shevchenko (1970, 1976), and later compiled by Lindquist & Oldfield (1996) are presented in the introduction of Chapter 4.

- Eriophyoid-host plant co-evolution and species radiation

It is generally assumed, because of their close and frequently unique ecological relationships with their host plants by being very host specific, and causing very specific growth reactions on particular hosts, that eriophyoid mites co-evolved and co-speciated closely with the host plant taxa. Sabelis & Bruin (1996) argued that co-evolution itself might be the driving force for the evolution of the high host specificity observed in Eriophyoidea, and that this offers the most important alternative to the predation *versus* competition explanation they favour. They further speculated that the role eriophyoids play in virus transmission is the most promising area for revealing close co-evolution between eriophyoids and their hosts.

In their treatise of eriophyoid species occurring on Gymnospermae, Boczek & Shevchenko (1996) argued, based on distribution patterns of eriophyoid taxa on different extant gymnosperm and angiosperm taxa, that eriophyoid taxa co-speciated with their host taxa. Smith (1984) presented some examples of co-evolution between Nearctic and Palaearctic *Trisetacus* spp. and their host plants. He found that morphologically similar species utilize similar sites on closely related host species. According to Sukhareva (1994), ancient members of the Poaceae are inhabited by more specialized species (and thus presumably species that co-evolved with their plant hosts the longest) of eriophyoid mites. Boczek & Shevchenko (1996) postulated that the same situation exists on gymnosperm plants where the hypothetically oldest eriophyoid genus, *Pentasetacus*, occurs on a member of the Araucariaceae, the oldest gymnosperm taxon with extant representatives.

On the other hand, Fenton *et al.* (2000) found that the molecular phylogenetic tree structure of seven morphologically closely related *Cecidophyopsis* spp. and that of their *Ribes* host species differed significantly. This implies that in this group of species (colonizing species of one host genus), mite speciation did not closely follow the speciation events in the plant hosts (no strict co-speciation took place) on this level, despite a long co-existence between these hosts and eriophyoid mites. However, the *Ribes* infesting *Cecidophyopsis* spp. in his study included gall-formers and open-living vagrants not inducing distorted plant growth, and these grouped together and not with another gall-forming *Cecidophyopsis* sp. from a gymnosperm host, and a gall-forming *Phyllocoptes* sp. from a *Rubus* sp. in the analysis. At the level of the gymnosperm-infesting *Cecidophyopsis* sp. not grouping with the *Ribes*-infesting *Cecidophyopsis* spp., the molecular phylogenies of the plant hosts and mite species are in concordance (Fenton *et al.*, 2000). The results also indicate that the species grouped together due to their colonization of a specific host genus, and not due to their gall-forming ability (Fenton *et al.*, 2000). Further, it seemed the *Ribes* infesting mites evolved and speciated much more recently and for a shorter time than their hosts, similarly it seemed that *Ribes*-infesting *Cecidophyopsis* spp. and the *Cecidophyopsis* sp. living on the gymnosperm separated much more recently than the separation of Gymnospermae and Angiospermae (Fenton *et al.*, 2000).

In their analysis of Eriophyoidea collected in northeast India, among which no Phytoptidae occurred, apparently because their "probable" hosts were not surveyed, Das & Chakrabarti (1989) did not find any indication of co-evolution between the 94 species in 38 genera and their hosts from this region. They discussed these findings in view of the hypothesized co-evolution between eriophyoids and their hosts based on the close associations between eriophyoids and their host plants, and the occurrence of intra-generic complexes of morphologically very similar species occurring on particular plant families (closely related host species). They considered that both environmental (e.g., pressure by predators, availability of plant species-rich environments, difference in speciation rate between mites and their hosts and changes between sheltered and exposed life-styles) and factors favouring co-evolution (e.g., intimate associations with their hosts, possibly lack in successful colonization of potentially new host species), are equally important in determining the evolution of the Eriophyoidea.

The distribution of known eriophyoid species on host plant taxa (presumably the earlier derived members of the Phytoptidae largely occur on Gymnospermae, and most members of the presumably more recently derived Eriophyidae and Diptilomiopidae occur on Angiospermae) seems to indicate that co-speciation may occur in the case of the higher taxa of the mites and

plants. These arguments are partly based on the assumption that the families within Eriophyoidea are monophyletic and that the polarization from early to more recently derived families are true, and the same for plants.

1.2.2 Extant and described diversity and biogeography

- Number of species

Recently the count of known eriophyoid species worldwide was 4 000 species (De Lillo & Skoracka, 2010). This probably represents only a tiny proportion of extant species. Several new genera and nearly 100 new species are described annually despite relatively limited systematic studies in the Eriophyoidea (Amrine *et al*., 2003). Conservatively, it is estimated that the world extant eriophyoid fauna may range from 35 000 to 50 000 species (Amrine *et al*., 2003). Based on the experience with collecting eriophyoids, including a fairly comprehensive survey of all eriophyoids to be found on the indigenous trees in the Magaliesberg region in South Africa, the number of eriophyoid species extrapolates to as many as 250 000 species worldwide, using the numbers per plant species[1] (S. Neser, *pers. comm.* & *unpubl. data*, 2003). These extrapolations indicate that less than 1% to possibly about 20%, depending on the country and area, may be known.

In comparison with Europe and North America, very few Eriophyoidea have been described from Africa. In South Africa, for example, Tucker (1926) was the first to describe five new species, and only 13 species, mostly cosmopolitan economically important pest species, were reported in 1960 (Ryke & Meyer, 1960). Since then, M.K.P. Smith Meyer and/or E.A. Ueckermann have described more than 190 new species and nine new genera from South Africa, from the *ad hoc* collections of mainly one collector, S. Neser (almost 100% of collected eriophyoid mites were new). Another *ca*. 200 unknown species (mostly *Aceria* spp.) have already been collected and are awaiting description and S. Neser from his collecting experience regards this as only the "tip of the iceberg" (S. Neser, *pers. comm*., 2008). It is unlikely that all eriophyoid species will be described before they are lost, and it is thus important to plan surveys and studies in order to gather data that will be useful to extrapolate on the shortfall.

- Biogeography of eriophyoids

During the evolution of life on earth, habitat occupation, niches, movement and evolution of plants and animals were not universally dispersed throughout the earth's environment, but were

[1] It should be noted that when eriophyoids were collected for the SEM study reported on in this dissertation, even more species per plant species were found than originally discovered by S. Neser. These additional new species usually were vagrant mites not causing any visible symptoms.

"restricted" by barriers to different and changing geographical areas over time. Today, spatial boundaries of biogeographical regions can be clearly- or less clearly-defined on biological similarity, and biological differences between the areas.

The morphology and diversity of living organisms coincide with biogeographical regions and biomes. Biogeographical areas and biomes for plants and animals are not exactly the same. Eriophyoid mites are obligatory plant-feeders, closely associated with their host plants, and may have originated as early as the Late Carboniferous when all land was part of the Pangaean supercontinent. On some classification levels, eriophyoid mites probably followed the divergence of the angiosperms and conifers. It thus seems feasible to presume that extant eriophyoid diversity may resemble extant plant diversity and biogeographical distribution more closely than that of other animals that are not closely associated with plants.

Eriophyoids occur widely on ferns, coniferous plants, monocots and dicots worldwide. They occur in the Arctic regions and at altitudes as high as 3 300 m (Oldfield, 1996). The distribution of many eriophyoid species on crops and exotic plants was probably expanded with them being transported with their host plants to other countries than their native areas. In his treatise of the diversity and host plant specificity of Eriophyoidea, Oldfield (1996) also listed and particularly presented the geographical ranges of eriophyoid genera and suprageneric groups. He, however, didn't come to any conclusions about the geographic distribution of Eriophyoidea.

- Future surveys and identification of eriophyoids

In practice when revising a higher taxon, or having to identify whether a species is new or previously described, comparing with all species of, for example, a specific genus on a global scale may be too laborious and impracticable. This is particularly so when no comprehensive and global keys for a group are available (this is particularly a problem in some of the larger genera, such as the genus *Aceria*, with a worldwide distribution and with more than 900 described species). It seems sensible in such studies to compare specimens or species in "similar" biotas. Additionally, one should also compare new material with phylogenetically closely related species, if it can not be compared with all species within a genus, or morphologically similar genera. This is not possible in the Eriophyoidea, however, because the classification is most probably still very artificial and not based on phylogenetic relationships (see Chapter 4).

In previous taxonomic studies of Eriophyoidea in South Africa, comparisons with described species were restricted to other species occurring in Africa (the Afrotropical Region) and occurring on the same host species, or host genus if it was not practical to compare such new material with

all species described in the particular genus under study (E.A. Ueckermann, *pers. comm.*, 2008). For species comparisons with new material, the larger floral geographical areas and similar biomes should rather be chosen for restriction of study, and not, as it has been traditionally done, to the Afrotropical Region, which is essentially an animal geographical area. In addition, eriophyoid mites mainly disperse with wind, and wind currents (Zhao & Amrine, 1997), and this may artificially enlarge the distribution area of species, particularly when only single specimens are collected, that may be "accidentals".

Several major biomes are defined in South Africa with reasonably sharp transitions between them (Mucina & Rutherford, 2006). These biomes and their constituent vegetation types are regularly used as a framework for the ecology and biogeography of the flora, and as a foundation for conservation assessments and actions (Van Rensburg *et al.*, 2004). They may also serve as an appropriate framework for planning future surveys of Eriophyoidea in South Africa. In addition, the role physical aspects of the environment play, such as altitude, climate, relative humidity, and temperature should be taken into account. A further indicator could be the biogeographical patterns in phytophagous insects that have been studied more comprehensively. Whatever plan for surveying is drawn up, biodiversity sampling should lend itself to extrapolation of the data.

1.2.3 Systematics

- History of eriophyoid taxonomy

Lindquist & Amrine (1996) included the most recent comprehensive review of the taxonomic history of the Eriophyoidea. An abbreviated rendition is presented here.

Early descriptive work (1737-1885): The first published descriptions of eriophyoid mites described the symptoms caused by the mites on their plant hosts, and not the mites themselves (Keifer, 1975a; Lindquist & Amrine, 1996). Réaumur (1737), 273 years ago, appears to be the first author that commented on some of these growth abnormalities, mistaking the eriophyoid mites for tiny maggots (Keifer, 1975a; Lindquist & Amrine, 1996). Afterwards, early post-Linnaean taxonomists proposed the first generic names for the symptoms caused by the mites, but mistook them for fungi, such as *Erineum* and *Phyllerium* (Persoon, 1797). During the next century, the mites themselves were named according to taxonomic convention, such as *Eriophyes* von Siebold, 1850 and *Phytoptus* Dujardin, 1851.

Nalepa Period (1886-1929): Alfred Nalepa, working in Vienna, Austria, published the first adequate eriophyoid descriptions and was the prominent taxonomist on these mites during his career, setting the standard followed by his European counterparts. He described some 479

species, and 12 genera, and presented the first classificatory schemes for them. His last work was a catalogue of the then-described eriophyoid mites, their symptoms and host plants (Nalepa, 1929). This remained a standard work used worldwide for information on names, hosts and references until the next catalogue published by Davis *et al*. (1982). Nalepa published in "old" German, and unfortunately, his work is somewhat difficult to access and comprehend by non-German-speaking researchers, and even difficult to translate by modern German-speaking translators (one translator commented that she suspect that Nalepa's native language might not have been German). Detailed information on the "Nalepa Period" is provided by Keifer (1975a), Newkirk (1984), and Lindquist & Amrine (1996). The bulk of eriophyoid systematic literature from the work of Nalepa up to the present includes alpha taxonomic publications on descriptions of new genera and species.

Keifer Period (1938-1982): Another major contributor to the taxonomy and biology of the Eriophyoidea was H. H. Keifer working in California, the United States of America. He was author or co-author of 711 species and 113 generic descriptions, most still recognized today (Amrine & Stasny, 1994). Keifer established a standard of illustrative and descriptive format which is in essence presently followed by most eriophyoid taxonomists. He also developed the classification of the Eriophyoidea to almost that widely accepted today. He further contributed a comprehensive review and compilation of systematic and other information on Eriophyoidea of the world in two chapters on Eriophyoidea and injurious eriophyoid mites (Keifer, 1975a, b in Jeppson *et al*., 1975), and an appendix to the book: *Synoptic keys to the groups and genera of Eriophyoidea* (Newkirk & Keifer, 1975).

During this period, European authors also contributed significantly to the systematics of the Eriophyoidea, including descriptions of 64 species by Farkas, 83 species by Liro and Roivainen, and 91 species by Boczek (Lindquist & Amrine, 1996). Other more comprehensive works, including catalogues, were published for Finland (Liro & Roivainen, 1951), central Europe (Farkas, 1965b), North America (Keifer *et al*., 1982), California (Keifer, 1952b), Kansas (Hall, 1967), South Dakota (Briones & McDaniel, 1976) and India (Channabasavanna, 1966).

1982-present: The post-Keifer period saw an increase in alpha taxonomic studies on Eriophyoidea from areas outside North America and Europe. These include descriptions of some new genera, and major contributions of newly described species (in brackets) among others from India (*ca*. 240), South Africa (*ca*. 190), New Zealand (*ca*. 55), Brazil (*ca*. 200), China (*ca*. 280), Thailand (*ca*. 130), Taiwan (*ca*. 170), and Yugoslavia (*ca*. 50).

- Morphology used in systematics

Characteristics from the entire body and all appendages are already used in the description of taxa, and the character list largely follows the descriptions done by Keifer during his career. Amrine & Manson (1996) reviewed taxonomic characters and their use, and proposed what should be included in a description of an eriophyoid species. Eriophyoid morphology and its application in systematics of the group are dealt with in Chapters 3 and 4.

- Morphometric studies

Linear measurements of setal lengths and of other morphological structures form an integral and large part (more than half of the descriptive information) of a "standard" eriophyoid species description. Additionally, some structures are also counted (meristic data). Unfortunately, these measurements and counts are frequently presented vaguely and inaccurately and without proper statistical structure. For example, frequently single measurements are not defined, and can either be random single or holotype measurements or means; ranges are not always included with means; or ranges are recorded without the means and number of specimens measured. This carelessness renders the published data almost useless, other than when the gap between two measurements being compared is robust and large enough to differentiate between taxa.

In a landmark study, Amrine, Fenton and co-workers (Fenton *et al*., 1993; Amrine *et al*., 1994; Kumar *et al*., 1999; Fenton *et al*., 2000) studied a complex of five morphologically very similar *Cecidophyopsis* spp. on *Ribes* spp. (currants and gooseberries). Some of these species could not be distinguished morphologically from each other in earlier studies, and were regarded as physiological strains based on their apparent host specificity to different plant species. Amrine *et al.* (1994) statistically separated the five species using one-way analysis of variance (ANOVA) and the Least Significant Difference (LSD) test based on careful and accurate measurements of some morphological features. Their findings were supported by biological and molecular studies.

Geometric morphometric analyses are a relatively recent method that can be utilized to quantify and visualize shape variation and change (eliminating the effect of size, position and orientation). Shape variation may provide information that may be used in order to obtain evidence of similarity among taxa/populations and may be useful in testing hypotheses related to ecology and systematics. The first geometric morphometric analysis of eriophyoids was undertaken by Navia *et al*. (2006) in which they investigated the morphological variation between populations of *Aceria guerreronis* (the coconut mite) across its almost cosmopolitan distribution wherever coconuts occur, and to relate this variation with the geographic distribution of the studied populations. They found significant correlation between shape variation in the coxigenital and ventral mite body

regions and the geographic origin of the populations sampled. These results agreed with results obtained in a similar study by Navia *et al*. (2005) using mitochondrial (16S) and nuclear (ITS) sequences. Both these studies corroborated the hypothesis that the species originates from America. Navia *et al*. (2006) proposed that multivariate and geometric morphometry may contribute to improving systematic studies of eriophyoid mites, if good and standardized preserved specimens are available.

- Molecular studies

It is evident from the first phylogenetic studies based on morphological characters (Hong & Zhang, 1996a, b, 1997; this study), that many problems are associated with studying relationships using morphological data. Currently, there are too few phylogenetically-informative morphological characters available or known for analyses. This is probably due to the difficulty in studying such microscopic animals, the relative simplification of the eriophyoid body and the seemingly high incidence of homoplasy in the morphological structures of Eriophyoidea. There is also a problem with separating particularly sibling eriophyoid species, or determining whether observed variation can be attributed to intra-specific variation, or whether it defines separate species.

By studying mite DNA one may circumvent many of the problems with morphological characters. The results can also be used to estimate the approximate timescale for the evolution of speciation (Fenton *et al*., 2000). The first studies on the chromosomes of Eriophyoidea for systematic use, were done by Huang & Huang (1990), Kuang *et al*. (1992) and Kuang *et al.* (1995). The first molecular study on Eriophyoidea was undertaken by Fenton and co-workers (Fenton *et al*., 1993, 1995, 1996; Kumar *et al*., 1999; Fenton *et al*., 2000; Jones, 2000). They studied a complex of morphologically closely related *Cecidophyopsis* spp. living on *Ribes* spp. Fenton *et al*. (1993) used polymerase chain reaction (PCR) amplification of ribosomal DNA (rDNA) and restriction fragment length polymorphism (RFLP) analyses to show that three of the then five *Cecidophyopsis* spp. found in the complex are probably valid species. The host species, distribution (Fenton *et al*., 1995) and niches (Fenton *et al.*, 1996) of the different *Cecidophyopsis* spp. on *Ribes* spp. were also determined from the series of molecular studies. Jones (2000) reported that the three known *Cecidophyopsis* spp. on *Ribes* could be rapidly identified unambiguously, and that additionally four new species were identified, using rDNA data of the mites. The systematic process of one of the four new species specified by the molecular analyses (Kumar *et al.*, 1999) was not completed, and the species is yet to be described morphologically and named. Fenton *et al.* (2000) analysed the phylogeny of the seven known *Cecidophyopsis* spp. on *Ribes* hosts, as well as a *Cecidophyopsis* sp. from a gymnosperm host, and a *Phyllocoptes* sp. from a *Rubus* sp. using

equivalent rDNA sequences. Three groups of closely related mite species were found: two groups of gall-forming species, and one group with the non gall-forming species. This is an example of an excellent holistic systematic study including not only molecular studies, but also careful and comprehensive morphological studies (including morphometric analyses, see above) (Amrine *et al*., 1994) and biological studies (Easterbrook, 1980).

Carew *et al*. (2004) showed with PCR-RFLP analyses that the bud and leaf gall mites on grapevine, previously believed to be morphologically identical strains of the grapevine eriophyid pest, *Colomerus vitis* (Pagenstecher, 1857), (Smith & Stafford, 1948), are two closely related but distinct species. The two species were not morphologically described and named. Navia *et al*. (2005) used analyses of mitochondrial ribosomal (16S) and nuclear ribosomal internal transcribed spacer (ITS) sequence data to study the geographical origin, ancestral host associations and invasion history and routes of the invasive coconut eriophyid mite pest, *Aceria guerreronis* Keifer, 1965. The results suggested that it originates from America, and the original host of the mite is a non-coconut palm. Goolsby *et al*. (2006) identified the haplotype and location of an eriophyid species, *Floracarus perrepae* Knihinicki & Boczek, 2002, which offers the most potential for control of its fern host, *Lygodium microphyllum* (Cav.) R. Br. which became an exotic weed in Florida, USA, by matching the overlapping geographical relationships between the fern and mite haplotypes and match it with the haplotype and origin of the plants which invaded Florida. They determined the mite haplotypes with parsimony and maximum-likelihood analyses of sequence data from the domain 2 gene region (D2) of the 28s rDNA gene and a portion of the mitochondrial CO1 region. Navajas & Fenton (2000) reviewed the used of molecular markers in the study of diversity in acarology, including molecular studies of the Eriophyidae.

A molecular study is currently underway studying the phylogeny of the Eriophyoidea (M. Lekveishvili, *pers. comm*., 2008). See Chapter 4 for more detail about this study.

- Species descriptions, concepts and delimitation

There are uncertainties about the species-level systematics of Eriophyoidea. The description and differentiation of many species in essence rely heavily on the assumption that species of particularly some groups generally tend to be extremely host specific (specific to one host plant species, or sometimes even specific to bio- or ecotypes of one plant species). Very few studies have been undertaken to actually study host specificity and inter- and intra-species variation.

On the one hand, it seems as if some species may have extensive intra-specific variation in some characters, especially when the populations occur on different host plants. For example,

significant morphological differences and variation between populations of *Aculus fockeui* (Nalepa & Trouessart, 1891) occurring on different host plants were found, or even between populations collected from the same host species (Boczek *et al*., 1984). This variation included differences in the shape and ornamentation of the prodorsal shield.

On the other hand, only slight morphological differences were found between morphologically very similar *Cecidophyopsis* spp. occurring on *Ribes* spp. (Amrine *et al*., 1994). Only after studying thousands of specimens (J.W. Amrine Jr., *pers. comm*., 1995) could Amrine finally find very slight differences in their very similar dorsal shield patterns, together with mainly slight morphometric differences, to separate and identify the different species morphologically (Amrine *et al*., 1994). Amrine *et al*. (1994) mentioned that this study indicates that with careful biological, morphological and molecular studies we may discover complexes of sibling species occurring on several different host species. Some species complexes may already be lumped under present day species names, for example, among many others, *Calacarus citrifolii* Keifer, 1955 and *Diptacus gigantorhynchus* (Nalepa, 1892).

These occurrences of morphologically similar groups of species are a recurrent theme in Eriophyoidea, including the following studies: When describing *Epitrimerus rumicis*, Farkas (1968a) noted the extraordinary similarity between some *Epitrimerus* spp. These species could practically not be distinguished from each other, at least not morphologically. Published observed differences used to differentiate species were from intra-specific variation between individuals of the same colonies, and errors resulting from faulty measurements. He suggested two explanations. There is a single, polyphagous species occurring on various host species, or there are ecologically distinct, but morphologically identical species living on different kinds of plants. In his opinion, the latter possibility is the more probable. Das & Chakrabarti (1989) mentioned that within some eriophyoid genera, complexes of morphologically very similar species occur on specific host families (closely related host species). Skoracka *et al*. (2002) found discontinuous variation among populations of *Abacarus hystrix* on different hosts during their research on grass-feeding eriophyoid mites. Skoracka (2009) described a cryptic new species from *A. hystrix* populations using molecular studies, careful morphological, including morphometric study, and information about the host specificity of the populations. Huang (2001c) studied eriophyoid mites from the Tengchih area in Taiwan. He found several incidences of intra-specific morphological variation. Some species varied in the shape of their microtubercles (e.g., *Trisetacus taiwanensis* Huang, 2001), some in the shield design (e.g., *Abacarus bambusae* Channabasavanna, 1966), and some in the number of empodial rays in specimens from different localities, or between legs I and II. He

commented that in future we may find that the range of morphological features used to delimit a species of eriophyoid mites is too broad, and may overlap in morphologically similar species.

The practice of identifying or even describing new species, based mainly on the host plant and the symptoms and niche thereon, is problematic. It has, for instance, been demonstrated that two or more species of *Trisetacus* exploit the same feeding sites and host species (Smith, 1984). In the present study, the same was found for two *Diptilomiopus* spp. on *Apodytes dimidiata* E. Mey ex Arn. (Appendix M).

- Genera, suprageneric groupings and phylogeny

This aspect is dealt with in Chapter 4.

CHAPTER 2

GENERAL MATERIAL AND METHODS

2.1 INTRODUCTION

Methods used for collecting, preparation, study and eventual description in alpha-taxonomic studies are particularly crucial for the Eriophyoidea, which are microscopically tiny, fragile and delicate, and easily distort during preparation. They are slide-mounted to facilitate morphological study, but type material is lost over time, because permanent slides with specimens cannot be prepared. Therefore, the quality, exactness and comprehensiveness of taxon descriptions are extremely important and can not be stressed enough (De Lillo *et al*., 2010). Morphological descriptions are further complicated because some of the detailed morphology is so minute that it doesn't fall within the resolution range of light microscopy. Knowing and using the correct and most appropriate and technologically advanced techniques and apparatus are crucial in securing the highest integrity and quality of data as is practicably possible. Even the improvement of studying of mites (including Eriophyoidea) over time is closely associated with the development and improvement of apparatus including different kinds of microscopes and microscopic techniques. A basic knowledge of the strengths and weaknesses of each technique and the resulting data are in some regards fundamental to presenting and analyzing systematic data of the Eriophyoidea. Although the current study at first largely concerned the appraisal and study of existing systematic data, it soon became apparent that such a study is essentially incomplete if the material and methods used in obtaining published data are not taken into account as well.

2.2 DATA SOURCES USED FOR THE PRESENT STUDY INCLUDING DISCUSSION THEREOF

2.2.1 Mite specimens included and collection methods

Mite specimens representing a wide variety of eriophyoid taxa from South African indigenous plants were collected particularly for the SEM study (Chapter 3). Collecting efforts were designed to focus on re-collecting described species, and particularly genera described from South Africa. Slide-mounted specimens were prepared when enough material was available, both in the SEM study (Chapter 3), and the phylogenetic study of the Eriophyoidea (Chapter 4). Specimens already collected and slide-mounted before the present study were available to it, and were studied if they

were suitable. Preferably, live specimens from freshly collected plant material were used for the SEM study (see "Material and methods" in Chapter 3). Slide-mounted specimens and SEM studies were used for the description of three new *Diptilomiopus* spp. from South Africa (Appendix M). In a few instances, mite material from other countries was also available, for example, a *Trisetacus* sp. collected from pines in France, and these were included in the present study.

Eriophyoid mites require special collection methods. They are frequently excluded from biodiversity surveys, even when other mites are included, because they cannot be collected by general methods, such as beating. Collection methods of Eriophyoidea are reviewed by Amrine & Manson (1996) and De Lillo *et al.* (2010). Plant material of the known host plants of eriophyoid species selected for the study were hand-collected in the field from localities where they were collected before. The material included the structures on or within which the species normally live, which are frequently symptoms caused by their feeding. In many cases, the particular host on which they were collected before was surveyed. It was sometimes necessary to continuously re-sample a particular plant species to find the targeted eriophyoid species, especially when it was a vagrant causing no detectable symptoms. Three or four non-target species were frequently found on the same sampled plant material (Table 3.1). Many of these were undescribed species. After being collected, the plant material was kept as fresh as possible, and brought into the laboratory for further preparation as soon as possible. The collected material was kept fresh by first wrapping it in damp paper towel, and then putting it into a plastic bag. The bags with material were kept in a cooler box at the collection site, and if the material could not be used immediately on arrival at the laboratory, it was stored in a fridge at about 4 °C, usually not longer than a week, until it could be processed (see collecting and SEM processing dates in Table 3.1). In this way mite colonies can be kept alive for a month or longer (De Lillo *et al*., 2010). Field collected plant material was searched for eriophyoid mites *in situ* with the aid of a high end quality dissecting stereo microscope with a cold light source, at magnifications ranging from 20–80x.

Mites were collected from the plant material by hand, using a minuten pin or hair lash mounted on a stick or other appropriate holder (De Lillo *et al*., 2010), with the aid of a stereo microscope. Whenever possible, large samples were collected, trying to include entire colonies with both females and males and all developmental stages.

In my experience even when plant material is searched thoroughly with the aid of a dissecting microscope, some species that are sparsely distributed on the plant material, may be missed. To alleviate this limitation, parts of the infested plant material can additionally be washed with a solution containing bleach and detergent. The mites in the solution can be concentrated by sieving

through fine mesh screens or with centrifugation (Monfreda *et al*., 2007). This method could be at least twice as effective and time-saving as *in situ* inspection of plants and their parts (Monfreda *et al*., 2007), and should be seriously considered for biodiversity surveys. Because the specimens in the present study were largely collected for SEM study, and had to be kept as natural and alive as possible, they were not washed from the plant material.

2.2.2 Physical preparation and study of specimens

- Light microscopy

The mites destined for slide-mounting were collected into an isopropanol-sorbitol solution (Keifer, 1975a; De Lillo *et al*., 2010). They were subsequently cleared and mounted in batches of about 100 specimens at a time, using the three media, "F-medium", "HCl-solution" and "Phenol-solution" developed and recipes provided by Keifer (1975a). Specimens were transferred from the collecting liquid into a solution in a depression slide, made up of a droplet of each of the three mentioned media of Keifer (1975a) which are kept in separate holders. The depression slide with solution and mites was briefly heated over an open flame, without boiling the solution, to clear the specimens. After clearing the specimens, and removing them from the heat, the clearing solution was diluted with two to three drops of F-medium to stop the clearing process and render the solution more fluid. The specimens were then mounted in a droplet of "F-medium" on a microscope slide (five specimens per slide), and covered with a cover slip. The slides with mounted specimens were left at room temperature for about two days for the fluid to "settle" and become more viscous. The cover slip was sealed ("ringed") afterwards with Glyptal®, a special moisture resistant paint (Amrine & Manson, 1996). See Keifer (1975a), Amrine & Manson (1996) and De Lillo *et al*. (2010) for alternative methods.

Slide-mounted specimens were studied with a Zeiss Axioskop microscope using phase contrast and Achroplan quality objectives. Drawings of the mites were made with a drawing tube (camera lucida) and the final realistic drawings were not modified to be semi-schematic. Digital images of some specimens studied with the said light research microscope were captured with a Wirsam Olympus CC12 digital camera and the analySIS® LifeScience ©2005 imaging system series by Soft Imaging System GmbH, an Olympus Company (http://www.soft-imaging.net).

- Scanning electron microscopy (SEM) (see Chapter 3)

2.2.3 Data from published descriptions

The goal of the present study was a broad appraisal and therefore published morphological descriptive data were used, rather than studying specimens, particularly for the explorative phylogenetic analyses of the Eriophyoidea (see "Material and methods" of Chapter 4). Published descriptions are the most reliable and available data, because it is almost impossible to obtain specimens, and particularly type specimens, of most taxa described worldwide, primarily because slide-mounted specimens frequently deteriorate over time until they are insufficient for studying (De Lillo *et al*., 2010). For example, Smith (1984), in his study on *Trisetacus* spp. of North America found that much of the type material of the large and important Keifer collection at the USDA in Beltsville, was in poor condition and that detailed study of specimens is difficult and re-illustration impossible. Some slide-mounted material in the South African National Collection of Arachnida–Acari was already badly deteriorated after five years.

Published eriophyoid species descriptions of acceptable standard are largely standardized, and they include morphological descriptive and morphometric data of a comprehensive range of the characters used in eriophyoid taxonomy. Additionally, descriptions should be, and are usually, accompanied by detailed descriptive line drawings. It is thus in theory possible to practice most taxonomy (comparing and identifying species, differentiating new species, and constructing identification keys), and to score a reasonably comprehensive descriptive data base from published descriptions. In taxonomic practice, it is further accepted, and is supported by surveys, that most eriophyoid species, particularly non-vagrants, are host-specific to a plant species, or at least a few closely related species within the same genus, and rarely have an extended host range across more than one plant family. The host plant information thus also aids in general taxonomic practices on these mites.

It is quite common practice, but not always defendable, to study published descriptions of those taxa for which specimens are not readily available, rather than the specimens themselves during taxonomic studies of the Eriophyoidea. This practice is not restricted to the Eriophyoidea; relatively few authors describing mites in general take time to study type material of previously described species (Lindquist, 2001).

The problems with obtaining type specimens of the Eriophyoidea are not an excuse for totally excluding the study of type specimens of described species in all systematic endeavours in this group. In practice, however, it is often unproductive to incorporate type material or try to collect additional specimens of a previously described species before proceeding with the taxonomic study at hand, especially in the light of the huge shortfall in description of extant diversity. With

the goal of describing the diversity as soon as possible, the quality of taxonomic studies of eriophyoids, in which study of type material was not included, is reasonable. However, whenever possible the study of specimens should be incorporated, and obviously particularly in cases of uncertainty. Using published descriptive data for the phylogenetic study in the present study was the optimal option, but restricted the character sample, and potentially incorporated many errors in the data sets of which the significance in influencing the results can not be measured.

2.3 DATA FROM SPECIMENS AND PUBLISHED DESCRIPTIONS: CAPTURE AND MANAGEMENT

Data capture formed a significant and problematic part of the present study mostly caused by the bulk of partly inconsistent and unstructured information to be captured for analyses. I attempted to capture descriptive data only once, and subsequently use the structured data set for taxon descriptions, keys (printed dichotomous keys and electronic interactive keys), and monographs and as data for phylogenetic analyses. This attempt was only partly successful (see discussion further on).

2.3.1 Software and protocol used

Descriptive data from published descriptions, and observations of slide-mounted specimens and SEM images were digitally captured and managed with *DeltaAccess*[1] (Hagedorn, 2007a).

DeltaAccess (a relational data base application) is a SQL interface to DELTA (the Description Language for Taxonomy) implemented in *Microsoft® Office Access* operating in *Microsoft® Windows* environment. During this study *DeltaAccess* was upgraded through several versions (Hagedorn, 1999, 2007a), and the final version used for the present study was *DeltaAccess* 1.9 for *Microsoft® Office Access* 2000 and 2002/XP (Hagedorn, 2007a). *DeltaAccess* will be renamed to *DiversityDescriptions* and a new version of *DiversityDescriptions* (= *DeltaAccess* 2.0) is currently being tested. With its release, the information of *DiversityDescriptions* (*DeltaAccess*) (also that at http://www.diversityworkbench.net/OldModels/Descriptions/index.html) will all be moved to Wiki at http://www.diversityworkbench.net/Portal/wiki/DiversityDescriptions (Hagedorn, 2007b). *DiversityDescriptions* will eventually form part of the *Diversity Workbench* –

[1] Copyright Gregor Hagedorn © 1995-2007. All rights reserved. Institute for Plant Virology, Microbiology and Biosafety, BBA, Federal Biological Research Center, Königin-Luise_Str. 19, 14195 Berlin, Germany. (email: G.Hagedorn@bba.de).

Software Components for Building and Accessing Biodiversity Information (Hagedorn, 2010). The advantages of capturing and managing data as structured data are given and discussed by Hagedorn *et al*. (2005).

Among the other positive attributes of relational data bases, *DeltaAccess* (a data base with a standard industry software interface) makes it possible to link data from other sources (such as nomenclatorial, specimen, or literature reference data bases) with DELTA data. It thus makes data in DELTA format accessible to relational data bases, which is not possible with data exclusively in DELTA format. Data in relational data base structures can be imported to or exported from *DeltaAccess*, as well as from or into DELTA coded text files through *DeltaAccess*.

DELTA is a descriptive data exchange format (Dallwitz, 1980; Dallwitz & Paine, 1999) and the basic directives of DELTA are endorsed by the International Taxonomic Database Working Group (TDWG) (TDWG, 2009), a section of the International Union of Biological Sciences (IUBS). DELTA as an international taxonomic data standard is currently being enhanced and extrapolated with the development of the SDD (Structure of Descriptive Data) standard (Hagedorn *et al*., 2005a). DELTA is a standard for formatting descriptive data and not a computer program. It can be used by several major taxonomic software packages (including the DELTA program packages) that can be used to analyze taxonomic data, generate natural language descriptions, or produce printed keys as well as interactive keys. Some of the DELTA software sources on the internet have been listed and hyperlinked by Hagedorn (2005b).

DeltaAccess can be used in several ways, but for this study it was primarily used as the central data repository and management system around which this and future systematic work will be organized. The Access Basic source code of *DeltaAccess* is included with the application and its information model and documentation thereof is available (Hagedorn, 2005a). This aspect was of particular importance to this study, since particularly the numeric (real and discrete) fields had to be modified to accommodate morphometric data in published eriophyoid descriptions, which were frequently not defined and structured statistically. This necessitated additional official definitions (for example “single value, not defined”) of a particular numeric entered into the data base that was not provided for in the data base. Additional data extraction queries and reports were also created for the data base as needed.

2.3.2 Problems

The terminology, definition and delimitation of many characters and character states are not standardized in eriophyoid descriptions. I decided not to subjectively standardize and reinterpret the data while capturing it in the descriptive data base, particularly because the type specimens were not studied concurrently, and standardization will be more advantageous when a large data bank of descriptive data has been compiled for comparison. This caused a problem for the exact definition and delimitation of character and character state data base fields, leading to, among other shortcomings, redundant data in the data base. Redundancy was caused by duplication of character state fields, because some descriptive data did not clearly fit into already defined and named character state fields at that stage of capturing the data. Most morphometric data from the descriptions did not fit into statistically defined fields, and this is another weak point of the data base data. The data base is essentially still a working data base and the captured data and character and character state fields need to be redefined and reinterpreted, before it can be exported and used unmodified in other applications, including natural language descriptions, interactive keys, and data sets for phylogenetic analyses.

In classical taxonomy, apart from a core set of characters described for an entire larger group, for example the Eriophyoidea, many characters of the group are only recorded for smaller subgroups in which they are taxonomically applicable. In a comprehensive descriptive data set destined for applications like phylogenetic analyses and interactive keys, all systematically informative characters used in the larger group must be scored for all species in it.

In theory it is already possible to structure and enter descriptive data only once and use data exported from this single data base, with minimal modification, in other applications, and this was the goal in the present study. Standards for structuring descriptive data (TDWG, 2009), and programs for using such structured data (see for example Hagedorn, 2005b) are available. In practice, though, such holistic integration between currently available software programs is not fully functional at all levels yet, to my experience. There is also not one total user friendly software package available for capturing and managing structured descriptive data at the functionality possible in *DeltaAccess*, as well as application modules for utilizing the data in all systematic applications, including the export of data matrices for phylogenetic analyses. Some software companies, however, for instance the Centre for Biological Information Technology (CBIT) developing the Lucid programs (CBIT, 2010a), are progressing towards developing more comprehensive software packages for managing and using descriptive data. In the present study descriptive data in *DeltaAccess* exported to DELTA formatted text documents, could not be

utilized directly (without modification) in developing an interactive key (CBIT, 2010b) in Lucid v3.3 (CBIT, 2010c), although this Lucid version was reportedly able to use data in DELTA format. The developers of Lucid attempted to import the data, and worked on the problem, but could not solve the importation totally, and most of the data will probably have to be recaptured in Lucid. This is unnecessary duplication of effort, and hopefully capturing and utilizing descriptive data will become more integrated and functional in future.

2.3.3 Data captured in *DeltaAccess*

The character definition consists of 462 characters with a total of more than 2 000 character states (including numeric fields). The maximum number of states for a single character is 82. The descriptive data of 317 species (items) were captured. The characters include text, ordered and unordered discrete multistate and discrete and real numeric data.

2.4 PHYLOGENETIC STUDIES (SEE CHAPTER 4)

The taxon and character samples and construction and management of the data matrices for the phylogenetic studies, and the protocols and programs used for phylogenetic parsimony analyses are given and discussed in the "Material and methods" section of Chapter 4.

2.5 DISCUSSION

The electronic capturing and structuring of descriptive data of eriophyoid taxa and eventual use of the data for generating natural descriptions, developing identification keys and spawning data matrices for phylogenetic studies were only partly successful, and required intensive and time consuming set up time. The problems and eventual inability to capture the descriptive data once and use it with minimal modification for other applications, were partly caused by problems with integration between available software, but also by the inadequacies of the published descriptive data of eriophyoid mites, of which the most important were incomplete descriptions, lack of detail, precision and standardization, and sometimes pure mistakes. Despite these problems, I am still convinced that enough progress was made with compiling, structuring and managing descriptive data and identifying weak points in the description and taxonomy of eriophyoid mites to pursue these methods further. It is important in systematic studies to continuously search for better and more holistic electronic procedures for capturing and utilizing data, because one of the major requirements of systematics is to gather and manage descriptive data of taxa which will also be used as primary homologies for

phylogenetic studies. In the Eriophyoidea it is of particular importance, because of numerous new taxa being described. The most pressing immediate need, however, is to standardize and improve the descriptions of the Eriophyoidea (also see Appendix L – article of De Lillo *et al*., 2010). Close cooperation and a team effort from all scientists with a good knowledge of the group currently actively describing new eriophyoid taxa will enhance their quality and accuracy.

CHAPTER 3

MORPHOLOGY AND SYSTEMATICS

3.1 INTRODUCTION

Nalepa (1887) reported the first significant information on the external morphology of eriophyoid mites from studies on slide-mounted specimens using light microscopy. From the 1940s onwards phase contrast light microscopy facilitated improved study of eriophyoid mite morphology. This led to improved descriptions, with the standard set by the publications of Keifer (e.g., Keifer, 1952b, 1959a, Baker *et al.*, 1996). Eriophyoid morphology for systematic use is still, almost exclusively, studied on cleared and slide-mounted specimens, using phase contrast (Fig. 3.1a). These data form the basis of the classification and identification of the Eriophyoidea. Taxon descriptions are accompanied by drawings, either realistic (drawn with the aid of a drawing tube or camera lucida with little or no modification) (e.g., Craemer *et al.*, 1999 and Amrine *et al.*, 1994), semi-schematic (drawn with the aid of a drawing tube with modification to represent characteristics of the species clearly) (e.g., Keifer, 1954) – of which a part is depicted in Fig. 3.1b, and e.g., Denizhan *et al.* (2007), or more schematic (e.g., Kuang, 1986a). Eriophyoid descriptions still largely follow the standard and format set by Keifer (Nuzzaci & De Lillo, 1996; De Lillo *et al.*, 2010).

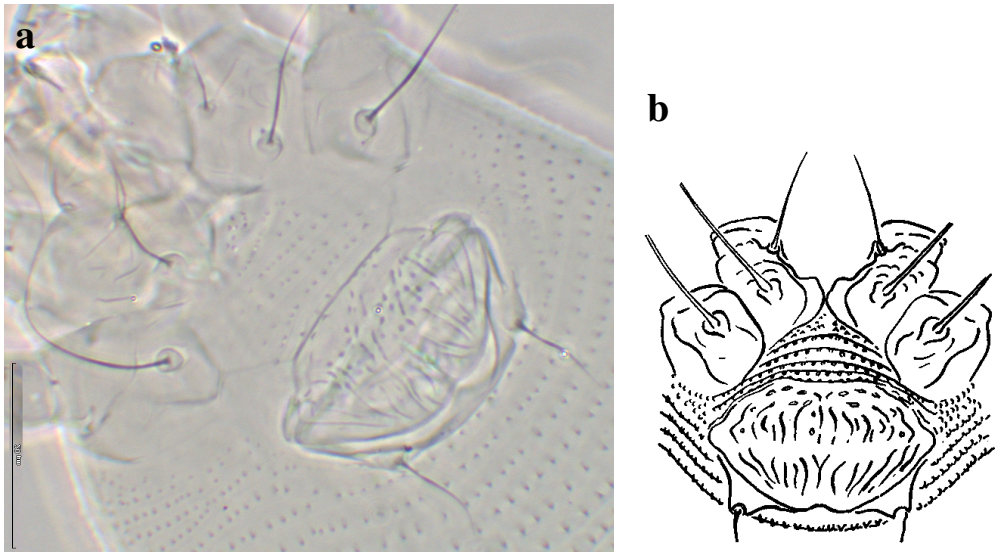


Fig. 3.1. Coxisternal plates and external genitalia of a slide-mounted female specimen of *Cecidophyopsis* sp. *cf. C. hendersoni* (Keifer, 1954): **a)** digital image of slide-mounted specimen viewed with phase contrast light microscopy; **b)** taxonomic drawing of the same area of *C. hendersoni* by Keifer (reproduced from Keifer, 1954).

The morphology of the Eriophyoidea is presented by various authors (including Channabasavanna, 1966; Shevchenko, 1970; Keifer, 1975a,b; Manson, 1984a; Amrine, 1996; Lindquist & Amrine, 1996; Amrine *et al.*, 2003), with a comprehensive review by Lindquist (1996a). Lindquist (1996a) additionally proposed hypotheses of primary homologies between eriophyoid structures and those of other acariform mites, applying the system of standardized terminology and notation of the Acariformes to the Eriophyoidea. This system is generally accepted and adopted by eriophyoid systematists worldwide and its terminology is used in this dissertation. Figures 3.2–3.6 depict the general morphological characters, and Figs 3.19–3.23 depict characters of the eriophyoid gnathosoma, as typified by some general schematic drawings and representative species.

The classification of the Eriophyoidea constructed from morphological studies of slide-mounted specimens (Newkirk & Keifer, 1975; Boczek *et al.*, 1989; Amrine, 1996 and Amrine *et al.*, 2003), despite some contention between the classifications, are relatively stable and workable. The groupings, however, may be artificial (see Chapter 4). Identification keys to the genera of the Eriophyoidea worldwide by Amrine (1996) and Amrine *et al.* (2003) are generally accepted today, and identification, description and differentiation of eriophyoid taxa at all levels are more or less satisfactory using data from only slide-mounted specimens, although problems in certain groups and in some morphological and taxonomic aspects exist.

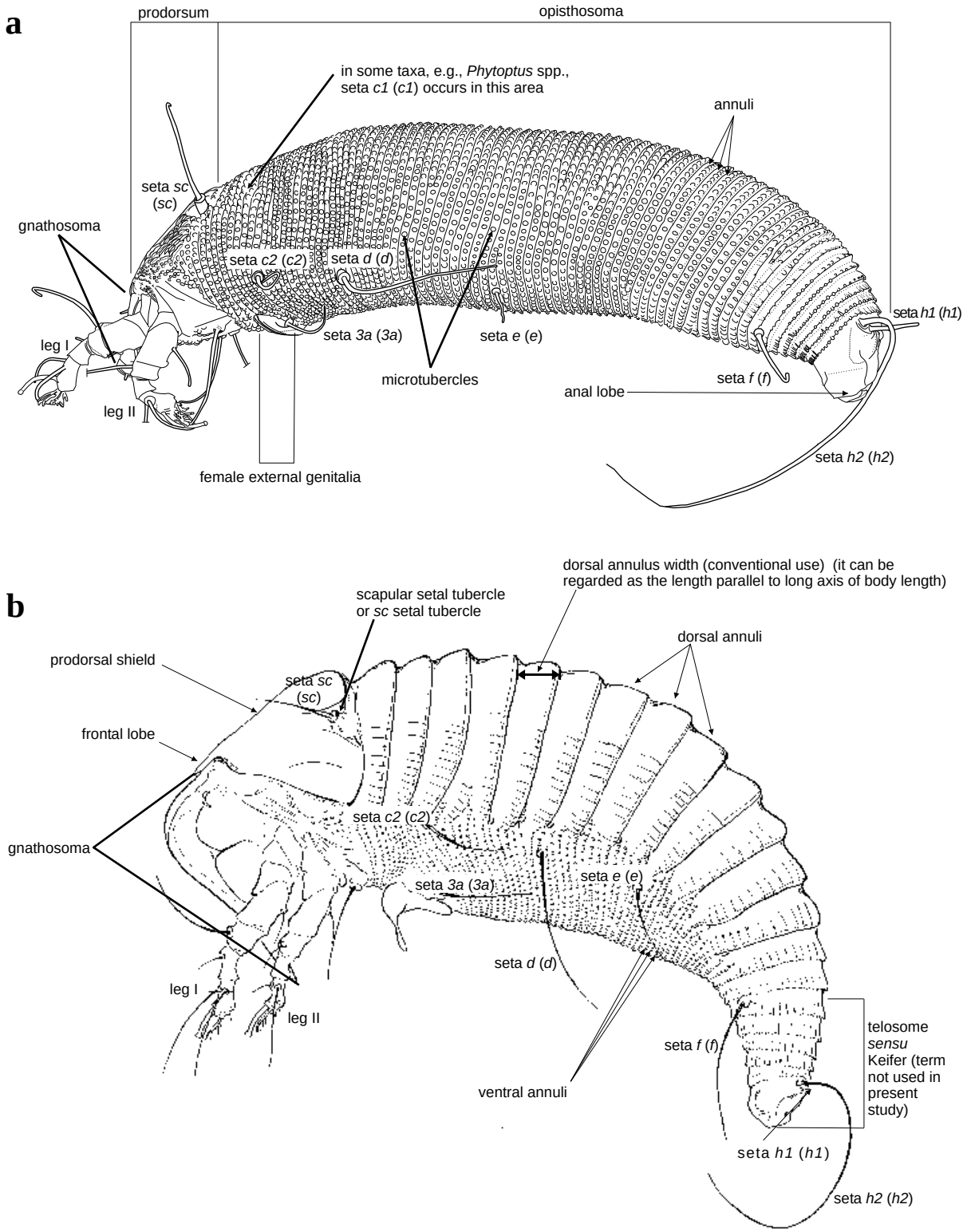


Fig. 3.2. Habitus of the two major forms of eriophyoid mites in lateral view: **a)** vermiform mite, *Aceria* sp. nov. (Eriophyidae), digitally drawn by C. Craemer from a SEM image. Vermiform eriophyoids usually live a relatively sheltered life within micro-spaces e.g., in galls or under bud scales; **b)** fusiform mite, *Rhynchaphytoptus ficifoliae* Keifer (Diptilomiopidae), drawn by E. de Lillo (De Lillo, 1988b) from slide mounted specimens, with confirmation of morphology from SEM images. Fusiform eriophyoids usually live a more exposed life, e.g., rust mites. Additionally *Rhyncaphytoptus* has the large, typical shaped gnathosoma characteristically of the Diptilomiopidae. Note that the quality of the two drawings can not be compared here, because (a) is a print of an original vector drawing and (b) is a scanned image of a photocopy of the original article by De Lillo (1988b). Drawing is used with permission from the author.

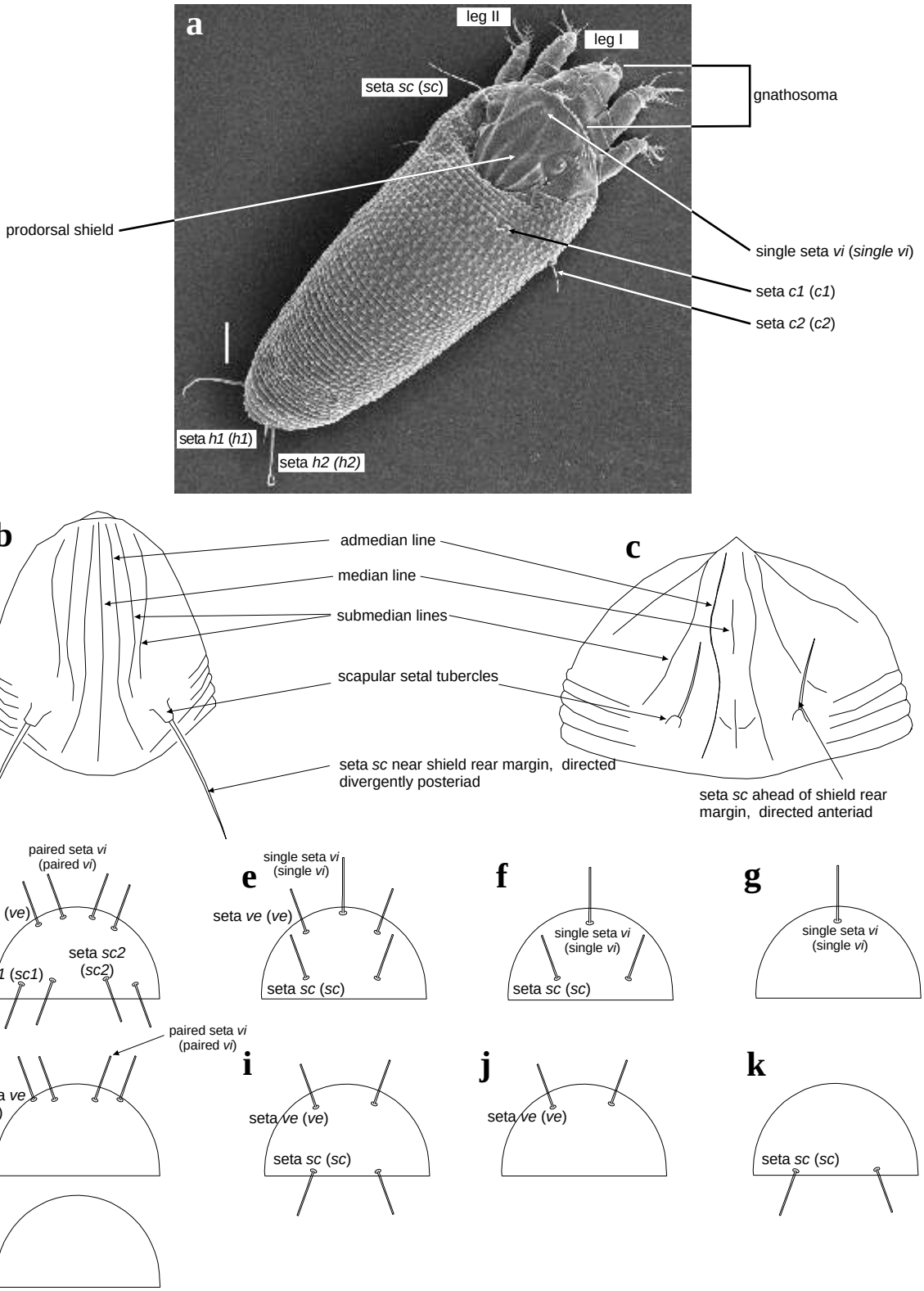


Fig. 3.3. a) Habitus of an eriophyoid mite, represented by the SEM image of *Trisetacus* sp. (Eriophyoidea: Phytoptidae) in dorsal view, scale line = 10 µm; **b, c)** schematic drawings of prodorsal shield in dorsal view with names of general lines of prodorsal shield pattern, and different positions and projections of *sc*. Schematic representation of different setal patterns on the prodorsum in dorsal view: **d)** eight setae, e.g., members of the Tydeidae; **e)** five setae (maximum number of prodorsal setae in the Eriophyoidea), only present in *Pentasetacus* (Phytoptidae: Nalepellinae); **f)** three setae, e.g., *Trisetacus* (Phytoptidae: Nalepellinae); **g)** one seta, e.g., *Boczekella* (Phytoptidae: Nalepellinae); **h)** four setae anteriorly on shield, e.g., *Prothrix* (Phytoptidae: Prothricinae), but the internal pair of setae may not be paired *vi*, but rather *sc* which moved far forward (see Chapter 4); **i)** four setae, two anteriorly on shield, two closer to the shield rear margin, e.g., *Novophytoptus* (Phytoptidae: Novophytoptinae); **j)** two setae anteriorly on shield, e.g., *Propilus* (Phytoptidae: Sierraphytoptinae: Mackiellini); **k**) two setae, *sc*, mostly on posterior part of dorsal shield, in most species of the Eriophyidae and Diptilomiopidae; **l)** no setae e.g., *Cecidophyes* (Eriophyidae: Cecidophyinae).

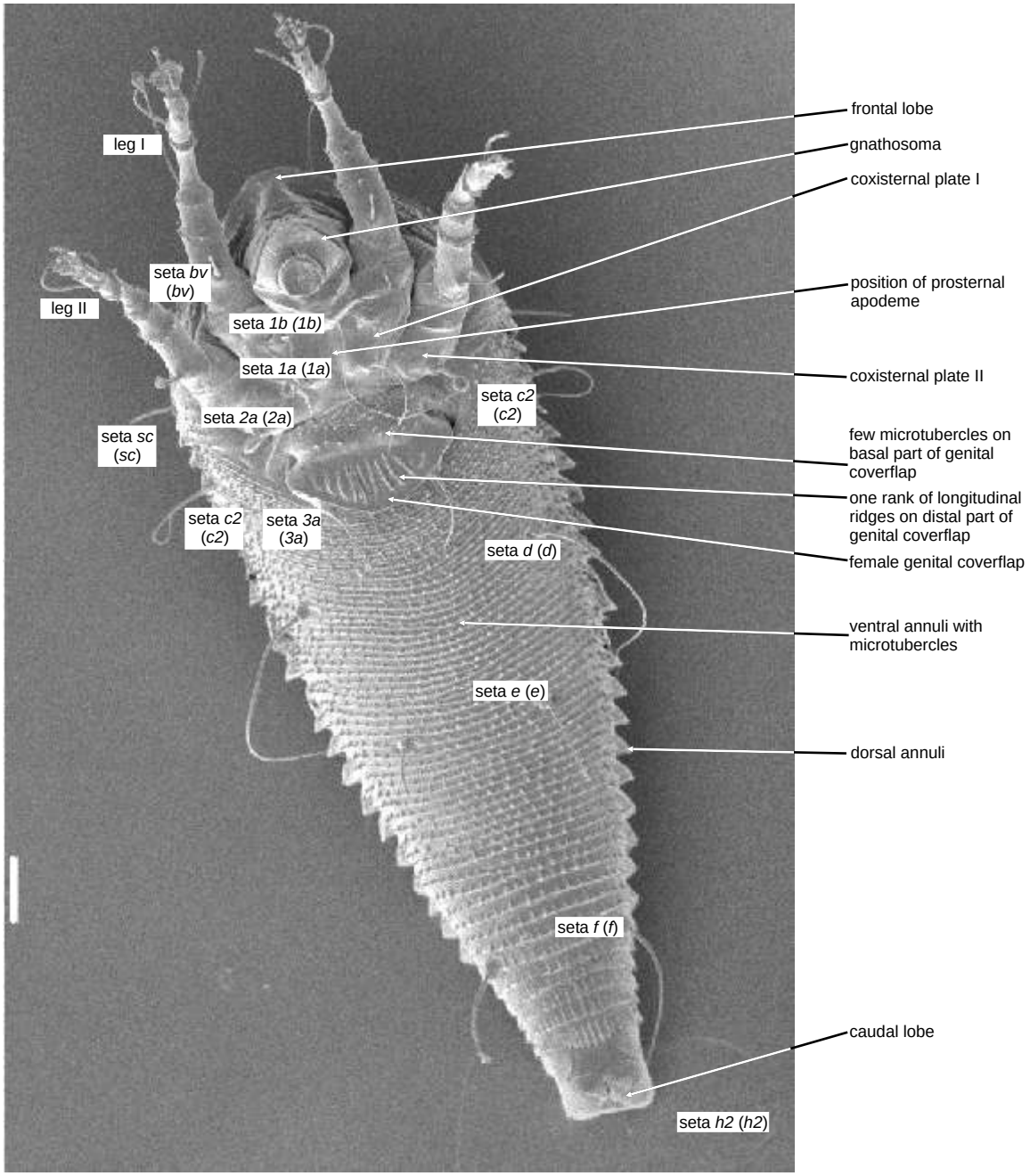


Fig. 3.4. Habitus of an eriophyoid mite, represented by the SEM image of an *Aculus* sp. (Eriophyoidea: Eriophyidae: Phyllocoptinae) in ventral view. Scale line = 10µm.

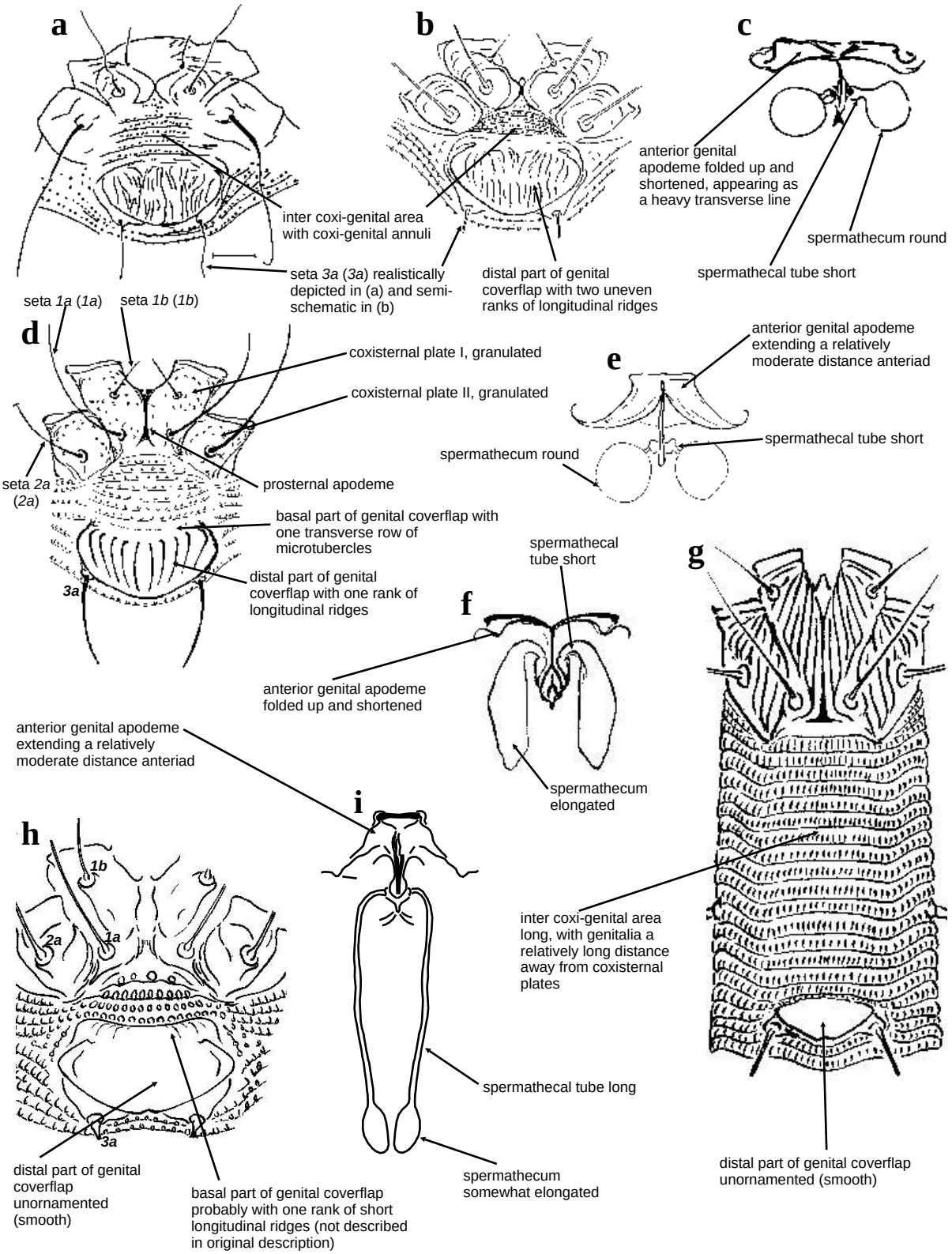


Fig. 3.5. Descriptive drawings of the coxi-genital areas and internal genitalia of slide-mounted adult females of different eriophyoid taxa. *Cecidophyes rouhollahi* Craemer, 1999 (Eriophyidae: Cecidophyinae), reproduced from Craemer *et al*. (1999), specimen depicted in (a) more flattened under coverslip than specimen depicted in (b): **a)** coxi-genital area, drawing by C. Craemer, **b)** coxi-genital area, drawing by H.H. Keifer, **c)** internal genitalia, drawing by C. Craemer; *Tegolophus califraxini* (Keifer, 1938b) (Eriophyidae: Phyllocoptinae), drawings by E. de Lillo, reproduced from De Lillo (1988b): **d)** coxi-genital area, **e)** internal genitalia; *Novophytoptus stipae* Keifer, 1962, drawings by H.H. Keifer, reproduced from Keifer (1962d): **f)** internal genitalia, **g)** coxi-genital area; *Trisetacus cupressi* Keifer, 1944, drawings by H.H. Keifer, reproduced from Keifer (1944): **h)** internal genitalia (modified from Keifer, 1944), **i)** coxi-genital area. All reproductions with permission where necessary.

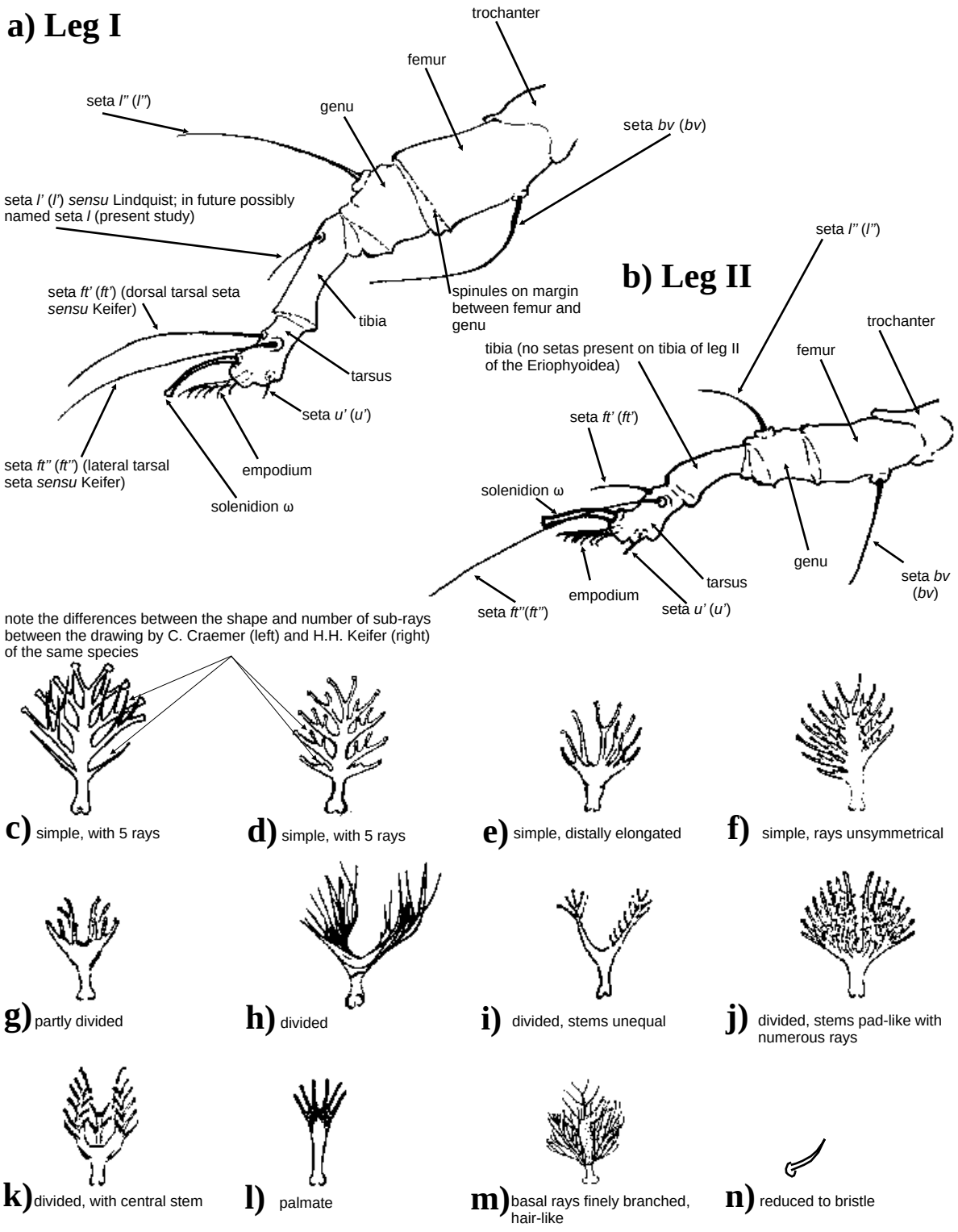


Fig. 3.6. Legs and leg structures of adult eriophyoid females. Legs of *Aculops rhodensis* (Keifer, 1957) as drawn by E. de Lillo, from De Lillo (1988b): **a)** leg I; **b)** leg II. Different shapes of eriophyoid empodia (featherclaws) of various species: **c)** *Cecidophyes rouhollahi*, drawing by C. Craemer (reproduced from Craemer *et al.*, 1999); **d)** *C. rouhollahi*, drawing by H.H. Keifer (reproduced from Craemer *et al.*, 1999); **e)** *Dicrothrix anacardii* Keifer, 1966 (reproduced from Keifer, 1966b); **f)** *Dechela epelis* Keifer, 1965 (reproduced from Keifer, 1965a); **g)** *Acaphyllisa parindiae* Keifer, 1978 (reproduced from Keifer, 1978); **h)** *Diptilomiopus faurius* sp. nov. (Appendix L); **i)** *Acarhis lepisanthis* Keifer, 1975 (reproduced from Keifer, 1975d); **j)** *Acarhynchus filamentus* Keifer, 1959 (reproduced from Keifer, 1959b); **k)** *Diptiloplatus megagrastis* Keifer, 1975 (reproduced from Keifer, 1975c); **l)** *Acritonotus denmarki* Keifer, 1962 (reproduced from Keifer, 1962b); **m)** *Brevulacus reticulatus* Manson, 1984, protogyne female (modified from Manson, 1984a); **n)** *Aberoptus samoae* Keifer, 1951, leg I (modified from Keifer, 1951). Terminology sensu Keifer not used in the present study.

Although the amount of character variation is roughly sufficient for standard taxonomy, some characters demarcating different genera, and even higher groupings, are not of good taxonomic value, and somewhat vague and subjective, and sometimes with intergradation between them (Amrine *et al.*, 2003). For instance, differentiation between the tribe Tegonotini (with lateral lobes or pointed projections from some or all annuli, or with a plate behind prodorsal shield bearing lateral extensions) and the tribes Phyllocoptini and Anthocoptini (without these lateral opisthosomal projections); between *Aculus* (anterior shield lobe broad and rounded) and *Aculops* (anterior shield more acuminate, frequently ending in a sharp point); between *Tegonotus* (*sc* ahead of rear shield margin, direction variable) and *Shevtchenkella* (*sc* on rear shield margin, directed posteriorly); between *Aceria* (posterior opisthosoma with annuli continuous and subequal dorsoventrally) and *Paraphytoptus* (posterior opisthosoma with wider annuli dorsally); and between *Epitrimerus* (middorsal ridge fading simultaneously with subdorsal or lateral ridges) and *Calepitrimerus* (middorsal ridge ending in a broad furrow before termination of subdorsal ridges) (Amrine *et al.*, 2003), are contentious.

Furthermore, the differentiation between species and the identification of these species of some very large genera, e.g., *Aceria* with more than 900 species worldwide, are also becoming problematic (Amrine *et al.*, 2003). Very few species identification keys are available for, example, *Aceria*, and those available pertain to species over limited geographic areas (e.g., Meyer & Ueckermann, 1990).

It is evident that there are not enough morphological characters documented and available for phylogenetic analyses, and most of these were found to be highly homoplasious by previous studies (Hong & Zhang, 1996a, b, 1997), as well as by the present phylogenetic study (see Chapter 4). Additional characters with more phylogenetic information (homologous or at least less homoplasious characters) will be of tremendous use in finding more clades and more robust and reliable hypothesized phylogenetic relationships between taxa.

Many of these systematic problems can be rectified or improved by the discovery of additional new systematically informative characters for the currently known species, apart from those characters that will be obtained from the discovery of new species. Despite the relative simplicity and reduction of the eriophyoid body, the group is unexpectedly diverse in morphology (Amrine, 1996; Lindquist, 1996a; Amrine *et al.*, 2003). There are, however, not many additional taxonomically informative and useful characters available from slide-mounted specimens. Taxonomic characters for the Eriophyoidea are already obtained from the entire body (Lindquist & Amrine, 1996; Amrine *et al.*, 2003), and most easily observable and taxonomically useful

characters are already utilized. The degree of morphological diversity is also limited by the lack of ontogenetic diversity in characters (characters have the same states throughout all life stages), and the lack of distinctive characters in the male (Lindquist & Amrine, 1996).

The quality of the systematics of the Eriophyoidea is dependent on the quality of the taxonomic descriptions, of which exact, detailed drawings should be an integral part (Keifer, 1975a, b; Amrine, 1996; Amrine *et al.*, 2003; De Lillo *et al.*, 2010). In practice, even in recent publications, many descriptions and drawings do not achieve the required standard and in particular do not always convey exact taxonomically important detailed characteristics (Amrine & Manson, 1996; De Lillo *et al.*, 2010). It also became clear during the present study (Chapters 4), particularly when using published descriptions, that the characters are frequently not well-defined and demarcated, and this presents problems for the determination of primary homologies in obtaining a taxon x character state matrix for phylogenetic analyses. Thorough and precise descriptions of eriophyoids are extremely important when it is taken into account that slide-mounted specimens are not permanent, and that most type material is lost over time (Amrine & Manson, 1996; De Lillo *et al.*, 2010).

There are many problems with the quality and standardization of slide-mounted specimens (Amrine & Manson, 1996; De Lillo *et al.*, 2010), and the resultant quality of eriophyoid descriptions. Another technique for studying morphology is electron microscopy (EM) which facilitates higher resolution than light microscopy, and is largely superior to light microscopy for studying minute organisms with ultra-fine structures. Following the development of electron microscopy and its eventual utilization for studying eriophyoid morphology, more information on the external and internal morphology of eriophyoid mites was obtained, and our understanding of and knowledge on their morphology have improved (Nuzzaci & De Lillo, 1996).

Information on the internal structures of eriophyoids was largely obtained with transmission electron microscopy (TEM), reviewed by Nuzzaci & Alberti (1996). Some of the first TEM studies undertaken on the Eriophyoidea were those of Paliwal & Slykhuis (1967) and Takahashi & Orlob (1969) on the intestines of *Aceria tosichella* with the focus on virus vectoring. Subsequent studies include Shevchenko & Silvere (1968), Nuzzaci & Liaci (1975), Nuzzaci (1976a, 1979), Thomsen (1987, 1988), Nuzzaci & Alberti (1996), and Nuzzaci & De Lillo (1991), and essentially focused on the functional morphology of various structures.

The first published studies on the external morphology of the Eriophyoidea with EM were undertaken with TEM (Proeseler & Eisbein, 1968; Eisbein & Proeseler, 1969). Hereafter, external

morphology was mainly studied with scanning electron microscopy (SEM) which is more appropriate for studying surface structures.

Scanning electron microscope images of eriophyoids can be found in Keifer (1975a, b) and Lindquist (1996a). Only a few comprehensive morphological studies, but on a single species or only a few species, using SEM have been published, and these mostly focused on the functional morphology of particular body regions, or demonstrated SEM techniques [e.g., Whitmoyer *et al.*, 1972; Gibson, 1974; McCoy & Albrigo, 1975 (mouth-parts and feeding); Hislop & Jeppson, 1976 (mouth-parts and feeding); Nuzzaci, 1976a, b; Nuzzaci & Vovlas, 1976; Schliesske, 1978; Baker *et al.*, 1987; Westphal *et al.*, 1990; Amrine *et al.*, 1994; Duffner *et al.*, 1998; Huang, 1999; Wergin *et al.*, 2000; Achor *et al.*, 2001; Freeman *et al.*, 2005]. Other SEM studies confirmed or elucidated internal gnathosomal structures (Thomsen, 1987; Freeman *et al.*, 2005), or focused on spermatophores deposited by eriophyoid males (e.g., Oldfield *et al.*, 1970; Duffner *et al.*, 1998).

Scanning electron microscope images are sporadically incorporated in taxonomic articles, but they are usually merely used to enhance and confirm taxonomic descriptions from slide-mounted specimens, and are included in the articles normally without particular comment or focus on them. They are mostly not used to add additional morphological or descriptive information (e.g., Keifer *et al.*, 1982; Boczek & Nuzzaci, 1985; Schliesske, 1985; De Lillo, 1988b; Chandrapatya & Boczek, 1991a,b; Boczek & Chandrapatya, 1992a; Amrine *et al.*, 1994; De Lillo, 1994; Huang & Wang, 2004). Only images of entire mites are usually included, while a few included some enlargements of particular body regions (e.g., Amrine *et al.*, 1994). The SEM images probably contributed to the correctness and detail of the descriptions. A few authors based descriptions on SEM images (e.g., Huang, 1992) without the inclusion of descriptive drawings. Amrine (1996) condemned this practice, and De Lillo & Skoracka (2010) likewise strongly advised against the use of SEM images in place of drawings.

De Lillo & Aldini (2001) combined TEM and SEM to study and compare the ultrastructure of sensory structures on the leg tarsi of a species of the Siteroptidae and *Phytoptus avellanae* (Phytoptidae), *Aculops lycopersici* (Tryon) (Eriophyidae) and *Diptacus hederiphagus* Nuzzaci (Diptilomiopidae) of the Eriophyoidea. They found the wall of the tarsal solenidion shaft of *P. avellanae* is smooth and without pores, but it has very small apical pores forming a complex system connected with pore tubules. They could not see the pores in SEM images. In contrast, the siteroptid solenidial shaft has a multiporous wall enclosing several dendritic branches, and no tubular bodies are associated with the solenidion. They concluded that the solenidia of these species are both isotropic, but based on clear differences in cuticular and cytological

characteristics these were found to be of different types. Before homologies between many structures, especially between structures in the Eriophyoidea and other mite groups, can be determined, anatomical and functional relevance should be taken into consideration, in addition to external morphological information (De Lillo & Aldini, 2001).

Alberti & Nuzzaci (1996) comprehensively reviewed the SEM and TEM techniques used for studying eriophyoid mites, focusing on conventional methods. Various techniques for SEM preparation and study of biological material are available. The microscopic size, soft and delicate bodies, and ultra-fine structural details of the Eriophyoidea causing difficulties with preparing and studying slide-mounted specimens, also pose problems for SEM techniques. Conventional SEM preparation methods broadly entail fixation, dehydration and final drying of the specimens. Unfortunately, these preparation methods are associated with artefacts in biological specimens (Sutherland & Hallett, 1987), of which deformation caused by shrinking of the material is the most prevalent, and shrinking is particularly a problem in the soft-bodied eriophyoid mites [Craemer & Hall, 2003 (Appendix J.1.)]. With these methods, the mites usually have to be removed from their natural habitat and position (Alberti & Nuzzaci, 1996).

It is possible to observe live or "fresh" specimens in the SEM, avoiding fixation and dehydration (Woolley, 1970). Nuzzaci & Vovlas (1976) and Alberti & Nuzzaci (1996) described a similar method modified for eriophyoid mites. Another method, the so-called "acrolein method", for successfully studying eriophyoids intact in a natural state was used by McCoy & Albrigo (1975) and Hislop & Jeppson (1976), and is also described by Alberti & Nuzzaci (1996). There are also SEM techniques available for preparing dry eriophyoid material, already preserved specimens and slide-mounted specimens (Nuzzaci & De Lillo, 1991; Alberti & Nuzzaci, 1996).

Low-temperature SEM, also known as cryo-SEM, with an integrated high vacuum freezing and sputter unit, seems to be the most successful SEM technique in obtaining highly magnified, largely artefact-free images of eriophyoid mites, particularly minimizing shrinkage (Sutherland & Hallett, 1987; Duffner *et al.*, 1998; Wergin *et al.*, 2000; Achor *et al.*, 2001). The first images of eriophyoid mites obtained by using cryo-SEM were published by Amrine *et al.* (1994). Achor *et al.* (2001) compared results of mites studied with ambient temperature SEM (using four preparation techniques), and low-temperature (cryo-) SEM. Low-temperature SEM was found to be superior to the conventionally used ambient temperature SEM. Wergin *et al.* (2000) described a modified cryo-fixation procedure that can be used for low-temperature SEM, retaining the mites in their living/feeding sites in natural behavioral

positions, and again confirmed that the turgor of eggs and the soft-bodied eriophyoids were maintained. Using a field emission SEM which provides superior resolution to what can be attained with conventional SEM, allowed better resolution and discrimination of ultra structural features (Wergin *et al.*, 2000).

The aims of and motivation for the present SEM study are set out in Chapter 1. One major aim is to investigate to what extent SEM studies may contribute to obtaining additional morphological characters, and how much it can improve the description of eriophyoid morphology, and to what extent it could or should be incorporated in the systematics of the Eriophyoidea, and particularly in phylogenetic analyses of this group.

The results and discussion of the SEM study of eriophyoid morphology is presented in two parts:

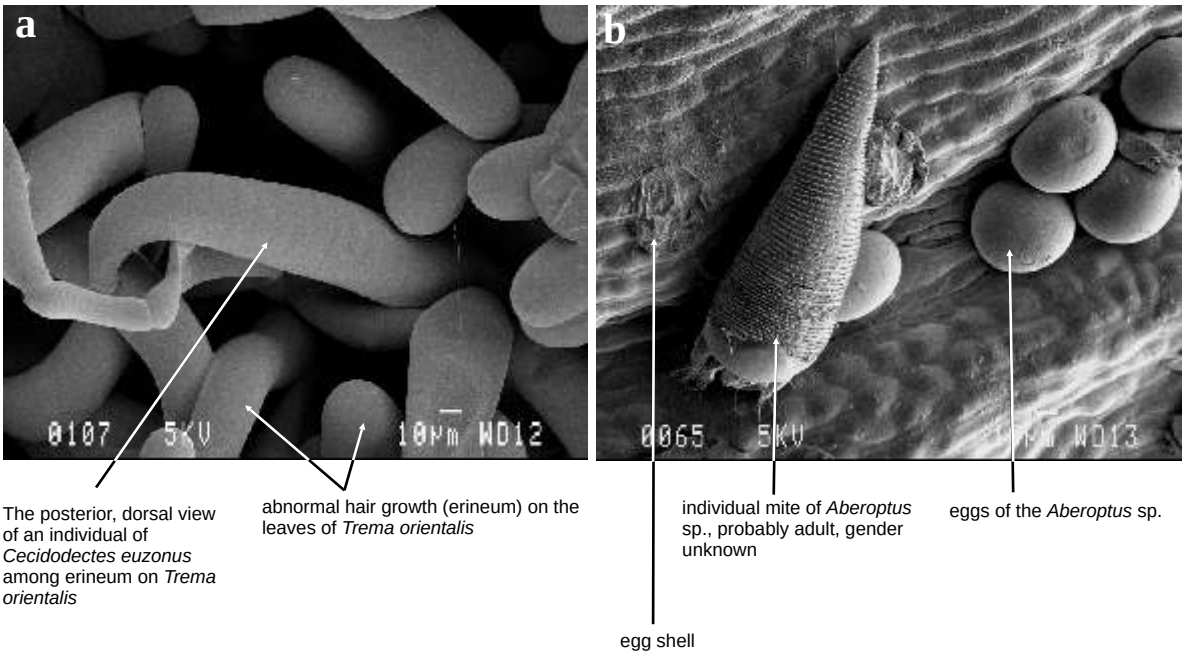
- Part I entails a general overview of the improvement of morphological study obtained in the present SEM study. Some results obtained with SEM are compared with slide-mounted specimens or published descriptions of these. Light microscopic study of the morphology of eriophyoid mites obtained from slide-mounted specimens and its application in their systematics is broadly appraised.
- Part II entails a comparative morphological study of the gnathosoma, of all the species in the present SEM study. It is included to illustrate to what extent SEM studies can contribute towards systematics, and to present the new data. Similar comparative studies, with significant results, of other structures studied during the present SEM study, including the legs, opisthosoma, coxisternal plates and external genitalia, are possible.

3.2 MATERIAL AND METHODS

3.2.1 Low-temperature SEM

A modified version of the cryo-fixation technique described by Echlin *et al.* (1970) was used for preparing specimens for the present study using a conventional JEOL JSM 840 SEM with a cryo-stage. This stage is one of the first developed, and was modified by placing a cold trap on the specimen holder directly above the specimen (A. Hall, *pers. comm.*). The cryo-stages and -systems available today are technically more advanced and produce better results than the stage used for the present study (A. Hall, *pers. comm.*). Preparation procedures are presented here because they were developed for the SEM infrastructure available, and are not published, and may be of use in developing similar procedures by others who would like to use this technique.

Fresh plant material preferably with live mites was used for study. Individual mites and mite colonies including eggs, spermatophores, etc. *in situ* on plant material, and later on in the study, single specimens collected from the material, were prepared and studied as follows: The gum of one side of a piece of double-sided adhesive carbon tape small enough to fit in the hollow button (specimen holder) was exposed and this side stuck onto a transparency sheet. The addition of the transparency sheet was necessary for manipulating the piece of carbon tape. The other side of the tape was also exposed. Tiny pieces of fresh plant material with as many live mites as possible on it (Fig. 3.7b), were arranged and stuck onto the exposed side of the tape (Fig. 3.7c). This was done with the aid of a dissecting stereo microscope. This procedure was not entirely satisfactory since many mites washed off during plunge-freezing in the nitrogen slush [Ebrahim *et al.*, 1996; Craemer & Hall, 2003 (Appendix J.1.)]. The remaining mites were also not representing all positions necessary for a morphological study for systematic purposes. Most of them could only be viewed in dorsal view. The adaptation to the cold stage as described above limited its maneuverability, and the specimens could not be tilted, limiting the observation and capturing of images on different aspects of a single specimen. It was frequently difficult to find the mites on the plant material when viewed in the SEM (Fig. 3.7a). This technique was still used, though, to study the mites *in situ* in order to observe their ecology and biology, including eggs and spermatophores, and to study their morphology without any prior mechanical manipulation of the specimens which might alter or damage them.



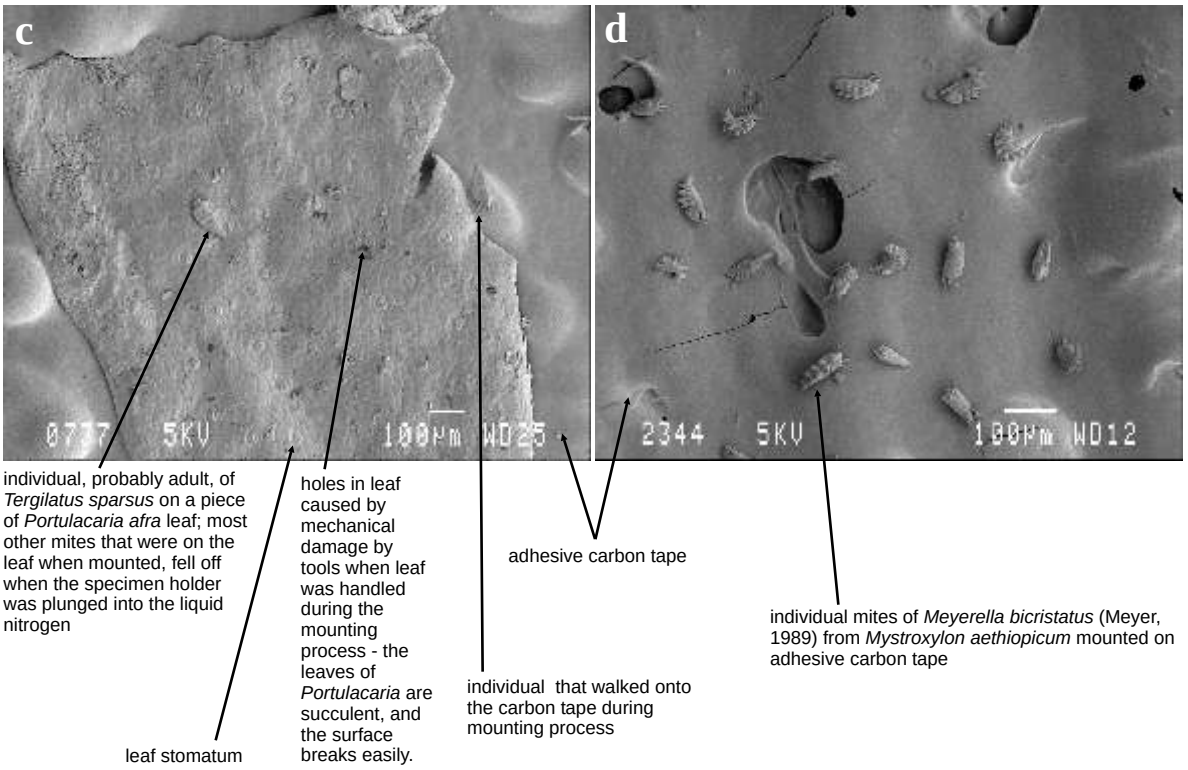


Fig. 3.7. Unmodified SEM images: **a)** Specimens of *Cecidodectes euzonus* Nalepa, 1917 among erineum hairs caused by them on *Trema orientalis*, illustrating the difficulty to sometimes find the mites within complicated plant structures when viewed with SEM. This and the need to view them from different aspects, creates the need to mount them individually for systematic purposes; **b)** Individual of *Aberoptus*, probably new species, *in situ* on a *Schotia brachypetala* leaf - note the good turgor, with no apparent shape distortion, of both plant and mite material, including mite eggs; **c)** *Tergilatus sparsus* Meyer & Ueckermann, 1995 on *Portulacaria afra* - a piece of plant material (leaf in this case) with live mites *in situ*, mounted on adhesive carbon tape; **d)** individual mites of *Meyerella bicristatus* (Meyer, 1989b) from *Mystroxylon aethiopicum* stuck onto adhesive carbon tape to facilitate observation of different aspects of the mite specimens. The lengths represented by the scale lines are given below the lines.

For these reasons, later on in the study, additional individual mites were taken off the plant material with an eyebrow hair mounted on a stick and mounted in the correct position on the carbon tape (Fig. 3.7d). After a specimen was mounted, it could not be moved again. Care was taken to mount live mites, and keep them alive through the mounting process to minimize distortion. The process of mounting the mites took about an hour, depending on the abundance and density of the mites and other factors. Unfortunately, the mites would still struggle after being put on the tape and in the process frequently damage themselves. This damage mostly involved the loss of limbs or attachments that could be identified as artefacts. Even with the relative shallow surface of the carbon tape, some structures, such as empodia and setae of the specimens, sunk into the surface and were partly covered. Frequently, the existence of an assortment of species was only realized when the mites were studied in the SEM.

When the piece of tape with plant material and mite specimens was ready, it was attached into a specimen holder with a sufficient amount of silver paint to earth the piece of tape. Hereafter the specimen holder was plunge-frozen in nitrogen slush. The holder with frozen specimens was then transferred via the pre-chamber of the cryo-system to the pre-cooled (about -170 °C) cryo-stage in the chamber of the SEM, where they were etched for *ca.* 30 minutes by increasing the temperature to *ca.* -80 °C to remove ice crystals. The completion of the etching was determined by observing a specific area of the material during the etching process. This was problematic because the specimen charged-up easily prior to sputter-coating. Ice was not always totally removed, or the specimens were rendered unstable by etching too extensively. The specimen holder was then transferred back to the cryo-stage of the pre-chamber and sputter-coated with gold. Hereafter it was returned to the cryo-stage in the SEM for observation at an accelerating voltage of 5 kV, and sometimes 2 kV, to prolong viewing time. This low current, particularly when using a conventional SEM, was also employed to alleviate charging and thereby increase resolution (A. Hall, *pers. comm.*).

The images were captured digitally in ".tiff" format employing a frame grabber controlled by Orion® rel 6.6, Belgium (A. Hall, *pers. comm.*). These were cropped and edited with Corel Photo-paint® Version 11.633. Obligatory text added by the SEM image-capturing system (image number, amount of accelerating voltage, etc.) (Fig. 3.7) was removed by cropping, or using the clone tool in Corel Photo-paint®, and the scale line was moved to a standardized position. Care was, however, taken not to alter any important image detail in the process. The images were laid out and labeled in Corel Draw® Version 11.633 or were inserted between text in Microsoft® Office

Word 2003. Some SEM images were compared with either a light microscope study of the morphology of slide-mounted specimens or their published descriptions.

3.2.2 Specimens studied

The SEM study was planned to deal with species described from South Africa, and in particular newly described species and genera in order to use the SEM images in future for redescription of these species, and particularly the new genera. Mites were collected from the same host plants mostly at the same localities at which they were originally collected from. Mixtures of species, often including new species, were obtained from these collections. Since most of these may be difficult to obtain again, and to maximize available SEM time and to increase the variation of the morphology observed, they were included in the SEM study, although they restricted work time on targeted species. One collection of mites (*Trisetacus* sp. from *Pinus pinaster* in France) was also opportunistically studied to include representatives of this phytoptid genus, not present in South Africa. About 3 500 SEM images of about 640 specimens of roughly 64 species (Table 3.1) were captured. This represents 23 genera of the 46 genera recorded from South Africa, including species of five [*Afromerus* Meyer, 1990 (Meyer, 1990b), *Costarectus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995), *Neserella* Meyer & Ueckermann, 1989 (Meyer & Ueckermann, 1989b), *Porosus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995) and *Quintalitus* Meyer, 1989 (Meyer, 1989c)] of the nine genera described from South Africa. These genera might be endemic to the southern hemisphere, which are important in the context of the present study which focuses on taxa from this region, and in particular from South Africa. Despite efforts to do so, species of *Adenocolus* Meyer & Ueckermann, 1997 (Meyer & Ueckermann, 1997), *Aequsomatus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995), *Africus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995) and *Pyelotus* Meyer, 1992 (Meyer, 1992c), all genera described from South Africa, could not be recollected during the study. *Phyllocoptes* sp. and *Tetraspinus* sp. were collected, and it is the first records of these genera from South Africa. About 46 of the 64 species are probably undescribed and about six of these can be assigned to new genera.

3.2.3 Convention and use of morphological terminology in present study

The descriptions of morphological structures refer to only one half of the body, particularly in regard to the use of singular or plural, e.g., seta *bv* is present on leg I, and not setae *bv* are present on legs I, and seta *sc* is on or near the rear shield margin, and not setae *sc* are on or near the rear shield margin. Usually the abbreviation of structures, and particularly setae, are used, e.g., *sc* and not "seta *sc*". These abbreviations are in brackets following the more complete names in Figs 3.2–

3.6, 3.19, 3.20, 3.23. The following are exceptions to this usage: the single, unpaired seta *vi* positioned on the dorso-median anterior prodorsum is referred to as single seta *vi*; the components of the prodorsal shield pattern refer to the entire surface of the prodorsum (refer to both sides of the body). The length, or related terms, of a structure, is always parallel to the long axis of the body, and width is perpendicular to the long axis of the body; these orientations in appendages are according to the long axis of the particular appendage, except the conventional use of "dorsal annuli are broader or wider than the ventral annuli", in stead of "dorsal annuli are longer than ventral annuli".

Table 3.1. List of eriophyoid species studied in the scanning electron microscope (SEM) study. Scientific names (and synonyms where given) of plant host species according to Germishuizen & Meyer (2003). Localities are in South Africa, except where otherwise given. Mite families, subfamilies and tribes in table arranged according to Amrine *et al.* (2003), the mite genera and species names are arranged alphabetically. Host plant names are followed by the plant family in brackets.

Mite species and higher classification	Host plant species from which collected	Mite habit and habitat	Location collected	Date collected, collector	Date(s) studied with SEM
PHYTOPTIDAE					
Phytoptidae: Nalepellinae: Trisetacini					
Trisetacus sp. *cf*. *T. pinastri* Nuzzaci, 1975	*Pinus pinaster* Aiton (Pinaceae)	colonies underneath bracts near collar of conelets and on conelets, no obvious symptoms detected	France, Lavercantiére (44°32'N, 1°19'E), and Sivaillan (45°03'N, 0°45'W)	2 June 2002; A. Rocque	04 June 2002 06 June 2002 07 June 2002 10 June 2002
Phytoptidae: Nalepellinae: Nalepellini					
Setoptus radiatae Meyer, 1991	*Pinus radiata* D.Don (Pinaceae)	between needles under needle sheaths	Mpumalanga Province, Sabie, Long Tom Educational Centre (24°13'S, 30°27'E)	16 June 2003; S. Neser	18 June 2003
Phytoptidae: Sierraphytoptinae: Mackiellini					
Mackiella sp.	*Phoenix reclinata* Jacq. Senegal (Arecaceae)	worm-like vagrants in grooves underneath brown wiry tissue towards leave bases	Gauteng Province, Pretoria, northern border of National Botanical Garden (25°44'S, 28°16'E)	13 May 2003; S. Neser	15 May 2003
ERIOPHYIDAE					
Eriophyidae: Aberoptinae					
Aberoptus sp. nov.?	*Schotia brachypetala* Sond. (Fabaceae)	colonies underneath spinned nests on leaf undersurfaces	Gauteng Province, Pretoria, ARC-PPRI Vredehuis terrain nr. Union Building (25°45'S, 28°12'E)	? 2003; S. Neser (NF2596)	05 February 2003
Aberoptus sp. *cf*. *A. platessoides* Meyer, 1989 (from *Ochna* sp.) or *Aberoptus* sp. nov.? (from *Schotia* sp.)	*Ochna pretoriensis* E.Phillips (Ochnaceae) or *Schotia brachypetala* Sond. (Fabaceae) (both prepared for SEM this day)	underneath spinned or waxy nests spinning, determine of which species the SEM images were taken	Gauteng Province, Pretoria Grid Reference for central Pretoria: (25°44'S, 28°12'E)	S. Neser	10 February 2003
Aberoptus sp. nov.?	*Schotia brachypetala* Sond. (Fabaceae)	colonies underneath spinned nests on leaf undersurfaces	Gauteng Province, Pretoria, ARC-PPRI Vredehuis terrain nr. Union Building (25°45'S, 28°12'E)	19 February 2003; C. Craemer	19 February 2003
Cecidophyopsis sp. *cf*. *C. hendersoni* (Keifer, 1954)	*Yucca guatemalensis* Baker (Agavaceae) (parts of cultivated plants from unknown nursery in Pretoria, submitted to ARC-PPRI for determining the "pathogen" causing the symptoms actually caused by the eriophyoid mites)	colonies among small papilla-like erineum on both leaf surfaces caused by the mites	Gauteng Province, Pretoria, unknown nursery Grid Reference for central Pretoria: (25°44'S, 28°12'E)	2 November 2001; C. Craemer	15 November 2001
	Yucca guatemalensis Baker (Agavaceae) (in door potted cultivated plant inoculated with *Cecidophyes* colonies from above material)	as above	Gauteng Province, Pretoria, Montanapark X1, Darter Street 1009 (25°45'S, 28°12'E)	22 January 2002; C. Craemer	22 January 2002
	Yucca guatemalensis Baker (Agavaceae) (in door potted cultivated plant inoculated with *Cecidophyes* colonies from above material)	as above	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	24 January 2002; C. Craemer	24 January 2002
	as above	as above	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station (25°43'S, 28°14'E)	18 July 2002; C. Craemer	18 July 2002
Eriophyidae: Cecidophyinae: Colomerini					
Afromerus sp. *cf*. *Afromerus lindquisti* Meyer, 1990	*Psydrax livida* (Hiern) Bridson (Rubiaceae)	white, worm-like mites in elongated leaf galls	Gauteng Province, Pretoria, Meiring Naude Road, nr. CSIR (25°47'S, 28°17'E)	15 March 2002; S. Neser	26 March 2002
				20 March 2003; S. Neser	28 March 2002
Ectomerus sp. *cf*. *Ectomerus systenus* Meyer, 1990	*Terminalia sericea* Burch. ex DC (Combretaceae)	whitish mites in leaf galls (not fruit galls)	Gauteng Province, Hartbeespoort, nr. Saartjiesnek (25°46'S, 27°56'E)	27 July 2003; S. Neser (NF2622)	30 July 2003
Neserella sp. *cf. N. tremae*	*Trema orientalis* (L.) Blume (Celtidaceae)	white-yellowish leaf vagrants on leaf undersurfaces, no in erineum patches on leaves	Gauteng Province, Magaliesberg, Tonquani Kloof, nr. Buffelspoort (25°50'S, 27°29'E)	18 January 2003; S. Neser (NF2593)	23 January 2003
					28 January 2003

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Eriophyidae: Eriophyinae: Aceriini					
Acalitus mallyi (Tucker, 1926)	*Vangueria infausta* Burch. subsp. *infausta* (Rubiaceae)	in leaf galls	no collection record; S. Neser (probably nr. Pretoria, South Africa) Grid Reference for central Pretoria: ((25°44'S, 28°12'E))	no collection record; S. Neser	22 May 2003
Aceria lantanae (Cook, 1909)	*Lantana* x *camara* L. (hybrid complex) (Verbenaceae) (material decomposed and mouldy)	leaf galls	Brazilia, nr. Palmeiras	date?; S. Neser	23 April 2002
Aceria lantanae (Cook, 1909)	*Lantana* x *camara* L. (hybrid complex) (Verbenaceae)	flower galls	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, Quarantine Glass House (25°43'S, 28°14'E)	2 October 2002; C. Craemer	03 October 2002
				27 August 2003, P. & C. Craemer	28 August 2003
Aceria ocellatum Meyer & Ueckermann, 1990	*Rhus lancea* L.f. (Anacardiaceae)	in relatively small, round leaf galls	Gauteng Province, Pretoria, University of Pretoria Campus (25°14'S, 28°11'E)	18 December 2001; C. Craemer	18 December 2001
				13 February 2002; C. Craemer	13 February 2002
				28 February 2002; C. Craemer	28 February 2002
				18 March 2002; C. Craemer	18 March 2002
Aceria sp. *cf. A. dichrostachyia* (Tucker, 1926) (check spelling of species name)	*Dichrostachys cinerea* (L.) Wight & Arn. subsp. and var. unknown (Fabaceae)	deformed, clustered leaflets (no galls or outgrowths from leaflet surfaces)	Gauteng Province, Pretoria, Wonderboom Fort, Northern slope (25°39'S, 28°13'E)	16 March 2003; S. Neser	19 March 2003
					20 March 2003
Aceria sp. *cf. A. giraffae* Meyer, 1990 (numerous yellow-orangey mites)	*Acacia erioloba* E.Mey. (Fabaceae)	vagrant amongst the indumentum of very young podlets	Northern Cape Province, Strydenburg (29°56'S, 23°39'E)	6 January 2002; S. Neser	24 January 2002
Aceria sp. *cf. A. neseri* Meyer, 1981	*Chrysanthemoides incana* (Burm.f.) Norl. (Asteraceae)	in brown erineum patches	Western Cape Province, Clifton, Round House Road (33°56'S, 18°23'E)	20 February 2002; T. Morley	28 February 2002
		among fine erineum hairs		8 May 2002; T. Morley	09 May 2002
Aceria sp. *cf. A. neseri* Meyer, 1981	*Chrysanthemoides monilifera* (L.) Norl. subsp. *monilifera* (Asteraceae)	in erineum patches (most mites already dead on plant material before cryo preparation)	Western Cape Province, Stellenbosch, Jan Marais Park (33°56'S, 18°51'E)	20 May 2002; A. Wood (for S. Neser)	22 May 2002
		in erineum patches	Western Cape Province, Stellenbosch, Jan Marais Park (33°56'S, 18°51'E)	5 June 2002; A. Wood (for S. Neser)	07 June 2002
Aceria sp. *cf. A. proteae* Meyer, 1981	*Protea caffra* Meisn. subsp. *caffra* (Proteaceae)	witches' broom	Gauteng Province, Magaliesberg, Tonquani Kloof, nr. Buffelspoort (25°50'S, 27°29'E)	18 January 2003; S. Neser	29 January 2003
Aceria sp. nov. (in preparation)	*Ipomoea batatas* (L.) Lam. var. *batatas* (Convolvulaceae)	erineum and distortion	South Africa, Mpumalanga Province, close to the border with Mocambique (very broadly - exact location unknown)	February 2002; R.W. Gibson	18 March 2002
Aceria sp. nov. (in preparation) ("new" seta on gnathosoma)	*Oxalis corniculata* L. (Oxalidaceae)	distortion, thickening and leaf edge rolling	Gauteng Province, Pretoria, Montanapark X1, Darter Street 1009 (25°45'S, 28°12'E)	25 November 2001; C. Craemer	26 November 2001
				18 December 2001; C. Craemer	18 December 2001
unknown species, must still be identified, and it should be determined whether it is the same *Aceria* sp. of 16 April and 24 April 2002	*Acacia* sp. *cf. A. rehmanniana Acacia rehmanniana* Schinz (Fabaceae)	leaf galls?			28 March 2002
Aceria sp.?	*Acacia rehmanniana* Schinz (Fabaceae)	leaf galls	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, Quarantine Glass House, cultivated plant (25°43'S, 28°14'E)	date; S. Neser	16 April 2002
				23 April 2002; A. Witt & S. Neser	24 April 2002
Aceria sp.?	*Cineraria* sp. *cf. C. lobata,* or near (Asteraceae)	blisters	Mpumalanga Province, Graskop, Pinnacle Rock Grid reference for Graskop: (24°56'S, 30°50'E)	2 September 2002; S. Neser (NF2590)	12 September 2002

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unknown species (eriophyinae-like mite) seems to be the same species (*Aceria* sp. nov.(?)) from *Apodytes* on 28 May but don't identify for now due to host uncertainty	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae) (flowers) cultivated tree in garden OR *Mystroxylon* (erineum)		Gauteng Province, Pretoria, Lynnwood Glen (25°46'S, 28°17'E)	26 May 2002; S. Neser	27 May 2002
Aceria sp.?	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae) cultivated tree in garden	among flower buds, and between leaf axils and axil buds	Gauteng Province, Pretoria, Lynnwood Glen (25°46'S, 28°17'E)	26 May 2002; S. Neser	28 May 2002
Aceria sp. nov.?	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae)	one of two species on this material: this one worm-like and whitish, the other orangey = Phyllocoptinae?	Gauteng Province, Pretoria, Meintjieskop, behind Union Building (25°44'S, 28°13'E)	22 July 2003; S. Neser & C. Craemer	23 July 2003
Aceria sp. nov.?	*Xymalos monospora* (Harv.) Baill. (Monimiaceae)	in growth points	Mpumalanga Province, Graskop, Pinnacle Rock Grid reference for Graskop: (24°56'S, 30°50'E)	2 September 2002; S. Neser (NF2586)	12 September 2002
Eriophyidae: Phyllocoptinae: Acaricalini					
Tumescoptes sp. *cf. T. dicrus* Meyer, 1992	*Phoenix reclinata* Jacq. (Arecaceae)	vagrant on green lamina	Gauteng Province, Pretoria, northern border of National Botanical Garden (25°44'S, 28°16'E)	13 May 2003; S. Neser	15 May 2003
Eriophyidae: Phyllocoptinae: Calacarini					
Calacarus sp.	*Rhus lancea* L.f. (Anacardiaceae)	large number of purple leaf vagrants with white "stripes" or ridges	Gauteng Province, Pretoria, University of Pretoria Campus (25°14'S, 28°11'E)	18 April 2002; C. Craemer	18 April 2002
				23 April 2002; C. Craemer	23 April 2002
Calacarus sp.?	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	leaf vagrant, SEM of only one specimen	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E), elevation 1 379m	2 April 2003; A. Witt	10 April 2003
Calacarus sp.?	*Psydrax livida* (Hiern) Bridson (Rubiaceae)	purple leaf vagrants with white "stripes" or ridges on mostly leaf upper surfaces	Gauteng Province, Pretoria, Meiring Naude Road, nr. CSIR (25°47'S, 28°17'E)	15 March 2002; S. Neser	26 March 2002
Eriophyidae: Phyllocoptinae: Tegonotini					
Shevtchenkella sp. *cf. S. lividae* (Meyer, 1990)	*Psydrax livida* (Hiern) Bridson (Rubiaceae)	orangey vagrants on leaf undersurfaces	Gauteng Province, Pretoria, Meiring Naude Road, nr. CSIR (25°47'S, 28°17'E)	15 March 2002; S. Neser	26 March 2002
Shevtchenkella sp. *cf. S. rothmanniae* (Meyer, 1990)	*Rothmannia capensis* Thunb. (Rubiaceae)	orange mites mostly in hairy gland cavities, sometimes on leaf surfaces	Gauteng Province, Pretoria, National Botanical Garden (25°44'S, 28°16'E)	14 August 2003; S. Neser & C. Craemer	15 August 2003
Shevtchenkella sp. *cf. S. rhusi* (Meyer, 1990)	*Rhus lancea* L.f. (Anacardiaceae)	vagrant	Gauteng Province, Pretoria, University of Pretoria Campus (25°14'S, 28°11'E)	18 March 2002; C. Craemer	18 March 2002
				23 April 2002; C. Craemer	23 April 2002
Neoshevtchenkella or *Shevtchenkella* sp.?	*Celtis africana* Burm. f. (Celtidaceae) (collected for pink vagrant with rows of lamellae on back (pers. comm., S. Neser))	leaf vagrants with wax structures	Gauteng Province, Pretoria, ARC-PPRI Vredehuis terrain nr. Union Building (25°45'S, 28°12'E)	6 February 2003; S. Neser (NF2598)	10 February 2003
Eriophyidae: Phyllocoptinae: Phyllocoptini					
Calepitrimerus sp.?	*Celtis africana* Burm. f. (Celtidaceae) (collected for pink vagrant with rows of lamellae on back (pers. comm., S. Neser))	leaf vagrant (species "B" and "C")	Gauteng Province, Pretoria, ARC-PPRI Vredehuis terrain nr. Union Building (25°45'S, 28°12'E)	6 February 2003; S. Neser (NF2598)	12 February 2003
Cecidodectes euzonus Nalepa, 1917	*Trema orientalis* (L.) Blume (Celtidaceae)	very long (some shorter) smooth, pink-orange mites, only in erineum	Gauteng Province, Magaliesberg, Tonquani Kloof, nr. Buffelspoort (25°50'S, 27°29'E)	18 January 2003; S. Neser (NF2593)	23 January 2003
					28 January 2003
Phyllocoptes sp.?	*Anthocleista grandiflora* Gilg (Gentianaceae)	leaf vagrant	Limpopo Province, Tzaneen (23°50'S, 30°09'E)	A. Witt	26 February 2003
					05 March 2003

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Tergilatus sparsus Meyer & Ueckermann, 1995	*Portulacaria afra* Jacq. ("(L.) Jacq." according to GRIN) (Portulacaceae) (potted plant outdoors)	leaf vagrant (one of possibly two species on this material: other "species" could be immatures of T. sparsus)	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	7 April 2002; S. Neser	08 April 2002
				12 May 2002; C. Craemer	13 May 2002
Eriophyidae: Phyllocoptinae: Anthocoptini					
Aculops or *Metaculus* sp.?	*Anthocleista grandiflora* Gilg (Gentianaceae)	leaf vagrant, one specimen (without wax)	Limpopo Province, Tzaneen (23°50'S, 30°09'E)	A. Witt	26 February 2003
Aculus sp. *cf. Aculops lycopersici* (Tryon, 1917) (according to the definition of *Aculus* and *Aculops* by Amrine, *Aculops lycopersici* resorts in *Aculus*)	*Physalis peruviana* (Solanaceae)	leaf vagrant	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	3 December 2002, C. Craemer	04 December 2002
Aculus sp.?	*Acacia burkei* Benth. (Fabaceae)	leaf vagrant without wax	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	7 May 2003; S. Neser	11 June 2003
Aculus sp.?	*Lantana trifolia* L. (Verbenaceae)	discolouration, slight distortion, retarded growth; large numbers of mites on leaves surrounding growth point, appearing like "pink powder" to the naked eye	Gauteng Province, Pretoria, Rietondale, Soutpansberg Road, ARC-PPRI Research Station, glass house, (25°43'S, 28°14'E)	25 September 2002; S. Neser	25 September 2002
Aculus sp.?	*Rothmannia capensis* Thunb. (Rubiaceae)	mites with wax, mostly in gland cavities, sometimes on leaf surfaces	Gauteng Province, Pretoria, National Botanical Garden (25°44'S, 28°16'E)	14 August 2003; S. Neser & C. Craemer	15 August 2003
Costarectus zeyheri Meyer & Ueckermann, 1995	*Dovyalis zeyheri* (Sond.) Warb. (Flacourtiaceae)	light orange vagrants with white wax stripes on undersurface of leaves	North West Province, Magaliesberg, Dome Kloof, nr. Buffelspoort (25°50'S, 27°32'E)	21 July 2002; S. Neser (NF2581)	24 July 2002
			North West Province, Magaliesberg, Castle Gorge (25°48'S, 27°34'E)	3 August 2003; S. Neser (NF2633)	13 August 2003
Meyerella bicristatus (Meyer, 1989)	*Mystroxylon aethiopicum* (Thunb.) Loes. subsp. *aethiopicum* (Celastraceae)	mites with humps or large lobes dorsally on opisthosoma, sometimes dense colonies among hairs on young growth (30 April 2003)	Gauteng Province, Pretoria, Lynnwood Glen, Argyle Street or near (25°46'S, 28°17'E)	19 May 2002; S. Neser	20 May 2002
				26 May 2002; S. Neser	27 May 2002
				30 April 2003; S. Neser	30 April 2003
				30 April 2003; S. Neser	07 May 2003
new genus? near *Costarectus*	*Mystroxylon aethiopicum* (Thunb.) Loes. subsp. *aethiopicum* (Celastraceae)	pinkish vagrant with wax ridges	Gauteng Province, Pretoria, Lynnwood Road (25°46'S, 28°16'E)	July 2003, C. Craemer	30 July 2003
new genus? near *Tetra*	*Protea caffra* Meisn. subsp. *caffra* (Proteaceae)	vagrant			29 January 2003
new genus? near *Mesalox*	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae)	among flower buds			13 May 2002
new genus? near *Mesalox*	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae) (cultivated tree in garden)		Gauteng Province, Pretoria, Lynnwood Glen (25°46'S, 28°17'E)	26 May 2002; S. Neser	27 May 2002
new genus? near *Mesalox*	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae)	orangey and more scarce	Gauteng Province, Pretoria, Meintjieskop, behind Union Building (25°44'S, 28°13'E)		23 July 2003
Porosus monosporae Meyer & Ueckermann, 1995	*Xymalos monospora* (Harv.) Baill. (Monimiaceae)	undersurface of younger leaves	Mpumalanga Province, Bridal Veil Falls nr. Sabie (25°06'S, 30°47'E)	16 June 2003; S. Neser	18 June 2003
					30 June 2003
Quantalitus squamosus Meyer, 1989	*Rothmannia capensis* Thunb. (Rubiaceae)	probably white, worm-like colonies in bullae	Gauteng Province, Pretoria, National Botanical Garden (25°44'S, 28°16'E)	14 August 2003; S. Neser & C. Craemer	15 August 2003
Tegolophus sp. *cf. T. orientalis* Meyer, 1990	*Trema orientalis* (L.) Blume (Celtidaceae)	white-yellowish mites	Gauteng Province, Magaliesberg, Tonquani Kloof, nr. Buffelspoort (25°50'S, 27°29'E)	18 January 2003; S. Neser (NF2593)	23 January 2003
Tetra retusa Meyer, 1992	*Bauhinia galpinii* N.E.Br. (Fabaceae)	vagrant on podlets and on leaf uppersurfaces, particularly against main vein in closely folded leaves	Gauteng Province, Pretoria, Montanapark X1, Darter Street 1009 (25°45'S, 28°12'E)	18 June 2002; C. Craemer	18 June 2002

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				20 June 2002; C. Craemer	20 June 2002
Tetra or *Tetraspinus* sp.?	*Chrysanthemoides monilifera* (L.) Norl. subsp. *monilifera* (Asteraceae)	vagrant (all specimens dead on material before cryo preparation)	Western Cape Province, Stellenbosch, Jan Marais Park (33°56'S, 18°51'E)	20 May 2002; A. Wood (for S. Neser)	22 May 2002
Tetraspinus sp.?	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	orange vagrants on leaf undersurfaces	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E), elevation 1 379m	2 April 2003; A. Witt	09 April 2003
Tetraspinus sp.? (one of five? species: orange mites (may have two vagrant species in these SEM images – compare with 9 April))	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	vagrant on leaf undersurfaces	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E), elevation 1 379m	2 April 2003; A. Witt	10 April 2003
Tetraspinus sp.? (one of five? species: orange mites (may have two vagrant species in these SEM images – compare with 9 April))	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	add images from description	Unknown	Unknown	22 August 2003
Eriophyidae: Phyllocoptinae (tribe uncertain)					
Anthocoptini?: *Aculus* sp.?	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	vagrant on leaf undersurfaces (possibly orange mite, not *Tetraspinus* nor *Metaculus*)	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E), elevation 1 379m	2 April 2003; A. Witt	09 April 2003
Eriophyidae (subfamily uncertain)					
unknown species, possibly in Aceriini	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	single worm-like mites in hairs, between young flowers and axil buds of leaves	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E) (elevation 1 379 m)	2 April 2003; A. Witt	16 April 2003
Eriophyinae?: Aceriini?	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae) ("*Faurea galpinii*" with smooth leaves (pers. comm., S. Neser)	second unknown species (worm-like), SEM images "B"	Mpumalanga Province, Graskop, Pinnacle Rock Grid reference for Graskop: (24°56'S, 30°50'E)	S. Neser (NF2589)	12 September 2002
Phyllocoptinae?	*Ekebergia capensis* Sparrm. (Meliaceae)	on distorted leaves (found only one dead specimen on material)	Gauteng Province, unknown location	April 2002; N. Basson	16 April 2002 (01-02)
new genus? in Phyllocoptinae or Cecidophyinae	*Acacia burkei* Benth. (Fabaceae)	vagrants with white wax ridges on leaf undersurfaces	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	7 May 2003; S. Neser	11 June 2003
Phyllocoptes? sp. (Phyllocoptinae: Phyllocoptini) (or may be a new genus in the Cecidophyinae)	*Dovyalis zeyheri* (Sond.) Warb. (Falcourtiaceae)	translucent white to dark puplish mites (not *Tetra zeyheri*, probably new species) colonies especially along veins, and in large "nests" and colonies in elongated galls with necrosis in vein axils	North West Province, Magaliesberg, Dome Kloof, nr. Buffelspoort (25°50'S, 27°32'E)	21 July 2002; S. Neser (NF2581)	24 July 2002
			North West Province, Magaliesberg, Castle Gorge (25°48'S, 27°34'E)	3 August 2003; S. Neser (NF2633)	13 August 2003
new genus? (subfamily uncertain)	*Cussonia* sp. (Araliaceae)	among and in flowers	Unknown	Unknown - S. Neser	12 February 2003
Eriophyidae (not *Neserella* or *Cecidodectes*) Eriophyidae (can not identify further but possibly Cecidophyinae: Colomerini: *Circases*)	*Trema orientalis* (L.) Blume (Celtidaceae)	shorter white mites, only from erineum; dorsal view of one specimen only	Gauteng Province, Magaliesberg, Tonquani Kloof, nr. Buffelspoort (25°50'S, 27°29'E)	18 January 2003; S. Neser (NF2593)	28 January 2003
DIPTILOMIOPIDAE					
Diptilomiopidae: Diptilomiopinae					
Diptilomiopus apobrevis sp. nov. (description in preparation)	*Apodytes dimidiata* E.Mey. ex Arn. ("E.Mey. ex Bernh." according to GRIM) subsp. *dimidiata* (Icacinaceae)	leaf vagrant add images from description	Mpumalanga Province, Nelspruit, Lowveld National Botanical Gardens (25°28'S, 30°59'E)	Arné	20 August 2003
Diptilomiopus faurius sp. nov. (description in preparation)	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae)	add images from description	Mpumalanga Province, Long Tom Pass picnic spot (25°08'S, 30°45'E)	2 April 2003; A. Witt	09 April 2003
					10 April 2003
					22 August 2003
Diptilomiopinae, unknown species	*Xymalos monospora* (Harv.) Baill. (Monimiaceae)	vagrant on undersurfaces of slightly younger leaves	Mpumalanga Province, Bridal Veil Falls nr. Sabie (25°06'S, 30°47'E)	16 June 2003; S. Neser	18 June 2003
					30 June 2003

Table 3.1. List of eriophyoid species studied in the scanning electron microscope (SEM) study. Scientific names (and synonyms where given) of plant host species according to Germishuizen & Meyer (2003). Localities are in South Africa, except where otherwise given. Mite families, subfamilies and tribes in table arranged according to Amrine *et al.* (2003), the mite genera and species names are arranged alphabetically. Host plant names are followed by the plant family in brackets.

new genus? nr. *Dacundiopus*	*Mystroxylon aethiopicum* (Thunb.) Loes. subsp. *aethiopicum* (Celastraceae)	vagrant scarcely distributed on leaves	Gauteng Province, Pretoria, Lynnwood Glen, Argyle Street or near (25°46'S, 28°17'E)	7 April 2002; S. Neser	08 April 2002
				15 April 2002; S. Neser	16 April 2002
				19 May 2002; S. Neser	20 May 2002
			Gauteng Province, Pretoria, Lynnwood Road (25°46'S, 28°16'E)	30 April 2003; S. Neser	30 April 2003
				6 May 2003; S. Neser	07 May 2003
Rhynacus sp.?	*Dovyalis zeyheri* (Sond.) Warb. (Falcourtiaceae)	shiny, light orange-amber-cream vagrants on leaf undersurfaces	North West Province, Magaliesberg, Castle Gorge (25°48'S, 27°34'E)	3 August 2003; S. Neser (NF2633)	13 August 2003
ERIOPHYOIDEA (family uncertain)					
gen. nov. unknown and unplaced species	*Rhus lancea* L.f. (Anacardiaceae)	in leaf blisters	Gauteng Province, Pretoria, Soutpansberg Road, ARC-PPRI Rietondale Research Station, (25°43'S, 28°14'E)	7 November 2001; C. Craemer	08 November 2001
Eriophyidae?: Phyllocoptinae: Anthocoptini?: close to *Tetra*?	*Faurea rochetiana* (A.Rich.) Chiov. ex Pic.Serm. (Proteaceae) ("*Faurea galpinii*" with smooth leaves (pers. comm., S. Neser))	vagrant, SEM images of only one specimen, SEM images "B"	Mpumalanga Province, Graskop, Pinnacle Rock Grid reference for Graskop: (24°56'S, 30°50'E)	S. Neser (NF2589)	12 September 2002
morphospecies one (family uncertain)	*Anthocleista grandiflora* Gilg (Gentianaceae)	vagrant with wax structures on leaf undersurface, SEM of one specimen	Limpopo Province, Tzaneen (23°50'S, 30°09'E)	A. Witt	26 February 2003
morphospecies two (family uncertain)	*Anthocleista grandiflora* Gilg (floribunda?) (Gentianaceae)	on green fruit	Sabie, bottom of Long Tom-pass, about 5 km from Hazeyview (25°03'S,30°59'E), 1342 m above sea level	14 August 2003; S. Neser or A. Witt?	28 August 2003
Eriophyoidea	*Psydrax livida* (Hiern) Bridson (Rubiaceae)	white vagrants with wax on leaf undersurfaces, SEM image of one specimen in dorsal view, identificaiton not possible	Gauteng Province, Pretoria, Meiring Naude Road, nr. CSIR (25°47'S, 28°17'E)	15 March 2002; S. Neser	26 March 2002
Eriophyoidea (one specimen)	*Rhus lancea* L.f. (Anacardiaceae) or *Lantana camara* L. (Verbenaceae) (plant material used this day)	unknown one specimen, two SEM images	*Lantana camara*, Brazilia, S. Neser; *Rhus lancea*, University of Pretoria Campus, Pretoria (25°14'S, 28°11'E)	*Lantana camara*, Brasil, S. Neser; *Rhus lancea*, University of Pretoria Campus, Pretoria; C. Craemer	23 April 2002
Eriophyoidea	*Sideroxylon inerme* L. subsp. *inerme* (Sapotaceae)	in open cup galls with white and brown erineum	Western Cape Province, Hermanus (34°25'S, 19°15'E)	1 February 2003; J.H. Giliomee	05 February 2003

PART I: GENERAL OVERVIEW OF THE CONTRIBUTION OF THE SEM STUDY TOWARDS THE SYSTEMATIC MORPHOLOGY OF THE ERIOPHYOIDEA[1]

The present SEM study contributed new and improved information towards the systematics of the species for which adequate images could be captured. Some examples are presented here in a general overview and, therefore, all structures that may be of systematic value are not dealt with, or indicated in this part. A comprehensive comparative study of the gnathosoma is presented in Part II.

3.3 PART I: RESULTS AND DISCUSSION

3.3.1 Comparison between SEM images and slide-mounted specimens

Some of the minute morphological structures of eriophyoid mites cannot be seen, or not clearly seen, when studying slide-mounted specimens using light microscopy. The resolution and study of these ultra-small and some larger features are significantly improved when utilizing SEM.

- Spinules and other structures on legs

Minute structures, with variation that may be of systematic value, are present on eriophyoid legs. Some of these are visible with light microscopy, but typically may be difficult or impossible to describe or quantify accurately, and are not utilized in the systematics of the Eriophyoidea. Some descriptive drawings of eriophyoid species include spinules (spicules) (small, spine-like cuticular processes according to Walter, 2008) and other structures on the legs (e.g., De Lillo, 1988b: 18, Fig. 4; Keifer, 1953: 74, Fig. 221), but these are not included in most descriptions, even if they may be present. Amrine *et al.* (1994) noted that numerous spinules can be seen on the lateral and distal margins of the femora and distal margins of the genua and tibiae in the SEM images of *Cecidophyopsis grossulariae*, but that these are difficult to observe with light microscopy. Lindquist (1996a) noted that various spine-like projections or serrations can occur on the legs, but that the smaller of these are probably more generally present than indicated in descriptions.

[1] Note that most of the comparisons and critique on observations from slide-mounted material, quality of slide-mounting, and descriptions thereof, entail the work of M.K.P. (Smith) Meyer and/or E.A. Ueckermann from South Africa. This is because the material included in the study was collected in South Africa, and the aim was to collect material that has already been described for comparison. The critique is not brought about by the quality of the taxonomic research of the Eriophyoidea by M.K.P. (Smith) Meyer and/or E.A. Ueckermann. Their work is regarded as representing some of the better quality descriptions published on Eriophyoidea in the world, and is only arguably surpassed in some aspects (more detail, and better mounting of specimens) by a few other eriophyoid taxonomists.

Similar spinules were broadly quantified in the present study. Spinules were present in some species (e.g., indicated by open triangles on legs I and II of *cf. Calacarus* sp. from *Psydrax livida*, Figs 3.8h, i) on congruent leg segment margins of different species. Sometimes these spinules are absent: there are for instance no appreciable spinules visible in the aspects viewed, between the femur and genu in specimens of *Trisetacus* sp. and *Afromerus* sp. (solid white arrows in Figs 3.8a and d, respectively). When these spinules are present on this margin (solid white arrows in Figs 3.8c, e-l), they broadly differ in size, position and number between species. For example, most spinules on this margin are probably present in the unknown species depicted in Fig. 3.8e.

Apart from these small structures, other characteristics, including shape and morphometrics of leg segments, and the position and shape of leg setae, can also be investigated for useful systematic information, and some of these are discussed here. The margin visible on the surface of the division between the femur and genu varies dorsally in the degree of fusion (solid white arrows in Fig. 3.8). The femur and genu are fused in *Diptilomiopus* sp. (Fig. 3.8b), partly fused dorsally in *Trisetacus* sp., *Afromerus* sp., *Acalitus mallyi* and two *Aceria* spp. (Figs 3.8a, d, j, k and l, respectively), while separated in the remainder of the species (Figs 3.8c, e, f, g, and h). Various types of ornamentation may be present on the femur (black arrows in Fig. 3.8), for example, ridges on the femora of leg I in *Cecidophyopsis* sp. and *Calacarus* sp. (Figs 3.8c and h, respectively), and granules on the femur of the unknown species (Fig. 3.8e). These three species are vagrants, living exposed. The shape of the leg segments also vary between species. In particular, the tibiae (open arrows in Fig. 3.8) are more rounded without sharp edges and ridges in *Trisetacus* sp., *Afromerus* sp., *Acalitus mallyi* and *Aceria* sp. on *Acacia rehmanniana* (Figs 3.8a, d, j and k, respectively). The tibiae of *Diptilomiopus* sp., *Aculus* sp., *Calacarus* sp. and *Aceria* sp. on *Ipomoea batatas* (Figs 3.8b, f, h, i, and l) have more straight and angular sides and ribs on the edge corners to varying degrees.

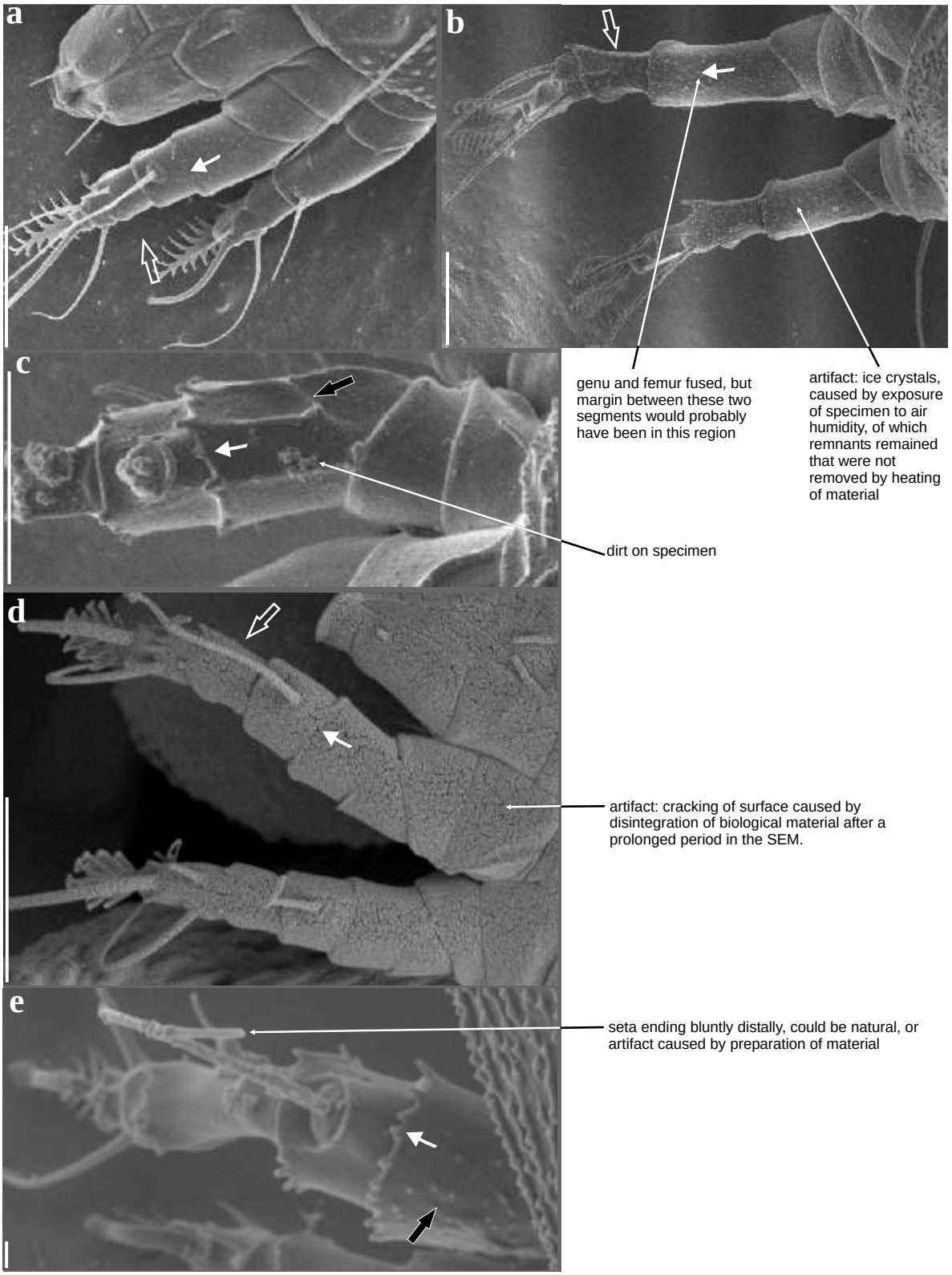


Fig. 3.8. (continued on next page) Dorsal views of legs of: **a)** *Trisetacus* sp. (Phytoptidae: Nalepellinae: Trisetacini), bud mite on *Pinus pinaster;* **b)** *Diptilomiopus faurius* sp. nov. (Diptilomiopidae: Diptilomiopinae), leaf vagrant on *Faurea rochetiana*; **c)** *Cecidophyopsis* sp. (Eriophyidae: Cecidophyinae: Cecidophyini), leaf vagrant on *Yucca guatemalensis*, **d)** *Afromerus* sp. (Eriophyidae: Cecidophyinae: Colomerini), leaf galls on *Psydrax livida*, (the fine cracks are artificial, caused by deterioration of specimen in SEM); **e)** unknown family (Eriophyoidea), vagrant on green fruit of *Anthocleista grandiflora*. Solid white arrows: dorsal completeness of margin between femur and genu on leg I, and presence, position and number of spines on this margin; solid black arrows: ornamentation on femur of leg I; open arrows: shape of tibia of leg I; **a, b, c, d)** scale lines = 10 µm; **e)** scale line = 1 µm.

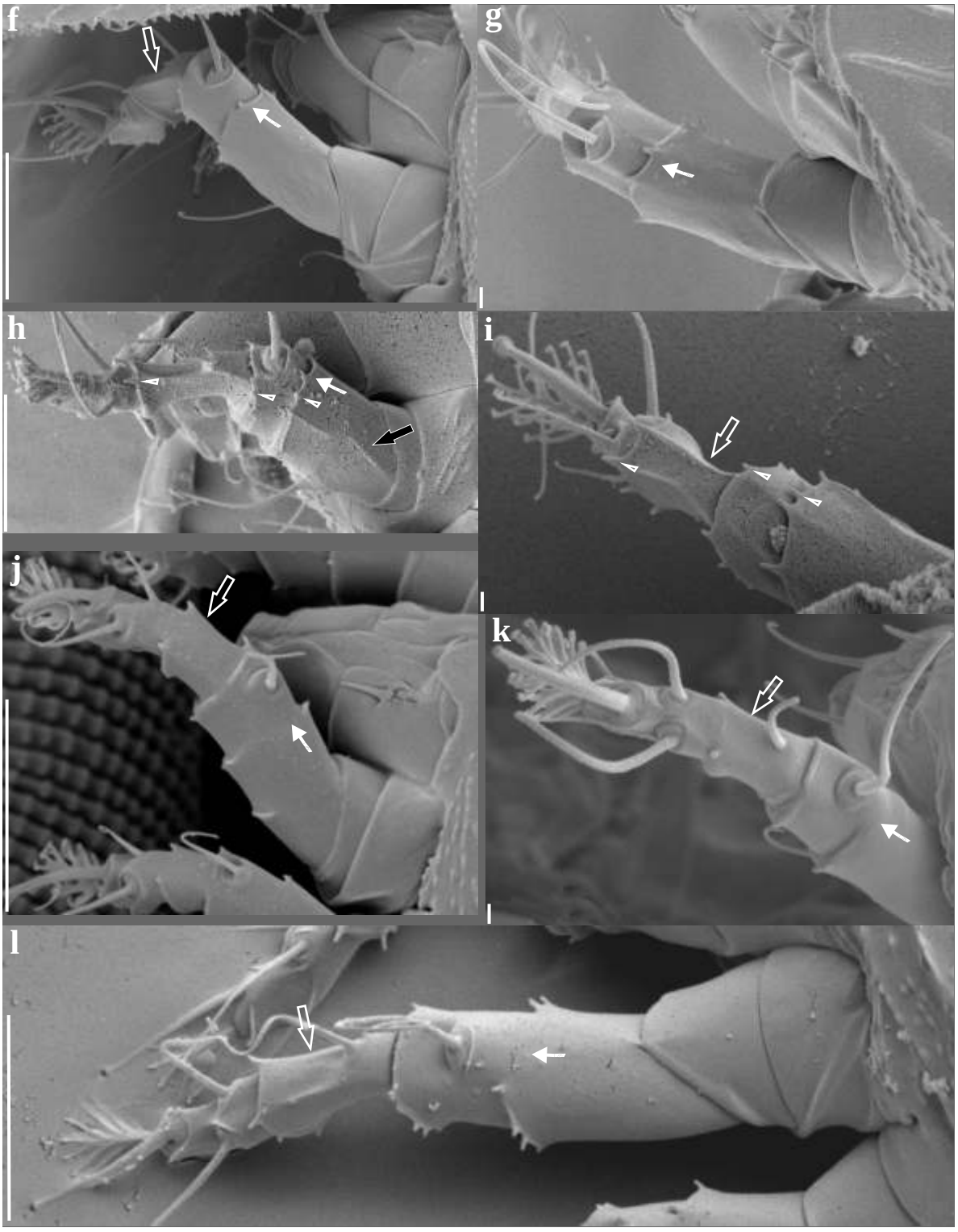


Fig. 3.8. (continued from previous page) **f, g)** *Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini), vagrant on *Lantana trifolia*; **h)** leg I and **i)** leg II of *cf. Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini), leaf vagrant on *Psydrax livida*; **j)** *Acalitus mallyi* (Eriophyidae: Eriophyinae: Aceriini), leaf galls on *Vangueria infausta* subsp. *infausta*; **k)** *cf. Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini), leaf galls on *Acacia rehmanniana*; **l)** *Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini), erineum and distortion on *Ipomoea batatas* var. *batatas*. Solid white arrows: dorsal completeness of margin between femur and genu on leg I, and presence, position and number of spines on this margin; solid black arrows: ornamentation on femur of leg I; open arrows: shape of tibia on leg I; open white triangles: segment margins on which spicules are present; **f, h, j, l)** scale lines = 10 µm; **g, i, k)** scale lines = 1 µm.

It seems that in species living in less exposed situations such as in buds and galls, the margin between the femur and genu is partly fused with no or a few slight spinules, they have little or no ornamentation on the legs, and the tibiae are more smoothly rounded. In vagrant species living in more exposed situations, the margin between the femur and genu is complete and with spinules, and some species have ornamentation on some leg segments, and the tibiae are more angular with ribs. This extrapolation is preliminary, though, because so few species were studied.

A pattern of ridges ventrally on particularly the femur of leg I of *Diptilomiopus faurius* sp. nov. from *Faurea rochetiana* is another example of structures clearly visible in the SEM images (Fig. 3.9a), but hardly visible in slide-mounted specimens, which are represented by a realistic line drawing (Fig. 3.9b).

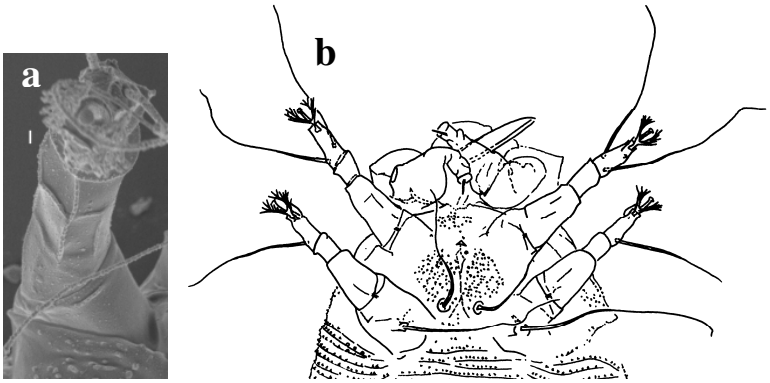


Fig. 3.9. *Diptilomiopus faurius* sp. nov. from *Faurea rochetiana* (Appendix M), ventral view of leg I, with a pattern of ridges, **a)** clearly visible in the SEM images, but, **b)** barely visible in the slide-mounted specimens. This descriptive drawing was drawn from the specimen with the most complete visibility of these ridges. Scale line = 1 µm.

- Leg tarsus: empodium

The Eriophyoidea do not have paired true claws on the leg tarsi – they only have one empodium, the empodial "featherclaw", on each (Lindquist, 1996a). The empodium is generally about 5 – 7 µm long, and some of its features cannot be studied using light microscopy.

The number of empodial rays is frequently used to separate species, although there may be intra-specific variation. It is usually possible to count them on slide-mounted specimens using phase contrast light microscopy, but in some groups it is difficult to count the number accurately. For example, the accurate counting of the number of empodial rays in *Diptilomiopus* from slide-mounted specimens is problematic, due to the empodial rays diagonally folding-in underneath the stem of each branch (Fig. 3.10a). This might be the reason why the number of empodial rays was not included in descriptions of *Diptilomiopus* spp. by A. Chandrapatya and/or J. Boczek, for

example, *D. aglaiae* (Chandrapatya & Boczek, 2002a), and *D. barringtoniae* (Boczek & Chandrapatya, 1992b). In some of these problematic cases, SEM studies may contribute this information. For example, eight rays are visible on each sub-branch of the divided empodium of *D. faurius* sp. nov. (Appendix M) collected from *Faurea rochetiana* (Fig. 3.10b).

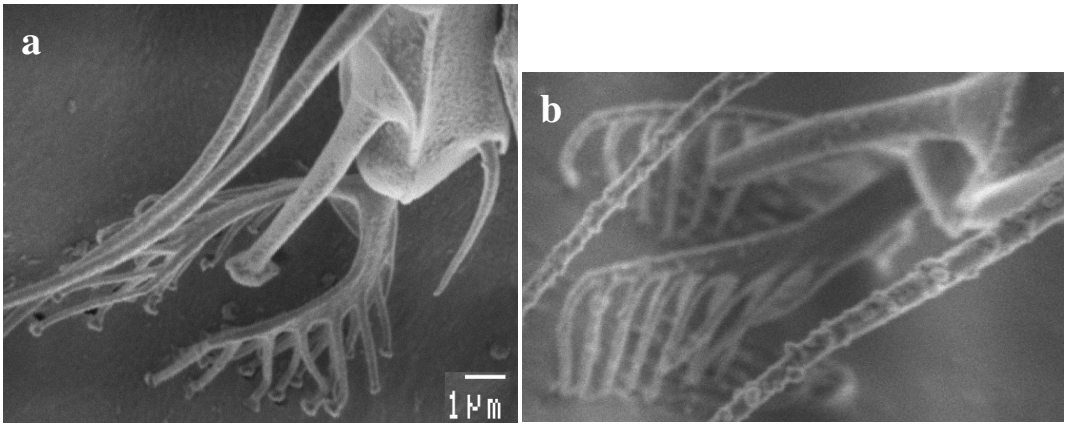


Fig. 3.10. Empodium on tarsus of leg I of *Diptilomiopus faurius* sp. nov. (Appendix M) from *Faurea rochetiana*: **a)** dorsal view depicting shape, **b)** lateral view facilitating count of rays – eight in this species.

Systematically informative characters which are not currently studied or recorded, mainly because they are not readily visible when studying slide-mounted specimens with light microscopy, may be found in the fine morphology of the empodium. The number of sub-rays and other small attachments to the main rays are difficult and frequently nearly impossible to detect or describe using light microscopy (Fig. 3.11). The numbers of sub-rays counted from the most distal ray for the first four species (a, b, c, d) in Fig. 3.11 are presented in Table 3.2. Before comparing this information for use in phylogenetic analyses, the homologies between specific rays must be established. Three scenarios may be possible for the development of added rays on the empodium: added at 1) the proximal end, 2) between the distal and proximal end, and 3) at the distal end. Because the distal rays do not have sub-rays, unlike those more proximally, it is here proposed that the rays are added or lost basally (see Table 3.2), but it can possibly also be added centrally, for example, see Table 3.3.

Table 3.2. Number of sub-rays present on the most distal main ray to the basal or proximal ray (numbered as they are present in the 7-rayed *Trisetacus* sp.), when added rays develop proximally, in a *Trisetacus* sp. from *Pinus pinaster* (Fig. 3.11a), *Cecidophyopsis* sp. from *Yucca guatemalensis* (Fig. 3.11b), *Shevtchenkella* sp. from *Psydrax livida* (Fig. 3.11c) and an unknown species from *Dovyalis* (Fig. 3.11d).

Eriophyoid species	*Trisetacus* sp.	*Cecidophyopsis* sp.	*Shevtchenkella* sp.	Unknown sp.
distal ray (ray 7)	0	0	0	0
ray 6	1	1	1	1/2
ray 5	2	2	2	2
ray 4	3	3	1	
ray 3	3/4	3		
ray 2	3	2		
ray 1	2			

Table 3.3. Number of sub-rays present from the most distal main ray to the basal or proximal ray (numbered as they are present in the 7-rayed *Trisetacus* sp.), when added rays develop centrally, in a *Trisetacus* sp. from *Pinus pinaster* (Fig. 3.11a), *Cecidophyopsis* sp. from *Yucca guatemalensis* (Fig. 3.11b), *Shevtchenkella* sp. from *Psydrax livida* (Fig. 3.11c) and an unknown species from *Dovyalis* (Fig. 3.11d).

Eriophyoid species	*Trisetacus* sp.	*Cecidophyopsis* sp.	*Shevtchenkella* sp.	Unknown sp.
distal ray (ray 7)	0	0	0	0
ray 6	1	1	1	1/2
ray 5	2	2	2	
ray 4	3	3		
ray 3	3/4			
ray 2	3	3		
ray 1	2	2	1	2

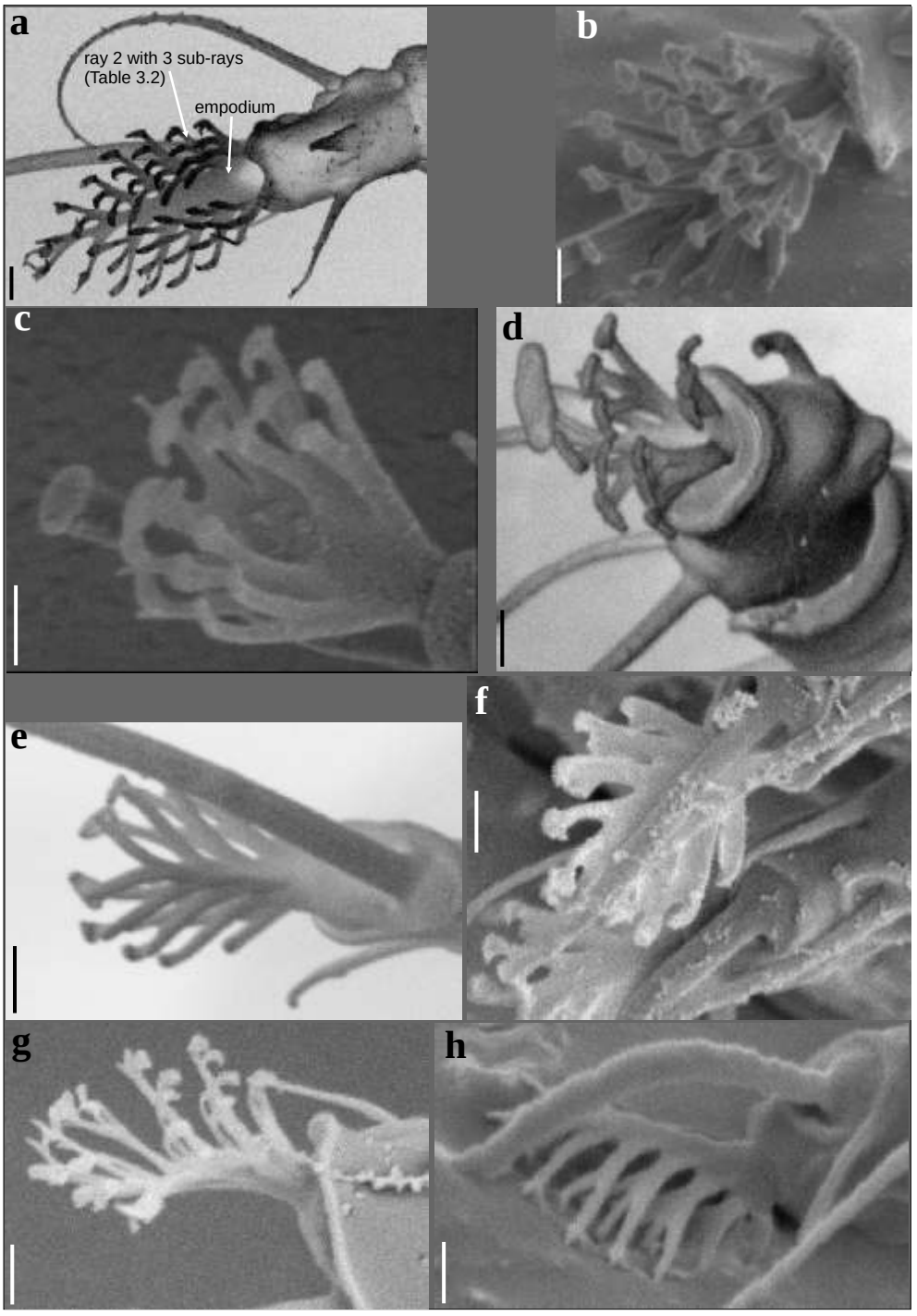


Fig. 3.11. Distal parts of tarsi with focus on the empodia: **a)** *Trisetacus* sp. from *Pinus pinaster*; **b)** *Cecidophyopsis* sp. from *Yucca guatemalensis*; **c)** *Shevtchenkella* sp. from *Psydrax livida*; **d)** unknown species from *Dovyalis*; **e)** unknown species from *Faurea rochetiana*; **f)** *Acalitus mallyi*; **g)** *Aceria* sp. from *Ipomoea batatas*; **h)** unknown species from *Apodytes dimidiata*. Scale lines = 1 µm.

The shape of the empodium (simple or divided) is important in defining subfamilies (e.g., Diptilomiopinae and Rhyncaphytoptinae) and tribes (e.g., Diphytoptini of the Phyllocoptinae) (Fig. 3.6, also see Lindquist, 1996a: 21). Other differences in more detailed shape may also occur, but have not been defined, and their visibility on slide-mounted species has not been recorded, but should be investigated. One example is the variation in the shape of the empodial rays. The rays of *Acalitus mallyi* (Fig. 3.11f) are flattened and the sub-rays are not clearly-defined, and the tips are not clearly tenent-like (the tips of tenent setae or seta-like processes are flattened perpendicularly to the longitudinal shaft of the ray, resembling the head of a nail), whereas the rays in other species, such as *Shevtchenkella* sp. (Fig. 3.11c), an unknown species from *Faurea rochetiana* (Fig. 3.11e), and a new genus from *Apodytes dimidiata* (Fig. 3.11h) are more rounded and end in tenent-like tips. The size of the enlarged and flattened membrane-like attachment (Fig. 3.13f) distally on the tenent-like empodial rays differs among species. It may be large and conspicuous in some species, such as in the unknown species from *Dovyalis* (Fig. 3.11d) and *Aberoptus* sp. (Figs 3.7e, f), and small or possibly absent in others such as *Trisetacus* sp. (Fig. 3.11a), *Acalitus mallyi* (Fig. 3.11f) and *Aceria* sp. from *Ipomoea batatas* (Fig. 3.11g).

The empodial rays of *Aceria* sp. nov. from *Ipomoea batatas* (Fig. 3.11g) appear generally thin and fragile in comparison with the other species depicted here. These differences in shape are currently not used, but could possibly be used in eriophyoid systematics in future.

- Detailed morphology of structures included in descriptive drawings, and frequently used to differentiate species

Some structures, such as the fine detail of the prodorsal shield and coxisternal plate ornamentation, and the external genitalia and surrounding areas, can essentially not be described or drawn from slide-mounted specimens to depict the exact true morphology of living specimens. This is caused by the distortion of slide-mounted specimens, and the resolution and essentially two-dimensional view in one plane of light microscopy. SEM alleviates these problems by revealing the true shape, orientation and ornamentation of structures. It may also improve the comprehension of these structures, and hopefully serve as impetus to describe and draw them from slide-mounted specimens in more accurate detail.

A case study: The structure and ornamentation of the external female genitalia are frequently depicted simplified and schematically in eriophyoid descriptions (e.g., Fig. 3.12b). In the SEM image of the coverflap of *Tergilatus sparsus* (Fig. 3.12c) the area basal to (anteriad of) the longitudinal ribs, for example, is much broader and the shape of the area is different to that depicted in the drawing (Fig. 3.12b). The fine detail and exact three-dimensional structure cannot

be seen in the slide-mounted specimen (Fig. 3.12a) due to inadequate clearing and staining of the specimen which can be rectified by improved slide-mounting, but also due to factors inherent to study of slide-mounted specimens using light microscopy already mentioned. Even with the slide-mounted specimens at hand (e.g., Fig. 3.12a), the drawing can be rectified to depict the true morphology more closely, but never to the degree possible with the addition of information from a SEM study. This inaccuracy of conventional eriophyoid descriptions renders the determination of primary homologies between specific areas impossible or ambiguous.

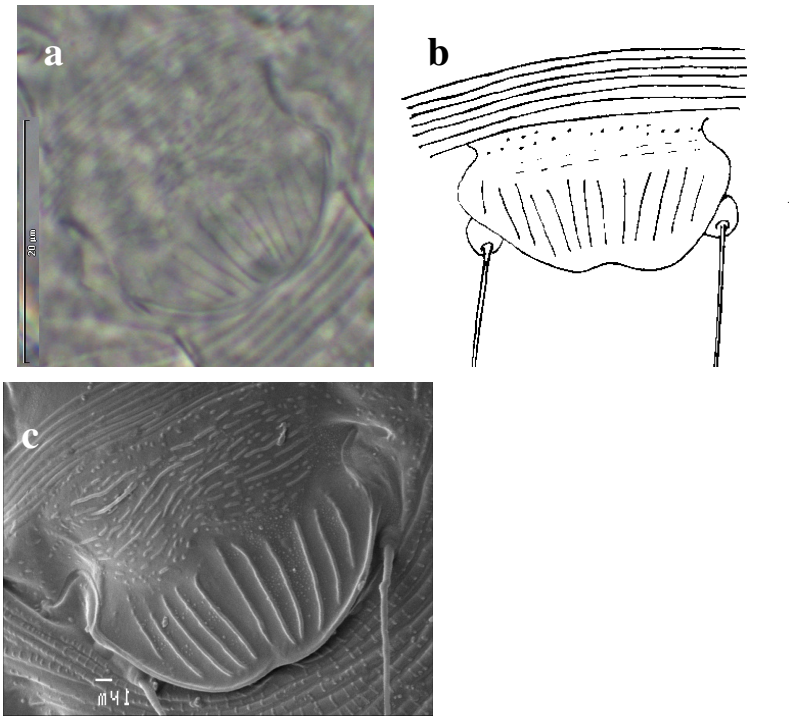


Fig. 3.12. External female genitalia of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995): **a)** a slide-mounted specimen (holotype) viewed with phase contrast; **b)** a drawing made from slide-mounted specimen; **c)** SEM image of same area in another specimen. Drawing reproduced from the original unpublished drawing with permission from the authors.

- Determining primary homologies between Eriophyoidea and other mite groups

Comparative studies of fine external morphology using SEM will aid in elucidating the similarity in structure, and primary homology between structures of Eriophyoidea and those of other mites, which is currently problematic. For example, studying the fine morphology of, and particularly of the tip of the empodial rays in the Eriophyoidea and homologous structures in other mite groups, will give better results when using SEM studies. Lindquist (1996a) hypothesizes that the empodial rays with enlarged tips in the Eriophyoidea are "equivalent to" (homologous to) the tenent hairs present in various superfamilies of trombidiform (including prostigmatid) mites. Several specimens of prostigmatid mites were included *ad hoc* in the present SEM study as they were encountered while collecting the eriophyoid mites. The morphology of the tenent hairs of Tetranychidae, Tenuipalpidae and Stigmaeidae (Fig. 3.13) are roughly the same as the empodial rays of the Eriophyoidea in having an enlarged, frequently flattened tip, but there are some differences. The enlarged and flattened area is at the distal end of the seta (ray) in the other mites (open arrows in Figs 3.13a, b, c), while in the Eriophyoidea, it is rather a thin, seemingly membrane-like attachment or enlargement behind the tip of the ray (or the tip of the ray extends beyond the enlargement) (Figs 3.13e, f). The empodium of a new genus from *Apodytes dimidiata* (Fig. 3.13f) illustrates how the rays, and particularly the tips, are probably orientated when the empodium is resting on a surface. The empodial hairs of *Tydeus* sp. in the present study (Fig. 3.13d) are different from tenent hairs in not having a flattened tip apically, but rather a slight knob [in spiders a similar type of hair and tip is also referred to as a "tenent hair" (A.S. Dippenaar-Schoeman, *pers. comm.*)]. When compared with the empodial rays in eriophyoid species, the empodial hairs in *Tydeus* also differ by not having side branches. Therefore, although the empodium of *Aberoptus* sp. (Figs 3.13e, f) may be homologous to the *Tydeus* empodium in having a central stem or pad with numerous radiating rays, the rays of the two structures are not similar. The level of detail in which the structures were studied in this example, is not possible when studying slide-mounted specimens with light microscopy.

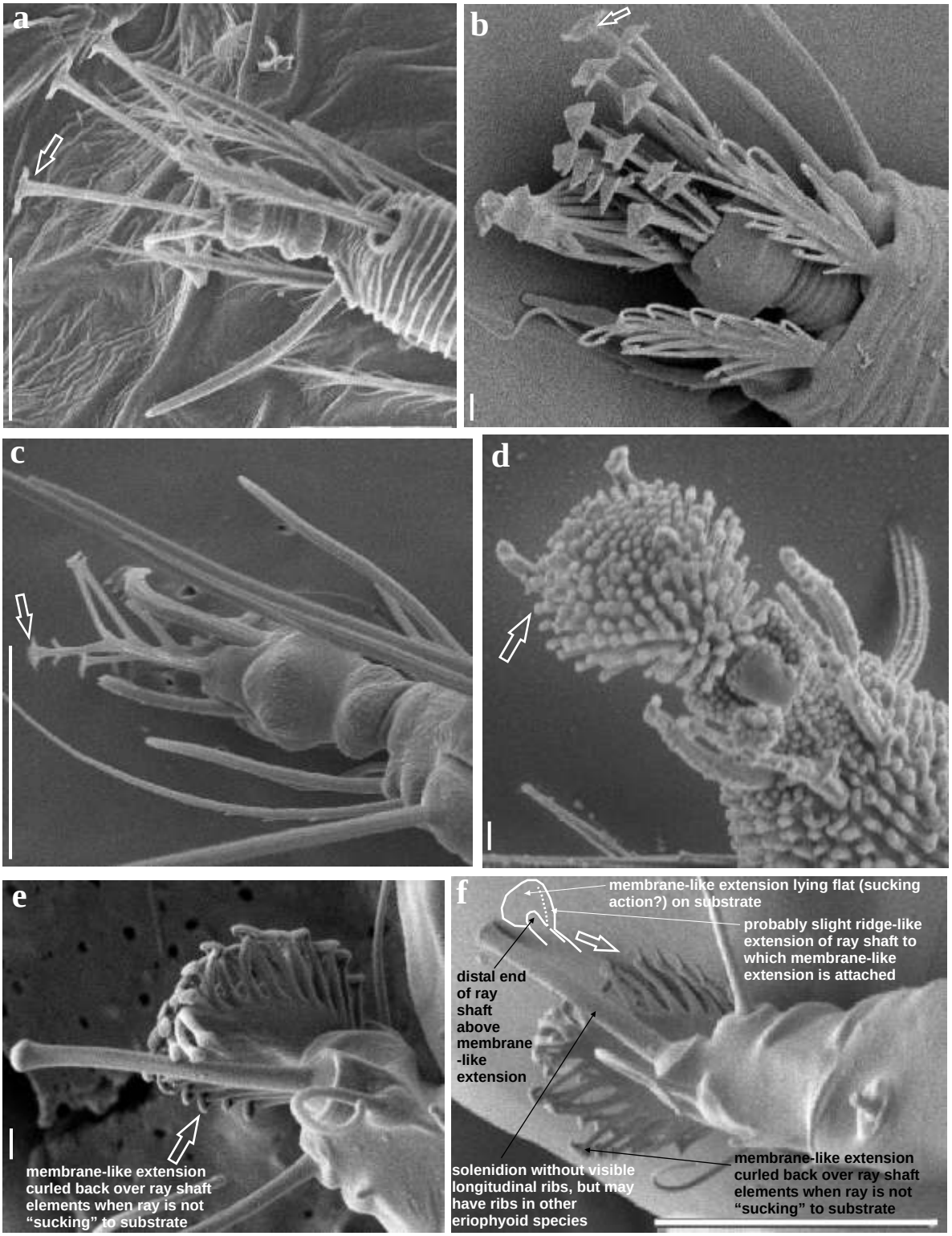


Fig. 3.13. Ambulacra with tenent hairs: **a)** leg II of an *Aponychus* sp. (Tetranychidae) from *Solanum mauritianum*; **b)** leg I of a species of the Tenuipalpidae from a *Senecio* sp.; **c)** leg I of a species of the Stigmaeidae from *Apodytes dimidiata*. Empodia with slightly knobbed hairs or rays (*Tydeus*) and "tenent" hairs or rays (*Aberoptus*) of: **d)** leg I of *cf. Tydeus* sp. (Tydeidae) from *Ekebergia capensis* Sparrm.; **e, f)** leg II of an *Aberoptus* sp. (Eriophyidae) from *Schotia brachypetala*; **a, c, f)** scale lines = 10 µm; **b, d, e)** scale lines = 1 µm. Arrows pointing towards tips of hairs of rays, with an enlarged drawing of the tip of the ray of the empodium of the *Aberoptus* sp. in Fig. 3.13f.

3.3.2 Artefacts caused by preparation and slide-mounting of specimens

Slide-mounted specimens have preparation / mounting artefacts varying in degree, and influence on the taxonomic process. The significance and number of artefacts caused will vary according to the technique used and the quality of and the way in which the process is done, and the influence of the person's experience and skill. Every batch processed may vary in the exact treatment and result from other batches. Artefacts are thus not standardized and comparable across specimens mounted in different batches. For example, rib-like ornamentation may still be present in specimens, but absent in specimens on another series of slides. This causes even more confusion. Examples of artefacts caused by slide-mounting are here discussed and illustrated with examples from the SEM study.

- Loss and/or distortion of fine-detail such as microtubercles, and ridges on annuli and legs

The clearing process for slide-mounting of eriophyoid mites may destroy fine external structures to various degrees, either by eroding them or "stretching" the cuticle, smoothing them out. Even in the final mounting fluid, clearing may continue. This is particularly prevalent when slides are stored in collections for extended periods. Over time, the specimens may become lighter and loose definition, until some of the structures vanishes, making the specimens unusable for systematic study (De Lillo *et al.*, 2010). Various other factors influence the visibility of fine-structures in slide-mounted specimens, including the amount of staining of specimens, the distance and amount of mounting fluid between specimens and the cover-slip and the quality of the microscope used and the ability of the observer (De Lillo *et al.*, 2010).

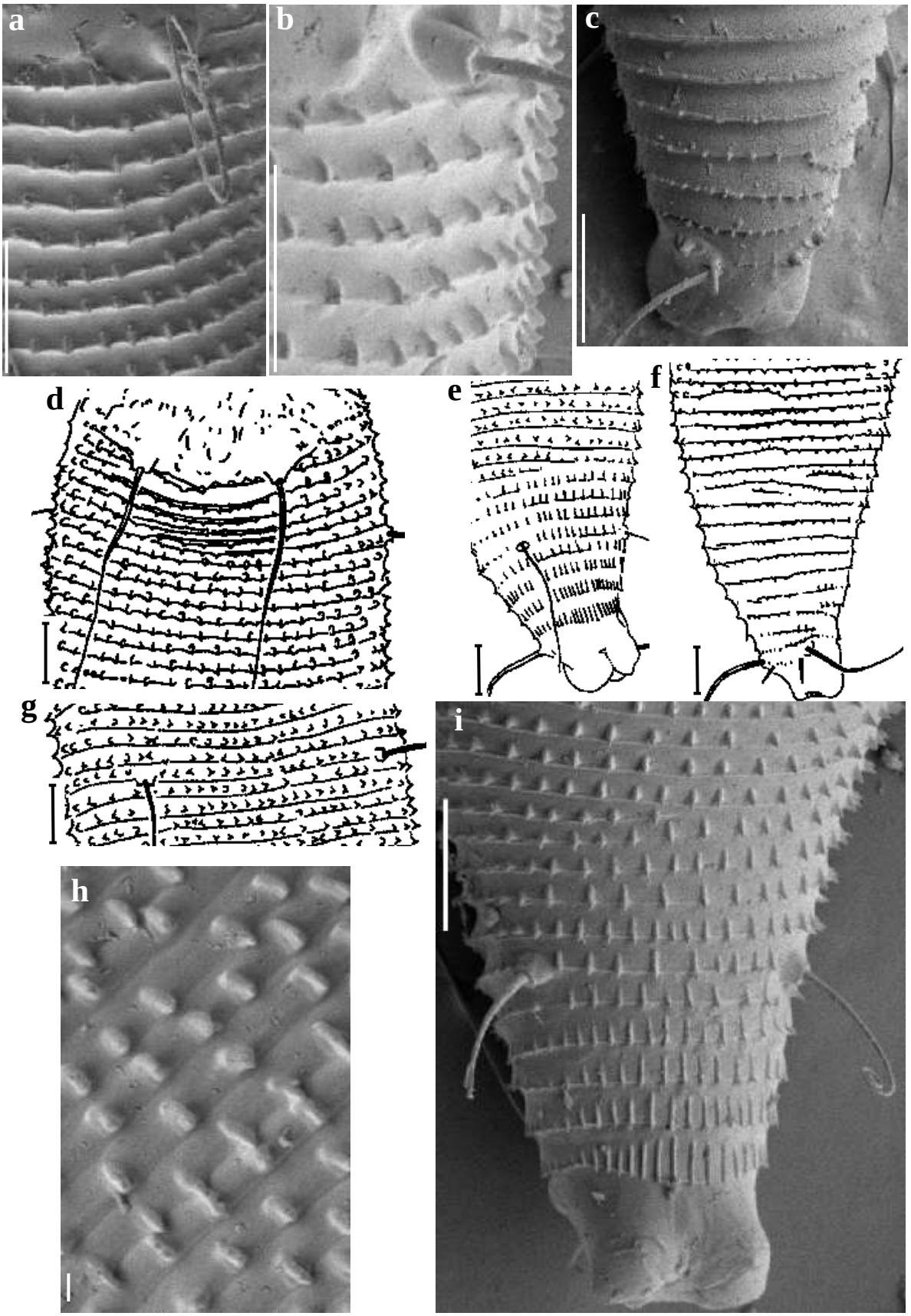
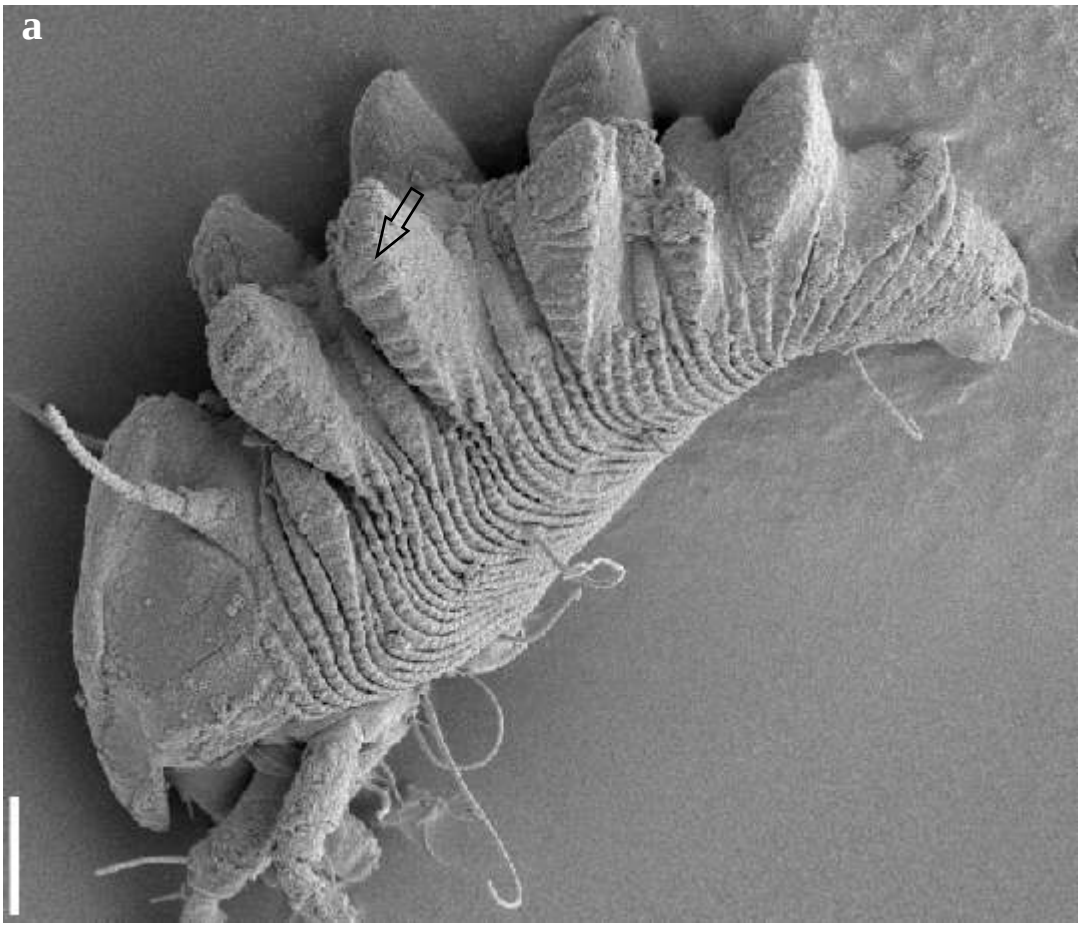
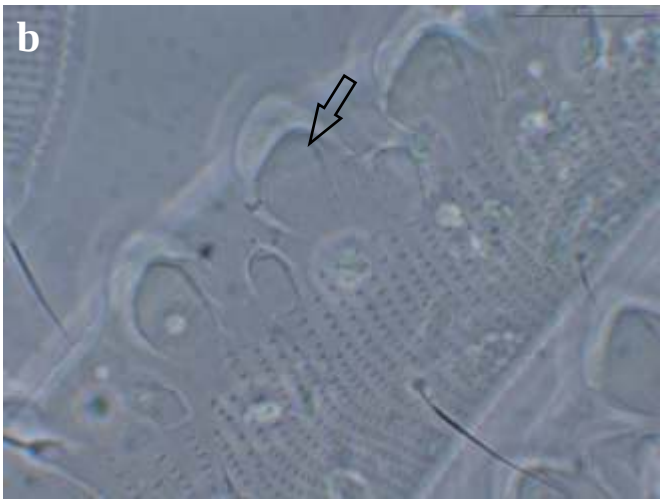


Fig. 3.14. Microtubercles of *Aceria* sp. nov. from *Ipomoea batatas*: dorsally on first annuli behind the prodorsal shield rear margin - **a, b)** SEM images, **d)** line drawing; dorsally on rear caudal annuli - **c)** SEM image, **f)** line drawing; on ventral annuli between setae *e* - **g)** line drawing, **h)** SEM image; on rear, caudal ventral annuli - **e)** line drawing, **i)** SEM image; all scale lines = 10 µm except **h)** scale line = 1 µm.

The presence, shape, size and position of microtubercles and small granules or other ornamentation on the eriophyoid body are extensively used in the differentiation of eriophyoid taxa, particularly at species level. Microtubercles are extremely small, and resolution is not always satisfactory with light microscopy and necessitates the improvement of resolution provided by SEM (Fig. 3.14). Iodine, added to the preparatory and mounting media, may help to make such fine, shallow and vague structures more visible by colouring them (De Lillo *et al.*, 2010; J.W. Amrine, Jr., *pers. comm.*). Three-dimensional images provided by SEM in contrast to slide-mounted specimens where one may only be able to view these very small structures in one two-dimensional plane instead of more planes possible through larger structures, improves their study the most. The microtubercles may also be distorted and displaced during the slide mounting process. Another problem that may occur with slide-mounted specimens is that some microtubercles are extremely small and fine and their presence and shape may be obscured by a heavily sclerotized cuticle (J.W. Amrine, Jr., *pers. comm.*). The improvement provided by SEM to study microtubercles in their natural shape and position can be seen when the line drawings of slide-mounted specimens and SEM images of the same areas of the same species in Fig. 3.14, are compared.

Another example of an artefact caused by slide-mounting is the obliteration of fine ridges on the body surface. Fine striae or ridges are present on the dorsal lobes and annuli of *Meyerella bicristatus* (Meyer, 1989) and can be clearly seen in SEM images of the species (Fig. 3.15a). These ridges are essentially invisible in the slide-mounted specimens of the same species (Fig. 3.15b), either because they are so shallow and without colour differentiation that they cannot be discriminated from surrounding surfaces, or they may have been destroyed by the clearing or mounting process. The ridges are thus also absent from the descriptive drawing of the species (Figs 3.15c). This character was used in the couplet descriptive states in the identification key to genera by Amrine *et al.* (2003) to differentiate *Neophantacrus* Mohanasundaram, 1981 in which the lobes are striated from *Meyerella* Amrine *et al.*, 2003 in which the lobes are smooth. In this case, fortunately it does not influence the outcome of the key, because additionally there are three rows of lobes in *Neophantacrus*, and only two in *Meyerella*.





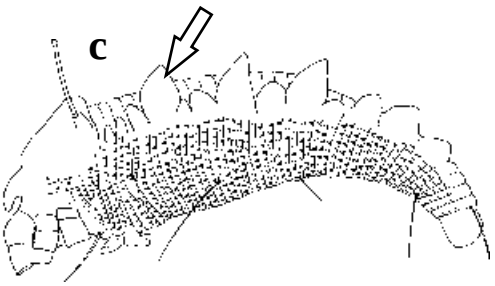


Fig. 3.15. *Meyerella bicristatus* (Meyer, 1989), leaf vagrant on *Mystroxylon aethiopicum* subsp. *aethiopicum*: **a)** SEM image of dorso-lateral aspect (scale line = 10 µm); **b)** part of lateral aspect of slide-mounted specimen (female) viewed with phase contrast light microscopy; **c)** line drawing [reproduced with permission from the original drawing by Meyer (1989b)] of the specimen digitally-imaged in 3.15b. Arrows indicating: ribs or striae on lobes in SEM image; striae very vaguely present in this one slide-mounted specimen of a series of about 100 specimens in which they were invisible (the lines are hardly visible in the printed copy, but when this image is enlarged on computer screen, the lines are vaguely visible); and the lobes are smooth in the descriptive drawing.

- Distortion of body shape

The general shape and presence of depressions, ridges, furrows or other modifications of the basic rounded body form of genera such as *Aceria* are extensively used in eriophyoid classification, delimiting mostly genera, but also subfamilies and tribes (Amrine *et al.*, 2003). The loss and distortion of shape, including body shape, are some of the more serious artefacts caused by slide-mounting.

During the clearing process for slide-mounting, it is possible to see how the bodies of the specimens contract and expand alternately during the different collecting and clearing steps (*pers. obs.*). One would suspect that this should cause some distortion, but it has not been investigated. When the specimens on the final mounting-slide are covered by a cover-slip, the specimens are flattened and squashed to varying degrees (De Lillo *et al.*, 2010).

The shape of the slide-mounted specimens of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Fig. 3.16) is an example of serious shape distortion. In the lateral view of a slide-mounted specimen (Fig. 3.16b), the body seems to be globose while in real life it is dorsoventrally flattened (Figs 3.16a, d). The shape of the body could have been seen by observing live specimens under a dissecting stereo microscope before mounting. Of more concern and importance, however, is the more subtle depression caudally behind the middorsal ridge visible in SEM (open white arrows in Figs 3.16a, h) that is not visible in live or slide-mounted specimens studied with light microscopy (open arrows in Figs 3.16c, g, i). The three-dimensional orientation of the broad ridge-like structure just posterior of the prodorsal rear shield margin (black arrows in Figs 3.16a, h, l) is not retained. This “collar” is flattened in the slide-mounted specimens (Figs 3.16b, j, k) and in the drawings thereof (Figs 3.16c, g). These artefacts in body shape may lead to wrong morphological information being built into the eriophyoid classification. It may be tolerated in the classification and identification of species in practical taxonomy, if the artefacts in slide-mounted specimens are standardized enough to avoid errors in identification using slide-mounted specimens. It is inappropriate data, however, for determining primary homologies for phylogenetic analyses.

Tergilatus sparsus (Fig. 3.16) again illustrate the improved information regarding fine morphology obtained from SEM images in comparison with slide-mounted specimens and drawings thereof. There is a rounded thickening at one end of the elongated microtubercles on the dorsal annuli (Fig. 3.16f) which are not clearly visible in slide-mounted specimens, and consequently this detail has not been included in the descriptive drawing (Fig. 3.16e). These ridges are also much finer in comparison to the size of the mite than what could be portrayed in the drawing. The intricacies of

detail, shape and relative positions of structures on the ventral aspect (Fig. 3.16d) were not visible in such detail in the slide-mounted specimens.

- Loss of secreted structures, and their study

Secreted body layers of eriophyoid mites such as wax, may be lost during preparation of specimens for slide-mounting. *Tetra retusa* Meyer, 1992 was described by Meyer (1992b) (Fig. 3.17b) without depicting or mentioning the wax structures present on the species (Figs 3.17a, c, e). Although the presence of wax on a species may be observed in live specimens before collection and mounting, using stereo dissection microscopy, it is not always clearly visible, even on live mites (*pers. obs.*). Studying the fine structure, shape and position of these secreted structures (Figs 3.17 a, c-e) and the external morphology of body parts possibly secreting the wax is by far superior using SEM.

3.3.3 Ecological and biological information

Finally, when studying the mites *in situ* with the low-temperature method, one has the added advantage of being able to study some aspects of the biology and ecology of the mites (Duffner *et al.*, 1998; Wergin *et al.*, 2000; Ochoa *et al.*, 2000). This includes studying the structure, position and other aspects of for example, their eggs and spermatophores. The shape, biology and ecology of spermatophores have been studied by a few authors (e.g., Oldfield *et al.*, 1970; Sternlicht, 1970; Sternlicht & Griffiths, 1974; Chandrapatya & Baker, 1986; Duffner *et al.*, 1998). Oldfield *et al.* (1970) speculated that the shape of the spermatophores may differ between species, and that it may have systematic value. The spermatophores of the possibly new *Aculus* sp. from *Lantana trifolia* (Figs 3.18a, b), and eggs and immatures of an unidentified species, probably a *Rhynacus* sp. (Fig. 3.18c) are examples of observations on *in tact* eriophyoid colonies in the present study. In the latter species, it was interesting to note how close together the eggs were laid, to the extent that they pressed against each other, changing their normally round shape slightly (Fig. 3.18c). Biological and ecological information can also be investigated for their possible potential as systematic characters, and this information can also be used for phylogenetic studies.

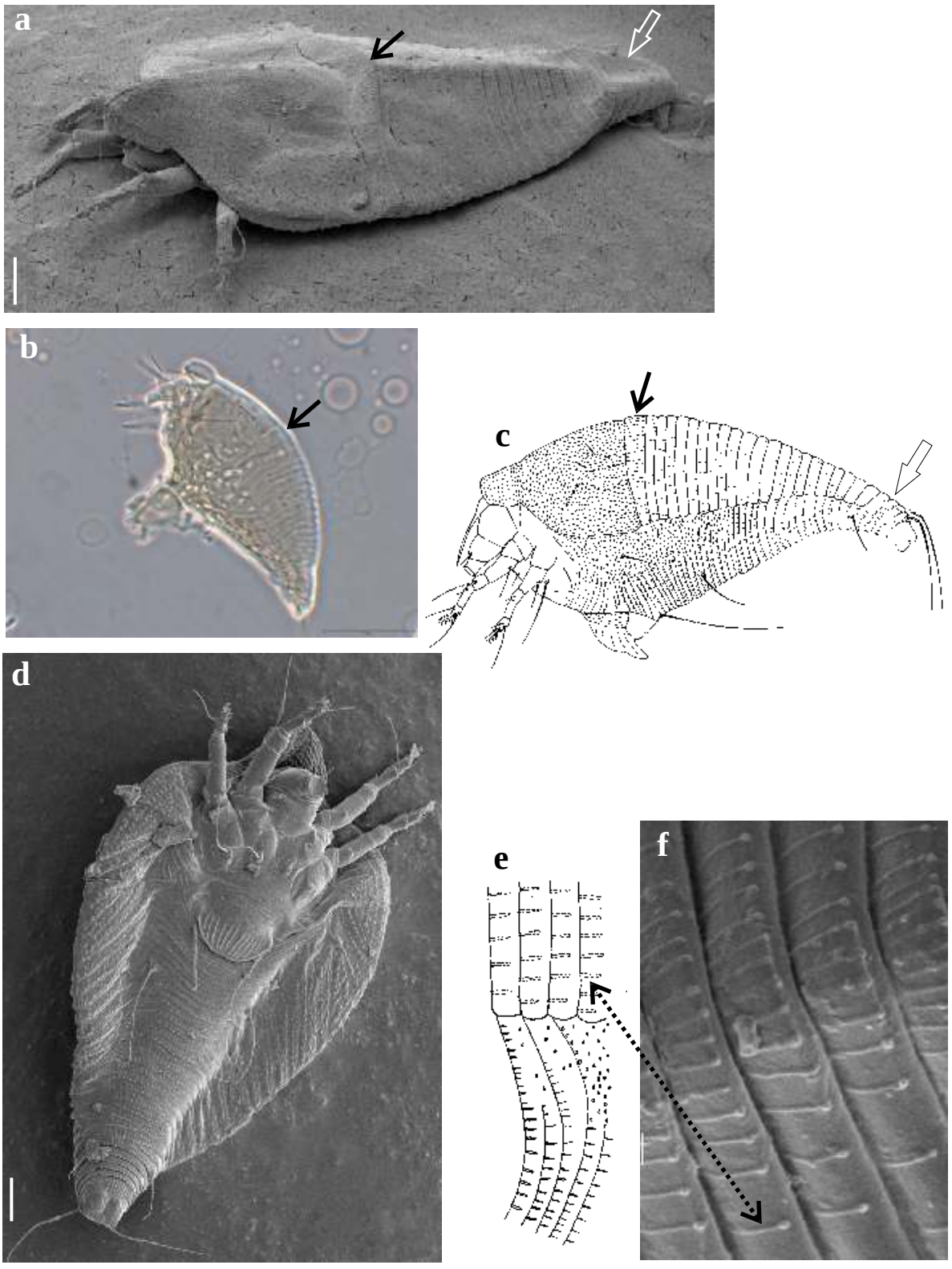


Fig. 3.16. (continued on next page). *Tergilatus sparsus* Meyer & Ueckermann, 1995, leaf vagrant on *Portulacaria afra*: SEM images (a, d, f, h, j), line drawings (c, d, g) [from Meyer & Ueckermann (1995)], and slide mounted specimens viewed with phase contrast (b, i, j, k): **a)** dorsal view; **b, c)** lateral view; **d)** ventral view; **e, f)** enlargement of opisthosomal microtubercles, alternatively lateral and dorsal; **g, h)** dorsal view; **i)** dorsal view of opisthosomal rear end; **j, k, l)** prodorsum (lateral in j, dorsal in k, l) including rear shield margin and first dorsal annuli; **a, d, h, l)** scale lines = 10 µm; **f)** scale line = 1 µm. Open arrows – rear end of opisthosoma; solid black arrows – first annulus behind rear prodorsal shield margin, black dashed arrow – pointing towards dorsal microtubercles in drawing and SEM image.

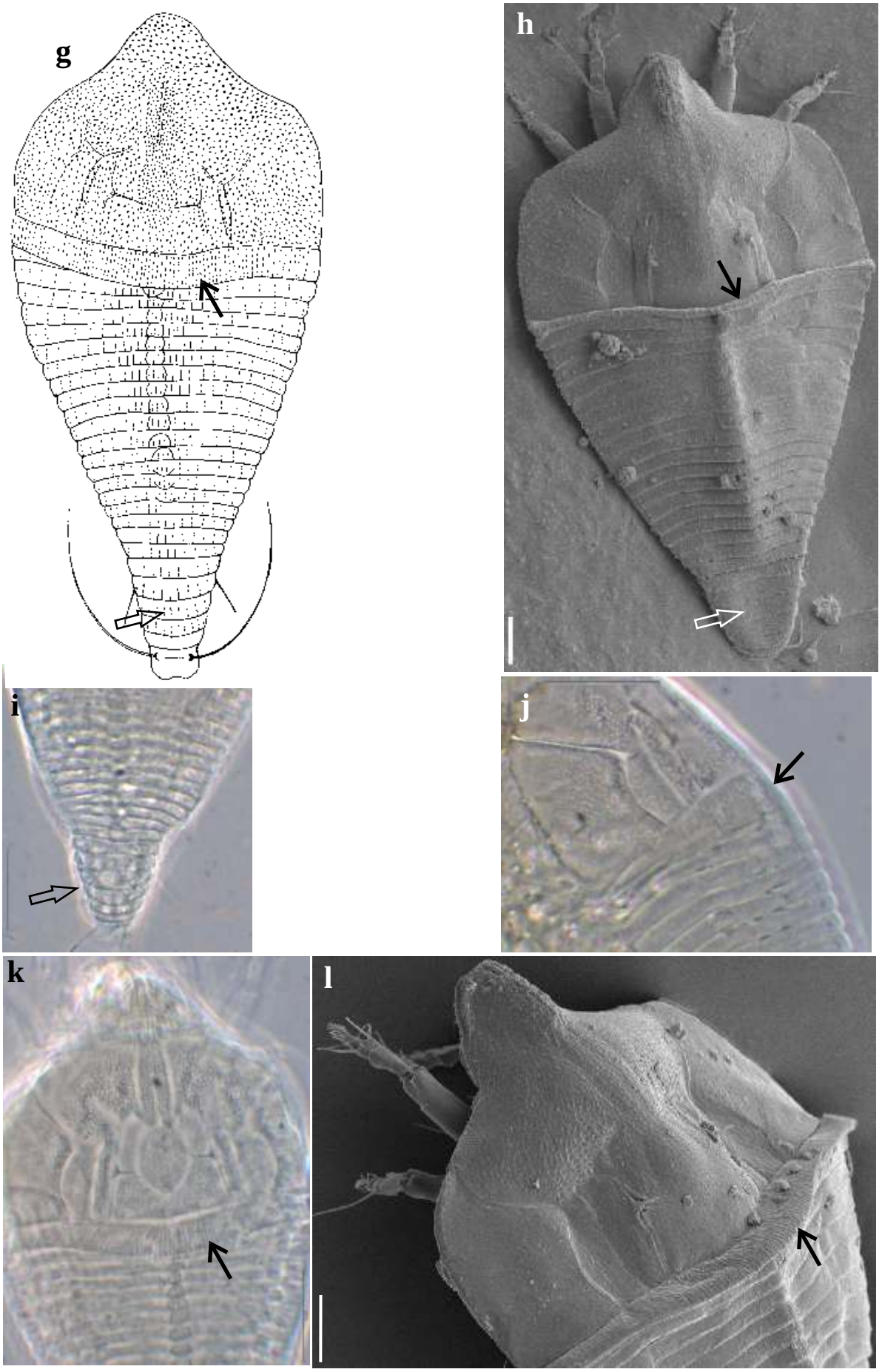


Fig. 3.16. (continued from previous page).

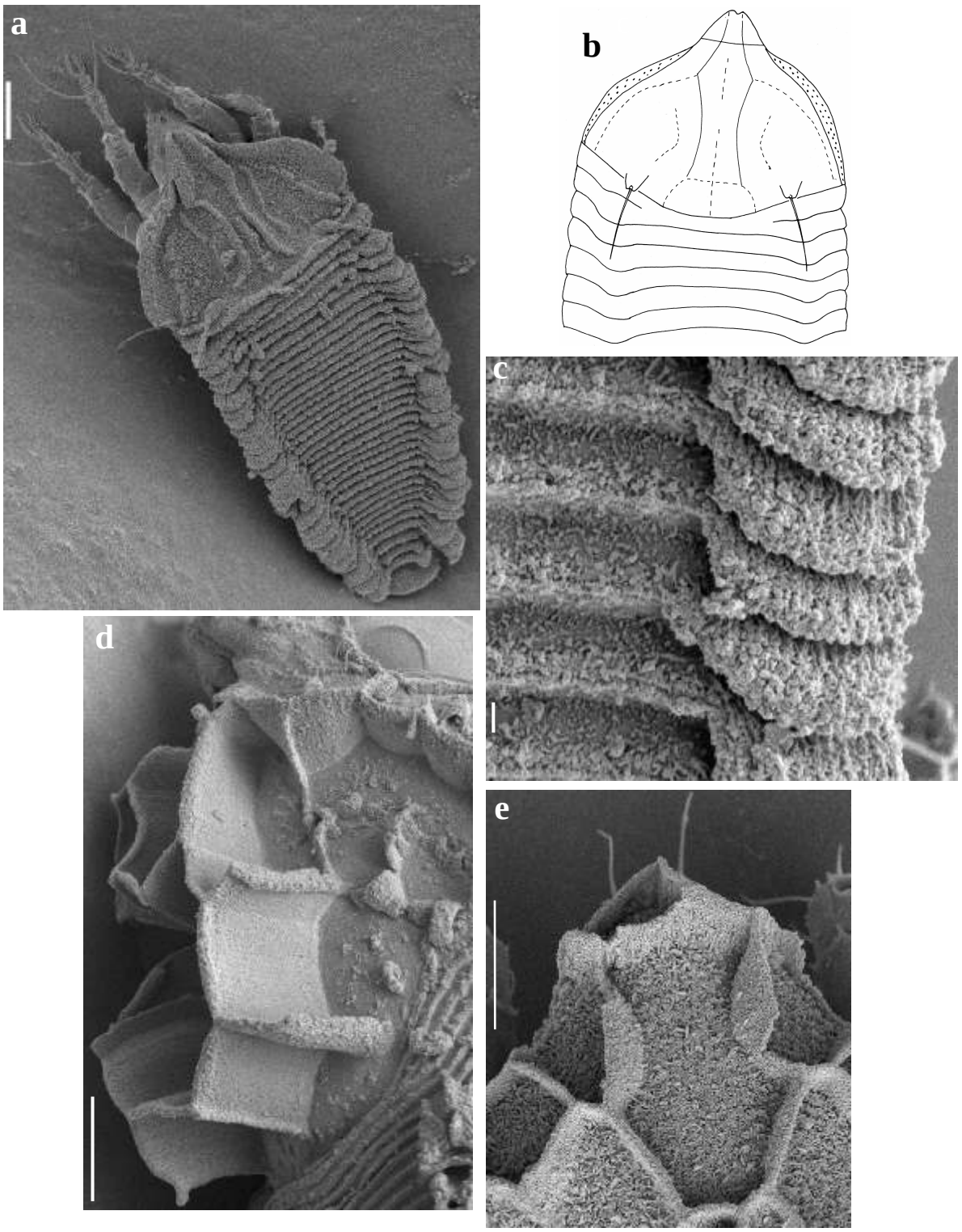


Fig. 3.17. *Tetra retusa* Meyer, 1992 from *Bauhinia galpinii* (Meyer, 1992b): **a, c, e)** wax secretions and enlargements thereof on about the entire body, but particularly on the ridges of the opisthosoma and prodorsal shield, all specimens in dorsal view; **b)** descriptive drawing (Meyer, 1992b) in dorsal view, without the wax, which was also not mentioned in the text description. *Calacarus* sp. from *Searsia lancea* (previously *Rhus lancea*): **d)** dorso-lateral aspect of the prodorsum with wax formations, the image of a specimen with some of the wax disturbed and broken off was chosen to be presented, to illustrate the inside and structure of wax cells; **a, d, e)** scale lines = 10 µm; **c)** scale line = 1 µm.

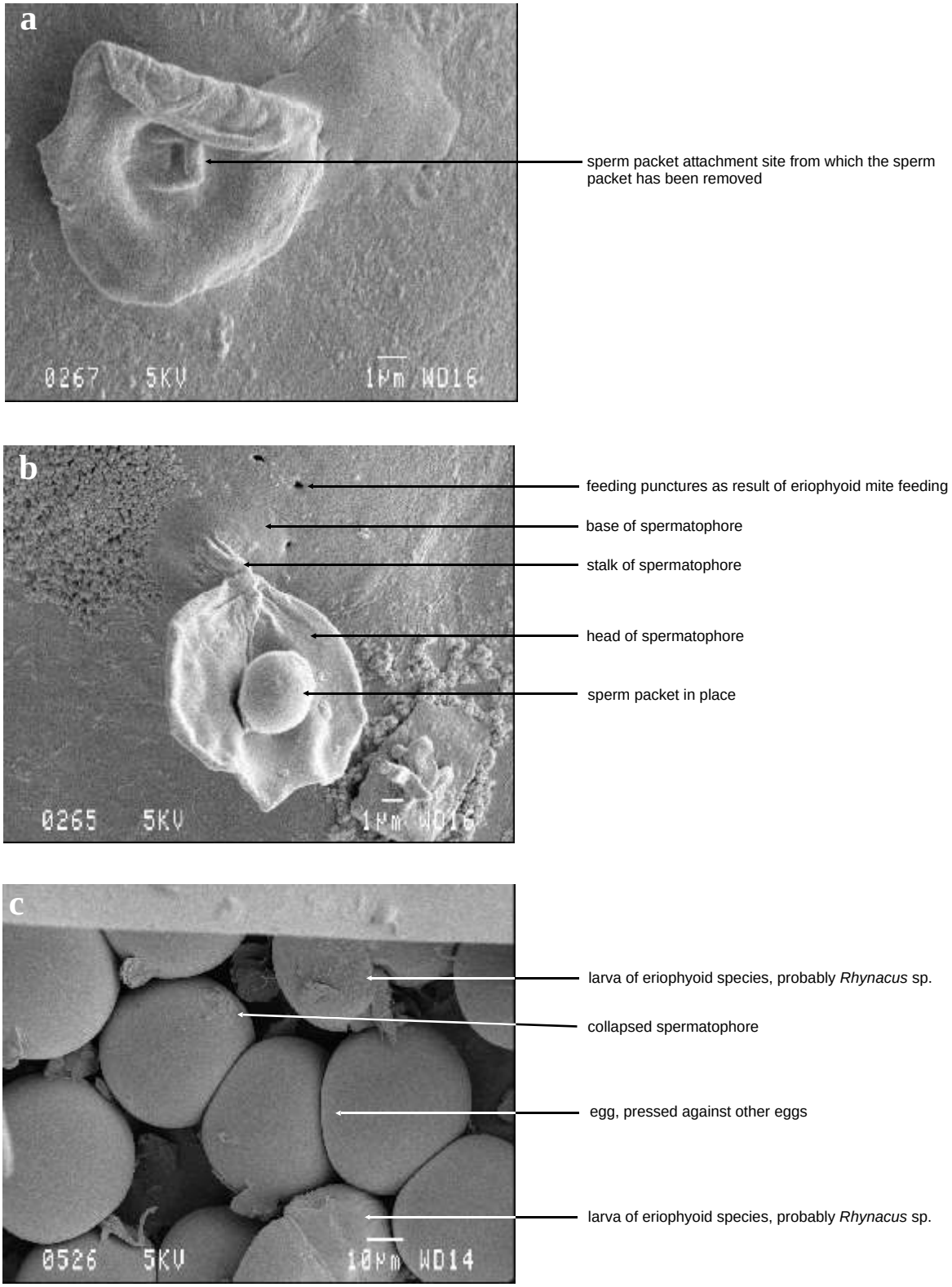


Fig. 3.18. Spermatophores of *Aculus* sp. from *Lantana trifolia*: **a)** with sperm packet in tact; **b)** without sperm packet. Possibly *Rhynacus* sp. from *Mystroxylon aethiopicum* subsp. *aethiopicum*: **c)** eggs and immatures; scale line length representations given below scale lines. SEM images are unmodified.

PART II. COMPARATIVE MORPHOLOGICAL STUDY OF THE GNATHOSOMA USING SEM[2]

3.4 PART II. INTRODUCTION

Understanding and knowing the structures and relative positions of the different structures of body parts to each other, are crucial in identifying, delimiting and comparing characters and character states in different taxa. Therefore, the structure and comparative morphology of the eriophyoid gnathosoma, and confusion in the use of terminology, are here briefly discussed.

The mouth-parts of the Arachnida typically comprise the labrum, mouth, in some taxa the so-called labium (the sternite of the palp segment), and the chelicerae and palpi (Evans, 1992). In the Ricinulei and Acari, construction of the pre-oral channel or chamber for food reception, involves the enlargement and ventral fusion or approximation of the palpcoxae and their apophyses to form a unit underneath the chelicerae. This unit is called the subcapitulum (infracapitulum or hypognathum), incorporating the labrum, mouth and pharynx (Evans, 1992). The subcapitulum, chelicerae and the free-moving parts of the palpi that are not incorporated in the subcapitulum, together form the gnathosoma (capitulum), a discrete, sensory-trophic movable structure (Evans, 1992) which is also present in the Eriophyoidea (Keifer, 1959a; Nuzzaci & Alberti, 1996) (Figs 3.19, 3.20, 3.22).

Several different terms are used for the same gnathosomal structures of mites (De Lillo *et al*., 2001) and likewise the terminology and fundamental understanding of the eriophyoid gnathosoma and the manner in which this information is used in taxon descriptions are not standard and are often used vaguely and arbitrarily. The same term frequently does not refer to the same structure. For example, the term “rostrum”: Lindquist (1996a) remarked that the infracapitulum is also named the rostrum or hypostome in eriophyoid literature. The term rostrum is, however, also frequently used to denote the subcapitulum together with the chelicerae, or even to denote the entire gnathosoma. For example, in the same book where there is a chapter by Lindquist (1996a), Lindquist & Amrine (1996) use gnathosoma and rostrum as synonyms, and similarly, Nuzzaci (1979) uses capitulum and rostrum as synonyms. Keifer (1959a) stated that the mouth-parts of the eriophyoids are collectively named the rostrum, thus rostrum is an alternative term for gnathosoma. In the same article, however, when the gnathosoma is discussed, the subcapitulum is

[2] Note that some duplication of information presented in the first part of the chapter occurs in this part, because it will be submitted as an article separate from the first part.

regarded as the rostrum, and the chelicerae and palpi as separate entities in association with the "rostrum". Keifer (1975a) remarks that the rostrum of the Diptilomiopidae (called Rhyncaphytoptidae by him) is always large in comparison to the body, implying that the chelicerae and oral stylet form part of the rostrum. Amrine *et al.* (1994) refer to the dorsal view of the gnathosoma in an SEM image as "paired palpi functioning as a rostrum". These and similar inconsistencies in the terminology lead to misunderstanding of the morphology and the specific parts being described.

Studies on the eriophyoid gnathosoma (including, Nalepa, 1887, 1898b, 1910; Keifer, 1959a; Orlob, 1966; Shevchenko & Silvere, 1968; Krantz, 1973; Gibson, 1974; McCoy & Albrigo, 1975; Hislop & Jeppson, 1976; Nuzzaci, 1979; Thomsen, 1987, 1988; Freeman *et al.*, 2005) were undertaken on a few species. These studies focused primarily on functional anatomy and morphology, feeding mechanisms, and salivary glands and their secretions. Lindquist (1996a), Nuzzaci & Alberti (1996) and Nuzzaci & De Lillo (1991, 1996) reviewed the anatomy and morphology of the eriophyoid gnathosoma.

The eriophyoid gnathosoma is uniquely specialized for piercing plant cells and sucking their sap (Lindquist & Oldfield, 1996). The dorsomedial surface of the subcapitulum has a longitudinal u-shaped open channel or stylet sheath extending from the base to the apical end of the palpi (Keifer, 1959a; Shevchenko & Silvere, 1968; Nuzzaci, 1979; Lindquist, 1996a; Nuzzaci & Alberti, 1996; Nuzzaci & De Lillo, 1996). This sheath encloses either seven (Thomsen, 1987) or nine (Nuzzaci & Alberti, 1996; De Lillo *et al*., 2001) stylet-like structures. These include a pair of cheliceral stylets that may divide apically into two stylets (Shevchenko & Silvere, 1968; Lindquist, 1996a; Freeman *et al.*, 2005), an oral stylet (labrum), a pair of auxiliary stylets (Keifer, 1959a, 1975a), or inner infracapitular stylets (Nuzzaci & Alberti, 1996), and a pair of cheliceral guides (Keifer, 1959a, 1975a), or outer infracapitular stylets (Nuzzaci & Alberti, 1996) (Fig. 3.22a). The outer infracapitular stylets project freely in the Phytoptidae and Diptilomiopidae (Nuzzaci & Alberti, 1996). SEM studies by Thomsen (1987) and Freeman *et al.* (2005) confirmed or elucidated internal gnathosomal structures.

Nuzzaci & De Lillo (1991) compared the anatomy of the eriophyoid gnathosoma with that of other phytophagous groups. Lindquist (1996a) homologized the gnathosomal structures used in eriophyoid taxonomy with those of other mites and named them accordingly. In comparison with the relatively simplified body of the Eriophyoidea, their gnathosoma is complex, and homologies of some of the structures with other mites are problematic (Shevchenko & Silvere, 1968; Lindquist, 1996a, b; Lindquist & Oldfield, 1996; Nuzzaci & Alberti, 1996). Only a few studies (e.g., Keifer, 1959a) focused specifically on comparative morphology for application in the systematics of the Eriophyoidea.

3.4.1 Gnathosomal characters currently used in eriophyoid taxonomy

- The two major gnathosomal forms

The most pertinent character, and one of the few hypothetical synapomorphies used in the classification of the Eriophyoidea (Lindquist, 1996b), is the presence of two fundamental forms of the cheliceral and oral stylets and associated structures differentiating the Diptilomiopidae ("big-beaked" eriophyoids) from the other eriophyoid families (Keifer, 1959a, 1975a; Lindquist, 1996a) (Figs 3.22a, b). In the Eriophyidae and Phytoptidae, the cheliceral stylets are slightly and evenly curved and relatively small to moderate in size and the oral stylet are of the so-called "short form" and mostly associated with a generally smaller and less robust gnathosoma than in the Diptilomiopidae (Fig. 3.22a). The cheliceral stylets of the Diptilomiopidae are generally longer and more robust with an abrupt basal curvature, correlated with the "long form" oral stylet (Fig. 3.22b). These two major gnathosomal forms are easily discernible in slide-mounted specimens, particularly in lateral view (Figs 3.22a, b). They can even be distinguished in live specimens when using a very good quality stereo dissecting microscope with sufficient illumination and magnification (preferably x 100 magnification).

- Other gnathosomal characters

According to Lindquist (1996a), gnathosomal morphology, including the setation on and segmentation of the palpi, are relatively stable throughout the Eriophyoidea. Very few gnathosomal characters are currently used in eriophyoid taxon differentiation and classification, and identification keys. In practice very few of even these are constantly included in species descriptions.

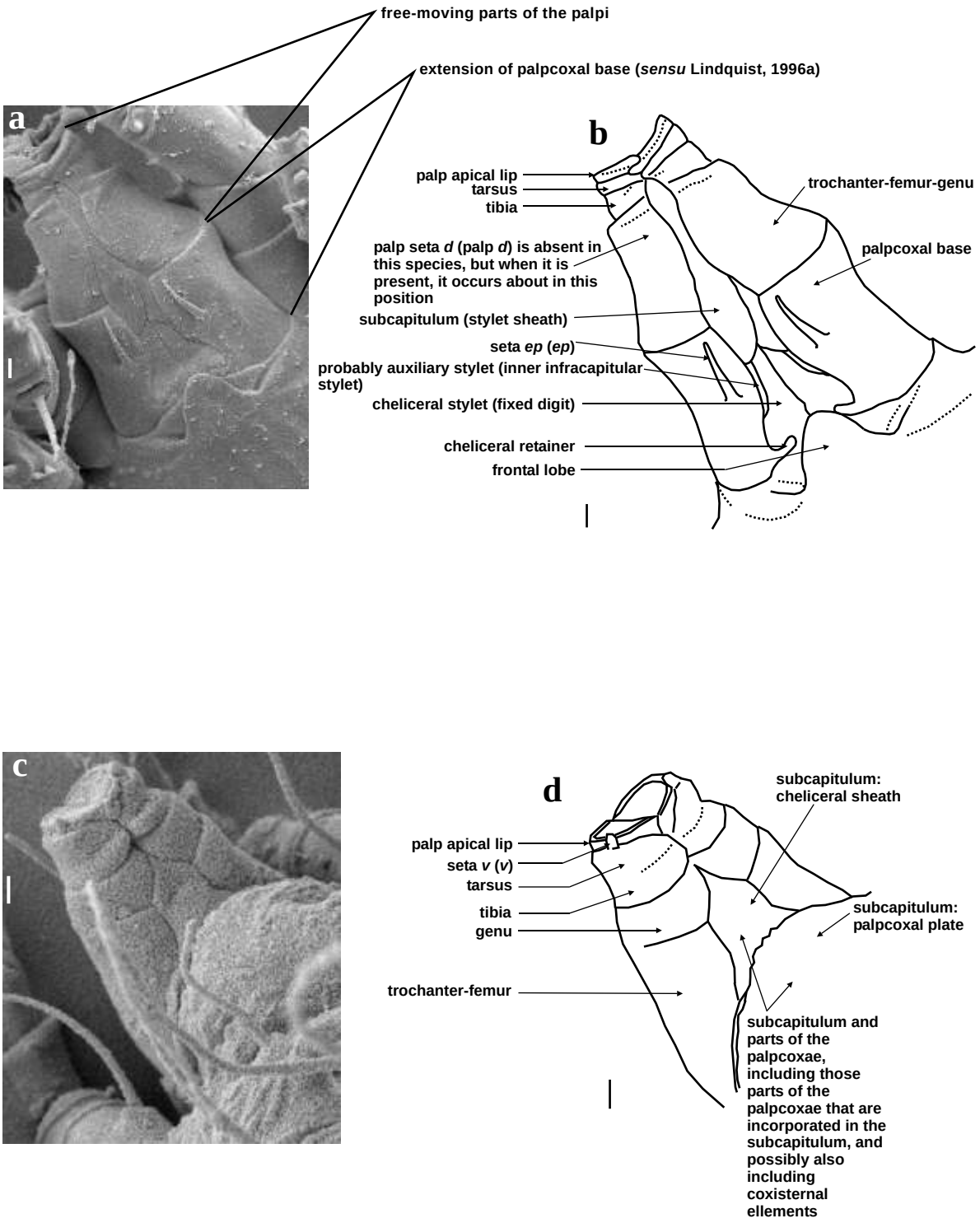
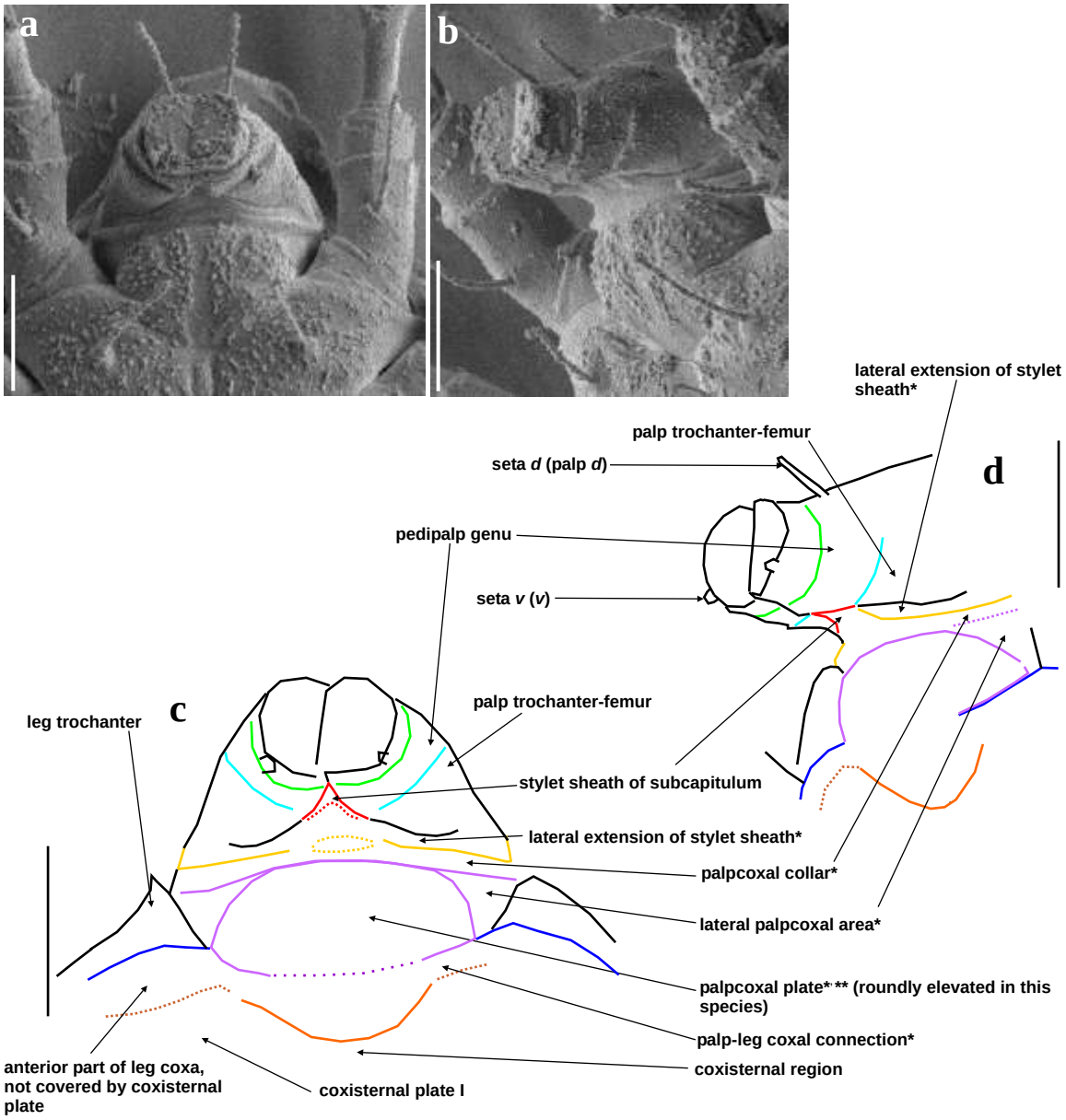


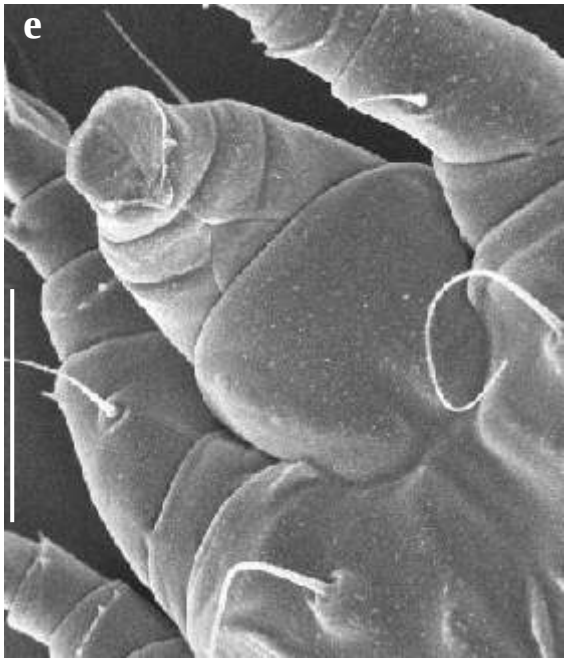
Fig. 3.19. Eriophyoid gnathosoma: **a)** dorsal view; **b)** line drawing of gnathosoma in image 3.19a; **c)** ventral view; **d)** line drawing of the gnathosoma in image 3.19c. Scale lines = 1 µm.

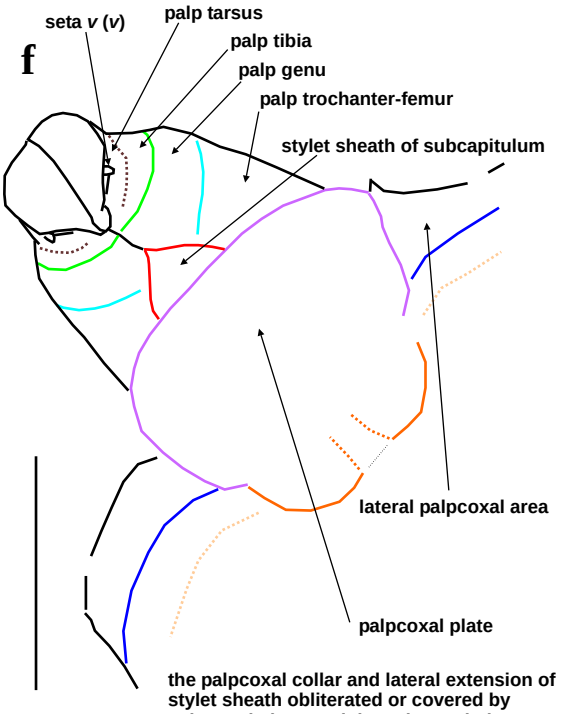


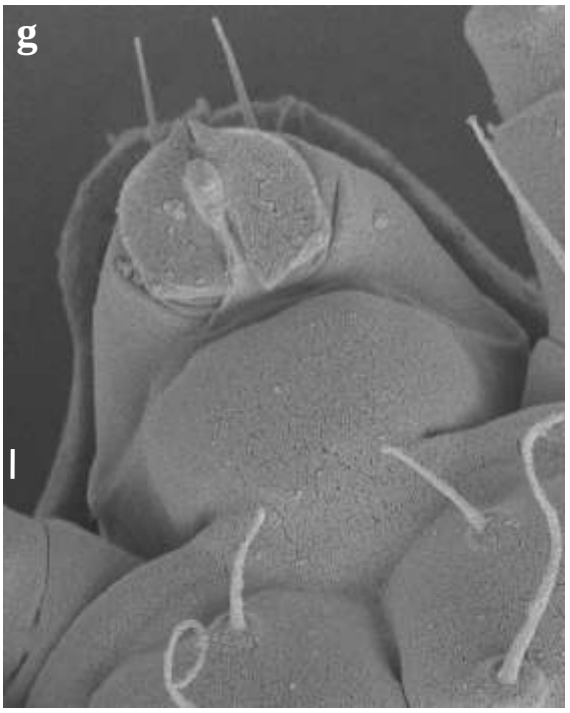
Key to colours in Figs 3.20 and 3.21

- green: margin between palp genu (ventrally) or trochanter-femur-genu segment (dorsally) and the palp tibia
- light blue: margin between palp genu and trochanter-femur (only present ventrally)
- red: anterior outlines of stylet sheath, but only of visible parts in a particular view
- yellow: proximal (posterior) margin of the stylet sheath and lateral extension of the stylet sheath; the anterior visible edge of the stylet sheath is red, and that of the lateral extension of the stylet sheath, black
- purple: outlines of the anterior part of the palpcoxal plate and the lateral palpcoxal area
- dark blue: margin between the leg coxa and leg trochanter
- orange: posterior (towards rear) edge of the palpcoxal plate, which is the margin between the palpcoxal plate and the coxisternal area and also between the anterior part of the leg coxa and the coxisternal plate
- area between the posterior part of the palpcoxal plate and the coxisternal plates or coxisternal area is here named the "palp-leg coxal connection" and is outlined anteriorly with purple, and posteriorly with orange

Fig. 3.20. (continued on next page). Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini): **a)** ventral view; **b)** ventro-lateral view; **c)** line drawing of Fig. 3.20a; **d)** line drawing of Fig. 3.20b; **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm. * These are preliminary new names or terms devised in the present study for these gnathosomal structures on the ventral aspect of eriophyoid mites. ** This structure was named the "basal palp segment" (Keifer, 1975a) or the "oral plate". It is just ahead of the coxisternal plates of coxae I, and is situated about on the same vertical level as the pharyngeal pump (Krantz, 1973; *own observations*) and may include elements of the coxisternum.







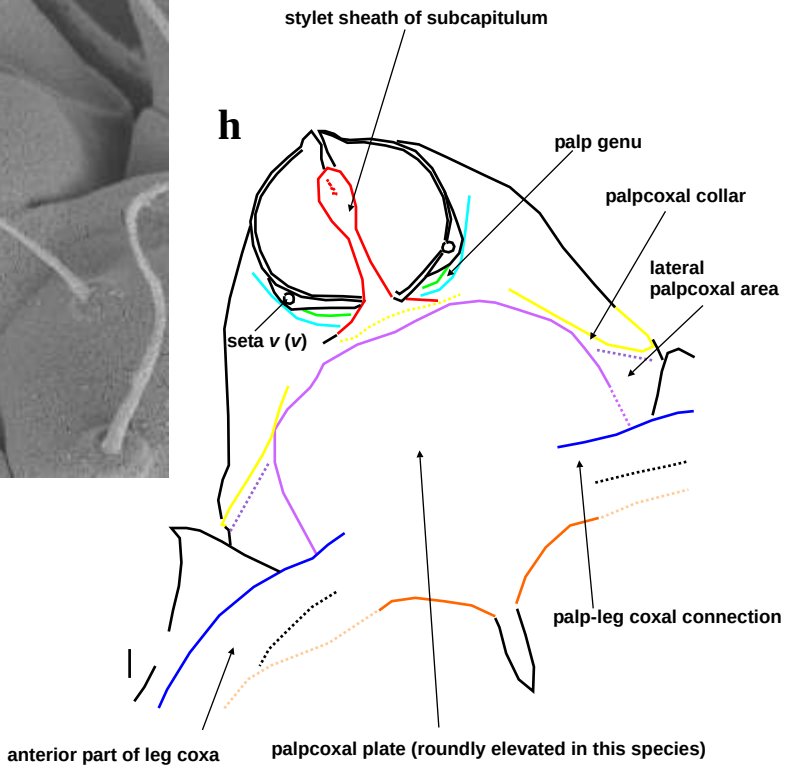
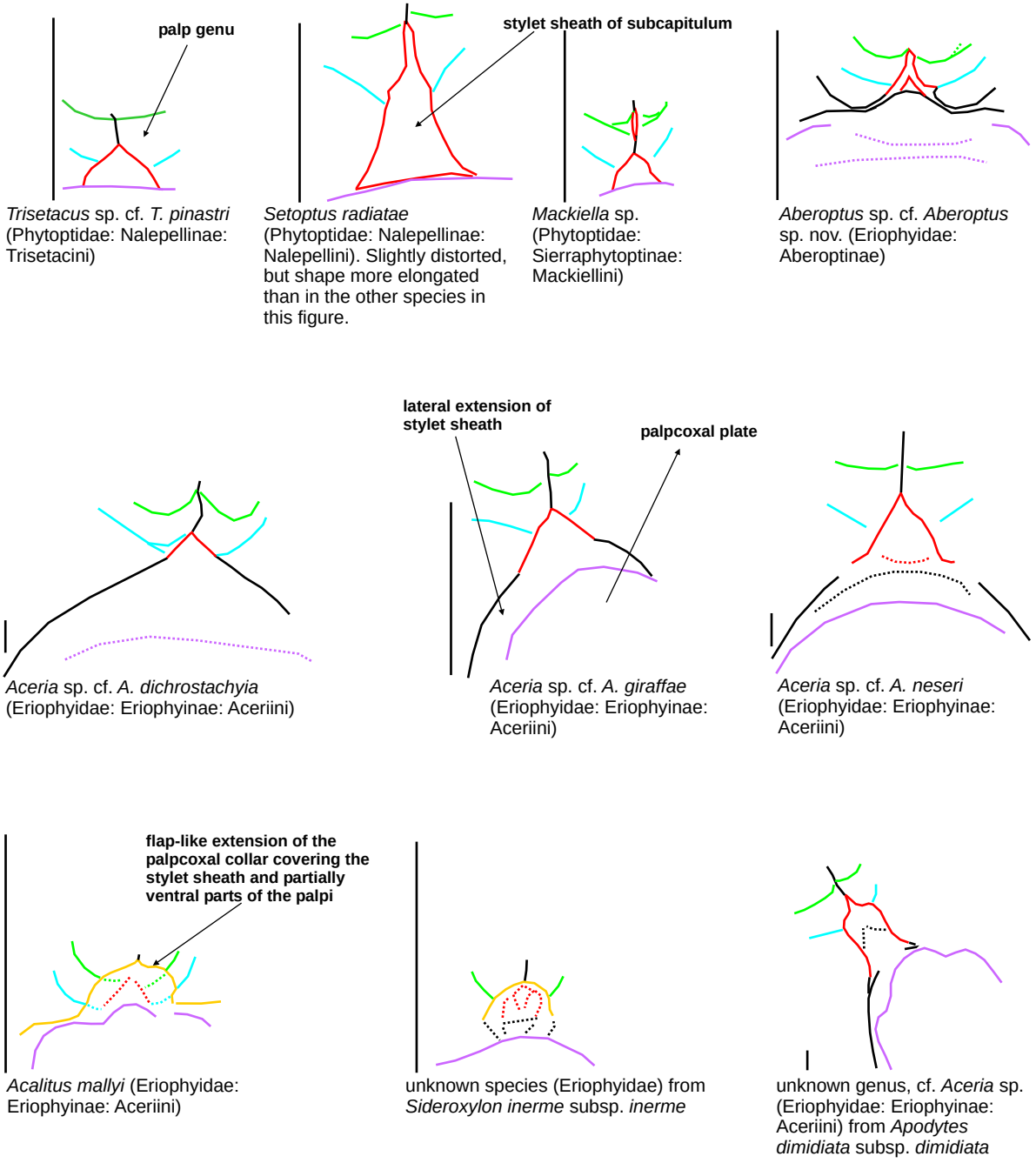


Fig. 3.20. (continued from previous page). Eriophyoid gnathosomas in ventral view. *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from *Pinus* sp.: **e)** SEM image; **f)** line drawing of Fig. 3.20e. *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Psydrax livida*:**g)** SEM image; **h)** line drawing of Fig. 3.20g; **e, f)** scale lines = 10 µm; **g, h)** scale lines = 1 µm.



Trisetacus sp. cf. *T. pinastri* (Phytoptidae: Nalepellinae: Trisetacini)

Setoptus radiatae (Phytoptidae: Nalepellinae: Nalepellini). Slightly distorted, but shape more elongated than in the other species in this figure.

Mackiella sp. (Phytoptidae: Sierraphytoptinae: Mackiellini)

Aberoptus sp. cf. *Aberoptus* sp. nov. (Eriophyidae: Aberoptinae)

Aceria sp. cf. *A. dichrostachyia* (Eriophyidae: Eriophyinae: Aceriini)

Aceria sp. cf. *A. giraffae* (Eriophyidae: Eriophyinae: Aceriini)

Aceria sp. cf. *A. neseri* (Eriophyidae: Eriophyinae: Aceriini)

Acalitus mallyi (Eriophyidae: Eriophyinae: Aceriini)

unknown species (Eriophyidae) from *Sideroxylon inerme* subsp. *inerme*

unknown genus, cf. *Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini) from *Apodytes dimidiata* subsp. *dimidiata*

Fig. 3.21. Eriophyoid gnathosoma: Ventral views of largely the subcapitulum and part of the palpi and palpcoxal plate of various species to show the differences in structures. The shape of the ventral part of the stylet sheath is visible between the free palp-segments. Its shape is probably strongly influenced by the angle at which imaged, and the anteriad extension of the gnathosoma at the moment of cryo freezing. However, there are some obvious differences in shape not influenced by these factors, that may be of use in classification and phylogeny. The data were not evaluated and this figure purely demonstrates that there are indeed differences that may be of systematic use. The colours correspond to probably homologous areas between the species. The longer scale lines = 10 µm, and the three shortest scale lines = 1 µm.

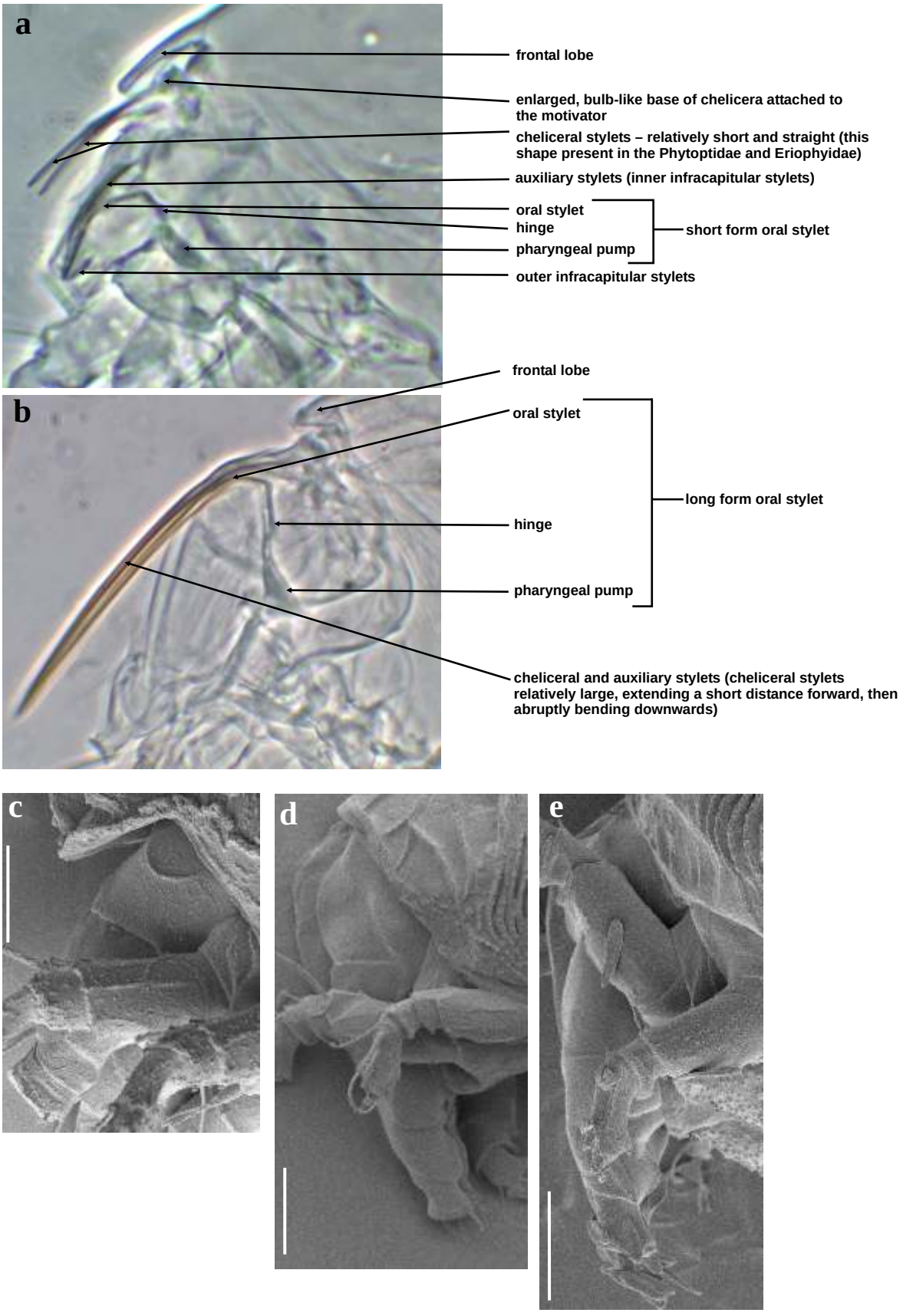


Fig. 3.22. Eriophyoid gnathosoma. The gnathosoma of all the Eriophyoidea except the Diptilomiopidae has relatively short and straight chelicerae, and the short form oral stylet: **a)** digital image of slide-mounted specimen viewed with light microscope; **c)** SEM image of lateral view. "Diptilomiopid"-like gnathosoma with large chelicerae sharply bent down at the base and the long form oral stylet: **b)** digital image of slide-mounted specimen**, d, e)** lateral views of gnathosomas. Scale lines = 10 µm.

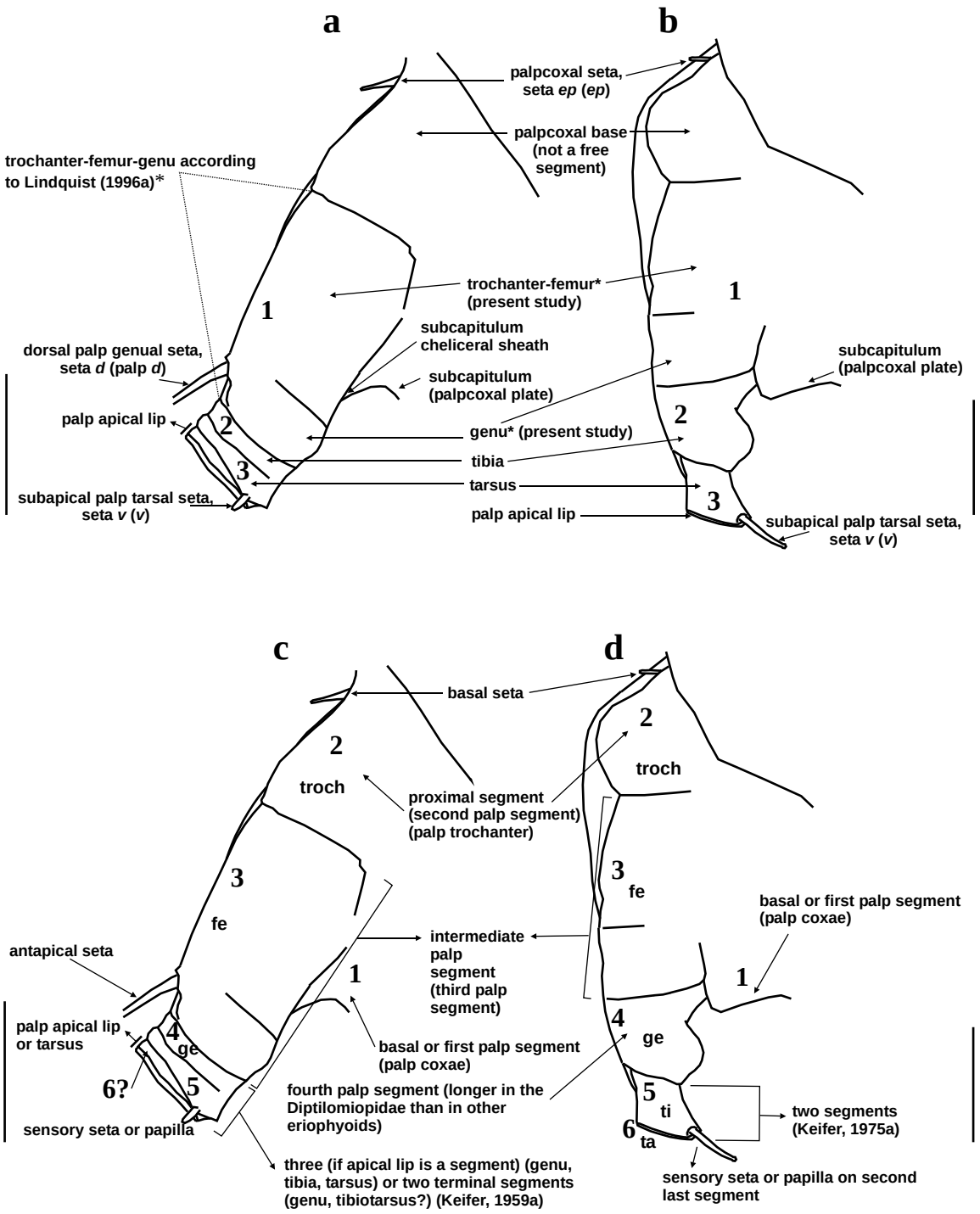


Fig. 3.23. Different hypotheses regarding the homology of the pedipalpal segments of the Eriophyoidea with other Acariform pedipalpi: **a, b)** segments according to Lindquist (1996a) (according to him palpi with three free segments), and present study, *according to Lindquist (1996a) the first free segment is a fusion of the trochanter, femur and genu, according to the present study, however, the genu is dorsally fused with the other segments, but ventrally separated from them; **c)** segments and terminology according to Keifer (1959a); **d)** segments and terminology according to Keifer (1975a); terminology not used by Keifer (1959a, 1975a) but added to Figs. 3.32c, d to homologize with usual segment names: troch = trochanter, fe = femur, ge = genu, ti = tibia, ta = tarsus, tibiotarsus; 1, 2, 3, 4, 5 = numbers of free segments (Lindquist, 1996a) or segments (Keifer, 1959a, 1975a) (to indicate number of segments according to each hypothesis [not included here: five segments according to Shevchenko & Silvere (1968)]). Scale lines = 10 µm.

Characters that have been included in some published species descriptions to date are:

i. The angle at which the gnathosoma projects from the body is frequently described, especially in earlier descriptions such as "the rostrum is projecting down" in *Diptilomiopus jevremovici* (Keifer, 1960) and *D. knorri* (Keifer, 1974) and "rostrum curved downwards" in *Acalitus mallyi* (Tucker) (Meyer, 1990a). Generally, the eriophyoid gnathosoma has about a hypognathous orientation (directed ventrally) reducing the ventral surface. It is reported to be more prognathous (directed anteriorly) in the Phytoptidae and Eriophyidae (e.g., Figs 3.27c, 3.38c), and more hypognathous in the Diptilomiopidae (e.g., Fig. 3.79b), with many intermediates between these two positions (Nuzzaci & Alberti, 1996);

ii. The length of the gnathosoma and of the chelicerae is regularly recorded;

iii. The presence (or absence) and length of the palp setae, or some of the palp setae, are sometimes recorded. Mostly, these setae are not depicted in the descriptive drawings of the gnathosoma, even when recorded in the text description. Some attention is given to the shape of palp *d*, if it is different from the usual simple shape, for example, it is bifurcate in some species (e.g., in *Tumescoptes* sp., Fig. 3.47d; and in *Porosus monosporae*, Figs 3.68a-c);

iv. Amrine described the shape of the cheliceral retainer, and found it to be different between morphologically similar species (Amrine *et al.*, 1994); and

v. In some species, such as *Aceria pretoriensis* (Meyer, 1989) (= *Cisaberoptus pretoriensis* Meyer, 1989), the apical ends of the palpi have triangular projections (Meyer, 1989a).

In their guidelines for describing eriophyoid species, Amrine & Manson (1996: 384) suggested that the following gnathosomal characters should be included in descriptions:

i. Length of the gnathosoma measured from the base of the chelicerae to the apical palp ends;

ii. Lengths of the palp *ep*, *d* and *v* (Figs 3.23a, b); and

iii. Description of the shape and position of the cheliceral guide (refer to the definition, description of these structures below).

One of the problems in studying and incorporating gnathosomal characters from slide-mounted specimens is the quite severe "squashing" and deformation of the gnathosoma. Additionally, the

"halo" created by phase-contrast light microscopy is particularly bad in this area due to the complex of stylets and other dense structures present.

Not much attention has been given to the morphology of the gnathosoma in the description of taxa, and particularly not the shape and relative position of structures. When the morphology of the gnathosoma is studied in more detail, however, using techniques such as the low-temperature SEM (present study), it becomes apparent that very few of the potentially useful and available systematic characters are used.

3.4.2 Gnathosomal characters currently used in phylogenetic treatises

In comparison with the gnathosoma of many free-living acariform mites, there is loss or reduction in eriophyoid gnathosomal structures (Lindquist & Oldfield, 1996) as follows:

- The ventral surface of the subcapitulum is reduced and lacks adoral and infracapitular setae;
- The palpi are reduced in segmentation and lack most of the setae and the tarsal solenidion; and
- The chelicerae are without setae, and the cheliceral bases are relatively small and do not form a stylophore which is present in, e.g., Tetranychidae.

Structures with similar form and function than most of the eriophyoid gnathosomal components are not found among other acariform mites (Lindquist, 1996a; Lindquist & Oldfield, 1996; Nuzzaci & Alberti, 1996), apart from possible homologies postulated by Nuzzaci & de Lillo (1991). In particular, the small, knob-like motivator between the cheliceral bases is unique to the eriophyoids (Shevchenko & Silvere, 1968; Lindquist & Oldfield, 1996).

Nuzzaci & De Lillo (1991) compared gnathosomal morphology and feeding mechanisms of phytophagous mite groups, and particularly the different structures constituting the gnathosoma, including the lateral labia, subcapitulum, labrum, chelicerae and feeding process. They largely studied them using TEM. Additional stylets and a cheliceral sheath are present in the Eriophyoidea, and a salivary pump in the Tetranychidae and Tenuipalpidae. They could not find major differences between the families Tetranychidae and Tenuipalpidae, and similarly not between the three eriophyoid families, Eriophyidae, Phytoptidae and Diptilomiopidae, except the larger and more robust gnathosoma in the Diptilomiopidae. They identified three gnathosomal types, or three evolutionary lines, representing the Tetranychoidea, Penthaleidae and Eriophyoidea (only taking into consideration the representative groups they studied). According to the

characteristics they studied, they concluded that the Eriophyoidea and Penthaleidae are morphologically more similar to each other than both are to the Tetranychidae and Tenuipalpidae, and thus the Eriophyoidea and Penthaleidae may be more closely related than either is to the Tetranychidae and Tenuipalpidae.

A comprehensive comparative morphological study of the gnathosomas of about 64 species studied with SEM (Table 3.1) is presented here (including Table 3.4), except seven species where the gnathosoma could not be studied sufficiently due to the frontal lobe obscuring the gnathosoma entirely, or where too few specimens were available or in the correct position: *Shevtchenkella* sp. *cf. S. rothmanniae* (Meyer, 1990); *Quantalitus squamosus* Meyer, 1989; unknown genus, possibly of the Anthocoptini, and specimens that could not be identified to family level, from *Faurea rochetiana*; unknown genus of the Eriophyidae from *Trema orientalis*; morphospecies one from *Anthocleista grandiflora*; and specimens that could not be identified to family level from *Psydrax livida*. The SEM images and some accompanying drawings are presented in Figs 3.25-3.85.

3.5 PART II: RESULTS AND DISCUSSION

3.5.1 Chelicerae

Only two characteristics of the chelicerae are currently used in eriophyoid taxonomy: the length of the chelicerae, and the two general shapes differentiating the Diptilomiopidae from the remainder of the Eriophyoidea (Fig. 3.22, and see above for more detail). However, other characteristics of the chelicerae may be useful for systematics. One such character is the division of the cheliceral shaft into a dorsal and ventral digit or filament, proposed to be modified from the fixed and movable cheliceral digits, respectively, as in some of the species investigated in previous studies (Shevchenko & Silvere, 1968; Krantz, 1973; Keifer, 1975a; Nuzzaci, 1979; Thomsen, 1987; Freeman *et al.*, 2005). The lower, thinner digit seems to be articulated to the upper digit in an SEM image presented by Freeman *et al.* (2005). It is unknown whether the cheliceral shaft is divided in all eriophyoid species (Lindquist, 1996a), but may be of use if it is present or absent in some groups, or may vary in other respects. This character can only be observed using TEM (Nuzzaci & Alberti, 1996) and where the internal stylets are sufficiently exposed in SEM studies (e.g., Thomsen, 1987; Freeman *et al.*, 2005) or in slide-mounted specimens (Krantz, 1973). In slide-mounted specimens, it is more difficult to detect because the two digits may lie very close together, appearing as one undivided stylet or the lower digits or filaments may be thin and fragile and obscured by other gnathosomal structures.

Table 3.4. New potentially useful gnathosomal characters for systematics. Character states were scored from SEM images (Figs 3.25-3.85). char = character; cs = protuberances (possibly papillae, setae or spines) proximally on the chelicerae; approximation = dorsal approximation of pedipalp coxal base segment edges; *ep* orientation = orientation of seta *ep* in relation to the palp surface; *ep* direction = anteriad direction of seta *ep* ; *ep* position = distance of seta *ep* from palpcoxal base segment distal margin; *ep* r-position = relative position of seta *ep* on basal segment (basal segment length / distance of seta *ep* from distal margin); stylet elevation = elevation of chelicerae and other stylets above palpi at about level of proximal margin; ? = unknown (could not be determined, or scored state uncertain).

		Char 1	Char 2	Char 3	Char 4	Char 5	Char 6	Char 7	Char 8	Char 9
		dorsal aspect of palpcoxal base segment								
Fig.	Mite species and classification	cs	approximation & shape	length	*ep* orientation	*ep* direction	*ep* position	*ep* r-position	ridges or depressions	ornamentation (other than ridges)
	PHYTOPTIDAE									
	Nalepellinae: Trisetacini									
3.25	*Trisetacus* sp. *cf*. *T. pinastri* from *Pinus pinaster*	? (may be covered by palpi)	touching; curved	10.6	appressed	parallel	5.5	1.9	no ridges	unornamented
	Nalepellinae: Nalepellini									
3.26	*Setoptus radiatae* from *Pinus radiata*	?	touching; straight	20.0	erect?	parallel	18.8	1.1	longitudinal ridge along the extended inside margin of *ep* terminating in an ovalish depression, margined with a slight ridge, distally (Fig. 2a)	unornamented
	Sierraphytoptinae: Mackiellini									
3.27	*Mackiella* sp. from *Phoenix reclinata*	?	?	?	?	?	?	?	?	?
	ERIOPHYIDAE									
	Aberoptinae									
3.28	*Aberoptus* sp. *cf*. *Aberoptus* sp. nov. from *Schotia brachypetala*	absent	separated; straight, parallel	7.5	erect	medially	4.0	1.9	ridge on the outer side of the enlarged cheliceral bases and insertion of *ep* , causing these structures to be enclosed in a hollow with *ep* inserted on vertical edges (Fig. 4a)	unornamented
	Cecidophyinae: Cecidophyini									
3.29	*Cecidophyopsis* sp. *cf. C. hendersoni* from *Yucca guatemalensis*	present in immature, could not be determined in adult	touching; straight	11.2	erect	medially	8.1	1.4	ridge extending in a half circle from seta ep to the proximal margin on the outer side of the palpcoxal base; setae ep inserted in relatively vertical palp edges, causing the setae to project medially	unornamented
	Cecidophyinae: Colomerini									
3.30	*Afromerus lindquisti* from *Psydrax livida*	absent	separated; curved	5.0	erect	medially	2.8	1.8	no ridges	unornamented
3.31	*Ectomerus* sp. *cf*. *E. systenus* from *Terminalia sericea*	?	separated; slightly curved	4.0	erect	converging	2.2	1.8	no ridges	unornamented
3.32	*Neserella* sp. *cf. N. tremae* from *Trema orientalis*	absent	separated; curved	2.7	erect	converging	1.3	2.0	no ridges	unornamented
	Eriophyinae: Aceriini									
3.33	*Acalitus mallyi* from *Vangueria infausta* subsp. *infausta*	absent	separated; slightly curved	6.8	appressed	parallel	3.0	2.3	no ridges	unornamented
3.34	*Aceria lantanae* (flower gall race) from *Lantana* x *camara* (hybrid complex)	present	separated; curved	7.0	erect	parallel	3.2	2.2	no ridges	unornamented
3.35	*Aceria ocellatum* from *Searsia lancea*	absent	separated; curved	4.8	appressed	converging	2.5	1.9	no ridges	unornamented
3.36	*Aceria* sp. *cf. A. dichrostachyia* from *Dichrostachys cinerea* subsp. and var. unknown	absent or very slight	separated; slightly curved	4.6	erect	parallel	2.3	2.0	strong ridge running to outside from seta *ep* , forking; strong diagonal ridge from below *ep* to distal coxal base margin (Fig. 12a)	unornamented
3.37	*Aceria* sp. *cf. A. giraffae* from *Acacia erioloba*	present	separated?	7.0	appressed	converging	3.6	2.0	slight ridge running from seta *ep* diagonally to outside	unornamented
3.38	*Aceria* sp. *cf*. *Aceria* sp. nov. from *Chrysanthemoides incana*	absent	separated	6.5	erect	parallel?	2.8	2.3	two slight parallel ridges antaxially of seta *ep* , forming a slight trough	unornamented
3.39	*Aceria cf. Aceria* sp. nov. from *C. monilifera* subsp. *monilifera*	absent	separated	6.7	erect	parallel?	2.8	2.4	two slight parallel ridges antaxially of seta *ep* , forming a slight trough	two tubercles close to proximal margin?
3.40	*Aceria* sp. *cf. A. proteae* from *Protea caffra* subsp. *caffra*	absent or very slight	separated; straight?	8.0	appressed	converging	4.8	1.7	possibly very slight ridge running to outside from seta *ep*	unornamented
3.41	*Aceria* sp. *cf. Aceria* sp. nov. from *Ipomoea batatas* var. *batatas*	present	separated	6.0	erect	parallel	3.6	1.7	possibly very slight ridge running to outside from seta *ep*	unornamented
3.42	*Aceria* sp. *cf*. *Aceria* sp. nov. from *Oxalis corniculata*	present	separated	7.0	erect	parallel	3.6	2.0	no ridges	unornamented
3.43	*Aceria* sp. *cf. Aceria* sp. nov. from *Acacia rehmanniana*	present?	separated	6.4	erect	parallel	3.0	2.1	no ridges	unornamented
3.44	Unknown genus, nr. *Aceria* from *Apodytes dimidiata* subsp. d*imidiata*	present	separated; straight?	6.4	appressed	converging	3.4	1.9	no ridges	unornamented
3.45	*cf. Aceria* sp. from *Cineraria* sp.	absent?	separated	? (too slanted)	erect	parallel	? slanted)	?	possibly very slight ridge running to outside from seta *ep*	unornamented

Fig.	Mite species and classification	Char 1	Char 2	Char 3	Char 4	Char 5	Char 6	Char 7	Char 8	Char 9
		dorsal aspect of palpcoxal base segment								
		cs	approximation & shape	length	*ep* orientation	*ep* direction	*ep* position	*ep* r-position	ridges or depressions	ornamentation (other than ridges)
3.46	*Aceria* sp. *cf. Aceria* sp. nov. from *Xymalos monospora*	?	separated	5.5 (lateral)	erect	converging	3 (lateral)	2 (lateral)	no ridges	tubercles or granula particularly in area distally of insertion of seta *ep* from anterior to lateral region (Fig. 22b)
	Phyllocoptinae: Acaricalini									
3.47	*Tumescoptes* sp. *cf. T. dicrus* from *Phoenix reclinata*	present?	separated	?	erect	converging?	?	?	possibly no ridges	possibly unornamented
	Phyllocoptinae: Calacarini									
3.48	*Calacarus* sp. from *Searsia lancea*	?	separated?	?	erect	?	4 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
3.49	*Calacarus* sp. from *Faurea rochetiana*	?	separated?	?	erect	parallel?	0 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
3.50	*Calacarus* sp. from *Psydrax livida*	absent?	separated	?	erect	converging	0 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
	Phyllocoptinae: Tegonotini									
3.51	*Shevtchenkella* sp. *cf. S. lividae* from *Psydrax livida*	absent?	separated	?	erect	converging	1 (lateral)	?	no ridges?	unornamented?
3.52	*Shevtchenkella* sp. *cf . S. rhusi* from *Rhus lancea*	?	separated?	?	erect	parallel	?	?	no ridges?	unornamented?
3.53	*Neoshevtchenkella* or *Shevtchenkella* sp. (with wax) from *Celtis africana*	absent?	separated?	?	erect	converging	?	?	no ridges?	unornamented?
	Phyllocoptinae: Phyllocoptini									
3.54	*cf. Calepitrimerus* sp. from *Celtis africana*	present	separated?	?	erect	converging	3 (lateral)	?	no ridges?	unornamented?
3.55	*Cecidodectes euzonus* from *Trema orientalis*	absent	separated	7 (lateral)	erect	parallel?	4 (lateral)	2.0	no ridges	unornamented
3.56	*cf. Phyllocoptes* sp. from *Anthocleista grandiflora*	present	separated	?	erect	converging	0 slanted)	?	granulated ridge diagonally downwards from seta *ep* (similar to this ridge in other species) (Fig. 33a)	granulated (Fig. 33a)
3.57	*Tergilatus sparsus* from *Portulacaria afra*	present	separated	?	erect	converging	?	?	transverse ridge proximally on palpcoxal base in immature, presence not determined in adult	unornamented
	Phyllocoptinae: Anthocoptini									
3.58	*Aculops* or *Metaculus* sp. from *Anthocleista grandiflora*	absent?	separated	?	erect	converging?	4.5	?	no ridges?	unornamented?
3.59	*Aculus* sp. *cf . Aculops lycopersici* from *Physalis peruviana*	present	separated	7.9	erect	converging	3.7	2.1	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base, more vague and larger circle than those in *Calacarus* spp.	unornamented
3.60	*cf. Aculus* sp. from *Acacia burkei*	present	separated?	?	erect	parallel?	?	?	half circular ridge running diagonally on outside of *ep*	unornamented
3.61	*cf. Aculus* sp. from *Lantana trifolia*	present	separated	6.3	erect	converging	3.3	1.9	slight ridge running from seta *ep* diagonally to outside	few slight granules
3.62	*cf. Aculus* sp. or possibly immature of *Quantalitus* from *Rothmannia capensis*	?	separated?	?	erect	converging?	?	?	single lobe like ridge on the outside of seta *ep*	unornamented
3.63	*Costarectus zeyheri* from *Dovyalis zeyheri*	?	separated?	?	erect	converging?	1 (lateral)	?	single vertical lobe like ridge antaxially of seta *ep*	unornamented
3.64	*Meyerella bicristatus* from *Mystroxylon aethiopicum*	present	separated	6.0	erect	converging	4.0	1.5	no ridges	unornamented
3.65	possibly a new genus nr. *Costarectus* from *Mystroxylon aethiopicum*	present	separated?	?	erect	converging?	1 (lateral)	?	no ridges	unornamented
3.66	possibly a new genus nr. *Tetra* from *Protea caffra* subsp. *caffra*	?	separated?	?	?	?	?	?	probably a lobe like vertical ridge on the outside edge of a diagonal ridge running from *ep* backwards	unornamented
3.67	possibly a new genus nr. *Mesalox* from *Apodytes dimidiata*	present	separated	9.4 (lateral)	erect	converging	1 (lateral)	1.5	no ridges or possibly very slight ovalish area diagonally on coxal base demarcated by very slight ridges, barely visibly	unornamented
3.68	*Porosus monosporae* from *Xymalos monospora*	?	?	?	?	?	?	?	?	?
3.69	*Tegolophus* sp. *cf. T. orientalis* from *Trema orientalis*	?	separated?	?	erect	converging	?	?	no ridges?	unornamented?
3.70	*Tetra retusa* from *Bauhinia galpinii*	present	separated	5.5	erect	converging	3.0	1.8	single diagonal ridge from *ep* to distal margin of palp coxal base	unornamented

Fig.	Mite species and classification	Char 1 dorsal aspect of palpcoxal base segment cs	Char 2 approximation & shape	Char 3 length	Char 4 *ep* orientation	Char 5 *ep* direction	Char 6 *ep* position	Char 7 *ep* r-position	Char 8 ridges or depressions	Char 9 ornamentation (other than ridges)
3.71	*Tetraspinus* sp. from *Chrysanthemoides monilifera* subsp. *monilifera*	present	separated	?	erect	converging	?	?	no ridges	unornamented
3.72	*cf. Tetraspinus* sp. from *Faurea rochetiana*	present	separated	?	erect	converging	5 (lateral)	?	single vertical lobe like ridge antaxially of seta *ep*	unornamented
	Eriophyidae (subfamily uncertain)									
3.73	possibly new worm-like genus (Eriophyinae?: Aceriini?) from *Faurea rochetiana*	absent	separated	9.5	appressed	converging	4.5	2.1	two slight parallel ridges one extending from seta *ep* , and the other antaxially of seta *ep* , forming a slight trough	unornamented
3.74	unknown genus (Phyllocoptinae?) from *Ekebergia capensis*	?	?	?	erect	converging	?	?	?	?
3.75	possibly a new genus in Phyllocoptinae or Cecidophyinae from *Acacia burkei*	present	separated?	?	erect	converging?	3 (lateral)	?	single ridge roundish diagonally from the outside of seta *ep* towards lateral outside of palpcoxal base	unornamented
3.76	*Phyllocoptes* sp. (Phyllocoptinae) or new genus (Cecidophyinae) from *Dovyalis zeyheri*	?	separated?	?	erect	converging?	?	?	possibly with a diagonal rounded slight ridge from *ep* to the outside	unornamented
3.77	probably a new genus (subfamily uncertain) from *Cussonia* sp.	present	separated?	8.9	erect	medially	5.0	1.8	no ridges?	unornamented?
	DIPTILOMIOPIDAE									
	Diptilomiopinae									
3.78	*Diptilomiopus apobrevis* sp. nov. from *Apodytes dimidiata*	absent	slightly separated; elevated	18.4 (lateral)	erect	converging	8 (lateral)	1.2	slight depressions ahead of and laterally on palpcoxal base	unornamented
3.79	*Diptilomiopus faurius* sp. nov. from *Faurea rochetiana*	absent	separated; elevated	23.7 (lateral)	erect	diverging	5 (lateral)	1.1	short ridges alongside *ep* , depression ahead of *ep*	unornamented
3.80	unidentified species (Diptilomiopinae) from *Xymalos monospora*	absent	separated; elevated	10.7 (lateral)	erect	converging?	0 (lateral)	1.1	*ep* in slight depression	unornamented
3.81	probably a new genus nr. *Dacundiopus* from *Mystroxylon aethiopicum*	absent	separated; elevated	20.0 (lateral)	erect	diverging	0 (lateral)	1.1	half round "platform" proximally and pointed "knob" towards the outside of palpcoxal base	unornamented
3.82	*Rhynacus* sp. *cf. Rhynacus* sp. nov. from *Dovyalis zeyheri*	absent?	separated; elevated	20.0	erect	?	18.8	1.1	longitudinal ridge on lateral aspect of palpcoxal base?	unornamented
	ERIOPHYOIDEA (family uncertain)									
3.83	probably a new genus (Eriophyidae) from *Searsia lancea* blisters	absent	separated?	?	absent?	absent?	?	?	?	?
3.84	unidentified morphospecies 2 (*cf.* Eriophyidae) from *Anthocleista grandiflora*	? (may be covered by palpi)	touching	8.5 (lateral)	erect	medially	6 (lateral)	1.5	longitudinal ridge on the outside of seta *ep*	unornamented
3.85	unidentified species (Eriophyoidea) from *Sideroxylon inerme*	absent	separated?	5.5 (lateral)	erect	converging	2 (lateral)	2.5	three longitudinal ridges: one extending from *ep* , and two ridges antaxially of *ep*	unornamented

Table 3.4. New potentially useful gnathosomal characters for systematics. Character states were scored from SEM images (Figs 3.25-3.85). char = character; cs = protuberances (possibly papillae, setae or spines) proximally on the chelicerae; approximation = dorsal approximation of pedipalp coxal base segment edges; *ep* orientation = orientation of seta *ep* in relation to the palp surface; *ep* direction = anteriad direction of seta *ep* ; *ep* position = distance of seta *ep* from palpcoxal base segment distal margin; *ep* r-position = relative position of seta *ep* on basal segment (basal segment length / distance of seta *ep* from distal margin); stylet elevation = elevation of chelicerae and other stylets above palpi at about level of proximal margin; ? = unknown (could not be determined, or scored state uncertain).

		Char 1	Char 2	Char 3	Char 4	Char 5	Char 6	Char 7	Char 8	Char 9
		dorsal aspect of palpcoxal base segment								
Fig.	Mite species and classification	cs	approximation & shape	length	*ep* orientation	*ep* direction	*ep* position	*ep* r-position	ridges or depressions	ornamentation (other than ridges)
	PHYTOPTIDAE									
	Nalepellinae: Trisetacini									
3.25	*Trisetacus* sp. *cf*. *T. pinastri* from *Pinus pinaster*	? (may be covered by palpi)	touching; curved	10.6	appressed	parallel	5.5	1.9	no ridges	unornamented
	Nalepellinae: Nalepellini									
3.26	*Setoptus radiatae* from *Pinus radiata*	?	touching; straight	20.0	erect?	parallel	18.8	1.1	longitudinal ridge along the extended inside margin of *ep* terminating in an ovalish depression, margined with a slight ridge, distally (Fig. 2a)	unornamented
	Sierraphytoptinae: Mackiellini									
3.27	*Mackiella* sp. from *Phoenix reclinata*	?	?	?	?	?	?	?	?	?
	ERIOPHYIDAE									
	Aberoptinae									
3.28	*Aberoptus* sp. *cf*. *Aberoptus* sp. nov. from *Schotia brachypetala*	absent	separated; straight, parallel	7.5	erect	medially	4.0	1.9	ridge on the outer side of the enlarged cheliceral bases and insertion of *ep* , causing these structures to be enclosed in a hollow with *ep* inserted on vertical edges (Fig. 4a)	unornamented
	Cecidophyinae: Cecidophyini									
3.29	*Cecidophyopsis* sp. *cf. C. hendersoni* from *Yucca guatemalensis*	present in immature, could not be determined in adult	touching; straight	11.2	erect	medially	8.1	1.4	ridge extending in a half circle from seta ep to the proximal margin on the outer side of the palpcoxal base; setae ep inserted in relatively vertical palp edges, causing the setae to project medially	unornamented
	Cecidophyinae: Colomerini									
3.30	*Afromerus lindquisti* from *Psydrax livida*	absent	separated; curved	5.0	erect	medially	2.8	1.8	no ridges	unornamented
3.31	*Ectomerus* sp. *cf*. *E. systenus* from *Terminalia sericea*	?	separated; slightly curved	4.0	erect	converging	2.2	1.8	no ridges	unornamented
3.32	*Neserella* sp. *cf. N. tremae* from *Trema orientalis*	absent	separated; curved	2.7	erect	converging	1.3	2.0	no ridges	unornamented
	Eriophyinae: Aceriini									
3.33	*Acalitus mallyi* from *Vangueria infausta* subsp. *infausta*	absent	separated; slightly curved	6.8	appressed	parallel	3.0	2.3	no ridges	unornamented
3.34	*Aceria lantanae* (flower gall race) from *Lantana* x *camara* (hybrid complex)	present	separated; curved	7.0	erect	parallel	3.2	2.2	no ridges	unornamented
3.35	*Aceria ocellatum* from *Searsia lancea*	absent	separated; curved	4.8	appressed	converging	2.5	1.9	no ridges	unornamented
3.36	*Aceria* sp. *cf. A. dichrostachyia* from *Dichrostachys cinerea* subsp. and var. unknown	absent or very slight	separated; slightly curved	4.6	erect	parallel	2.3	2.0	strong ridge running to outside from seta *ep* , forking; strong diagonal ridge from below *ep* to distal coxal base margin (Fig. 12a)	unornamented
3.37	*Aceria* sp. *cf. A. giraffae* from *Acacia erioloba*	present	separated?	7.0	appressed	converging	3.6	2.0	slight ridge running from seta *ep* diagonally to outside	unornamented
3.38	*Aceria* sp. *cf*. *Aceria* sp. nov. from *Chrysanthemoides incana*	absent	separated	6.5	erect	parallel?	2.8	2.3	two slight parallel ridges antaxially of seta *ep* , forming a slight trough	unornamented
3.39	*Aceria cf. Aceria* sp. nov. from *C. monilifera* subsp. *monilifera*	absent	separated	6.7	erect	parallel?	2.8	2.4	two slight parallel ridges antaxially of seta *ep* , forming a slight trough	two tubercles close to proximal margin?
3.40	*Aceria* sp. *cf. A. proteae* from *Protea caffra* subsp. *caffra*	absent or very slight	separated; straight?	8.0	appressed	converging	4.8	1.7	possibly very slight ridge running to outside from seta *ep*	unornamented
3.41	*Aceria* sp. *cf. Aceria* sp. nov. from *Ipomoea batatas* var. *batatas*	present	separated	6.0	erect	parallel	3.6	1.7	possibly very slight ridge running to outside from seta *ep*	unornamented
3.42	*Aceria* sp. *cf*. *Aceria* sp. nov. from *Oxalis corniculata*	present	separated	7.0	erect	parallel	3.6	2.0	no ridges	unornamented
3.43	*Aceria* sp. *cf. Aceria* sp. nov. from *Acacia rehmanniana*	present?	separated	6.4	erect	parallel	3.0	2.1	no ridges	unornamented
3.44	Unknown genus, nr. *Aceria* from *Apodytes dimidiata* subsp. d*imidiata*	present	separated; straight?	6.4	appressed	converging	3.4	1.9	no ridges	unornamented
3.45	*cf. Aceria* sp. from *Cineraria* sp.	absent?	separated	? (too slanted)	erect	parallel	? slanted)	?	possibly very slight ridge running to outside from seta *ep*	unornamented

Fig.	Mite species and classification	Char 1	Char 2	Char 3	Char 4	Char 5	Char 6	Char 7	Char 8	Char 9
		dorsal aspect of palpcoxal base segment								
		cs	approximation & shape	length	*ep* orientation	*ep* direction	*ep* position	*ep* r-position	ridges or depressions	ornamentation (other than ridges)
3.46	*Aceria* sp. *cf. Aceria* sp. nov. from *Xymalos monospora*	?	separated	5.5 (lateral)	erect	converging	3 (lateral)	2 (lateral)	no ridges	tubercles or granula particularly in area distally of insertion of seta *ep* from anterior to lateral region (Fig. 22b)
	Phyllocoptinae: Acaricalini									
3.47	*Tumescoptes* sp. *cf. T. dicrus* from *Phoenix reclinata*	present?	separated	?	erect	converging?	?	?	possibly no ridges	possibly unornamented
	Phyllocoptinae: Calacarini									
3.48	*Calacarus* sp. from *Searsia lancea*	?	separated?	?	erect	?	4 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
3.49	*Calacarus* sp. from *Faurea rochetiana*	?	separated?	?	erect	parallel?	0 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
3.50	*Calacarus* sp. from *Psydrax livida*	absent?	separated	?	erect	converging	0 (lateral)	?	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base	unornamented
	Phyllocoptinae: Tegonotini									
3.51	*Shevtchenkella* sp. *cf. S. lividae* from *Psydrax livida*	absent?	separated	?	erect	converging	1 (lateral)	?	no ridges?	unornamented?
3.52	*Shevtchenkella* sp. *cf . S. rhusi* from *Rhus lancea*	?	separated?	?	erect	parallel	?	?	no ridges?	unornamented?
3.53	*Neoshevtchenkella* or *Shevtchenkella* sp. (with wax) from *Celtis africana*	absent?	separated?	?	erect	converging	?	?	no ridges?	unornamented?
	Phyllocoptinae: Phyllocoptini									
3.54	*cf. Calepitrimerus* sp. from *Celtis africana*	present	separated?	?	erect	converging	3 (lateral)	?	no ridges?	unornamented?
3.55	*Cecidodectes euzonus* from *Trema orientalis*	absent	separated	7 (lateral)	erect	parallel?	4 (lateral)	2.0	no ridges	unornamented
3.56	*cf. Phyllocoptes* sp. from *Anthocleista grandiflora*	present	separated	?	erect	converging	0 slanted)	?	granulated ridge diagonally downwards from seta *ep* (similar to this ridge in other species) (Fig. 33a)	granulated (Fig. 33a)
3.57	*Tergilatus sparsus* from *Portulacaria afra*	present	separated	?	erect	converging	?	?	transverse ridge proximally on palpcoxal base in immature, presence not determined in adult	unornamented
	Phyllocoptinae: Anthocoptini									
3.58	*Aculops* or *Metaculus* sp. from *Anthocleista grandiflora*	absent?	separated	?	erect	converging?	4.5	?	no ridges?	unornamented?
3.59	*Aculus* sp. *cf . Aculops lycopersici* from *Physalis peruviana*	present	separated	7.9	erect	converging	3.7	2.1	ridge extending in a half circle from seta *ep* to the proximal margin on the outer side of the palpcoxal base, more vague and larger circle than those in *Calacarus* spp.	unornamented
3.60	*cf. Aculus* sp. from *Acacia burkei*	present	separated?	?	erect	parallel?	?	?	half circular ridge running diagonally on outside of *ep*	unornamented
3.61	*cf. Aculus* sp. from *Lantana trifolia*	present	separated	6.3	erect	converging	3.3	1.9	slight ridge running from seta *ep* diagonally to outside	few slight granules
3.62	*cf. Aculus* sp. or possibly immature of *Quantalitus* from *Rothmannia capensis*	?	separated?	?	erect	converging?	?	?	single lobe like ridge on the outside of seta *ep*	unornamented
3.63	*Costarectus zeyheri* from *Dovyalis zeyheri*	?	separated?	?	erect	converging?	1 (lateral)	?	single vertical lobe like ridge antaxially of seta *ep*	unornamented
3.64	*Meyerella bicristatus* from *Mystroxylon aethiopicum*	present	separated	6.0	erect	converging	4.0	1.5	no ridges	unornamented
3.65	possibly a new genus nr. *Costarectus* from *Mystroxylon aethiopicum*	present	separated?	?	erect	converging?	1 (lateral)	?	no ridges	unornamented
3.66	possibly a new genus nr. *Tetra* from *Protea caffra* subsp. *caffra*	?	separated?	?	?	?	?	?	probably a lobe like vertical ridge on the outside edge of a diagonal ridge running from *ep* backwards	unornamented
3.67	possibly a new genus nr. *Mesalox* from *Apodytes dimidiata*	present	separated	9.4 (lateral)	erect	converging	1 (lateral)	1.5	no ridges or possibly very slight ovalish area diagonally on coxal base demarcated by very slight ridges, barely visibly	unornamented
3.68	*Porosus monosporae* from *Xymalos monospora*	?	?	?	?	?	?	?	?	?
3.69	*Tegolophus* sp. *cf. T. orientalis* from *Trema orientalis*	?	separated?	?	erect	converging	?	?	no ridges?	unornamented?
3.70	*Tetra retusa* from *Bauhinia galpinii*	present	separated	5.5	erect	converging	3.0	1.8	single diagonal ridge from *ep* to distal margin of palp coxal base	unornamented

Fig.	Mite species and classification	Char 1 dorsal aspect of palpcoxal base segment cs	Char 2 approximation & shape	Char 3 length	Char 4 *ep* orientation	Char 5 *ep* direction	Char 6 *ep* position	Char 7 *ep* r-position	Char 8 ridges or depressions	Char 9 ornamentation (other than ridges)
3.71	*Tetraspinus* sp. from *Chrysanthemoides monilifera* subsp. *monilifera*	present	separated	?	erect	converging	?	?	no ridges	unornamented
3.72	*cf. Tetraspinus* sp. from *Faurea rochetiana*	present	separated	?	erect	converging	5 (lateral)	?	single vertical lobe like ridge antaxially of seta *ep*	unornamented
	Eriophyidae (subfamily uncertain)									
3.73	possibly new worm-like genus (Eriophyinae?: Aceriini?) from *Faurea rochetiana*	absent	separated	9.5	appressed	converging	4.5	2.1	two slight parallel ridges one extending from seta *ep* , and the other antaxially of seta *ep* , forming a slight trough	unornamented
3.74	unknown genus (Phyllocoptinae?) from *Ekebergia capensis*	?	?	?	erect	converging	?	?	?	?
3.75	possibly a new genus in Phyllocoptinae or Cecidophyinae from *Acacia burkei*	present	separated?	?	erect	converging?	3 (lateral)	?	single ridge roundish diagonally from the outside of seta *ep* towards lateral outside of palpcoxal base	unornamented
3.76	*Phyllocoptes* sp. (Phyllocoptinae) or new genus (Cecidophyinae) from *Dovyalis zeyheri*	?	separated?	?	erect	converging?	?	?	possibly with a diagonal rounded slight ridge from *ep* to the outside	unornamented
3.77	probably a new genus (subfamily uncertain) from *Cussonia* sp.	present	separated?	8.9	erect	medially	5.0	1.8	no ridges?	unornamented?
	DIPTILOMIOPIDAE									
	Diptilomiopinae									
3.78	*Diptilomiopus apobrevis* sp. nov. from *Apodytes dimidiata*	absent	slightly separated; elevated	18.4 (lateral)	erect	converging	8 (lateral)	1.2	slight depressions ahead of and laterally on palpcoxal base	unornamented
3.79	*Diptilomiopus faurius* sp. nov. from *Faurea rochetiana*	absent	separated; elevated	23.7 (lateral)	erect	diverging	5 (lateral)	1.1	short ridges alongside *ep* , depression ahead of *ep*	unornamented
3.80	unidentified species (Diptilomiopinae) from *Xymalos monospora*	absent	separated; elevated	10.7 (lateral)	erect	converging?	0 (lateral)	1.1	*ep* in slight depression	unornamented
3.81	probably a new genus nr. *Dacundiopus* from *Mystroxylon aethiopicum*	absent	separated; elevated	20.0 (lateral)	erect	diverging	0 (lateral)	1.1	half round "platform" proximally and pointed "knob" towards the outside of palpcoxal base	unornamented
3.82	*Rhynacus* sp. *cf. Rhynacus* sp. nov. from *Dovyalis zeyheri*	absent?	separated; elevated	20.0	erect	?	18.8	1.1	longitudinal ridge on lateral aspect of palpcoxal base?	unornamented
	ERIOPHYOIDEA (family uncertain)									
3.83	probably a new genus (Eriophyidae) from *Searsia lancea* blisters	absent	separated?	?	absent?	absent?	?	?	?	?
3.84	unidentified morphospecies 2 (*cf.* Eriophyidae) from *Anthocleista grandiflora*	? (may be covered by palpi)	touching	8.5 (lateral)	erect	medially	6 (lateral)	1.5	longitudinal ridge on the outside of seta *ep*	unornamented
3.85	unidentified species (Eriophyoidea) from *Sideroxylon inerme*	absent	separated?	5.5 (lateral)	erect	converging	2 (lateral)	2.5	three longitudinal ridges: one extending from *ep* , and two ridges antaxially of *ep*	unornamented

I could not study the division of the cheliceral shaft, because the gnathosoma was studied intact and in a natural condition, and the shafts of the chelicerae were largely not visible. The cheliceral shafts are directly linked and hinged to the medial motivator (De Lillo *et al*., 2001). The bases of the cheliceral shafts are bulbous, thicker and more robust and may be articulated to the distal needle-like dorsal and ventral cheliceral digits (Shevchenko & Silvere, 1968; Thomsen, 1987). Only the bulbous cheliceral shaft bases, with medially possibly part of the dorsal aspect of the motivator, and the proximal part of the more slender distal digit of the dorsal cheliceral shaft or modified fixed digit, are usually exposed (e.g., Figs 3.33a, b). The remaining parts of the chelicerae and other stylets in the Phytoptidae and Eriophyidae are covered by the overlapping stylet sheath (e.g., Figs 3.33a, b), which was also recorded by, e.g., Nuzzaci & Alberti (1996). In the SEM images by Thomsen (1987) and Nuzzaci & Alberti (1996: 107 – Fig. 1.2.4) this sheath can also be seen enclosed around the distal end of the stylets, forming the tip of the subcapitulum. The shape of the chelicerae, stylet sheath and palpi are different in the Diptilomiopidae. The chelicerae, partly covered by the sheath, are elevated above the palpi (Fig. 3.79b), and the stylet sheath overlaps the cheliceral shafts more distally (Fig. 3.79a).

Two additional cheliceral characters are recorded in the present study:

a. <u>Character 1</u> (Table 3.4). **Protuberances on cheliceral shafts**

Cheliceral setae occur in other mite groups, but are absent in the Eriophyoidea (Lindquist, 1996a). The internal sensillar structures of eriophyoid chelicerae were described by De Lillo *et al*. (2001). The external morphology of these structures, however, and whether there are obvious external protuberances associated with them, their shape and location on the chelicerae were not reported. In the present study a protuberance that could be a papilla, spine, or seta, was detected on the proximal and dorsally exposed aspect of each dorsal cheliceral shaft of some species, mostly closely above the upper margin of the overlapping stylet sheaths (e.g., Figs 3.29b, d; 3.54c, d; 3.57a-d). This character could not be scored in many species, and no comprehensive attempt was made to determine particular patterns in the occurrence and size of these protuberances. They, however, broadly seem to be more frequently present and more pronounced in species of the Phyllocoptinae (e.g., *Aculus* sp., Figs 3.60a, b, d), and are smaller or absent in species from other subfamilies included in present study (e.g., *Acalitus mallyi*, Figs 3.33a, b). In most species the protuberances do not seem to be symmetrical, with the protuberance of one chelicera being larger than the other (e.g., *Phyllocoptes* sp., Figs 3.56a, b, d). In the latter species, it further seems as if the structures might be setae, because they seem to be inserted on tubercles (Figs 3.56a, b, d), but this is inconclusive, and as with the uncertain presence of additional setae on the palpi (Fig. 3.42) discussed later on, further

investigation, especially whether the structures are birefringent in polarized light, is needed to clarify the matter.

b. Inter-locking mechanism (Fig. 3.25) at the cheliceral bases

In *Trisetacus* sp. (Fig. 3.25) in the present SEM study, structures of the cheliceral bases seem to inter-lock with the palpcoxal base segments (Figs 3.25a, b, c, d). This mechanism may be in place of the cheliceral retainer mechanism which is usually present. The cheliceral retainers are structures of the palpi which inter-lock with parts of the cheliceral bases. These mechanisms probably keep the stylets and palpi in place when the mite is not feeding. Unfortunately, this basal gnathosomal area is obscured by the frontal lobe in the other two phytoptine species studied (Figs 3.26 & 3.27), and no similar cheliceral base inter-locking structures are present in any of the other species in which this area was visible. This character is thus unique (autapomorphic) to *Trisetacus* sp. and has not been scored as a character in Table 3.4.

3.5.2 Palpi (pedipalpi)

The palpi of the Actinotrichida [of which the Acariformes (including the Prostigmata, and the Eriophyoidea) is a subgroup] show considerable variation in their segmentation and shape (Evans, 1992; Kethley, 1990). Primitively within the Prostigmata, the palp is a leg-like, tactile structure comprising five homogenous articulating free segments (trochanter, femur, genu, tibia and tarsus) (Kethley, 1990). The palpcoxa is never a free segment in the Acariformes (Lindquist, 1996a).

Eriophyoid palpi are well-developed stout structures with truncated flattened surfaces apically, and they flank and support the subcapitulum. They may be reduced in segmentation due to fusion of some of the segments, depending on the interpretation of the palp structures. It is important to identify the palp segments and homologize them and their structures with those of other acariform mites in order to study the relationships between eriophyoids and other acariform mites. Keifer (1959a) noted that: "*These (eriophyoid) palpi have a series of segments, and while this recital will not attempt to definitely designate what each of these segments is, there is a possibility that all six segments of the Acarine palp are actually present*". He designated the "oral plate" in front of coxisternal plates I to be the basal or first palp segment (Figs 3.23c, d), and denoted the palp base (*sensu* Lindquist, 1996a) as the second palp segment and called it the "proximal segment". Nuzzaci (1979) stated that the palpi are articulated post-oral appendages [four free segments according to Keifer (1975a) (Fig. 3.23d), and five segments according to Shevchenko & Silvere

(1968) (Fig. 3.23c)]. Lindquist (1996a) hypothesized that each palp appears to consist of a base and three free segments (Figs 3.23a, b).

The palpcoxal base (called the "proximal segment" or "basal palp segment" by Keifer, 1959a, 1975a) is situated at the proximal end of the palpi. It is presumed that, similar to the gnathosoma of other Acari, the enlarged coxae of the palpi of the Eriophyoidea form the external walls of the subcapitulum by meeting and fusing ventrally (Evans, 1992), and thus the palpcoxa is not a free segment. The basal segment appears to be a projection of the dorsal portion of the palpcoxal base (Lindquist, 1996a).

- Palpcoxal base ("basal palp segment")

The present study confirms Lindquist's (1996a) observation that the basal segment is a projection of the dorsal portion of the palpcoxal base, because it is clear the segment extends uninterruptedly dorso-ventrally (Figs 3.41g, h). Ventrally, it extends to form the subcapitulum that consists of the basal part of the stylet sheath and the "oral plate" of Keifer (Figs 3.20 & 3.41g, h). It could be possible that leg coxisternal elements contribute to the "oral plate" structure.

- Shape of the palpcoxal base segment (dorsally)

Characteristics of the shape of the dorsal aspect of the palpcoxal base have not previously been used in the systematics of the Eriophyoidea. Some discrete differences may be of use particularly in studying the phylogeny. This segment is usually deformed in the slide-mounting process so the shape characteristics cannot be determined in slide-mounted specimens.

Characters from the shape of the palpcoxal base that are recorded in the present study:

a. **Character 2** (Table 3.4). **Approximation of inner margins of the palpcoxal segments dorsally**

Dorsally, the inner margins of the palpcoxal bases differ, as well as their relationship or approximation towards each other. The approximation of the margins (either touching or separate) could be scored most of the time, but the shape of the inner margins was not clear in most species. However, there are shape differences in the margin, such as rounded in *Trisetacus* sp. and *Afromerus* sp. (Figs 3.25 & 3.30, respectively), and straight or parallel in *Setoptus radiatae* and *Aberoptus* sp. (Figs 3.26 & 3.28, respectively). In the Diptilomiopinae, this segment is partly elevated against the stylets, and is separated by the stylets. The character states are presented in Table 3.4 (Character 2), and are given as approximations, followed by the shape of the margins. These two character states can be scored separately if they turn out to be informative.

b. <u>Character 3</u> (Table 3.4). **Length of the palpcoxal base segment**

The length was measured on the SEM images on the straight-most and shortest distance from the base of the segment where it borders the frontal margin of the prodorsal shield areas, not including the anterior shield lobe, up to the furthest distance on the anterior margin, preferably in line with the base of *ep* if possible (dashed black lines in Figs 3.25c, 3.28c, 3.38b, 3.55a, 3.79b). It was preferably measured on the dorsal view image, but if this is not optimal, it was measured on the lateral view image (e.g., dashed black lines in Figs 3.55a, 3.79b) and has been indicated as such in Table 3.4. The length of the scale bar was used to calculate the real length in µm.

- <u>Structures on the dorsal surface of the palpcoxal base</u>

Two structures on the dorsal surface of the palpcoxal base are sometimes included in eriophyoid taxonomy:

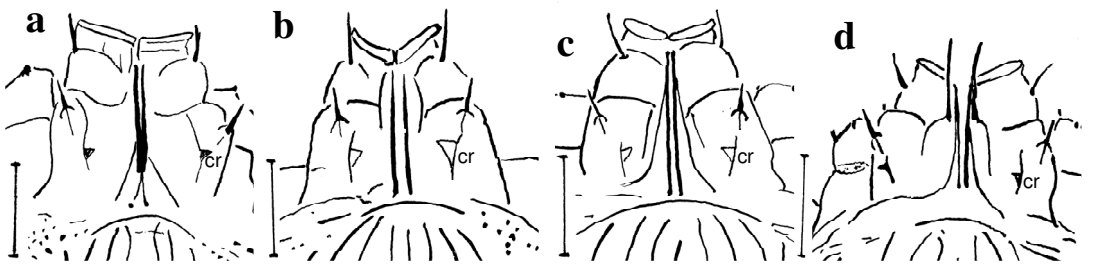
c. Cheliceral retainer

A seemingly flexible, spine-like process which is slightly darker than the surrounding dorsal palpcoxal surface is visible, one on each palpcoxal base, in slide-mounted specimens, and in some species it is easily discernable. It is directed almost centrally. It was named the "cheliceral retainer" by Keifer (1959a, 1975a). Similar to other structures on the gnathosoma, the cheliceral retainer is pushed out of place, usually out-wards, by the slide-mounting process: for example see drawings of *Cecidophyopsis* spp. (Fig. 3.24) from Amrine *et al.* (1994). This is also the case in most published SEM images of the gnathosoma and in the present study they are out of place in *Cecidophyopsis* sp. specimen (Fig. 3.29j). Sometimes the retainer itself flips towards the outside (Fig. 3.24d).

The shape of the cheliceral retainer was not scored, because it is not visible in most of the images of specimens in the current study, because the gnathosomas were not distorted, and are in their natural "non-feeding" state. The retainer is inter-locked with, or partly hooked around the enlarged knob-like base of the chelicera (e.g., Fig. 3.41b). It is obscured by the anterior shield lobe and anterior structures of the prodorsum. Part of the base of the cheliceral retainer is probably covered by the enlarged cheliceral base when they are "inter-locked", and therefore, it may appear narrower in the SEM image. The "true" shape of the cheliceral retainer is thus probably as exposed in slide-mounted specimens, or when the mouth-parts are "pulled apart" and the cheliceral retainer exposed in SEM images, such as that of *Cecidophyopsis grossulariae* (Fig. 10c, p. 160 in Amrine *et al.*, 1994) and *Cecidophyopsis* sp. specimen (Fig. 3.29j). In the case of the cheliceral retainer, it might not be the best option to study the shape on intact SEM images as

found in the current study, but rather in either slide-mounted specimens or in SEM images where the cheliceral retainer is exposed.

Amrine *et al.* (1994) included the shape of the cheliceral retainer of the species in his description of *Cecidophyopsis* spp. from *Ribes* spp.: *C. ribis* and *C. selachodon* (Fig. 3.24a) with cheliceral retainers similar, fairly large, triangular, directed mesally or upward; *C. grossulariae* with cheliceral retainers depicted in drawing (Fig. 3.24b), but not described in text; *C. aurea* (Fig. 3.24c) with cheliceral retainer nearer to *ep* than the other species, narrowly triangular; *C. alpina* (Fig. 3.24d), with the cheliceral retainer fairly large, triangular and directed mesally or upward. The shape and position as described in the text by Amrine *et al.* (1994) do not correspond with the selective depiction of it for the species, showing that it is not easy to score this character, but even if it corresponded, the differences are not particularly marked.



C. selachodon	***C. grossulariae***	***C. aurea***	***C. alpina***
"as in *C. ribis*: fairly large, triangular, directed mesally or upward"	not described in text	"nearer to basal setae than other species, narrowly triangular"	"fairly large, triangular and directed mesally or upward"

Fig. 3.24. Dorsal view of gnathosomas of: **a)** *Cecidophyopsis selachodon*; **b)** *C. grossulariae*; **c)** *C. aurea* and **d)** *C. alpina*. cr = cheliceral retainer. Below drawings with species names are the descriptions of the cheliceral retainers from Amrine *et al.* (1994). Cheliceral retainers of *C. ribis* are not depicted in Amrine *et al.* (1994). The cheliceral retainer on the right *in C. selachodon* and on the left in *C. alpina* flipped over, caused by the slide-mounting process. Drawings were scanned from Amrine *et al.* (1994) (with permission from the author), and were cropped and enlarged or made smaller so that scale lines (10 µm) are all the same length, and thus drawings are at about the same scale.

The shape of the cheliceral retainer in the SEM images of the current study is clearly different between species. It should be taken into account that the differences are between species of different genera, and not between morphologically very similar species such as the *Cecidophyopsis* spp. (Amrine *et al.*, 1994). For example, compare the cheliceral retainer in the adults of *Acalitus mallyi* (Fig. 3.33), *Aceria* sp. from *Ipomoea batatas* (Fig. 3.41) (more structured) and *Aceria lantanae* (Fig. 3.34) (shallower and more rounded than in *Acalitus mallyi* and *Aceria* sp. from *Ipomoea batatas*) and immatures of *Neserella tremae* (Fig. 3.32), and *Tergilatus sparsus* (Fig. 3.57). This character has potential as a systematic character, but it needs to be determined how the

specimens should be preserved and studied from which it must be scored. The enlarged cheliceral base around which the cheliceral retainer is "locked" also differs in size and shape, and may be of systematic use, but it was not scored in the present study. For example, it is quite rounded in *Aberoptus* sp. from *Schotia brachypetala* (Figs 3.28a, c), and more oval-shaped and less bulbous in *Aceria ocellatum* (Fig. 3.35a).

d. Seta *ep*

The second structure of possible taxonomic importance is a seta, one present on each palpcoxal base, named "basal seta" by Keifer (1959a; 1975a). Lindquist (1996a) hypothesized that this seta appears to represent the palpcoxal seta, *ep*, based on its dorsoproximal position. He regarded it to be surprisingly well-developed in the Eriophyoidea, compared with its usually reduced size in other trombidiform or prostigmatid mites, when present. He thought that this may be due to its exposed position, in contrast with being covered by the basis of chelicera in the other groups.

In other prostigmatid groups the seta homologous to *ep* in the Eriophyoidea (according to Lindquist, 1996a) is named supracoxal seta (*e*) and is normally present and situated above the palp base, one on each side of the subcapitulum, and occurs additionally to the infracapitular seta of the gnathosoma that is usually present (Evans, 1992). The "pair of palp supracoxal setae", *e*, occurs dorsally at the bases of the palpi in the Tetranychoidea, but is often difficult to discern in the Tetranychidae (Lindquist, 1985). Seta *e* in the Tetranychidae is spine-like in comparison to the "normal" *ep* in the Eriophyoidea (E.A. Ueckermann, *pers. comm.*, 2008).

Currently, the presence of *ep* is sometimes recorded and/or depicted in eriophyoid descriptions. The length of *ep* is not always given, but should be included based on advice of Amrine & Manson (1996). J.W. Amrine Jr. (*pers. comm.*, 2008) suggested that the position of *ep* may be of taxonomic value. Seta *ep* is always present in eriophyoid species so far known.

In the present explorative study, the characteristics already used in taxonomy, namely presence and length of *ep*, were not recorded. Three new characteristics of *ep* that may be of use to systematics were observed and scored as an attempt to identify new characters of potential systematic value. These are:

i. **<u>Character 4</u>** (Table 3.4). **Orientation of *ep* in relation to palp surface, either flat on the surface or projecting away (up) from it:**
e.g., they are lying flat in *Trisetacus* sp. from *Pinus pinaster* (Fig. 3.25e) and *Aceria ocellatum* (Figs 3.35a, c), In general, they seem to be lying flat in some *Aceria* and

other species of the Aceriini, and in *Trisetacus* (Trisetacini) and projecting up in all others (e.g., in *cf. Aculus* sp. from *Lantana trifolia* Figs 3.61b, c, h). When lying flat, they are either projecting parallel or convergent anteriorly.

ii. **Character 5** (Table 3.4)**. Anteriad direction of *ep*:**
e.g., they are projecting parallel anteriad in *Trisetacus* sp. from *Pinus pinaster* (Figs 3.25a, c), anteriad converging in *Aceria ocellatum* (Fig. 3.35a), and anteriad medially in *Aberoptus* sp. from *Schotia brachypetala* (Figs 3.28a, c).

iii. **Character 6** (Table 3.4). **Position of *ep* from distal margin of palpcoxal base segment** (gray line in Fig. 3.25c).

iv. **Character 7** (Table 3.4). **Relative position of *ep***:
Relative position of *ep* was calculated by dividing the palpcoxal base segment length (Character 3) by the position of *ep* on the palpcoxal base segment (character 6).

- Possible additional setae on the palpcoxal base

A structure, first thought to be a second seta, was found antaxially of *ep* on the palpcoxal base (Figs 3.42a, b, d, e, g) of a new *Aceria* sp. collected on *Oxalis corniculata*. The shape of this structure did not seem to be similar to that of spines or other known protuberances observed in the SEM images in the present study. Although the structure seems like a small version of *ep*, thus probably being a seta, it is difficult to verify this in slide-mounted specimens studied with phase contrast light microscopy. E.E. Lindquist (*pers. comm.*, 20 September 2007) commented that it is generally accepted that the seta occurring dorsally on the palpcoxa of many superfamilies of the acariform mites is the palp supracoxal seta (*ep* in the case of the Eriophyoidea), and that no other seta is known to occur in this area, and that it is thus not likely that it is, in fact, a seta. The structure is very small and stretches the limits of resolution in phase contrast light microscopy. Using 1600 x magnification on slide-mounted specimens, it appears rather more spine-like than seta-like, but it is not conclusive. Further investigation, especially whether the structure is birefringent with polarized light, is needed to clarify this matter. A probably homologous structure in the same position has been described in *Acaphyllisa limitata* (Flechtmann & Etienne, 2001) (Fig. 3.42f reproduced from Flechtmann & Etienne, 2001). Flechtmann & Etienne (2001) regarded it to be a seta, but did not comment on the occurrence of this seta in the Eriophyoidea, or speculated on the possible homology of this seta with setae in other acariform mites. It is not common in the Eriophyoidea that *ep* is inserted on a tubercle, and *ep* and the new seta are depicted by them to be inserted on tubercles. Material of the latter species should be re-examined to verify the matter. In the new *Aceria* sp. from *Oxalis corniculata* in the present study, a third extremely

small protuberance is present on the adaxial side of the second protuberance, if *ep* is regarded as the first seta (Figs 3.42a, b, e). It was clearly present in all SEM images taken of this aspect of the palpi in this species.

- Ornamentation of the palpcoxal base segment

Ornamentation is present on the dorsal surface of the palpcoxal segment of some species. In so far as could be established, similar ornamentation of palp segments has not been used in taxonomy of the Eriophyoidea, and may be of use, particularly for phylogenetic studies. It is doubtful whether these ornamentations will be clearly visible in slide-mounted specimens.

i. **Character 8** (Table 3.4). **Presence of ridges or depressions on palpcoxal base segment:**
   e.g., a longitudinal ridge is present along the extended inside margin of *ep*, terminating in a distal ovalish depression margined with a slight ridge in *Setoptus radiatae* from *Pinus radiata*.

ii. **Character 9** (Table 3.4). **Ornamentation, other than ridges, on the palpcoxal base segment:**
   e.g., tubercles or granula are present from the dorsal to the lateral region, particularly in the area distally of the insertion of *ep* in *Aceria* sp. nov. from *Xymalos monospora* (Fig. 22b).

- First or proximal articulating palp segment (dorsally)

The next palp segment, apical to the palpcoxal base, considered by Lindquist (1996a) to be the first articulating palp segment, is formed by the fusion of the trochanter, femur and genu. Presently only the presence, shape and length of *d* on this segment are sometimes used in taxonomy. The scoring of Characters 17 – 20 (Table 3.4) is from this segment.

i. **Character 17** (Table 3.4). **Position of *d*:**
   Although the position differed slightly between species [e.g., it seems to be on the genu, close to the proximal genu margin in *Setoptus radiatae* (Fig. 3.26d) and possibly closer to the distal genu margin in *Aceria* sp. from *Acacia erioloba* (Fig. 3.37d)], it turned out to be less variable than was perceived before scoring. It is still included, however, because the character may turn out to be useful for systematics in future.

ii. **Character 18** (Table 3.4). **Ornamentation or structures present dorsally:**

The trochanter-femur-genu was usually unornamented, except some structures which are autapomorphic for a single species. This character may become more informative when more species are studied in future.

iii. **Character 19** (Table 3.4). **General shape:**

This character needs further study for evaluating its possible systematic value.

iv. **Character 20** (Table 3.4). **Elevation of chelicerae above the palpi:**

The chelicerae are sometimes elevated above the palpi at the level of the proximal margin of the trochanter-femur-genu segment, and the presence of and extent of elevation were scored (Character 19). They are particularly elevated above the palpi in the diptilomiopid species, such as *Diptilomiopus faurius* sp. nov. (Fig. 3.79b). It is slightly elevated in many other species, such as the possibly new genus from *Apodytes dimidiata* (Fig. 3.67b), but not elevated in, for example, *Neserella* sp. from *Trema orientalis* (Figs 3.32a, c).

- The ventral aspect of the gnathosoma

The ventral surface of the gnathosoma is reduced because of the hypognathous position of the gnathosoma in most eriophyoid species. Several characters were scored from this aspect (Characters 10–16, 21, Table 3.4).

i. **Characters 10–16** (Table 3.4). **Morphology of the gnathosomal ventral aspect:**

The structures and externally identifiable separate areas in these parts of the gnathosoma have hardly been studied, and separate areas were identified for the first time (Figs 3.20, 3.21) in the present study. The identification of homologies between the areas of different species was attempted (Fig. 3.21). The hypothetically homologous areas were indicated in similar colours in Figs 3.20 & 3.21. Several characters were tentatively scored, and mostly involve the shape and position of structures and margins, and ornamentation present. These can be viewed in the SEM figures of the particular species for each character state (Table 3.4). No attempt was made in present study to evaluate these characters, but there are clear differences that may be of systematic value (Fig. 3.21).

ii. **Character 21** (Table 3.4). **Seta *v*:**

Seta *v* is present ventrally, on the palptarsus *sensu* Lindquist (1996a). It is uncertain whether it is a seta or solenidion in most species, because it is so small that the presence or absence of birefringence in polarized light cannot be determined. In some diptilomiopid species, however, this seta is quite long (e.g., in the diptilomiopid species included in the present study, Figs 3.78 – 3.82), and was

determined to be a seta in some diptilomiopid species (Lindquist, 1996a). Seta *v* is inserted right on the distal edge of the tarsus, and frequently lays closely against an indentation of the palp apical lip (e.g., Figs 3.27d, 3.29h, 3.30b). In some species it is inserted on a slight bulge or lobe of the distal part of the tarsus, allowing the seta to be positioned more distally (e.g., in *Cecidophyopsis* sp. from *Yucca guatemalensis*, Fig. 3.29h; in *Afromerus lindquisti*, Fig. 3.30b; and in *cf. Aculus* sp. from *Lantana trifolia*, Fig. 3.61 e), probably to facilitate it to touch the surface when the palpi are pressed down for feeding. This seta is sometimes hardly visible in slide-mounted specimens of some species, and is usually not described. Studying the SEM images, it was found that it differs in shape and length in different species, and since these characteristics have potential for systematic use, they were scored (Character 21, Table 3.4).

- Artefacts in SEM images

Smooth, rounded drop-like bumps are frequently present on the surface of the gnathosoma. These may be some liquid that froze, or some growth occurring randomly on some species [e.g., the relatively short, white arrows in Figs 3.25 (*Trisetacus* sp. from *Pinus pinaster*), 3.31 (*Ectomerus systenus*), 3.33a (*Acalitus mallyi*), 3.34a (*Aceria lantanae*), 3.41a,b (*Aceria* sp. from *Ipomoea batatas*), 3.43a (*Aceria* sp. from *Acacia rehmanniana*) and 3.57b (*Tergilatus sparsus*)]. It is, however, easily distinguishable from approximately rounded or oval tubercles [e.g., relatively short, white arrows in Figs 3.27d (*Mackiella* sp. from *Phoenix reclinata*), 3.29a (*Cecidophyopsis* sp. from *Yucca guatemalensis*), and 3.84f (species from *Anthocleista grandiflora*)].

Other artefacts on specimens are indicated in some figures, but are generally present on many specimens. These include ice crystals and/or dirt, fine cracks, some charging, and the breaking-off of some setae. These are usually identifiable, and can be separated from morphological features, and can be largely rectified by using better equipment for cryo-SEM (see general discussion further on).

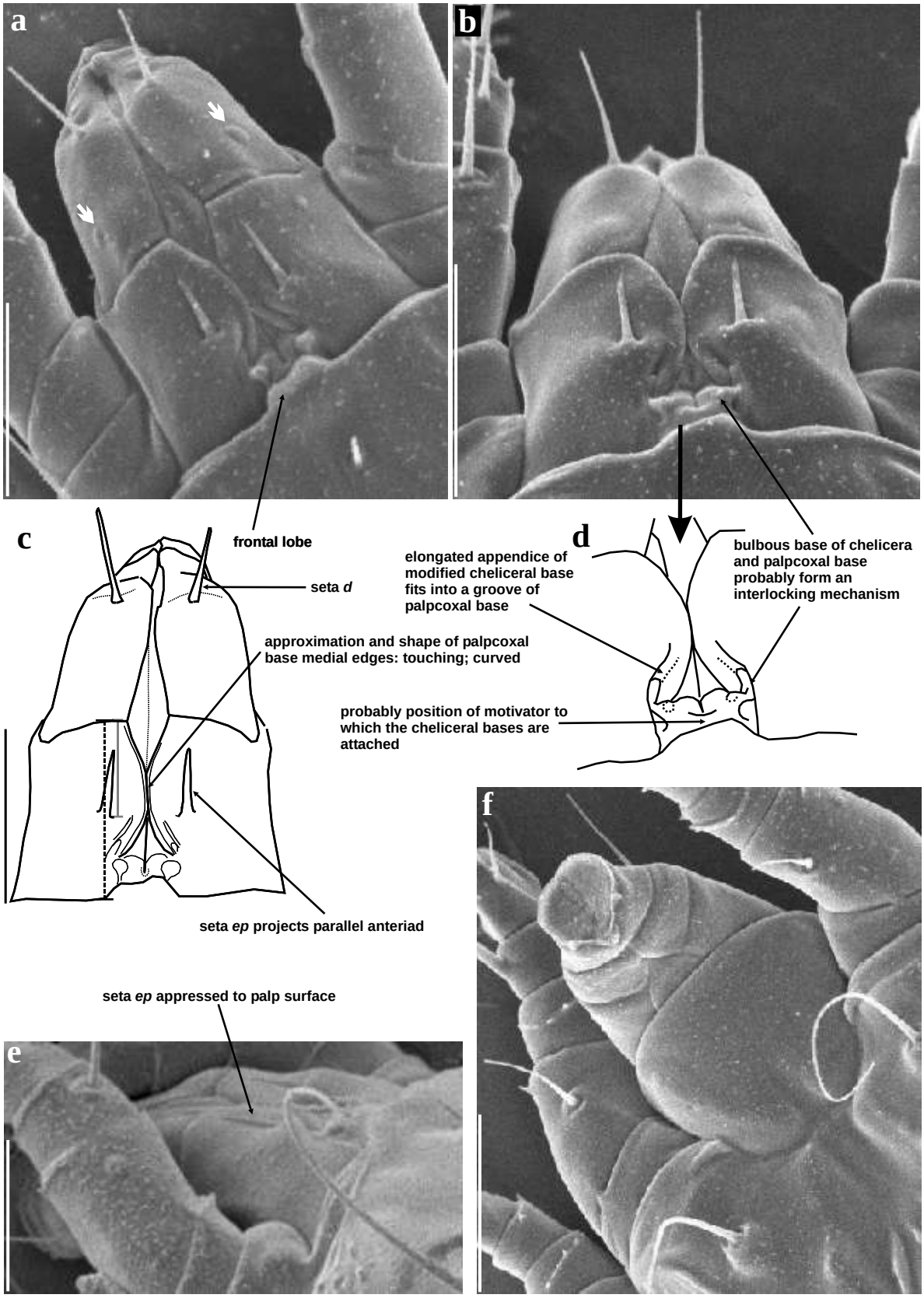


Fig. 3.25. Gnathosoma of *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from *Pinus pinaster*: **a, b)** dorsal views (probably adults, genders unknown), white arrows indicate droplet-like structures that are probably not part of the mite, but artefacts; **c)** line drawing of Fig. 3.25a, dashed black line indicates length of palpcoxal base, grey line indicates distance of seta *ep* from distal margin of palpcoxal base, measured as the shortest distance from the base of seta to distal margin; **d)** line drawing of enlargement of "cheliceral lock mechanism" in Fig. 3.25b; **e)** dorsolateral view (probably adult, gender unknown); **f)** ventral view (male). Scale lines = 10µm.

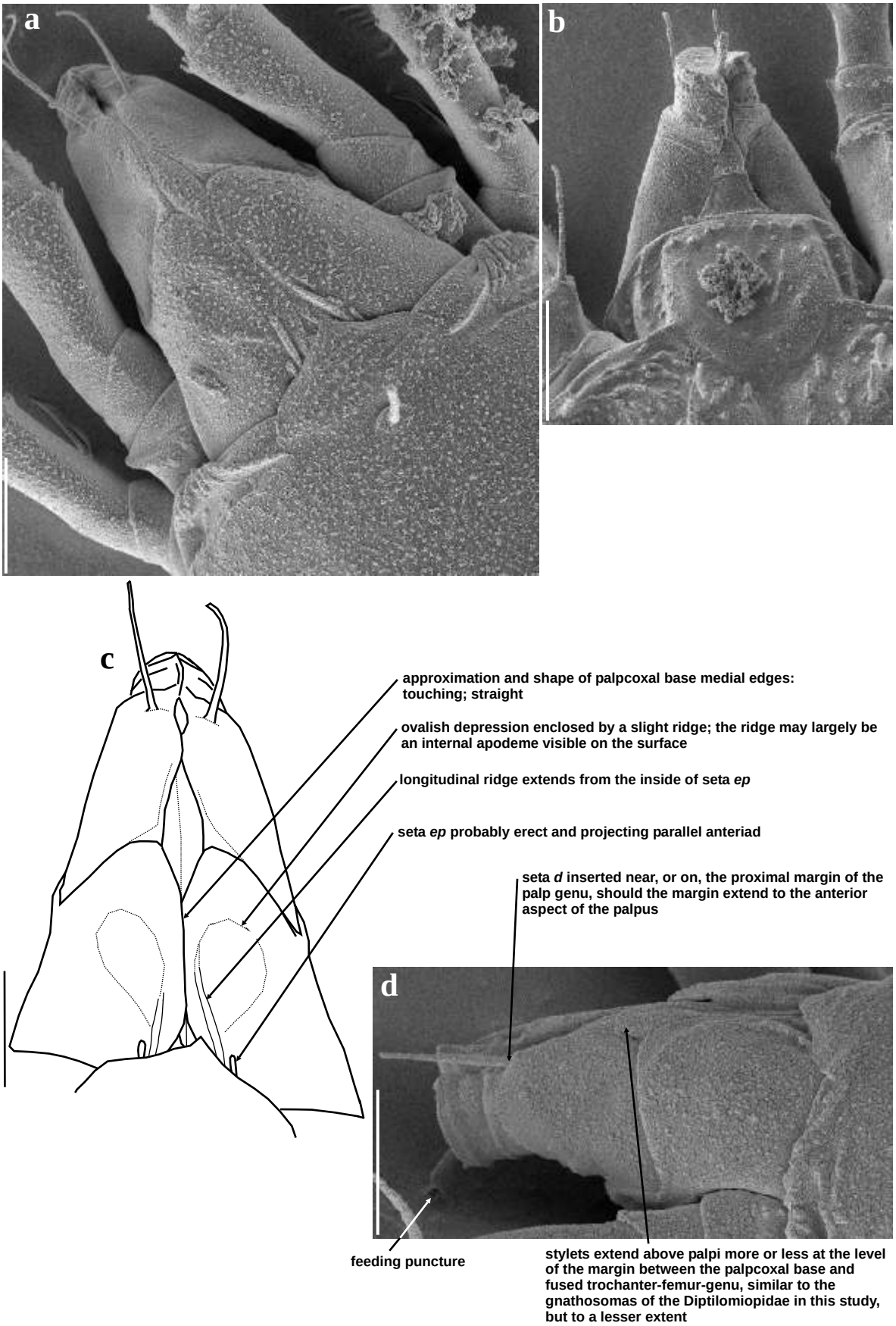


Fig. 3.26. Gnathosoma of *Setoptus radiatae* Meyer, 1991 (Phytoptidae: Nalepellinae: Nalepellini) from *Pinus radiata*: **a**) dorsal view (probably adult, gender unknown); **b**) ventral view (female); **c**) line drawing of Fig. 3.26a; **d**) lateral view (probably adult, gender unknown). Scale lines = 10µm.

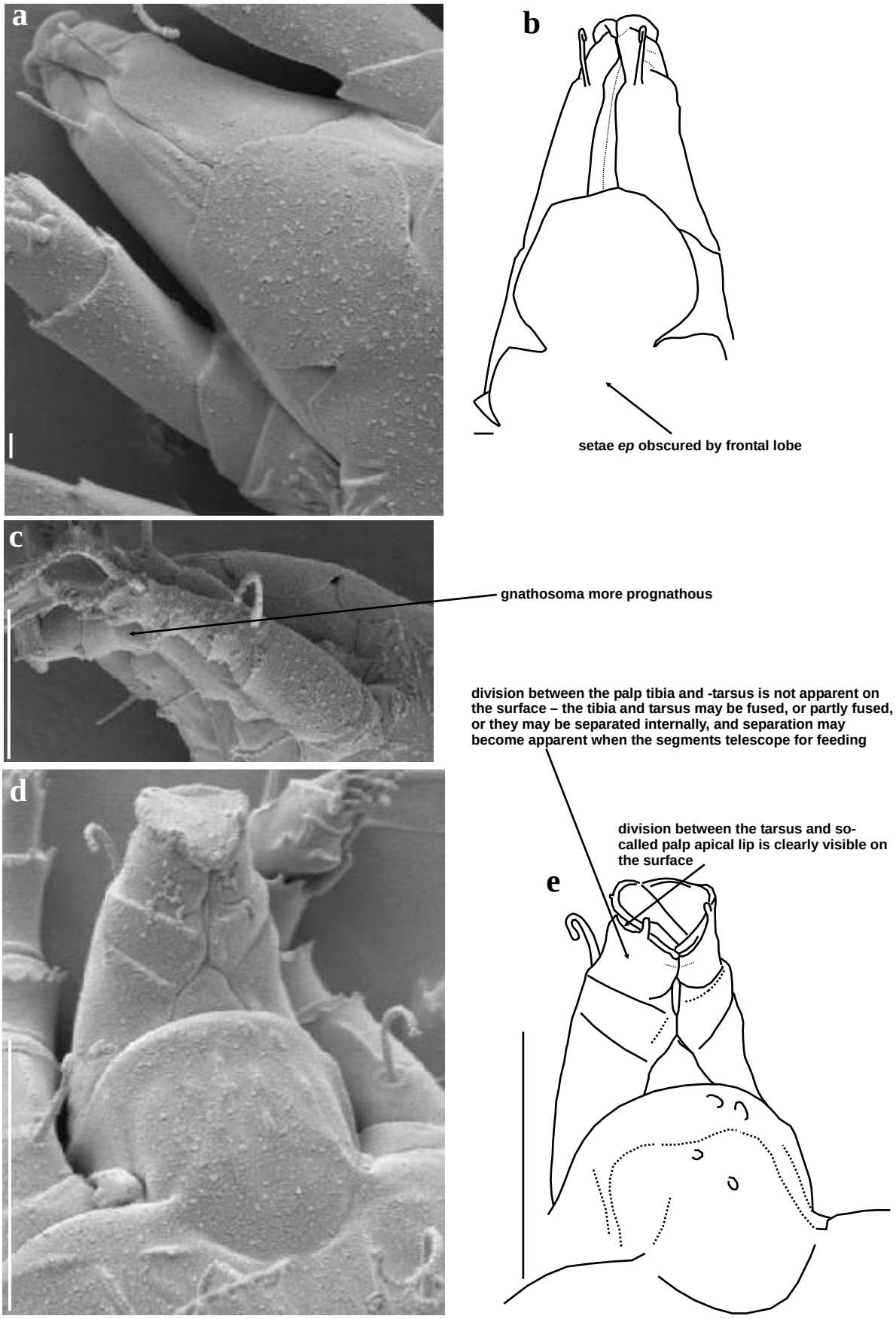


Fig. 3.27. Gnathosoma of *Mackiella* sp. (Phytoptidae: Sierraphytoptinae: Mackiellini) from *Phoenix reclinata*: **a**) dorsal view (probably adult, gender unknown); **b**) line drawing of Fig. 3.27a; **c**) lateral view (male); **d**) ventral view (male); **e**) line drawing of Fig. 3.27d; **a, b)** scale lines = 1 µm; **c, d, e)** scale lines = 10 µm.

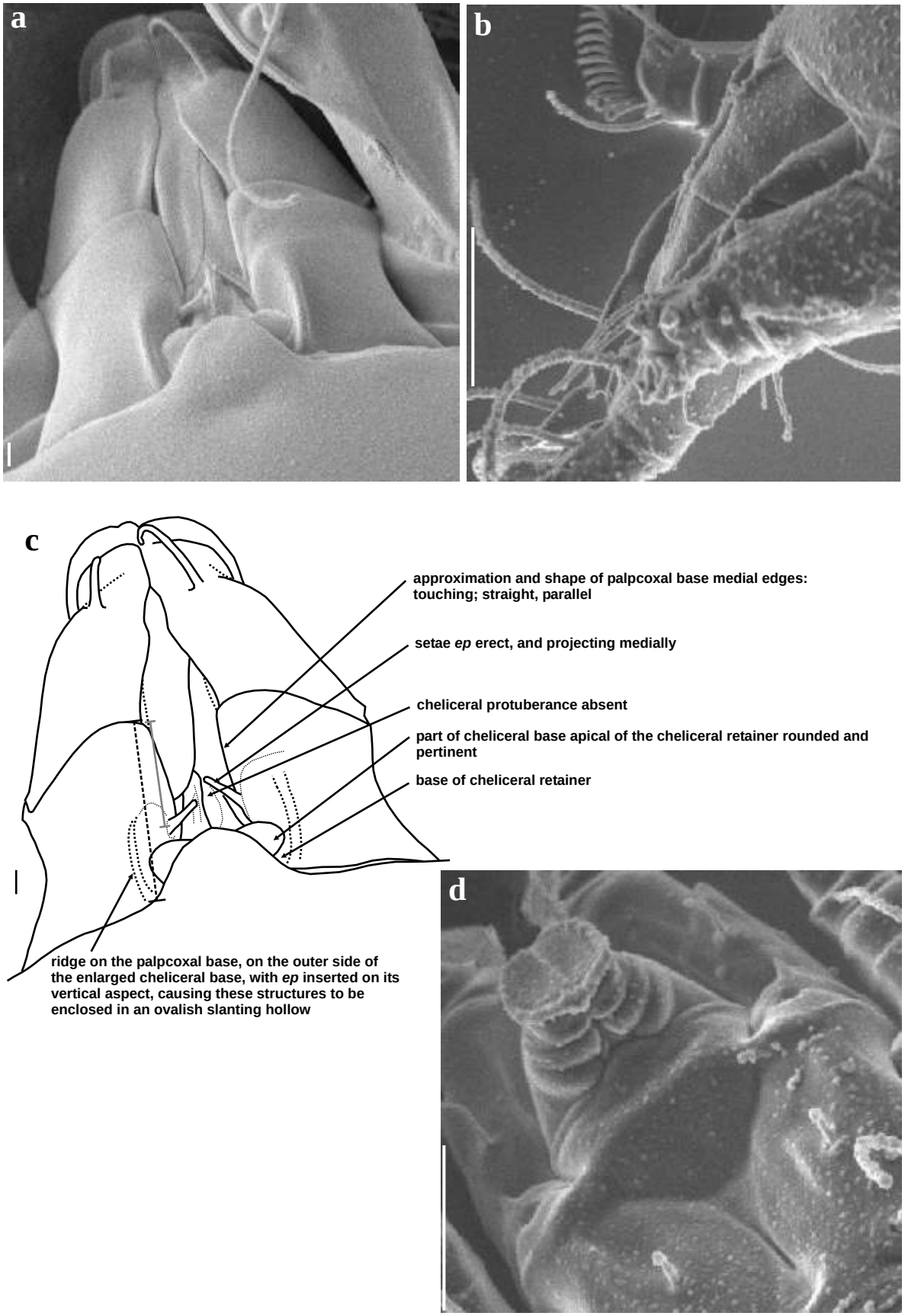


Fig. 3.28. Gnathosoma of *Aberoptus* sp. *cf. Aberoptus* sp. nov. (Eriophyidae: Aberoptinae) from *Schotia brachypetala*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female); **c)** line drawing of Fig. 3.28a, dashed black line indicates length of palpcoxal base, grey line indicates distance of seta *ep* from distal margin of palpcoxal base, measured as the shortest distance from the base of seta to distal margin; **d)** ventral view (female); **a, c)** scale lines = 1 µm; **b, d)** scale lines = 10 µm.

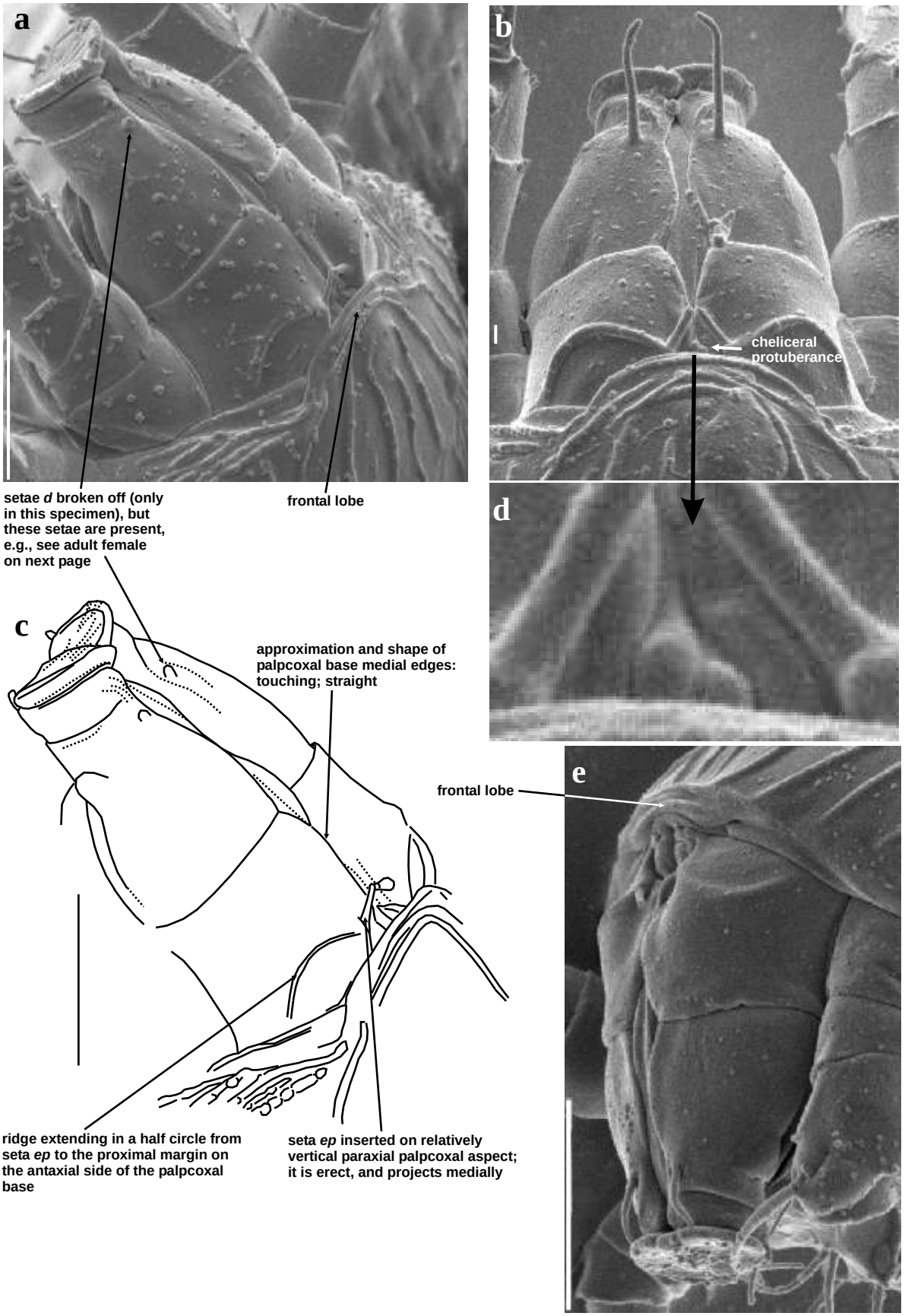


Fig. 3.29. (continued on next page). Gnathosoma of *Cecidophyopsis* sp. *cf. C. hendersoni* (Keifer, 1954) (Eriophyidae: Cecidophyinae: Cecidophyini) from *Yucca guatemalensis*: **a)** dorso-lateral view (female); **b)** dorsal view (possibly immature based on gnathosoma morphology); **c)** line drawing of Fig. 3.29a, showing broken off setae which is possibly an artefact caused by cryo-praparation; **d)** enlargement of protuberances basally on the chelicerae; **e)** dorso-lateral view of gnathosoma of just-born larva still emerging from egg; **a, c, e)** scale lines = 10 µm; **d)** scale line = 1 µm.

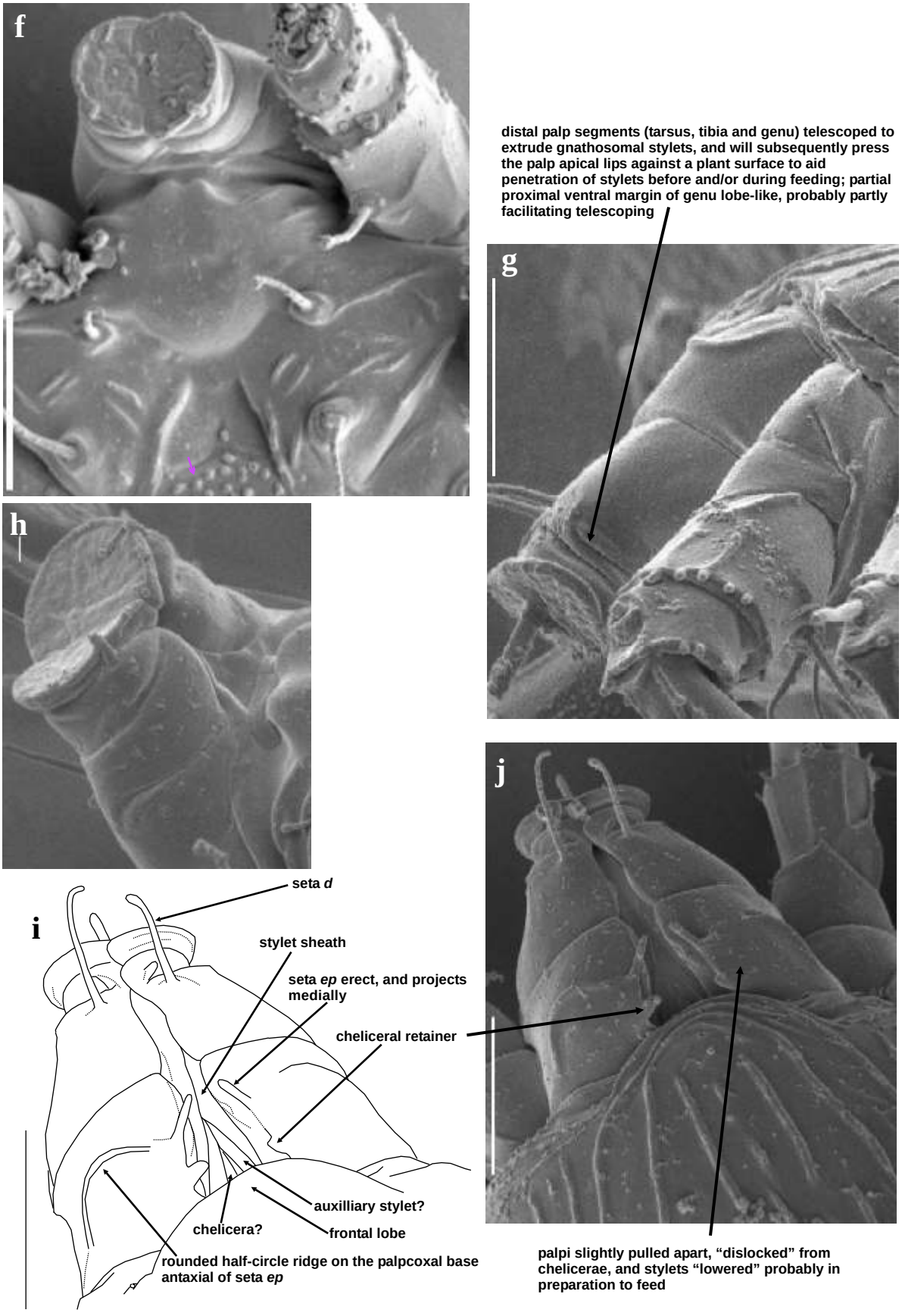


Fig. 3.29. (continued from previous page). Gnathosoma of *Cecidophyopsis* sp. *cf. C. hendersoni*: **f)** ventral view (female); **g)** lateral view, gnathosoma with apical palp segments telescoping for feeding (female); **h)** lateral view (female); i) line drawing of Fig. 3.29j; **j)** ventro-lateral view of gnathosoma (female); **f, g, h, j)** scale lines = 10 µm; **i)** scale line = 1 µm.

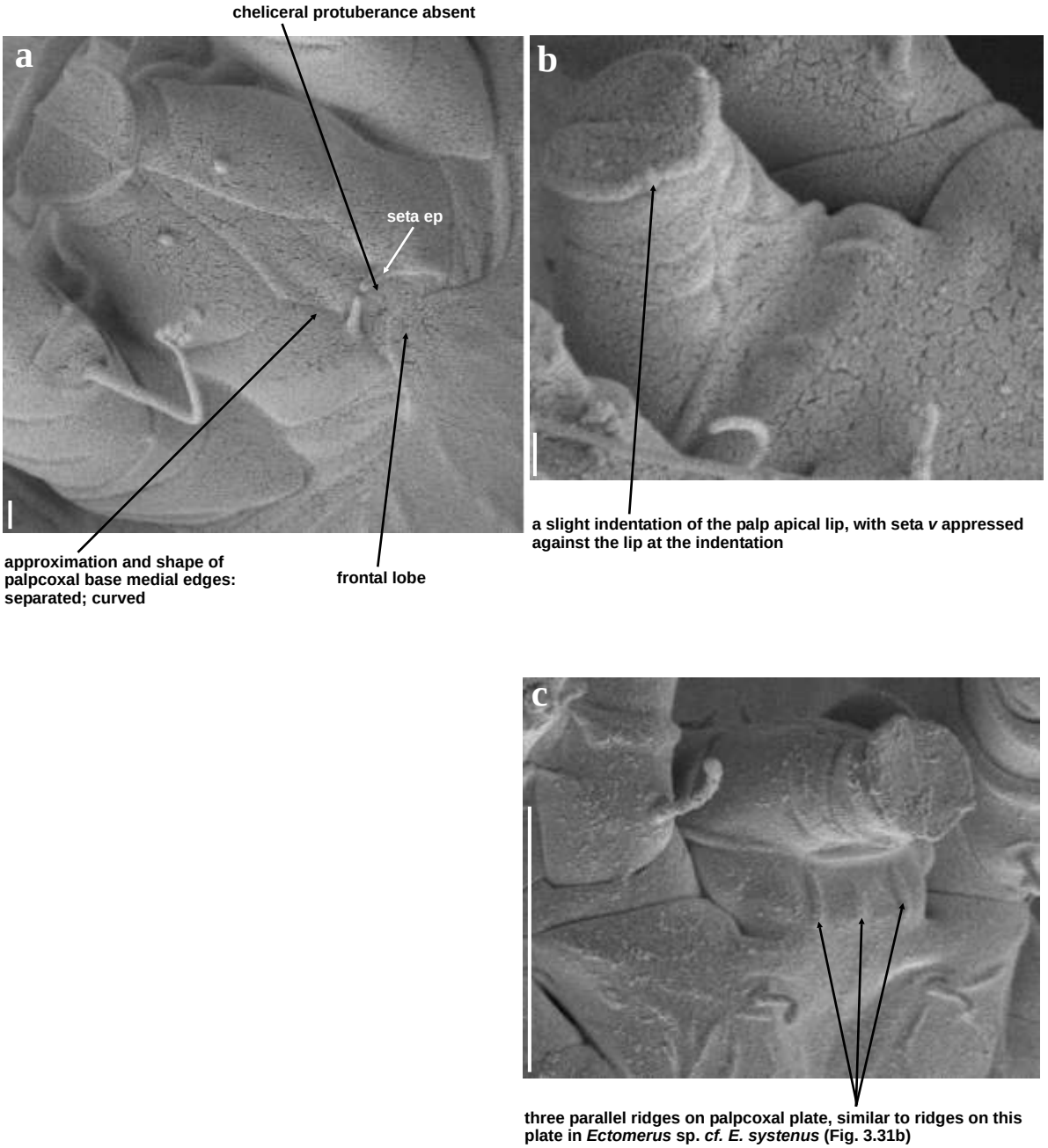


Fig. 3.30. Gnathosoma of *Afromerus lindquisti* Meyer, 1990 (Eriophyidae: Cecidophyinae: Colomerini) from *Psydrax livida*: **a)** dorsal view (female); **b, c)** ventro-lateral views (males); **a, b)** scale lines = 1 µm; **c)** scale line = 10 µm.

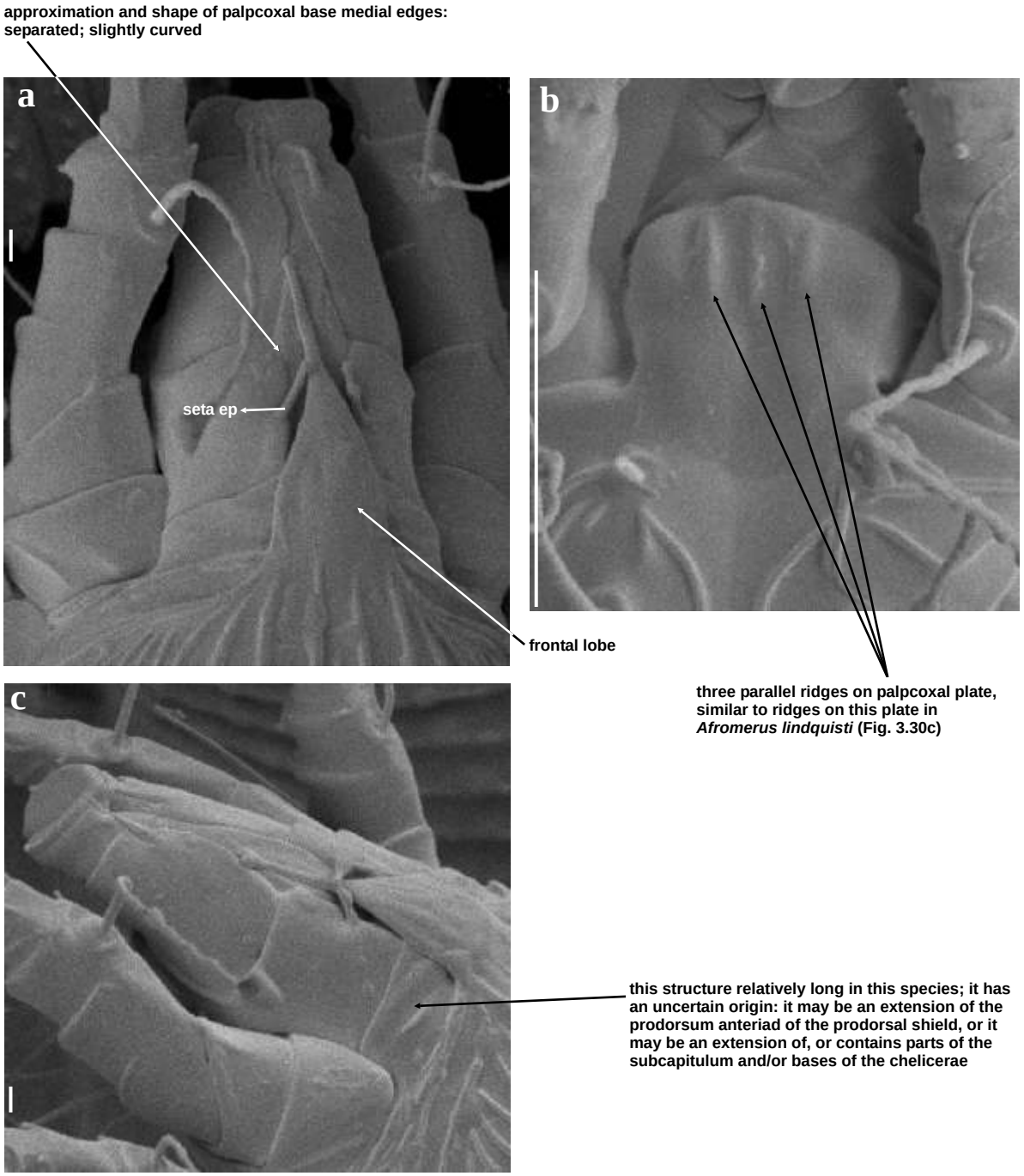


Fig. 3.31. Gnathosoma of *Ectomerus* sp. *cf. E. systenus* Meyer, 1990 (Eriophyidae: Cecidophyinae: Colomerini) from *Terminalia sericea*: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (female); **c)** dorso-lateral view (probably adult, gender unknown); **a, c)** scale lines = 1 µm; **b)** scale line = 10 µm.

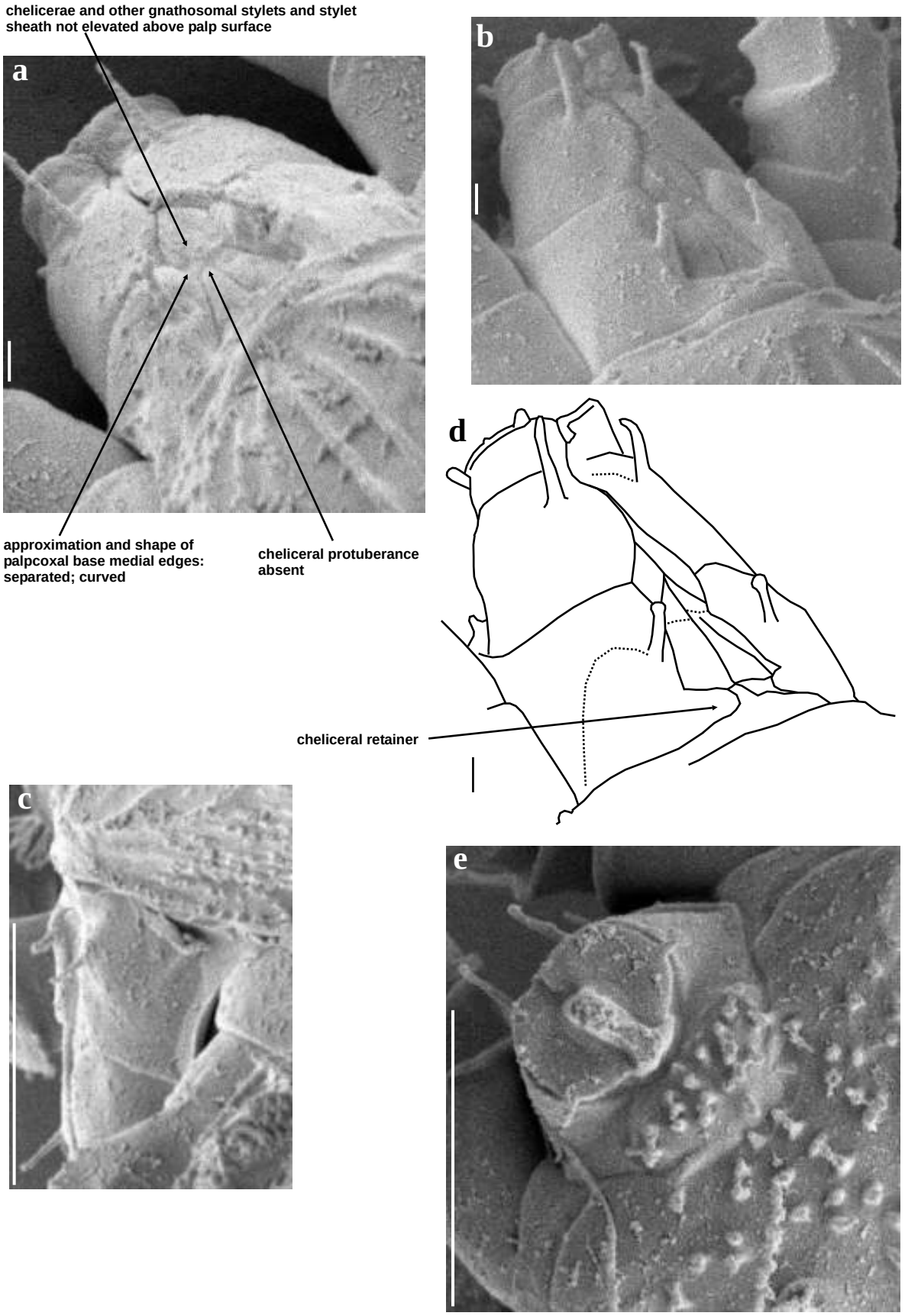


Fig. 3.32. Gnathosoma of *Neserella* sp. *cf. N. tremae* Meyer & Ueckermann, 1989 (Eriophyidae: Cecidophyinae: Colomerini) from *Trema orientalis*: **a)** dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (immature); **c)** lateral view (probably adult, gender unknown); **d)** line drawing of Fig. 3.32b; **e)** ventral view (female); **a, b, d)** scale lines = 1 µm; **c, e)** scale lines = 10 µm.

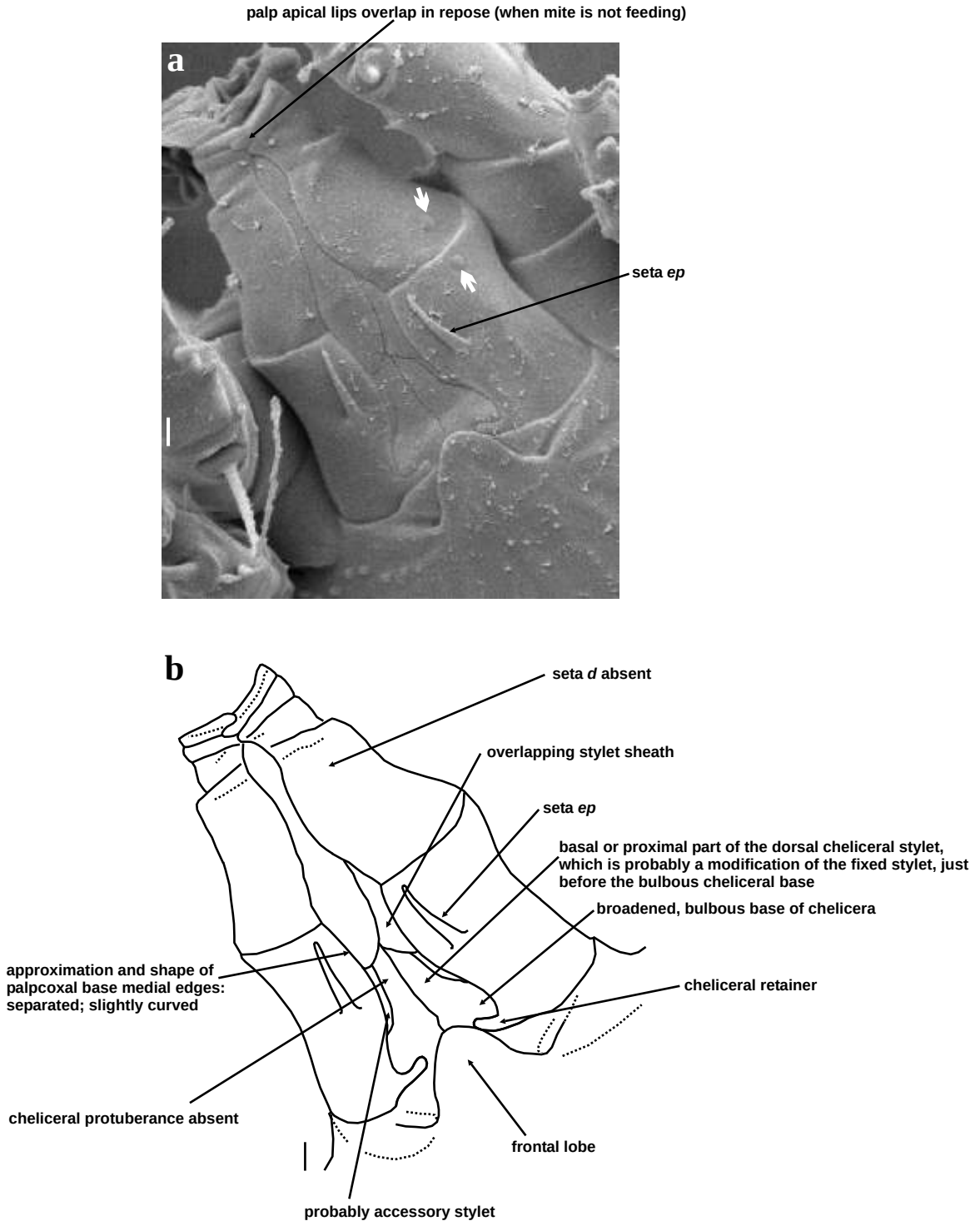


Fig. 3.33. (continued on next page). Gnathosoma of *Acalitus mallyi* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Vangueria infausta* subsp. *infausta* leaf galls: **a)** dorsal view (probably adult, gender unknown), white arrows indicate droplet-like structures that are probably not part of the mite, but artefacts; **b)** line drawing of Fig. 3.33a; scale lines = 1 µm.

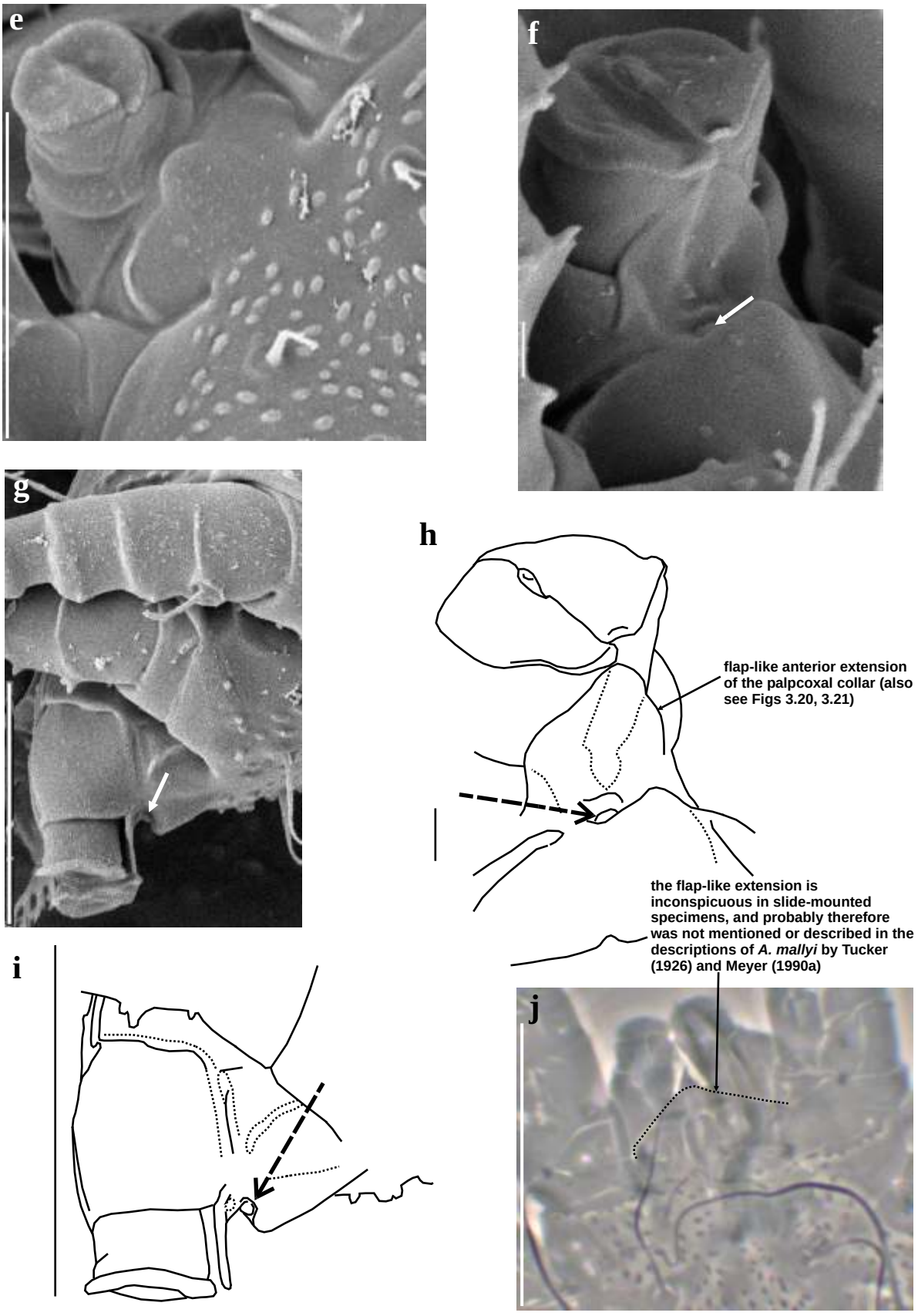


Fig. 3.33. (continued from previous page). Gnathosoma of *Acalitus mallyi*: **e)** ventral view (female); **f)** ventro-lateral view (female); **g)** lateral view (female); **h)** line drawing of Fig. 3.33f; **i)** line drawing of Fig. 3.33g; **j)** digital image captured of slide-mounted female specimen, outline of flap extension of coxal plate very unclear, traced with a red stipple line; a knob-like structure in a hollow formed by the anterior edge of the ventral coxal base indicated by the white arrows in f, g, and dashed black arrows in h, i; **e, g, i)** scale lines = 10 µm; **f, h)** scale lines = 1 µm; **j)** scale line = 20 µm.

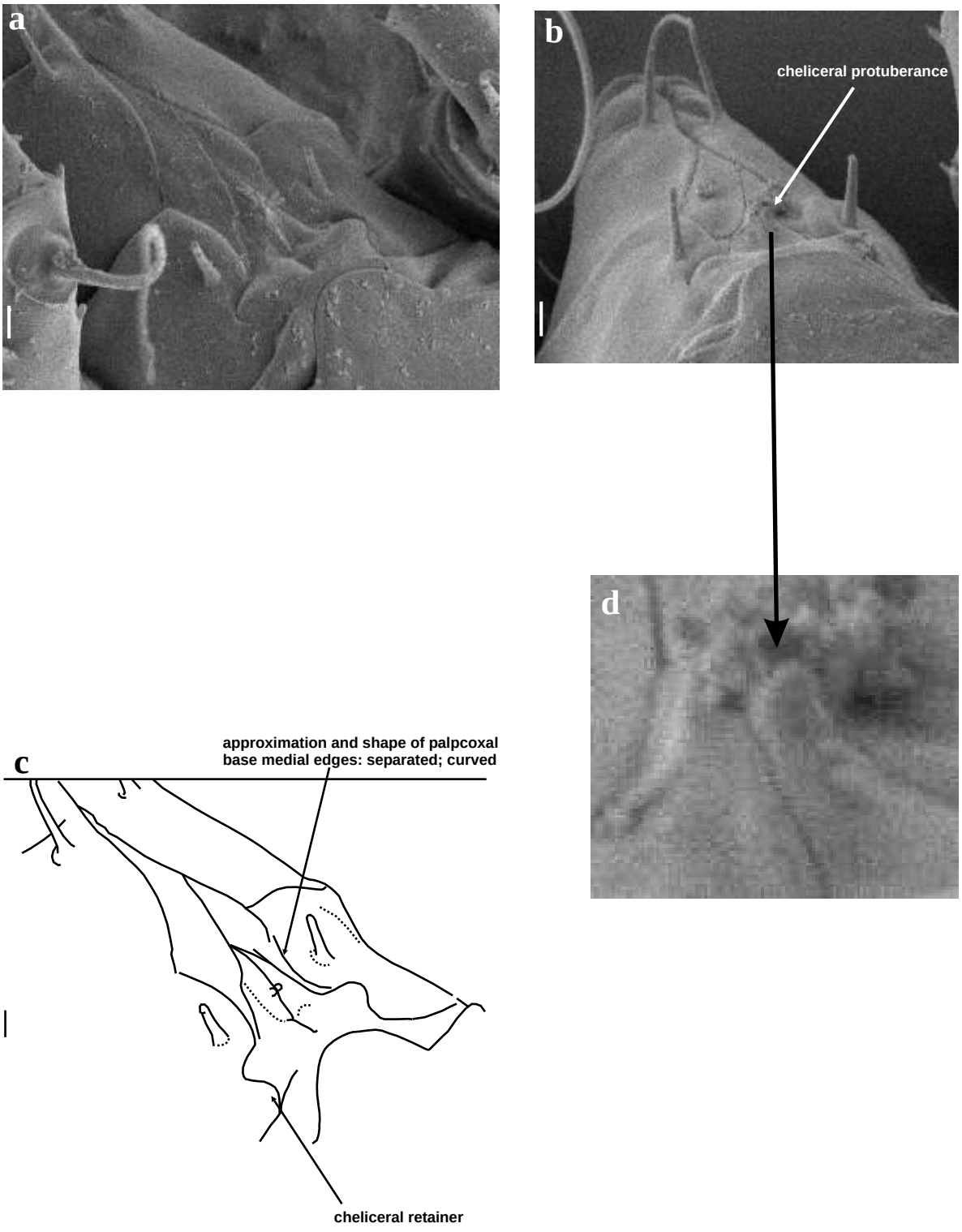
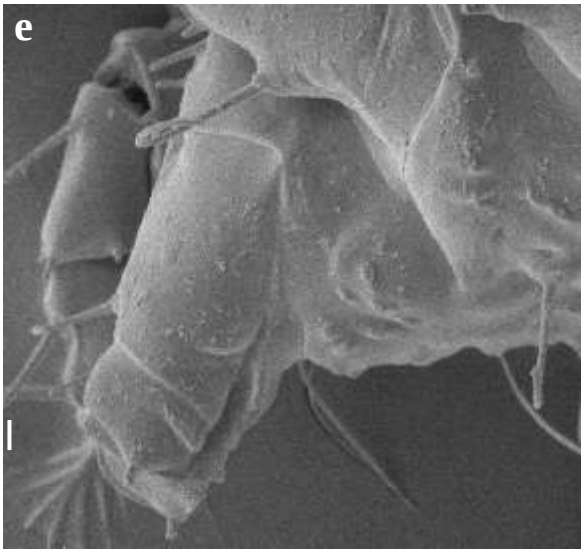
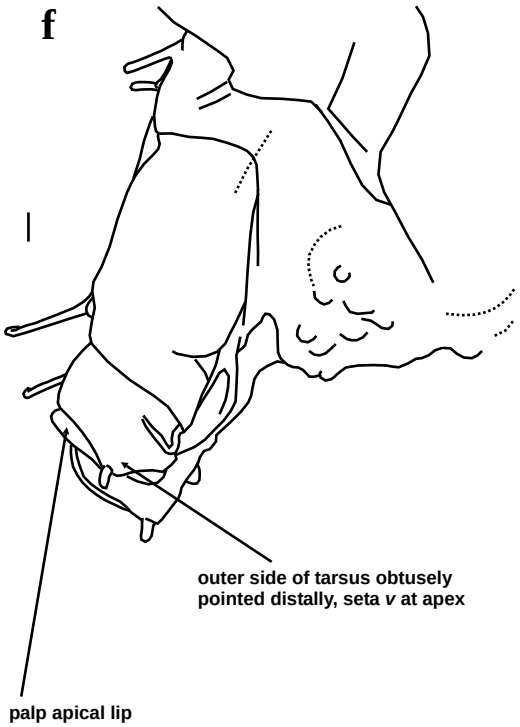
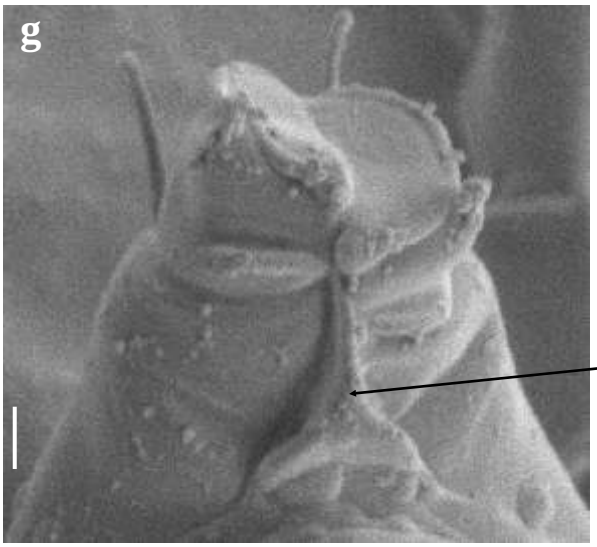


Fig. 3.34 (continued on next page). Gnathosoma of *Aceria lantanae* (Cook, 1909) (Eriophyidae: Eriophyinae: Aceriini) from *Lantana* x *camara* (hybrid complex) flower galls: **a, b)** dorsal views (probably adults, gender unknown); **c)** line drawing of Fig. 3.34a; **d)** enlargement of cheliceral protuberances in Fig. 3.34b. Scale lines = 1 µm.







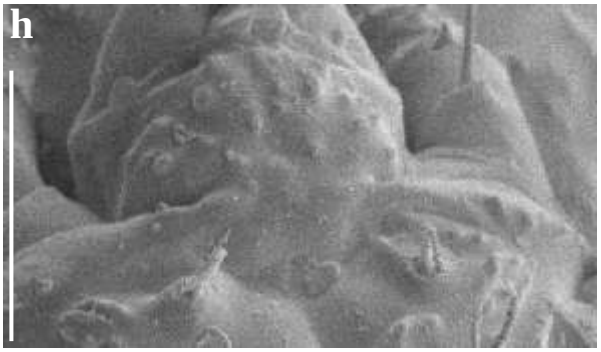


Fig. 3.34. (continued from previous page). Gnathosoma of *Aceria lantanae*: **e)** lateral view (female); **f)** line drawing of Fig. 3.34e; **g, h)** ventral views of the same specimen (female); **e, f, g)** scale lines = 1 µm; **h)** scale line = 10 µm.

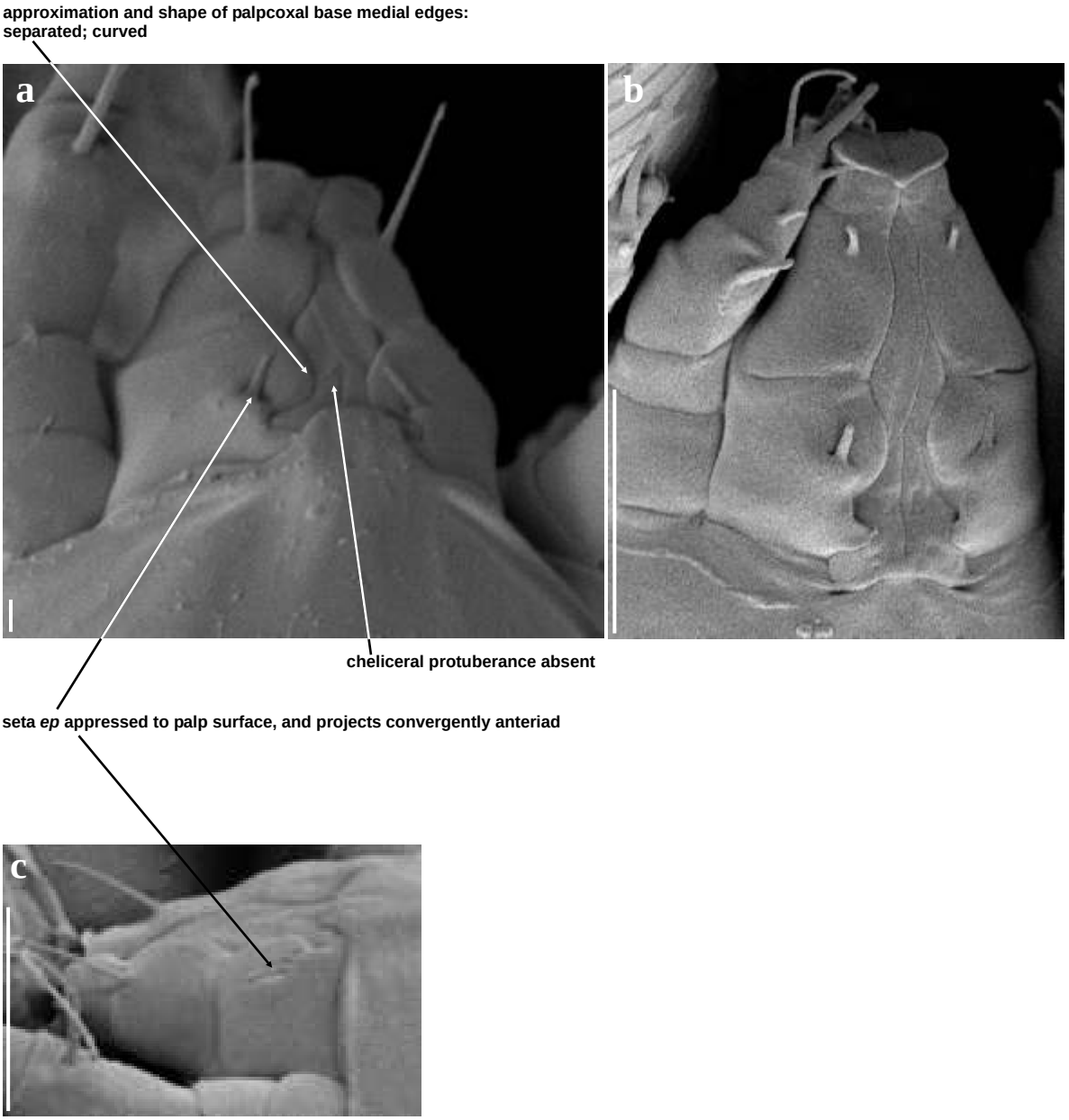


Fig. 3.35. Gnathosoma of *Aceria ocellatum* Meyer & Ueckermann, 1990 (Eriophyidae: Eriophyinae: Aceriini) from *Searsia lancea* (previously *Rhus lancea*) leaf galls: **a)** dorsal view (probably adult, gender unknown); **b)** dorsal view (immature); **c)** dorso-lateral view (probably adult, gender unknown); **a)** scale line = 1 µm; **b, c)** scale lines = 10 µm.

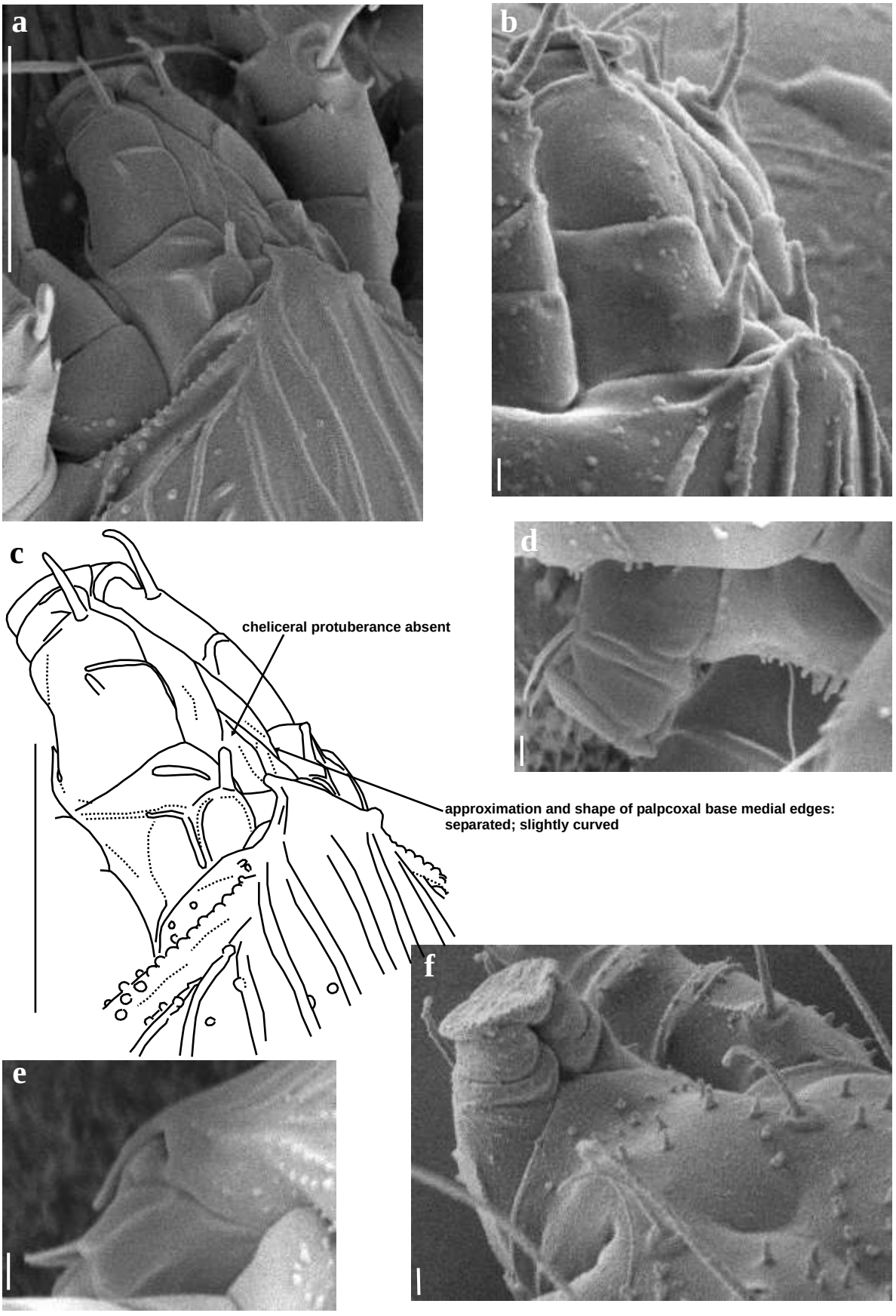


Fig. 3.36. Gnathosoma of *Aceria* sp. *cf. A. dichrostachyia* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Dichrostachys cinerea* subsp. and var. unknown: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorso-lateral view (larva); **c)** line drawing of Fig. 3.36a; **d, e)** lateral view of the same specimen (female); **f)** ventral view (female); **a, c)** scale lines = 10 µm; **b, d, e, f)** scale lines = 1 µm.

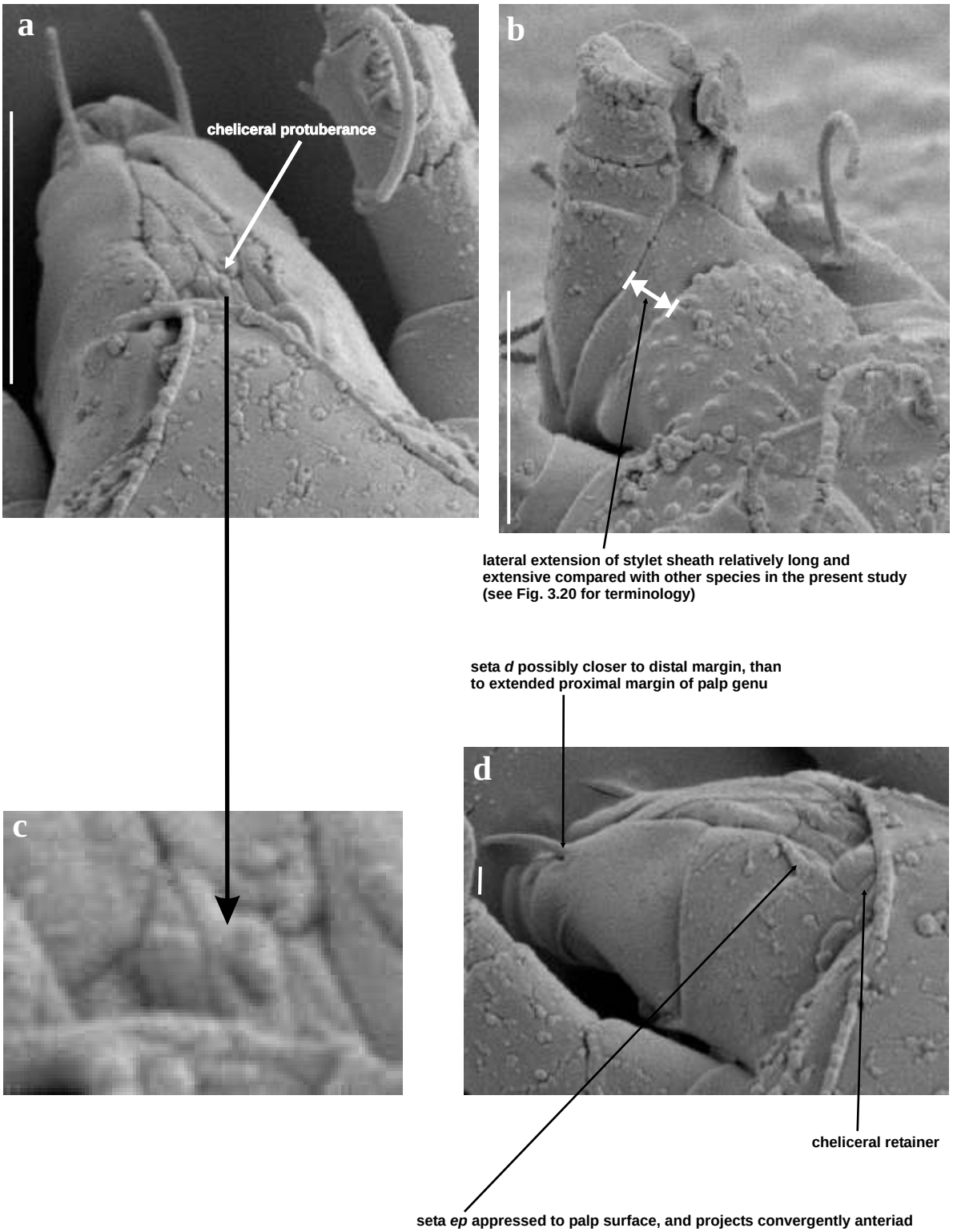


Fig. 3.37. Gnathosoma of *Aceria* sp. *cf. A. giraffae* Meyer, 1990 (Eriophyidae: Eriophyinae: Aceriini) from *Acacia erioloba*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** enlargement of cheliceral protuberances in Fig. 3.37a; **d)** dorso-lateral view (probably adult, gender unknown); **a, b)** scale lines = 10 µm; **d)** scale line = 1 µm.

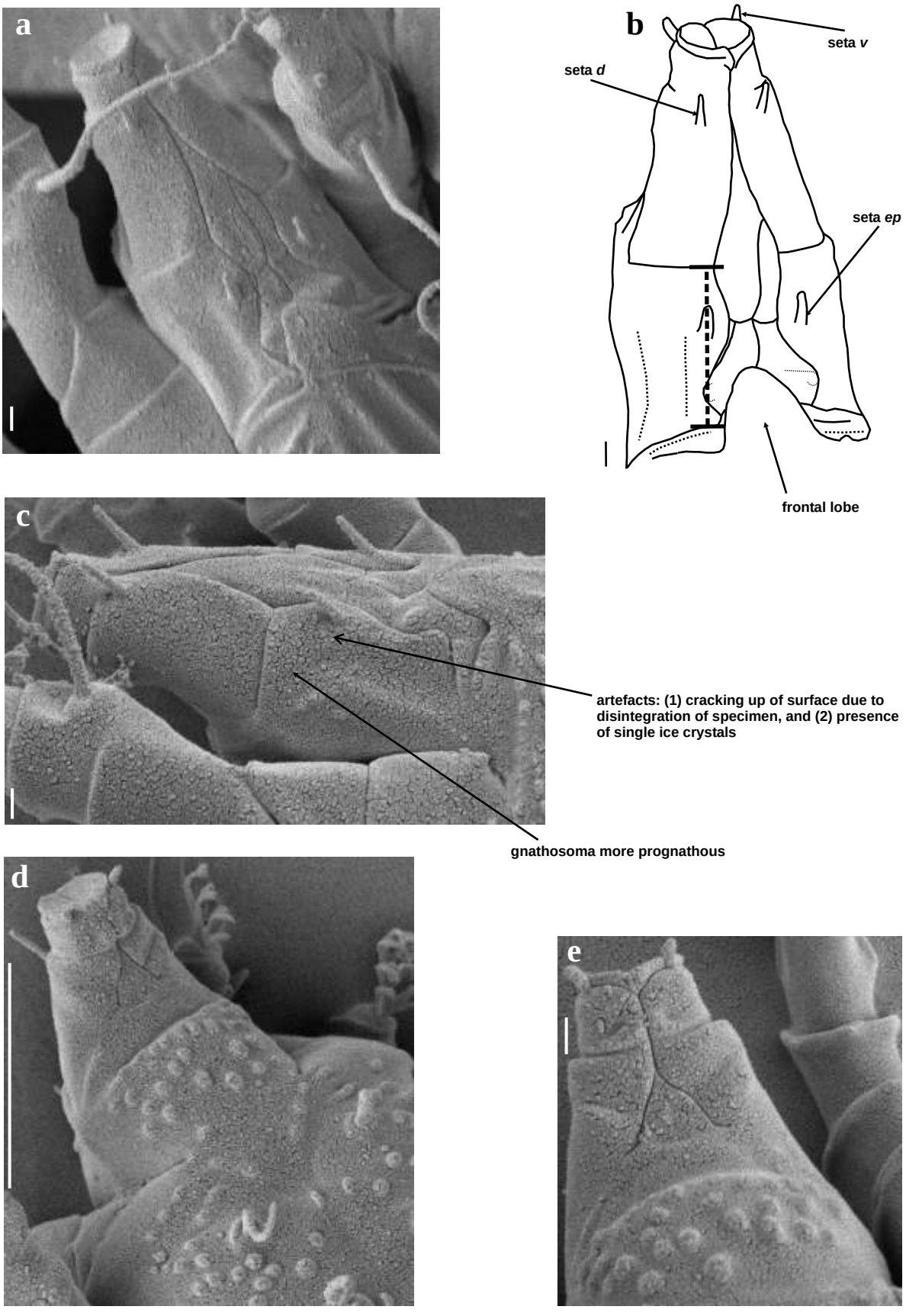


Fig. 3.38. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Chrysanthemoides incana*: **a)** dorsal view (probably adult, gender unknown); **b)** line drawing of Fig. 3.38a, dashed black line indicates length of palpcoxal base; **c)** lateral view (female); **d)** ventral view (female); **e)** ventral view (male); **a, b, c, e)** scale lines = 1 µm; **d)** scale line = 10 µm.

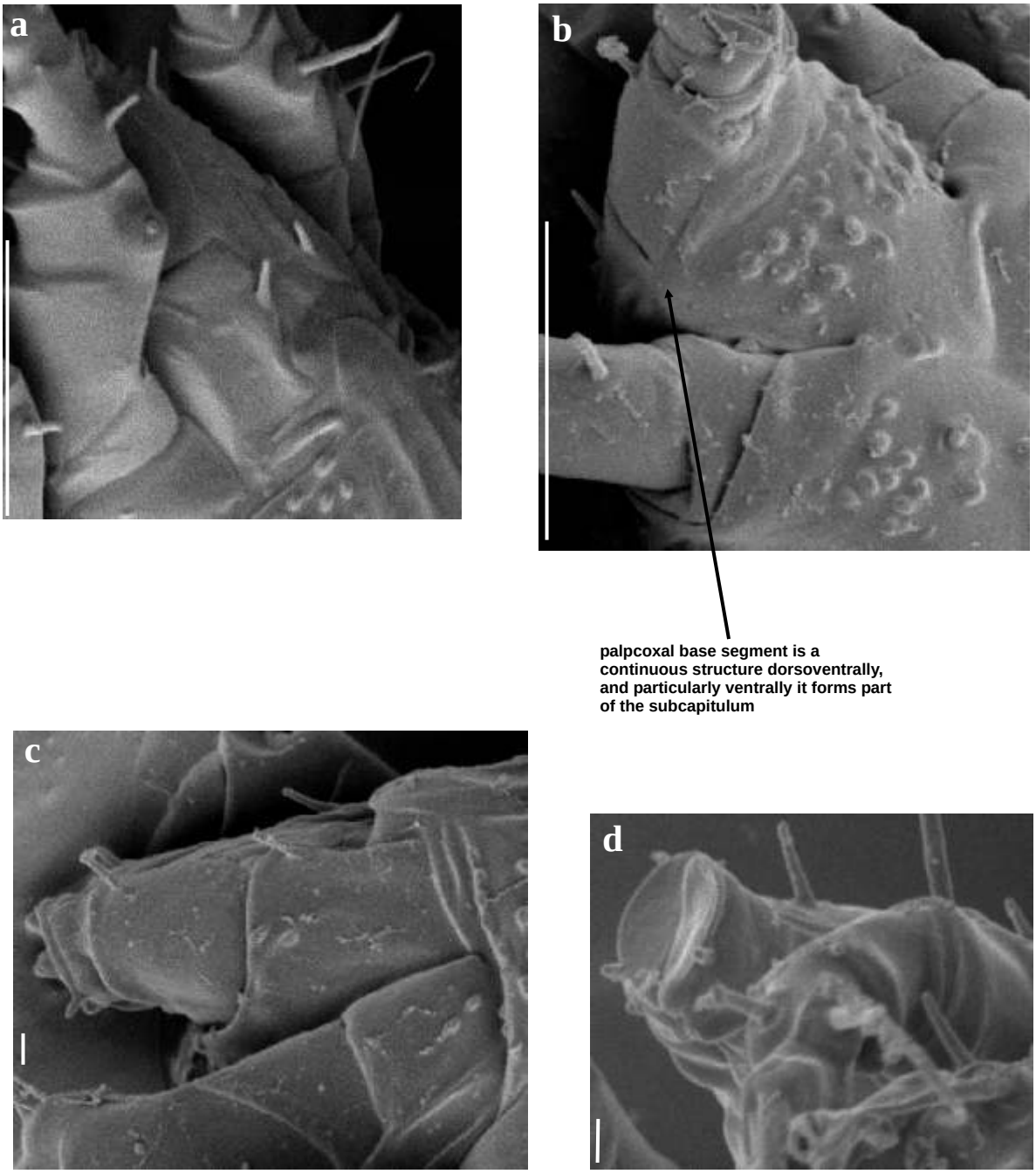


Fig. 3.39. Gnathosoma of *Aceria* sp. nov. females (Eriophyidae: Eriophyinae: Aceriini) from *Chrysanthemoides monilifera* subsp. *monilifera*: **a)** dorso-lateral view; **b)** ventro-lateral view; **c)** lateral view; **d)** ventro-lateral view of apical tip of the pedipalpi; **a, b)** scale lines = 10 µm; **c, d)** scale lines = 1 µm.

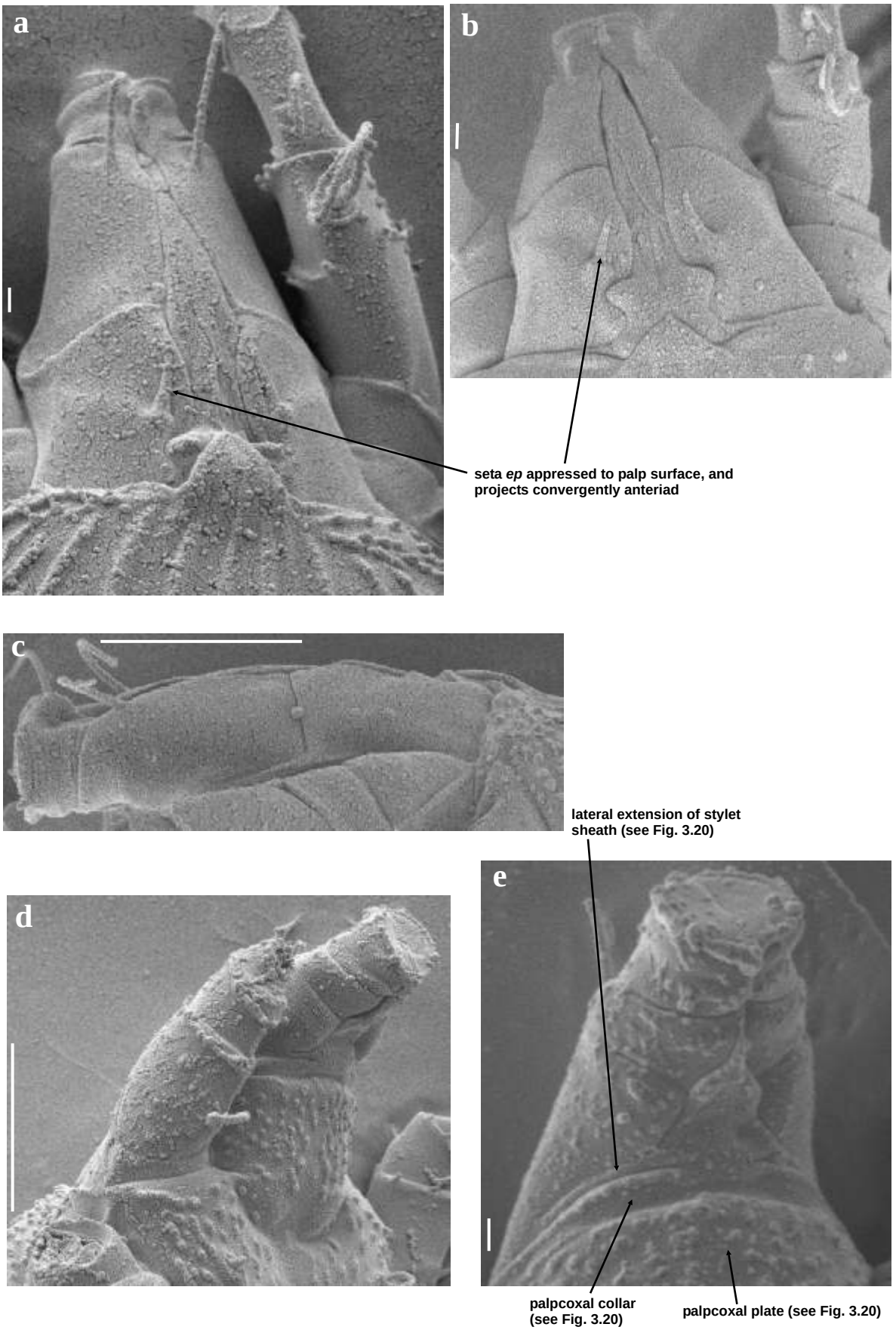


Fig. 3.40. Gnathosoma of *Aceria* sp. *cf. A. proteae* Meyer, 1981 (Eriophyidae: Eriophyinae: Aceriini) from *Protea caffra* subsp. *caffra*: **a)** dorsal view (probably adult, gender unknown); **b)** dorsal view (larva); **c)** lateral view (female); **d, e)** ventro-lateral views (females); **a, b, e)** scale lines = 1 µm; **c, d)** scale lines = 10 µm.

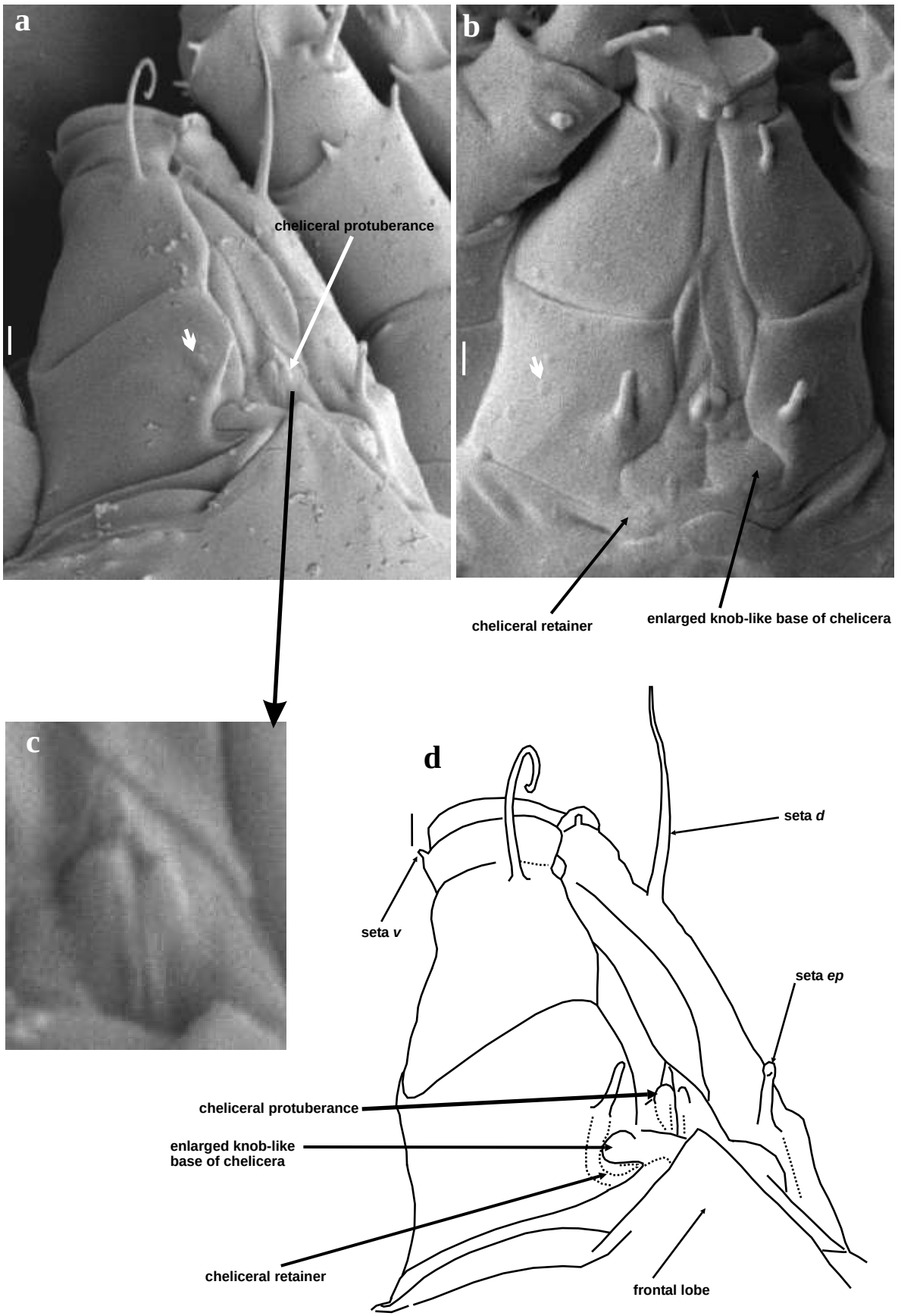


Fig. 3.41. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Ipomoea batatas* var. *batatas*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably larva); **c)** enlargement of cheliceral protuberances in 3.41a; **d)** line drawing of Fig. 3.41a. White arrows indicate droplet-like structures that are probably not parts of the mites, but artefacts. Scale lines = 1 µm.

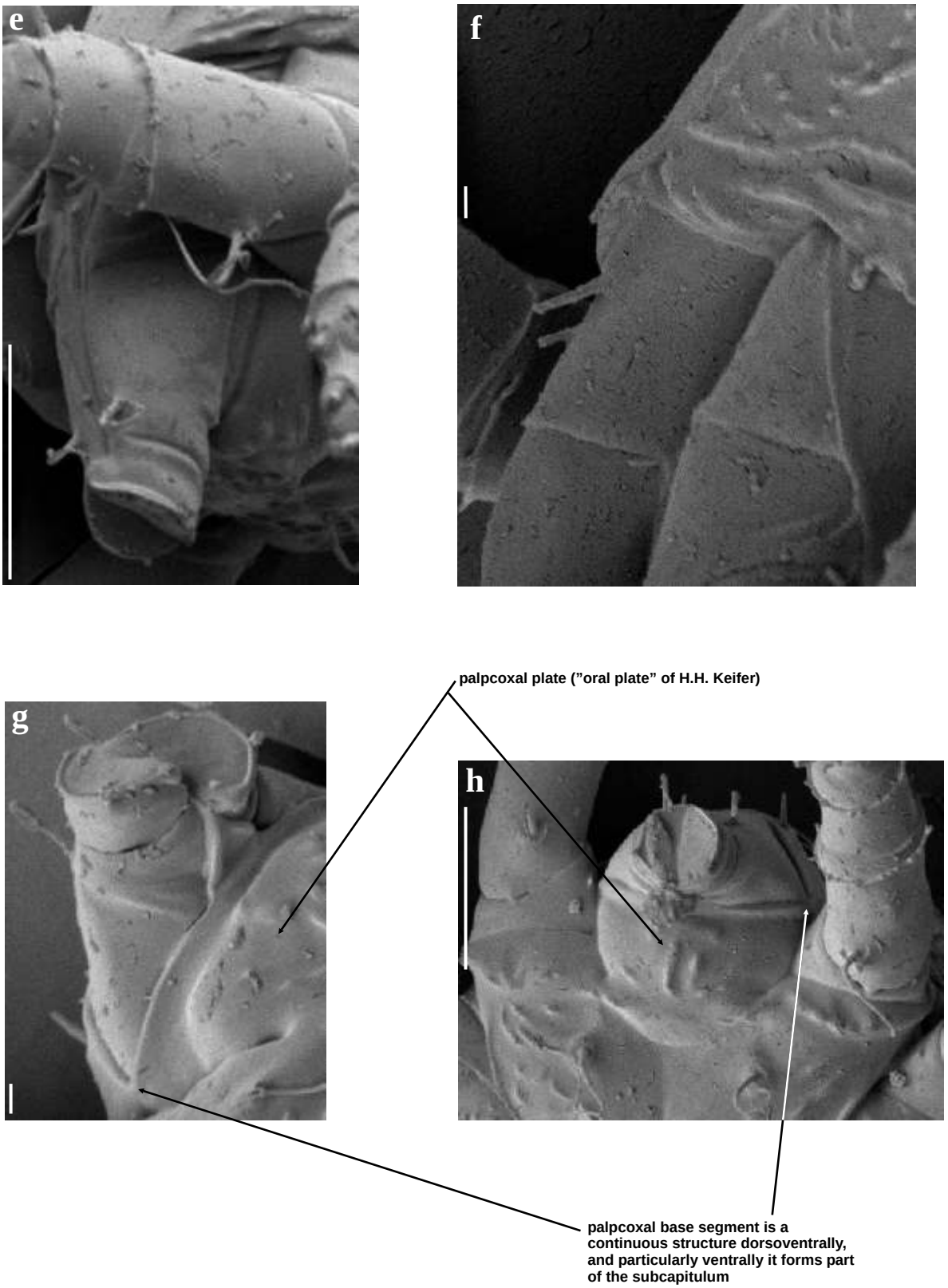


Fig. 3.41. (continued from previous page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **e)** dorso-lateral view (male); **f)** lateral view of basal part of gnathosoma (female); **g)** ventro-lateral view (female); **h)** ventral view (female); **e, h)** scale lines = 10 µm; **f, g)** scale lines = 1 µm.

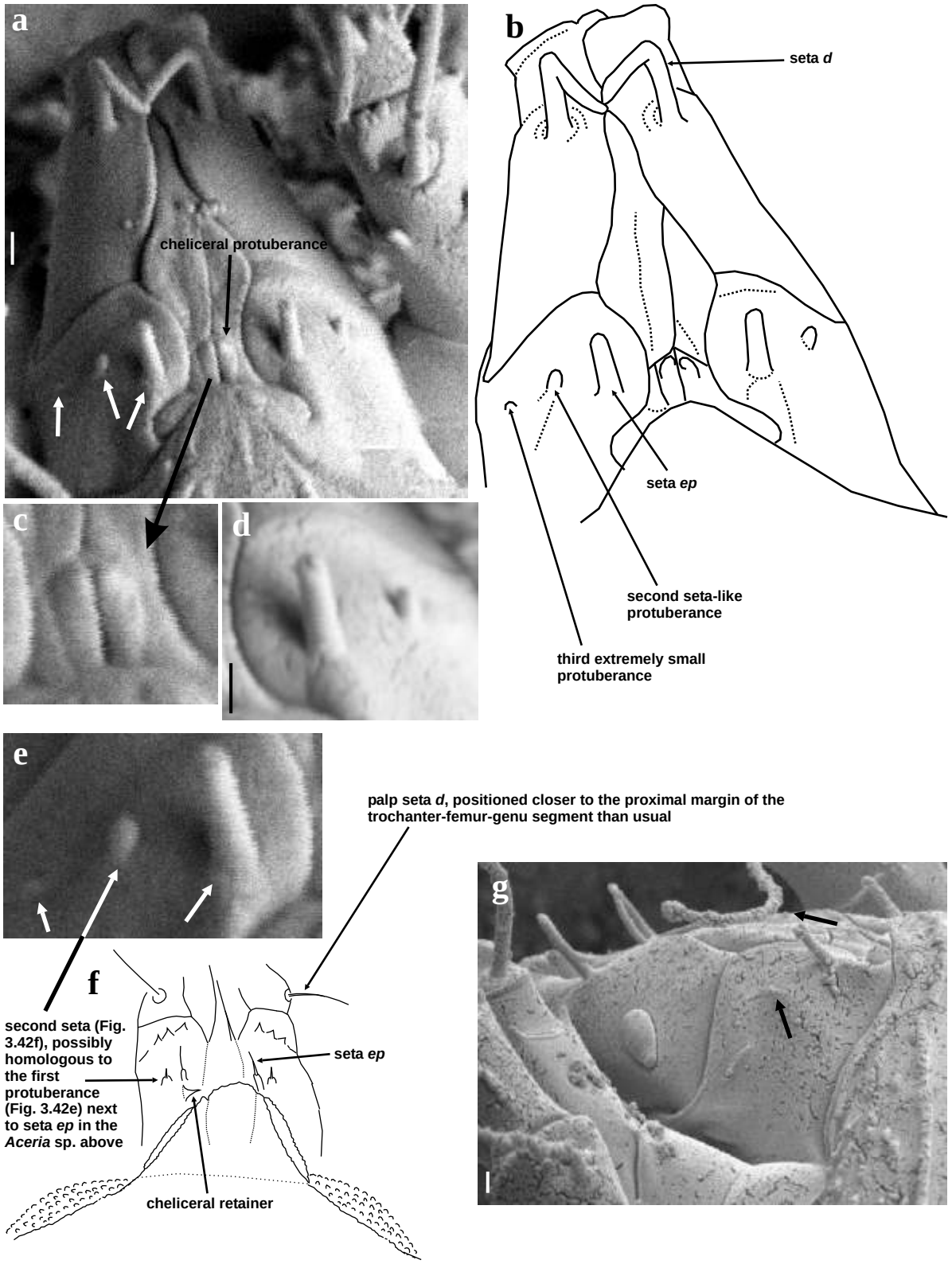


Fig. 3.42. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Oxalis corniculata*: **a)** dorsal view (probably adult, gender unknown), white arrows indicate seta *ep* (closest to dorsal exposed parts of the chelicerae), and two protuberances on the side of it; **b)** line drawing of Fig. 3.42a; **c)** enlargement of cheliceral protuberances in Fig. 3.42a; **d)** enlargement of seta *ep* on the right hand side of the specimen in Fig. 3.42a and the first protuberance alongside it; **e)** enlargement of seta *ep* and two protuberances indicated by white arrows in Fig. 3.42a, also here indicated by white arrows; **f)** seta *ep*, and seta (still unnamed, but mentioned in the text description) alongside it on the gnathosomal palpcoxal base of *Acaphyllisa limitata* (drawing from Flechtmann & Etienne, 2001), which might be homologous with the first protuberance alongside seta *ep* in the *Aceria* sp. from *O. corniculata*; **g)** lateral view (probably adult, gender unknown) with black arrows indicating the first protuberance next to seta *ep*. Scale lines = 1 µm.

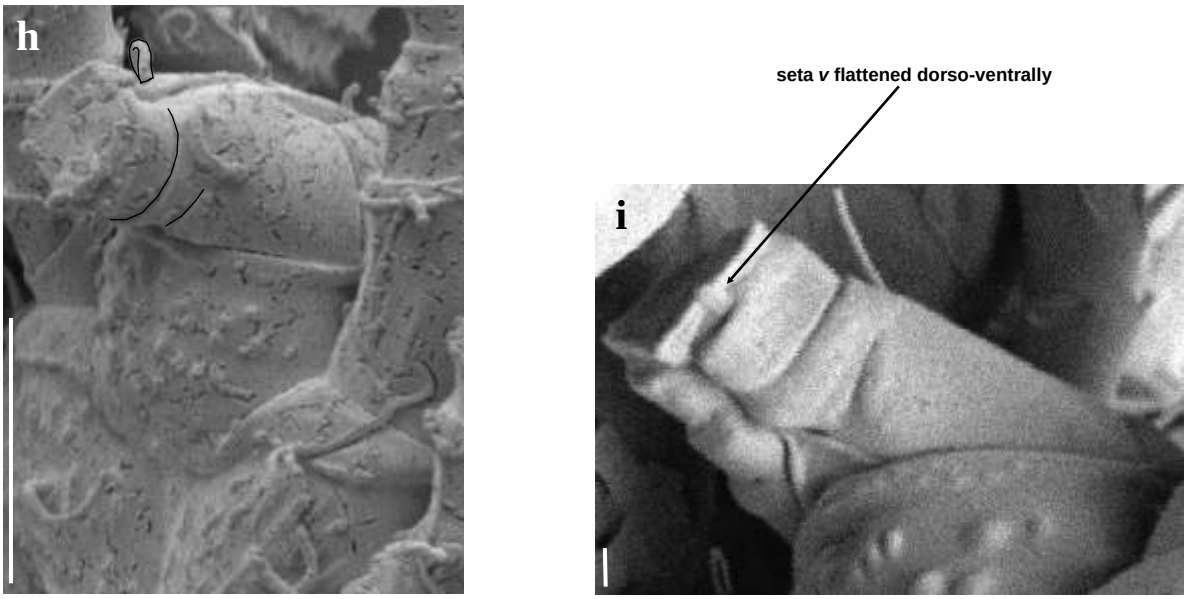


Fig. 3.42. (continued from previous page).Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **h)** ventro-lateral view (male), some detail enhanced with black drawing line to make it more visible; **i)** ventro-lateral view (male); **h)** scale line = 10 µm; **i)** scale line = 1 µm.

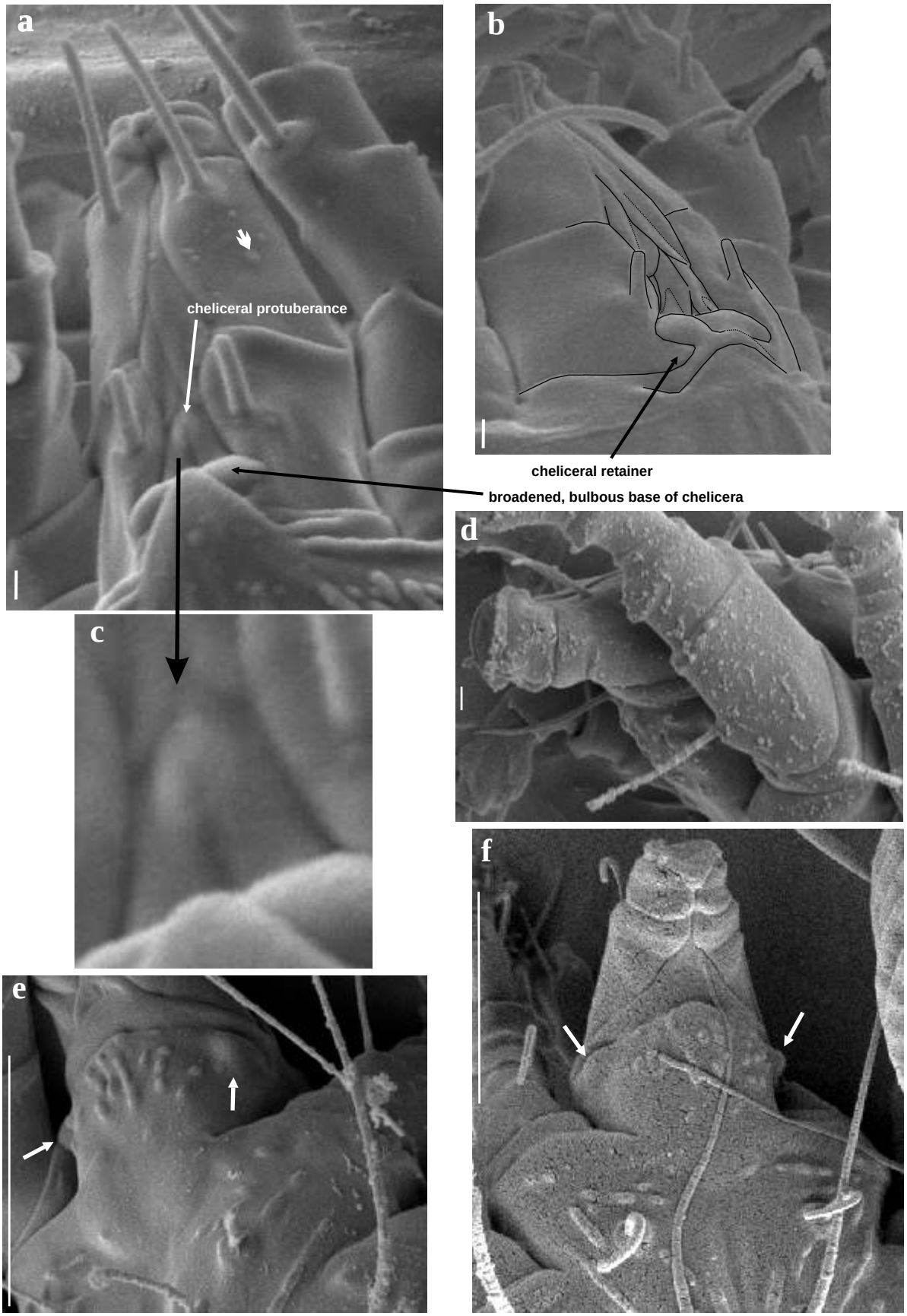


Fig. 3.43. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Acacia rehmanniana*: **a)** dorso-lateral view (probably adult, gender unknown), short white arrow indicates one of the droplet-like structures which are probably not part of the mite, but artefacts; **b)** dorso-lateral view (larva), some lines traced in black to make them more clear; **c)** enlargement of cheliceral protuberances in Fig. 3.43a; **d)** lateral view (female); **e)** ventro-lateral view (female), a rounded bump each side laterally on ventral palpcoxal base (indicated by white arrows); **f)** ventral view (female), a rounded bump each side laterally on ventral palpcoxal base (indicated by white arrows); **a, b, d)** scale lines = 1 µm; **d, f)** scale lines = 10 µm.

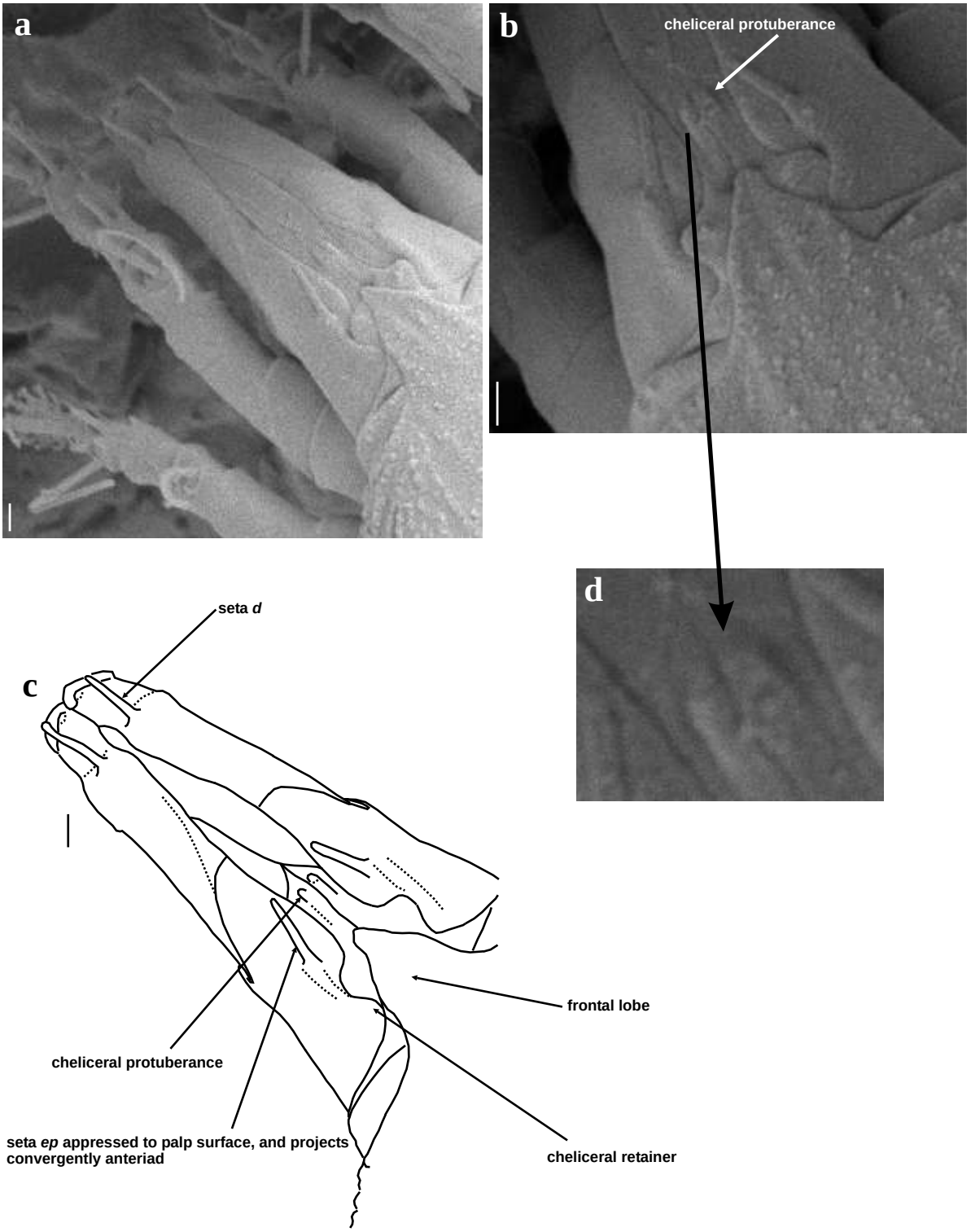


Fig. 3.44. (continued on next page). Gnathosoma of unknown genus, nr. *Aceria* (Eriophyidae: Eriophyinae: Aceriini) from *Apodytes dimidiata* subsp. *dimidiata* flower buds: **a, b)** dorsal views of the same specimen (probably adult, gender unknown); **c)** line drawing of Fig. 3.44a; **d)** enlargement of cheliceral protuberances in Fig. 3.44b. Scale lines = 1 µm.

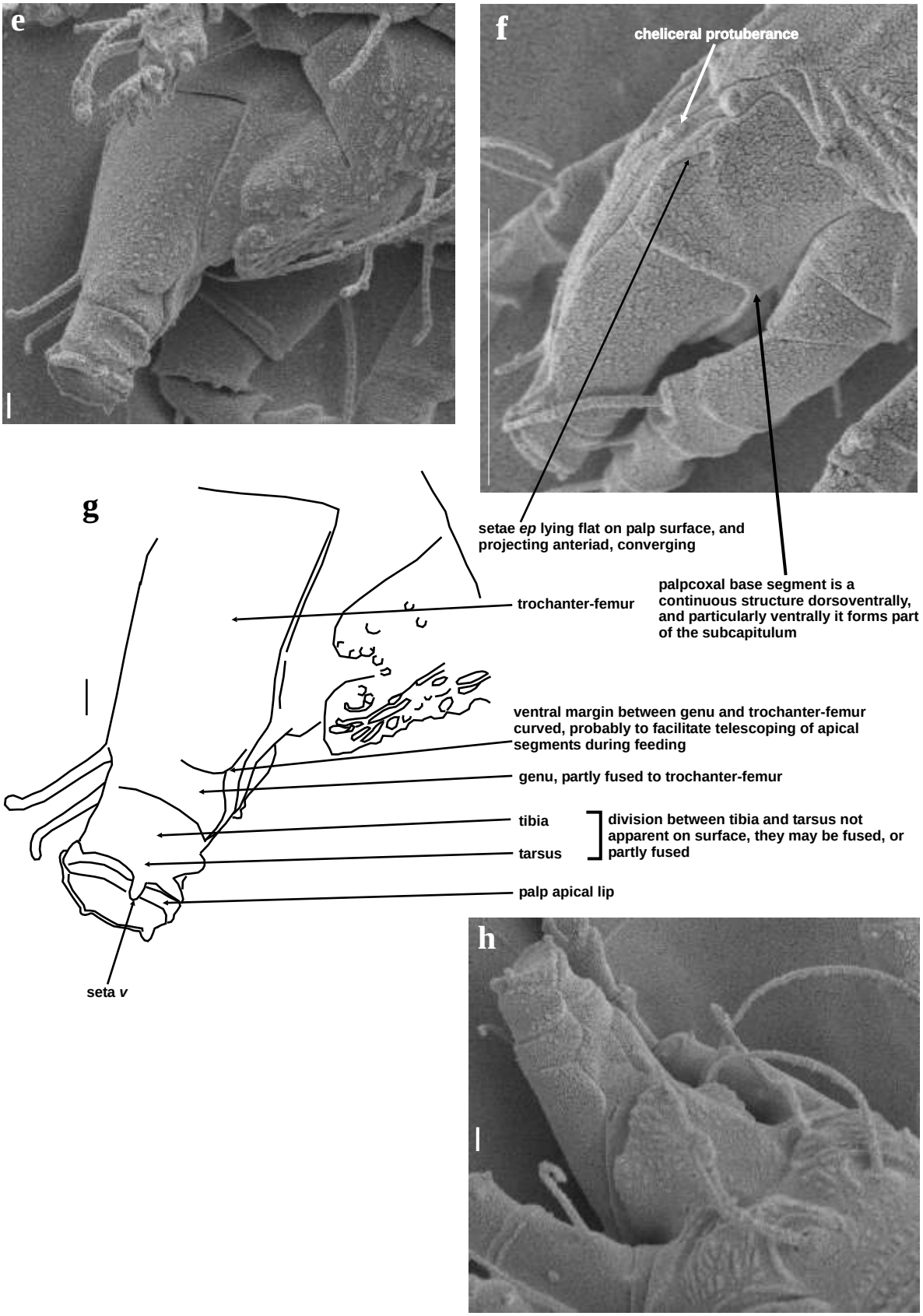


Fig. 3.44. (continued from previous page). Gnathosoma of unknown genus, nr. *Aceria*: **e)** ventro-lateral view (male); **f)** dorso-lateral view (probably adult, gender unknown); **g)** line drawing of Fig. 3.44e; **h)** ventro-lateral view (female); **e, g, h)** scale lines = 1 µm; **b)** scale line = 10 µm.

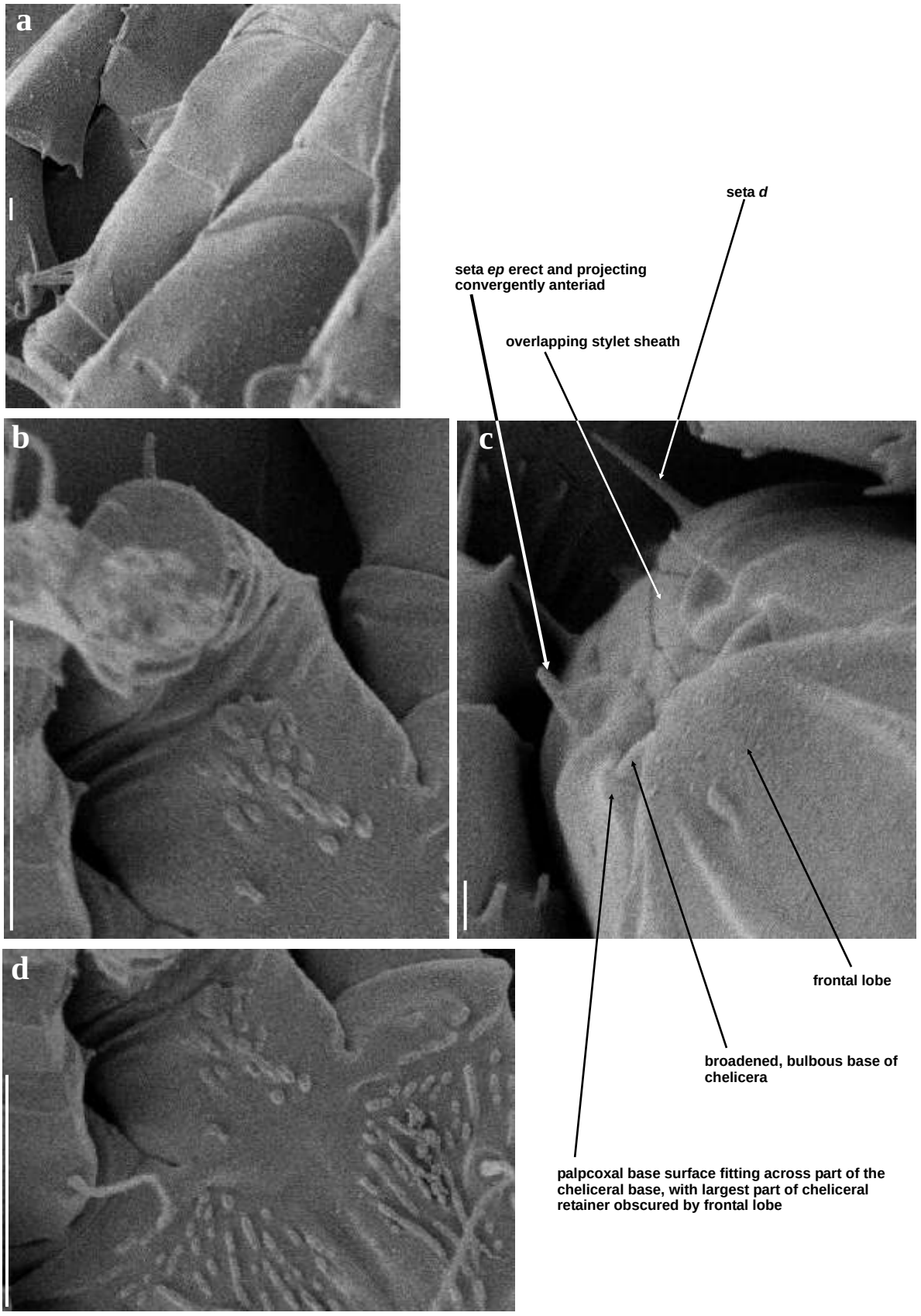


Fig. 3.45. Gnathosoma of *cf. Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini) from *Cineraria* sp. blisters: **a)** lateral view (female); **b, d)** ventral views of the same specimen (female); **c)** dorsal view (probably adult, gender unknown); **a, c)** scale lines = 1 µm; **b, d)** scale lines = 10 µm.

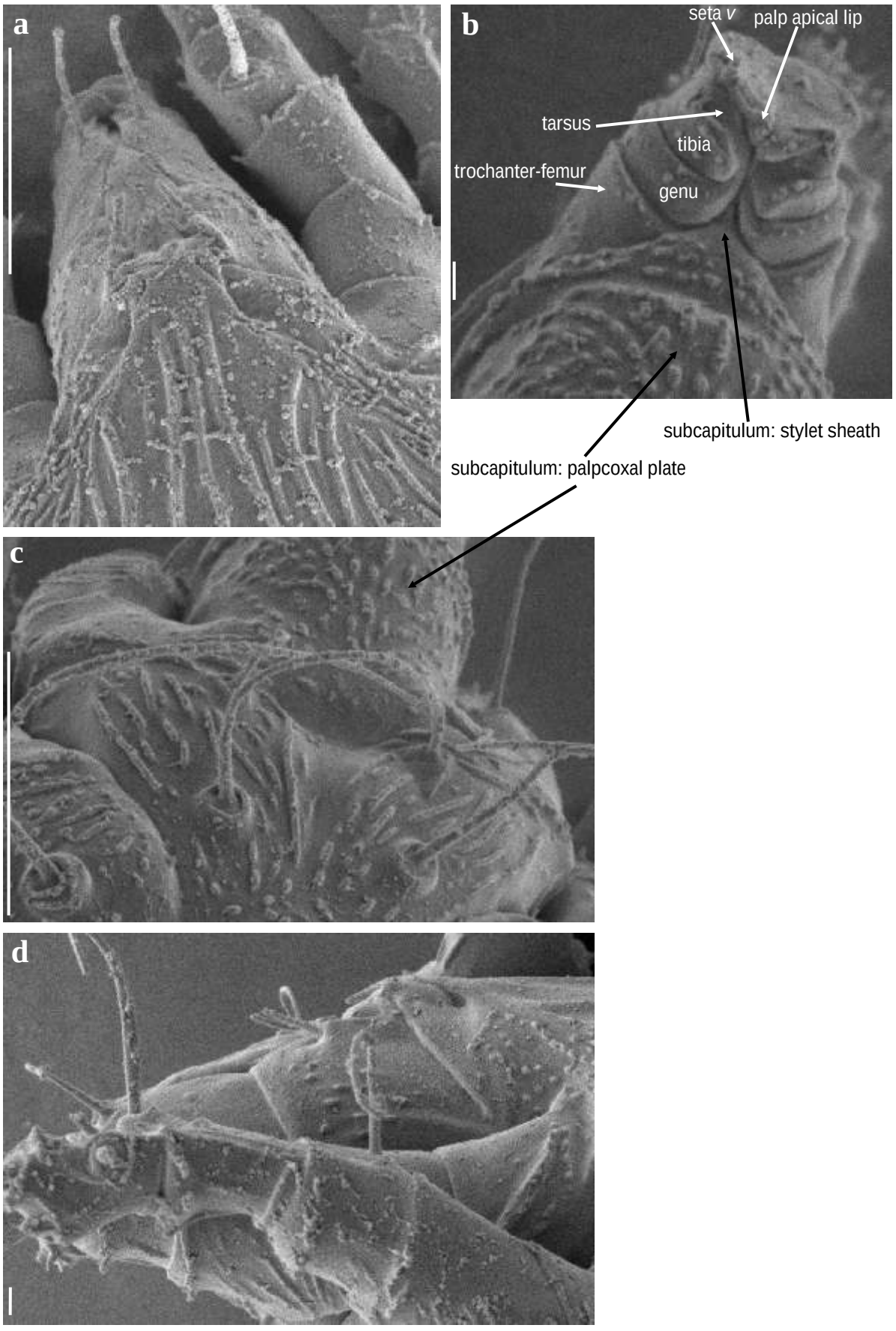


Fig. 3.46. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Xymalos monospora*: **a)** dorsal view (probably adult, gender unknown); **b, c)** ventral views of the same specimen (female); lateral view (female); **a, c)** scale lines = 10 µm; **b, d)** scale lines = 1 µm.

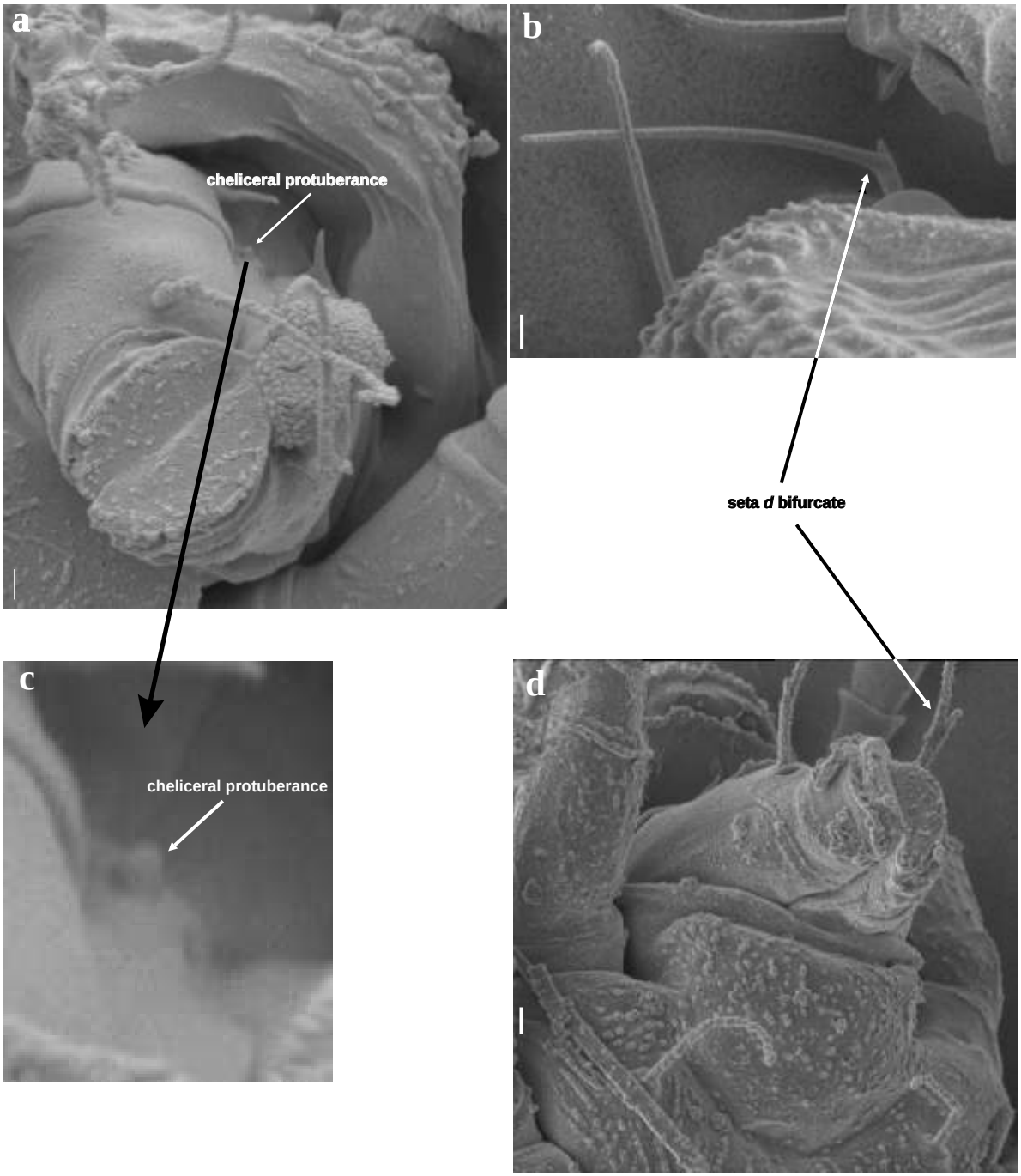
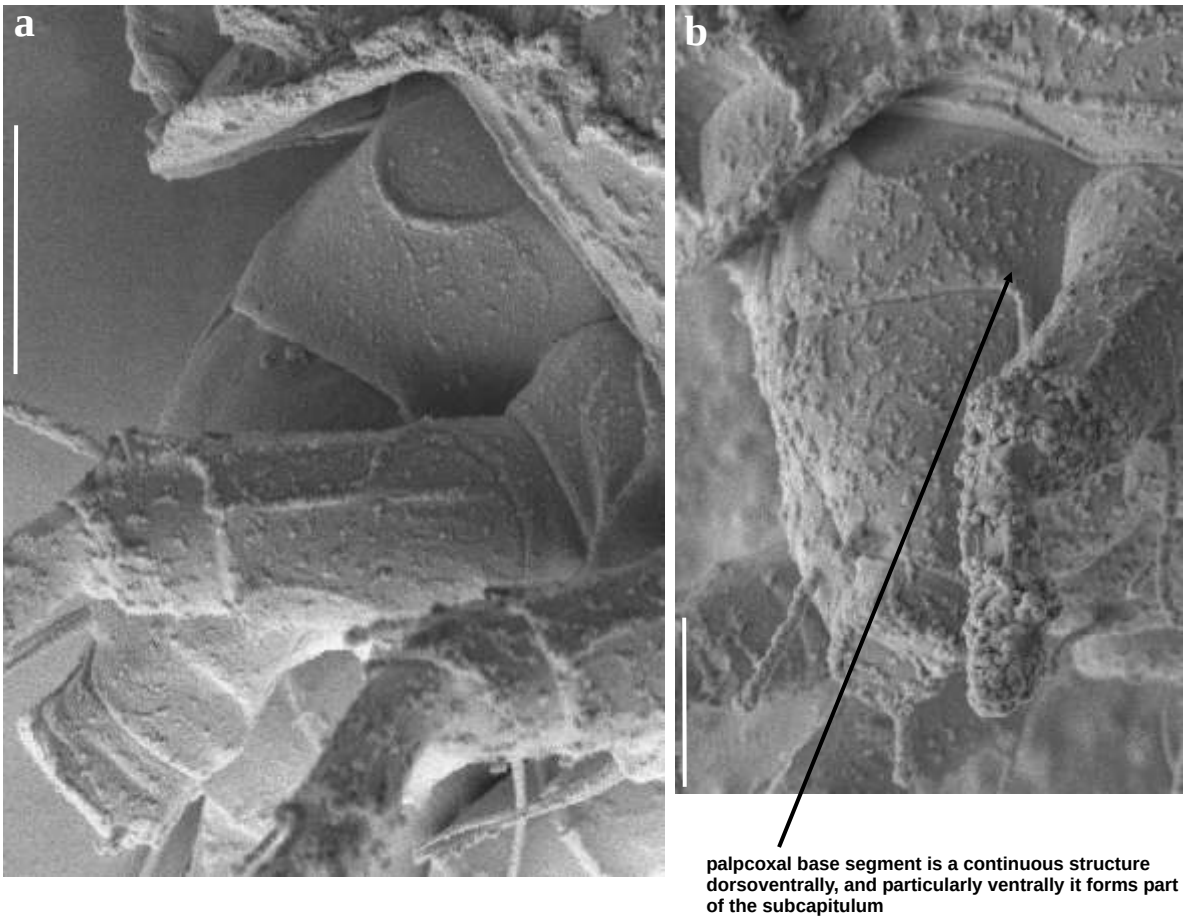


Fig. 3.47. Gnathosoma of *Tumescoptes* sp. *cf. T. dicrus* (Eriophyidae: Phyllocoptinae: Acaricalini) from *Phoenix reclinata*: **a)** ventro-dorsal view (female); **b)** bifurcate setae *d* enlarged to show tiny side branch (probably adult, gender unknown); **c)** enlargement of cheliceral protuberance in Fig. 3.47a; **d)** venro-lateral view (female). Scale lines = 1 µm.



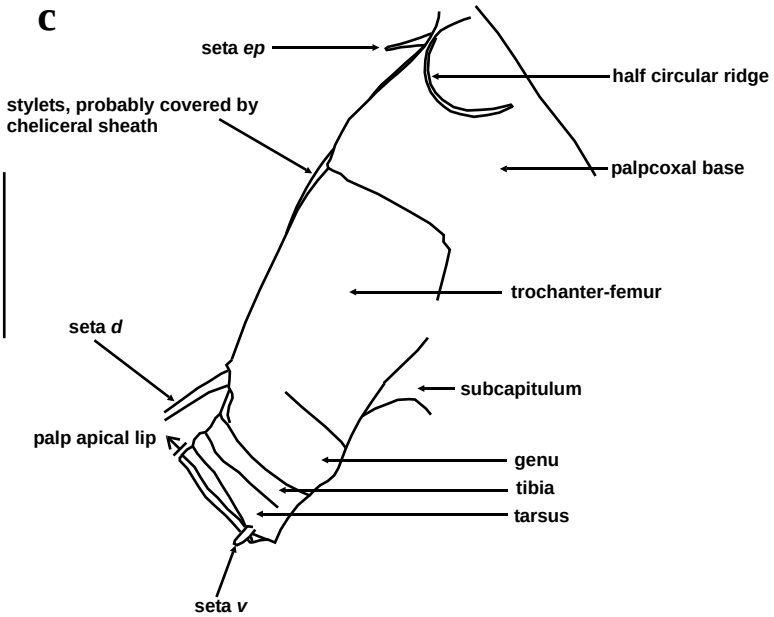
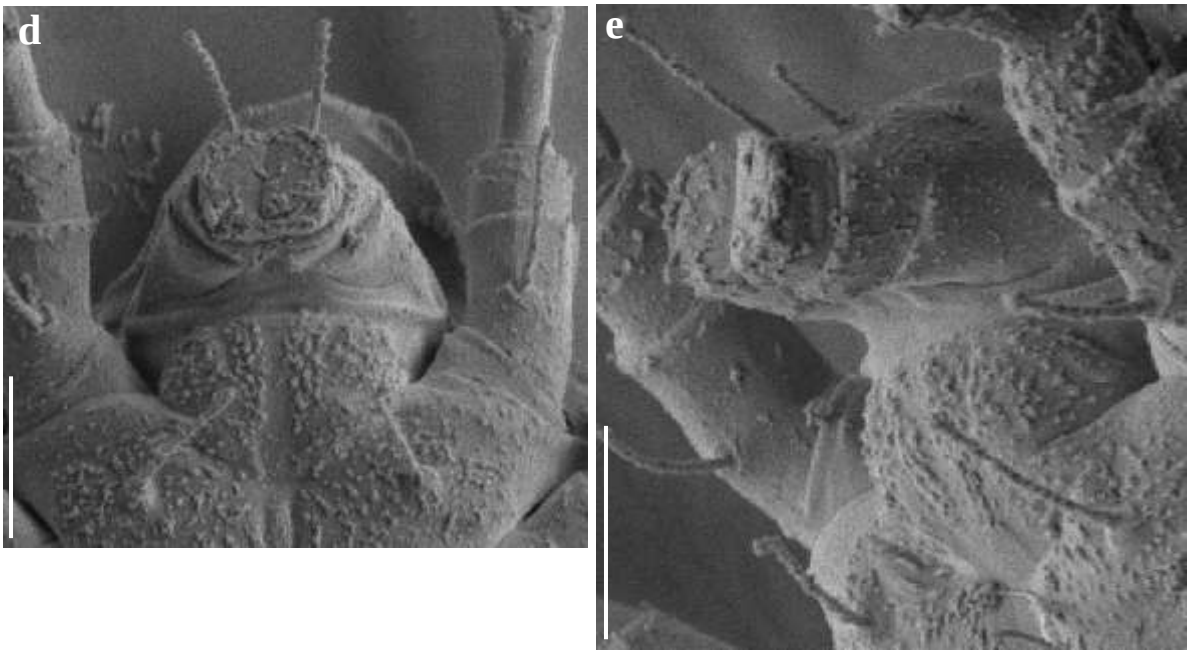


Fig. 3.48. (continued on next page). Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Searsia lancea* (previously *Rhus lancea*): **a)** lateral view (female); **b)** dorso-lateral view (female); **c)** line drawing of Fig. 3.48a. Scale lines = 10 µm.



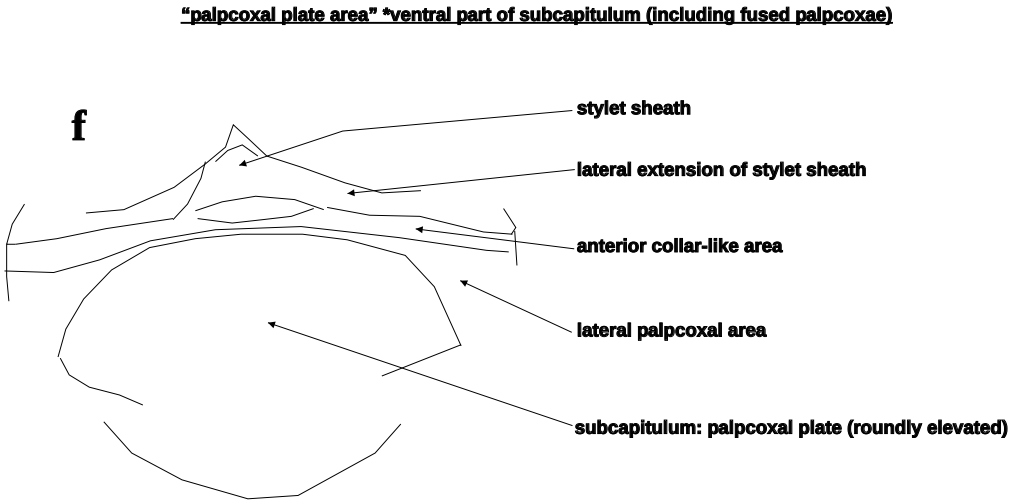


Fig. 3.48. (continued from previous page). Gnathosoma of *Calacarus* sp.: **d)** ventral view (female); **e)** ventro-lateral view (female); **f)** line drawing of "palpcoxal plate area" of Fig. 3.48d, *names for different areas are preliminary (also see Fig. 3.20). Scale lines = 10 µm.

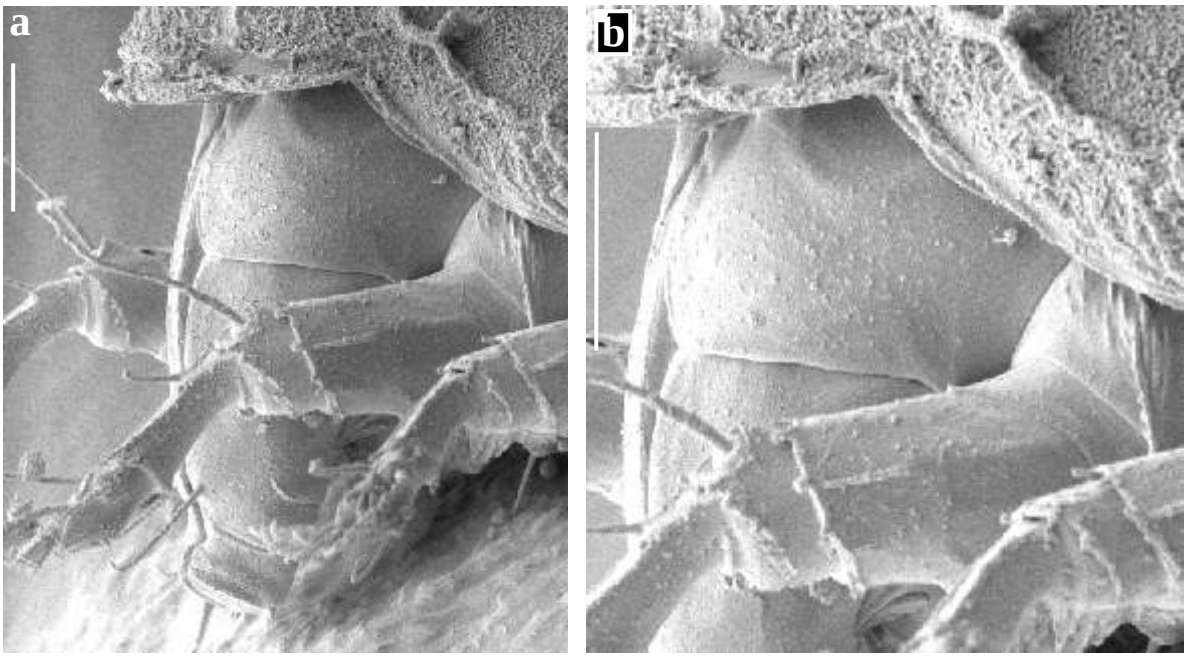


Fig. 3.49. Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Faurea rochetiana*: **a, b)** lateral view of the same specimen (probably adult, gender unknown). Scale lines = 10 µm.

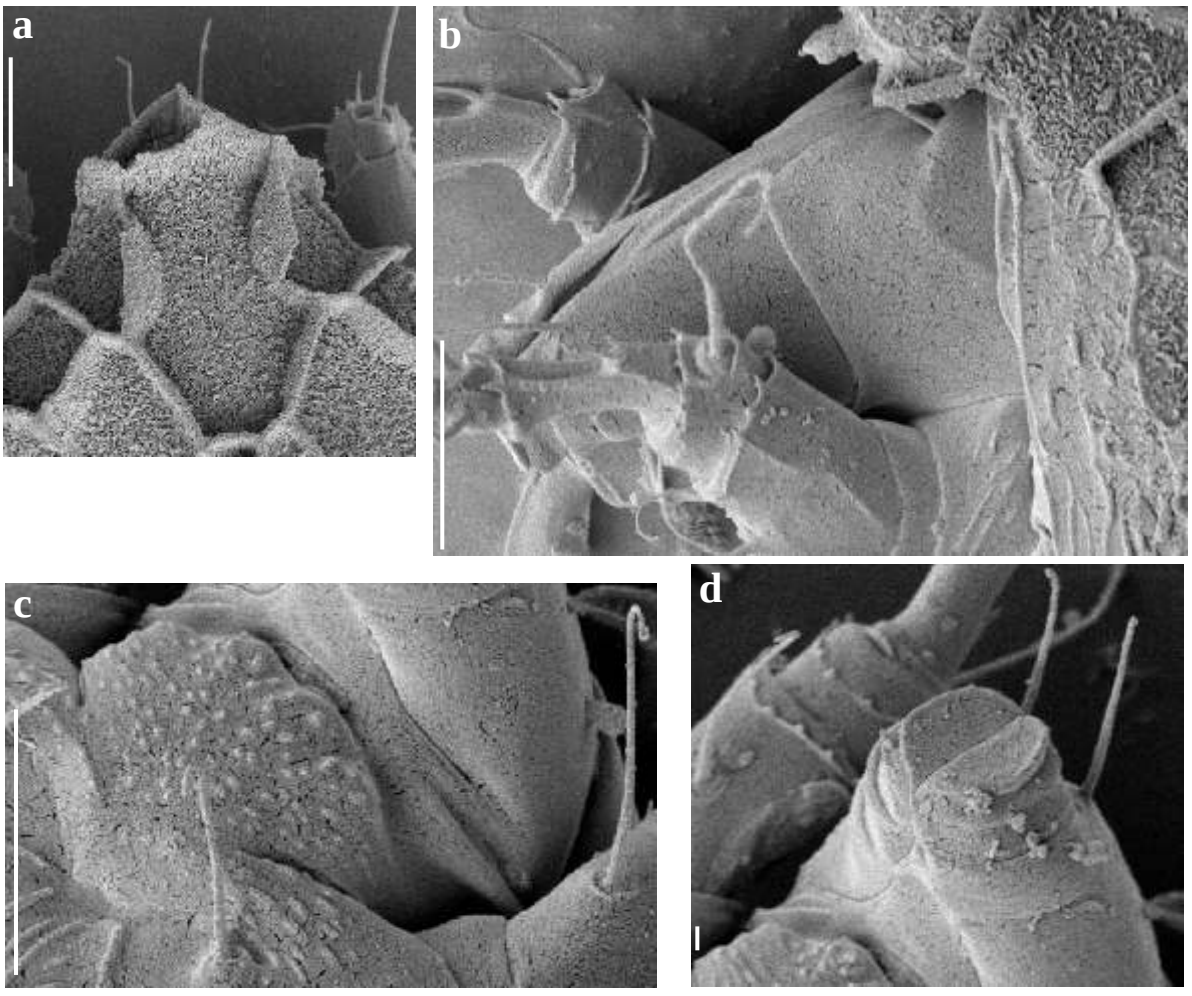


Fig. 3.50. Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Psydrax livida*: **a)** dorsal view (probably adult, gender unknown), in vagrants, like this *Calacarus* sp., the frontal lobe obscures the gnathosoma which is also usually more hypognathous in these species, in dorsal view; **b)** lateral view (probably adult, gender unknown); **c, d)** ventro-lateral views of the same specimen (female); **a, b, c)** scale lines = 10 µm; **d)** scale line = 1 µm.

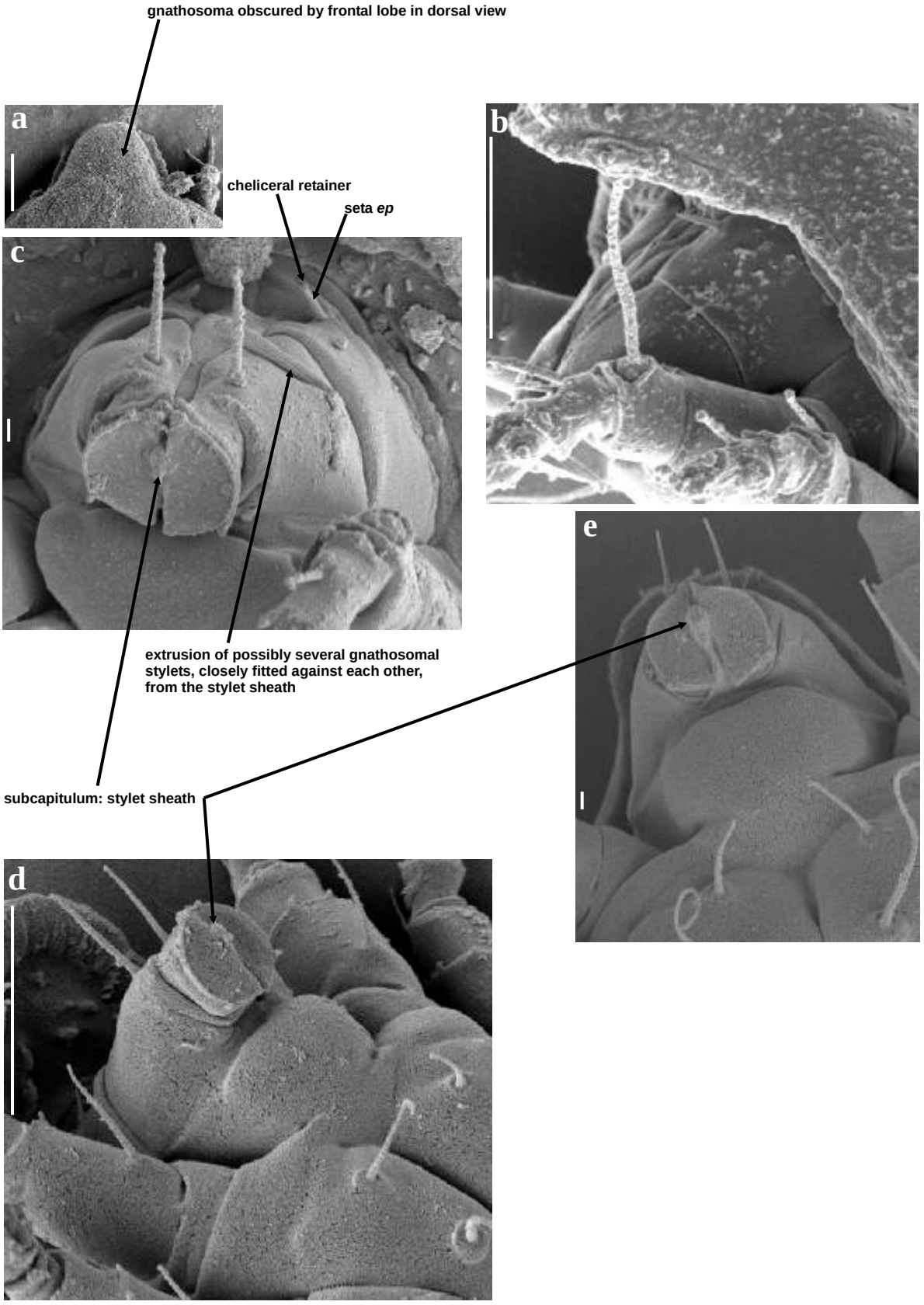


Fig. 3.51. Gnathosoma of a *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Psydrax livida*: **a)** gnathosoma obscured by frontal lobe in dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (male); **c)** ventral-dorsal view (female), note extrusion of possibly several gnathosomal stylets, closely fitted against each other, from the stylet sheath; **d)** ventro-lateral view male; **a, b, d)** scale lines = 10 µm; **c, e)** scale lines = 1 µm.

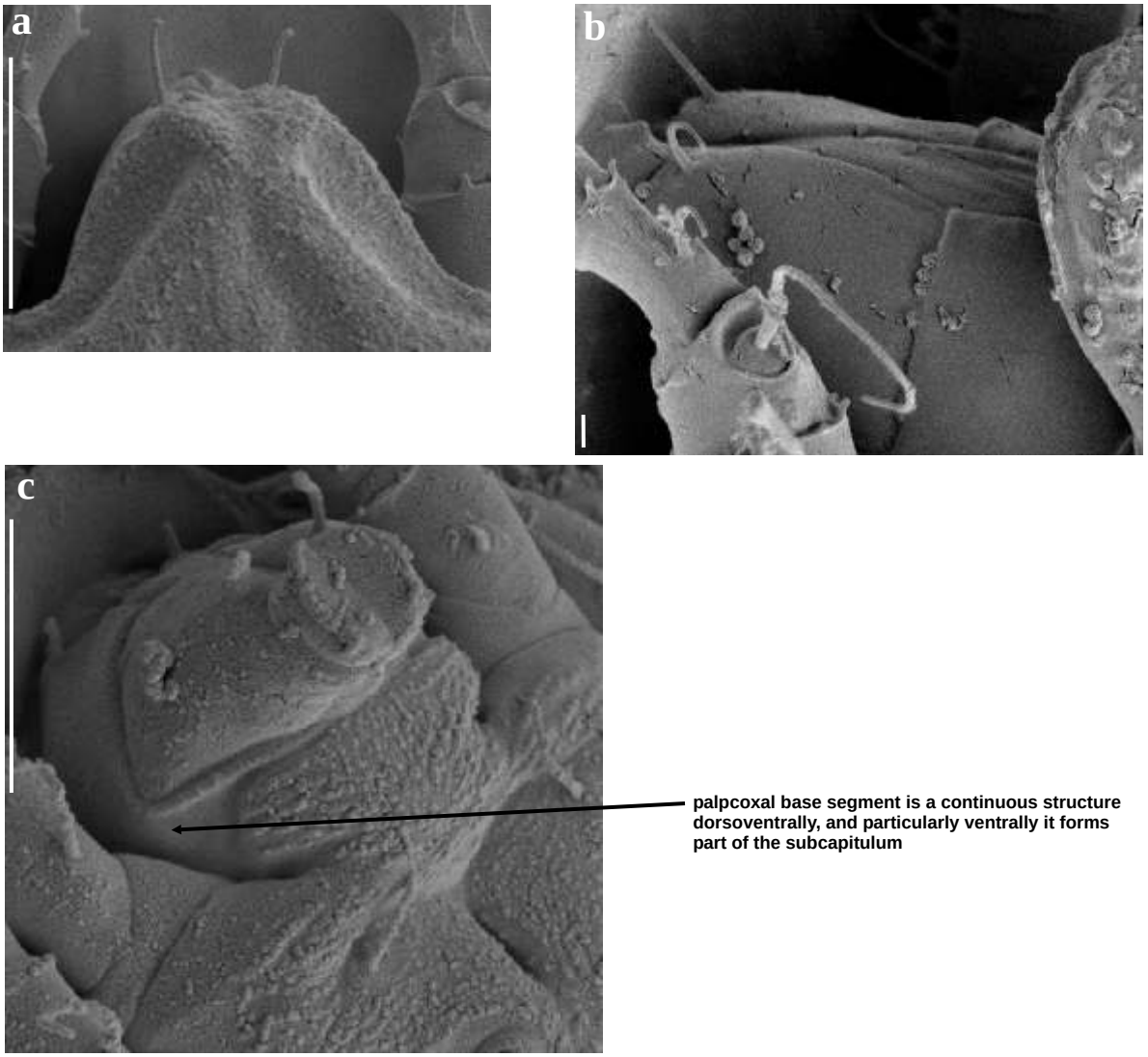


Fig. 3.52. Gnathosoma of *Shevtchenkella* sp. *cf. S. rhusi* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Searsia lancea* (previously *Rhus lancea*): **a)** frontal lobe largely obscures gnathosoma in dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (probably adult, gender unknown); **c)** ventro-lateral view (female); **a, c)** scale lines = 10 µm; **b)** scale line = 1 µm.

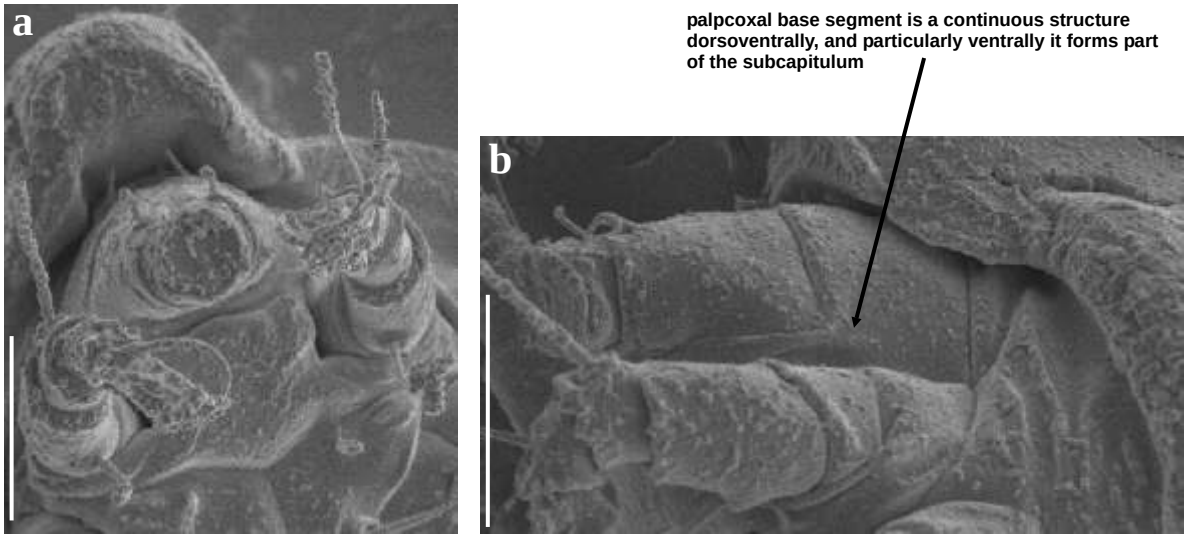


Fig. 3.53. Gnathosoma of *Neoshevtchenkella* or *Shevtchenkella* sp. (with wax) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Celtis africana*: **a)** dorso-ventral view (female); **b)** lateral view (female). Scale lines = 10 µm.

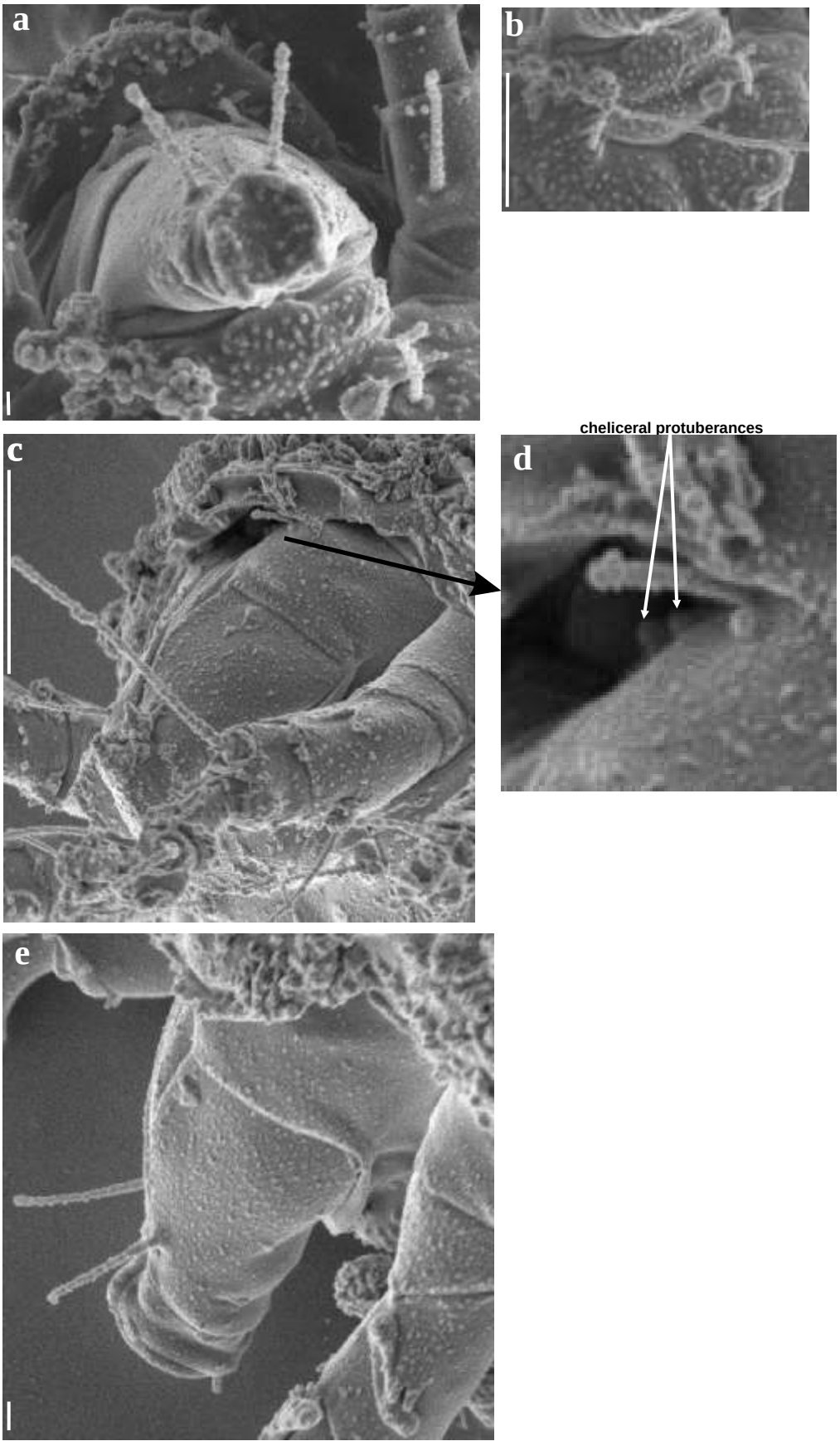


Fig. 3.54. Gnathosoma of *cf. Calepitrimerus* sp. (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Celtis africana*: **a, b)** ventral views of the same specimen (female); **c)** dorso-lateral view (female); **d)** enlargement of cheliceral protuberances in Fig. 3.54c; **e)** dorso-lateral view (probably adult, gender unknown); **a, e)** scale lines = 1 µm; **b, c)** scale lines = 10 µm.

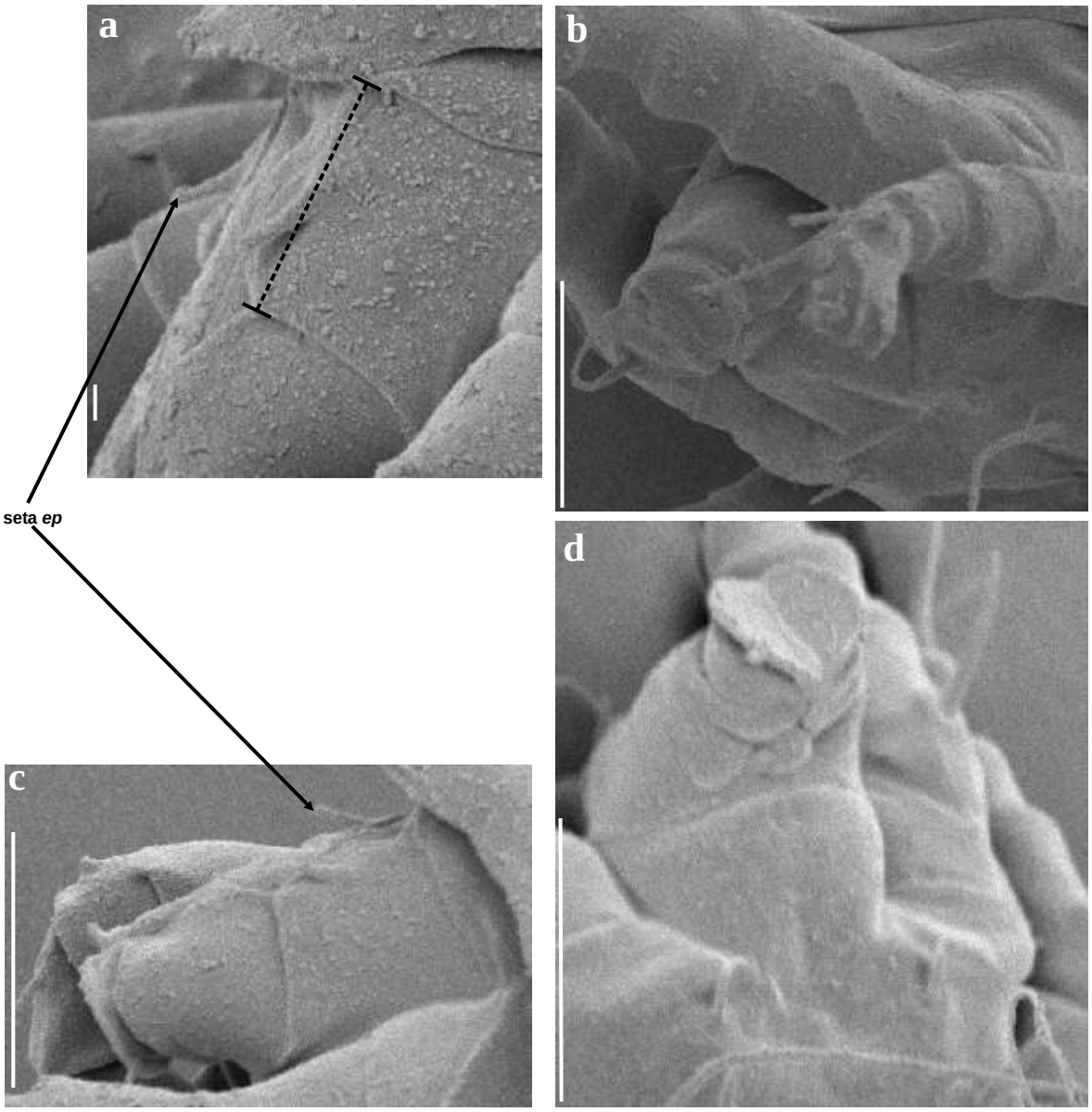


Fig. 3.55. Gnathosoma of *Cecidodectes euzonus* Nalepa, 1917 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Trema orientalis*: **a)** dorso-lateral view (probably adult, gender unknown), dashed black line indicates length of palpcoxal base; **b)** ventro-lateral view (female); **c)** lateral view (probably adult, gender unknown); **d)** ventro-lateral view (female); **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm.

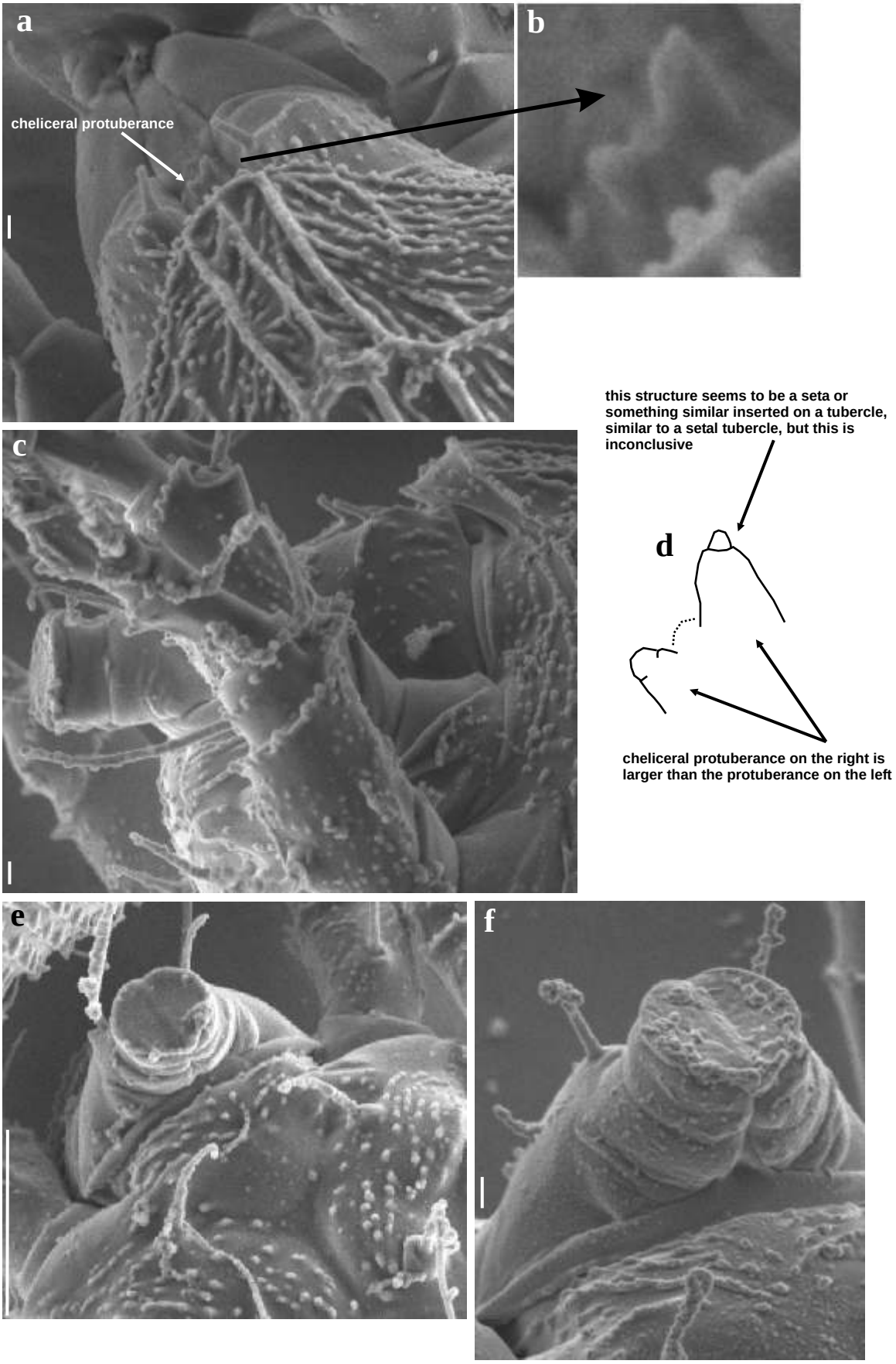


Fig. 3.56. Gnathosoma of *cf. Phyllocoptes* sp. (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Anthocleista grandiflora*: **a)** dorsal view (probably adult, gender unknown); **b)** enlargement of the cheliceral protuberances in Fig. 3.56a; **c)** lateral view (female); **d)** line drawing of cheliceral protuberances enlarged in Fig. 3.56b; **e, f)** ventral views (females); **a, c, f)** scale lines = 1 µm; **e)** scale line = 10 µm.

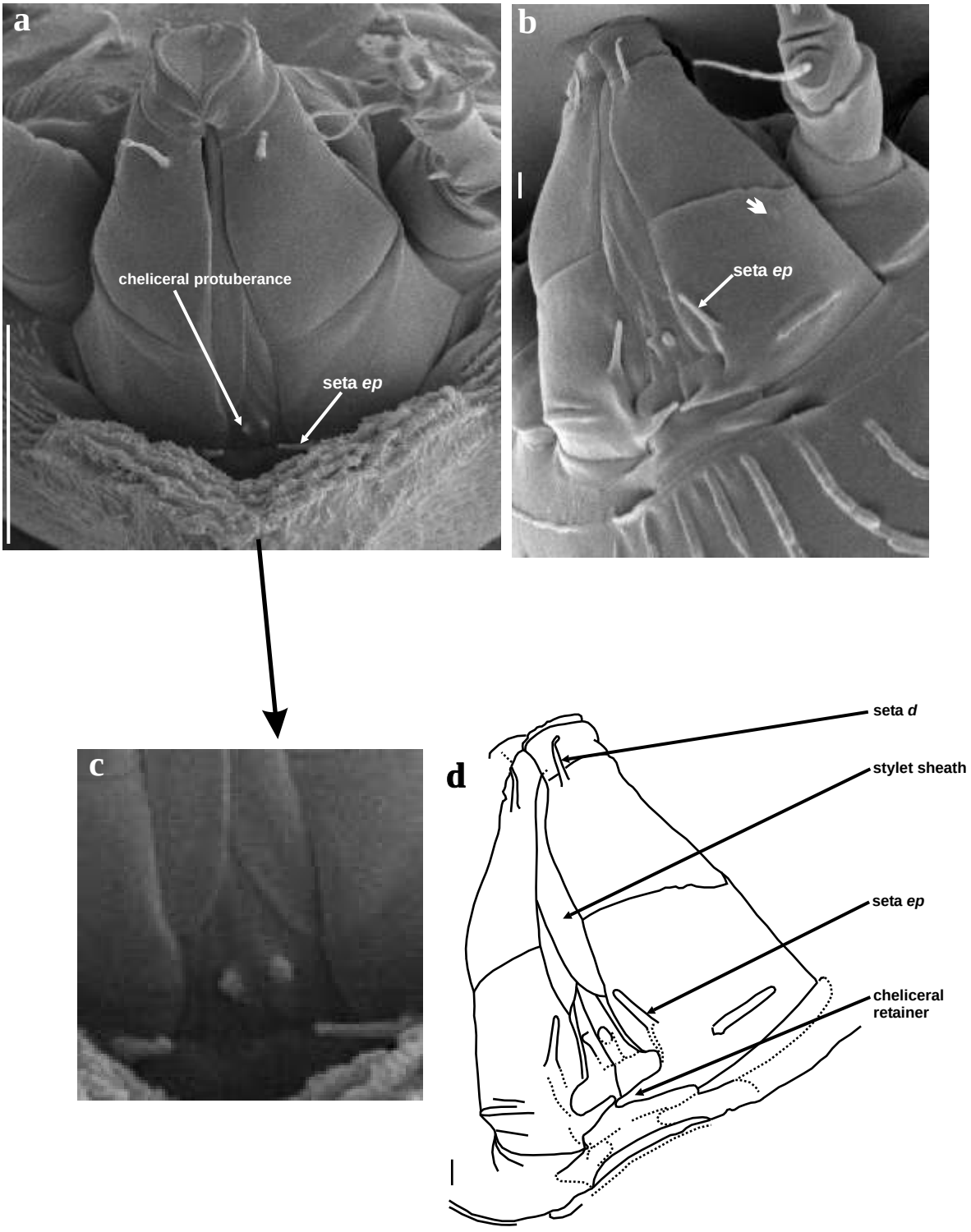


Fig. 3.57. (continued on next page). Gnathosoma of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Portulacaria afra*: **a)** dorsal view (female); **b)** dorso-lateral view (larva), short white arrow indicates droplet-like structure that is probably not part of the mite, but an artefact; **c)** enlargement of cheliceral protuberances in Fig. 3.57a; **d)** line drawing of Fig. 3.57b; **a)** scale line = 10 µm; **b, d)** scale lines = 1 µm.

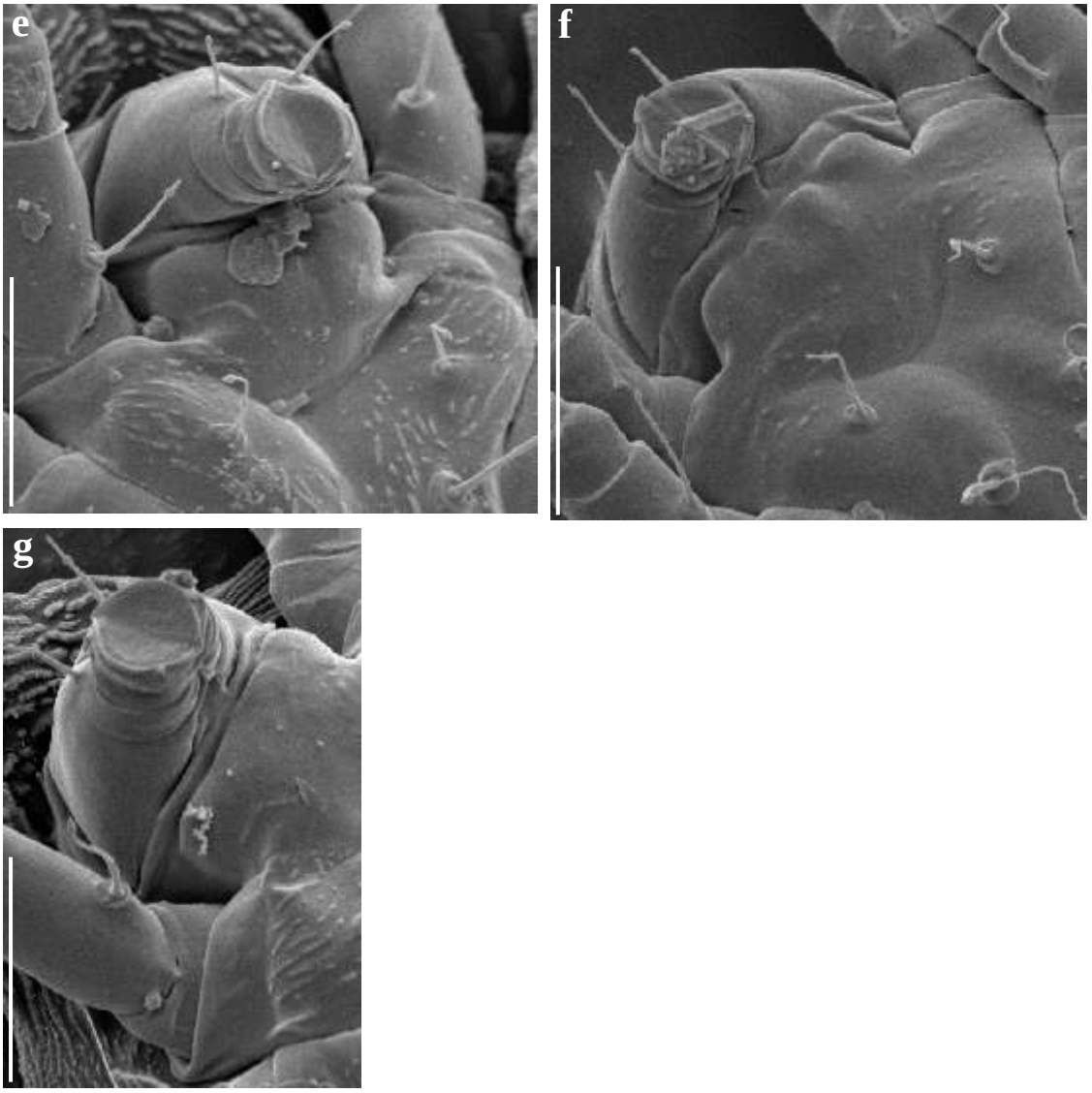


Fig. 3.57. (continued from previous page). Gnathosoma of *Tergilatus sparsus*: **e)** ventro-lateral view (male); **f)** ventral view (immature, stage unknown); **g)** ventro-lateral view (female). Scale lines = 10 µm.

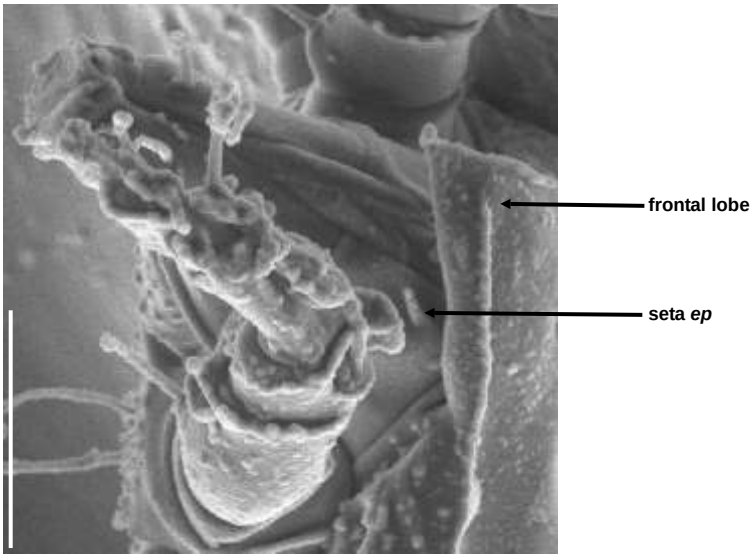


Fig. 3.58. Gnathosoma of possibly *Aculops* or *Metaculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Anthocleista grandiflora*: dorso-lateral view (probably adult, gender unknown). Scale line = 10 µm.

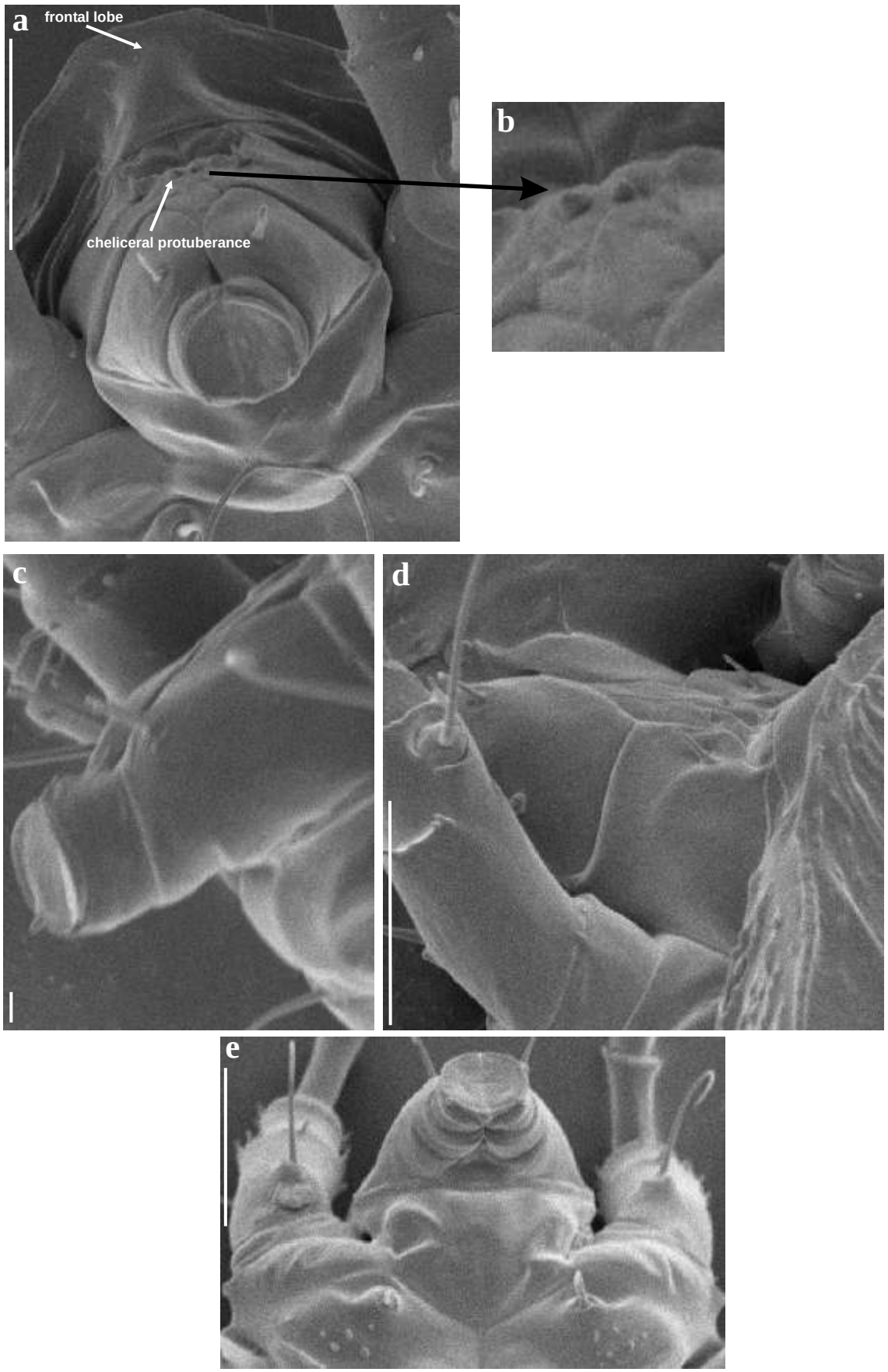


Fig. 3.59. Gnathosoma of *Aculus* sp. *cf. Aculops lycopersici* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Physalis peruviana*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in Fig. 3.59a; **c)** lateral view (female); **d)** dorso-lateral view (female); ventral view (female); **a, d, e)** scale lines = 10 µm; **c)** scale line = 1 µm.

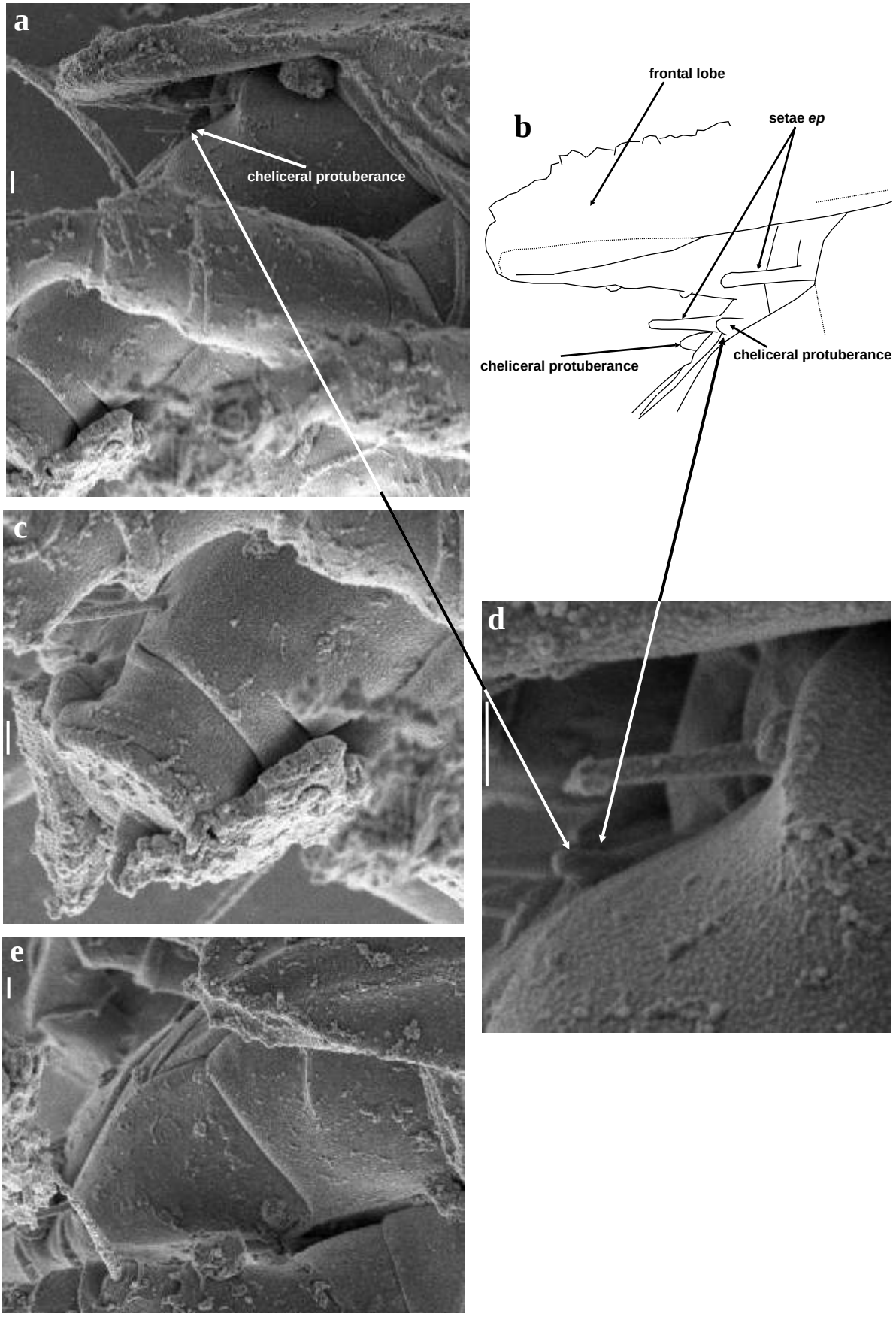


Fig. 3.60. Gnathosoma of *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Acacia burkei*: **a, c, d)** lateral views of different areas and enlargements of the same female specimen; **b)** line drawing of the cheliceral protuberances in Fig. 3.60a (enlarged in Fig. 3.60d); **e)** dorso-lateral view, basal part of gnathosoma obscured by frontal lobe (probably adult, gender unknown). Scale lines = 1 µm.

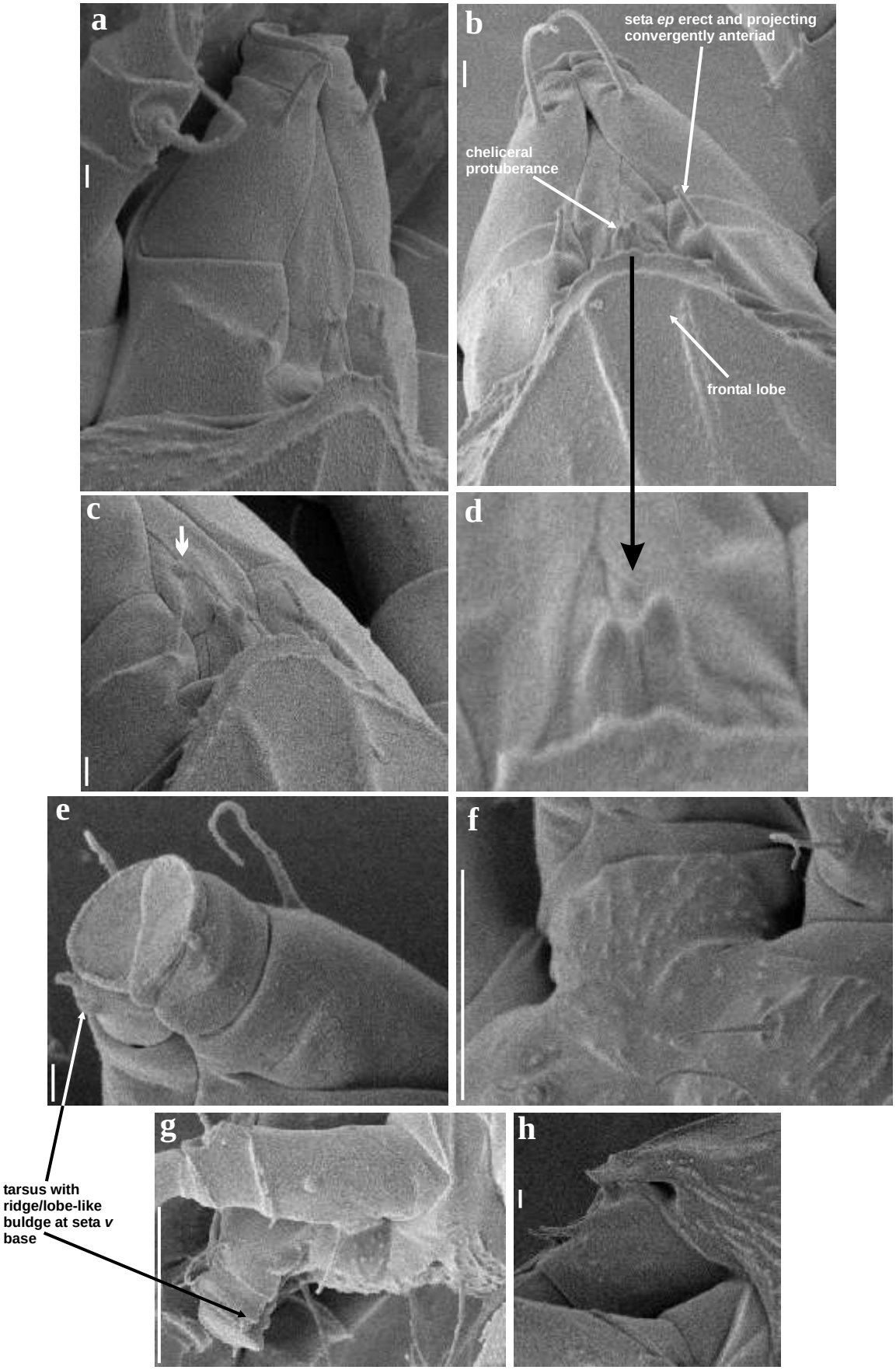


Fig. 3.61. Gnathosoma of *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Lantana trifolia*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably adult, gender unknown); **c)** basal part, dorso-lateral view (probably adult, gender unknown), short white arrow indicates droplet-like structure that is probably not part of the mite, but an artefact; **d)** enlargement of cheliceral protuberances in Fig. 3.61b; **e)** distal part, ventro-lateral view (female); **f)** palpcoxal plate region, ventro-lateral view (female, same specimen as in Fig. 3.61e); **g)** distal part, lateral view (female); **h)** basal part, lateral view (female); **a, b, c, e, h)** scale lines = 1 µm; **f, g)** scale lines = 10 µm.

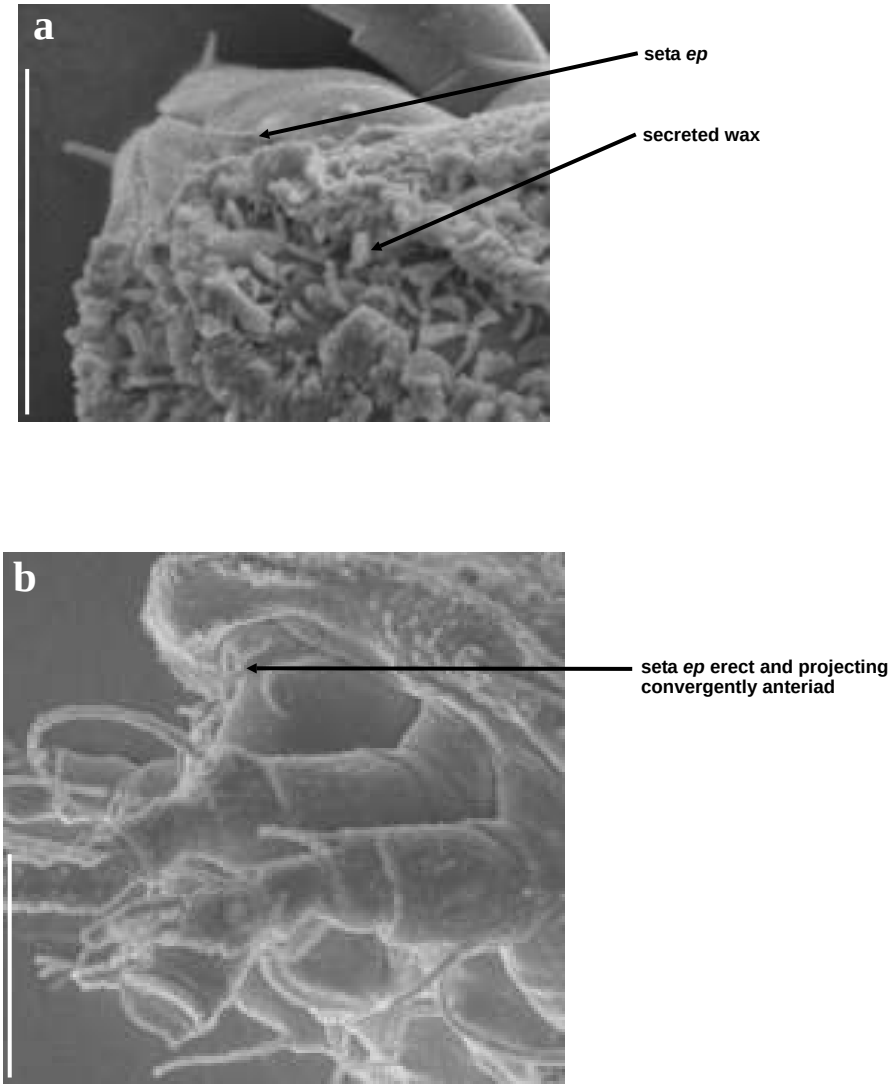


Fig. 3.62. Gnathosoma of *cf. Aculus* sp. or possibly an immature of *Quantalitus* (Eriophyidae) from *Rothmannia capensis*: a) dorsal view, frontal lobe obscures most of gnathosoma (possibly immature); b) lateral view (immature). Scale lines = 10 µm.

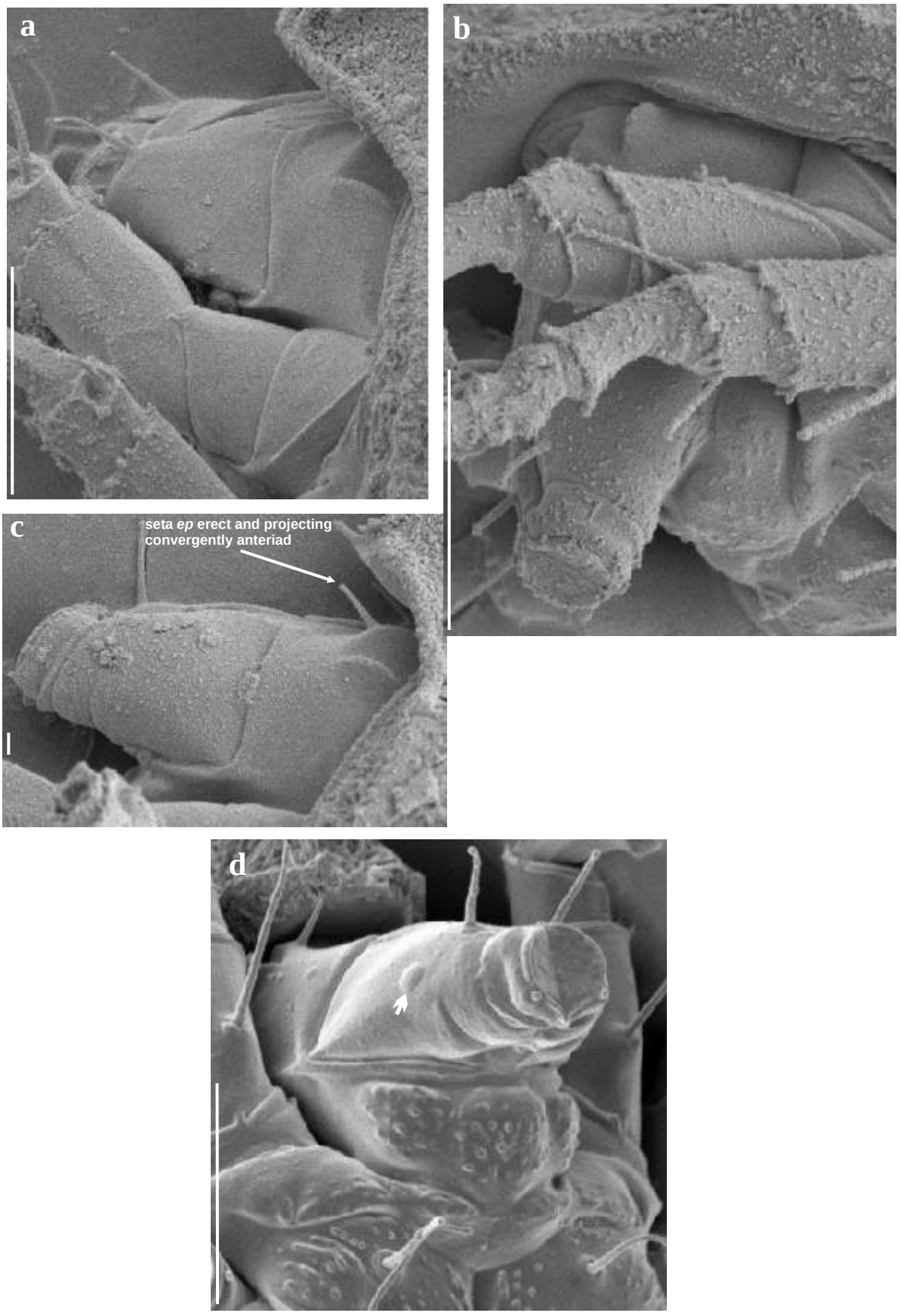


Fig. 3.63. Gnathosoma of *Costarectus zeyheri* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Dovyalis zeyheri*: **a)** dorso-lateral view (adult, probably female); **b)** dorso-lateral view (male); **c)** lateral view (female); **d)** ventro-lateral view (female), short white arrow indicates droplet-like structure that is probably not part of the mite, but an artefact; **a, b, d)** scale lines = 10 µm; **c)** scale line = 1 µm.

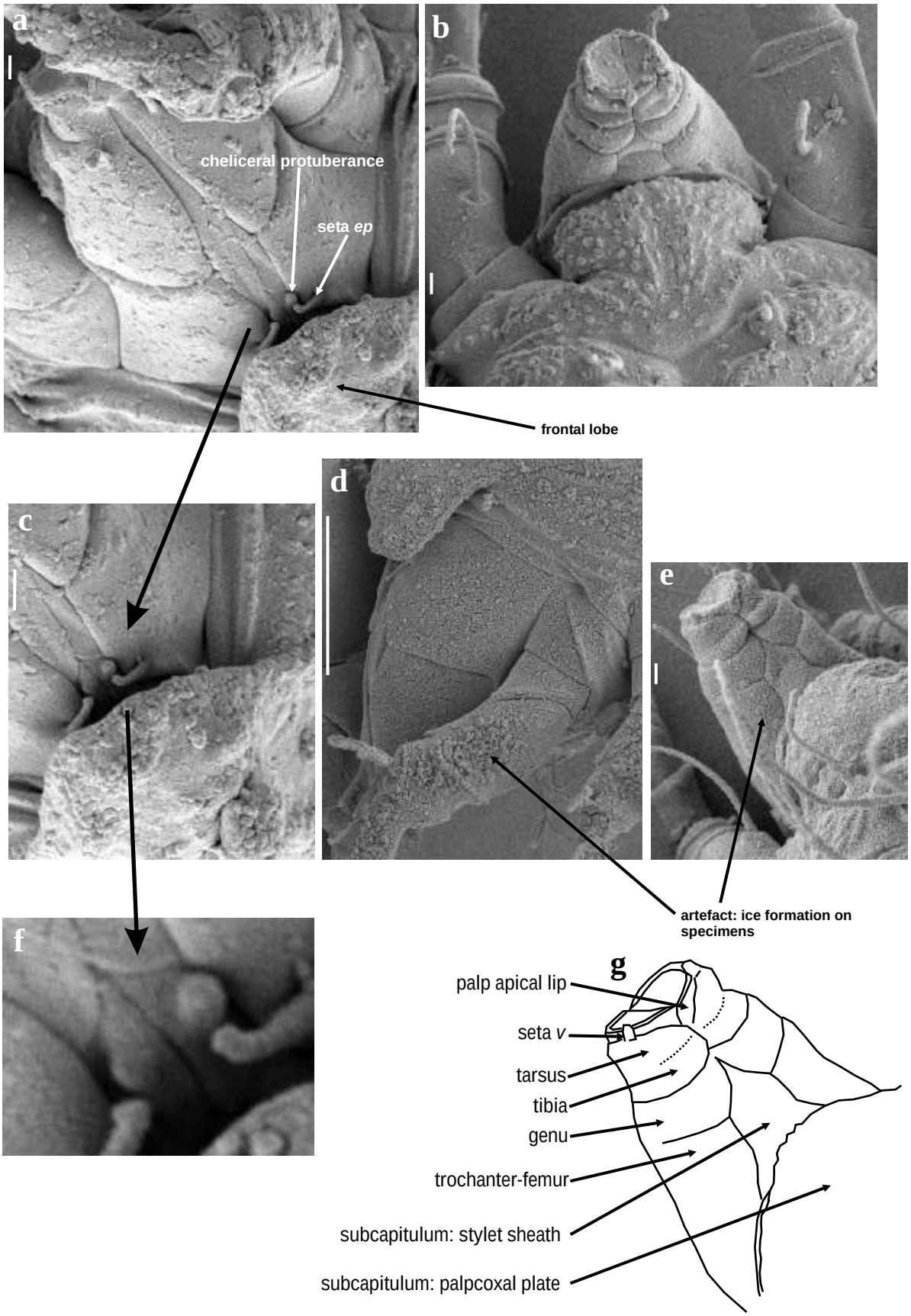


Fig. 3.64. Gnathosoma of *Meyerella bicristatus* (Meyer, 1989) females (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Mystroxylon aethiopicum*: **a, c, f)** ventro-dorsal views of the same specimen, with cheliceral protuberances in Fig. 3.64a enlarged in c and further enlarged in f; **b)** ventral view; **d)** lateral view; **e)** ventro-lateral view; **g)** line drawing of Fig. 3.64e; **a, b, c, e)** scale lines = 1 µm; **d)** scale line = 10 µm.

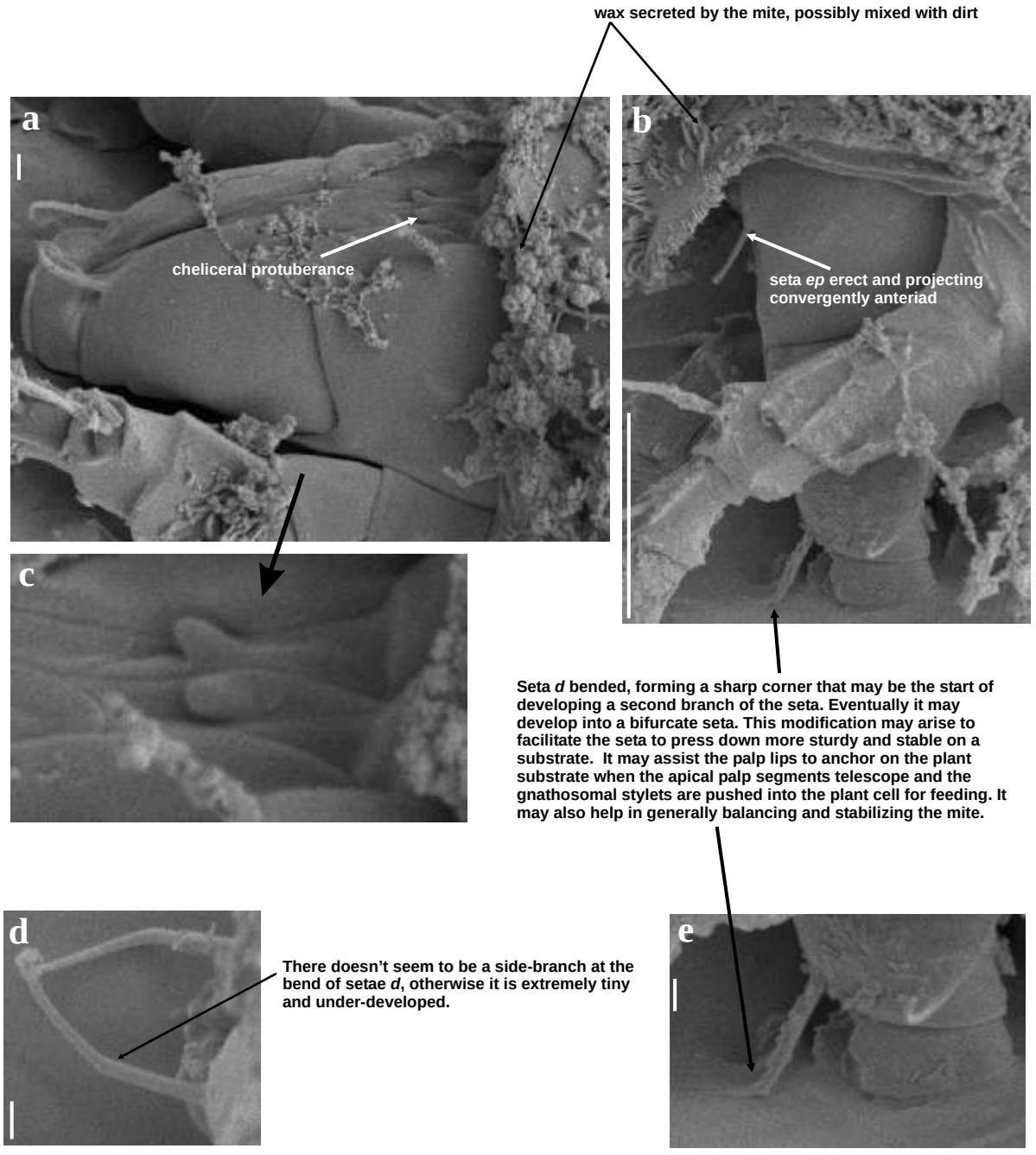


Fig. 3.65. (continued on next page). Gnathosoma of possibly a new genus nr. *Costarectus* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Mystroxylon aethiopicum*: **a)** dorso-lateral view (probably adult, gender unknown); **b, e)** lateral views of the same specimen (male); **c)** enlargement of cheliceral protuberances in Fig. 3.65a; **d)** dorsal view to show the shape of the dorsal pedipalp genual setae (setae *d*) (probably adult, gender unknown); **a, d, e)** scale lines = 1 µm; **b)** scale line = 10 µm.

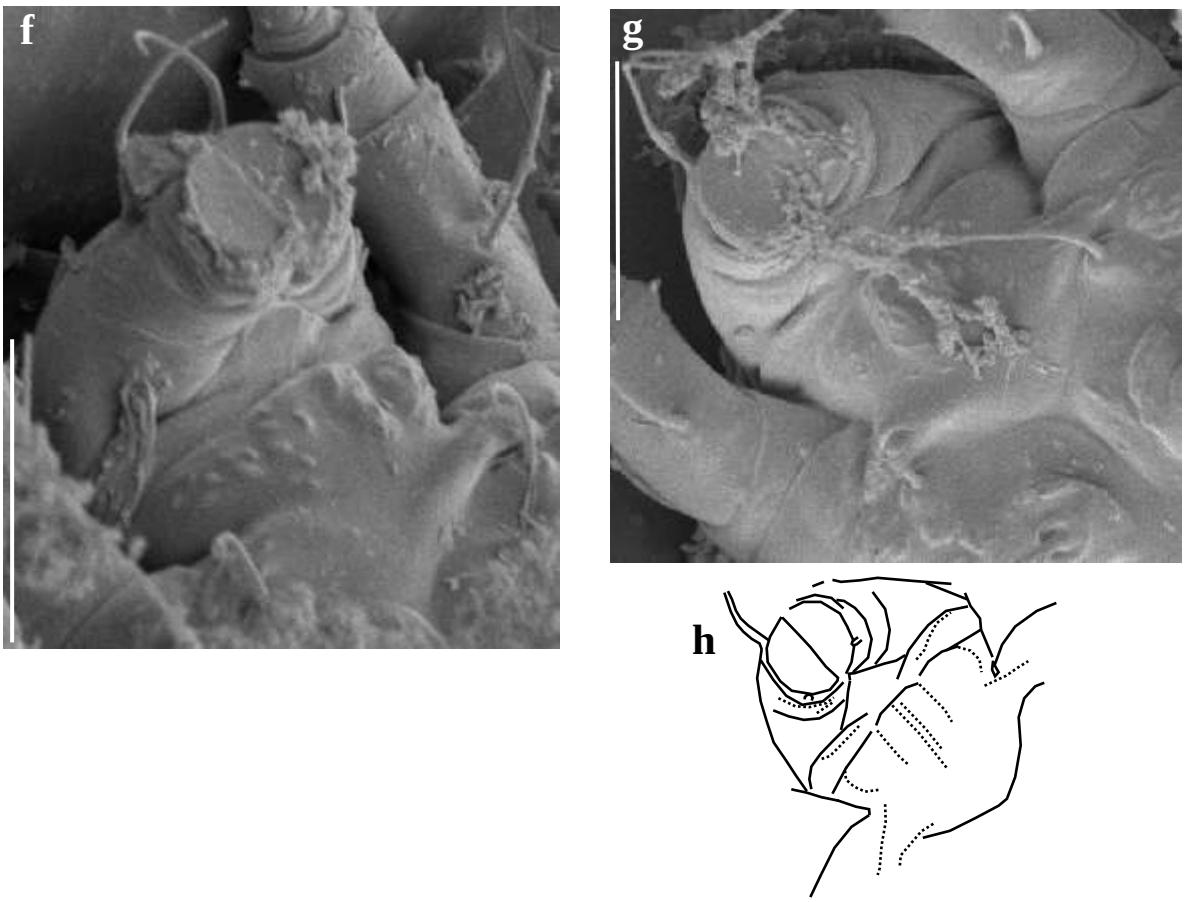


Fig. 3.65. (continued from previous page). Gnathosoma of possibly a new genus nr. *Costarectus*: **f)** ventro-lateral view (male); **g)** ventral view (male); **h)** line drawing of Fig. 3.65g. Scale lines = 10 µm.

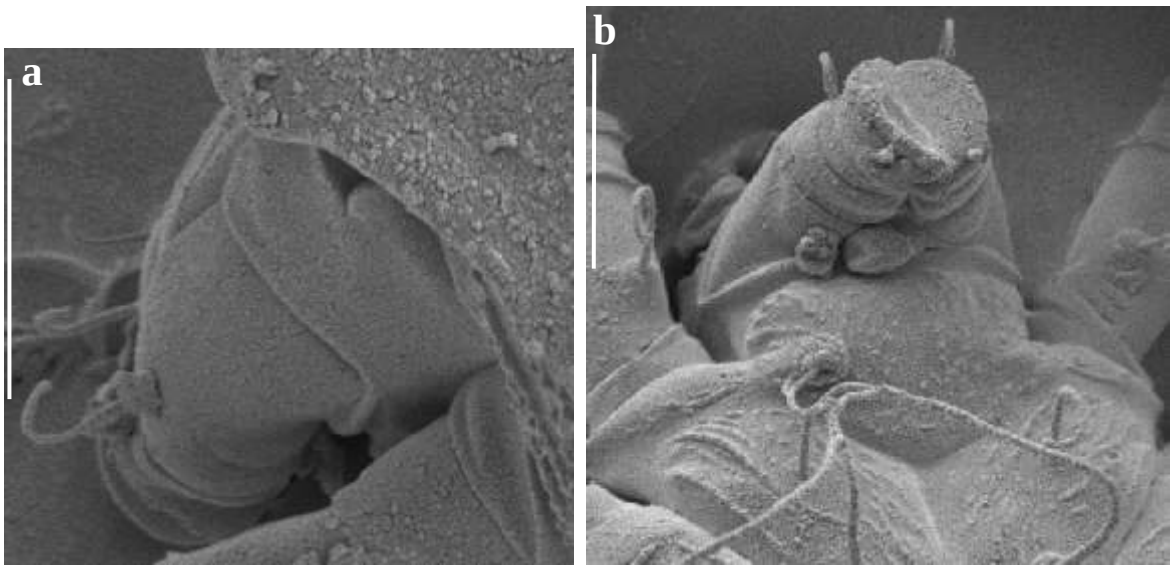


Fig. 3.66. Gnathosoma of possibly a new genus nr. *Tetra* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Protea caffra* subsp. *caffra*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female). Scale lines = 10 µm.

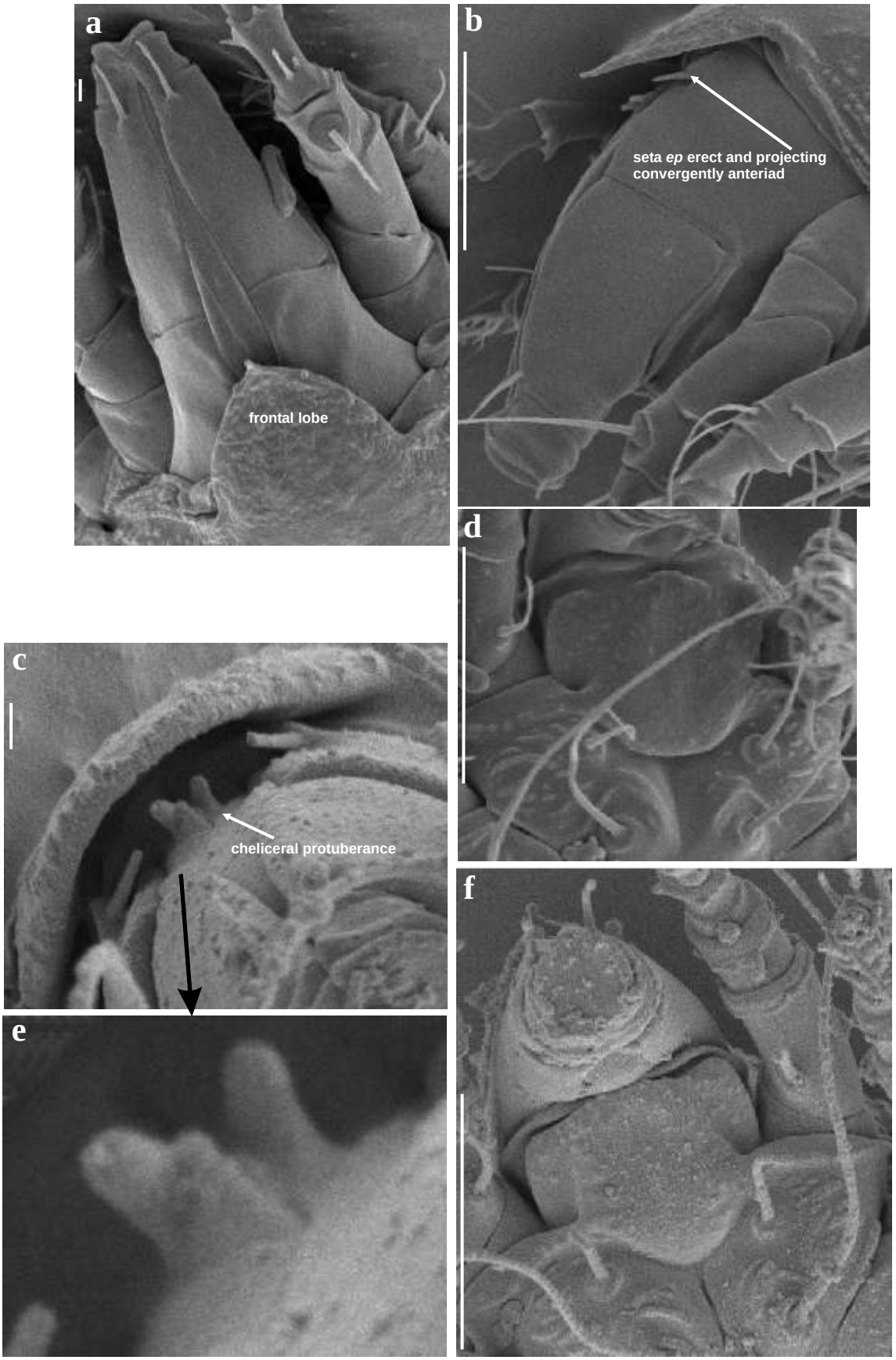


Fig. 3.67. Gnathosoma of possibly a new genus nr. *Mesalox* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Apodytes dimidiata*: **a)** dorsal view (probably adult, gender uknown); **b)** lateral view (female); **c)** ventro-dorsal view (female); **d)** ventro-lateral view (female); **e)** enlargement of the cheliceral protuberances in Fig. 3.67a; **f)** ventral view (male); **a, c)** scale lines = 1 µm; **b, d, f)** scale line = 10 µm.

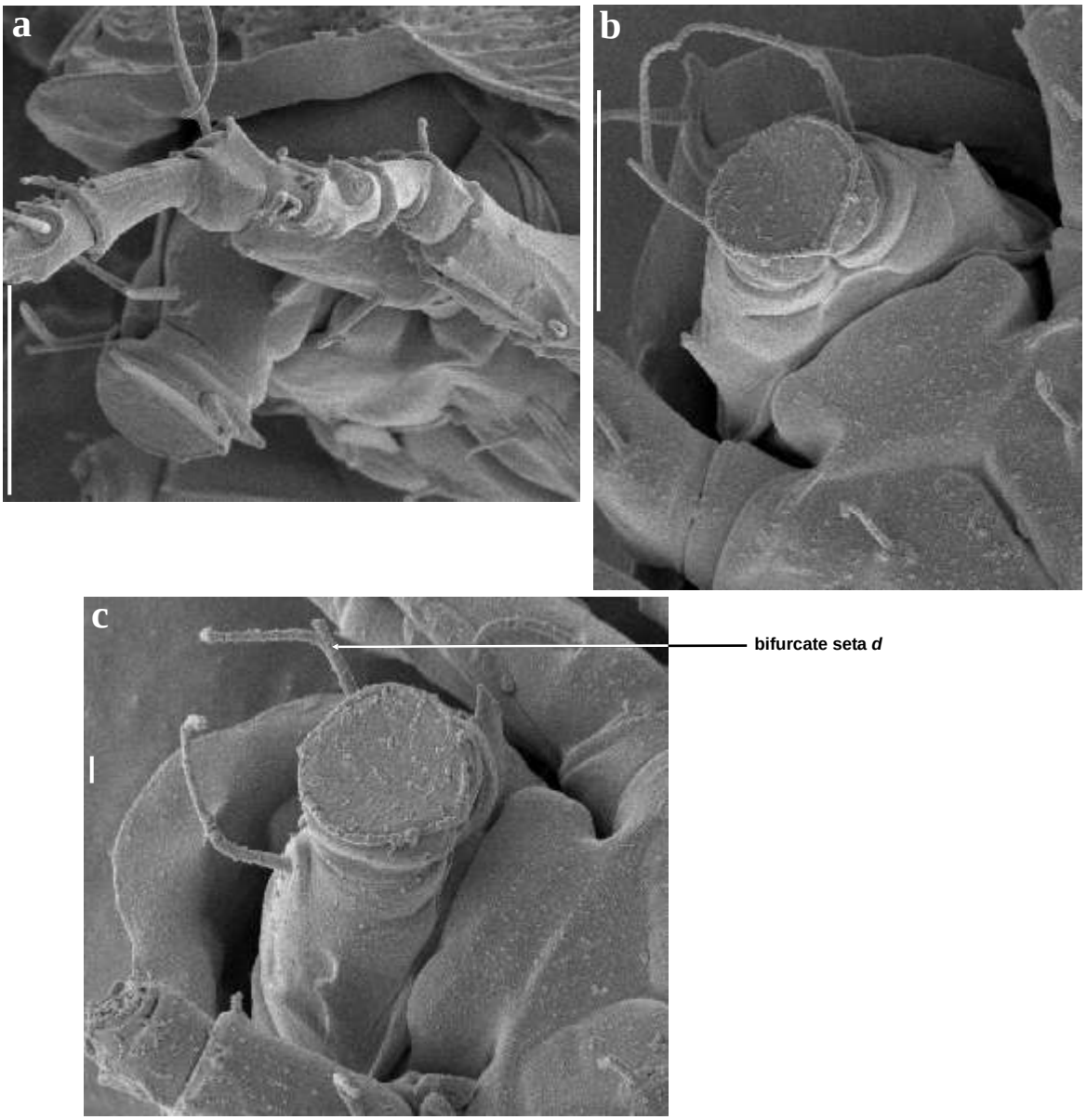


Fig. 3.68. Gnathosoma of *Porosus monosporae* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Xymalos monospora*: **a)** ventro-lateral view (female); **b)** ventral view (female); **c)** ventro-lateral view (male); **a, b)** scale lines = 10 µm; **c)** scale line = 1 µm.

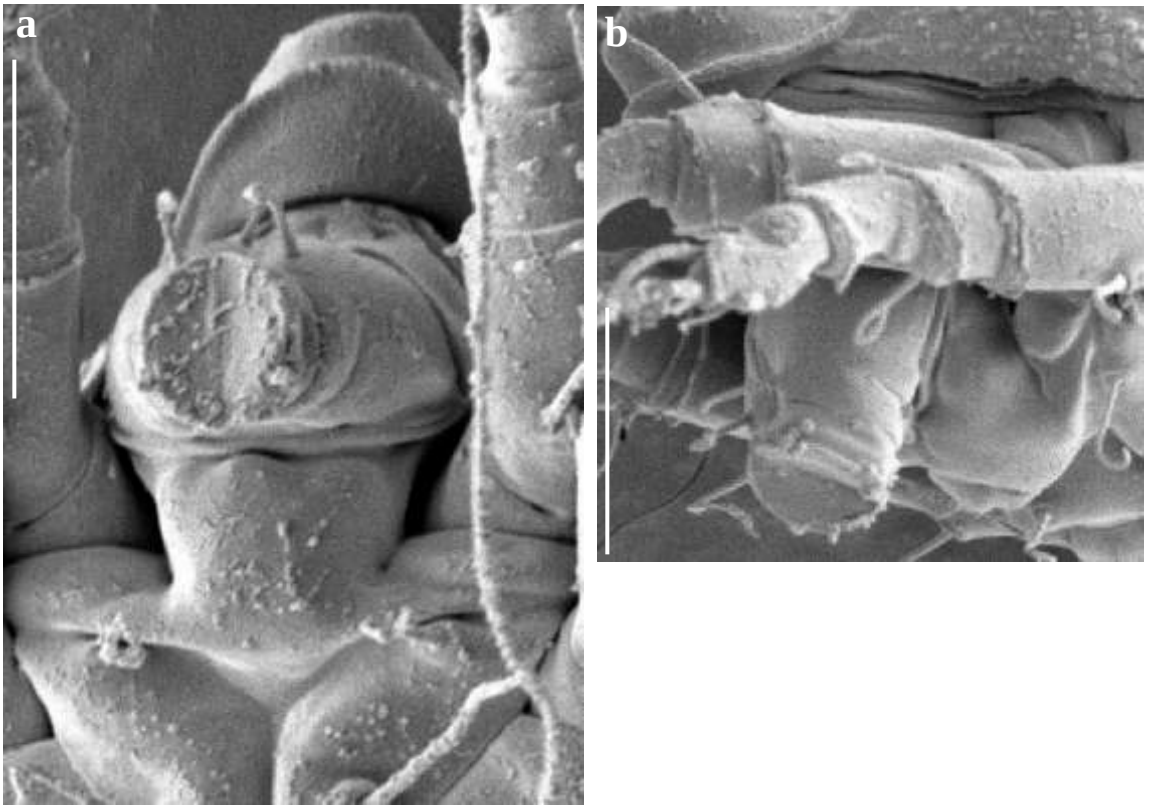


Fig. 3.69. Gnathosoma of *Tegolophus* sp. *cf. T. orientalis* Meyer, 1990 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Trema orientalis*: **a)** ventro-lateral view (female); **b)** lateral view (female). Scale lines = 10 µm.

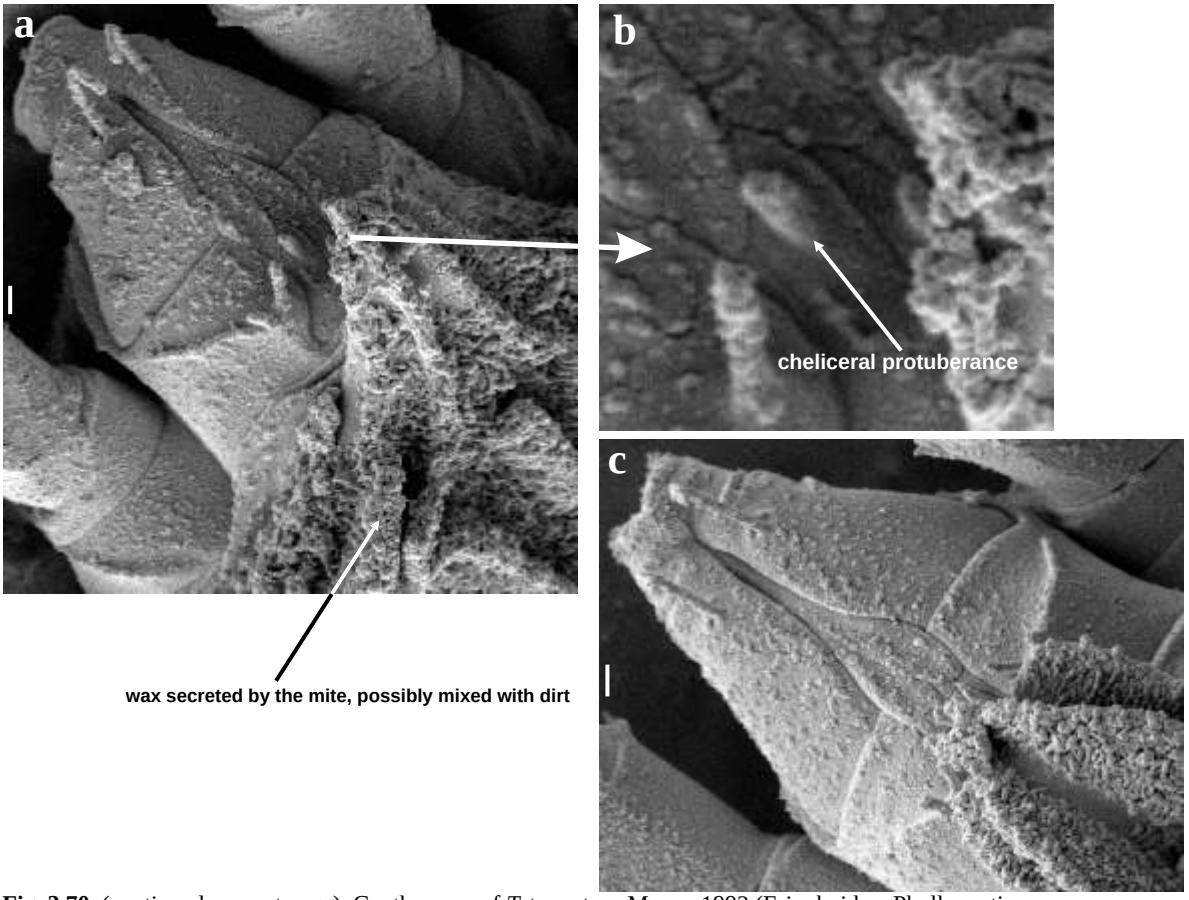


Fig. 3.70. (continued on next page). Gnathosoma of *Tetra retusa* Meyer, 1992 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Bauhinia galpinii*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** enlargement of cheliceral protuberances in Fig. 3.70a; **c)** dorsal view (probably adult, gender unknown). Scale lines = 10 µm.

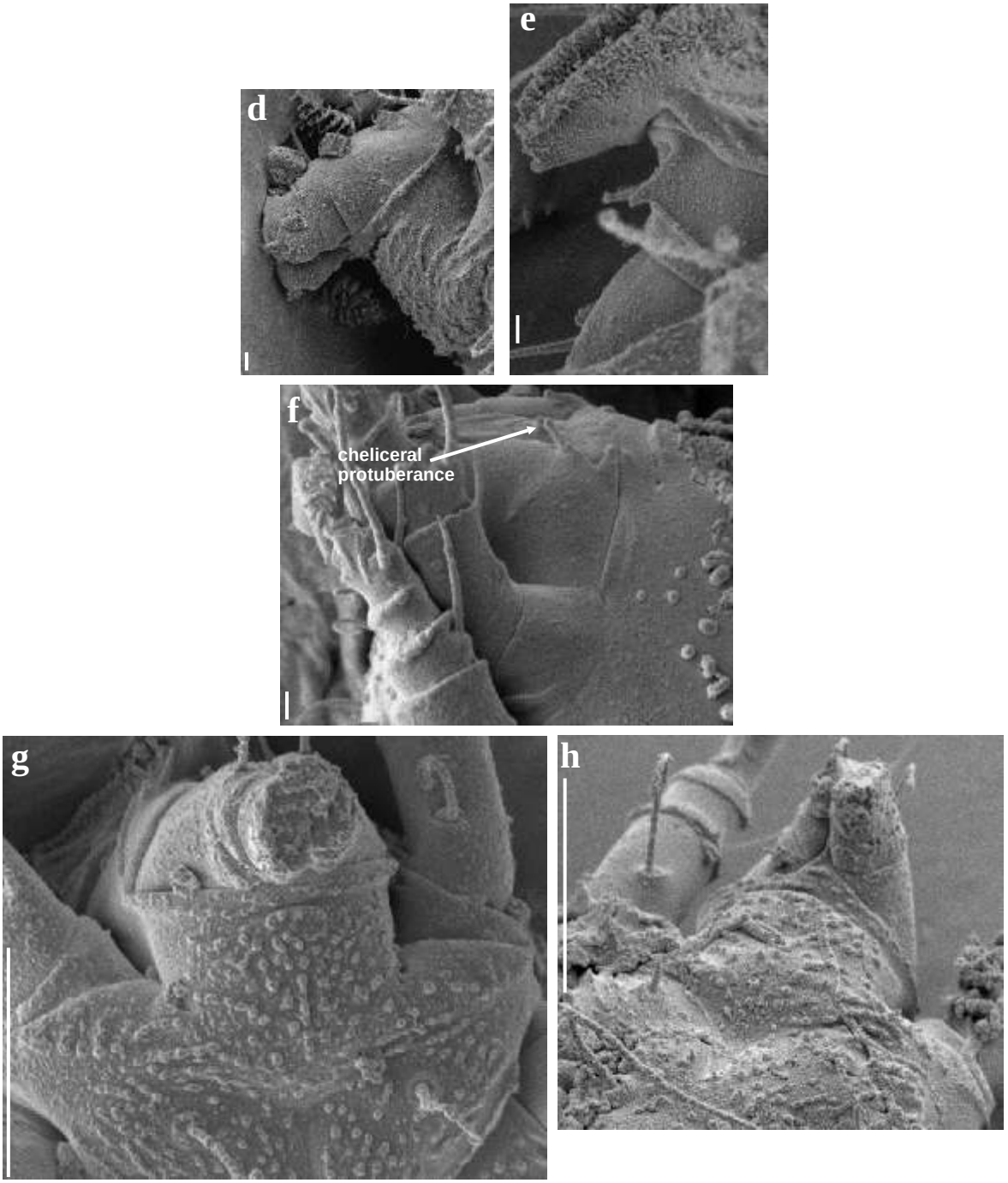


Fig. 3.70. (continued from previous page). Gnathosoma of *Tetra retusa*: **d)** ventro-lateral view (female); **e)** lateral view (female); **f)** dorso-lateral view (larva); **g)** ventral view (female); **h)** ventral view (male); **d, e, f)** scale lines = 1 µm; **g, h)** scale lines = 10 µm.

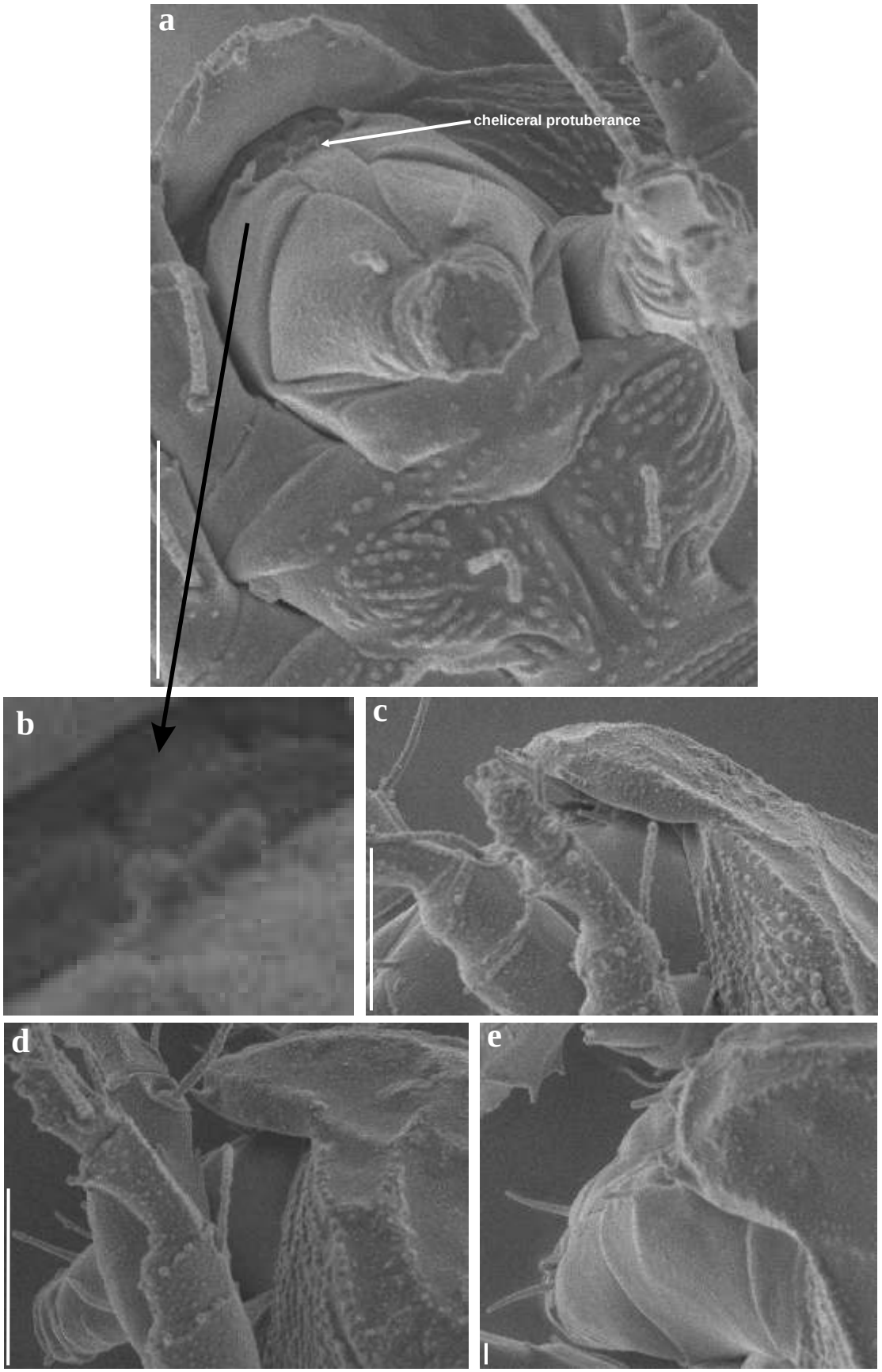


Fig. 3.71. Gnathosoma of *Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Chrysanthemoides monilifera* subsp. *monilifera*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in Fig. 3.71a; **c, d)** lateral views (females); **e)** dorso-lateral view (probably adult, gender unknown); **a, c, d)** scale lines = 10 µm; **e)** scale line = 1 µm.

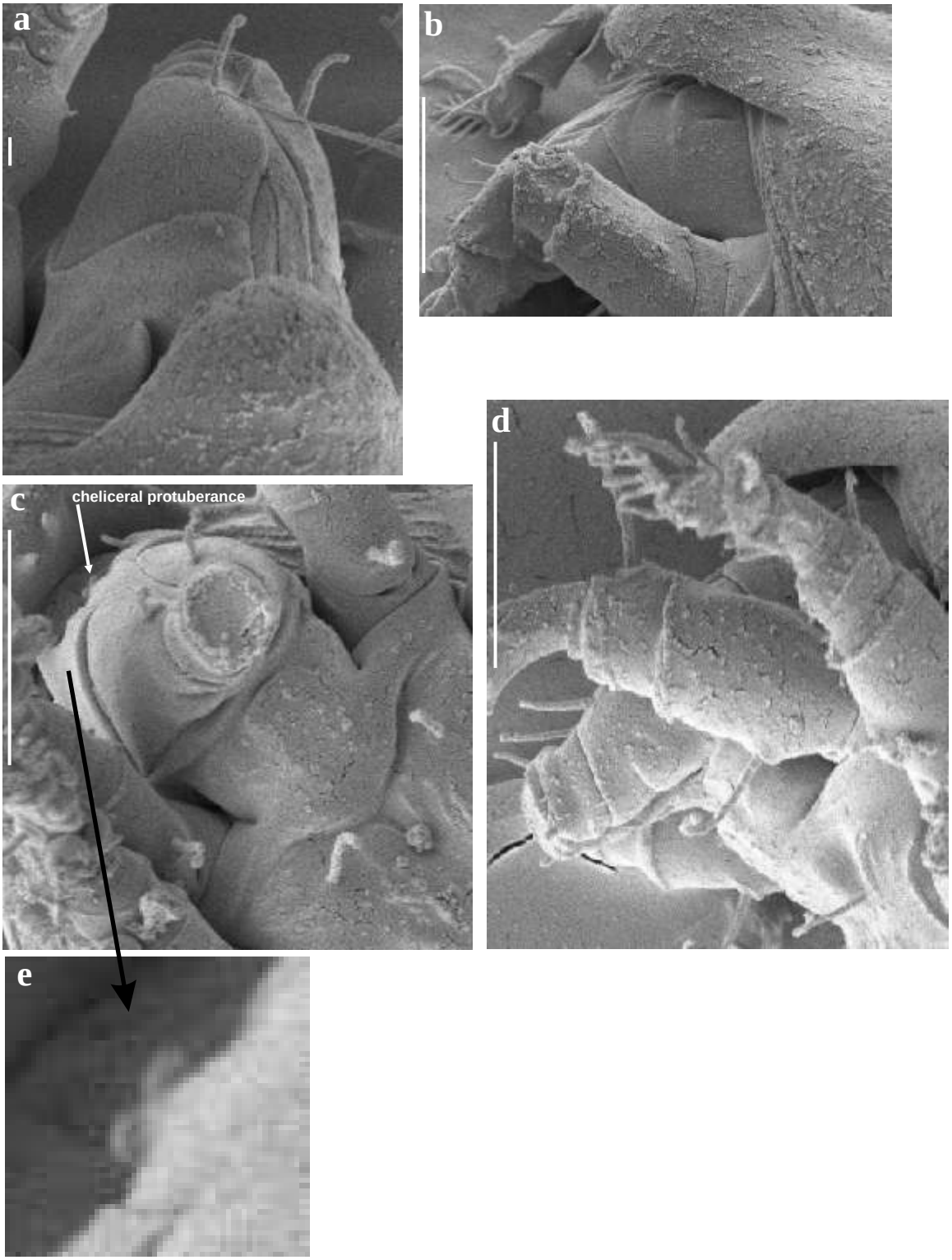


Fig. 3.72. Gnathosoma of *cf. Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Faurea rochetiana*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** lateral view (female); **c)** dorso-ventral view (female); **d)** lateral view (female); **e)** enlargement of cheliceral protuberances; **a)** scale line = 1 µm; **b, c, d)** scale lines = 10 µm.

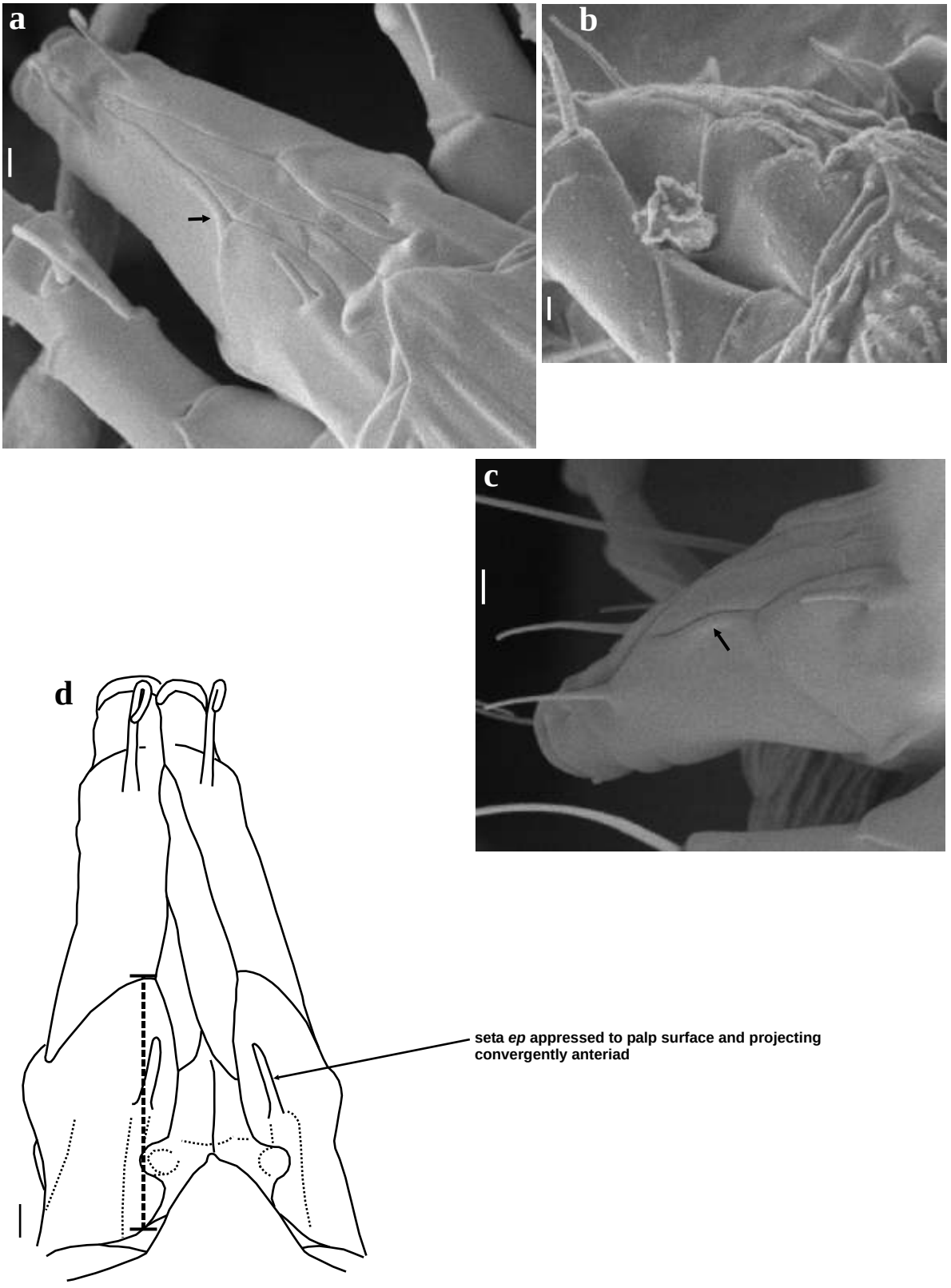


Fig. 3.73. (continued on next page). Gnathosoma of a possibly new worm-like genus (Eriophyidae: Eriophyinae?: Aceriini?) from *Faurea rochetiana*: **a)** dorsal view (probably adult, gender unknown), the black arrow indicates the slight ridge shaped inner edge of the palp trochanter-femur; **b)** dorso-lateral view (probably adult, gender unknown); **c)** dorso-lateral view (probably adult, gender unknown), the black arrow indicates the slight ridge shaped inner edge of the palp trochanter-femur; **d)** line drawing of Fig. 3.73a, dashed black line indicates length of palpcoxal base. Scale lines = 1 µm.

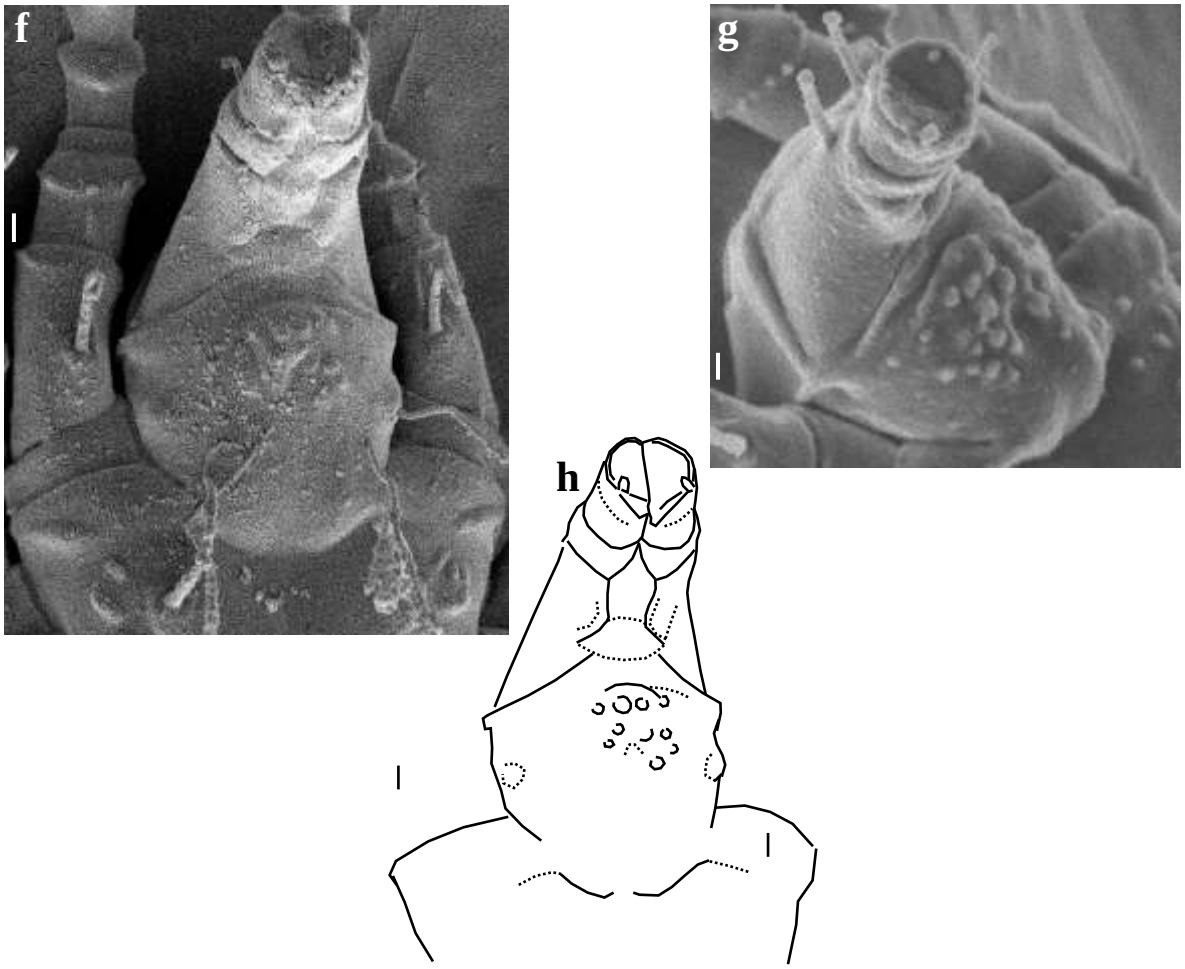


Fig. 3.73. (continued from previous page). Gnathosoma of a possibly new worm-like genus (Eriophyidae: Eriophyinae?: Aceriini?): f) ventral view (female); g) ventro-lateral view (male); h) line drawing of Fig. 3.73f. Scale lines = 1 µm.

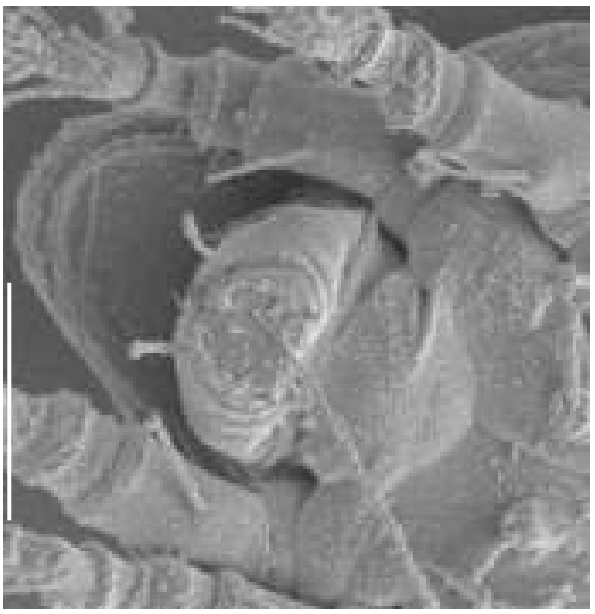


Fig. 3.74. Gnathosoma of an unknown genus (could not be identified) (Eriophyidae: Phyllocoptinae?) from *Ekebergia capensis*: ventral view (male). Scale line = 10 µm.

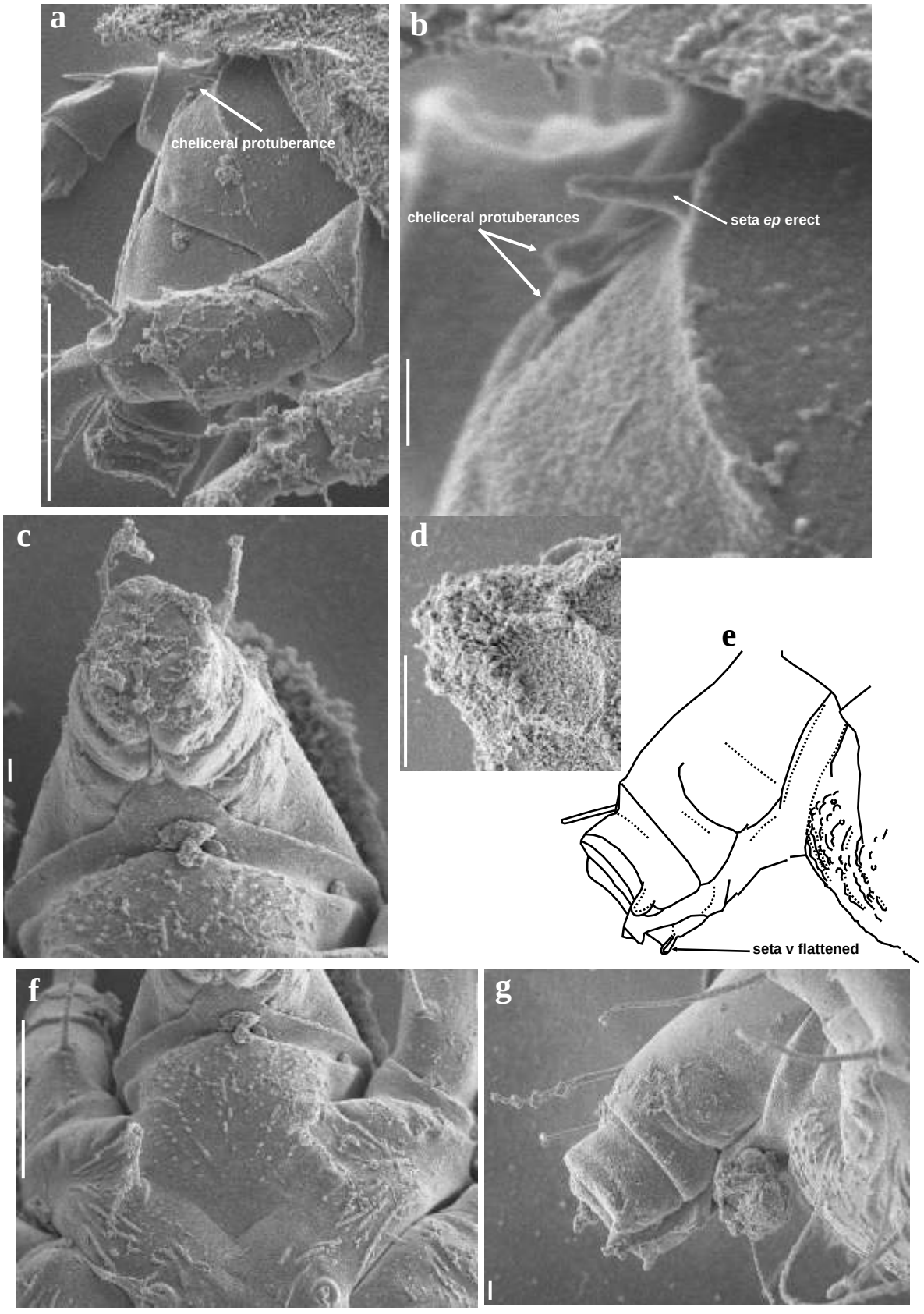


Fig. 3.75. Gnathosoma of a possibly new genus in the Phyllocoptinae or Cecidophyinae (Eriophyidae) from *Acacia burkei*: **a)** lateral view (possibly nymph); **b)** same specimen as in Fig. 3.75a, enlargement of cheliceral protuberances; **c, f)** ventral views of the same specimen (female); **d)** dorsal view, gnathosoma obscured by frontal lobe (probably adult, gender unknown); **e)** line drawing of Fig. 3.75g; **g)** lateral view (female) with dorso-ventrally flattened and oval shaped setae *v*; **a, d, f)** scale lines = 10 µm; **b, c, g)** scale lines = 1 µm.

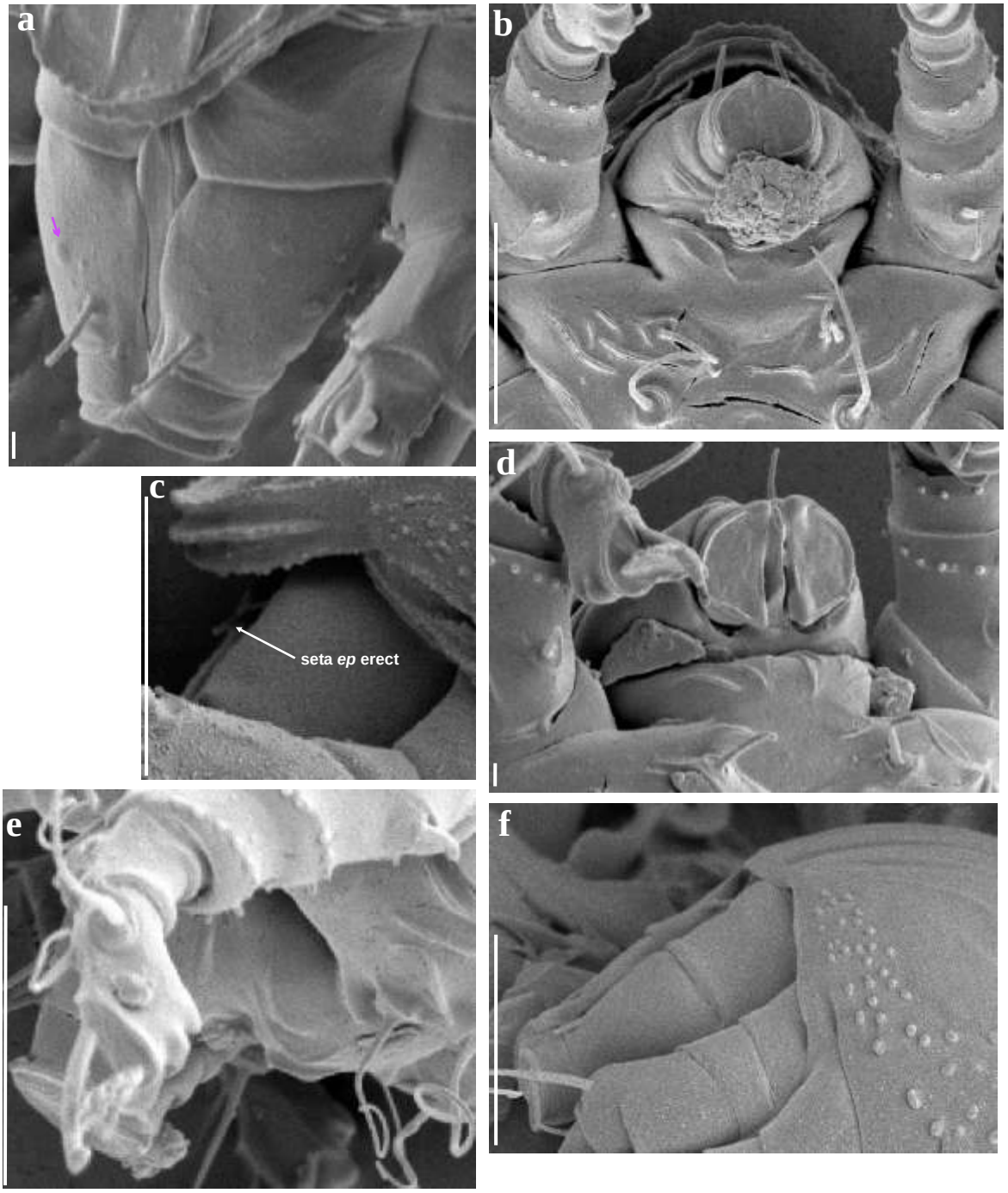


Fig. 3.76. Gnathosoma of *Phyllocoptes* sp. (Phyllocoptinae) or new genus (Cecidophyinae) from *Dovyalis zeyheri*: **a)** dorsal view, basal part of gnathosoma obscured by frontal lobe (probably adult, gender unknown); **b)** ventral view (male); **c)** lateral view of basal part of gnathosoma (female); **d)** ventro-lateral view (female); **e)** lateral view of distal part of gnathosoma (female); **f)** dorso-lateral view (larva); **a, d)** scale lines = 1 µm; **b, c, e, f)** scale lines = 10 µm.

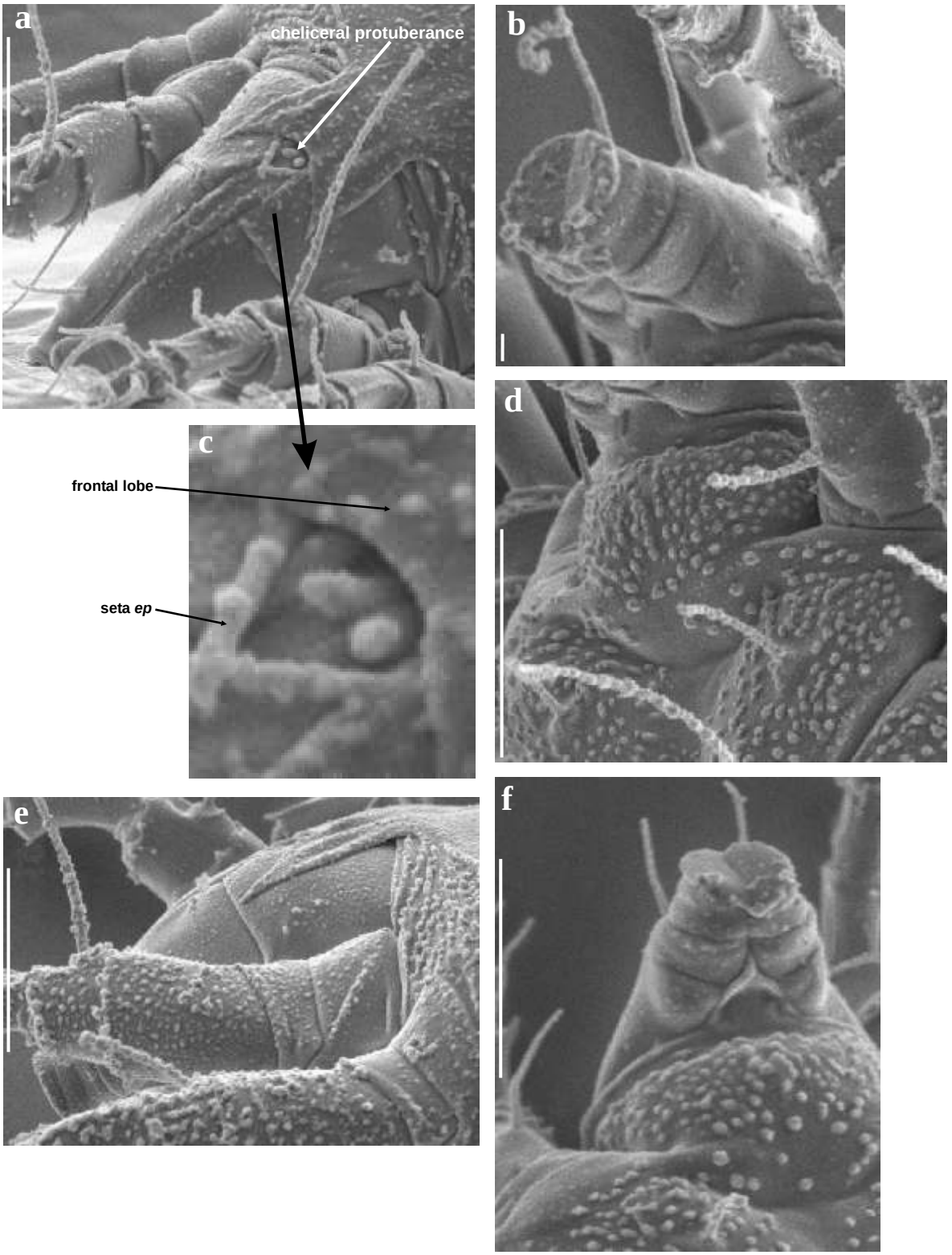


Fig. 3.77. Gnathosoma of a probably new genus (Eriophyidae, subfamily uncertain) from *Cussonia* sp. flowers: **a)** dorso-lateral view (probably adult, gender unknown); **b, d)** ventro-lateral views of the same specimen (female); **c)** enlargement of cheliceral protuberances in Fig. 3.77a; **e)** lateral view (female); **f)** ventral view (male); **a, d, e, f)** scale lines = 10 µm; **b)** scale line = 1 µm.

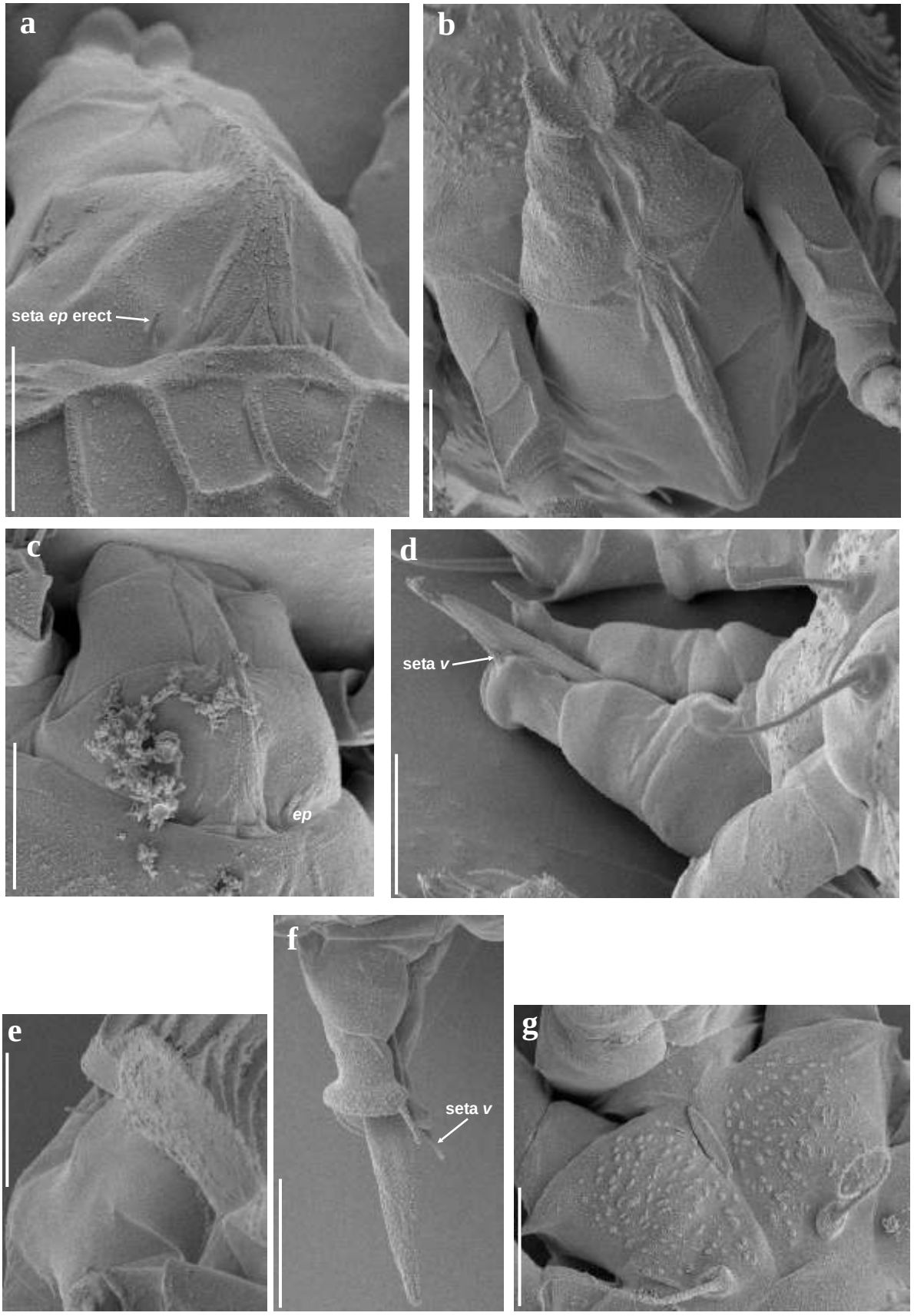


Fig. 3.78. Gnathosoma of *Diptilomiopus apobrevis* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Apodytes dimidiata*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorso-lateral view (larva); **d)** ventro-lateral view (female); **e)** lateral view, basal part (possibly nymph, or male); **f)** ventro-lateral view, apical part (female); **g)** ventral view (female). Scale lines = 10 µm.

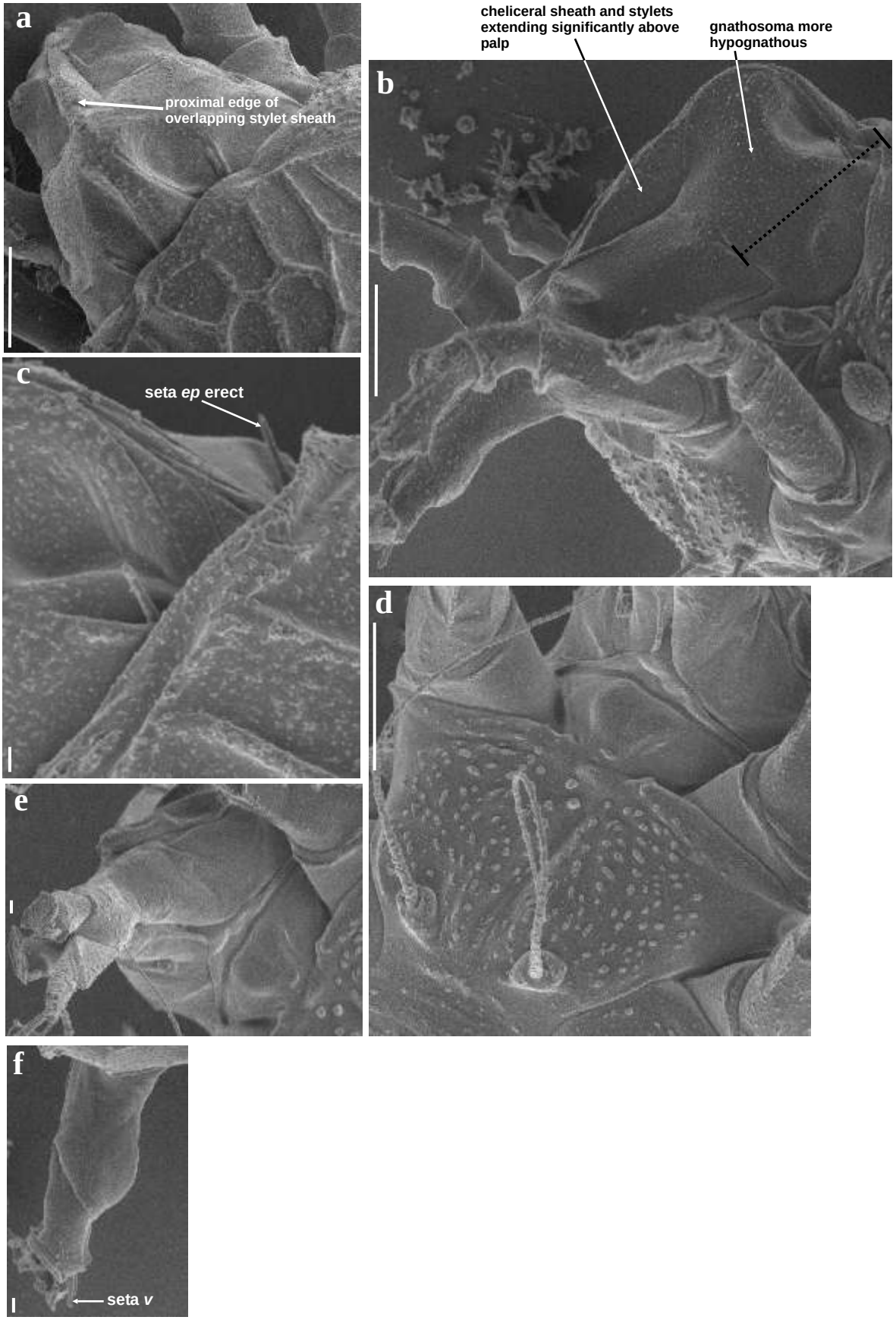


Fig. 3.79. Gnathosoma of *Diptilomiopus faurius* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Faurea rochetiana*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female), dashed black line indicates length of palpcoxal base; **c)** dorso-lateral view, basal part (female); **d, e)** ventro-lateral views of the same specimen (female); lateral view (distal part of gnathosoma); **a, b, d)** scale lines = 10 µm; **c, e, f)** scale lines = 1 µm.

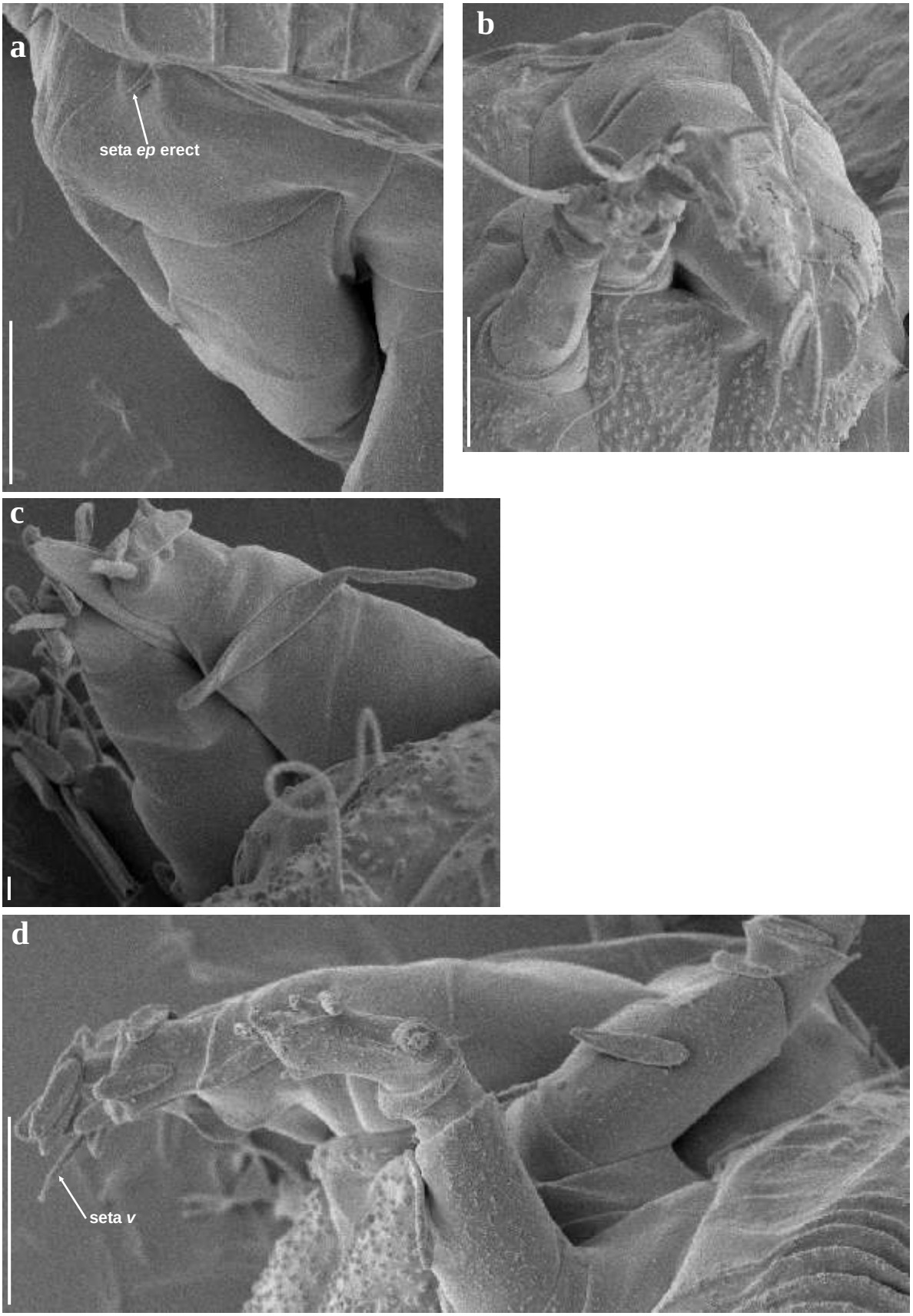


Fig. 3.80. Gnathosoma of unidentified species (genus and species could not be identified) (Diptilomiopidae: Diptilomiopinae) from *Xymalos monospora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** ventral view (male); **d)** lateral view (female); **a, b, d)** scale lines = 10 µm; **c)** scale line = 1 µm.

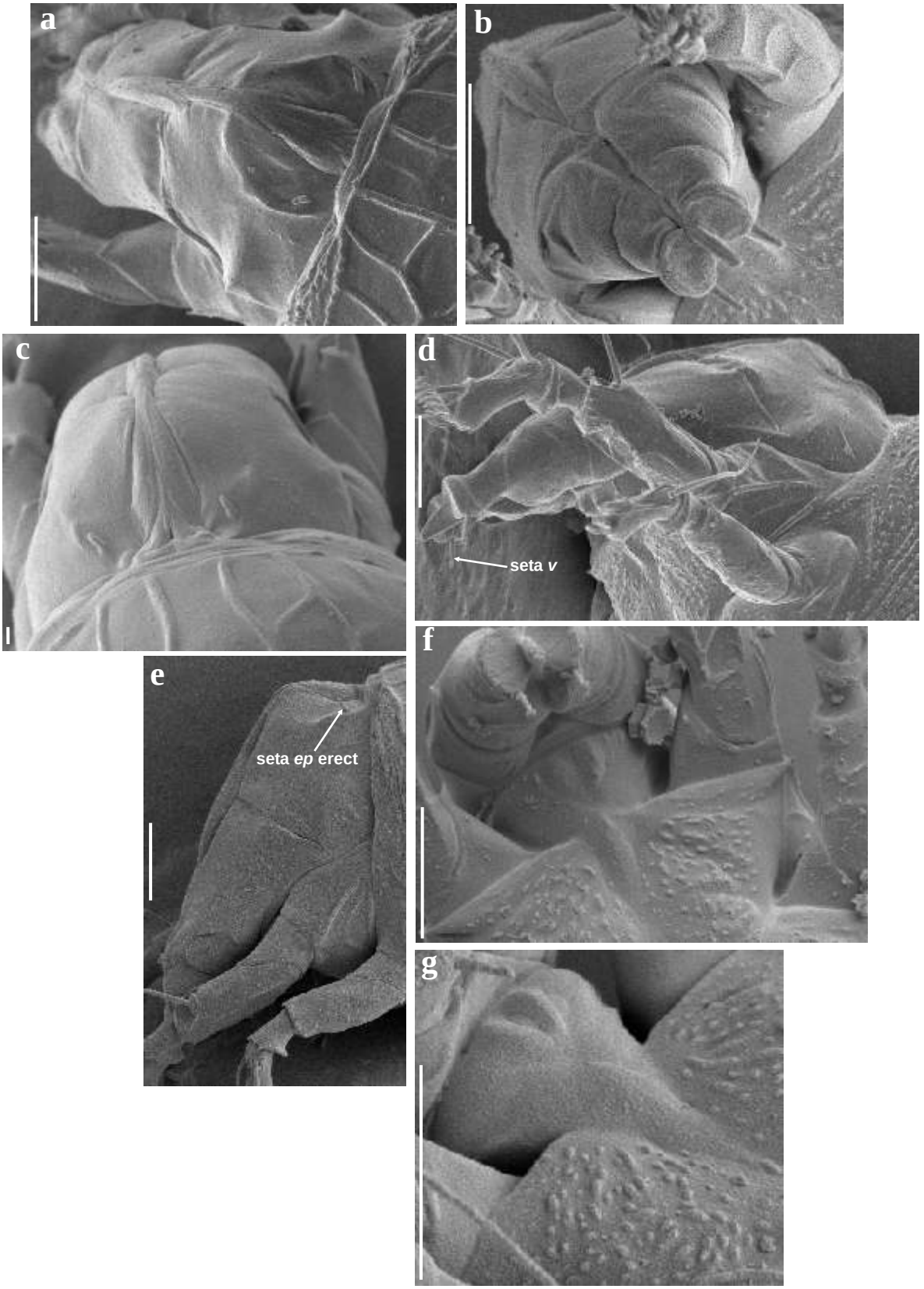


Fig. 3.81. Gnathosoma of probably a new genus nr. *Dacundiopus* (Diptilomiopidae: Diptilomiopinae), from *Mystroxylon aethiopicum*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorsal view (immature); **d, e)** lateral views (females); **f)** ventral view (female); ventro-lateral view (female); **a, b, d, e, f, g)** scale lines = 10 µm; **c)** scale line = 1 µm.

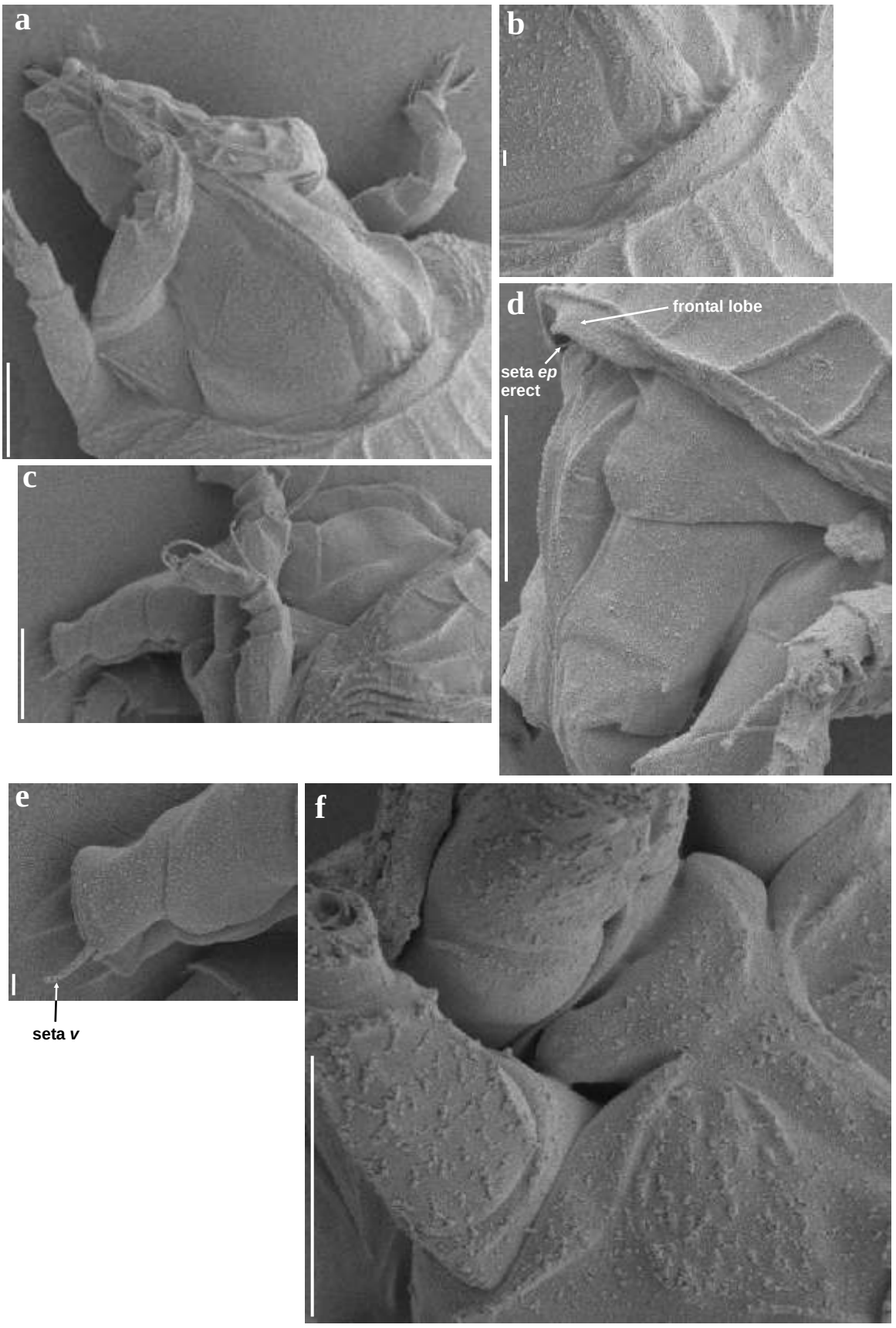


Fig. 3.82. Gnathosoma of *Rhynacus* sp. *cf. Rhynacus* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Dovyalis zeyheri*: **a, b)** dorso-lateral view and enlargement of the basal area respectively of the same specimen (probably adult, gender unknown); **c, e)** lateral view and enlargement of the distal part respectively of the same specimen (male); **d)** dorso-lateral view (female); **f)** ventro-lateral view (male); **a, c, d, f)** scale lines = 10 µm; **b, e)** scale lines = 1 µm.

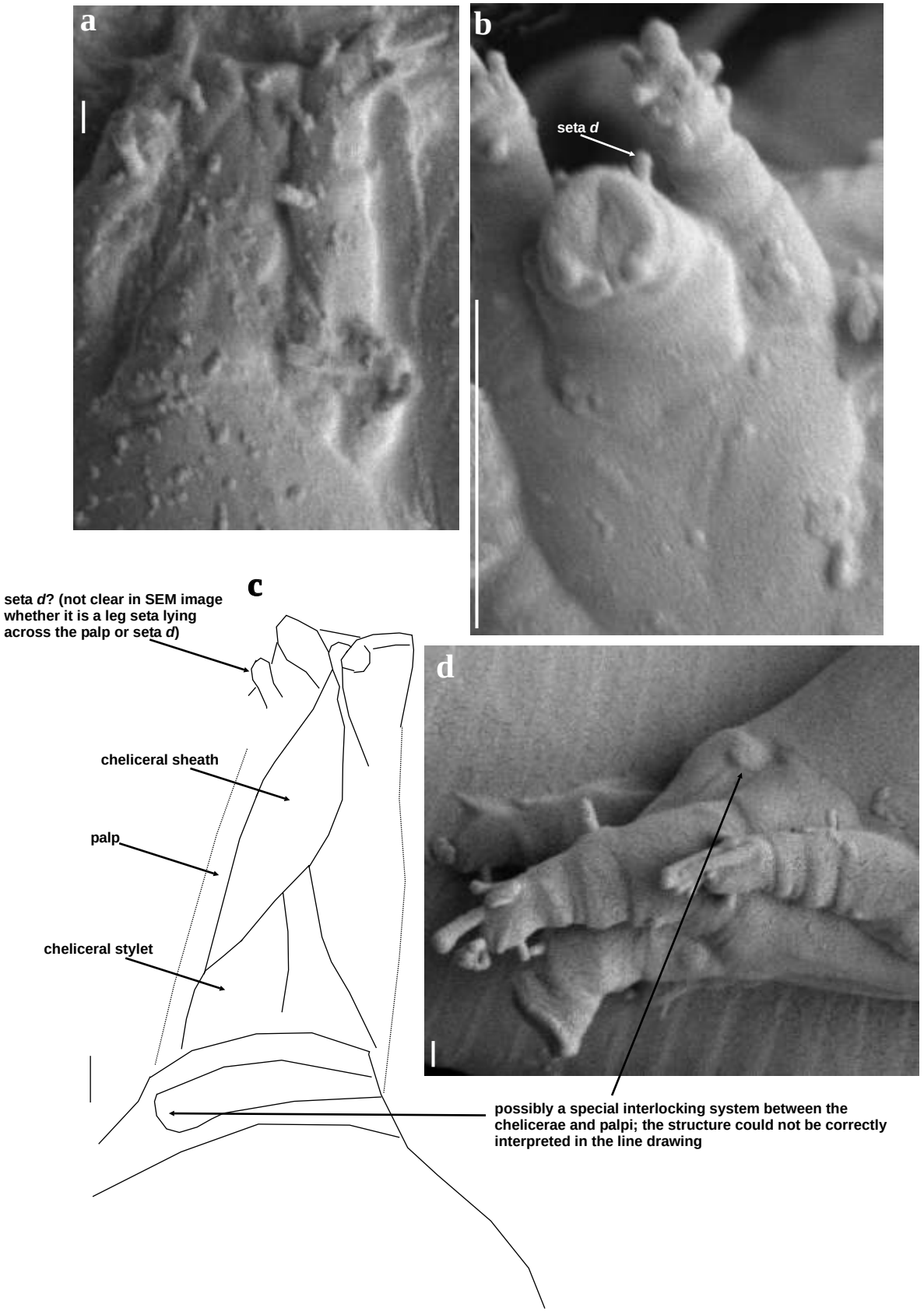


Fig. 3.83. Gnathosoma of probably a new genus (Eriophyidae) from *Searsia lancea* (previously *Rhus lancea*) leaf blisters: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (immature); **c)** preliminary attempt at a line drawing (which is probably still wrong and incomplete, because the SEM images that could be obtained from this species were very unclear, probably due to a sticky substance covering the mites) of the dorsal view of the gnathosoma, from Fig. 3.83a; **d)** lateral view (probably adult, gender unknown); **a, c, d)** scale lines = 1 µm; **b)** scale line = 10 µm.

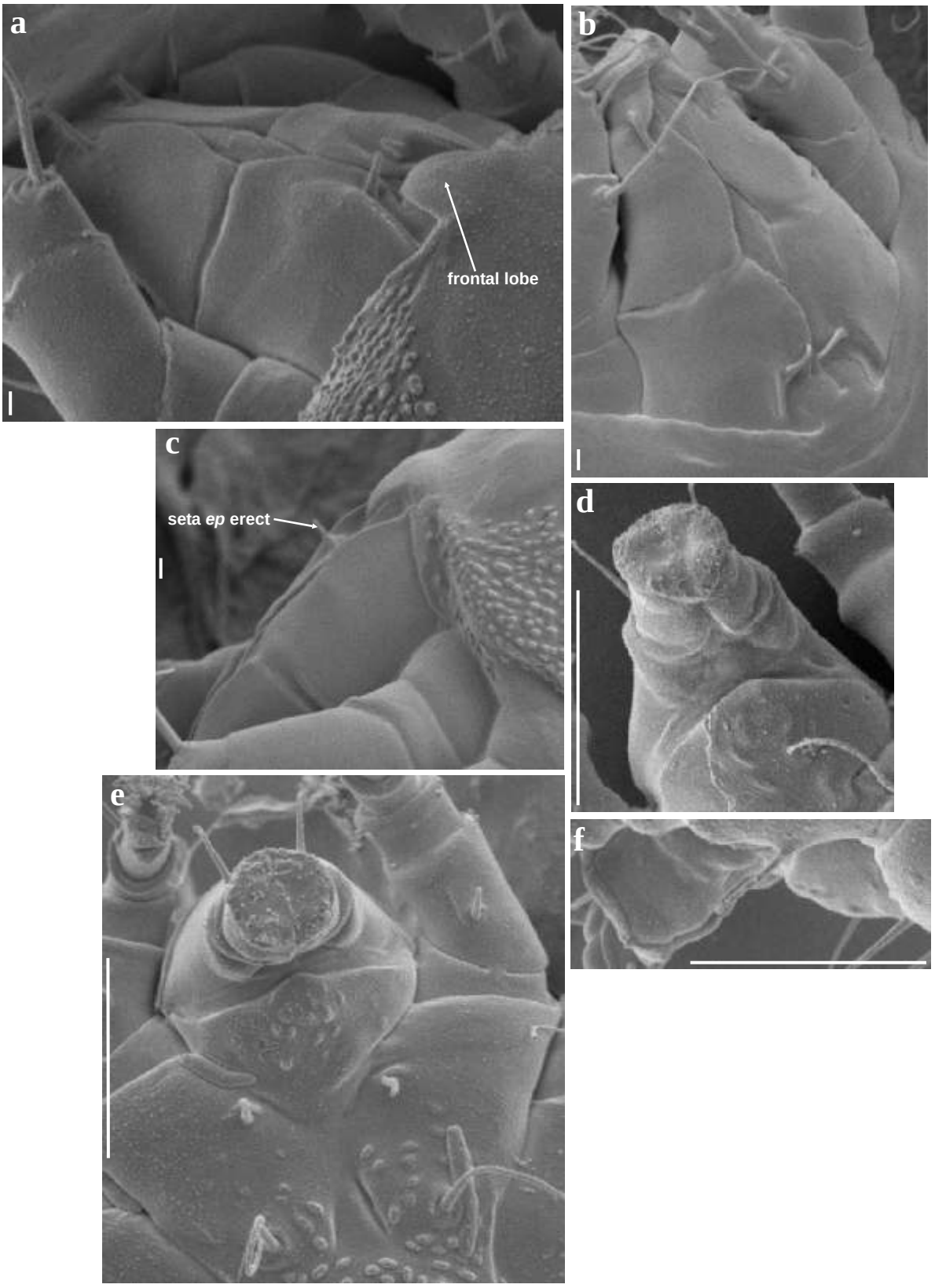


Fig. 3.84. Gnathosoma of unidentified morphospecies 2 (Eriophyoidae: Eriophyidae or Phytoptidae, but it is probably Eriophyidae) from green fruit of *Anthocleista grandiflora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (larva); **c, f)** lateral views of the same specimen (probably adult, gender unknown); **d)** ventral view (female); **e)** ventral view (male); **a, b, c)** scale lines = 1 µm; **d, e, f)** scale lines = 10 µm.

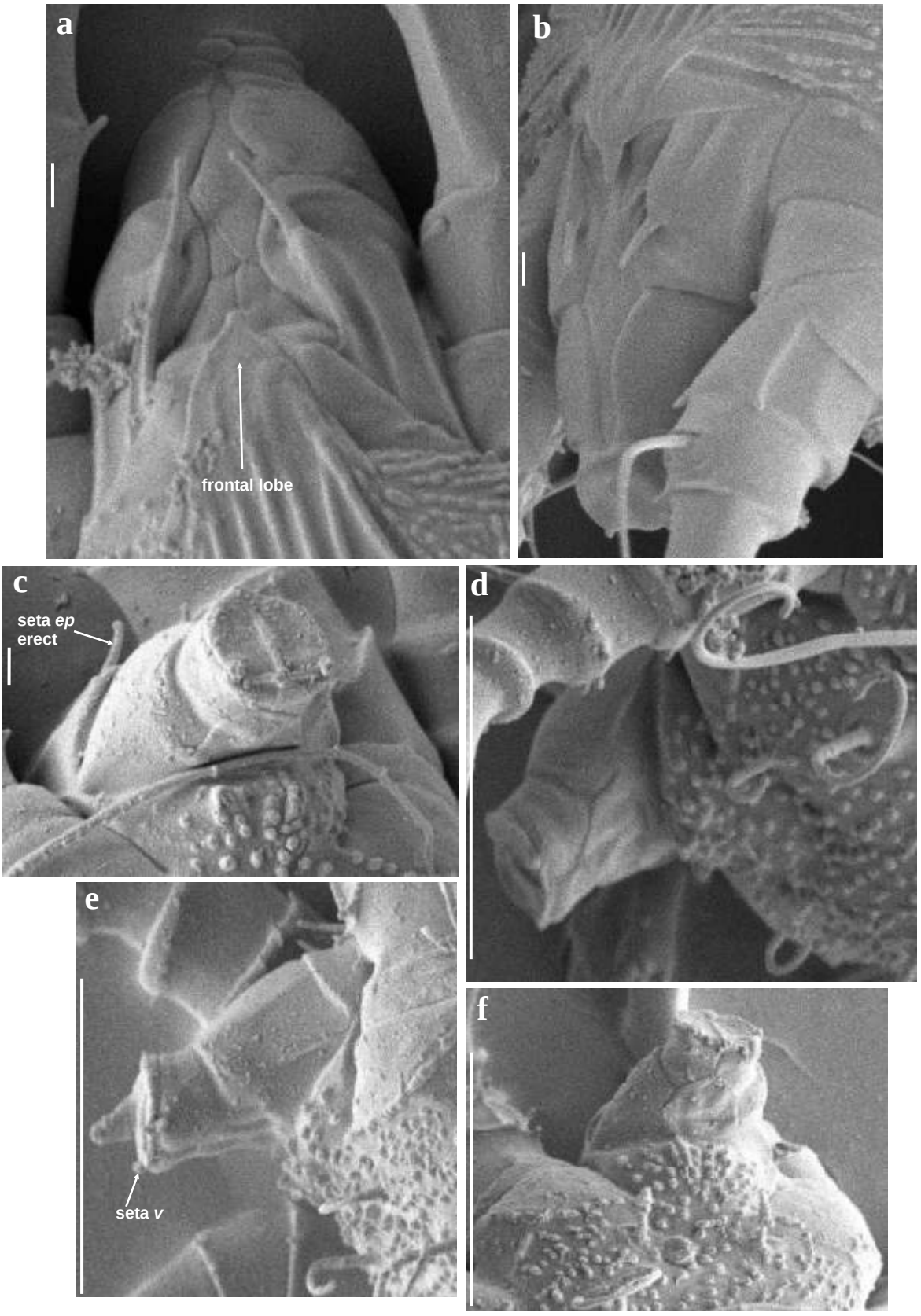


Fig. 3.85. Gnathosoma of unidentified species (genus and species could not be identified) (Eriophyoidea) from *Sideroxylon inerme* subsp. *inerme*: a) dorso-lateral view (probably adult, gender unknown); b) dorso-lateral view (female); c) ventro-lateral view (female); d) ventro-lateral view (female); e) lateral view (female); f) ventro-lateral view (female); **a, b, c)** scale lines = 1 µm; **d, e, f)** scale lines = 10 µm.

3.6 GENERAL DISCUSSION

Similar to other organisms, the quality of the systematics of the Eriophyoidea is associated with the quality of the morphological character descriptions of its taxa. Additional information such as molecular, biological and ecological data can also be incorporated into studies. The quality of eriophyoid systematics also depends on the quality of specimens studied and the observations that are possible. These depend on the collection, preparation, mounting and storage of specimens, and the technology and techniques used to study the specimens.

In practice, there are various short-comings in the systematics of the Eriophyoidea which are almost solely based on morphological information obtained from light microscopic studies of slide-mounted specimens. Often, descriptions and drawings do not achieve the required standard and do not convey taxonomically important characteristics. Much of the weakness in published morphology is caused by the quality and standard of slide-mounted specimens and the quality of their study (Amrine & Manson, 1996; De Lillo *et al.*, 2010). To begin with, the quality of morphological descriptions and systematics of eriophyoid mites can be improved to a large extent, at least for classification and identifications, by improving slide-mounting and description of slide-mounted specimens.

There are, however, inherent inadequacies in light microscopic studies of slide-mounted specimens. Additionally, even when using optimal slide-mounting techniques and study of such specimens, there are problems with standardization of results (De Lillo *et al.*, 2010). Descriptions based on the study of slide-mounted specimens, however, are in essence useful and robust. Some eriophyoid researchers such as E. De Lillo, J.W. Amrine Jr. and V.G. Shevchenko (*pers. comm.*), strongly advise that the *status quo* of obtaining the core taxonomic description solely from slide-mounted specimens, should be retained.

There are, indeed, many advantages to the conventional practice in the systematics of the Eriophyoidea, namely:

- A large amount of descriptive data are already documented and available;
- Some published descriptions are of slide-mounted material that is not available anymore, including type material. For these, the only representation of the taxon is the description (De Lillo *et al.*, 2010). An attempt can be made to re-collect these taxa for re-descriptions from slide-mounted specimens, as well as incorporating other techniques of study, such as SEM, but this sets additional problems. As a result there are no characters described for these species to compare with SEM observations on other species;

- The characters and character states are relatively uncomplicated and easily observable;
- The classification and identification of known eriophyoid species are largely possible using the present set of characters and descriptions and their associated identification keys; and
- Probably most importantly, the slide-mounting technique is reasonably cheap and simple, and equipment for study of slide-mounted specimens is at least available to eriophyoid taxonomists worldwide.

According to some eriophyoid taxonomists, morphological information from SEM studies should not be extensively used and as an obligation incorporated in the systematics and particularly the practical taxonomy of the Eriophyoidea. Unfortunately, the study of slide-mounted eriophyoid specimens has inherent inadequacies and problems that cannot be totally rectified with improved techniques and study. These are demonstrated in part I of present study and briefly entail:

- Structures are viewed in two-dimensions and depth and three-dimensional images of structures are formed by the interpretation of the observer, and is subject to error;
- Phase contrast light microscopy, necessary to study eriophyoid specimens, causes a light halo around specimens and this obscures some detail;
- The size of many eriophyoid morphological structures is at the limits of the resolution of light microscopy. The margin of error in the current descriptions based on light microscopy is too large to be acceptable in phylogenetic studies (see Chapter 4). This may be due to poor descriptions, but can also partly be attributed to the inability to observe precise detail when using light microscopy; and
- Slide-mounting causes some artefacts which can be alleviated by using mounting methods that will cause the least artefacts in taxonomically important characters such as the dorsal shield pattern (Denizhan *et al.*, 2008). These alternative methods have their own problems, and it may even be disputed which method will offer the best results for the comparison and identification of specimens. The lack of representation of exact morphology will not always be a problem for identification, because the purpose is mainly to compare certain characters, even if they are incorrectly described, as long as these artefacts are robust, stable and roughly standardized. Such erroneous data, however, are unacceptable for phylogenetic studies (see Chapter 4).

Studying specimens with electron microscopy provides higher resolution and three-dimensional images and can be superior to light microscopy and can improve and alleviate most short-comings

with light microscopic studies of slide-mounted specimens. SEM studies of eriophyoid mites are, on the other hand, not without inadequacies, limitations and problems of their own such as:

- SEM facilities in general are not readily available. In comparison with studying slide-mounted specimens with light microscopy, SEM studies are cumbersome, expensive, complicated, time-consuming and unavailable to many researchers worldwide who are studying eriophyoid systematics.
- Employing those techniques that may contain the least artefacts, such as cryo-SEM, are even more complicated than conventional SEM and require special SEM equipment and special skills. These skills and equipment are scarce, and probably represent the major constraint facing the incorporation of SEM studies in the systematics of the Eriophyoidea. Even the SEM research undertaken in the present study may not be able to continue due to funding and easy availability of SEM facilities; and
- Specimens prepared for and studied with SEM are not always without artefacts. The amount of distortion and artefacts in specimens are, similar to slide-mounting of specimens, dependent on various factors of which the choice of SEM technique, quality of equipment, and experience and skill of the person preparing and studying the specimens are the most noteworthy. The choice of SEM technique should take into consideration the aim of the SEM study. Elimination of shape distortion, and improvement on observing ultra-structural detail, and general representation of true morphology, as found in live specimens, are the main aims. Some SEM techniques (including conventional techniques) may cause shrinking and even more severe shape distortion than what is found in slide-mounted specimens. In many cases, the quality of SEM images is inferior to line drawings, particularly caused by shrinking of specimens and sub-standard image-capturing. Some minute details can, however, still be successfully studied in such images, depending on the quality of resolution and contrast, but studying shape and relative positions of structures is not reliable when any kind of appreciable distortion occurred.

  In the present study, the results of the SEM study were not always satisfactory: surface ice could not always be entirely removed; material often degraded after prolonged examination; and some mites intact on plant pieces were washed off during sample preparation in the nitrogen slush. These were mostly caused by the equipment available for the study, and are not inherent to optimal utilization of the cryo-SEM technique. The use of a field emission SEM with cryo-attachment will enhance results (Wergin *et al.*, 2000), especially for the resolution of fine-structure such as specialized setae, and will

prevent some of the artefacts experienced (Achor *et al.*, 2001), but this option was not available for the present study;

- Not all morphological information necessary for the classification and identification of eriophyoids is available from one specimen when studied with SEM, because all aspects of it cannot be observed as is possible with slide-mounted specimens. In the present study, for instance, the gender, and sometimes even the life stage of specimens in dorsal view could not be determined, and similarly, the dorsal and some lateral characteristics of specimens in ventral view could not be studied. Unfortunately, the cryo-stage of the SEM available could not be tilted. The classification and identification of eriophyoid mites also include the evaluation of internal structures, such as the internal female genitalia, and without this information from slide-mounted specimens, specimens studied with SEM cannot always be identified;
- There are frequently not enough specimens available from a collection to incorporate SEM studies, especially when it is combined with light microscopic studies. The manner in which, for example, the cryo-technique for the present study was done, specimens studied with the SEM were inevitably destroyed after one continuous study session. This meant that there was only one change per SEM session to obtain clear and useful images;
- Another practical and important problem with published SEM images, although it may at first seem to be a minor problem, is the frequently poor reproduction of printed SEM images, especially when the original article is not available and the article must be obtained through inter-library system which usually provides inferior electronic or photocopied versions of the original publication. In many instances, the SEM images are rendered obscure and unusable, far worse than ever experienced with line drawings. In the present study, for instance, this turned out to be a real constraint. SEM images published in several photocopied articles obtained for present study were not usable (e.g., Fig. 3.86). In present study, it was in many such instances not possible to obtain the original SEM images or at least scanned versions of the published printed images. Even the original images, however, may be of poor quality; and
- Another problem is the enlargement at which SEM images are presented. For example, despite control over the size of the images on paper in the present study, observations for writing-up the information were usually made on images viewed on screen, where images can be interactively enlarged to the limit of usable resolution. Less clear and smaller paper printed versions (also necessary in the present study), make the observation of particularly smaller detail difficult, ambiguous or impossible. These limitations will be drastically improved in future, with an increase in the use of electronic-capturing and

distribution and when paper format will be supplemented or replaced by electronic versions of articles, including published SEM images.

Although SEM images have been sporadically used in descriptions of new eriophyoid taxa to enhance light microscopic studies, additional morphological data from SEM studies have hardly been incorporated into eriophyoid systematics. SEM images and descriptive morphological data from them are not seriously advocated, neither compulsory for describing new taxa. Comprehensive comparative morphological studies utilizing SEM, with focus on use in systematics, are few and limited in scope.

Understandably, there are reservations about incorporating morphological information from SEM studies in the classification and identification of eriophyoids, especially because SEM facilities are not readily available worldwide. Some authors went as far as basing entire descriptions on even inadequate SEM images (e.g., Huang, 1992). This practice was condemned by Amrine (1996). The addition of SEM studies to enhance eriophyoid descriptions based on slide-mounted specimens and including detailed descriptive line drawings are propagated, but basing the description of eriophyoid taxa exclusively on SEM studies is not advised (Amrine *et al.*, 2003; De Lillo & Skoracka, 2010). It is concurred in the present study that descriptions should not be based exclusively on SEM studies, and particularly not when they are not up to standard. Therefore, light microscopy and line drawings should remain the basis for practical identification and identification keys for the time being.

Nevertheless, although morphological data used in taxon descriptions is used for classification and identification which are frequently more practical applications, it still remains a scientific study of the group. Results of morphological studies should represent the actual morphology of life specimens as closely as possible. Artefacts, mistakes in observations and insufficient detail for application and analyses of the data should be avoided at all costs. This will improve all aspects of eriophyoid systematics. In a phylogenetic study, for example, flawed data can result in wrong hypotheses of groupings and relationships between taxa. Scientific study of a group of organisms must not be constrained by the practical applications and problems with infrastructure.

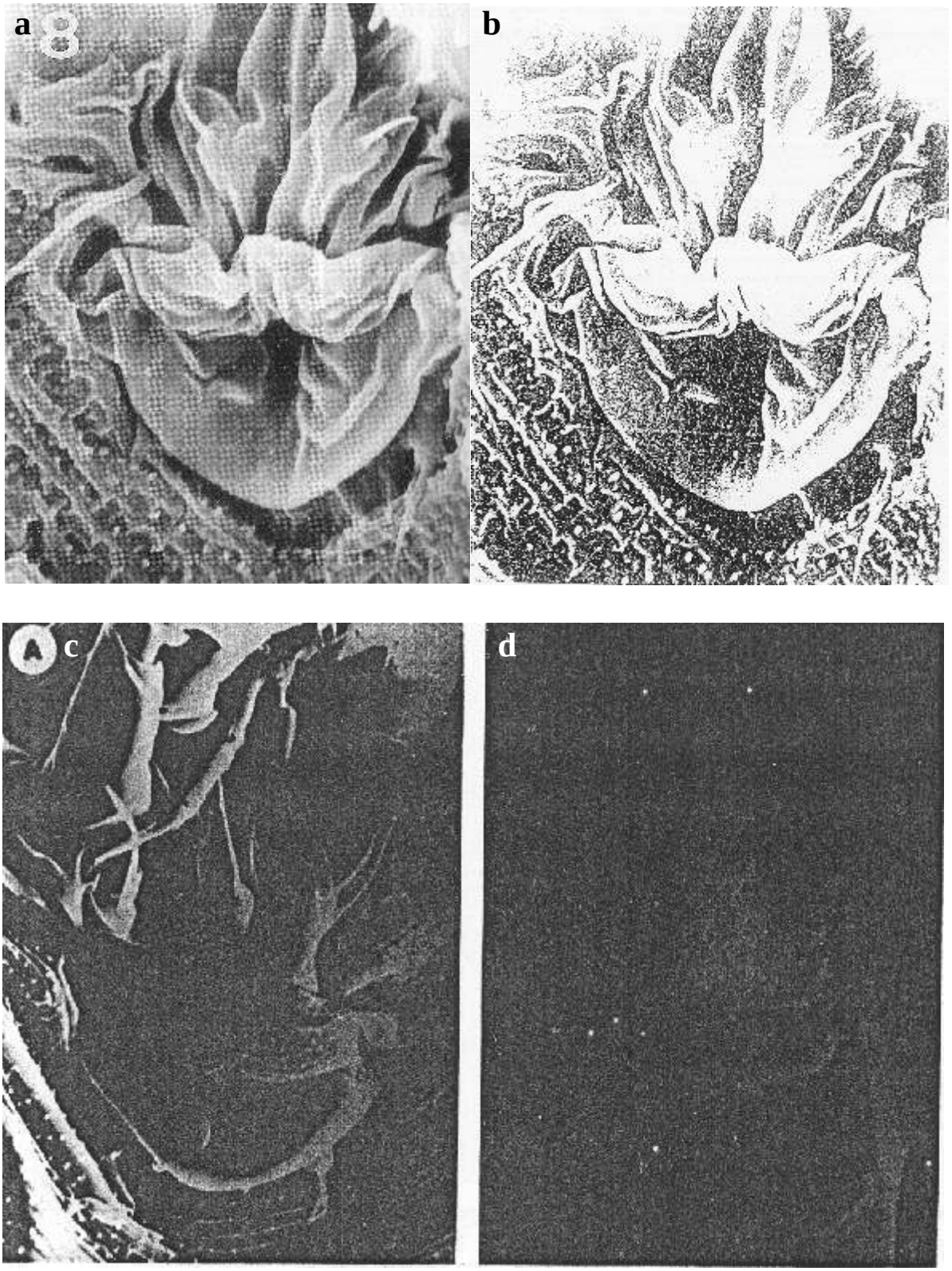


Fig. 3.86. Examples of loss of quality of SEM images of species in the current study, in the publishing and photocopying processes, all printed images scanned with the same scanner in Grayscale at a resolution of 200 dpi, and saved as *.tiff: **a)** original printed image Fig. 6, p. 232 in Huang (1992); **b)** photocopy of image received from library, before the original reprint was obtained; **c, d)** photocopies of SEM images (Plate 1 image A and B here c and d alternatively) originally published on p. 441 in Chandrapatya & Boczek (1991b), original article / reprint or original SEM images not yet obtained.

It has been confirmed and demonstrated in the present study that the morphological study of eriophyoid specimens incorporating the most appropriate SEM techniques such as cryo-SEM, is in many respects scientifically superior to light microscopic study of slide-mounted specimens. Despite some problems, the results from the SEM study were satisfactory and contributed considerable amounts of new data. The present study indicates new features not previously reported, or not seen in eriophyoid mites with such clarity of detail. The SEM images also simplify or sometimes clarify the division of structures into homologous substructures for determining primary homologies between characters and character states. The determination of the exact area and structures constituting the so-called basal and distal area of the female genital coverflap, the relative position, and the precise description of these, are examples of this.

In the present study, it was also shown that in the Eriophyoidea too few systematically informative characters are available, particularly for phylogenetic studies (see Chapter 4). To partly alleviate this problem, molecular and other data such as biological and ecological data could also be utilized. Although sound morphological data in these studies are essential, it is also essential to test information from other data sets (that may also have their own problems and limitations), in order to increase information available for phylogenetic studies (Hillis & Wiens, 2000; Jenner, 2004). The comparative study of the gnathosoma of the species included in the present study demonstrated that there are many "new" morphological structures available that may be of systematic value. SEM images can also be duplicated and stored and archived in separate international mite collections in addition to slide-mounted material and other collections of eriophyoid mites, such as dry collections, to accompany and represent type-specimens which will be lost over time.

Aspects that still need discussion and clarification include how much SEM studies can or should contribute to improve the systematics of the Eriophyoidea, and to what extent morphological information that is obtained from SEM studies that may sometimes not be observable in slide-mounted specimens, should be incorporated into eriophyoid systematics, taking into account the problems and limitations of SEM studies in eriophyoid research.

The investigation and testing of new techniques for morphological study are not just confined to the SEM, TEM and light microscopic techniques discussed in this chapter. Numerous modifications for electron and light microscopy have been published, and new equipment is available and more powerful computer technology contributes to these (Alberti & Nuzzaci, 1996). Eriophyoid taxonomists should continuously investigate these developments for possible improvement of morphological studies of the eriophyoids, since this aspect is such an important part of the systematics of this group.

3.7 CONCLUSIONS

While undertaking the research for this chapter on morphology, as well as coding characters states for phylogenetic analyses in Chapter 4, the importance of using the best techniques for slide-mounting of specimens as an important aspect of improving the morphological study of eriophyoid mites (De Lillo *et al*., 2010) became increasingly clear. These techniques used to date in mounting of specimens in South Africa must be improved. Apart from this, it is clear from the present study that many artefacts are present in slide-mounted specimens, and there are limitations inherent in light microscopy of these specimens that cannot be enhanced and rectified by improving these techniques, and these inadequacies are already built into eriophyoid descriptions and classifications.

Cryo-SEM is a technique that offers excellent improvement to morphological studies, and seems to cause the least artefacts to specimens, and enhances their study. Information from SEM studies not only improved on and rectified information from light microscopic studies and resultant descriptions, but additionally provided a surprisingly large number of new structures that have not been previously reported, that may be of use in systematics. This increase in characters is essential for phylogenetic studies of the Eriophyoidea, and will also improve conventional taxonomy. Information from SEM studies additionally improves the information and clarity of morphological characters to such a degree that it will aid in the improvement of the identification and delimitation of characters and character states which is also urgently needed in eriophyoid systematics. For all these reasons, the inclusion of SEM studies should not just be a mere enhancement of primary light microscopic studies for taxon descriptions. Morphology studied with SEM should be seriously and routinely incorporated into descriptions of taxa, and making it a requirement in some instances should be considered. The inclusion of SEM studies is compulsory for the description of many nematode groups, largely implemented by peer review practices, and a description will hardly be accepted for publication if these are not included without acceptable reasons (M. Marais,

pers. comm.). Numerous phylogenetic studies in spiders are also extensively incorporating information from SEM studies.

In reality, however, SEM facilities are not readily and widely available worldwide. Consequently, morphological information from SEM studies cannot be solely incorporated in the practical description, classification, differentiation and identification of eriophyoid mites, without concurrent and corroborating usable character states from slide-mounted specimens. This is similar to the situation with information from molecular studies.

CHAPTER 4

PHYLOGENY AND CLASSIFICATION OF THE ERIOPHYOIDEA

4.1 INTRODUCTION

The results of an explorative phylogenetic study of the Eriophyoidea at genus level are presented in this Chapter. The present eriophyoid classification is appraised and particularly the monophyly of suprageneric taxa is tested, and an alternative classification is proposed. Additionally, groups within the Eriophyoidea recovered with the phylogenetic analyses are proposed for further study as alternative hypotheses to taxa in the existing eriophyoid classifications. Nearly all *Diptilomiopus* spp. are included in the data set, as well as all the described species or more than one species of a few other genera. The monophyly of these genera is also tested to a more or lesser extent, depending on the comprehensiveness of the species sample of each. It is pertinent to commence with phylogenetic studies of the Eriophyoidea to determine the true relationships between eriophyoid taxa, and to improve their classification (Lindquist, 1996b; Lindquist & Amrine, 1996; Nuzzaci & De Lillo, 1996). Despite different views on the phylogeny of the Eriophyoidea, only a few phenetic and cladistic studies (Huang & Huang, 1990; Kuang *et al.*, 1992; Sukhareva, 1994; Kuang *et al.*, 1995; Hong & Zhang, 1996a, b, 1997) have been undertaken. These studies were inadequate in putting forward reliable hypotheses for various reasons, such as small taxon samples. The present study expands on these studies with data from additional taxa and characters, and their results and hypotheses are independently tested.

4.1.1 Eriophyoid classifications

The eriophyoid classification generally accepted today, and followed in the present study, is presented in Amrine (1996), up-dated by Amrine *et al.* (2003) (Table 1.1). It was developed mainly by Nalepa (1898b), Keifer (1944, 1956, 1964a, 1966b, c) later in collaboration with Newkirk (Newkirk & Keifer, 1971, 1975), Roivainen (1953), Farkas (1968b) and Amrine & Stasny (1994). In this classification the *ca.* 4000 eriophyoid species (De Lillo & Skoracka, 2010) belong to the superfamily **Eriophyoidea** with the families **Phytoptidae** (21 genera), **Eriophyidae** (227 genera) and **Diptilomiopidae** (53 genera) (Amrine *et al.*, 2003).

The Eriophyoidea were grouped together in one taxon since the first suprageneric classification proposed by Nalepa (1892, 1898b, 1929). They remained recognized as a monophyletic taxon, despite

the addition of the majority of described species since then. The present study mainly concerns the eriophyoid suprageneric taxa (families, subfamilies and tribes). The Phytoptidae have five subfamilies – three without tribes, one with three and one with two tribes; Eriophyidae have six subfamilies – two without tribes, two with two tribes each, one with three, and one with five tribes; and the Diptilomiopidae have two subfamilies without tribes (Table 1.1). Amrine (1996), Lindquist & Amrine (1996) and Amrine *et al.* (2003) presented synopses of the classification. Diagnoses of the suprageneric groups recognized within the Eriophyoidea are provided by Amrine & Stasny (1994), Lindquist & Amrine (1996) and Amrine *et al.* (2003).

A different classification was proposed primarily by Shevchenko[1] (1971, 1974a, b, 1976) and Boczek *et al.* (1989). Shevchenko (1971, 1974a) proposed three superfamilies, **Trisetoidea**, **Phytoptoidea** and **Eriophyoidea,** within the **Tetrapodili** which is a taxon at the suborder level (taxon author uncertain – see Lindquist, 1996c). Shevchenko (1976) changed the two superfamilies, Trisetoidea and Phytoptoidea, to family level (Nalepellidae and Phytoptidae *sensu* Shevchenko, 1976), the same as in the classification presented by Boczek *et al.* (1989), but stressed that he still regards them as two separate, natural lineages. Additionally, Shevchenko (in Boczek *et al.*, 1989) proposed a family rank taxon, **Pentasetacidae** (same group as Pentasetacini *sensu* Amrine & Stasny, 1994) for *Pentasetacus* Schliesske, 1985 (with single *vi*, *ve* and *sc* present), based on his interpretation that the family rank taxa is based on the number of prodorsal shield setae. This classification was not accepted widely, but is considered an alternative hypothesis of eriophyoid phylogeny. The suprageneric groupings are similar in the two major classifications, respectively presented in Amrine *et al.* (2003) and in Boczek *et al.* (1989) as generic keys. They mainly differ in the taxonomic levels on which particularly the taxa of the Phytoptidae *sensu* Keifer (1964a) were classified (Lindquist, 1996b). The differences between the two classifications and phylogenetic hypotheses underlying them are discussed in more detail in the "Appraisal of the monophyly of Eriophyoidea suprageneric taxa" section of the Results and Discussion further on.

The eriophyoid classifications were probably developed to be primarily practical, sound and stable systems for identifying and classifying eriophyoid taxa, requirements inherent to taxonomy. The classifications were also developed, however, to comprise natural (monophyletic) taxa, based on the evolution and phylogeny of the group (Farkas, 1968b; Shevchenko, 1971, 1974b; Newkirk & Keifer, 1975; Shevchenko *et al.*, 1991). There is some sense that the family level classification of the Eriophyoidea broadly reflects natural groupings, and thus approximates the phylogeny of these mites (Farkas, 1968b; Das & Chakrabarti, 1989). On the other hand, it is proposed that the majority of the eriophyoid supraspecific taxa (families, subfamilies, tribes and genera), defined by classical taxonomy,

[1] The surname Shevchenko has also been erroneously transliterated from Russian as Shevtchenko. In this dissertation, "Shevchenko" is used, even when referring to previous instances (including reference authors) where the name was spelled "Shevtchenko".

are probably based on artificial groupings (polyphyletic or paraphyletic groups), apart from the Diptilomiopidae which is probably monophyletic (Lindquist, 1996b; Lindquist & Amrine, 1996).

Farkas (1968b) regards the classification of the Eriophyoidea as an attempt to develop a "natural system" in so far as it has the hypothetically more primitive members on "one side" (the Phytoptidae) and the hypothetically more derived members on the "other side" (the Diptilomiopidae). He evaluated the classification of the Eriophyoidea and proposed it is mainly based on two evolutionary developments, from earlier to more recently derived. These are the gradual reduction in the number of setae (Shevchenko, 1962) and the increased complicated morphology of the body from a simpler body plan, similar to that of the larvae and more vermiform shaped species, to species with various body modifications including ridges, annular extensions, and longer and more rigid dorsal annuli.

4.1.2 Different eriophyoid life forms in classification and phylogeny

The life forms, deuterogyny, diapause and seasonal development of the Eriophyoidea are reviewed by Manson & Oldfield (1996). Some eriophyoid species have alternating generations with structurally two different female types, usually with one male type, referred to as deuterogyny (Keifer, 1942). The protogyne female is regarded as the primary female; it resembles the primary male, and reproduces rapidly during favourable conditions. The deutogyne female is regarded as the secondary female, with no male counterpart, which can carry the species through unfavourable periods usually by either hibernation or aestivation (Keifer, 1975a; Manson & Oldfield, 1996). Shevchenko (1961, 1962) proposed that the "deutogyne" of Keifer (1942) actually is the primary female (earliest derived form), while the "protogyne" of Keifer (1942) is secondary and more derived.

Some species may have a range of structural forms between the protogyne and deutogyne, and not just two distinct forms (Keifer, 1969a). Sometimes the deutogyne female form may be present, with the protogyne form, similar to the male, non-existent (Oldfield, 1969). Alternate forms of females as well as males were found in *Trisetacus kirghisorum* Shevchenko, 1962 (Shevchenko & De-Millo, 1968) and in *Aceria inusitata* Britto & Navia, 2008 (Britto *et al.*, 2008).

The presence of morphologically different females and/or males causes problems for and has a definite influence on the systematics of the Eriophyoidea. Sometimes deutogyne and protogyne females of the same species were described as two different species [e.g., first descriptions of *Tegonotus aesculifoliae* (Keifer, 1938) (Keifer, 1938b)], were assigned to different genera due to the distinctive morphology of the deutogyne female [e.g., *Rhyncaphytoptus ulmivagrans* (Keifer, 1939) (Keifer, 1939a) (= *Abacoptes ulmivagrans* (Keifer, 1939) (Keifer, 1939e))]. Some were placed in different suprageneric taxa (Roivainen, 1953; Shevchenko, 1961). This happened and may still happen if they were identified and classified according to the current classification which is almost exclusively based on protogyne

females (Roivainen, 1953), and also according to the characters used in the differentiation of taxa (Shevchenko, 1961). The differences between the two forms may be slight, though, and it is necessary to confirm their presence with breeding experiments (Manson & Oldfield, 1996). The deutogyne frequently has reduced or suppressed microtuberculation, or the microtubercles may have a different shape, there may be less ornamentation on the prodorsal shield, and ridges or furrows on the protogyne opisthosoma may be absent in the deutogyne (Keifer, 1975a).

The diagnosis of the Aberoptinae particularly illustrates the role of the morphology of deutogyne females in eriophyoid classification (and in effect phylogenetic hypotheses, if the classification is developed to be natural). The Aberoptinae comprised two genera, *Aberoptus* and *Cisaberoptus*, the latter assigned to the Aberoptinae based on the morphology of the deutogyne female (Keifer, 1966b: 2). Amrine *et al.* (2003: 2) re-assigned *Cisaberoptus*, the deutogyne female of *Aceria kenyae* (Keifer, 1966), to the tribe Aceriini based on the morphology of the protogyne female. They strongly recommended that eriophyoid generic concepts should not be based on the "unusual" structure of the deutogyne female, but on the morphology of the protogyne female alone. Shevchenko (1961) proposed that the morphology of the deutogyne female *sensu* Keifer (1942) should also be incorporated in the identification process. I agree with Shevchenko (1961), and inclusion of deutogyne morphology in differentiation of genera can not be taken *a priori* phylogenetic analyses including all the life stages, in particular, the morphology of both the deutogyne and protogyne females in determining the retrieval of groups of species which may be interpreted as separated genera. Deutogynes should also be scored for phylogenetic analyses otherwise; it excludes morphological variation which may contribute towards the phylogenetic resolution of relationships and retrieval of clades. The morphology of the deutogyne female *sensu* Keifer (1942) may have more phylogenetic signal than that of the protogyne female *sensu* Keifer (1942) (V.G. Shevchenko, *pers. comm*., 2009). It may also cause errors or retrieval of artificial groups if the same life stages are not compared with each other, e.g., protogyne female characters should not be scored in the same character columns in the data matrix than those of the deutogyne females.

Incorporating morphology of the deutogyne female *sensu* Keifer (1942) in phylogenetic analyses and classification is problematic, though. Most published eriophyoid species and genus descriptions are probably incomplete, because all the possible life forms (protogyne and/or deutogyne, and male) have not been described (Roivainen, 1953). This may remain the situation, because most descriptions are based on a single collection of specimens, but to collect the different life forms, at least more than one collection, one in each season, are necessary. Deutogyne forms are probably present in more species than previously thought (Manson & Oldfield, 1996). Due to the general lack of deutogyne descriptive data, and even the lack in determining the presence of a deutogyne form in a species, deutogynes were not scored and included in the present phylogenetic study.

4.1.3 Phylogeny

4.1.3.1 Relationships between taxa of the Eriophyoidea (including hypotheses on the evolution of the group)

Apart from hypotheses of relationships between eriophyoid taxa presented as classifications (above), specific hypotheses and treatises on the evolution and phylogeny of the Eriophyoidea have been published. Lindquist (1996b) reviewed some phylogenetic aspects, focusing on the relationship of the Eriophyoidea with other mite groups. He did not include phylogenetic analyses, which he regarded to be beyond the scope of that treatise.

Eriophyoid evolution and phylogeny in relation to their ecology (Sabelis & Bruin, 1996), and plant hosts (Boczek & Shevchenko, 1996; Gerson, 1996; Lindquist & Oldfield, 1996; Oldfield, 1996) were comprehensively dealt with. General evolutionary trends in the Eriophyoidea, first presented by Farkas (1966, 1969) and Shevchenko (1970, 1976), and later compiled by Lindquist & Oldfield (1996) include the following:

- Eriophyoid ancestors were vagrant mites colonizing minute natural cavities (e.g., fine crevasses in axils, underneath sheaths and scales, and in buds) of relatively ancient ever-green plants including conifers and monocotyledonous palms and grasses.
- Adapting to these small spaces, the body of early derived Eriophyoidea evolved into an elongated, vermiform, annulated shape, covered more or less with microtubercles and with elimination of the posterior two pairs of legs.
- Hereafter, some mites adapted to living on seasonal dicotyledonous plants, perhaps repeatedly and independently (homoplastically). This involved movement between protected over-wintering sites on hosts, and new plant growth of the following season for successful reproduction. Along with this, a deuterogynous life cycle developed.
- Subsequently, two major trends took place (Silvere, 1973), primarily as alternatives, and probably homoplastically (in parallel, convergently and with reversals):
    - Some mites retained a more vulnerable, non-vagrant, vermiform body living in small natural spaces. Some of these adapted, probably during the early stages of eriophyoid evolution, by causing abnormal growth in their hosts to create living spaces where they were not naturally available. These alterations became more specialized to specifically benefit the mites, such as erinea and galls. Most of these species are in the Eriophyinae.
    - A second trend entailed adaptation to live on exposed plant surfaces, able to resist desiccation. This adaptation included various modifications of body structures including a more fusiform, often more robust, body; fewer, longer and more rigid

dorsal opisthosomal annuli; sometimes the loss of particularly dorsal opisthosomal microtubercles; and a larger, stronger prodorsal shield with a frontal lobe extending over the gnathosoma. Most of these species are in the Phyllocoptinae.

Expression of these two trends occurs together in for example, *Paraphytoptus* spp., with the anterior part of the body mostly covered among erineal hairs with a non-vagrant body shape; and the posterior part sticking out of the erineum, exposed, with characteristics similar to vagrant species (Keifer, 1975a).

- An additional evolution to the "diptilomiopid-like" form of the gnathosoma (Figs 3.22b, d, e) occurred, enabling these mites to probe deeper into tissue or through thicker, waxy leaf surface layers (Lindquist & Oldfield, 1996). These species are in the Diptilomiopidae which are proposed to be monophyletic.

Silvere (1973) proposed that eriophyoids may be neotenous organisms (the origin of the eriophyoids may entail paedomorphosis), because some of the structures and tissues of the adults of the Eriophyoidea are similar to those in embryonic or immature arthropod stages. Neoteny is the retention by adults in a species, of traits previously seen only in juveniles, resulting in a sexually mature juvenile or larval form. During the evolutionary process a species' neotenous form may become its "normal" mature form (Ryke, 1986). Apart from the hypothesis of neoteny from the original article by Silvere (1973), Lindquist & Oldfield (1996) reviewed the concept of a Russian school of acarologists, including A.P. Silvere, V.G. Shevchenko and A.B. Lange who took this hypothesis further. In essence the Russian researchers proposed that the eriophyoid lineage evolved by reaching sexual maturity at a stage preceding the prelarval stage, and accordingly they regarded the Eriophyoidea as an ancient, independent suborder, Tetrapodili, outside the Prostigmata. Lindquist & Oldfield (1996) opposed this hypothesis, but in pointing out neotenic trends in other Prostigmata, they agreed that some degree of neoteny probably took place in the evolutionary development of the Eriophyoidea.

Shevchenko (1962, 1971, 1974a, b), Farkas (1968b) and Shevchenko *et al.* (1991) regarded the retainment or loss of setae on the anterior part of the prodorsal shield as phylogenetically highly informative. The Phytoptidae is regarded by them as the most primitive of the Eriophyoidea because Phytoptidae species usually retain the most setae (e.g., they are the only eriophyoid species that retain the setae anteriorly on the prodorsum) and many Phytoptidae species have a vermiform body shape without intricate body modifications (Farkas, 1968b). These authors also proposed that the Phytoptidae consists of two major phylogenetically distinct lineages: Phytoptidae species with an odd number of prodorsal setae (thus with single *vi* present) and with all species occurring on conifers without

exception, and those with an even number of prodorsal setae living on a variety of hosts, but none occurring on conifers.

Shevchenko *et al.* (1991) proposed hypotheses of evolution and phylogeny of the Eriophyoidea (named Tetrapodili by the authors) primarily based on prodorsal shield setal numbers and patterns. They regarded *Pentasetacus araucariae* Schliesske, 1985 to be the most primitive or earliest derived in the Eriophyoidea, because it possesses the largest number of prodorsal shield (including *ve* and single *vi*), and occurs on an ancient conifer, *Araucaria araucana*. Starting from this complete set of prodorsal shield setae, they proposed all possible pathways and development of prodorsal shield setal patterns. They also observed that the developmental pathways of setal patterns in eriophyoid mites are closely related to the phylogeny of their host plants.

They identified two pathways. One pathway starts with the five prodorsal setae in *Pentasetacus*, including single *vi* and *ve* (Fig. 3.3e), followed by the loss of *ve* which results in species with three prodorsal (single *vi* and *sc*) (Fig. 3.3f), namely *Trisetacus*, *Nalepella*, *Setoptus* and *Phantacrus*. The next step entails the loss of *sc* and only single *vi* remains (Fig. 3.3g), as found in *Boczekella*. All these genera occur only on conifers. Shevchenko *et al.* (1991) further noted that these genera also have other characteristics that are regarded by them as being primitive: relatively long spermathecal tubes and the presence of the tibial solenidion *φ* in all, and the presence of *c1* in some genera (*Pentasetacus*, *Trisetacus* and *Boczekella*).

The other pathway entails the loss of single *vi* resulting in the retainment of only *ve* and *sc*. This setal arrangement (Fig. 3.3i) is present in the Phytoptidae genera *Phytoptus*, *Anchiphytoptus*, *Sierraphytoptus*, *Novophytoptus*, *Austracus*, *Mackiella* and *Retracrus* (Shevchenko *et al.*, 1991). These genera occur mainly on monocotyledons (Shevchenko *et al.*, 1991). In some species *sc* is also lost and only *ve* remains (Fig. 3.3j), e.g., *Propilus* spp., and these particularly occur on palms (Monocotyledones: Arecaceae) (Shevchenko *et al.*, 1991). The tibial solenidion *φ*, and *c1* is present in some of these genera, but all have relatively short spermathecal tubes different from the long spermathecal tubes found in the genera with single *vi* present (Shevchenko *et al.*, 1991). Most eriophyoid species (all Eriophyidae and Diptilomiopidae), however, are without single and paired *vi* and *ve*, and have only *sc* present (Fig. 3.3k), or in some species all prodorsal are absent (Fig. 3.3l). It thus seems that single *vi* and *ve* were easily lost, but *sc* is more resistant to loss (Shevchenko *et al.*, 1991). These species occur on a wide variety of plants. Shevchenko *et al.* (1991) concluded that there are too few eriophyoid taxa known from particularly relict plants to propose a complete and final classification for the Eriophyoidea, but that some aspects of its phylogeny can already be gathered from morphology, such as prodorsal shield setae, and its relation to their plant hosts.

Although Farkas (1968b) regarded the retainment or loss of setae on the prodorsal shield phylogenetically highly informative, he noticed that *Platyphytoptus* (Eriophyidae) and *Setoptus* (Phytoptidae) might be closely related phylogenetically. *Platyphytoptus* is in the Eriophyidae because it lacks setae anteriorly on the prodorsum, but occurs on conifers, and is morphologically similar to *Setoptus* (with single *vi*) in the Phytoptidae. He, however, refrained from placing *Platyphytoptus* in the Phytoptidae, because it would cause a major upset in the classification of the Eriophyoidea.

Farkas (1969) proposed that only a few original forms or lineages gave rise to the forms found in the Eriophyoidea. He postulated that the original lineage from which the Eriophyoidea developed was similar to *Phytoptus avellanae* Nalepa, 1889, a typical non-vagrant, vermiform species living in distorted buds of its host, with *ve* and *sc* present. He regarded the following as important evolutionary changes:

- reduction of the number of prodorsal setae,
- direction in which *sc* is projected, from anteriad to posteriad, or up, or mediad,
- development of a larger and more robust frontal lobe from a small, thin prodorsal shield anterior extension,
- change of body shape from more vermiform to a shorter and more stout fusiform shape, and
- opisthosomal annuli changing from uniformly annulated dorsoventrally to larger dorsal annuli in contrast with thinner ventral annuli.

Apart from the reduction of the prodorsal setae and the direction in which *sc* is projected, the remaining three characters are related to a sheltered (non-vagrant, e.g., gall-living) or an exposed vagrant life-style (Farkas, 1969).

Farkas (1969) also proposed that forms similar to *Eriophyes* and *Aceria* (non-vagrant forms) gave rise to forms similar to *Phyllocoptes* and *Vasates* (vagrant forms), respectively, thus suggesting that the Phyllocoptinae had a diphyletic origin, and that characters due to an exposed life-style developed convergently (homoplastically).

When extrapolated to phylogenetic relationships between taxa, species with *sc* ahead of the rear shield margin, projected anteriad, mediad or up, including *Eriophyes* and *Phyllocoptes*, will be phylogenetically more closely related than they are related to species with *sc* near or on the rear shield margin, projected posteriad, including *Aceria* and *Vasates*. Likewise, it seemed that a gall-former was the ancestor, and some species evolved to a vagrant life-style, in a complex of morphologically similar *Cecidophyopsis* spp. (Fenton *et al.*, 2000). Farkas (1969) used the transitional forms existing between *Eriophyes* and *Phyllocoptes*, and between *Aceria* and *Vasates*, with a corresponding lack of transitional forms between, for example, *Eriophyes* and *Aceria*, and the deutogyne stages of *Phyllocoptes* and

Vasates being similar to *Eriophyes* and *Aceria*, respectively, as reasons for his hypothesis. According to Farkas (1969) the deutogyne stage of a species has the same characteristics than the lineage from which the particular species originated. Farkas (1969) also postulated that the Diptilomiopidae originated from the Phyllocoptinae, because all Diptilomiopidae species then had *sc* projecting anteriad or up. Farkas (1969) did not extend his hypotheses on evolution and phylogeny into changing the classification of the Eriophyoidea.

4.1.3.2 Relationship of the Eriophyoidea with other mite groups

It is largely accepted among acarologists that the Eriophyoidea is a robust clade and this is reiterated by among others, Lindquist (1996b) and Hong & Zhang (1996a). They presented lists of autapomorphic and synapomorphic characters for the Eriophyoidea to support this hypothesis, but it was not tested with empirical phylogenetic analyses. It is problematic to determine primary homologies and the phylogenetic relationships of the Eriophyoidea with other mite groups, because their morphology is so unique and specialized (Smith, 1984; Lindquist, 1996b; Silvere, 1973).

Lindquist (1996b) comprehensively reviewed previous hypotheses on the relationships of the Eriophyoidea with other mite groups. He argued against and for groups previously proposed as sister groups of the Eriophyoidea, namely the "Vermiformia" (including Demodicidae), Nematalycoidea, Tarsonemoidea, Raphignathae (including Stigmaeidae), Tetranychoidea, and Tydeoidea. The relationship of the Eriophyoidea with the Tetranychoidea and Tydeoidea is more important to the present study; because species of the Tetranychidae and Tydeidae are herein used as outgroup taxa for the cladistic analyses of the Eriophyoidea.

Various authors proposed a sister relationship between the obligate plant-feeding Tetranychoidea and the Eriophyoidea (e.g., Baker, 1948; Baker & Wharton, 1952). These hypotheses were based on similarities between the Eriophyoidea and some tetranychoids. Additionally, some derivative genera of the Tenuipalpidae also lost legs IV and some have elongated, annulated bodies (Baker, 1948; Farkas, 1969; Lindquist, 1996b), but Farkas (1969) agreed that the resemblance could be due to convergence, because these species also inhabits galls, with consequent adaptation to small spaces. Lindquist (1996b) argued that a close relationship with the Tetranychoidea is improbable, because it will entail the loss of characteristics synapomorphic to the Tetranychoidea.

Lindquist (1996b) argued strongly that the Tydeoidea are the closest relatives of the Eriophyoidea. Lindquist (in Nuzzaci & de Lillo, 1991) and Kethley (in Norton *et al.*, 1993) published dendograms in which the Eriophyoidea and Tydeoidea are sister taxa. In both publications no data were included to support this relationship. Lindquist (1996b) likewise did not include any empirical analyses, but discussed and explained characteristics that the two groups share which indicate a close relationship.

Lindquist (1998) did not regard the proposal of a sister relationship between the Eriophyoidea and Tydeoidea as conclusive. He additionally proposed an alternative, more ancient sister relationship between the Eriophyoidea and Pachygnathoidea, which may place the Eriophyoidea outside the Prostigmata.

4.1.3.3 Phenetic and phylogenetic analyses

Huang & Huang (1990) were the first to study the phylogenetic relationships between eriophyoid taxa with methods other than classical taxonomy and evolutionary hypotheses based on experience with and insight in the group's morphology and biology. They analysed morphometric data in ratio format and discrete descriptive character states with phenetic and cladistic algorithms, respectively. They included 15 species from the three eriophyoid families in both analyses. The species were one each from 10 subfamilies, and one species each from the five sections of the Phyllocoptinae, according to the classification of Newkirk & Keifer (1975). Their taxon sample was very small and did not sample all the suprageneric taxa of this classification.

The phenogram resulting from the phenetic analysis (cluster analysis, UPGMA, with the Average Manhattan Distance Coefficient) did not correspond with the existing classification of the Eriophyoidea or with the cladogram that resulted from their cladistic analysis (Huang & Huang, 1990). The taxa which clustered the closest to each other, e.g., *Sierraphytoptus* and *Aberoptus*; *Nalepella* and *Diptilomiopus*; and *Novophytoptus* and *Calacarus*, cannot be supported by any knowledge on the Eriophyoidea. Phenetic analyses for studying phylogenetic relationships between taxa are critisized, and it is usually not employed for this purpose anymore.

The preliminary cladistic analysis by Huang & Huang (1990), entailed an analysis of 14 morphological characters and one ecological character (degree of symptoms induced). This study has many shortcomings, and Lindquist (1996b) who reviewed the study found it to be fundamentally flawed. Nevertheless, the following information could be gained from the cladogram: the species of *Diptilomiopus* and *Rhyncaphytoptus* were found to group as a clade, supported by the synapomorphy, shape of the chelicerae being "diptilomiopid-like" (Figs 3.22b, d, e), and thus supports the monophyly of the Diptilomiopidae. The species of the Eriophyidae were retrieved as three separate groups. The relationships between the four species of the Phytoptidae (which were in a polytomy), the *Diptilomiopus–Rhyncaphytoptus* group and the three Eriophyidae groups were all unresolved, and no information about the relationships between them can be gained from the results, but it may indicate that the Phytoptidae and Eriophyidae are not monophyletic groupings.

Kuang *et al.* (1992) studied the relationships between five eriophyoid species using polyacrylamide gel electrophoresis to observe the differences between esterase isozymes. The species were from the

subfamilies Nalepellinae, Phyllocoptinae, and Rhyncaphytoptinae and can thus be regarded as exemplar species of the three eriophyoid families Phytoptidae, Eriophyidae and Diptilomiopidae, respectively. They did a cluster analysis with Euclidean distance as a measure of similarity, and used the bio-chemical and some morphological characters as data. In the resultant phenogram *Tegolophus fontanesiae* Kuang & Hong, 1991 and *Aculus ligustri* (Keifer, 1938) (both of the Eriophyidae: Phyllocoptinae: Anthocoptini) clustered together and were regarded as the most closely related. *Trisetacus juniperinus* (Nalepa, 1911) and *Boczekella pseudolaris* Kuang & Shen, 1994 (both of the Phytoptidae: Nalepellinae: Trisetacini) clustered together. *Rhyncaphytoptus lonicerae* Kuang & Zhao, 1987 (Diptilomiopidae: Rhyncaphytoptinae) clustered with the *T. fontanesiae–A. ligustri* (Anthocoptini) group. The taxa included are extremely limited, and represent only tiny portions of the morphological variation in the three families, and it is generally accepted that phenetic analyses are not appropriate for studying phylogenetic relationships between taxa. The results and conclusion are not highly significant. The Diptilomiopidae and Eriophyidae, nevertheless, were apparently more closely related to each other than the Diptilomiopidae and the Phytoptidae.

As a follow up on the previous study, Kuang *et al.* (1995) determined the karyotypes of 10 species from the three eriophyoid families. Although the study resulted in few valid or significant results and conclusions, it supported the relationships hypothesized by Kuang *et al.* (1992) that the Diptilomiopidae and Eriophyidae are more closely related to each other than the Diptilomiopidae and the Phytoptidae.

Sukhareva (1994) undertook a phenetic study of the Phytoptidae *sensu* Boczek *et al.* (1989) which comprises species with *ve* present, single and paired *vi* absent; and *sc*, *c1* and tibial solenidion *φ* present or absent. This group of species occurs mainly on sedges, grasses, lilies and palms of the Monocotyledones (Sukhareva, 1994). She included 43 operational taxonomic units (OTUs) (40 Phytoptidae species, the redescription of one species, and the deutogyne in addition to the protogyne females of another two species), and analysed 22 characters which are of identification importance at the species level, with correlation and principle component analyses.

With the correlation analysis, Sukhareva (1994) identified two groups of characters. One character group described wormlike mites with many subequal annuli, with the gnathosoma directed more forward, with the prodorsal shield pattern consisting of vertical, almost parallel lines characteristic of mites living in enclosed spaces, which she named the gall-living form (= non-vagrants). The other group described mites with more compact bodies, with fewer annuli and a large, often smooth prodorsal shield, and the gnathosoma directed downwards, typical of mites living exposed on various parts of the plant, which she named the free-living form (= vagrants). Sukhareva (1994) regarded the non-vagrants as the earlier derivative form or the form closer to the “original” form of the

Eriophyoidea. She also compared the host plant distribution of the two forms, incorporating principle component analysis of the morphological and morphometric data. She found that Phytoptidae species living on sedges (Cyperaceae), grasses (Poaceae) and lilies (Liliaceae) of the monocotyledons have the earlier derivative non-vagrant form; Phytoptidae species living on palms (Arecaceae) of the monocotyledons have an exposed life-style and corresponding vagrant form. Both mite forms are found in species living on various dicotyledons, and the loss of structures such as *c1* and the tibial solenidion *φ* is not correlated with body form or habitus. The earlier derived gall-living form on monocotyledons, although superficially the same as those of this form living on dicotyledons, actually differs in some regards, e.g., number of annuli posteriad of *f*. They differ to such a degree that Smith (1977) divided them in two groups, and proposed that the gall-living form on dicotyledons acquired this body shape as a reversal from "free-living forms" having secondarily acquired a confined and protected life-style, and is thus not the same lineage as the gall-living form on monocotyledons (Sukhareva, 1994). She concluded that the Phytoptidae (*sensu* Boczek *et al.*, 1989) are one of the earlier evolutionary stages of the Eriophyoidea on Angiospermae. Further, on dicotyledons there is no connection between the evolution of the plants and the morphological changes in the mites, and both life forms can be found on the same plant groups, and is probably rather correlated with the type of habitats the mites occupy on them, with free-living forms transforming to gall-living forms and *vice versa*, probably continuously involving many reversals. The study by Sukhareva (1994) was carefully executed and presented and testable hypotheses were generated, but a phenetic study cannot be defended for studying the phylogeny of a group, and the hypotheses should be tested incorporating sound phylogenetic analyses.

Hong & Zhang (1996a, b; 1997) published three phylogenetic studies on the Eriophyoidea, in which they analysed generic relationships: the phylogeny of the Eriophyoidea (to test monophyly of the families), the Cecidophyini, and the Diptilomiopinae, respectively. Hong & Zhang (1996a) analysed 35 discrete morphological characters of 17 eriophyoid genera to test the monophyly of the families. In the discussion of their preferred tree they regarded all characters, including homoplasies supporting groups, as synapomorphies. According to the more traditional literature on phylogenetic theory, only homologous characters can be named and regarded as synapomorphies, and a group is only a clade when it is supported by at least one synapomorphy (Kitching *et al.*, 1998; Brooks & McLennan, 2002). It is certainly recognized, however, that homoplasy is important in supporting groups, and may contribute to increased phylogenetic resolution and robustness of groups found (Källersjö *et al.*, 1999; also see discussion of support of groups and clades found in the present study later on in the discussion). Only those groups which are "real clades", and supported by homologous characters, are included in this presentation of their work. The other groups they regarded as monophyletic groupings are not recognized as monophyletic groups in the present study.

The preferred tree of Hong & Zhang (1996a) is presented in Fig. 4.3a. They found the Diptilomiopidae to be monophyletic. Within the Diptilomiopidae clade, *Diptacus* and *Diptilomiopus* were found as a smaller clade, supporting the monophyly of the Diptilomiopinae. The Diptilomiopidae clade is sister to a taxon group (not at the same node) including all the Eriophyidae included in the analysis and *Sierraphytoptus* of the Phytoptidae. These taxa, including the Diptilomipidae clade, grouped together as a well-supported clade. This implied a closer relationship between the Eriophyidae and the Diptilomiopidae, than the Diptilomiopidae have with the Phytoptidae (Hong & Zhang, 1996a), excluding *Sierraphytoptus*. *Nalepella* is sister to the latter clade, and *Trisetacus* sister to the clade which includes *Nalepella*. Within the Eriophyidae-*Sierraphytoptus* taxon group, *Cecidophyes* and *Aberoptus* were found as a clade and together with *Nothopoda* and *Eriophyes*, were found as a larger clade. The remainder of the Phytoptidae (*Phytoptus*, *Mackiella*, *Novophytoptus* and *Pentasetacus*) are outside the clade which includes the remainder of the Eriophyoidea in the data set, with relationships between them largely unresolved.

The Phytoptidae were found to be polyphyletic, and not paraphyletic as interpreted by Hong & Zhang (1996a) and they proposed a stronger division of the groups within the Phytoptidae in the eriophyoid classification, elevating Phytoptidae subfamilies to monophyletic families. They did not propose formal change of the Eriophyoidea classification. They commented though, that the classification by Boczek *et al.* (1989) is more natural in dividing the Phytoptidae into different families. They also concluded that the Phytoptidae have more plesiomorphic characters than the Eriophyidae and Diptilomiopidae, and that *Pentasetacus* was found to be the most primitive eriophyoid taxon. It is significant that these conclusions are not supported by the tree they presented.

The consistency indices for the trees they found were low, and indicated a high degree of homoplasy in the data. Their study included a very small sample of the Eriophyoidea, and they did not include taxa from all the suprageneric taxa in the Eriophyoidea. Their data set was corrected and re-analysed under different parameters in the present study, and the results and discussion thereof and more detail about their analysis are reported further on in this chapter under “Results and Discussion”.

Hong & Zhang (1996b) studied the phylogeny of the tribe Cecidophyini by analysing 21 morphological characters of nine genera of the Cecidophyini. They included four genera as outgroup taxa: *Phytoptus* (Phytoptidae), *Phyllocoptes* (Phyllocoptinae), *Eriophyes* (Eriophyinae) and *Colomerus* from the Cecidophyinae tribe Colomerini which they regarded as sister to the Cecidophyini. They presented one most parsimonious tree found after three successive re-weightings of the initial 63 most parsimonious trees found by the “branch-and-bound” parsimony procedure in PAUP 3.0 (Swofford, 1991). The Cecidophyini were found to be monophyletic, and the clade was supported by two synapomorphies: *sc* and its setal tubercle absent. They further defined two distinct clades in the Cecidophyini clade. One

clade included *Dechela* and *Neserella*, supported by the synapomorphies: *1b* and *l'* absent. Another clade contained the remainder of the Cecidophyinae genera in their analysis, and was supported by one synapomorphy: the opisthosoma divided into longer dorsal annuli, and narrower ventral annuli. Within this clade *Achaetocoptes* and *Johnella* were retrieved as a clade supported by two synapomorphies: dorsal annuli of variable width, and fewer, broad dorsal annuli with lateral extensions. This clade was found to group with *Cecidophyes*, *Coptophylla* and *Glyptacus* in the same clade with relationships between them unresolved. *Chrecidus* was sister to this clade, and *Cecidophyopsis* sister of the clade containing *Chrecidus*.

Hong & Zhang (1997) reviewed the Diptilomiopinae and studied their phylogeny. They analysed 19 characters of 23 Diptilomiopinae genera with *Rhyncaphytoptus*, of the Rhyncaphytoptinae which they regarded as sister to the Diptilomiopinae, as outgroup. In their analysis three successive weighting cycles of 1 048 most parsimonious trees found with a heuristic search, produced 83 most parsimonious trees and they presented a strict consensus of these. The Diptilomiopinae were retrieved as a clade, supported by one synapomorphy, a divided empodium. They regarded *Brevulacus* retrieved as sister to a clade with the remainder of the Diptilomiopinae as a distinct division of the subfamily into two groups. The one group consists of *Brevulacus* with *bv* on leg I, which is absent in the remainder of the Diptilomiopinae. Amrine (1996) placed the monospecific *Brevulacus* in the Rhyncaphytoptinae, because he regarded the empodium to be entire and not divided as Manson (1984a) interpreted it to be. The interpretation by Hong & Zhang (1997) of the tree they presented does not correspond with the presented tree, particularly regarding the characters mapped on it, and whether they are homoplasious or homologous. More detailed information will be provided in the comparisons of the results by Hong & Zhang (1997) with the results in the present study, but the tree groups were: *Levonga* was found to group with *Pseudodiptacus*, with *Dacundiopus* their sister; *Lambella* was sister to (*Dacundiopus* (*Levonga*, *Pseudodiptacus*)); and *Africus* was sister to this group. This group, and *Diptilomiopus* and *Diptilorhynacus* were retrieved in the same group, with relationships between them unresolved. *Neodiptilomiopus*, *Vimola*, *Rhynacus* and *Diptiloplatus* and the genera and groupings listed so far, were found to group together in a well-supported group (that seems to be a clade). This clade was recovered together with *Diptiloplatus* and *Neorhynacus* as a clade with unresolved relationships between them. The latter clade and *Acarhynchus*, *Asetadiptacus*, *Dialox*, *Diptacus*, *Neodialox* and *Pararhynacus* were retrieved as the same group. Within this group, *Neodialox* and *Pararhynacus* were a group. *Apodiptacus* and *Trimeroptus* were recovered as a group, and this group and *Bucculacus* are outside the previous larger group.

The first molecular phylogenetic study on the Eriophyoidea with the aim to study the phylogeny of the entire superfamily is being undertaken by M. Lekveishvili and co-workers (West Virginia University, USA). This study is in progress and the data still unpublished, although its preliminary results have

been presented at two congresses. Their analyses of 18S and COI gene sequence data (M. Lekveishvili, *unpubl. data*), showed that the 18S gene is probably the more informative at higher taxonomic levels. Their ingroup consisted of about 26 eriophyoid species, of which about 16 were *Aceria* spp., and a tydeid species was the outgroup species. Their preliminary analyses recovered some groupings of *Aceria* spp.; however, monophyly of the genus was not recovered. The Diptilomiopidae was poorly represented (one or two species). When only one species was included, it was positioned outside the Eriophyidae, but including another Diptilomiopidae species placed the family among the Eriophyidae. They included two species of two of the Phytoptidae subfamilies – Nalepellinae and Phytoptinae. These species were retrieved as a fairly well-supported clade outside a well-supported clade that included the Eriophyidae and Diptilomiopidae. The molecular data in their data set were similarly homoplasious than found in the morphological data sets in the present study, with CI and RI values ranging from about 0.55 to 0.65 for a 27-taxon data set. Their preliminary data had poor taxon sampling, and a current data set includes more than 80 taxa and sequence data of one more gene, EF-1alpha (M. Lekveishvili, *pers. comm.*, January 2010).

An unpublished phylogenetic study on the Phytoptidae was undertaken by R. Ochoa (USDA-ARS, Beltsville, USA) (R. Ochoa, *pers. comm.*). He derived character states of the hypothetical ancestor through analysis of the type genus of the Tydeidae, and included *Eriophyes* and *Ashieldophyes* (Eriophyidae) as outgroup taxa in his analysis of the Phytoptidae (ingroup) at generic level. He analysed the data set with parsimony analyses in PAUP 3.1.1 (Swofford, 1993). The unpublished results of the analysis broadly were: *Prothrix* and the Sierraphytoptinae (*Neopropilus*, *Propilus*, *Retracrus*, and *Sierraphytoptus*) were recovered as a clade (the "*Sierraphytoptus* clade"). *Mackiella* and *Austracus* (Sierraphytoptinae) were sisters to the "*Sierraphytoptus* clade". *Anchiphytoptus* and *Phytoptus* (both in the Phytoptinae); and *Novophytoptus* (Novophytoptinae) and *Acathrix* (Phytoptinae) were retrieved as two groups. *Fragariocoptes* (Sierraphytoptinae), *Boczekella* and *Setoptus* (both of the Nalepellinae) were in the same group with the two Eriophyidae taxa included as outgroups in the analysis, *Eriophyes* and *Ashieldophyes*, in an "*Eriophyes* clade". The Eriophyidae group is sister to the Phytoptidae in this "*Eriophyes* clade". R. Ochoa (*unpubl. data*) concluded that the grouping of the Eriophyidae and some Phytoptidae in the same clade indicates problems in the traditional division of the Phytoptidae based on external morphology.

4.2 MATERIAL AND METHODS

4.2.1 Taxon sampling

4.2.1.1 Ingroup taxa

In total, 318 worldwide taxa are included in the present study of which 316 are eriophyoid species, or ingroup taxa (taxa sampled are listed in Table 4.1 and Appendix A). Three different taxon samples from the same 318 taxa were sampled and analysed: 318, 66 and 18 taxa (Table 4.1). These different sizes taxon sets sampled formed part of a set of different parameters, under which the relationships, groups and clades found during the study, were evaluated.

Every suprageneric group in the Eriophyoidea classification (Amrine *et al.*, 2003; Table 1.1) is quite comprehensively represented in this sample. Care was taken to reflect the diversity at genus level of the Eriophyoidea as a whole. Type species of genera were chosen. Largely the type species of about 73% of genera then recognized (Amrine *et al.*, 2003), were sampled for the study (220 of 301 genera). Although care was taken to sample from all higher eriophyoid taxa, the sample was taken without using the classification as the only guideline for sampling, such as the percentage of each taxon sampled. The choice of taxa, however, was influenced by the quality of published species descriptions. Additionally, when the original description of a type species was too meagre or sub-standard, or in another language which could not be easily translated, another species of the genus was chosen, if there were more than one species in such a genus. This other species was chosen to be as representative as possible of the morphological variety in the genus. It was included, either additional to, or as substitute for the type species. Sometimes more than one species per genus were included on an *ad hoc* basis, when it was noticed that some of the species in the genus may not belong therein, or when a specific characteristic of the genus was proposed to be homologous, e.g., the position of the genitalia in *Novophytoptus*.

Table 4.1. Eriophyoid taxa and two outgroup taxa included in the cladistic analyses. The species included in the different data sets (318-taxon, 66-taxon, 18-taxon) are indicated by black (ingroup taxa) and open (outgroup taxa) circles.

This table will be printed from MS Excel, please see printed copy, or separate electronic copy.

Table 4.1. Mite species included in the 318, 66 and 18 taxon data sets, arranged according to their classification according to Amrine *et al* . (2003). Open circles indicate species included as outgroup taxa, and closed circles the ingroup taxa.

Classification	Species	318	66	18
	OUTGROUP TAXA			
Tetranychidae	*Mononychelus yemensis*	○	○	
Tydeidae	*Orfareptydeus stepheni*	○	○	○
	INGROUP TAXA			
PHYTOPTIDAE				
NALEPELLINAE				
Nalepellini	*Nalepella tsugifoliae*	●	●	●
	Pentaporca taiwanensis	●		
	Phantacrus lobatus	●	●	
	Setoptus jonesi	●		
Pentasetacini	*Pentasetacus araucaria*	●	●	●
Trisetacini	*Boczekella laricis*	●		
	Trisetacus ehmanni	●	●	●
	Trisetacus pini	●		
NOVOPHYTOPTINAE	*Novophytoptus rostratae*	●		●
	Novophytoptus stipae	●	●	
PHYTOPTINAE	*Acathrix trymatus*	●	●	
	Anchiphytoptus lineatus	●		
	Oziella yuccae	●		
	Phytoptus avellanae	●	●	●
PROTHRICINAE	*Prothrix aboula*	●	●	
SIERRAPHYTOPTINAE				
Mackiellini	*Mackiella phoenicis*	●		●
	Palmiphytoptus oculatus	●		
	Propilus gentyi	●		
	Retracrus johnstoni	●	●	
Sierraphytoptini	*Austracus havrylenkonis*	●		
	Fragariocoptes setiger	●		
	Neopropilus jatrophus	●	●	
	Sierraphytoptus alnivagrans	●	●	●
ERIOPHYIDAE				
ABEROPTINAE	*Aberoptus samoae*	●	●	●
	Cisaberoptus kenyae	●		
	Cisaberoptus pretoriensis	●		
ASHIELDOPHYINAE	*Ashieldophyes pennadamensis*	●		●
CECIDOPHYINAE				
Cecidophyini	*Achaetocoptes ajoensis*	●		
	Bariella farnei	●		
	Cecidophyes rouhollahi	●	●	●
	Chrecidus quercipodus	●		
	Coptophylla lamimani	●		
	Dechela epelis	●	●	
	Glyptacus lithocarpi	●		
	Johnella virginiana	●		
	Neserella decora	●		
Colomerini	*Afromerus florinoxus*	●		

Classification	Species	318	66	18
	Circaces chakrabarti	●		
	Colomerus gardeniella	●	●	
	Cosetacus camelliae	●	●	
	Ectomerus anysis	●		
	Epicecidophyes clerodendris	●	●	
	Gammaphytoptus camphorae	●		
	Indosetacus rhinacanthi	●		
	Neocecidophyes mallotivagrans	●		
	Paracolomerus casimiroae	●	●	
ERIOPHYINAE				
Aceriini	*Acalitus ledi*	●	●	
	Aceria tulipae	●	●	
	Acerimina cedrelae	●		
	Acunda plectilis	●	●	
	Baileyna marianae	●		
	Cenaca syzygioidis	●	●	
	Cymoptus spiniventris	●		
	Keiferophyes avicenniae	●		
	Notaceria tetrandiae	●		
	Paraphytoptella arnaudi	●		
	Ramaculus mahoe	●		
	Scoletoptus duvernoiae	●		
Diphytoptini	*Diphytoptus nephroideus*	●		
	Schizoempodium mesophyllincola	●	●	
Eriophyini	*Asetilobus hodgkinsi*	●		
	Brachendus pumilae	●		
	Cercodes simondsi	●		
	Eriophyes pyri	●	●	●
	Eriophyes quadrifidus	●	●	
	Nacerimina gutierrezi	●		
	Pareria fremontiae	●	●	
	Proartacris pinivagrans	●		
	Stenacis palomaris	●		
	Trimeracarus heptapleuri	●		
NOTHOPODINAE				
Colopodacini	*Adenocolus psydraxi*	●		
	Apontella bravaisiae	●		
	Colopodacus africanus	●	●	
Nothopodini	*Anothopoda johnstoni*	●		
	Cosella deleoni	●		
	Disella ilicis	●		
	Floracarus calonyctionis	●		
	Neocosella ichnocarpae	●		
	Nothopoda rapaneae	●	●	●
	Pangacarus grisalis	●		
PHYLLOCOPTINAE				
Acaricalini	*Acaphyllisa parindiae*	●	●	
	Acaricalus segundus	●	●	
	Cymeda zealandica	●		
	Dichopelmus notus	●		
	Knorella gigantochloae	●	●	
	Litaculus khandus	●	●	
	Neoacaphyllisa lithocarpi	●		
	Neodichopelmus samoanus	●		
	Notacaphylla chinensiae	●		

Classification	Species	318	66	18
	Paracaphylla streblae	●		
	Schizacea gynerii	●		
	Tumescoptes trachycarpi	●		
Anthocoptini	*Abacarus acalyptus*	●	●	
	Abacarus hystrix	●		
	Aculodes mckenziei	●		
	Aculops populivagrans	●	●	
	Aculus ligustri	●	●	
	Anthocoptes gutierreziae	●	●	
	Bakeriella ocimis	●		
	Catachella machaerii	●		
	Costarectus zeyheri	●		
	Ditrymacus athiasella	●		
	Epiphytimerus palampurensis	●		
	Heterotergum gossypii	●		
	Indotegolophus darjeelingensis	●		
	Keiferana neolitseae	●		
	Mesalox tuttlei	●		
	Metaculus syzygii	●		
	Meyerella bicristatus	●		
	Neocolopodacus mitragynae	●		
	Neomesalox kallarensis	●		
	Neophantacrus mallotus	●		
	Notallus nerii	●		
	Nothacus tuberculatus	●		
	Notostrix attenuata	●		
	Paraciota tetracanthae	●		
	Pentamerus rhamnicroceae	●	●	
	Porcupinotus humpae	●		
	Porosus monosporae	●		
	Pyelotus africanae	●		
	Quintalitus squamosus	●		
	Rectalox falita	●		
	Sinacus erythrophlei	●		
	Tegolophus califraxini	●	●	
	Tegoprionus dentatus	●		
	Tetra concava	●		
	Tetraspinus lentus	●		
	Thamnacus rhamnicola	●	●	
	Ursynovia ulmi	●		
	Vittacus mansoni	●		
Calacarini	*Calacarus pulviferus*	●	●	
	Jutarus benjaminae	●		
	Paracalacarus podocarpi	●	●	
Phyllocoptini	*Acadicrus bifurcatus*	●	●	
	Acamina nolinae	●	●	
	Acarelliptus cocciformis	●		
	Acritonotus denmarki	●	●	
	Aequsomatus lanceolatae	●	●	
	Arectus bidwillius	●		
	Calepitrimerus cariniferus	●		
	Caliphytoptus quercilobatae	●		
	Caroloptes fagivagrans	●		
	Cecidodectes euzonus	●		
	Cenalox nyssae	●	●	
	Criotacus brachystegiae	●		
	Cupacarus cuprifestor	●		
	Epitrimerus pyri	●		

Classification	Species	318	66	18
	Euterpia fissa	●		
	Indonotolox sudarsani	●		
	Keiferella juniperici	●		
	Latinotus wegoreki	●		
	Leipothrix solidaginis	●		
	Metaplatyphytoptus amoni	●		
	Monotrymacus quadrangulari	●		
	Neocupacarus flabelliferis	●		
	Neodicrothrix tiliacorae	●		
	Neometaculus bauhiniae	●		
	Neophytoptus ocimae	●		
	Phyllocoptes calisorbi	●		●
	Phyllocoptruta arga	●	●	
	Phyllocoptruta oleivora	●	●	
	Platyphytoptus sabinianae	●		
	Proneotegonotus antiquorae	●		
	Prophyllocoptes riveae	●		
	Rhombacus morrisi	●		
	Tergilatus sparsus	●		
	Vasates quadripedes	●	●	
Tegonotini	*Dicrothrix anacardii*	●	●	
	Neotegonotus fastigatus	●		
	Shevtchenkella juglandis	●		
	Tegonotus mangiferae	●	●	
DIPTILOMIOPIDAE				
DIPTILOMIOPINAE	*Acarhis diospyrosis*	●		
	Acarhis lepisanthis	●		
	Acarhis siamensis	●		
	Acarhynchus filamentus	●		
	Africus psydraxae	●		
	Apodiptacus cordiformis	●	●	
	Asetadiptacus emiliae	●		
	Bucculacus kaweckii	●		
	Chiangmaia longifolii	●		
	Dacundiopus stylosus	●		
	Davisella breitlowi	●		
	Dialox stellatus	●		
	Diptacus pandanus	●		
	Diptacus sacramentae	●	●	●
	Diptilomiopus acronychia	●		
	Diptilomiopus aglaiae	●		
	Diptilomiopus alagarmalaiensis	●		
	Diptilomiopus alangii	●		
	Diptilomiopus anthocephaliae	●		
	Diptilomiopus apolongus sp. nov.	●		
	Diptilomiopus apobrevis sp. nov.	●		
	Diptilomiopus aralioidus	●		
	Diptilomiopus artabotrysi	●		
	Diptilomiopus artocarpae	●		
	Diptilomiopus asperis	●		
	Diptilomiopus assamica	●	●	●
	Diptilomiopus averrhoae	●	●	
	Diptilomiopus azadirachtae	●		
	Diptilomiopus barringtoniae	●		
	Diptilomiopus bengalensis	●		
	Diptilomiopus benjaminae	●		
	Diptilomiopus boueae	●		

Classification	Species	318	66	18
	Diptilomiopus camarae	●		
	Diptilomiopus cerberae	●		
	Diptilomiopus championi	●		
	Diptilomiopus cocculae	●		
	Diptilomiopus combretae	●		
	Diptilomiopus combreti	●		
	Diptilomiopus commuiae	●		
	Diptilomiopus coreiae	●		
	Diptilomiopus cumingis	●		
	Diptilomiopus cuminis	●		
	Diptilomiopus cuminis Huang	●		
	Diptilomiopus cythereae	●		
	Diptilomiopus davisi	●		
	Diptilomiopus dendropanacis	●		
	Diptilomiopus elaeocarpi	●		
	Diptilomiopus elliptus	●		
	Diptilomiopus emarginatus	●		
	Diptilomiopus ervatamiae	●		
	Diptilomiopus eucalypti	●		
	Diptilomiopus euryae	●		
	Diptilomiopus faurius sp. nov.	●		
	Diptilomiopus ficifolius	●		
	Diptilomiopus ficus	●		
	Diptilomiopus ficusis	●		
	Diptilomiopus formosanus	●		
	Diptilomiopus gilibertiae	●		
	Diptilomiopus guajavae	●		
	Diptilomiopus hexogonus	●		
	Diptilomiopus holmesi	●		
	Diptilomiopus holopteleae	●		
	Diptilomiopus holoptelus	●		
	Diptilomiopus illicii	●		
	Diptilomiopus indicus	●		
	Diptilomiopus integrifoliae	●		
	Diptilomiopus jasminiae	●		
	Diptilomiopus javanicus	●		
	Diptilomiopus jevremovici	●	●	
	Diptilomiopus knorri	●		
	Diptilomiopus languasi	●		
	Diptilomiopus leeasis	●		
	Diptilomiopus leptophyllus	●		
	Diptilomiopus lobbianus	●		
	Diptilomiopus loropetali	●		
	Diptilomiopus maduraiensis	●		
	Diptilomiopus malloti	●		
	Diptilomiopus melastomae	●		
	Diptilomiopus meliae	●		
	Diptilomiopus morii	●		
	Diptilomiopus morindae	●		
	Diptilomiopus musae	●		
	Diptilomiopus octogonus	●		
	Diptilomiopus pamithus	●		
	Diptilomiopus perfectus	●		
	Diptilomiopus phylanthi	●		
	Diptilomiopus pocsi	●		
	Diptilomiopus racemosae	●		
	Diptilomiopus riciniae	●		
	Diptilomiopus sandorici	●		

Classification	Species	318	66	18
	Diptilomiopus securinegus	●		
	Diptilomiopus septimus	●		
	Diptilomiopus stephanus	●		
	Diptilomiopus strebli	●		
	Diptilomiopus swieteniae	●		
	Diptilomiopus thaianae	●		
	Diptilomiopus thangaveli	●		
	Diptilomiopus thunbergiae	●		
	Diptilomiopus trewier	●		
	Diptilomiopus ulmivagrans	●		
	Diptiloplatus megagrastis	●		
	Diptilorhynacus dioscoreae	●		
	Diptilorhynacus sinusetus	●		
	Diptilostatus nudipalpus	●		
	Duabangus chiangmai	●		
	Kaella flacourtiae	●		
	Lambella cerina	●		
	Levonga casearíasis	●		
	Levonga litseae	●		
	Levonga papaitongensis	●		
	Lithocarus thomsoni	●		
	Mediugum sanasaii	●		
	Neoacarhis aglaiae	●		
	Neodialox palmyrae	●		
	Neodiptilomiopus vishakantai	●		
	Neolambella ligustri	●		
	Neorhynacus rajendrani	●	●	
	Norma lanyuensis	●		
	Pararhynacus photiniae	●		
	Prodiptilomiopus auriculatae	●		
	Rhynacus arctostaphyli	●	●	
	Steopa bauhiniae	●		
	Suthamus chiangmi	●		
	Thailandus diospyrosae	●		
	Trimeroptes eleyrodiformis	●		
	Vimola syzygii	●		
RHYNCAPHYTOPTINAE	*Areekulus eugeniae*	●		
	Asetacus madronae	●	●	
	Brevulacus reticulatus	●		
	Catarhinus tricholaenae	●	●	
	Chakrabartiella ficusis	●	●	
	Cheiracus sulcatus	●	●	
	Hoderus roseus	●	●	
	Hyborhinus kallarensis	●		
	Konola hibernalis	●		
	Neocatarhinus bambusae	●		
	Peralox insolita	●		
	Quadracus mangiferae	●		
	Quadracus urticarius	●		
	Quadriporca indicae	●		
	Quadriporca mangiferae	●		
	Rhinophytoptus concinnus	●		●
	Rhinotergum schestovici	●		
	Rhyncaphytoptus ficifoliae	●	●	●
	Sakthirhynchus canariae	●		
	Stenarhynchus aristidus	●		

4.2.1.2 Outgroup taxa

In the present study, two exemplar species were used from taxa outside the Eriophyoidea (Table 4.1; Appendix A): *Orfareptydeus stepheni* Ueckermann & Grout, 2007 (Trombidiformes: Prostigmata: Eupodina: Tydeoidea: Tydeidae: Tydeinae) (Ueckermann & Grout, 2007) (Fig. 4.1), and *Mononychellus yemensis* Meyer, 1996 (Trombidiformes: Prostigmata: Eleutherengona: Tetranychoidea: Tetranychidae: Tetranychinae) (Meyer, 1996) (Fig. 4.2). These specific species were chosen on the basis of their relatively recent descriptions, presuming that species descriptions for these groups became more comprehensive over time. The species are more or less "typical" of their groups (E.A. Ueckermann, *pers. comm*.), and type material of the species, in decent condition, was available for study. By including these species, the monophyly of the groups they belong to was not implied, but they are certainly outside the ingroup, and both groups have been proposed as being closely related to the Eriophyoidea. Lindquist (1996b) argued that the Tydeidae is the sister taxon of the Eriophyoidea.

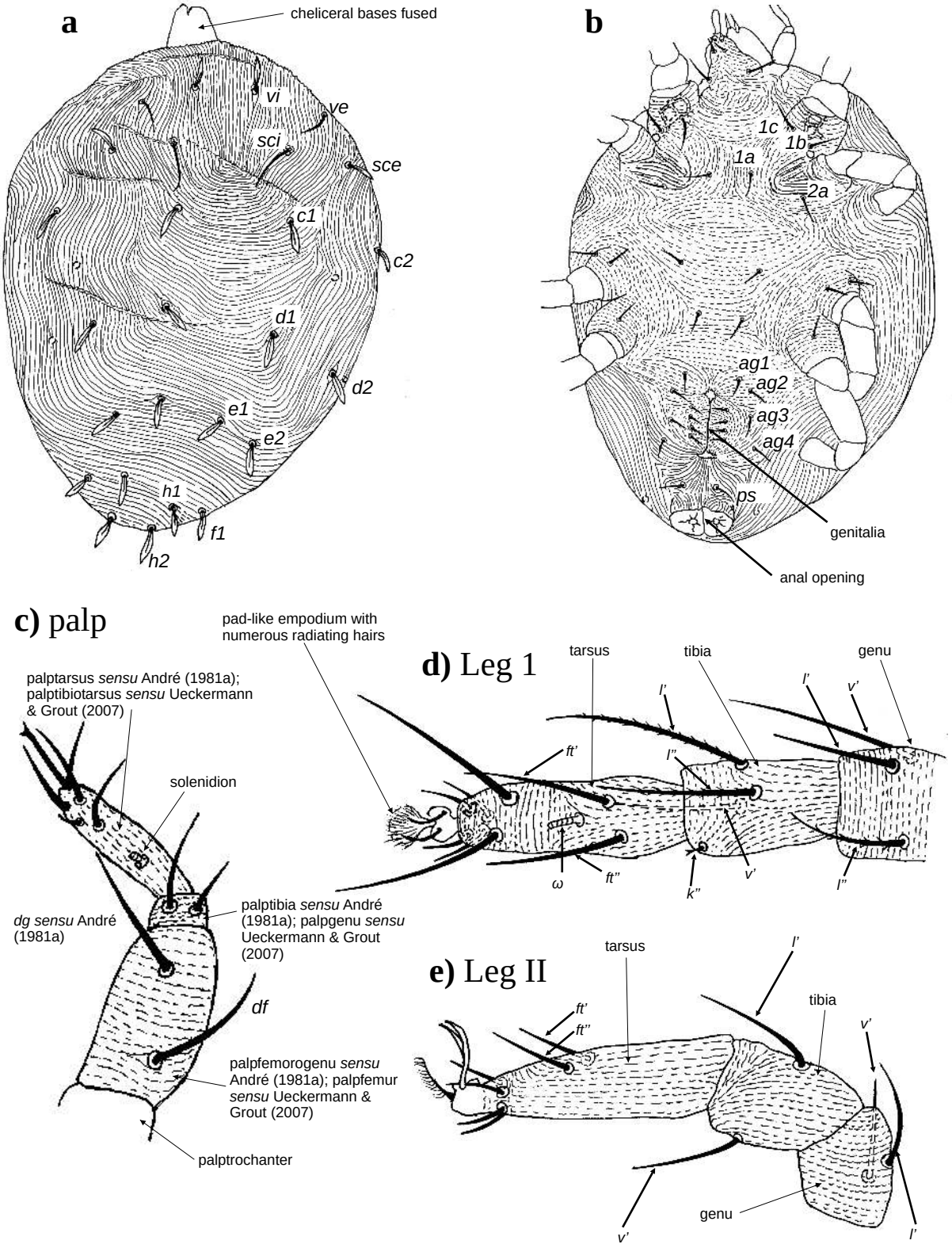


Fig. 4.1. *Orfareptydeus stepheni* Ueckermann & Grout, 2007 (Tydeidae: Tydeinae). Female: **a)** dorsal view; **b)** ventral view; **c)** palp; **d)** leg I; **e)** leg II. Original drawings in Ueckermann & Grout (2007), used with permission.

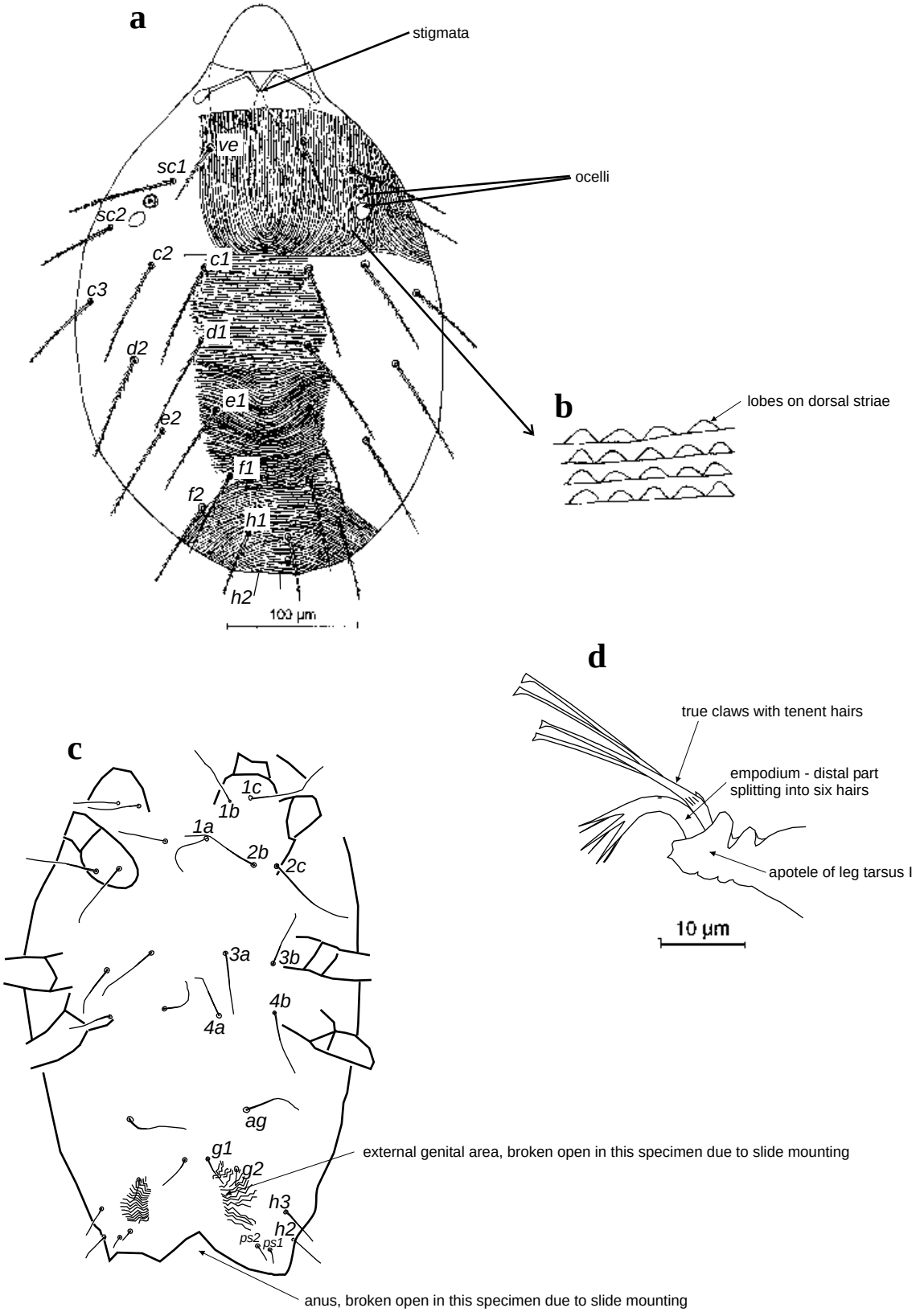


Fig. 4.2. *Mononychellus yemensis* Meyer, 1996 (Tetranychidae). Female: **a)** dorsal view [setae *h2* not included in original drawing by Meyer (1996)]; **b)** enlargement of lobes on dorsal striae; **c)** ventral view; **d)** apotele of tarsus I. Drawings a, b and d modified from Meyer (1996), drawing c original drawing by author from holotype.

Fig. 4.1. *Orfareptydeus stepheni* Ueckermann & Grout, 2007 (Tydeidae: Tydeinae). Female: **a)** dorsal view; **b)** ventral view; **c)** palp; **d)** leg I; **e)** leg II. Drawings modified from Ueckermann & Grout (2007).

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Fig. 4.2. *Mononychellus yemensis* Meyer, 1996 (Tetranychidae). Female: **a)** dorsal view [setae *h2* not included in original drawing by Meyer (1996)]; **b)** enlargement of lobes on dorsal striae; **c)** ventral view; **d)** apotele of tarsus I. Drawings a, b and d modified from Meyer (1996), drawing c original drawing by author from holotype.

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4.2.2 Character sampling

Only morphological data were used for this study. The descriptive data were primarily obtained from published original descriptions (Appendix A), including descriptive drawings. Information from additional published descriptions of a species was added if available. Published features of South African species were checked on slide-mounted type specimens or additional material, when type material was unavailable, and on scanning electron microscope (SEM) images if the particular species was included in the SEM study undertaken (Chapter 3). Morphological data for the three new *Diptilomiopus* spp. described in the present study were obtained from slide-mounted specimens and digital images of specimens obtained with the SEM study (Chapter 3).

Characters in the data matrices for phylogenetic analyses were restricted to those observable on slide-mounted specimens, and which were already included in published species descriptions, and which have been scored for most species in the data set. All discrete descriptive characters generally described in species descriptions were, however, included as far as possible, apart from the detail of ridges, furrows and other modifications (see species of the Phyllocoptinae in Amrine *et al*., 2003) of an evenly rounded eriophyoid body. Particularly those characters that are used in the current classification to define suprageneric taxa, those hypothesized as synapomorphic characters in evolutionary hypotheses of the groups, and characters used in previous cladistic analyses of the Eriophyoidea were included. Some characters informative at the species level, for example, substructures of the prodorsal shield ornamentation, were not included. These were, however, included in a parallel study on the phylogeny of *Diptilomiopus* spp., not included in this dissertation. Methods for initial capturing of the published data, and slide preparation of specimens are provided in Chapter 2, and the material and methods section for the SEM study in Chapter 3.

4.2.3 Definition, description and discussion of characters coded for phylogenetic analyses

A total of 117 characters (see character discussion in Appendix B) were scored for the 318-taxon (Table 4.1; Appendix A) data matrix (Appendix D). The 27 characters informative for the phylogenetic resolution of ingroup taxa cladistically analyzed by Hong & Zhang (1996a) were included. The character states of many of these were modified for the present study to study the influence of character state definitions on results. The modified states were also similar to the character states for the other analyses in the present study, and thus results could be compared without the influence brought about by different character definitions. Thirty-eight additional characters informative for the phylogenetic resolution of ingroup taxa, not previously used in phylogenetic studies of the Eriophyoidea, were added. Sixty-six of the 117 characters are informative for resolving relationships between the ingroup taxa. The characters informative of relationships in the ingroup consist of 17 binary characters and 49 multistate characters, with a maximum of 16 character states per character.

The uninformative characters comprise 44 autapomorphic characters of the Eriophyoidea, five autapomorphic characters of terminal eriophyoid taxa, and two characters that were the same for all taxa included in the analyses. Hypothetically, a diversity of synapomorphies strongly supports the monophyly of the Eriophyoidea. Many of these are autapomorphies of the Eriophyoidea within the Acari. Lindquist (1996b) provides a list of these hypothesized synapomorphies and some are included in the data matrix for the present analyses of the 318-taxon data set (Appendix D). The uninformative characters were included because they may be informative of relationships with some of the species excluded from the analyses, will test the relationship between outgroup and ingroup taxa, and will produce a more complete set of characters mapped on the trees and discussed in the character list. The matrix will eventually serve as a storage space for descriptive data. Some autapomorphies of eriophyoid terminal species pertinent in the key to genera (Amrine *et al.*, 2003) were included, but most were not, for example, the presence of a large extension projecting dorsally for the dorsal surface of anal lobes in *Schizoempodium mesophyllincola* Oldfield, Hunt & Gispert, 1998 (Oldfield *et al*., 1998).

The inclusion of these uninformative characters in the analyses causes an artificial increase in the CI (ensemble consistency index) which measures the amount of homoplasy in a given data set (Kitching *et al.*, 1998). These uninformative characters were excluded from the 66-taxon data matrix and analyses. Since fewer taxa were included in the 66-taxon data set, the accuracy of the CI was possibly improved in comparison with the CI of the 318-taxon data set – when the number of taxa increases values of CI decrease (Kitching *et al.*, 1998), and additional exclusion of uninformative characters further improved the accuracy. The exclusion of the uninformative characters from the 66- and 18-taxon character sets also prevented unnecessary duplication in the different sets.

A total of 60 characters (Appendices C & E) from the 117 character set were prepared for the 66-taxon sub-sample, including those characters and character states applicable to the taxa in the taxon sub-sample, and excluding uninformative characters. This data matrix is presented in Appendix F.

Three data matrices with the 35 characters (Appendix G), including uninformative characters, of Hong & Zhang (1996a) were constructed for the 18-taxon analyses. For re-analyses of the original data matrix of Hong & Zhang (1996a), their exact data matrix (Appendix H1) was used. For the corrected 18-taxon analyses, the characters and character states of Hong & Zhang (1996a) were used, but the scoring was corrected to produce a new corrected data matrix (Appendix H2). The third data matrix (Appendix H3) for the 18-taxon analyses were constructed by modifying the character states of Hong & Zhang (1996a) to be more similar to those constructed for the 318- and 66-taxon data matrices in the present study (Appendix G2).

4.2.4 Character scoring and coding

Character coding was preliminary and explorative, because many characters in the 117 character data set were coded from scratch, and some were modified from the previous character data set analyzed by Hong & Zhang (1996a). The character coding changed and improved as the knowledge on the eriophyoid characters and character states improved during the study and as data from the data base and original description were progressively interpreted. The character data sets can be regarded as work in progress and is by no standards sufficient as a final morphological data set, in character definition, scoring and coding, for presently known characteristics of eriophyoid species. The data are still highly ambiguous for many characters, mainly due to faulty published descriptions and lack of standardization of description of particular characters and their states among descriptions. The data matrices were compiled and managed in Excel© from data retrieved from the DeltaAccess© data base of descriptive data (Chapter 3) and checked with the original descriptions and any additional data available after retrieval from the data base to double check the data. The Excel data matrix was exported to a text file, and formatted for use as a data input file for Nona© (Goloboff, 1993b; Goloboff, 1999b) and eventually TNT© (Tree Analysis Using New Technology) (Goloboff *et al*., 2008b) (see discussion of analyses below).

4.2.5 Phylogenetic analyses

The 318-taxon data matrix was initially analysed with heuristic parsimony analyses in PAUP© 4.0* (Phylogenetic Analysis Using Parsimony and Other Methods version 4, Swofford, 2002), and Nona© version 1.6 (Goloboff, 1993b) and later version 2 (Goloboff, 1999b). Nona was run with WinClada© ver. 1.00.08 (Nixon, 2002). The eventual and final parsimony analyses, of which results are presented in this dissertation, were performed using the Willi Hennig Society edition of the program TNT ver. 1.1 November, 2008 (Goloboff *et al.*, 2008b). The 66- and 18-taxon character optimizations were additionally performed in WinClada ver. 1.00.08 (Nixon, 2002) for presentation of the trees from WinClada. Nona (free-ware), Winclada (share-ware to be bought from Kevin Nixon) and TNT (the Willi Hennig Society edition is free-ware) are available via http://www.cladistics.com/. TNT can be downloaded more directly from http://www.zmuc.dk/public/phylogeny/TNT (Goloboff *et al.*, 2008b). The analyses were performed under different weighting schemes, and due to the different sizes and complexities of the data matrices with 318, 66 and 18 taxa, different algorithms, parameters and approaches of analyses were used. *Orfareptydeus stepheni* (taxon 0) was designated as outgroup in all the analyses, and *Mononychellus yemensis* was included as an additional outgroup species in some.

For the 318-taxon matrix the 49 multistate characters of the 117 characters were set as non-additive (Fitch, 1971), except for characters 14, 15, 101 and 104 which were set as additive (Farris, 1970). In the 66-taxon data matrix the 46 multi-state characters of the 60 characters included were set as non-additive, except characters 4, 5, 49 and 52 which were set to be additive.

4.2.5.1 Different weighting schemes

The analyses in TNT of the 318-, 66- and 18-taxon data matrices were done with the characters weighted with 11 levels of weighting against homoplasy: equally weighted (weight for all character states = 1), and implied weighting (Goloboff, 1993a) with concavity constants (k) 999, 100, 50, 30, 20, 15, 10, 3, 1 and 0.1. The implied weighting algorithm maximizes total fit where k is a constant of concavity and can be between 0 and 1000 in TNT, allowing minimum (0.1) or most (999) influence by homoplasies.

4.2.5.2 Analyses of the 318-taxon data matrix

An account of the analyses of the 318-taxon data matrix is here presented to illustrate the problems caused by the complexity and conflict therein of morphological data sets of the Eriophyoidea in cladistic analyses. This is caused by the complexity of the data due to a high amount of character homoplasy, the small informative characters:taxa ratio, a relatively large proportion of multi-state characters, and the character states of many characters of the eriophyoid ingroup is all different from character states in the outgroup, or characters are present in the eriophoids but absent in the outgroup non-eriophyoid mites. Many of these restraints of eriophyoid morphological data sets will probably remain in future phylogenetic analyses.

Several heuristic parsimony analyses, as well as Ratchet searches (Nixon, 1999), of the 318-taxon data matrix were done with different parameters in the program Nona with WinClada (C. Craemer, *unpubl. data*). Single analyses were also attempted in PAUP (C. Craemer, *unpubl. data*). The results of these initial analyses were not optimal. The analyses ran unexceptable long times – a constraint frequently associated with parsimony analyses of large or complex data sets (Goloboff, 1999a). Extraordinary amounts of shortest trees were found, for example, one analysis resulting in 100 000 shortest trees, the number limited by the size of memory space allocated. When character weighting and bootstrap analyses were attempted, the programs aborted. Consequently the program TNT was used to analyse the 318-taxon, and consequently the other data matrices of the present study, using different parameters and algorithms. Results of the analyses in TNT are presented.

The data were analysed under different character weighting schemes (see information under different weighting schemes above). The 318-taxon matrix was initially analysed with heuristic searches ("traditional searches") in TNT under equal character weights, done with temporary collapsing of

branches if supported ambiguously ("rule 1"). Several analyses with different parameters were run. The most parsimonious solutions were continuously found in only a very few replications during these heuristic searches. For example, one of the searches: space were set for 35 000 trees in RAM, 3 000 replications of finding Wagner trees with RAS (random addition sequences) were completed, tree searches of each RAS were done with tree bisection and reconnection (TBR) combined with sub-tree pruning and re-grafting (SPR) and 10 trees were kept from each replication. The random seed was set as 0 (using time as the start of the set of random numbers for RAS). The best score was only hit once out of the 3 000 replications and some replications over-flowed. TBR branch-swapping was done on the 10 trees saved in RAM, and 35 000 trees were found with overflow. Clearly with the overflow and most parsimonious trees only found in one replication out of 3 000, the most parsimonious tree, and all possible most parsimonious trees, were most probably not found. The strategy with heuristic searches should be to maximise the number of hits and not the number of most parsimonious trees. With these heuristic methods the most parsimonious tree can usually be found for about 20 to 30 taxa, but with more taxa it becomes more problematic (P. Goloboff, *pers. comm*.) depending on the data set.

The 318-taxon data set clearly required the special and combined algorithms in the heuristic searches, “New Technology searches”, available in TNT for rapid parsimony analyses of large or complex data sets (Goloboff *et al.*, 2008b). The basic types of special algorithms implemented in TNT (Goloboff *et al.*, 2008b) are the ratchet (Nixon, 1999), tree-drifting (Goloboff, 1999a), sectorial searches (Goloboff, 1999a) and tree-fusing (Goloboff, 1999a). The present data set was, however, just too complex and problematic to allow for “straight forward”, default and more “usually” set parameters for these “New Technology searches”. The searches still took unacceptable and unusable long times to run. The following line commands for running the New Technology searches, with particular parameters that may suit the present complex 318-tax data set, were provided by P. Goloboff (*pers. comm*.):

```
rep+/1;
sec: xss 4-3+5-1 gocomb 10 combst 6 fuse 4 drif 8 self 60;
xmu = hit 10 gfuse 4 drif 20 rat 12 xss;
```

These commands instruct the algorithms to keep searching until it finds the best length tree 10 times independently ("hit 10”). The searches performed with the commands still each ran for days, and did not manage to find the best length tree 10 times in acceptable times. One of these searches (under implied weighting of k = 10) quickly (after 60 hours) found 10 shortest trees. This search was done as follows: space was set for 30 000 trees in memory, branches were collapsed if supported ambiguously (“rule 1”) and implied weighting strength was 10 (k = 10). The best score found was 40.56323 and 32 trees were retained. Tree length of these trees was 2 347 (Table 4.3). The strict consensus of the 32 trees was calculated and this tree is presented in Figs 4.5 – 4.23.

Due to the time constraint problems with the "New Technology searches" and explorative nature of the present study, I decided to rather find estimated consensus trees (Goloboff & Farris, 2001) of the 318-taxon data matrix. When a data set is very large and complicated, a consensus tree can be found with estimated consensus, which provides a conservative estimate of the actual consensus of most parsimonious trees without actually finding them (Goloboff *et al.*, 2008b). This method gives an idea of the approximate and conservative results for a data set, and under equal weighting the groups found are probably real groups (not groups that are overresolved) that are relatively well-supported (P. Goloboff, *pers. comm.*). The analyses are also completed very quickly – an estimated consensus for the 318-taxon data matrix was found in about 30 seconds under various parameters. The estimated consensus for the 318-taxon data matrix was found under equal weighting and 10 levels of implied weighting against homoplasy (see different weighting schemes above). The precision was set to 5 [recovering true nodes; precision increases the number of true groups you recover, and when you increase, more exhaustive search algorithms are used (P. Goloboff, *pers. comm.*)] and the accuracy was set to 4 [not finding false nodes; it decreases the number of incorrect groups found, as you increase accuracy, more stringent algorithms for tree collapsing is used (P. Goloboff, *pers. comm.*)] for all the estimated consensus analyses.

The tree length, total fit, adjusted homoplasy, CI, RI and number of nodes for each tree found under the different weighting schemes, as well as the strict consensus of the most parsimonious trees found with the new technology searches under implied character weighting with k = 10 (above) are presented in Table 4.3. The estimated consensus found under implied weighting with k = 20 had the highest total fit, was the shortest tree found and had the highest CI and RI values, and has the highest number of nodes (were the most resolved) of all the estimated consensus trees found (Table 4.3). This tree was chosen as the preferred of the estimated consensus trees and is presented in Figs 4.26 – 4.39. Because there are still debate about the appropriateness of using character weighting in parsimony analyses, and because more parsimonious trees are found under equal weighting, and thus probably largely preventing an over resolved consensus, the estimated consensus found under equal weighting is also presented (Figs 4.4; 4.5).

4.2.5.3 Analyses of the 66-taxon data matrix

Given the size of the data matrix which could still be regarded as "medium", the 66-taxon by 60 character data matrix was analysed with heuristic searches ("traditional searches" in TNT) under the eleven weighting schemes set out above. Under each weighting scheme a search was done of the data matrix with 7 000 replications of random addition sequences (RAS) with TBR branch swapping. Place for 70 000 trees was allocated in RAM. Ten trees were kept per replication and the final 10 trees in memory were subjected to TBR branch swapping (which is combined with SPR in TNT). Branches supported ambiguously were collapsed during the searches ("rule 1"). This can be regarded as a quite

comprehensive heuristic search using Wagner trees constructed with RAS combined with TBR branch swapping (e.g., see Arnedo *et al.*, 2009).

4.2.5.4 Analyses of the 18-taxon data matrices

The small 18-taxon by 35 character matrices were analysed with the Implicit Enumeration search in TNT that produces exact solutions, and which guarantees finding all trees optimal under current settings (Goloboff *et al.*, 2008b). Complete results were found in usually less than six minutes per run. Analyses of each of the three matrices were done under the eleven weighting schemes set out above.

4.2.6 Presentation of trees (cladograms)

Trees found from analyses of the 318-taxon data set were presented from TNT and those found from analyses of the 66- and 18-taxon data sets were presented from WinClada, because WinClada can produce trees with the characters and character states both mapped on the trees with indication of homoplasies, homologies and characters which are homoplasious but with a certain character state which is uninterrupted ("homologous"). This format of presentation was preferred for the present study. WinClada can only handle a maximum of 10 character states (0–9), and some characters in the 66-taxon data matrix had more states (with a maximum of 16), and mapping of character states on the branches of these were manually corrected. Final formatting of trees from WinClada and TNT, corrections of character states on trees from WinClada, and classification, group names and other information on the trees, were done in Corel Draw version 11.633 © Corel Corporation, 2002.

4.2.7 Group support

The simplest measure of support for individual groups is branch length (Kitching *et al.*, 1998). In the presence of homoplasy, however, the interpretation of branch length as support is subjective, and may be misleading (Kitching *et al.*, 1998), but the trees were presented as metric trees to give an indication of branch support.

Group supports were calculated with symmetric resampling in TNT with a change probability (P) of 33 (the default setting in TNT). Symmetric resampling is not influenced by uninformative characters and different weighting schemes as found with other resampling methods (Goloboff *et al.*, 2008c). For example standard Bootstrapping is influenced by uninformative characters, and Bootstrapping (both standard and Poisson) and Jacknifing are affected by character weight and transformation costs (e.g., additive characters) (Goloboff *et al.*, 2008c).

Symmetric resampling of the different data matrices was done with TNT's Traditional search as follows: the 318-taxon data matrix resampling was done under implied character weighting with k = 10, space for 80 000 trees was allocated in memory (RAM), and resampling was done with 1000

replicates. The 66-taxon data matrix resampling was done for characters under implied weighting with k = 999, space for 10 000 trees was set in memory, and resampling was done with 1000 replicates. The 18-taxon data matrix with corrected data was resampled for characters under implied weighting with k = 999, space for 80 000 trees was set in memory, and resampling was done with 5000 replicates. The 18-taxon data matrix with modified data was done for characters under implied weighting with k = 100, space for 80 000 trees were set in memory, and resampling was done with 5000 replicates.

The results of the symmetric resampling are presented as group frequencies with groups collapsed below 50. Group frequencies, however, cannot measure support for groups with very low support, because it may produce alterations in the apparent support for these groups (Goloboff *et al.*, 2008c). The results are, therefore, also presented as symmetric resampling group frequency differences (GC values in TNT), which do not have this problem (Goloboff *et al.*, 2008c). Groups were arbitrarily collapsed below a GC value of 20.

4.3 RESULTS AND DISCUSSION: PREFERRED TREES

The three following major groupings of trees are presented: trees obtained from analyses of data matrices with 318 taxa (including 2 outgroup species), 66 taxa (including 2 outgroup species) and 18 taxa (including one outgroup species). A shortened name is given to each data matrix and each tree. These abbreviations are given in parentheses and in bold in this section, and will be used from hereinafter. The groups and clades in these trees, with integrated evidence compiled from all the presented trees, and the evaluation of the eriophyoid classification with reference to these groups, are presented and discussed further on in the results and discussion.[2]

4.3.1 Preferred trees from the analyses of the 318-taxon data matrix

The tree statistics for the 318-taxon analyses are presented in Table 4.2.

a) From the results of the analyses of the 318-taxon (**318tax**) data matrix (Table 4.2), three trees are presented (**318tax trees**).
   - Only one of the final New Technology searches, namely the search of the data matrix under implied character weighting with k = 10, produced a final phylogenetic resolution. This search generated 32 most optimal trees of length 2347 (Table 4.2). The strict consensus of these trees (**318tax-k10 tree)** is presented in Figs 4.6–4.23. Results of the various data sets and analyses under various parameters were primarily used to evaluate the groups and clades found overall in the study. This strict consensus tree, however, was regarded as the most

[2] The complete lists of characters and character state changes at the tree nodes are not included in this dissertation but can be obtained from the author.

preferred tree. Symmetric resampling results of the 318tax data set under implied character weighting with k = 10 are presented in Figs 4.24 and 4.25. Tree statistics of the 318tax-k10 tree are given in Table 4.2, and the consistency indices (ci) and character retention indices (ri) of the characters are presented in Table 4.8.

Table 4.2. Tree statistics for estimated consensus trees of 318-taxon data matrix found under different weighting schemes, and for the 32 most parsimonious trees and the strict consensus (Fig. 4.) of these trees found with New Technology Searches in TNT under implied weighting of characters with k = 10. The statistics of the trees that are presented in the results are in bold.

	Tree length	Total fit	Adjusted homoplasy	CI	RI	Number of nodes
New technologies k = 10						
32 shortest trees	2347	72.36	57.64	0.128	0.633	316
Strict consensus	**2402**	**72.29**	**57.71**	**0.125**	**0.623**	**255**
Estimated consensus						
Equal weights	**5394**	**57.71**	**72.29**	**0.056**	**0.086**	**26**
Implied weighting:						
k = 999	5014	58.57	71.43	0.060	0.154	45
k = 500	5112	58.53	71.47	0.059	0.137	41
k = 100	3450	62.18	67.82	0.087	0.435	57
k = 80	3407	62.32	67.68	0.088	0.442	55
k = 50	3467	61.73	68.27	0.087	0.432	57
k = 40	3298	62.93	67.07	0.091	0.462	71
k = 30	3196	65.41	64.59	0.094	0.480	79
k = 20	**2970**	**68.10**	**61.90**	**0.101**	**0.521**	**103**
k = 15	3688	61.73	68.27	0.081	0.392	58
k = 10	3550	61.90	68.10	0.085	0.417	54
k = 3	4847	62.82	67.18	0.062	0.184	75
k = 1	5079	61.11	68.89	0.059	0.142	54
k = 0.1	5079	62.59	67.41	0.059	0.142	54

Two trees are presented from the estimated consensus trees (Table 4.2) found for the 318tax data matrix under the eleven different weighting schemes.

- The estimated consensus tree found under equal weighting of characters (**318taxEq tree**) is presented (Figs 4.4, 4.5), although it is not the most optimal estimated consensus tree found under the different weighting schemes (Table 4.2). It does not have the shortest tree length, or has maximum total fit, has a higher amount of adjusted homoplasy than the other trees, and some of the lowest CI and RI values (Table 4.2). It has been decided to present this tree, because there is criticism against differential character weighting in parsimony analyses (e.g., Maddison *et al.*, 1984; Kluge 1997a, b). There is also less chance that the tree is overresolved which may happen with trees found under implied weighting. Some of the few groups found (Fig. 4.5) seem to be relatively well-supported, either by group frequency and GC values of trees under other parameters, or being present in them. The tree under equal weighting was

thus regarded as a relatively good alternative "test" for the robustness of the groups and clades found in the remainder of the trees. The consistency indices (ci) and character retention indices (ri) of the characters in this tree are presented in Table 4.4.

- The estimated consensus tree found under implied character weighting with k = 20 (**318tax-k20 tree**) was chosen and presented (Figs 4.26–4.39). First of all it had the highest total fit of 68.10 of the estimated consensus trees found (Table 4.5). It also is the shortest tree, has the highest CI and RI values, the least adjusted homoplasy, and the highest phylogenetic resolution of the estimated consensus trees found. The ci and ri indices of the characters are presented in Table 4.6.

b) A summary tree (**318-summary tree**) (Fig. 4.40) of the 318tax-k10 tree was constructed manually to reflect the relative relationships between the taxa from the 318tax data set which were included in the 66-taxon data set. It was literally done by eliminating those taxa not included in the 66-taxon analyses from the 318tax-k10 tree (Figs 4.6–4.23), and to portray the relationships of the remaining taxa. The summary tree does not necessarily portray sister group relationships found in the 318tax-k10, but rather relative relationships and a hypothetical topology of what the topology of a 66-taxon tree in the present study would be if it fully supported the relative relationships between taxa found in the 318tax-k10 tree. This was done to make it simpler and easier to compare the results from the 66-taxon analyses with that found for the 318tax analyses, and to particularly evaluate whether the groups found in the preferred tree of the 318tax analyses (318tax-k10 tree) are supported by the trees found for the preferred tree of the 66-taxon analyses, the tree found under implied weighting with k = 999.

4.3.2 Preferred trees from the analyses of the 66-taxon data matrix

The tree statistics for the 66-taxon analyses are presented in Table 4.3.

c) From the results of the analyses of the 66-taxon (**66tax**) data matrix (Table 4.2), four trees are presented (**66tax trees**).

- The consensus tree found under equal weighting of characters (**66taxEq tree**) is presented (Figs 4.41; 4.42) basically for the same reasons given above for choosing the 318taxEq tree for presentation, although it is not the most optimal tree found under the different weighting schemes (Table 4.2).

Table 4.3. Tree statistics for most parsimonious (MP) and strict consensus trees of the 66-taxon data matrix found under different weighting schemes. The statistics of the trees that are presented in the results are in bold.

	Tree length	Total fit	Adjusted homoplasy	CI	RI	Number of nodes
Equal weights						
768 MP trees	648	44.20	41.80	0.292	0.501	64
consensus	**942**	**38.91**	**47.09**	**0.201**	**0.181**	**13**
Implied weighting:						
k = 999						
3 MP trees	648	85.55	0.45	0.292	0.501	64
consensus	**649**	**85.54**	**0.46**	**0.291**	**0.499**	**61**
k = 500						
3 MP trees	648	85.10	0.90	0.292	0.501	64
consensus	649	85.10	0.90	0.291	0.499	61
k = 100						
3 MP trees	648	81.87	4.13	0.292	0.501	64
consensus	649	81.86	4.14	0.291	0.499	61
k = 80						
3 MP trees	648	80.96	5.04	0.292	0.501	64
consensus	649	80.95	5.05	0.291	0.499	61
k = 50						
3 MP trees	648	78.46	7.54	0.292	0.501	64
consensus	649	78.45	7.55	0.291	0.499	61
k = 40						
3 MP trees	648	76.95	9.05	0.292	0.501	64
consensus	649	76.94	9.06	0.291	0.499	61
k = 30						
1 MP tree	**651**	**74.68**	**11.32**	**0.290**	**0.497**	**61**
k = 20						
1 MP tree	**659**	**70.86**	**15.14**	**0.287**	**0.489**	**64**
k = 15						
3 MP trees	660	67.73	18.27	0.286	0.487	64
consensus	663	67.69	18.31	0.285	0.484	59
k = 10						
1 MP tree	671	62.79	23.21	0.282	0.476	64
k = 3						
3 MP trees	700	47.08	38.92	0.270	0.444	64
consensus	701	47.08	38.92	0.270	0.443	62
k = 1						
1 MP tree	715	34.76	51.24	0.264	0.428	64
k = 0.1						
5 MP trees	733	23.08	62.92	0.258	0.408	64
consensus	736	23.08	62.92	0.257	0.405	57

- The same number of most parsimonious trees, with the same topologies, and resultantly the same strict consensus trees were found for each of the analyses under implied character weights with k = 999, 500, 100, 80, 50 and 40. The strict consensus trees of these analyses were the shortest, had the highest relative CI and RI values, and were the most resolved of all the strict consensus trees found under all the weighting schemes. The consensus tree found under implied character weighting with k = 999 (**66tax-k999 tree**) was chosen as the most preferred tree for this data set, however, and is presented (Figs 4.43–4.48). It had the highest total fit of 85.54 and the least adjusted homoplasy of 0.46 of the strict consensus trees with

the same topology, as well as most of the most parsimonious trees found, and the highest total fit of all the strict consensus trees found under the other weighting schemes (Table 4.2). Symmetric resampling results of the 66tax data set under implied character weighting with k = 999 are presented in Figs 4.49 and 4.50.

- The single parsimonious trees found under implied character weighting with k = 30 (**66tax-k30**) and k = 20 (**66tax-k20**) are also presented. The 66tax-k30 tree is presented in Figs 4.51–4.53, and the 66tax-k20 tree is presented in Fig. 4.54. These trees were additionally presented, to be investigated as additional evidence for the support or not of groups and clades found in the 66tax-k999 tree. They had a different topology from the strict consensus trees found under weighted characters with k = 999–40. Their homoplasious characters were slightly more heavily weighted against, but they were the first trees following the preferred tree, and their statistics and topology were still close enough to those of the preferred 66tax-k999 to be regarded as near optimal. The 66tax-k30 tree was chosen and presented first, but its topology was so close to that of the preferred 66tax-k999 tree, that the 66tax-k20 tree, which also has the same weighting against homoplasy than the more preferred 318tax-k20 estimated consensus tree (Fig. 4.54), was included for additional scrutiny. The latter has not been evaluated and presented so extensively as the 66tax-k30 tree.

4.3.3 Preferred trees from the analyses of the 18-taxon data matrices

d) Three different versions of the 18-taxon (**18tax**) data matrices were analysed with the Implicit Enumeration searches in TNT:
   i. the uncorrected, unmodified original data matrix of Hong & Zhang (1996a);
   ii. the data matrix of Hong & Zhang (1996a) with corrected scoring; and
   iii. the 18tax data matrix with characters included in the data matrix of Hong & Zhang (1996a), but which were corrected and modified to resemble, and be a sub-sample of those characters used for the 318tax and 66tax data sets.

The trees found for these three data matrices are presented separately for each data matrix.

The tree statistics for the re-analyses of the original 18-taxon data matrix of Hong & Zhang (1996a) are presented in Table 4.4.

Table 4.4. Re-analysis of the original data matrix of Hong & Zhang (1996a) without any changes to original published data; all characters ordered (similar to original analyses by Hong & Zhang, 1996a). Tree search with implicit enumeration algorithm in TNT. * Uninformative characters included; ** uninformative characters excluded; ◆ rounded to 51 and 47, respectively, in WinClada.

Analysis	Tree length		Total fit	Adjusted homoplasy	CI		RI		Number of nodes	Topology
	with*	without**			with*	without**	with*	without**		
Equal weights										
3 trees	77	69	24.05 – 24.15	7.85 – 7.95	0.519◆	0.46	0.63	0.63	16	
consensus	**80**	**72**	**23.75**	**8.25**	**0.5**	**0.44**	**0.6**	**0.6**	**13**	**A**
Implied weighting										
k = 999										
1 tree	**77**	**69**	**31.96**	**0.04**	**0.519**	**0.46**	**0.63**	**0.63**	**16**	**B**
k = 100										
1 tree	77	69	31.64	0.36	0.519	0.46	0.63	0.63	16	B
k = 50										
1 tree	77	69	31.29	0.71	0.519	0.46	0.63	0.63	16	B
k = 30										
1 tree	77	69	30.84	1.16	0.519	0.46	0.63	0.63	16	B
k = 20										
1 tree	77	69	30.31	1.69	0.519	0.46	0.63	0.63	16	B
k = 15										
1 tree	77	69	29.80	2.2	0.519	0.46	0.63	0.63	16	B
k = 10										
1 tree	77	69	28.86	3.14	0.519	0.46	0.63	0.63	16	B
k = 3										
1 tree	**80**	**72**	**24.22**	**7.78**	**0.5**	**0.44**	**0.6**	**0.6**	**16**	**C**
k = 1										
1 tree	80	72	18.67	13.33	0.5	0.44	0.6	0.6	16	C
k = 0.1										
3 trees	83	75	11.44	20.56	0.482	0.42	0.57	0.57	16	
consensus	84	76	11.44	20.56	0.476◆	0.42	0.56	0.56	13	D

i. The original tree published by Hong & Zhang (1996a) and three trees found for the unchanged – uncorrected, unmodified – original data matrix of Hong & Zhang (1996a) under different weighting schemes (Table 4.3) are presented. These analyses and trees are merely included to illustrate the different results that can be obtained from different parsimony analyses and different character weighting methods of the same data set (see more detailed results and discussion later on), and are not used any further in the evaluation of taxon relationships, groups and clades found in this study.

   - The tree originally published by Hong & Zhang (1996a) (**18PublishedHZ96**) is presented (Fig. 4.3a). It is a strict consensus (Length, CI and RI unknown) of three shortest trees obtained under successive weighting.

   Trees obtained during this study:

   - Three most parsimonious trees were found under equal character weights and the strict consensus (**18origEq**) of these is presented (Fig. 4.3b). This tree was presented for the same reasons that the previous shortest trees were presented.
   - Only one most parsimonious tree (**18orig-k999**) (Fig. 4.3c) and another (**18orig-k3**) (Fig. 4.3d) was found under implied character weighting with k = 999 and 3, respectively. The 18orig-k999 tree is the preferred tree, because it has the highest

total fit, but even a much heavier weighting against homoplasy (k = 3) resulted in a tree that had a higher total fit than the three optimal trees found under equal weighting. The trees were also presented, because they were weighted to compare with the tree after weighting found by the analyses of Hong & Zhang (1996a). The two trees also have different topologies, and three of the four topologies found with the different analyses are presented. The strict consensus tree found under extremely heavy weighting against homoplasy, k = 0.1, almost not allowing any influence of homoplasy, had the lowest total fit (11.44; Table 4.3) and is not presented.

The tree statistics for the analyses of the corrected scoring of the 18-taxon data matrix of Hong & Zhang (1996a) are presented in Table 4.5.

Table 4.5. Re-analysis of the corrected scoring of the original 18-taxon data matrix of Hong & Zhang (1996a); Character 32 (length of *sc*) ordered, remaining characters unordered. Characters and states as defined and used by Hong & Zhang (1996a). Tree search with implicit enumeration algorithm in TNT. * Uninformative characters included (statistics from TNT); ** uninformative characters excluded (statistics from WinClada); ◆ truncated to 45 (for 0.459), 44 (for 0.448), 0.42 (for 0.427), 0.41 (for 0.419) in WinClada.

Analysis	Tree length		Total fit	Adjusted homoplasy	CI		RI		Number of nodes	Topology
	with*	without**			with*	without**	with*	without**		
Equal weights										
141 trees	85	77	≈ 18.75–18.83	≈ 9.17–12.44	0.459◆	0.40	0.483	0.48	16	
consensus	**118**	**110**	**15.56**	**8.25**	**0.331**	**0.28**	**0.112**	**0.11**	**3**	**A**
Implied weighting										
k = 999										
1 tree	**85**	**77**	**27.95**	**0.05**	**0.459◆**	**0.40**	**0.483**	**0.48**	**16**	**B**
k = 100										
1 tree	85	77	27.55	0.45	0.459◆	0.40	0.483	0.48	16	B
k = 50										
1 tree	85	77	27.13	0.87	0.459◆	0.40	0.483	0.48	16	B
k = 30										
1 tree	85	77	26.59	1.41	0.459◆	0.40	0.483	0.48	16	B
k = 20										
1 tree	85	77	25.96	2.04	0.459◆	0.40	0.483	0.48	16	B
k = 15										
1 tree	85	77	25.37	2.63	0.459◆	0.40	0.483	0.48	16	B
k = 10										
1 tree	85	77	24.31	3.69	0.459◆	0.40	0.483	0.48	16	B
k = 3										
2 trees	86	78	19.38	8.62	0.453	0.39	0.472	0.47	16	
consensus	**87**	**79**	**19.28**	**8.72**	**0.448◆**	**0.39**	**0.461**	**0.46**	**14**	**C**
k = 1										
9 trees	90	82	14.04	13.96	0.433	0.37	0.427◆	0.42	16	
consensus	93	85	13.46	14.54	0.419◆	0.36	0.393	0.39	12	D
k = 0.1										
9 trees	90	82	8.09	19.91	0.433	0.37	0.427◆	0.42	16	
consensus	93	85	7.17	20.83	0.419◆	0.36	0.393	0.39	12	D

ii. The scoring of the data matrix analysed by Hong & Zhang (1996a) was corrected and three trees are presented from the trees found (Table 4.4) in the searches on this corrected data matrix.

- One-hundred-and-forty-one most parsimonious trees were found under equal character weights (Table 4.4) and the strict consensus (**18correctEq**) of these is presented (Fig. 4.55a). This tree was presented for the same reasons that the previous trees found under equal weighting were presented.
- One most parsimonious tree (**18correct-k999**) was found under implied character weighting with k = 999, and is presented (Fig. 4.55b). It is the most preferred tree, primarily because it has the highest total fit of the trees found (Table 4.4). The

topologies of the single most parsimonious trees found under implied character weights with k = 100, 50, 30, 20, 15 and 10 were the same as the most parsimonious tree found under k = 999. Symmetric resampling results of the 18tax corrected data set under implied character weighting with k = 999 are presented in Fig. 4.56.

- Two most parsimonious trees were found under implied character weighting with k = 3 (Table 4.4). The strict consensus (**18correct-k3**) of these is presented (Fig. 4.57), because it represents results found under heavy weighting against homoplasy, still has a higher total fit (19.28) than the most parsimonious trees found under equal character weights, and it represents another topology found, apart from that of the strict consensus under equal character weights, and the topology of trees found under weighting that is similar to equal weighting.

The tree statistics for the analyses of the modified character states and corrected scoring of the 18-taxon data matrix of Hong & Zhang (1996a) are presented in Table 4.6.

Table 4.6. Trees found for the 18-taxon data set with characters included in the data matrix of Hong & Zhang (1996a) but which were corrected and modified to resemble, and be a sub-sample of those characters used for the 318tax and 66tax data sets. Character 32 (length of *sc*) ordered, remaining characters unordered. Tree search was done with the implicit enumeration algorithm in TNT. * Uninformative characters included (statistics from TNT); ** uninformative characters excluded (statistics from WinClada); ◆ 0.64 (TNT 0.650), 0.57 (TNT 0.576), 0.41 (TNT 0.420) in WinClada.

Analysis	Tree length		Total fit	Adjusted homoplasy	CI		RI		Number of nodes	Topology
	with*	without**			with*	without**	with*	without**		
Equal weights										
10 trees	117	109	21.58–21.90	8.10–8.43	0.650◆	0.62	0.494	0.49	16	
consensus	**132**	**124**	**19.92**	**10.08**	**0.576◆**	**0.54**	**0.309**	**0.30**	**8**	**A**
Implied weighting										
k = 999										
4 trees	117	109	29.96	0.04	0.650◆	0.62	0.494	0.49	16	
consensus	**120**	**112**	**29.96**	**0.04**	**0.633**	**0.60**	**0.457◆**	**0.45**	**13**	**B**
k = 100										
3 trees	117	109	29.6	0.4	0.650◆	0.62	0.494	0.49	16	
consensus	**118**	**110**	**29.59**	**0.41**	**0.644**	**0.61**	**0.481**	**0.48**	**14**	**C**
k = 50										
4 trees	117	109	29.22	0.78	0.650◆	0.62	0.494	0.49	16	
consensus	120	112	29.16	0.84	0.633	0.60	0.457◆	0.45	13	B
k = 30										
4 trees	117	109	28.73	1.27	0.650◆	0.62	0.494	0.49	16	
consensus	120	112	28.65	1.35	0.633	0.60	0.457◆	0.45	13	B
k = 20										
3 trees	117	109	28.16	1.84	0.650◆	0.62	0.494	0.49	16	
consensus	118	110	28.13	1.87	0.644	0.61	0.481	0.48	14	C
k = 15										
10 trees	117	109	27.59 – 27.63	2.37 – 2.41	0.650◆	0.62	0.494	0.49	16	
consensus	132	124	26.86	3.14	0.576◆	0.54	0.309	0.30	8	A
k = 10										
4 trees	117	109	26.65	3.35	0.650◆	0.62	0.494	0.49	16	
consensus	120	112	26.47	3.53	0.633	0.60	0.457◆	0.45	13	B
k = 3										
1 tree	**118**	**110**	**22.05**	**7.95**	**0.644**	**0.61**	**0.481**	**0.48**	**16**	**D**
k = 1										
1 tree	123	115	16.90	13.10	0.618	0.59	0.420◆	0.41	16	E
k = 0.1										
1 tree	123	115	11.09	18.91	0.618	0.59	0.420◆	0.41	16	E

iii. Four trees are presented for the 18tax data set with characters included in the data matrix of Hong & Zhang (1996a) but which were corrected and modified to resemble, and be a sub-sample of those characters used for the 318tax and 66tax data sets.

- Ten most parsimonious trees were found under equal character weights (Table 4.6) and the strict consensus (**18modifyEq**) of these is presented (Fig. 4.58). This tree was presented for the same reasons that the previous trees found under equal weighting were presented.
- Four most parsimonious trees were found under implied character weighting with k = 999 (Table 4.6). The strict consensus (**18modify-k999**) of these is presented (Fig. 4.59). This is the most preferred tree for these analyses, primarily because it has the highest total fit (29.96) of the trees found (Table 4.6). The topologies of the strict

consensus trees of most parsimonious trees found under implied character weights with k = 50, 30, and 10 were the same as the most preferred tree.

- Three most parsimonious trees were found under implied character weighting with k = 100 (Table 4.6). The strict consensus (**18modify-k100**) of these is presented (Fig. 4.60). This consensus tree is presented, because it has a different topology than the most preferred tree, but still has a high total fit of 29.59, similar to that of the preferred tree (Table 4.6). The topology of the strict consensus trees of most parsimonious trees found under implied character weights with k = 20 is the same as the most preferred tree (Table 4.6). Symmetric resampling results of the 18tax modified data set under implied character weighting with k = 100 are presented in Fig. 4.61.
- One most parsimonious tree (**18modify-k3**) were found under implied character weighting with k = 3, and is presented (Fig. 4.62). It is presented because it represents results found under quite heavy weighting against homoplasy, still has a higher total fit (22.05) than the most parsimonious trees found under equal character weights, and it represents another topology found for this data set.

4.4 RESULTS AND DISCUSSION: MATERIAL AND METHODS

4.4.1 Re-analyses of the original, unchanged published data matrix of Hong & Zhang (1996a)

Hong & Zhang (1996a) analysed 35 discrete morphological characters of 17 eriophyoid genera of the about 240 genera then described. Eight of the characters were uninformative regarding the relationships between eriophyoid taxa, and thirteen of the 35 characters were presence or absence of or solenidia. The characters used by them were included in the present analysis, but some were modified (see modified characters, Appendix G2).

The taxa sampled for their analysis were from all three eriophyoid families: the type genera of six tribes in the Phytoptidae, the type genera of six subfamilies of the Eriophyidae and two genera each of the two subfamilies of the Diptilomiopidae. The ingroup consisted of genera and not of exemplar species. This is a very small taxon sample and did not represent all the suprageneric groupings in the eriophyoid classification.

There are a few discrepancies in the study of Hong & Zhang (1996a). Generalized Tydeidae was included as outgroup, based on the hypothesis by Norton *et al.* (1993) that the Tydeidae is sister to the Eriophyoidea. Hong & Zhang (1996a) did not explain what they meant by “generalized Tydeidae”,

though. The character states they scored for the outgroup were more similar to scoring a hypothetical outgroup than scoring a real Tydeidae exemplar. For example, among many other examples, they coded the body shape of the outgroup to be worm-like, and not rounded or oval as the body of the Tydeidae is in reality.

They reportedly determined character states by examining specimens and original descriptions, but did not specify of what genera and what species within the genera they investigated specimens, and some of the characters were scored erroneously. They stated that all characters were ordered except character 5 (the presence of the frontal lobe). However, this character is binary, and being ordered or unordered is not applicable, and the state transformation is treated in the same way in either scenario. In practice, all the multistate characters in their analysis were thus set as being ordered.

Polymorphic characters were scored and dealt with as unknown (coded as "?") characters in the data matrix constructed by Hong & Zhang (1996a), because the programs then could not analyse these characters. Today, algorithms, for example, those used in Nona and TNT, are able to handle and analyse polymorphic characters.

They analysed the character state matrix with parsimony analysis in PAUP 3.0 (Swofford, 1991), using the "branch-and-bound" procedure. With equal weighting the result was 33 shortest (most parsimonious) trees with length 79, CI 0.506 and RI 0.606. In the current analysis, analysing the exact same data matrix, with equal weighting of characters, the implicit enumeration algorithm (similar to "branch-and-bound" in Paup) in TNT produced three shortest trees with length 77, CI 0.519 (with uninformative characters included, probably the same way Hong & Zhang (1996a) determined the CI), CI 0.46 (calculated with exclusion of the uninformative characters) and RI 0.63 (Table 4.4). The trees from the current re-analyses are more parsimonious with slightly higher CI (when uninformative characters were included) and RI, and thus is a better result.

After analysing the data under equal character weighting, Hong & Zhang (1996a) proceeded by weighting the characters with successive weighting (Farris, 1969, 1988), with a result of three equally parsimonious trees after the first and second reweighting, using the "branch-and-bound" procedure. The strict consensus tree of these was presented as their preferred tree (Fig. 4.3a). They did not report the length or any other tree statistics and support estimations of the three most parsimonious trees, or the resultant consensus tree, and no comparison of these statistics can be made with the re-analysed results in the present study.

The strict consensus of the three equally parsimonious trees found in the present re-analyses under equal character weights is presented in Fig. 4.3b. The unchanged data matrix of Hong & Zhang (1996a)

was further re-analysed with implicit enumeration searches in TNT under implied character weighting with k set to the values 999, 100, 50, 30, 20, 10, 3 and 0.1 (Table 4.4). See the discussion of implied weighting further on for more detail about the implied weighting method.

The preferred tree for the present re-analyses is the tree found under character weighting with k = 999 (Fig. 4.3c). This tree has the same topology as one of the three most parsimonious trees found in the re-analysis under equal weighting, and the one tree found in each analyses with implied weighting of characters with k = 100, 50, 30, 20, 15 and 10 (Table 4.4). The tree found under implied character weighting with k = 3 is also presented (Fig. 4.3d) to present an alternative topology found under heavier weighting against homoplasy for comparison with the tree presented by Hong & Zhang (1996a) and with the preferred tree of the present analyses, to study the type of influence different amounts of weighting against homoplasy (less homoplasy allowed), may have on results.

The topologies of the preferred tree of Hong & Zhang (1996a) (18PublishedHZ96 tree, Fig. 4.3a) and the preferred tree of the present study (18orig-k999 tree, Fig. 4.3c), and the tree obtained under implied character weighting with k = 3 (18orig-k3 tree, Fig. 4.3d) obtained from the same data matrix, differ. The overall retrieval of the families in groups is more or less the same in the trees. Diptilomiopidae was retrieved as a monophyletic group, with the same internal topology in all three trees. The Phytoptidae was never retrieved as one group or clade, but most Phytoptidae taxa are at the base of the trees, with some of them outside a group with the remainder of the Eriophyoidea, but with relationships unresolved between them and the Eriophyoidea group. *Sierraphytoptus* groups with Eriophyidae taxa in the 18PublishedHZ96 tree (Fig. 4.3a) and the 18orig-k999 tree (Fig. 4.3c), but is positioned outside a clade with the Diptilomiopidae and Eriophyidae in the 18orig-k3 tree (Fig. 4.3d). The Eriophyidae was never retrieved as a monophyletic group, and usually was found in one group with the Diptilomiopidae clade, with or without *Sierraphytoptus* included.

Seven clades were found in the 18PublishedHZ96 and 18orig-k3 trees, supported by nine and seven synapomorphies, respectively. Four clades were found in the 18orig-k999 tree supported by four synapomorphies. These include the Diptilomiopidae clade found in all three trees. Additionally, within the Diptilomiopidae clade *Diptacus–Diptilomiopus* was found as a clade, positioned within the Eriophyidae. *Aberoptus–Cecidophyes* was retrieved as a clade in all three trees. Within the Eriophyidae, the positions of *Ashieldophyes* (either found grouping with *Sierraphytoptus*, or with *Nothopoda* constituting a clade), *Phyllocoptes* (either found grouping with *Sierraphytoptus*, or with *Sierraphytoptus–Ashieldophyes*, or as a single species within a clade with all Diptilomiopidae and Eriophyidae, but with its relationship with these taxa unresolved), *Nothopoda* (either found to group with *Eriophyes*, or with *Ashieldophyes* constituting a clade). There are other topology differences within the Eriophyidae which include different relationships between smaller groupings or clades, and

the relationships between the Eriophyidae taxa and the Diptilomiopidae clade, and the inclusion or exclusion of *Sierraphytoptus*.

The largest differences between the three trees are in the basal topology, entailing relationships between the Phytoptidae taxa, and the positions of these taxa. Except for *Sierraphytoptus*, they are all basal in the three trees and outside the group comprising the remainder of the Eriophyoidea in the data set.

The differences include the positions and relationships of the only three genera (*Trisetacus*, *Nalepella* and *Pentasetacus*) of the Nalepellinae in the data set. In the tree presented by Hong & Zhang (1996a) [the 18PublishedHZ96 tree (Fig. 4.3a)], *Pentasetacus*, *Mackiella, Novophytoptus* and *Phytoptus* are outside a clade which includes *Trisetacus* and *Nalepella* and the remainder of the Eriophyoidea, with relationships between the clade and genera outside the clade unresolved. *Pentasetacus* may be sister to a *Novophytoptus-Mackiella* group, and *Nalepella* is sister to a clade constituting the Diptilomiopidae, Eriophyidae and *Sierraphytoptus*, and *Trisetacus* a basal sister to *Nalepella*. In the preferred tree of the re-analyses [18orig-k999 tree (Fig. 4.3c)], *Pentasetacus*, *Trisetacus*, *Novophytoptus* and *Phytoptus*, with relationships between them unresolved, are outside a group with the remainder of the Eriophyoidea, which include a group constituting the Diptilomiopidae, Eriophyidae and *Sierraphytoptus*; and *Nalepella* which is sister to this group and *Mackiella* which is sister to *Nalepella*. The relationships between *Trisetacus*, *Pentasetacus*, *Novophytoptus* and *Phytoptus*, and the group with the remainder of the Eriophyoidea are unresolved. In the 18orig-k3 tree (Fig. 4.3d), *Pentasetacus*, *Trisetacus*, and *Nalepella* are outside a clade which contains the remainder of the Eriophyoidea in the data set. *Trisetacus* and *Nalepella* was found as a weakly supported group, and the relationships between this group, *Pentasetacus*, and the clade with the remainder of the Eriophyoidea are unresolved. The relationships and groupings of the other Phytoptidae also differ, but these are not discussed here.

This exercise was done and included to demonstrate that there can be significant difference in the results of parsimony analyses of the same data set due to the different algorithms used, as well as the execution thereof, and different weighting schemes used. Particularly in the case of analysing the relatively complex character state matrix of the Eriophyoidea, with a weak phylogenetic signal (large amount of homoplasy in the characters), it is very important which algorithm is used, and how the procedure is done, to ascertain that the most parsimonious tree is found, and that all parsimonious trees, with different topologies, are discovered. The problem and necessity of optimal analyses increases with the addition of more data from both taxa and characters to the data set. Different weighting methods and the amount of weighting against homoplasy is also of importance, and should be done in a scientifically defendable manner. The data set of Hong & Zhang (1996a) was further modified, by correcting the scored character states (Appendix H2, and trees in Figs 4.55–4.57), and by modifying the

character definitions and consequent scoring (Appendices H3, G.3, and trees in Figs 4.58–4.62). The largest difference between the topologies of the three series of analyses was caused by the modification of the character definitions. This stresses how immensely important the definition of characters and character states (primary homologies which already defined and scored during alpha taxonomy), and sample thereof, are in the eventual results of phylogenetic analyses. The results of the latter two series of analyses are presented and discussed together with the other analyses in the present study.

4.4.2 Discussion of taxon and character sampling, analyses chosen, and reliability of information from trees, groups and clades found in the present study

4.4.2.1 Taxon sample

The study was designed to be explorative, using published species descriptions, rather than focusing on producing a reliable, robust hypothesis on the phylogeny of the superfamily. The latter is probably impossible at this stage of our knowledge on eriophyoid biodiversity, phylogeny, morphology and molecular data anyway. Despite the small amount of descriptive morphological data available (eventually 66 characters informative for relationships between the eriophyoid ingroup taxa were included), the taxon sample was chosen to represent a major part of morphological variation within the Eriophyoidea at genus level, regardless of the theoretical phylogenetic resolution that one can expect from the number of characters and character states. The largest data matrix analysed in the present study, contained 318 species (including the two outgroup species). The ratio of characters and character states to the number of taxa included is very small. The fewest characters needed for full phylogenetic resolution is one more character than the number of taxa, or in terms of character states, at least two character states per taxon.

When empirically analysing or testing a hypothesis, it is ideal to examine all critical evidence. When testing phylogenetic hypotheses with analyses, e.g., parsimony analyses used in the present study, one will theoretically approach a reliable answer when including all taxa and all possible and particularly more critically important characters, sampled randomly. This is practically impossible though, and one has to take samples of the taxa and characters for inclusion in analyses. The taxon and character sampling is crucial in finding reliable results in a phylogenetic analysis. One way of improving the reliability of an empirical phylogenetic analysis will be to increase characters or taxa. Without extensive additional morphological studies, the number of characters available for studying the phylogeny of the Eriophyoidea is limited, and the sample used in the present study includes a major portion of the published morphological information presently available, and increasing it will not be an explorative exercise. In future the improvement of the quality of morphological studies and the addition of molecular data will hopefully improve the size, value and information of the character sample.

The other option to improve the results and reliability of phylogenetic analyses of the Eriophyoidea would be to increase the number of taxa sampled, and to sample it without bias. Increasing the number of taxa is one of the most important ways to significantly improve the overall accuracy of the phylogenetic analyses (Zwickl & Hillis, 2002). Testing the hypotheses on phylogeny of the Eriophyoidea already starts with an inherent problem regarding the amount of taxa in the data set, because so little of the extant taxa is known and described. The number of taxa included in the analyses, however, could be significantly increased over the 17 taxa included in the previous analysis by Hong & Zhang (1996a). Their taxon choice was also biased in only including one typical taxon of some of the suprageneric taxa, ignoring a significant portion of evidence from the remaining taxa. In a small data set where there are only a few representatives of a given group, the probability of the species appearing together in a phylogenetic analysis *a priori* is much larger, and results are thus less reliable in comparison with a more comprehensive sample where each taxonomic group is represented by significantly more representatives, where each representative have much more alternative placements (Goloboff *et al*., 2009). It was thus decided to sample the taxa from the Eriophyoidea for the present study comprehensively and as unbiased in favour of the current classification as practically possible, by sampling almost maximum amount of genera from each suprageneric grouping.

The complexity of phylogenetic analyses increases exponentially with an increase in taxa (Goloboff *et al*., 2009), though. Combined with the small characters:taxa ratio, and apparent high homoplasy in the large data set for the present study, and also conflict that may be partly caused by errors in descriptive data, analysing the data set only became possible with the availability of the program TNT to the study (see “Material and Methods”). Parsimony algorithms implemented in TNT can successfully process very large and/or complex data sets (Goloboff *et al*., 2009).

The type species of genera were preferably chosen as taxa for the present analyses, conforming to the exemplar method, because individual species were sampled from each suprageneric taxon, and scored as separate terminals (Prendini, 2001). Monophyly of the genera is not implied in this method (Prendini, 2001), and the sample species in the present study were not chosen to completely represent the variation within a genus. The type species were merely chosen to ensure a cross-cutting, representative inclusion of morphological character variety at the genus level within the Eriophyoidea. At least as the name bearing taxa, the sampled type species are supposed to be close to the average characteristics of, and characteristics that delineate the genera. Additional species to test the monophyly of larger genera such as *Aceria* were not included, but by including a large representative sample of species from each suprageneric taxon, the monophyly of the suprageneric taxa were tested while simultaneously testing the relationships between them (Prendini, 2001). This sampling choice was not biased in favour of the present classification, because the genera were sampled randomly and

comprehensively from all suprageneric taxa, and was only biased in favour of groupings of species within the genera.

During preliminary analyses of the data set, it was noticed that most phylogenetic resolution and phylogenetic structure was found within the Diptilomiopidae, and particularly in the Diptilomiopinae (C. Craemer, *unpubl. data*). This subfamily was chosen for a next phylogenetic study where a smaller group from the Eriophyoidea can be studied, and where a largely species specific character–character state data set can be developed. *Diptilomiopus*, with *ca.* 84 species (up to about 2006), is the largest genus in the Diptilomiopinae, and includes new undescribed species from South Africa, and it seems to be largely restricted to the southern hemisphere, which influenced the choice. While scoring the characteristics for the taxon sample for the eriophyoid cladistic analyses, *Diptilomiopus* spp. were scored for the same characters, and was included in the analysis to explore whether the sampled characters would largely give phylogenetic resolution of suprageneric taxa, or may possibly be informative regarding relationships at the species level for the specific species sample. A test analysis of a data set excluding the bulk of *Diptilomiopus* spp. was also run, but it did not have much influence on the phylogenetic resolution of taxa within the remainder of the Eriophyoidea (C. Craemer, *unpublished data*), and they were kept in the data set. Three new *Diptilomiopus* spp. from South Africa were described (Appendix M) and are included in the present study.

Because of the very low characters:taxa ratio sampled when including 318 taxa, it was decided to sample a smaller number of exemplar species from the 316 eriophyoid species, using the preliminary results of the 318-taxon analyses and the eriophyoid classification as guidelines. Sixty-six species were sampled, and 60 characters were included in this data set. The characters/character states:taxa ratio was drastically improved. The size of the data matrix allowed analyses with "traditional searches" (incorporating RAS and TBR branch swapping). Quite comprehensive analyses were done ("Material and Methods"), but there was overflow and for example for the analysis under implied character weighting with k = 999, the best score was only hit 15 times out of 7000, indicating that the shortest, and all the shortest trees for the data matrix were probably not found. It is thus still not certain whether the most optimal tree was found, and it presents the same problem as for the results of the analyses of the 318-taxon data matrix. The results were not necessarily more "accurate" or reliable; although some groupings supported the groupings found in the 318tax trees. Many of the useful hypotheses found in the 318tax trees were lost, due to the exclusion of taxa. The "best" and most informative results for the exploratory aim of the present study, and for presenting new hypotheses, was obtained from analysing the 318 taxa, despite the low characters:taxa ratio.

It was additionally decided to include analyses of the very small sample of 18 taxa (including one outgroup species), representing some of the suprageneric groupings in the Eriophyoidea, analysed by

Hong & Zhang (1996a) to test their study, properly test the results obtainable from such a small set, with "enough" (27 informative) characters, and to compare it with the results obtained from the more comprehensive 318- and 66-taxon analyses as further tests of the robustness of groupings, and presentation of alternative hypotheses, and possible homologies that were not retrieved by the larger analyses. This provided a useful comparison of groupings, and alternative hypotheses, but the groupings found in these small data sets were not regarded as reliable.

4.4.2.2 Character sample

It was decided to largely include characters currently used in eriophyoid taxonomy. It was the best design for a first exploratory study on this scale not to add many new characters which are not yet used in eriophyoid taxon descriptions. This sample also made it possible to code a matrix for a large and comprehensive sample of taxa, and it additionally tested the phylogenetic signal in characters currently used in eriophyoid taxonomy. The available descriptive data were sampled as comprehensively as possible, though, including all characters from the published species descriptions, largely described from slide-mounted specimens, that were appropriate or near appropriate data for phylogenetic analyses. Detailed variation in opisthosomal ridges, furrows and other body shape modifications which are extensively used characters, particularly in the Phyllocoptinae, was however excluded. An attempt was made to score and code the variation, but the determination of homologies was too complex and ambiguous, and a high level of inaccuracies in the description of these characters is suspected due to distortion of slide-mounted specimens (see Chapter 3). Omitting these characters also avoided the inclusion of additional ambiguous data in the data set, but it is important to include this suite of characters in an improved data set, where primary homologies can be defined.

There are too few morphological characters investigated and described, particularly for characters informative for taxa above species level, to allow for any complete phylogenetic resolution of the phylogenetic relationships within the Eriophyoidea. Not many more published characters are available than those used in the present study (see Chapter 3). The number of characters necessary will also depend on the phylogenetic signal inherent in the characters and for what level (higher classification or groupings or relationships between species) this signal is largely informative. The character set used in the present study, turned out to be highly homoplasious, as was suspected from the results of the phylogenetic analysis by Hong & Zhang (1996a), and the biology and simplified morphology of the group. The lack of retrieval of synapomorphies was exacerbated by the low characters:taxa ratio, and consequent lack of congruence.

The data set (taxa and characters and coded character states) is the crucial factor in finding reliable phylogenetic hypotheses using empirical analyses such as parsimony analyses. The analyses themselves are empirical and repeatable, although they should be well executed. It is clear from the

present study that the most important aspect which needs improvement in future studies of the phylogeny of the Eriophyoidea, is the character sample and descriptive data. It is not ideal to use published descriptive data, and usually the person doing the phylogenetic study should study the specimens personally and specifically for the study, with incorporation of new characteristics if necessary. For analyses with higher numbers of taxa, this may not be possible or practically feasible for the Eriophyoidea. It is important that the description of taxa should be standardized, to be able to incorporate the data into standardized data sets for use in data bases; phylogenetic studies and development of electronic integrative keys (see Chapter 2). The improvement of character data, both by the person doing the analyses, and those that are purely describing new taxa, may be partly achieved by improving preparation of the specimens for study, and by improving the quality, detail and accuracy of description (De Lillo *et al.*, 2010). It can also be improved by incorporating better techniques (e.g., SEM) in studying the morphology of specimens (Chapter 3).

Before the development of the algorithms incorporated in TNT, continuous morphometric data had to be gap-coded to change it into discrete data for parsimony analyses. Some of the characters in the present study, e.g., tibial length, were dealt with in this way. In TNT it is now possible to include continuous data in data sets. This will allow the addition of more morphometric data for the Eriophyoidea, but this can not be done from many published descriptions, because the morphometric data are inaccurate and vague. Biological and ecological data can also be carefully included in the character set. Probably most importantly molecular data should be added which will expand the amount of character data available significantly. Like morphological data, molecular data will have problems of its own, though. In a first molecular phylogenetic study on the Eriophyoidea with the aim of studying the phylogeny of the entire superfamily undertaken by M. Lekveishvili and co-workers (West Virginia University, USA), the molecular data in their data set with 27 taxa (including the outgroup taxon) had CI and RI values ranging from about 0.55 to 0.65 (M. Lekveishvili, *unpubl. data*). It seems that homoplasy in molecular data of the Eriophyoidea is as high as found in the morphological data.

4.4.2.3 Analyses

It was decided to analyse the data with parsimony analyses, primarily first of all not to make any prior assumptions about evolution, and to find the most parsimonious and thus most defendable hypotheses or trees for explaining the distribution of character states in the Eriophyoidea. The phylogenetic resolution and groupings found in the preliminary runs of the 318tax data set was largely based on homoplasy with very little retrieval of synapomorphies. Judged on the conventional indications for tree reliability and robustness (different resampling methods, and Bremer's support) almost none of the phylogenetic resolution was reliable, and the trees usually largely collapsed under these criteria. (Some may also regard the collapse of trees under equal character weights e.g., Fig. 4.4, as an indication of weak group supports.) The phylogenetic resolution found under implied weighting is almost complete,

and are probably overresolved (groupings largely supported solely by homoplasy), but the groups are significant and make biological sense. It was decided to rather "test" the robustness of the groups somewhat by congruence between analyses of the data under various parameters, than to solely test it with the conventional methods. Different taxon sample sizes (one of 66 taxa, and another with 18 taxa) was sampled from the original 318-taxon data set (also for the reasons set out above). The analyses were additionally analysed with different algorithms, and under different character weighting schemes (different amounts of weighting (not *a priori*, though) against the influence by homoplasy in the construction of the trees). See "Character weighting" below.

4.4.2.4 Character weighting (implied weighting) used in the present analyses

Characters in real organisms are not equally weighted, and some characters show a lot of homoplasy while others may be completely hierarchical (Goloboff, 1993a). Equally weighted characters are thus based on the wrong assumption that all characters provide equally strong evidence of relationships, and can in fact not be considered unweighted. Characters with more homoplasy are less reliable. Parsimony does not prohibit weighting, but it rather requires weighting (Goloboff, 1993a). Implied weighting is, similar to successive weighting (Farris, 1969), using evidence on homoplasy provided by parsimony analyses, which provides a method for weighting characters (Goloboff, 1993a), and is not an *a priori* weighting method. The implied weighting algorithm is an examination of self-consistency, based on the idea that the trees themselves should give the information about the reliability of characters, and extra steps in highly homoplasious characters should count less (Goloboff, 1993a). Traditionally, trees are compared on the basis of how many steps they require for the data. Implied weighting is based on searching trees with maximum total fit. Those trees which imply the characters to be more reliable, explain the data better (Goloboff, 1993a). Implied weighting "prefers" trees with higher weights. The "weight" of a character is a function of its fit to a tree, and the total fit or weight of a tree is the sum of the fits of the characters (Goloboff, 1993a). Trees found under implied weighting typically produce more resolved, and better supported trees than standard unweighted parsimony (Goloboff, 1993a), and if the data are properly weighted, the results found under weighting should always be preferred, regardless of the results found under equal weights (Goloboff, 1993a). It is important to note, however, that Goloboff *et al*. (2008c) strongly advised that support of trees found under implied weighting should be tested, because in the way implied weighting is computed (with floating point numbers), it may result in overresolved trees.

4.4.2.5 Reliability and robustness of groupings and clades found in the present study

Although the study was not meant to be an exercise in the theory of phylogeny and cladistic analyses, some interesting questions and aspects came to the fore, largely related to the reliability of the results. This dilemma is caused by the phylogenetic resolution and retrieved groupings in the preferred trees

which are largely supported by homoplasy, and additionally, the majority of phylogenetic resolution is not robust (for example, not supported by symmetric resampling), and analyses of the data sets result in huge numbers of equally parsimonious trees. Do the results match or approach good hypotheses about true genealogical relationships between extant eriophyoid species? Or are the results just a coincidence or mimicking the current classification because it is based on the same homoplasious data set, where homology is swamped by homoplasy, and totally unreliable? Will the results largely confuse the systematics of the Eriophyoidea, rather than contribute valid, useful phylogenetic hypotheses to it? To argue the usefulness of the presentation of tree groups found in this study, we need to consider the general phylogenetic concepts and the discovery of natural, monophyletic groupings.

There are only two types of natural taxa that are the products of evolutionary processes: species and monophyletic groups (Brooks & McLennan, 2002). A monophyletic group or clade is a group that consists of a common ancestor and all, and only all, of its descendants (Kitching *et al*., 1998). A natural classification consists of monophyletic groups or taxa (named groups). Artificial taxa represent incomplete or invalid evolutionary units. These are paraphyletic groups (one or more descendants of an ancestor are excluded from the group, making the group an incomplete evolutionary unit) (Brooks & McLennan, 2002), and polyphyletic groups (a group that does not include the most recent common ancestor of all its members) (Kitching *et al*., 1998).

We use characteristics (characters and character states) to describe groups and taxa, and these are also studied or analysed to present hypotheses on the relationships between taxa. Relationship in phylogeny only refers to connections based on genealogy. Characteristics between taxa can differ or be the same. Similar or same characteristics can be the result of a novel feature that developed and is present in the common ancestor (homologous character) – i.e., an apomorphic character in the descendants. Another origin of a similar or same feature shared by organisms, is not due to genealogy, but is a result of convergent or parallel evolution, or reversal, and this type of character is a homoplasious character. Similarity between organisms does not equate with the degree of phylogenetic relatedness (Brooks & McLennan, 2002).

Apomorphic characters (homologies) allow us to specify monophyletic groups when they are shared between taxa (synapomorphies). Only synapomorphies provide evidence of common ancestral relationships (Brooks & McLennan, 2002). Symplesiomorphies (general homologies – a relative status) and homoplasies are useless in this regard (Brooks & McLennan, 2002). Monophyletic groups are discovered by finding synapomorphies, and discovery of homology is at the heart of cladistic analyses (Kitching *et al*., 1998). Monophyletic groups supported by homology are the only groups that can be justified objectively (Kitching *et al*., 1998) and empirically. Homoplasies are *ad hoc* incidences (P. Goloboff, *pers. comm*.), and in finding the most parsimonious explanation of character distribution,

homologies are empirical and the simplest explanation. Homologies are not fixed, though, homologies are hypotheses discovered by analyses, and they can be tested, and also falsified (Kitching *et al*., 1998). Following the equating of homology with synapomorphy, only homologous characters (and not homoplasies) supporting nodes will be called synapomorphies in the present study.

A group only supported by homoplasy is a polyphyletic group (Kitching *et al*., 1998). [In the presented study the definitions by Kitching *et al*. (1998) is followed in this regard, and only groups supported by at least one homology (synapomorphy) will be called clades.] It is thus an artificial group that does not exist in nature, and should not be a taxon in a natural classification. Results (e.g., trees) with groups largely supported by homoplasies thus did not recover evidence of phylogenetic relationships, and can be regarded as "bad" trees. "If the only available tree is a bad one, should you use it? No" (Coddington, 1985 as referred to by Brooks & McLennan, 2002). The biologically logical and robust method of dealing with a weakly supported tree is to collect more data (Brooks & McLennan, 2002).

Homoplasy, however, may contribute to the improvement of the retrieval of well-supported phylogenetic groups (Källersjö *et al*., 1999). They found that the number of well-supported groups and average jackknife resampling frequencies were significantly decreased when the most homoplasious characters which are at the third position were excluded, as is the usual practice, when they analysed a large molecular rbcL matrix. Goloboff *et al*. (2008a) illustrated that proper down-weighting of characters according to their homoplasy also produces more strongly supported groups, and more stable results in morphological data sets. These examples of the influence of homoplasy on the results of parsimony analyses are, however, not exactly applicable to the present study. Although the phylogenetic resolution, support, feasibility and biological sense of groupings in the present study increased highly significantly with down-weighting of homoplasy to the level where maximum total fit was found, and the groups and phylogenetic resolution are obviously provided by homoplasy, the support of the groups were weak when measured on basis of the amount of support by synapomorphies, and in terms of symmetric resampling values.

It is presumed that only one evolutionary history of living organisms exists which resulted in the diversity of extant and extinct organisms we study systematically today, and there is thus only one true phylogeny. In reality homoplasy exists in organisms, and in some groups, e.g., in the Eriophyoidea, homoplasy may be very high in their evolutionary development. It may be so high that it may literally mask the few incidences of "true" homologous characters. The descendants of one ancestor will also inherit an entire suite and certain combination of homoplasies that became part of its lineage. It is plausible that a complex and extensive combination of homoplasies may provide evidence of genealogical relationship if properly retrieved, and if sufficient data were analysed.

Some authors (e.g., Coddington, 1985 and Brooks & McLennan, 2002) may argue that the trees found in the present study are so poor that they should not be used at all. Many of the groups retrieved, however, make biological sense and are feasible in view of the knowledge on the ecology and biology of the species involved, and/or when evaluated on the morphological similarity of the included species. Although similarity does not equate genealogical relationships, if genealogically related, one will expect in many groups that the included species will be morphologically more similar than to species of particularly more distantly related groupings. This might especially be the case if overall, random, and well-defined morphology are compared. These similarities of species within certain groups are additionally in characters, e.g. the genitalia, which are generally found to have good phylogenetic signal.

The analyses in the present study also retrieved groups and positions of single species that brought more insight to the current classification, more than what would have been retrieved by traditional taxonomic practices. Some groups were congruent under the different parameters used in the present study, albeit no additional taxa and characters were added to the largest data set which formed the basis of all analyses. Some groupings (not only the few clades retrieved) were supported by the previous phylogenetic analyses (Hong & Zhang, 1996a, b; 1997) of the Eriophyoidea and its subtaxa. The groups found in the analyses provide good alternative hypothesized groupings, besides those taxa proposed in the classification of the group. Resampling methods largely did not support the groups found, but although these methods test robustness, they do not simulate the addition of new character and taxon data which are not random.

The data were analysed with parsimony analyses, and if the analyses are properly executed, the trees found will be the most parsimonious answer for the available data, which are significantly comprehensively sampled from available data. The results are thus the most defendable given the data, regardless of the robustness, reliability and correctness of the groupings. Under implied weighting, the best fit for the characters was also sought, by down-weighting excessive influence by homoplasy in the analyses. When the homoplasy was heavily down-weighted, up to k = 0.1, when weighting against homoplasy was about 100%, most groupings could not be defended by biological sense, although they may provide alternative hypotheses. Implied weighting may possibly weight the homoplasy down to about the level that really exists in the evolutionary development of the group in nature.

It is impossible to compare any cladogram retrieved with the real phylogeny that exists in nature to determine how close the cladogram (tree) comes to portraying true phylogeny. In theory, groups supported by at least one synapomorphy will always be more defendable (more parsimonious, and with more unambiguous evidence), though, than groups based on *ad hoc* homoplasy, it does not matter how homoplasious a group is in reality. Therefore, although the results and hypotheses of the present study

are presented, it is understood that extreme caution should be followed in the incorporation of the groupings in the current classification, and many groups might be totally artificial. When smaller taxon samples were analysed in the present study, more synapomorphies were retrieved, but this does not mean that the groupings (clades) supported by them are more reliable, because synapomorphies are just hypotheses, and some synapomorphies, alternatively, were retrieved as homoplasies in the analyses with more taxa and more evidence.

The only way to test the robustness of the groups will be to gather more and more data and continuously test the hypothesized groupings. Whether the topologies presented here will change drastically and whether the groupings will be supported, and genealogical relationships in this group are truly retrievable with combinations of homoplasious characters, will only be resolved in future. In the mean time it provides useful information, and parsimony analyses will continue to add useful information to systematic endeavours on the Eriophyoidea, despite “poor” trees.

4.5 RESULTS AND DISCUSSION: GROUPS AND CLADES RECOVERED BY THE DIFFERENT ANALYSES, PROPOSED AS ADDITIONAL HYPOTHETICAL SUPRAGENERIC GROUPINGS FOR THE ERIOPHYOIDEA

In this part of the results and discussion the tree clades and groups recovered from different data sets, under different parameters, are identified, described and named. These groupings will be used and incorporated by names and chronological numbers in the next part of the results and discussion, where the monophyly of suprageneric taxa in the current Eriophyoidea classification will be appraised, without detailed information about them. It should be noted that the groups are proposed on the basis of the data sets (taxon and character samples) in the present study, and the robustness and convergence towards monophyletic groups are particularly uncertain for the present study (see the discussion of reliability and robustness of groups and clades above). The groups did not contain random species, though, and many of the groups found made biological sense. The tree groups and clades are proposed as hypotheses of suprageneric groups additional to existing Eriophyoidea classifications.

The group and clade names (e.g., "*Nalepella* group") usually originate from a taxon name of species within the group or some characteristic of the group, but they are merely handles for referring to a group. These names do not hypothesize anything, or preamble officially incorporating these groups in the eriophyoid classification at this stage. A group is not necessarily a group of species at one node, but may refer to a group of species with about the same topology and making "biological sense" or which seems to be consistent under all parameters. The named groups and clades are chronologically numbered for ease of reference. When a group or clade has already been discussed prior to its use, it, and its chronological number are given in bold and underlined. Any list of taxa given in parentheses does not imply relationships in parenthetic notation, except when so noted.

In the presentation and discussion of results in the text mostly only the genus name is used, but the genus name in these cases is a substitute or alternative name for the species included in the analysis, and does not refer to the entire genus. In the single cases where more than one species of a genus were included in the analyses, the genus and species names are used. Sometimes genus names refer to the entire genus, but this will be clear from the context. The abbreviation "*D.*" before the species name always refers to "*Diptilomiopus*".

Some of the genera are small (see Appendix A), therefore, some extrapolation to the position or relationships of the genus was inferred during the discussion, but these are highly hypothetical, since

the monophyly of genera has not been determined. This is particularly true for the large genera such as *Aceria* (with close to 900 species). Naturally, for monospecific genera, the relationships of the species also extrapolate to the relationships of the genus as it is currently defined.

The complete terminology of characters and character states should be ascertained in the character description and discussion in Appendix B. Sometimes these may be shortened for the sake of brevity. For example, for Character 21 the setal tubercle of *c2* in the two outgroup species are primary absent (State 0), and if absent in the Eriophyidae, they are secondary absent (State 2), but in results and discussion, it is merely noted that the setal tubercles are absent.

The Phytoptidae is traditionally regarded as important in understanding the evolution and phylogeny of the Eriophyoidea, is relatively well discussed and tested in previous hypotheses on the phylogeny and evolution of the Eriophyoidea, and it is a relatively small family in comparison to the Eriophyidae and Diptilomiopidae. The results for this family are, therefore, given and discussed in more detail than for the Eriophyidae and Diptilomiopidae. The detailed topology of a group of species retrieved in the analyses is not necessarily given in the text, or discussed, because the main aim is to find some structure and hypotheses for future phylogenetic studies, and not necessarily to discuss the position found for each species in the data sets.

The groups and clades recovered by the analyses are evaluated more or less according to morphological similarity, host plants, habit, biogeography and any other knowledge about the species involved that may give insight to their relationships. Geographic distribution is used with caution, except where the origins of the host plants are known, because these mites are so closely associated with their host plants, and they are so small and “part” of the plant, that they might have moved with their host plants to different regions of the world where they and their host may not be native. Thus the collection sites may not necessarily be the places where the mites originated and may not be part of their natural distribution.

PHYTOPTIDAE

4.5.1 Groups retrieved comprising largely Phytoptidae [*sensu* Amrine *et al.* (2003)] species

I. Nalepellinae groups (eight groups)

1.) ***Nalepella* groups.**

1a.) ***Nalepella* group 1a:** *Nalepella*, *Phantacrus* (Nalepellinae: Nalepellini).

This is the most supported and robust group of the *Nalepella* groups. It occurs in all the presented 318tax (Figs 4.5, 4.8, 4.28) and 66tax trees (Figs 4.42, 4.43), under all weighting schemes, including the trees obtained under equal weighting. This group is also supported by a relatively high symmetric resampling absolute group frequency (hereon GF) and symmetric resampling group frequency difference (GC in TNT) values in the 318tax-k10 tree: GF value of 64 (Fig. 4.24), and GC value of 61 (Fig. 4.25); and in the 66tax-k999 tree: GF value of 69 (Fig. 4.49), and GC value of 61 (Fig. 4.50) particularly when compared with other groups found in the present study.

The 66tax-k999 (Fig. 4.44) and -k30 (Fig. 4.51) trees: the group (node 122) is supported by three homoplasies: single *vi* and tibial solenidion *φ* present, and tibia length twice tarsal length. The latter character state can be regarded as homologous, although the character itself is homoplasious, because the character is a multistate character, and this state only supports this group in these two trees. The 318taxEq and 66taxEq trees: the group (node 341, Fig. 4.5) is supported by 11 homoplasies, and node 76 (Fig. 4.42) supported by 12 homoplasies, respectively. These homoplasies include the three homoplasies supporting the group in the 66tax-k999 and -k30 trees. Two other homoplasies which support the group in the unweighted trees are: long spermathecal tubes, and very long *sc*.

Nalepella and the monospecific *Phantacrus* are needle vagrants on coniferous trees, a *Pseudotsuga* and *Tsuga* sp., respectively, and are essentially native to the Nearctic Region. The 15 species of the genus *Nalepella* (Amrine *et al.*, 2003) live on conifers (including *Pinus* and *Tsuga* spp.) in largely the Holarctic Region, with possibly single species occurring in the Oriental Region depending on the natural distribution of their hosts. These two species being sister species thus makes biological sense in so far their host plants, niche, geographical distribution and current classification are concerned.

Both species are exposed needle vagrants, with vagrant-like body shapes, however, the dorsal opisthosomal annuli of *Phantacrus* have large projecting lobes (Keifer, 1965c) while *Nalepella tsugifoliae* has an evenly arched body with annuli about subequal (Keifer, 1953). These differences were scored as different states for the two species in the data matrix (see characters 72 and 74 in

Appendices A & C). The relatively strongly supported sister relationship between the species indicate that detailed body shape (the presence of ridges and dorsoventral differentiation of annuli) may not be important in the determining the relationship between *Nalepella* and *Phantacrus*. It may also indicate that detailed body shape, e.g., presence and shape of ridges, may not have a strong phylogenetic signal. *Nalepella triceras* (not included in the present data sets) from Europe, has opisthosomal annuli with strong dorsoventral differentiation (Amrine *et al.*, 2003), which makes it morphologically more similar to *Phantacrus*. *Phantacrus* may eventually be designated a junior synonym of *Nalepella*. These results partly support the view of Boczek *et al*. (1989) that eriophyoid genera are differentiated on species level features, including the shape of opisthosomal ridges and troughs.

1b.) ***Nalepella* group 1b:** *Pentaporca*, *Nalepella, Phantacrus* (Nalepellinae: Nalepellini).

The 318tax-k10 and 318tax-k20 trees: the monospecific *Pentaporca* is sister to and in the same group as *Nalepella-Phantacrus* (***Nalepella* group 1a**). This group (node 558, Fig. 4.8 and node 416, Fig. 4.28, respectively) is supported by the same two homoplasies: single *vi* present, and *1a* slightly ahead of *2a*. The delimitation of the character to which the latter state belongs and its description is frequently ambiguous and the character is not generally used for separating taxa in the Eriophyoidea. The group is not supported by a GF value of 50 or above and weakly by a GC value of 24 (Fig. 4.25) in the 318tax-k10 tree. The group is feasible when evaluating host plants, niche, and current classification. *Pentaporca* is an exposed needle vagrant on *Tsuga chinensis*, a coniferous species indigenous to the Oriental Region. *Pentaporca* was not included in the 66tax and 18tax analyses to test its inclusion in this *Nalepella* group.

2.) ***Trisetacus* group:** *T. pini*, *T. ehmanni* (Nalepellinae: Trisetacini).

The two *Trisetacus* spp. above were included in the 318tax data set. The 318taxEq tree: under equal character weights the group (node 344, Fig. 4.5) is supported by 18 homoplasies, including some that partly differentiates the genus: presence of *c1*, and single *vi*, and long spermathecal tubes. Additionally various character states of *sc*, and character states relating to a more vermiform shaped body are included. These species are in the same genus, and therefore their sister relationship is viable. They were found to group together with *Boczekella* and *Setoptus* under the 318tax-k10 and -k20 character weighting schemes as **Trisetacini-Nalepellini group 3a**, discussed hereafter.

3.) **Trisetacini-Nalepellini groups**

3a.) **Trisetacini-Nalepellini group 3a:** *Trisetacus pini*, *T. ehmanni, Boczekella* (Nalepellinae: Trisetacini); *Setoptus* (Nalepellinae: Nalepellini).

The 318tax-k10 tree: the two *Trisetacus* spp. were found to group with *Setoptus* (node 572, Fig. 4.14) supported by three homoplasies: tibia I with *l'* and *φ*, and prodorsal shield circular. The latter character

state is particularly subjective and ambiguous. Relationships between these species are unresolved. *Boczekella* is sister to this group and included with them (node 491, Fig. 4.14). This group is supported by five homoplasies, and some are more robust and less ambiguous: single *vi* and *c1* present, genital coverflap smooth, and coxisternal plates I and II slightly and faintly ornamented. The 318tax-k20 tree: the four species were recovered in the same group, but with relationships between them unresolved. The group (node 386, Fig. 4.34) is supported by 12 homoplasies including those supporting this group in the 318tax-k10 tree. The group is not supported by a GF value of 50 or above and/or a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree. A GC value of 46 in the same tree for the sister relationship between the two *Trisetacus* spp. [***Trisetacus* group (2)**] within **Trisetacini-Nalepellini group 3a, is higher** (Fig. 4.25).

These species mainly occur on *Pinus* spp. and closely related relatives in the Holarctic Region, with *T. ehmanni* (a refuge-inhabiting mite) and *Setoptus* (vagrant mite) more prevalent in the Nearctic, and *T. pini* (a gall-inhabiting mite) in the Palearctic Region, and *Boczekella* (vagrant mite) occurs on *Larix decidua* (Panacea) native to the mountains of central Europe. The ecological data and their classification in the Nalepellinae, support the group. The division of the species in different tribes based on the presence of *c1* is not supported by the results, and this agrees with the key to genera, and implied classification, proposed by Boczek *et al*. (1989).

3b.) **Trisetacini-Nalepellini group 3b:** *Trisetacus ehmanni* (Nalepellinae: Trisetacini); *Nalepella*, *Phantacrus* (Nalepellinae: Nalepellini).

Only the three species above from the Nallepelinae groups dealt with so far were included in the 66tax data set. The 66tax-k20 tree (Fig. 4.54): *Nalepella-Phantacrus* (***Nalepella* group 1a**) was retrieved in a group with *T. ehmanni* of **Trisetacini-Nalepellini group 3a**, the only other taxon within the Nalepellinae included in the analyses except *Pentasetacus*. This is a less preferred tree due to its longer length than found under other weighting schemes, but which was included because it presents alternative hypotheses. The 66tax-k999 and -k30 trees are the more preferred 66tax trees, and herein *T. ehmanni* is in the **Trisetacini-Phytoptinae group (4)** (discussed below).

3c.) **Trisetacini-Nalepellini group 3c:** *Trisetacus* (Nalepellinae: Trisetacini); *Nalepella* (Nalepellinae: Nalepellini).

When *Phantacrus* was also excluded from the analyses (in the 18tax data set) and only *Nalepella* (Nalepellini) and *Trisetacus* (Trisetacini) were included, *Nalepella* and *Trisetacus* were recovered as sisters when the relationship between them was resolved. The 18correct-k999 tree: this group (node 20, Fig. 3.55b) is supported by one homoplasy: *ve* absent. Sometimes *Nalepella-Trisetacus* groups together with *Pentasetacus* as a **Nalepellinae group or clade (5)** (Figs 4.57, 4.59, 4.60, 4.62) (see below, and under discussion of *Pentasetacus* groups).

4.) **Trisetacini-Phytoptinae group:** *Trisetacus ehmanni* (Nalepellinae: Trisetacini); *Acathrix* (Phytoptinae)**.**

The 66tax-k999 and -k30 trees: *Trisetacus ehmanni* is not closely related to *Nalepella-Phantacrus* (***Nalepella* group 1a**), but was retrieved as the sister of *Acathrix*. This group (66tax-k999 tree, node 103, Fig. 4.44) is supported by three homoplasies: *c1* absent, tibial solenidion *φ* present and coxisternal plates II faintly ornamented. It is not supported by a GF value of 50 or above or by a GC value above 20 (Fig. 4.50) in the 66tax-k999 tree.

Acathrix does not live on a conifer such as *Trisetacus* and other species of the Nalepellinae, but lives in the frond folds of the coconut palm, *Cocos nucifera*, in the Nearctic, Neotropical, and Oriental Regions. The closer relationship between *Trisetacus* and other Nalepellinae species is biologically more meaningful than a close relationship between *Trisetacus* and Phytoptinae species, but the latter is an alternative hypothesis.

5.) **Nalepellinae group and clade:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Nalepella* (Nalepellinae: Nalepellini); *Trisetacus* (Nalepellinae: Trisetacini).

In the 18tax data sets the Nalepellinae is represented by three species (above), one from each of its three tribes, and not species of all seven genera in the Nalepellinae as in the 318tax data set. Where the relationships between the three taxa are resolved in the 18tax trees, they were found as a group.

In the 18taxcorrect trees, the relationships between the Nalepellinae genera are completely resolved in only the 18correct-k3 tree where *Pentasetacus* is sister to a *Trisetacus-Nalepella* group (node 19, Fig. 4.57). This Nalepellinae group is supported by one homoplasy: solenidion *φ* present. The group is not supported by the GF and GC values (Fig. 4.56) in the 18correct-k999 tree.

In the 18modify trees the group is a clade present in all the trees found under implied character weighting. In the 18modify-k999 tree the clade is at node 19 (Fig. 4.59) and in the 18modify-k100 and –k3 trees at node 20 (Figs 4.60, 4.62, respectively). The three clades are each supported by two synapomorphies: single *vi* present and spermathecal tubes long. These characters are used for differential diagnosis of the Nalepellinae. The relationships between the species in the clade are not resolved in the 18modify-k999 tree (Fig. 4.59), but in the 18modify-k100 and –k3 trees, *Pentasetacus* was found as the sister of *Trisetacus* at node 19 in both trees, supported by two homoplasies: *c1* present, and *1a* in line with *2a*. *Nalepella* is sister to the *Pentasetacus-Trisetacus* group. The Nalepellinae clade is not supported by a GF value of 50 or above and relatively weakly by a GC value of 20 (Fig. 4.61) in the 18modified-k100 tree. The unweighted 18modifiedEq tree (Fig. 4.58): the Nalepellinae group is not present, and the Phytoptidae in the analysis, including *Pentasetacus*,

Trisetacus, *Nalepella*, *Novophytoptus* and *Mackiella* (excluding *Phytoptus* and *Sierraphytoptus*), are part of a polytomy together with all other eriophyoid taxa in the analysis.

One could deduce that the modified characters and character states which are similar to the 318tax data set was more "successful and robust" in retrieving the Nalepellinae clade. The loss of this clade when more evidence from more taxa and characters are added with the similar structured characters may thus be real.

II. The Phytoptinae and Sierraphytoptinae groups (10 groups)

6.) *Pentasetacus*-Sierraphytoptini groups.

6a.) ***Pentasetacus*-Sierraphytoptini group 6a:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Austracus* (Sierraphytoptinae: Sierraphytoptini).

The 318taxEq tree: the group is not present. The 318tax-k10 tree: the group (node 490, Fig. 4.11) is weakly supported by one homoplasy: tibial length equal to tarsal length in leg II. It is part of the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (node 409), which is in turn part of the **Phytoptinae-Sierraphytoptinae group (9)** (node 412), both groups are discussed later on. The 318tax-k20 tree (Fig. 4.33, Group 13): *Pentasetacus* and *Austracus* are in the same group (node 356, Fig. 4.33), which includes a group at node 355, consisting of Phytoptinae and Sierraphytoptinae species. Relationships between *Pentasetacus*, *Austracus* and the group at node 355 are unresolved. All these are part of a group at node 358 [the **Phytoptinae-Sierraphytoptinae group (9)**, discussed later on] which includes *Pentasetacus* and all Phytoptidae with single and paired *vi* absent, except the two *Novophytoptus* spp. included in the analysis. *Pentasetacus-Austracus* is not supported by the GF (Fig. 4.24) or GC value (Fig. 4.25) in the 318tax-k10 tree.

6b.) ***Pentasetacus*-Sierraphytoptini group 6b:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini).

In the presented 66-tax trees, including the 66taxEq tree, *Pentasetacus* was recovered as sister of *Sierraphytoptus*. The 66taxEq tree: the group (node 79, Fig. 4.42) is supported by 10 homoplasies: *ve*, *c1* and *h1* present, genital coverflap and coxisternal plates unornamented, prodorsal shield ornamentation obscure, 3-rayed empodium, and *1b* the same distance apart than *1a*. The 66tax-k999 tree: the group (node 125, Fig. 4.46) is supported by three of the 10 homoplasies supporting the group in the 66taxEq tree: prodorsal shield ornamentation obscure, and coxisternal plates I and II unornamented. These supportive homoplasies are characters usually used to differentiate species. *Pentasetacus-Sierraphytoptus* and *Phytoptus* are part of a larger group (node 126, Fig. 4.46) supported by three homoplasies: *ve* and *c1* present, and *1a* slightly ahead of *2a*. The presence of *ve* and *c1* are character states used for differentiating subfamilies and tribes. *Pentasetacus-Sierraphytoptus* is also

present in the 66tax-k30 (Fig. 4.51) and the 66tax-k20 (Fig. 4.54) trees. It is not supported by a GF value of 50 or above and by a GC value of 30 (Fig. 4.50) in the 66tax-k999 tree.

Pentasetacus-Sierraphytoptus in the 66tax trees is more supported than *Pentasetacus-Austracus* in the 318tax trees, but *Austracus* was not included in the 66tax data set. *Pentasetacus* causes galling on an ancient relict coniferous species, *Araucaria araucana* (Gymnospermae: Araucariaceae), in the Chilean Andes in South America (Schliesske, 1985). *Austracus* has also been collected from South America, causing fruit galls on *Nothofagus dombeyi* (Monocotyledones: Nothofagaceae) in Argentina (Keifer, 1944). Their host plants are not closely related, but are more primitive than the Angiospermae on which the bulk of the Eriophyoidea lives. *Sierraphytoptus alnivagrans* is a vagrant on *Alnus tenuifolia* (Betulaceae) which occurs essentially in North America (Keifer, 1939a). Purely based on ecology, one may propose that *Pentasetacus* is rather more closely related to *Austracus*.

7.) **Dorsal-rear-fused clade:** *Prothrix* (Prothricinae); *Neopropilus* (Sierraphytoptinae: Sierraphytoptini); *Propilus*, *Retracrus* (Sierraphytoptinae: Mackiellini).

This clade was recovered by most of the 318tax and 66tax analyses, and is supported by the synapomorphy: dorsal fusion of the rear annuli beyond *f.* The 318tax-k10 tree: the clade (node 562, Fig. 4.11) is additionally supported by two homoplasies: *h1* present, and frontal lobe edge blunt and rounded. The 318tax-k20 tree: the clade (node 418, Fig. 4.33) is additionally supported by three homoplasies: *l'*, *sc* and its setal tubercle absent. Although the supportive homoplasies of the two clades differ, they share the support of the synapomorphy. The clade is confirmed by a clade consisting of a reduced number of species from it, *Prothrix*, *Neopropilus* and *Retracrus*, in all the 66-taxon trees, including in the tree found under equal character weights (66taxEq tree, Fig. 4.41). In these trees, the clade is supported by the same synapomorphy as in the 318tax trees. None of the species were included in the 18-taxon analyses. A subgroup of the clade (*Prothrix-Neopropilus*) is supported by a GF value of 53 (Fig. 4.24) and the entire clade is supported with a GC value of 25 (Fig. 4.25) in the 318tax-k10 tree.

The 318tax analysis under equally weighted characters did not retrieve the clade (318taxEq tree, Figs 4.4, 4.5). This result is regarded to be less reliable, given the morphological similarity of these species (see descriptive drawings in Amrine *et al.*, 2003), and the relatively strong support for the clade in the other trees.

The clade and the phylogenetic resolution found within the clade at first glance seem to be supported by the host plants and distribution of the taxa involved. Within the clade *Prothrix* and *Neopropilus* were always recovered as sisters. Both genera are monospecific and they occur in the Oriental Region, with *Prothrix* collected on an unknown host plant in probably the Philippines (Amrine *et al.*, 2003),

and *Neopropilus* a vagrant from *Jatrophus curcas* (Euphorbiaceae) in Taiwan (Huang, 1992). *Retracrus* was recovered to be sister to, or in the same group as *Prothrix-Neopropilus* with relationships unresolved. In the 318tax-k10 and –k20 trees (Figs 4.11 and 4.33, respectively) *Propilus* is sister to *Retracrus-Prothrix-Neopropilus*. The two known species of *Retracrus* and the four known *Propilus* spp. (Amrine & de Lillo, 2003) were collected on palms (Arecaceae) in mainly the central and southern Americas (Keifer, 1975c; Navia & Flechtmann, 2002).

8.) **Smaller-Phytoptinae-Sierraphytoptinae group (8):** *Phytoptus*, *Anchiphytoptus*, *Oziella*, *Acathrix* (Phytoptinae); *Austracus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini); *Pentasetacus* (Nalepellinae: Pentasetacini) – [these species, apart from *Pentasetacus*, are all the Phytoptinae and Sierraphytoptinae in the data sets, excluding the **Dorsal-rear-fused clade (7)**, *Fragariocoptes*, and *Sierraphytoptus*].

This group is at node 409 in the 318tax-k10 tree (Fig. 4.11) and at node 357 in the 318tax-k20 tree (Fig. 4.33). Apart from relationships mentioned here, the topology of the Smaller-Phytoptinae-Sierraphytoptinae group is not discussed in detail for the present study, because it is not well-supported, and not central to the question about the more important relationships in the Phytoptidae. *Pentasetacus* is sister to *Austracus* in the 318tax-k10 tree (***Pentasetacus*-Sierraphytoptini group 6b**). In an unpublished phylogenetic study of the Phytoptidae by R. Ochoa (R. Ochoa, *pers. comm.*), *Mackiella* and *Austracus* had a close relationship with other Sierraphytoptinae, as found in the present study, but were outside a clade which largely coincides with the **Dorsal-rear-fused clade (7)**. *Anchiphytoptus* and *Phytoptus* were not found to be sisters in the present study, but were found to be relatively closely related, and this partly supports the sister relationship between these taxa found by R. Ochoa (R. Ochoa, *pers. comm.*), and the designation of *Anchiphytoptus* as a junior synonym of *Phytoptus* by Chetverikov *et al*. (2009).

9.) **Phytoptinae-Sierraphytoptinae group: Dorsal-rear-fused clade (7); Smaller-Phytoptinae-Sierraphytoptinae group (8)**; *Fragariocoptes*, *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Pentasetacus* (Nalepellinae: Pentasetacini).

This group comprises the Phytoptinae and Sierraphytoptinae in the data sets. These consist broadly of two groups, namely the **Dorsal-rear-fused clade (7)** and the **Smaller-Phytoptinae-Sierraphytoptinae group (8)**, and two Sierraphytoptinae species, namely *Fragariocoptes* and *Sierraphytoptus*, which were either recovered as closely related taxa and in the same group as the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (318tax-k10 tree, node 411, Fig. 4.11) or the relationships between the two species, and their relationships with the two mentioned groups of the Phytoptinae-Sierraphytoptinae group, are unresolved (318tax-k20 tree, Fig. 4.33). The group includes *Pentasetacus* under some parameters. The two *Novophytoptus* spp. whose relationships with the Phytoptidae and Eriophyidae are uncertain, and *Palmiphytoptus* that does not have a close relationship with the

Phytoptidae and which will be discussed under "species not correctly classified" further on, are not part of the group.

The 318tax-k10 tree: the group (node 412, Fig. 4.11) is supported by the homoplasies: *ve* present and *sc* ahead of rear shield margin. The 318tax–k20 tree: the group (node 358, Fig. 4.33) is supported by a longer branch with the same two homoplasies supporting the group in the 318tax-k10 tree, as well as five others: *c1* present, *1a* slightly ahead of *2a* (an ambiguous state), no opisthosomal ridges or furrows present, coxisternal plates I unornamented and genital coverflap smooth. The presence of *ve* in combination with the other homoplasies, thus support the Phytoptinae-Sierraphytoptinae group, rather than the absence or presence of single *vi*. The topology of the group in the 318tax-k10 and –k20 trees, differs slightly from each other.

R. Ochoa (*pers. comm*.) found *Fragariocoptes* to be closely related to *Boczekella* and *Setoptus* of the Nalepellinae, and these were in the same clade with the outgroup Eriophyidae species (*Eriophyes* and *Ashieldophyes*) in his unpublished study of the phylogeny of the Phytoptidae. These results were not supported by the present study.

10.) Groups retrieved in the 66tax trees of the four species from the **Phytoptinae-Sierraphytoptinae group (9)** included in the 66tax analyses: *Acathrix*, *Phytoptus* (Phytoptinae); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Pentasetacus* (Nalepellinae: Pentasetacini).

Many species in **Phytoptinae-Sierraphytoptinae group (9)** in the 318tax trees are excluded from the 66-tax data set, and only four species, listed above, are included of those species that are not part of the **Dorsal-rear-fused clade (7)**. The **Dorsal-rear-fused clade (7)** was not found to have a close relationship with the remainder of the species of the Phytoptinae-Sierraphytoptinae group (9) by any of the 66-tax analyses and is not taken into consideration for the discussion of this group. With the reduced taxon set, the Phytoptinae-Sierraphytoptinae group (9) as a whole at one node is not present in the 66-taxon trees, and thus these results do not support **Phytoptinae-Sierraphytoptinae group (9)**.

10a.) ***Pentasetacus*-Sierraphytoptini group 6b** (already discussed)

The 66taxEq tree: *Pentasetacus* and *Sierraphytoptus* are in the same group (the ***Pentasetacus*-Sierraphytoptini group 6b**). These are the only species from the **Phytoptinae-Sierraphytoptinae group (9)** exemplar species that were recovered as a group in this tree. The relationships of the group and other eriophyoid taxa and groups in the tree have not been resolved.

10b.) ***Pentasetacus-Sierraphytoptus-Phytoptus*** **group:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Phytoptus* (Phytoptinae).

In the three 66tax trees under implied character weighting, *Phytoptus* is sister to the ***Pentasetacus*-Sierraphytoptini group 6b**, and constitute the *Pentasetacus-Sierraphytoptus-Phytoptus* group. This group (66tax-k999 tree, node 126, Fig. 4.46) is supported by three homoplasies: *ve* and *c1* present, and *1a* slightly ahead of *2a*. The presence of *ve*, rather than the absence of single *vi*, also supports the recovered relatively close relationships between *Pentasetacus* and species without *vi* in this group, similar to the support for other groups with these suprageneric taxa.

10c.) **Trisetacini-Phytoptinae group (4)** (already discussed)

Acathrix is the closest related to *Trisetacus ehmanni* in the 66tax-k999 and –k30 trees.

10d.) ***Pentasetacus-Sierraphytoptus-Phytoptus-Acathrix*** **group (in 66tax-k20 tree):** *Acathrix*, *Phytoptus* (Phytoptinae); *Pentasetacus-Sierraphytoptus* (Nallepellinae – Sierraphytoptinae).

An alternative hypothesis to consider: *Acathrix*, *Phytoptus* and *Pentasetacus-Sierraphytoptus* are in the same group in the less preferred 66tax-k20 tree (Fig. 4.51). The *Acathrix-Phytoptus-Pentasetacus-Sierraphytoptus* group is the only group in the 66tax trees that supports the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** in the 318tax trees, and is sister to the remainder of the Eriophyoidea included in the analysis.

11.) Groups in the 18tax trees recovered from the four species of the **Phytoptinae-Sierraphytoptinae group (9)** – *Phytoptus* (Phytoptinae), *Sierraphytoptus* and *Mackiella* (both of the Sierraphytoptinae, and of the tribes Sierraphytoptini and Mackiellini, respectively) and *Pentasetacus* (Nalepellinae: Pentasetacini).

11a.) **Sierraphytoptinae group 11a:** *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini); and *Phytoptus* (Phytoptinae) positioned separately.

The 18correct-k999 tree (Fig. 4.55b): the three species from the Phytoptinae and Sierraphytoptinae in the 18tax data set (above), were not found as a group at one node, but are single terminal species, with *Mackiella* splitting of first, then *Sierraphytoptus* and then *Phytoptus*. They are part of and basal in a clade containing all the Eriophyoidea in the 18tax data set, except the **Nalepellinae group** (*Pentasetacus*, *Trisetacus*, *Nalepella*). This "Eriophyoidea minus the Nalepellinae" clade (node 25, Fig. 4.55b) is supported by two synapomorphies, single *vi* absent, and spermathecal tubes short; and a homologous character state of a homoplastic character: long *sc*. This clade is not supported by a GF

value of 50 or above (Fig. 4.56a) but is supported by a GC value of 30 (Fig. 4.56b) in the 18correct-k999 tree.

11b.) Sierraphytoptinae group 11b: *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini).

The 18correct-k3 tree: the Phytoptinae and Sierraphytoptinae species are again part of an "Eriophyoidea minus the Nalepellinae" clade (node 22, Fig. 4.57) supported by one synapomorphy: single *vi* absent. In this clade, *Sierraphytoptus* is the sister of *Mackiella* (node 24, Fig. 4.57) supported by two homoplasies: frontal lobe present, and opisthosoma differentiated dorsoventrally in longer dorsal annuli, and narrower ventral annuli. These are characteristics of vagrant eriophyoid mites, and differentiate the Sierraphytoptinae from the Phytoptinae.

11c.) *Mackiella*-Nalepellinae clade: *Mackiella* (Sierraphytoptinae: Mackiellini); *Pentasetacus* (Nalepellinae: Pentasetacini); *Nalepella* (Nalepellinae: Nalepellini); *Trisetacus* (Nalepellinae: Trisetacini).

Mackiella was recovered with the **Nalepellinae clade** (*Pentasetacus*, *Trisetacus*, *Nalepella*) as a clade in all the 18modify trees under implied weighting. This *Mackiella*-Nalepellinae clade is at nodes 20 (18modify-k999 tree, Fig. 4.59), and 21 (18modify-k100 tree, Fig. 4.60 and 18modify-k3, Fig. 4.62) supported by one synapomorphy: solenidion *φ* present.

III. The *Novophytoptus* groups (three groups)

12.) *Novophytoptus* groups.

12a.) *Novophytoptus* group: *Novophytoptus rostratae*, *N. stipae* (Novophytoptinae).

The 318taxEq tree: the two *Novophytoptus* spp. were recovered as sisters (node 342, Fig. 4.5) supported by 16 homoplasies, including the genital area far removed from the coxae, which is a diagnostic characteristic of *Novophytoptus* spp., but which was found to be homoplastic, because the genital area is also far removed from the coxae in *Stenarhynchus* (Rhyncaphytoptinae) which was not found to be closely related to the *Novophytoptus* spp., but to other Rhyncaphytoptinae in the **Diptilomiopidae groups or clades (27)**. The other supportive homoplasies are: *ve* and *h1* present, *sc* very long and near rear shield margin, *bv* on femur I and II absent, anterior genital apodeme folded up, and spermathecae elongated.

12b.) ***Novophytoptus-Tetra*** **group:** *Novophytoptus rostratae*, *N. stipae* (Phytoptidae: Novophytoptinae), *Tetra*, *Ursynovia* (Eriophyidae: Phyllocoptinae: Anthocoptini).

The 318tax-k10 tree: the group (node 565, Fig. 4.14) is supported by three homoplasies, of which only one is not reversing, but changing towards another state in the included species, namely *sc* very long, which changes to *sc* exceptionally long at node 566 of the group *Ursynovia-N. stipae*. The relationships between *Tetra* and *Ursynovia,* and the *Novophytoptus* spp. are not strongly supported.

The 318taxEq tree: *Ursynovia* and *Tetra* were recovered as a group (node 343, Fig. 4.5). This supports the synonymy of *Ursynovia* with *Tetra* by Amrine *et al.* (2003). The relationships of this group with other taxa are unresolved.

12c.) ***Novophytoptus-Eriophyes*** **group:** *Novophytoptus* (Phytoptidae: Novophytoptinae), *Eriophyes* (Eriophyidae: Eriophyinae: Eriophyini).

Only one *Novophytoptus* sp. is included in each of the 66-tax (Appendix F) and 18-tax (Appendix H) data sets, and a strong relationship between it and any other taxon was not recovered, except in the 18modify-999k (node 23, Fig. 4.59) and -100k (node 24, Fig. 4.60) trees where a sister relationship between it and *Eriophyes* was recovered. This group is weakly supported by one homoplasy: long *sc*. It is not supported by a GF or GC value (Fig. 4.61) in the 18modify-k999 tree.

ERIOPHYIDAE

4.5.2 Groups retrieved comprising largely Eriophyidae [*sensu* Amrine *et al.* (2003)] species

I. The Eriophyidae groups (six groups)

Determination of what constitutes an Eriophyidae group in the presented trees is subjective, but the groups were largely chosen as the smallest group including all Eriophyidae taxa.

13.) Eriophyidae group and clades

13a.) Eriophyidae group 13a (in the 318tax-k10 tree): all Eriophyidae and Phytoptidae [except ***Nalepella* group 1b**] included, and the Diptilomipidae excluded.

The 318tax-k10 tree: the group (node 344, Fig. 4.8) is weakly supported by three homoplasies: *sc* length short in relation to prodorsal shield length, opisthosomal ridges or furrows present, and genital coverflap ornamented and divided into a basal and distal part. The group is not present in the 318taxEq tree, and is not supported by the symmetric resampling values for the 318tax-k10 tree (Figs 4.24, 4.25).

13b.) Eriophyidae clade 13b (in the 318tax-k20 tree): all Eriophyidae, Diptilomiopidae and Phytoptidae included, except ***Nalepella* group 1b**.

In the 318tax-k20 tree (Fig. 4.26), for which weighting against homoplasy was lighter than for the 318tax-k10 tree, the **Diptilomiopidae clade – 318tax trees (27a)** was not recovered outside, but as part of **Eriophyidae group 13a**. Eriophyidae clade 13b (318tax-k20 tree, node 323, Fig. 4.28) is supported by two homoplasies, *sc* short in relation to prodorsal shield length, and long tibia I, and one synapomorphic character state, short spermathecal tubes. The short spermathecal tubes is a state of one of the more reliable characters in the data set: when the internal genitalia are preserved and observable in slide-mounted specimens, the relative length of the spermathecal tubes are easily and unambiguously scorable, and the spermathecal tubes are long in only the Nalepellinae. In other organisms (e.g., spiders) the internal genitalia provide good phylogenetic signal, and the amount of homoplasy in the character seems to be low in comparison with the other characters in the data sets, for example in the present study it has a ci of 0.4. The state is reversed in **Trisetacini-Nalepellini group 3a** (318tax-k20 tree, Fig. 4.34). Most species and groups in **Eriophyidae clade 13b** were retrieved as part of a polytomy with relationships between the taxa and the **Diptilomiopidae clade – 318tax trees (27a)** unresolved, apart from a few phyllocoptine species outside and at the base of the polytomy (Fig. 4.28).

The group at node 320 (Fig. 4.28) may also be regarded as an Eriophyidae group, and exclude four phyllocoptine species, additional to **Nalepella group 1b**. This node is supported by four homoplasies:

sc length average in relation to prodorsal shield length, *1b* slightly further apart than *1a*, tibia I of average length, 4-rayed empodium I. None of these characters are entirely unambiguous, and they are mostly used to differentiate species, and this Eriophyidae group is regarded to be less likely than **Eriophyidae clade 13b.**

13c.) **Eriophyidae clade 13c** (in the 66tax-k999 and –k30 trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but ***Nalepella* group 1a** excluded.

Eriophyidae clade 13c is at node 79 (Fig. 4.44) and the Diptilomiopidae groups are included in this clade and positioned among the Eriophyidae. This clade is supported by two synapomorphic character states: tibia I of average length, and short spermathecal tubes. The short spermathecal tubes are reversed to being relatively long in *Trisetacus ehmanni*. Alternatively, the group at node 76 (Fig. 4.44) may be regarded as an Eriophyidae group. It is supported by two homoplasies: *sc* directed divergently anteriad, *1b* slightly further apart than *1a*. It excludes ***Nalepella* group 1a**, *Novophytoptus stipae*, and two Aceriini species: *Aceria* and *Acunda*. The group at node 75 (Fig. 4.44) may also be regarded as an Eriophyidae group. It is weakly supported by one homoplasy: 6-rayed empodium I. It excludes ***Nalepella* group 1a**, the **Trisetacini-Phytoptinae group (4)** (*Trisetacus-Acathrix*), *Novophytoptus stipae*, and the two Aceriini species.

The same Eriophyidae groups are found in the 66tax-k30 tree. None of the groups are supported by the symmetric resampling values (Figs 4.49, 4.50). The clade at node 79 is the more reliable retrieval, because it is supported by two synapomorphic character states, including the length of the spermathecal tubes which may have a strong phylogenetic signal.

13d.) **Eriophyidae group 13d** (in the 66tax-k20 tree): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but the group comprising the Phytoptinae, Sierraphytoptinae and *Pentasetacus* in the data set, excluded.

This group (Fig. 4.54) is supported by three homoplasies: *ve* and *c1* absent, and the number of empodial rays. This is an important alternative hypothesis.

13e.) **Eriophyidae clade 13e** (in the 18correct trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but the Nalepellinae in the data set, *Pentasetacus*, *Trisetacus* and *Nalepella* comprising the **Nalepellinae group**, excluded.

The 18correct-k999 tree: The clade (node 25, Fig. 4.55b) is supported by two synapomorphic character states of homologous characters, single *vi* absent, and spermathecal tubes short, and one synapomorphic character state, long *sc*, which changes to other states for groups and taxa within the clade. The clade is not supported by a GF value of 50 or above (Fig. 4.56a) but is supported by a GC

value of 30 (Fig. 4.56b). The clade at node 22 in this tree (Fig. 4.55b) can also be regarded as an Eriophyidae clade. This clade includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and *Novophytoptus* of the Phytoptidae. The other Phytoptidae in the tree are not part of this clade and are positioned at the base of the clade, with *Phytoptus* the sister of the clade. The clade is supported by one synapomorphy, *sc* at or near the rear shield margin, and one homoplasy, *c1* absent. It is not supported by the symmetric resampling values (Fig. 4.56a, b). Based on the character supporting the clades, and the symmetric resampling results, the clade at node 25 may be more robust.

Likewise in the 18correct-k3 tree the Eriophyidae clade at node 22 (Fig. 4.57) includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and all Phytoptidae excluding the Nallepelinae, and is supported by one synapomorphy: single *vi* absent. The alternative Eriophyidae group at node 29 in this tree (Fig. 4.57) includes all Eriophyidae and the **Diptilomiopidae clade – 18tax trees (27b)**, but excludes all Phytoptidae in the 18tax data set. This node is weakly supported by two homoplasies: *ve* absent, and *sc* at or near rear shield margin. The exclusion of the Nalepellinae from, and the inclusion of *Novophytoptus* and possibly other Phytoptidae species with single *vi* absent in a predominantly Eriophyidae + Diptilomiopidae group are the strongest hypothesis from the 18correct trees.

13f.) **Eriophyidae clade 13f** (in the 18modify trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but *Phytoptus* and *Sierraphytoptus* (sometimes grouped in the **Phytoptinae-Sierraphytoptini group**), excluded.

This clade is present in all the 18modify trees, including the 18modifyEq tree. It is at nodes 19 (18modifyEq tree, Fig. 4.58), 21 (18modify-k999 tree, Fig. 4.59) and 22 (18modify-k100 tree, Fig. 4.60), supported by three synapomorphic character states: *ve* and *c1* absent, and *sc* projected divergently anteriad. At node 26 (18modify-k3 tree, Fig. 4.62), it is supported by only two synapomorphic character states: *c1* absent, and *sc* on or near rear shield margin. The clade is not supported by symmetric resampling values in the 18modify-k100 tree. The Phytoptidae included in this Eriophyidae clade, under some parameters, may constitute the **Nalepellinae clade (5)** and *Mackiella*, or the ***Mackiella-Nalepellinae* clade (11c)**, and *Novophytoptus*.

II. The Nothopodinae groups (six groups)

14.) **Nothopodinae groups and clade.**

14a.) **Nothopodinae group 14a:** *Anothopoda*, *Nothopoda*, *Pangacarus*, *Floracarus*, *Neocosella*, *Cosella* (Nothopodinae: Nothopodini); *Colopodacus*, *Adenocolus* (Nothopodinae: Colopodacini).

The 318tax-k10 tree: all the Nothopodinae species included in the analysis, except *Disella* and *Apontella*, were recovered as a group at node 446 (Fig. 4.16) supported by two homoplasies: tibia entirely fused with tarsus in leg II, and prosternal apodeme absent (coxae I fused medially). Primarily

the reduction or complete fusion of the tibia with the tarsus differentiates the Nothopodinae from the remainder of the Eriophyidae. Tibia I is absent (entirely fused with the tarsus) in all species in this group, except in *Anothopoda*, where tibia I is distinct, but short and without *l'*. Within the group *Colopodacus* and *Adenocolus* (Colopodacini), are in the same group (node 442) supported by two homoplasies: *1b* and the setal tubercle of *1b* present. The presence of *1b* in the latter species is a reversal within Nothopodinae where *1b* is absent.

14b.) ***Disella-Apontella* group:** *Disella* (Nothopodinae: Nothopodini); *Apontella* (Nothopodinae: Colopodacini).

The 318tax-k10 tree: The *Disella-Apontella* group (node 476, Fig. 4.16) is supported by three homoplasies: tibia partly fused with tarsus in legs I and II, genital coverflap entirely ornamented, and ornamentation divided into a clearly defined basal and distal part. The *Disella-Apontella* group is part of a larger group (node 478, Fig. 4.16), weakly supported by one homoplasy: 5-rayed empodium. The latter group also includes species from the Eriophyinae, Cecidophyinae and Phyllocoptinae, and is in the same group with **Nothopodinae group 14a** at node 447, but with the relationship between these two groups unresolved. Within the group at node 478, *Notacaphylla* (Phyllocoptinae: Acaricalini) is sister to *Disella-Apontella* and they group at node 477 (Fig. 4.16) supported by five homoplasies: *sc* ahead of rear shield margin, frontal lobe present, body fusiform flattened with ridges and furrows present, and dorsal annuli smooth (without microtubercles). The close relationship between some Nothopodinae species and *Notacaphylla chinensiae* is feasible, because the tibia of this species also seems quite shortened, and *l'* is absent (Mohanasundaram & Singh, 1988).

14c.) **Nothopodinae group 14c**: all Nothopodinae in the data set are included (including *Disella* and *Apontella*), but *Anothopoda* is excluded.

The 318tax-k20 tree: This group (node 374, Fig. 4.32) is relatively well-supported by 10 homoplasies, but many states change in individual terminal taxa within the group. The supporting homoplasies are: tibia of legs I and II completely fused to tarsus; *l'* absent; *sc* ahead of rear shield margin; *h1* absent, body elongated fusiform, opisthosomal ridges or furrows absent, dorsal annuli with microtubercles, prosternal apodeme absent (coxae I fused), and 5-rayed empodium. *Anothopoda* is part of a large polytomy (Fig. 4.29) including species of which the relationships with most other Eriophyoidea and groups within the Eriophyoidea are not resolved.

The relationships of species within **Nothopodinae groups 14a and 14c** are not conclusive. *Neocosella* and *Cosella* may be more closely related to each other than to other Nothopodinae (nodes 502, Fig. 4.16 and 393, Fig. 4.32), and the *Neocosella-Cosella* group may be closely related to *Floracarus* and *Disella*, supported by the solenidion of leg tarsus I situated on the lateral tarsus aspect, and not dorsally

above the empodium as in most other eriophyoid taxa (node 393, Fig. 4.32). *Colopodacus* may be closely related to either *Adenocolus* (Fig. 4.16) or *Apontella* (Fig. 4.32).

The 318tax-k20 tree (Fig. 4.32): the relationship of the Nothopodinae species with other eriophyoid groups and taxa was not resolved.

Nothopodinae in the 66tax trees.

Nothopoda and *Colopodacus* were sampled from the Nothopodinae for inclusion in the 66tax data set. They were included mainly because they are the type genera of Nothopodini and Colopodacini, respectively, and both are part of **Nothopodinae groups 14a and 14c** in the 318tax-k10 and -k20 trees, respectively.

14d.) Nothopodinae in the 66tax-k999 tree.

A close relationship between *Nothopoda* and *Colopodacus* is not supported in this tree. *Nothopoda* was recovered as the sister of *Cenaca* (Eriophyinae: Aceriini) (node 112, Fig. 4.46), supported by three homoplasies: *1b* and setal tubercle of *1b* absent, and 4-rayed empodium. *Cenaca-Nothopoda* is sister to a group (node 84, Fig. 4.46) including largely Cecidophyinae, and single Eriophyinae and Aberoptinae. These two groups were recovered as a group (node 85, Fig. 4.46) supported by homoplasies: *l'* and *h1* absent, and *sc* directed divergently posteriad. *Colopodacus* is in a group (node 101, Fig. 4.48) which includes *Epicecidophyes* (Cecidophyinae) and a weakly supported group (node 100, Fig. 4.48) with Phyllocoptinae species and the Phytoptidae group *Retracrus-Neopropilus-Prothrix*, but the relationship of *Colopodacus* with these taxa was not resolved.

14e.) Nothopodinae clade: *Colopodacus* (Nothopodinae: Colopodacini); *Nothopoda* (Nothopodinae: Nothopodini).

The 66tax-k30 tree: The relationship between *Colopodacus* and *Nothopoda* supports the hypothesis gained from the 318tax analyses that at least part of the species in the Nothopodinae may be a monophyletic group. Only one tree was obtained under this weighting scheme, and in this tree *Colopodacus* and *Nothopoda* are retrieved as a clade (node 116, Fig. 4.52) relatively well-supported by two synapomorphies: reduction of tibia and its complete fusion with tarsus in legs I and II. The *Colopodacus-Nothopoda* clade is included in a group (node 86, Fig. 4.52) that comprises the same species than the group (node 85, Fig. 4.46) to which *Nothopoda* belongs in the 66tax-k999 tree, except for the addition of *Colopodacus*. Node 86 (Fig. 4.52) is supported by four homoplasies: *l'* absent (with reversals in *Cecidophyes* and *Colomerus*) and *h1* absent (all species in the group with *h1* absent); *sc* directed divergently posteriad (several character state changes within the group); and *1b* slightly closer together than *1a* (state changes within group, but none of the included species with *1b* further apart than *1a*).

The 66tax-k30 and -20 trees: the "Nothopodinae" group (with *Nothopoda* and *Colopodacus*) is in the same group with two other groups: a group with several Cecidophyinae species (including *Cecidophyes-Dechela*) and *Aberoptus* (Aberoptinae), and another group with the Aceriini (Eriophyinae) *Cenaca* and *Acalitus*. *Ashieldophyes* was not included in the 66tax analyses. The relationship of the Nothopodinae or part of the Nothopodinae with other eriophyoid taxa is not clear, but there is a weak hypothesis that they may have a somewhat close relationship with the Aberoptinae, some Cecidophyinae and some Eriophyinae (Aceriini).

15.) *Nothopoda* in the 18tax trees.

Only *Nothopoda* of the Nothopodinae was included in the 18tax data set. In the 18correct-k999 (Fig. 4.55b) and –k3 (Fig. 4.57) trees *Nothopoda* is sister to a clade with *Aberoptus-Ashieldophyes-Cecidophyes*, and *Phyllocoptes* is sister to *Nothopoda*. In the 18modify trees *Nothopoda* is included in the *Aberoptus-Ashieldophyes-Cecidophyes* group, with the closest relationship to *Aberoptus* in a weakly supported group. In the 318tax-k10 tree the nothopodine species were not in a close relationship with *Aberoptus* (Aberoptinae), *Ashieldophyes* (Ashieldophyinae) or with *Cecidophyes* (Cecidophyinae), but the nothopodine species were in the same larger, weakly supported group (node 447, Fig. 4.16) than *Dechela* (Cecidophyinae).

III. The Aberoptinae groups (two groups)

16.) Aberoptinae groups.

16a.) *Cisaberoptus* deutogyne group: *Cisaberoptus pretoriensis*, *C. kenyae* [originally Cecidophyinae: Aberoptinae reassigned to Eriophyinae: Aceriini by Amrine *et al.* (2003)].

The inclusion of the *Cisaberoptus* spp. is essentially flawed, because the characteristics of the presumed deutogyne females of *Cisaberoptus* were scored in the data set, while all other species in the data set were scored for the same characters from protogyne females. Nevertheless, in the 318tax-k10 tree (the same groups are in the 318tax-k20 tree), the two *Cisaberoptus* spp. were recovered as sisters (node 499, Fig. 4.18) supported by the homoplasies: palp apical ends spatulate or with triangular projections, and body shape flattened fusiform. *Palmiphytoptus* (currently probably erroneously classified in the Phytoptidae) is sister to this group, and *Acunda* (Eriophyinae: Aceriini) sister to the *Palmiphytoptus-Cisaberoptus* group. These four species were recovered as a group at node 440 (Fig. 4.18) supported by four homoplasies: *1a* slightly ahead of *2a*, opisthosomal ridges or furrows absent, coxisternal plates II unornamented, and 8-rayed empodium I. These are used as largely species differentiating characters (except the presence of opisthosomal ridges or furrows).

16b.) ***Aberoptus* groups:** *Aberoptus samoae* (Eriophyidae: Aberoptinae).

Aberoptus samoae is the only species from the Aberoptinae *sensu* Amrine *et al*. (2003) in the present data sets. The 318tax-k10 tree: *Aberoptus* and *Cymoptus* (Eriophyinae: Aceriini) were recovered as sisters (node 348, Fig. 4.18) supported by four homoplasies: *l'* absent, frontal lobe absent, and coxisternal plates I and II unornamented. *Aberoptus-Cymoptus* is part of a group also including *Tergilatus* and *Phyllocoptruta arga* (Phyllocoptinae: Phyllocoptinae) at node 350 (Fig. 4.18). The Aberoptinae were not found to be closely related to the Nothopodinae or the Cecidophyinae in the 318tax trees.

Aberoptus is in the 66tax data set, but *Cymoptus* and *Tergilatus*, both in the same group (node 349, Fig. 4.18) and relatively closely related to *Aberoptus* in the 318tax trees, were not included. *Phyllocoptruta arga*, the other species that was relatively closely related to *Aberoptus* in the 318tax trees, was not found to have a close relationship with *Aberoptus* in the 66tax trees. *Aberoptus* was found rather to have a close relationship with four of the six Cecidophyinae included in the 66tax data set, within the **Cecidophyinae group 17c** (66tax-k999 tree, node 83, Fig. 4.46, and the same group in Fig. 4.51) to be discussed further on.

The 18correct-k999 (Fig. 4.55b) and -k3 (Fig. 4.57) trees: *Aberoptus* is sister to an *Ashieldophyes-Cecidophyes* group, and these three taxa are in a clade supported by one synapomorphy: female genitalia appressed to coxae II. *Nothopoda* (Nothopodinae) is sister to this three taxon group. *Aberoptus* under these parameters is thus more closely related to *Ashieldophyes* and *Cecidophyes* than to *Nothopoda*. *Phyllocoptes* is sister to *Nothopoda*, and these five species were recovered as an "Eriophyidae group" which is included in the same weakly supported group as the group that contains all the Diptilomiopidae in the analysis. The only taxon of the Eriophyidae that is not part of this grouping is *Eriophyes*, which is sister to the Eriophyidae-Diptilomiopidae group. Broadly, the same relationships are found in the 18modify trees.

IV. The Cecidophyinae groups (five groups)

17.) **Cecidophyinae groups.**

17a.) **Cecidophyinae group 17a** (in 318tax trees)**:** *Achaetocoptes*, *Johnella*, *Glyptacus*, *Chrecidus*, *Coptophylla*, *Cecidophyes*, *Bariella* (Cecidophyinae: Cecidophyini); *Epicecidophyes*, *Neocecidophyes*, *Ectomerus*, *Colomerus*, *Indosetacus*, *Circaces* (Cecidophyinae: Colomerini).

The 318tax-k10 tree: Thirteen of the nineteen Cecidophyinae species included in the 318tax data set were recovered as a group (node 424, Fig. 4.13) supported by three homoplasies: dorsoventral differentiation variably different, opisthosoma without ridges or furrows, and genital apodeme folded up, appearing as a thick transverse line. The latter character state is the primary characteristic

diagnosing the Cecidophyinae. The retrieval of the Cecidophyinae as a group on the basis of similarity in female genitalia makes biological sense. The genitalia are a more complex character, less exposed to the outside environment, and this type of character may have strong phylogenetic signal. Unfortunately, it is difficult to study the internal genitalia of the Eriophyoidea accurately, and requires excellent slide-mounting of specimens, and there may be errors in the description of this character in some species. The species of this group are morphologically not particularly uniform, and if the grouping is monophyletic, it serves as a reminder that similar morphology should not be the major or sole reason for evaluating groupings retrieved by phylogenetic analyses.

Not many subgroups were recovered within the group, but rather sister relationships, with taxa splitting off one after the other. The species of the Cecidophyini are generally closer related to each other than to the Colomerini, and *vice versa*. Most of the Cecidophyini species are in the group at node 437 (Fig. 4.13) supported by six homoplasies: *sc* short in relation to prodorsal shield length (which is interesting, because *sc* is absent in the Cecidophyini, and was coded as inapplicable, a state which is computed the same way as unknown characters, substituted with all states possible during the analysis), *l'* vertically on half of tibia, tibia as long as tarsus, frontal lobe edge blunt and rounded, opisthosoma with ridges and/or furrows, and dorsal annuli without microtubercles. *Neocecidophyes* and *Epicecidophyes* of the Colomerini are part of this group. They are the only two Colomerini species of those species included in the 318tax data set with smooth, and much longer dorsal than ventral annuli, and may possibly belong in the Cecidophyini.

Johnella and *Achaetocoptes* were recovered as sisters at node 430 (Fig. 4.13), supported by two homoplasies: shield ornamentation faint and obscure, and dorsal annuli extremely longer than ventral annuli. *Achaetocoptes* and *Johnella* were also found to be sister taxa in the phylogenetic analysis of the Cecidophyini by Hong & Zhang (1996b), supported by two synapomorphies: fewer, broad dorsal annuli which extend laterally, and dorsal annuli of variable width. The sister-taxon relationship between *Johnella* and *Achaetocoptes* is possible. They are morphologically similar, and both are vagrants on *Quercus* spp. in the northern hemisphere. *Johnella* and *Achaetocoptes* each have two species (Amrine *et al*., 2003) and may eventually be placed in one genus, pending results of a phylogenetic analysis of all species in these two and related genera.

The group consisting of only Cecidophyini (node 435, Fig. 4.13), with relationships between the species presented in parenthetical notation are: (*Bariella* (*Cecidophyes* (*Coptophylla* (*Chrecidus* (*Glyptacus* (*Achaetocoptes*, *Johnella*)))))). This group of species is about the same group ("Clade A") found by the analysis of Hong & Zhang (1996b) which includes all the Cecidophyini in their analysis, except *Dechela* and *Neserella* which were part of "Clade B" in their tree. The present results thus supports the retrieval of "Clade A" in the Hong & Zhang (1996b) analysis. In the present study, this

Cecidophyini group seems to be somewhat robust, but apart from *Achaetocoptes-Johnella*, the relationships found between the other species in the group, are weakly supported.

The Colomerini (*Circaces*, *Indosetacus*, *Colomerus* and *Ectomerus*) which are not part of the group at node 437 (Fig. 4.13) are from the southern hemisphere.

The 318tax-k20 tree: Cecidophyinae group 17a is also present (node 368, Fig. 4.34). The topology of the group is slightly different found for the same group in the 318tax-k10 tree, though. The group consisting primarily of Cecidophyini species, together with the Colomerini *Neocecidophyes* and *Epicecidophyes* is still present (at node 367), but particularly the phylogenetic resolution of relationships between the Colomerini species in Cecidophyinae group 17a are unresolved. *Cenalox* (Phyllocoptinae: Phyllocoptini) is sister to Cecidophyinae group 17a, and it seems feasible, primarily because the genitalia of *Cenalox* also seems to be pressed up against the coxae, although the anterior genital apodeme is not folded up in the characteristic single line (Keifer, 1961b).

17b.) *Dechela-Neserella* groups

Dechela and *Neserella* are not in **Cecidophyinae group 17a** in the present study, and was not recovered as part of the broadly corresponding "Clade A" (which includes all other Cecidophyini species) in the tree presented by Hong & Zhang (1996b). In the present study, they were found to be closely related to and in the same group as the **Extended southern-Aceriini group (19)** which is discussed later on. The 318tax-k20 tree: They were found as sisters at node 395 (Fig. 4.30). The 318tax-k10 tree: they are in a group at node 427 (Fig. 4.16) which includes **Nothopodinae group 14a**, as well as a group with diverse species and genera of the Eriophyinae [including the **Extended southern-Aceriini group (19)**], and Calacarini. The group consisting of species from diverse subfamilies (excluding **Nothopodinae group 14a**) is at the base of the group at node 427 and largely originates from the southern hemisphere, and particularly the Oriental, Australian and Afrotropical Regions. The group may be a natural group, or species may be part of natural groupings different from their present classification *sensu* Amrine *et al.* (2003).

17c.) **Cecidophyinae group 17c** (in the 66tax weighted trees): *Colomerus*, *Epicecidophyes* (Cecidophyinae: Colomerini); *Cecidophyes* (Cecidophyinae: Cecidophyini).

Three species (above) of **Cecidophyinae group 17a** were included in the 66tax data set. If the 66tax trees support the close relationships between Cecidophyinae species found by the 318taxon analyses, these species should be positioned in close proximity to each other, and to *Cosetacus* (Fig. 4.40). This is partly the case. The 66tax-k999 tree (Fig. 4.46): They were found in the same group, which includes *Aberoptus* (Aberoptinae) and *Cosetacus* and *Dechela* of the Cecidophyinae which were not part of

Cecidophyinae group 17a in the 318tax trees. The group is at node 83, supported by two homoplasies: genitalia appressed against coxae, and anterior genital apodeme folded up to appear as a thick transverse line. The 66tax-k30 and –k20 trees: the same group is present.

If the Cecidophyinae is monophyletic, the data set as it is at the moment is not sufficient to facilitate discovery of the shape of the genitalia diagnostic of the Cecidophyinae as a synapomorphy for the group. The group with largely Cecidophyinae is converging on being a natural grouping.

17d.) ***Cecidophyes* groups in 18tax trees**: *Cecidophyes* (Cecidophyinae: Cecidophyini); *Ashieldophyes* (Ashieldophyinae); *Aberoptus* (Aberoptinae); sometimes including *Nothopoda* (Nothopodinae: Nothopodini).

Only *Cecidophyes* of the Cecidophyinae was included in the 18tax data sets. The 18correct trees under implied weighting: *Cecidophyes*, *Aberoptus* and *Ashieldophyes* was found as a clade at node 26 (18correct-k999 tree, Fig. 4.55b) and at node 25 (18correct-k3 tree, Fig. 4.57) supported by one synapomorphy: genitalia appressed to coxae. The 18modify-k3 tree: The same clade is present at node 29 (Fig. 4.62) supported by the same synapomorphy, and *Cecidophyes-Ashieldophyes* is at node 31 (Fig. 4.62) supported by one synapomorphy: setal tubercles of *sc* absent. *Cecidophyes* is sister to *Ashieldophyes* in all three clades. All 18modify trees under implied weighting: *Nothopoda* was found in a group with *Cecidophyes*, *Ashieldophyes* and *Aberoptus*. In the 318tax analyses *Ashieldophyes* was thus not found to have close relationships with the Cecidophyinae, but rather with the Phyllocoptinae (Figs 4.10, 4.32).

18.) **Broadly-folded-apodeme group:** *Keiferophyes*, *Acunda* (Eriophyinae: Aceriini); *Brachendus* (Eriophyinae: Eriophyini); *Paracolomerus* (Cecidophyinae: Colomerini); *Palmiphytoptus* (Sierraphytoptinae *sensu* Amrine *et al*., 2003); *Cisaberoptus pretoriensis*, *C. kenyae* (Aberoptinae).

The 318tax-k10 and -k20 trees: This group is at node 441 (Fig. 4.18) and node 373 (Fig. 4.33), respectively, supported by one homoplasy: female genital apodeme broadly folded up, but not forming a characteristic, thin line as found in most Cecidophyinae. The 66tax trees: Only *Acunda* and *Paracolomerus* from this group were included in in the 66tax data set. If the group was supported in the 66-taxon trees, *Acunda* and *Paracolomerus* should have been recovered as sister taxa (Fig. 4.40), or being relatively closely related, but they were not. *Acunda* was recovered to have a closer relationship with *Aceria* at the base of the Eriophyoidea groups (with *Novophytoptus stipae* basal to them and sister to *Aceria*) (66tax-k999 tree, Fig. 4.44). *Paracolomerus* was not recovered in a close relationship with *Acunda* or the other Cecidophyinae in the analyses. It was found to be sister to *Eriophyes pyri* at node 119 (66tax-k999 tree, Fig. 4.46) supported by one homoplasy: *sc* long in relation to prodorsal shield length. No taxa from the **Broadly-folded-apodeme group** was included in the 18tax data sets

The **Broadly-folded-apodeme group** is viable. The description of the anterior genital apodeme, however, may be inaccurate, or not in enough detail, and the grouping may be entirely artificial. Attempts should be made to study the female genitalia in finer detail to find primary homologies. Additionally careful study of non-genitalia morphology study may find other common characteristics that may be of use in differentiating this group, such as the shape of the female genital coverflap.

V. The Eriophyinae group (one group)

19.) Extended southern-Aceriini group: *Acerimina*, *Cenaca*, *Ramaculus* and *Scoletoptus* (Eriophyinae: Aceriini); the group may also include the following species – *Dechela*, *Neserella* (Cecidophyinae: Cecidophyini); *Nacerimina* (Eriophyinae: Eriophyini); *Jutarus* (Phyllocoptinae: Calacarini).

The 318tax-k10 tree: *Ramaculus* and *Cenaca* were recovered as sister species (node 497, Fig. 4.16), supported by one homoplasy: *sc* long in relation to prodorsal shield length. *Scoletoptus*, *Neserella-Jutarus* and *Acerimina*, are outside and at the base of *Ramaculus-Cenaca*, in this order from closest to furthest related to the latter group. These six species were recovered in the same group as *Nacerimina* and species from the Cecidophyinae, Phyllocoptinae, and Nothopodinae (node 427, Fig. 4.16). The latter group is supported by the homoplasies: frontal lobe absent, body vermiform, annuli subequal and not differentiated dorsoventrally and the genital coverflap entirely ornamented but not divided into a basal and distal part. The 318tax-k20 tree: the four Aceriini species are in a relatively large polytomy (Fig. 4.29), and the relationships retrieved between these species in the 318tax-k10 tree are thus not supported.

Only *Cenaca* of the four Aceriini species was included in the 66tax data set. If the relationships of *Cenaca* with other eriophyoid species in the 318tax-k10 tree were supported by the 66tax trees, it should be roughly in the same group as *Dechela*, *Nothopoda*, and *Colopodacus*, and slightly less closely related to *Aequsomatus*. The 66tax-k999 tree: the fairly close relationship of *Aequsomatus* and *Colopodacus* to *Dechela*, *Nothopoda* and *Cenaca* in the 318tax trees is not supported. *Cenaca* and *Nothopoda* were recovered as sister species (node 112, Fig. 4.46), supported by the homoplasies: *1b* and its tubercle absent, and 4-rayed empodium. *Dechela* was found to be less related, but in the same general group (node 85, Fig. 4.46) as *Cenaca*, supported by the homoplasies: *sc* directed divergently posteriad, *h1* and *l'* absent. The 66tax-k30 tree: there is still a fairly close relationship between *Cenaca*, *Nothopoda*, *Colopodacus*, and *Dechela* (they are in the same group at node 86, Fig. 4.52), supported by the homoplasies: *sc* directed divergently posteriad, *h1* and *l'* absent, and *1b* slightly closer together than *1a*. The relationships between the species were retrieved as different from those in the 66tax-k999 tree, though.

Acerimina, *Cenaca*, *Ramaculus* and *Scoletoptus* key out together as a group with *1b* absent within the Aceriini (Amrine *et al.*, 2003). All the species (also those not included in the present analyses) of the four Aceriini genera (*Acerimina*, *Cenaca*, *Ramaculus* and *Scoletoptus*) occur in the southern hemisphere (Gondwana), and although the relationships are surely not well-supported, it is worth exploring the relationships between Aceriini species with *1b* and/or *l'* absent. Regarding the sister relationship found between *Ramaculus* and *Cenaca* in the 318tax-k10 tree: the genus *Ramaculus* has two species, and the species included in the present data sets causes galls on a Violaceae in New Zealand, and *Cenaca* has three species, and the species included in the present data sets causes witches' broom on a Myrtaceae in Singapore. The included species are morphologically similar, except for the differential absence of some setae. *Dechela* and *Neserella* also part of this **Extended southern-Aceriini group** did not form part of a group with most of the Cecidophyinae in the data set, **Cecidophyinae group 17a**, and also formed a separate clade from the other Cecidophyini in an analysis by Hong & Zhang (1996b). In their study, *Neserella* and *Dechela* were recovered as sisters which were found to be part of a larger clade supported by *1b* and *l'* absent.

In conclusion, *Acerimina*, *Neserella*, *Jutarus*, *Scoletoptus*, *Ramaculus*, *Cenaca*, *Nacerimina* and *Dechela* were not retrieved as one group or clade for example in the 318tax-k10 tree (Fig. 4.16), but they are positioned close to each other, they are all from the southern hemisphere, and *1b* and *l'* may be absent. It is hypothesized that these species or some of them, possibly with the inclusion of other closely related species, may be a natural grouping, which may have a close relationship with **Nothopodinae group 14a**.

VI. The Eriophyini (Eriophyinae) (five species positions)

20.) Eriophyini species positions.

20a.) Position *Proartacris*.

The 318tax-k10 tree: *Proartacris* is sister to a group (node 412, Fig. 4.11) including mostly the Phytoptidae species without *vi*, and *Pentasetacus* (**Phytoptinae-Sierraphytoptinae group (9)**). The group (node 413, Fig. 4.11) consisting of *Proartacris* and the **Phytoptinae-Sierraphytoptinae group (9)**, is weakly supported by one homoplasy: opisthosomal ridges or furrows absent. The 318tax-k20 tree: the sister relationship between the **Phytoptinae-Sierraphytoptinae group (9)** and *Proartacris* has not been found, and *Proartacris* is included in a large polytomy (Fig. 4.29). *Proartacris* was not included in the 66-tax and 18tax data sets. The relationship of *Proartacris* stays highly uncertain, but a close relationship with either the other Eriophyinae or Phyllocoptinae included in the 318tax analyses, was not found. A tentative weakly supported relationship was found with some Phytoptidae. This may be feasible, since the three known *Proartacris* spp. live on hosts in the Pinaceae and Arecaceae in the Oriental and Neotropical Regions. Amrine (in a personal communication to Navia & Flechtmann, 2002) pointed out that *Proartacris* spp. should rather be in the Phyllocoptinae based on the presence of

a frontal lobe, the differentiation in the appearance of their annuli dorsoventrally, and the more fusiform shape of the type species, *P. pinivagrans*.

20b.) Position *Trimeracarus*

The monospecific *Trimeracarus* was collected in Hungary from leaf galls on an Araliaceae tree. The 318tax-k10 tree: *Trimeracarus* was found to be closely related to some phyllocoptine species (Fig. 4.12). It was found to be the sister of *Thamnacus* (node 573, Fig. 4.12) weakly supported by one homoplasy: *l'* on vertical proximal quarter of tibia. The sister to this group is *Monotrymacus*, at node 555, weakly supported by two homoplasies: *1a* slightly ahead of *2a*, and frontal lobe edge bluntly rounded. The sister to the *Trimeracarus-Thamnacus-Monotrymacus* group is *Tegoprionus* at node 556, supported by two homoplasies: *sc* ahead, but less than half of shield ahead, of rear shield margin, and *h1* absent. The 318tax-k20 tree: *Trimeracarus* is part of the Eriophyidae polytomy (Fig. 4.29). *Trimeracarus* was not included in the 66-tax and 18-tax data sets. In conclusion, the relationship of *Trimeracarus* with other Eriophyidae species is uncertain. It may have a closer relationship with some phyllocoptine species.

20c.) Position *Eriophyes pyri*

Two *Eriophyes* spp., *E. pyri* and *E. quadrifidus*, were included in the 318tax data sets. Seta *sc* of *E. pyri* is situated very close to the rear shield margin, similar to their position in the Aceriini, and are slightly more ahead of the rear shield margin in *E. quadrifidus*, depending on the interpretation of the exact position and extent of the rear shield margin. Seta *sc* is directed anteriad in both species. *Eriophyes* is a fairly large genus with more than 299 species worldwide (Amrine *et al.*, 2003).

The 318tax-k10 tree: *E. pyri* is included in the same group (node 416, Fig. 4.14) than another group (node 415, Fig. 4.14) with Aceriini, Anthocoptini and the *Novophytoptus* spp. The group at node 416 is weakly supported by one homoplasy: 5-rayed empodium I. This group is one of two groups in a probably more robust larger group (node 418) supported by five homoplasies: *1b* slightly further apart than *1a*, *l'* situated on vertical half of tibia, coxisternal plates II ornamented, genitalia not appressed but close to coxae, and female genital apodeme moderately extended forward and not folded up. *Eriophyes pyri* is the only Eriophyini member in the latter group, and it does not seem to have a close relationship to other Eriophyini species, including *E. quadrifidus*. The 318tax-k20 tree: The latter, largest group is also present in this tree (node 361, Fig. 4.34) and is supported by homoplasies of which some are usually used in the differentiation of supraspecific taxa: long *sc*, body vermiform with annuli dorsoventrally subequal and similar, furrows or ridges absent, dorsal annuli with microtubercles, leg tibia shorter than tarsus, but longer than half tarsus length, and 5- or 6-rayed empodium I.

Eriophyes pyri was included in the 66tax and 18tax data sets. If the 66tax tree fully supported the relationships in the 318tax trees, *E. pyri* would be closely related to *Aceria*, *Novophytoptus*, and slightly further related to *Trisetacus* and *Cosetacus*. These relationships are not supported in the 66tax-k999 tree where *E. pyri* and *Paracolomerus* of the Cecidophyinae were recovered as sisters (node 119, Fig. 4.46). In the 18correct-k999 (Fig. 4.55b) and -k3 trees (Fig. 4.57), the Phytoptidae are at the base of the tree, and *Eriophyes pyri* is sister (at nodes 30 and 29, respectively) to a group consisting of the Diptilomiopidae and Eriophyidae. The *Eriophyes pyri*-Diptilomiopidae-Eriophyidae group (node 30, Fig. 4.55b) is supported by one homoplasy: *ve* absent. The same group is present in the 18correct-k3 tree. In the 18modify trees, *Eriophyes* and *Novophytoptus* were recovered as sisters (nodes 23, Fig. 4.59 and 24, Fig. 4.60). The *Eriophyes-Novophytoptus* group supports this close relationship in the 318tax-k10 tree, but the relationship of the group with other species is not the same.

20d.) Position *Nacerimina*

The 318tax-k10 tree (Fig. 4.16): The genus *Nacerimina* has two species. The species included in the analyses, *N. gutierrezi*, is a vagrant on a palm (Arecaceae) from Samoa and the other, *N. maesae*, was collected in the deformed inflorescence of a host in the Myrsinaceae in South Africa. *Nacerimina* was recovered to be the sister of the Philippine *Dechela* (Cecidophyinae) (node 515) supported by one homoplasy: *l''* on genu II absent. The two species also have other characteristics in common, e.g., the dorsal shield pattern is broadly similar, *1b* is absent, and the internal female genitalia may be similar. The recovered relationships of *Nacerimina* are very weakly supported, though, and in the 318tax-k20 tree *Nacerimina* is included in the Eriophyidae polytomy (Fig. 4.29), and so are most of the other eriophyine and phyllocoptine species in the group at node 427 (Fig. 4.16). *Nacerimina* was not included in the 66tax and 18tax data sets.

20e.) Positions *Eriophyes quadrifidus* and *Asetilobus*

See general information about the genus *Eriophyes* above under the discussion of the relationships of *E. pyri.* The 318tax-k10 tree (Fig. 4.18): the two eriophyine species were recovered in a group with *Phyllocoptes calisorbi* (Phyllocoptinae) (node 484), supported by one homoplasy: annuli subequal and similar dorsoventrally. *Neocolopodacus* (Phyllocoptinae) (a genus with two species from India) is sister to this group at node 485, supported by two homoplasies: body fusiform and fat, and opisthosomal ridges of furrows absent. *Eriophyes quadrifidus* causes the pinule edges of a Dennstaedtiaceae plant to thicken and curl, and was collected in South Africa. *Asetilobus* is monospecific and causes galls on a Verbenaceae in New Zealand. It is feasible that *Asetilobus* may be closely related to open living species currently of the Phyllocoptinae, because it has an obvious frontal lobe, but the lobe is flexible, and the species is without dorsoventral differentiation in the annuli, currently placing it in the Eriophyinae. None of these relationships are supported in the 318tax-k20 tree, and all four species are included in the Eriophyidae polytomy (Fig. 4.29).

VII. The Aceriini (Eriophyinae) (six species positions)

21.) Aceriini species positions.

21a.) Position *Acalitus* (and possibly *Cenaca*).

The genus *Acalitus*, with 87 species (Amrine *et al.*, 2003), occurs widely in all ecozones of the world, and include bud, erineum, and gall mites (Meyer, 1990a). The genus is distinguished by particularly: *bv* and *l'* on leg I absent, *h1* and palp *d* minute or absent, coxisternal apodeme usually weak or absent, with coxae fused medially, and coxisternal plates and female genital coverflap frequently granulated (Keifer, 1965b; Manson, 1984b; Meyer, 1990a; Amrine *et al.*, 2003). The 318tax-k10 tree: *Acalitus* was recovered in a group with two Anthocoptini mites, *Nothacus* and *Quintalitus* (node 361, Fig. 4.16), supported by four homoplasies: palp *d* and *l'* absent, tibia shorter than tarsus, but longer than half tarsus length, and *1b* clearly closer together than *1a*. This group is absent in the 318tax-k20 tree, though, and these three species are part of the Eriophyidae polytomy (Fig. 4.29). *Acalitus* was included in the 66tax data set. If the 66tax trees support the groups found in the 318tax analyses, *Acalitus* should be closely related to *Paracalacarus*, while the other Aceriini species in the 66tax data set, *Cenaca* and *Acunda*, are not closely related to *Acalitus*, but they are in the same larger group with mainly Eriophyinae and Phyllocoptinae species (Fig. 4.40). Particularly close relationships between these three Aceriini species were not found by the 318tax analyses. The 66tax-k999 tree: *Acalitus* and *Nothopoda* (Nothopodinae) were recovered as sisters (Fig. 4.46). *Acalitus* and *Cenaca* are more closely related than both are to other eriophyine species (Fig. 4.43). The 66tax-k30 tree: *Acalitus* and *Cenaca* were recovered as sisters (node 88, Fig. 4.52) supported by two homoplasies: palp *d* and *bv* on leg I absent. *Acalitus-Cenaca* is closely related to **Nothopodinae clade (14e)** and **Cecidophyinae group 17c** (Fig. 4.52). *Acalitus* may thus have a close relationship with *Cenaca*, and they may have a close relationship with, or eventually be in the same monophyletic group with some Nothopodinae. This is feasible, because *l'* and *1b* are absent, the tibia fused or short, ornamentation on the genital coverflaps are similar in these species, and they have 4- or 5-rayed empodia. The close relationship between *Acalitus*, *Nothacus* and *Quintalitus* found by the 318tax analyses is equally well-supported, though, and is a strong alternative hypothesis. Similar to other large eriophyoid genera, however, one exemplar for *Acalitus* is not nearly enough to represent the variation within the genus, and only after including more species will one be able to get a more accurate result regarding the relationships of *Acalitus* spp. with each other, and with other eriophyoid species.

21b.) Position: *Baileyna*.

The genus *Baileyna* has five species (Amrine *et al.*, 2003). The 318tax-k10 tree: *Baileyna* is at the base of a large group (node 426, Fig. 4.13) supported by four homoplasies: *1b* slightly closer together than *1a*, tibia shorter than tarsus, but half or more of tarsus length, body with slightly longer dorsal than ventral annuli, and lateral lobes absent. It is the closest related to *Cenalox* (Phyllocoptini), but the two

species were not recovered as a group at one node. The remainder of the group (excluding *Baileyna*) (node 425) is supported by the genitalia being appressed to the coxae (which is not the case in *Baileyna*). Most of the Cecidophyinae in the 318tax data set (**Cecidophyinae group 17a**) are present in the group at node 426, together with another group at node 418 (Fig. 4.14), which is supported by, among other homoplasies: genital area at "usual" distance from coxae (not appressed to coxae), and genital apodeme moderately extended forward. This differentiates the group from the cecidophyine-like genitalia of the Cecidophyinae in the group at node 426. Two Aceriini, *Paraphytoptella* and *Aceria*, are included in the group at node 418, but in the 318tax trees, *Baileyna* is not particularly closely related to them, but more closely related to *Cenalox* (Phyllocoptini) and some of the Colomerini (*Circaces*, *Indosetacus*, and *Colomerus*) in the group at node 426. These relationships are probably not robust, because *Baileyna* is part of the Eriophyidae polytomy in the 318tax-k20 tree (Fig. 4.29). *Baileyna* was not included in the 66tax and 18tax data sets.

21c.) Position *Cymoptus*.

The genus *Cymoptus* has five species, occurring in both the southern and northern hemispheres. The 318tax-k10 tree: *Cymoptus* and *Aberoptus* were recovered as sisters at node 348 (Fig. 4.18), supported by three homoplasies: *l'* and frontal lobe absent, and coxisternal plates I and II ornamented. *Tergilatus* is sister to the *Cymoptus-Aberoptus* group (node 349, Fig. 4.18) supported by one homoplasy: 2-rayed empodium I. *Phyllocoptruta arga* is sister to *Tergilatus* (node 350). This four-species group is also present in the 318tax-k20 tree, but it is weakly supported by one homoplasy in both trees: 3-rayed empodium I. These relationships are weakly supported. *Cymoptus* was not included in the 66tax and 18tax data sets.

21d.) Position *Notaceria*.

Notaceria is monospecific, and its species is a vagrant collected on *Cordia tetrandra* (Boraginaceae) in Guyana, described by Mohanasundaram and Muniappan (1990). The 318tax-k10 tree: *Notaceria* is the closest related to species of the Phyllocoptinae (Phyllocoptini and Anthocoptini). A sister relationship between it and *Sinacus* (Anthocoptini) was recovered (node 563, Fig. 4.18), supported by three homoplasies: *l'* and lateral opisthosomal lobes absent, and tibia and tarsus of leg I the same length. *Notaceria* itself has many character changes. *Notaceria-Sinacus* was recovered in a group (node 374) which contains other Phyllocoptinae species, weakly supported by two homoplasies: dorsal annuli smooth with slight lateral lobes. The relationships between the species in this group are not well-supported, and all are part of the Eriophyidae polytomy in the 318tax-k20 tree (Fig. 4.29). It is quite plausible, though, that *Notaceria* may be closely related to the vagrant-like species of the Phyllocoptinae. The descriptive drawings of *Notaceria tetrandiae* (Mohanasundaram & Muniappan, 1990) are very schematic. The presence of a frontal lobe is not recorded, and it is not clearly present in the drawings, but the prodorsal shield is quite robust and more rounded anteriorly than e.g., in most

Aceria spp., and it may be partly covering the cheliceral bases. Additionally *Notaceria* is a vagrant species, and both *Notaceria* and *Sinacus* are from the Oriental Region.

21e.) Position *Aceria* and *Paraphytoptella*

Aceria is the type genus of the Aceriini. It probably has close to a 1000 species, and a worldwide distribution. It is the largest genus in the Eriophyoidea (Amrine *et al.*, 2003), with many more unknown species likely to be described in the near future. The type species, *Aceria tulipae*, has been included in some of the analyses, but it is understood that only one species does not represent the potential variation found in such a large genus, even if the characters included in the analyses are focused on character states used for generic and higher taxon differentiation. The genus *Paraphytoptella* is a small genus with two species, but is morphologically (particularly in body shape) very similar to *Paraphytoptus* with 33 species, apart from the absence of opisthosomal *e* in *Paraphytoptella* (Amrine *et al.*, 2003). The 318tax-k10 tree: Although a sister relationship between *Aceria* and *Paraphytoptella* was not found, they are closely related (they are more closely related to each other, than to any other Aceriini species in the analysis), and are included in a group (node 415, Fig. 4.14) weakly supported by one homoplasy: *l'* inserted on proximal third of tibia. This group includes *Heterotergum* (Anthocoptini) as well as a more strongly supported group (node 565) which includes *Tetra*, *Ursynovia*, *Novophytoptus rostratae* and *N. stipae* (***Tetra-Novophytoptus* group**). *Eriophyes* is sister (node 416) to the group at node 415, supported by one homoplasy: 5-rayed empodium I. *Aceria* is sister to ***Tetra-Novophytoptus* group** (node 414), but this relationship is only weakly supported by one homoplasy: *sc* very long in relation to prodorsal shield length. The species and groups discussed so far, is part of a larger group (node 418, Fig. 4.14) supported by five homoplasies: genitalia "usual" distance from coxae, internal genital apodeme not folded up, *1b* slightly further apart than *1a*, coxisternal plates II ornamented, and *l'* inserted vertically on half of tibia. The 318tax-k20 tree: the latter group in the 318tax-k10 tree is also present in this tree (node 361, Fig. 4.34) and is fairly strongly supported by seven homoplasies: long *sc*, body vermiform with annuli dorsoventrally subequal and similar, furrows or ridges absent, dorsal annuli microtuberculated, leg tibia shorter than tarsus, but longer than half tarsus length, and 5- or 6-rayed empodium I. These character states broadly define a "normal, usual or average" vermiform Eriophyoidea species, similar to the morphology of *Aceria* spp., with no particular outstanding "modifying" characteristics. The relationships of the species in the group are roughly the same in the two trees, although some relationships present in the 318tax-k10 tree have not been found by the 318tax-k20 analysis.

Five species, *Cosetacus*, *Trisetacus* (exemplar of the **Phytoptidae group**), *Eriophyes*, *Aceria* and *Novophytoptus* [exemplar of the ***Novophytoptus* group (12a)**] of the largest group just discussed, were included in the 66-tax data set. If the 66tax analyses would broadly retrieve the relationships in the 318tax trees, these five species would be recovered in the same group, placed within a group with all

Eriophyidae in the analysis, and some Phytoptidae, except *Nalepella-Phantacrus* which was retrieved as sister to this group (Fig. 4.40). *Aceria* may be closely related to *Novophytoptus* and *Eriophyes* (Fig. 4.40). The 66tax-k999 and –k30 trees: the five species were not recovered in an exclusive group at one node, but some relationships between the species are supported. *Novophytoptus*, *Aceria* and *Trisetacus* were retrieved in, and at the base of a large group (node 79, Fig. 4.44) and Fig. 4.51, including all the Eriophyoidea in the analysis except *Nalepella-Phantacrus*. The latter is sister to this "Eriophyoidea" group. *Novophytoptus* is sister basally to *Aceria*. They were not recovered as sisters at the same node, but a relatively close relationship between them is supported. *Acunda* is also closely related to *Aceria* in these trees (Figs. 4.44, 4.51) although a close relationship between them was not found by the 318tax analyses. *Trisetacus* and *Acathrix* were recovered as sisters (node 103, Fig. 4.44), and is fairly closely related to *Aceria* and *Novophytoptus*. *Cosetacus* and *Eriophyes* are positioned separately from each other (Fig. 4.46), and from the other three of the five species. The relatively close relationships between them found by the 318tax analyses are thus not supported. *Cosetacus* was, however, found to be more closely related to *Eriophyes* than to the other three species (Fig. 4.46).

In summary, it roughly makes morphological sense that *Eriophyes* spp. (those morphologically similar to *Eriophyes pyri*), *Aceria*, *Paraphytoptella* and *Heterotergum* are closely related, based on a similar body shape, and particularly prodorsum and frontal lobe shapes. *Paraphytoptus* of the Aceriini (not included in the data sets) may also be included in this grouping. In essence, the longer dorsal annuli in *Heterotergum* can be regarded as an anterior extension of the longer dorsal annuli restricted to the posterior part of the opisthosoma in *Paraphytoptus* and *Paraphytoptella*. The relatively close relationships of species *Aculodes*, *Cosetacus*, *Catachela*, *Tetra*, *Ursynovia*, and the group with the two *Novophytoptus* spp., and the group with some of the Phytoptidae species with single *vi* present (namely *Trisetacus*, *Setoptus* and *Boczekella*), within the larger group discussed above based on relationships recovered by the 318tax analyses, are proposed for further study. These relationships could be supported by similar body characteristics, with the possible exception of *Catachela*. As mentioned earlier, it does not seem that the markedly longer distance of the genitalia of *Novophytoptus* from the coxae phylogenetically deeply separates it from the "average" Eriophyidae, however, in order to be positioned closely with these species, the *Novophytoptus* spp. had to undergo numerous character changes, based on the character sample in the present analyses. These are preliminary hypotheses, and should be tested rigorously.

Sixteen *Aceria* species were included in a data set with 26 eriophyoid species in an ongoing, molecular phylogenetic study on the Eriophyoidea (M. Lekveishvili, *unpubl. data*) (see Introduction of this chapter). The analysis of this preliminary data set showed that the genus *Aceria* is not monophyletic, and some species are clustered in small groups, with the other Eriophyidae species scattered among the *Aceria* spp. and retrieved in groups together with *Aceria*

spp. A *Tetra* sp. was found to group with two *Aceria* spp., an *Aculops* sp. was found to group with *Aceria* spp., and an *Acalitus* sp. seemed to be most basal in a (Eriophyidae + Diptilomiopidae) clade. Three *Eriophyes* spp., as well as two Diptilomiopidae species, were retrieved in clusters within the (Eriophyidae + Diptilomiopidae) clade.

21f.) Position *Acunda* and *Keiferophyes*.

Acunda is monospecific, and its type species, *A. plectilis* was collected on grass (Poaceae) in California, USA. *Keiferophyes* has two species, and the type species, included in the data sets, *K. avicenniae*, was collected in the inflorescences of a Verbenaceae in South India. The 318tax-k10 tree: *Acunda* and *Keiferophyes* are in the same group together with other species (node 441, Fig. 4.18) supported by one homoplasy: female genital anterior apodeme broadly folded up. This character is probably phylogenetically highly informative, the interpretation and description of it is unfortunately, surely flawed for most species. This group (node 441) consists of *Keiferophyes* and two groups (nodes 494 and 440), with the relationships between them unresolved. *Paracolomerus* (Colomerini) and *Brachendus* (Eriophyini) were recovered as sisters at node 494 (Fig. 4.18), supported by one homoplasy: *sc* longer in relation to prodorsal shield length. The group at node 440 (Fig. 4.18) is supported by four homoplasies: *1a* slightly ahead of *1b*, opisthosomal ridges or furrows absent, coxisternal plates II unornamented, and 8-rayed empodium I. *Acunda* is part of the latter group, and is sister to a group consisting of *Palmiphytoptus*, and two *Cisaberoptus* spp. (node 500, Fig. 4.18) supported by two homoplasies: *h1* minute, and frontal lobe present. The 318tax-k20 tree: The entire group (318tax-k10 tree, node 441, Fig. 4.18) is also present (node 373, Fig. 4.33) in this tree, supported by the same character state, and it has the same internal topology.

Acunda, but not *Keiferophyes*, was included in the 66tax data set and both were not included in the 18tax data sets. If the group was supported in the 66tax trees, *Acunda* and *Paracolomerus* should be recovered in the same group (Fig. 4.40). The 66tax-k999 and -k30 trees: this relationship is not confirmed. *Acunda* was found to have a greater affinity with *Aceria* at the base of the Eriophyoidea groups, and *Novophytoptus*, *Nalepella* and *Phantacrus* are closely related to them.

VIII. The Phyllocoptinae groups (six groups)

22.) *Schizacea-Knorella* group: *Schizacea*, *Knorella* (Phyllocoptinae: Acaricalini).

This group is present in all the presented 318tax trees. It is well-supported by a GF value of 84 (Fig. 4.24), and a GC value of 83 (Fig. 4.25) in the 318tax-k10 tree. Only *Knorella* was included in the 66tax analyses, and the robustness of the relationship was thus not additionally tested.

The 318taxEq tree (Fig. 4.5): the group (node 339) is supported by 14 homoplasies. A suite of setae are absent: *sc* and its tubercle, *d*, *e*, *bv* on femur I and II, and *l''* on genu II; *l'* vertically on half of tibia; and *1b* clearly further apart than *1a* (this is also reflected by the shape of the coxisternal plates). Two homoplasies are usually regarded as species level characters: coxisternal plates II ornamented, and genital coverflap basally ornamented. Three homoplasies reflect the placement of the species in the Acaricalini of the Phyllocoptinae: dorsal annuli longer than ventral annuli, frontal lobe present and divided empodium.The 318tax-k10 tree: the group (node 551, Fig. 4.17) is supported by five homoplasies: divided empodium, dorsal annuli longer than ventral annuli, and *sc* and its setal tubercle, and *l''* on genu II, absent. The 318tax-k20 tree: the group (node 413, Fig. 4.32) is supported by four homoplasies: three which supported the group in the 318tax-k10 tree – empodium divided, and *sc* and its setal tubercle absent, and additionally genital coverflap is ornamented basally.

This sister relationship is likely. The species are dorsoventrally flattened vagrants on Poaceae in the southern hemisphere. *Knorella* is from a bamboo species in Thailand (Keifer, 1975c) and *Schizacea* is from a large grass species in Colombia, South America (Keifer, 1977a). They are also morphologically very similar, and might have belonged to the same genus, if they did not have differently shaped dorsal ridges and troughs. It will only be possible to test the monophyly of the genera (*Knorella* with eight species, and *Schizacea* with two species Amrine *et al*., 2003) when all the species are included in analyses.

23.) Flat-monocot group: *Tumescoptes*, *Schizacea*, *Knorella* (Phyllocoptinae: Acaricalini); *Acamina*, *Euterpia*, *Neocupacarus* (Phyllocoptinae: Phyllocoptini).

This group is present in the 318tax-k10 and –k20 trees, but not in the 318taxEq tree. It is also not, as a group at one node, supported by a GF value of 50 or above (Fig. 4.24) or by a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree. The well-supported ***Schizacea-Knorella* group (22)** is part of this group.

The 318tax-k10 tree: the group (node 364, Fig. 4.17) is supported by five homoplasies: *bv* absent on femur I and II; *l'* vertically on half of tibia; dorsal annuli slightly longer than ventral annuli (becoming even longer in the ***Schizacea-Knorella* group (22)**, and in *Tumescoptes-Euterpia*); and genital coverflap ornamented, divided into a basal and distal part. The absence of *bv* on both legs is the most unambiguous character. The 318tax-k20 tree: the group (node 335, Fig. 4.32) is supported by three homoplasies: *d* and *e* absent, and tibia longer, but less than half tarsus length longer.

Acamina and *Knorella* from the group were included in the 66tax data set. Their relatively close relationship was not supported by the 66tax analyses, and therefore the monophyly of the group was not supported either. In particular, *Acamina* was recovered in a group with some Diptilomiopinae

species and it may have a diptilomiopid-like gnathosoma, and may be wrongly placed within the Phyllocoptinae (see ***Apodiptacus* group 32b** further on). This is not likely, though, because Keifer, who described *Acamina* (Keifer, 1939) was a careful and accurate taxonomist, and the long form oral stylet of the Diptilomiopidae is distinctively different from the short form oral stylet in the other families.

The group is defensible, although it was not supported in the 66tax trees. The species of the group included in the 318tax data set are all vagrants on Monocotyledones (particularly on grasses and palms), and probably all originated from the southern hemisphere, and particularly from South America and the Oriental Region. Although they are different in specific body modifications, they are all flattened dorsoventrally.

24.) One-Phyllocoptini group: *Neometaculus*, *Indonotolox*, *Metaplatyphytoptus*, *Aequsomatus* (Phyllocoptinae: Phyllocoptini).

The 318taxEq tree: *Neometaculus* and *Metaplatyphytoptus* were recovered as sister species at node 340 (Fig. 4.5), supported by 10 homoplasies, including: *sc* short in comparison with prodorsal shield length, *1b* and its setal tubercle absent, and coxae I medially fused. Three homoplasies are characteristics placing it in the Phyllocoptinae: frontal lobe present, body fusiform flattened, and dorsal annuli longer than ventral annuli. Three homoplasies are regarded as species level characteristics: coxisternal plates I unornamented, tibia longer than tarsus, but less than half tarsus length longer, genital coverflap ornamented, divided into a basal and distal part. The 318tax-k10 tree: the group (node 451, Fig. 4.16) is supported by two homoplasies: *sc* ahead of rear shield margin, and dorsal annuli without microtubercles. The 318tax-k20 tree: the group (node 376, Fig. 4.31) is supported by four homoplasies: *sc* ahead of rear shield margin, *1b* and its setal tubercle absent, and coxisternal plates unornamented. Only *Aequsomatus* of the group was included in the 66tax data set, and the robustness of the group was thus not tested in the 66tax analyses.

The rational for the close relationship between the species in this group is not obvious, apart from all are from the southern hemisphere. They are broadly morphologically similar, but for instance *Indonotolox* has a distinct narrow prodorsal shield projection to the rear. This kind of detail and variation in body modification was not included in the data sets. Nevertheless, the projection would have been autapomorphic for this species among the species in the data sets and could not have had an influence on the retrieval of relationships. The species of the group seem to belong to Phyllocoptini species in which *1b* are absent. Other species in this group (without *1b*), e.g., *Gilarovella*, *Visinus* and *Garcinyes*, have not been included in the data sets in the present study. *Neometaculus* and *Metaplatyphytoptus* are more similar than the other species in the group. Although their bodies do not seem to be equally thick (Mohanasundaram, 1983a; Hong & Kuang, 1989, respectively), it is probably

caused by different mounting procedures. They are differentiated in the same couplet in the genus key of Amrine *et al.* (2003).

25.) ***Tetra-Ursynovia*** **group:** *Tetra*, *Ursynovia* (Phyllocoptinae: Anthocoptini).

The 318taxEq tree: the group (node 343, Fig. 4.5) is supported by six homoplasies: *sc* very long, and in comparison with prodorsal shield length very long, *sc* on or near rear shield margin, *h1* present, body fusiform flattened, and dorsal annuli longer than ventral annuli. The latter two characteristics place the species in the Phyllocoptinae, and *sc* on or near the rear shield margin, place them in the Anthocoptini. The 318tax-k10 and –k20 trees: the species are still in the same groups, but these groups include the two *Novophytoptus* species in the data set. The relationships between them are weak. See the discussion of the ***Novophytoptus-Tetra group*** **(12b)**.

These results do not conclusively confirm, but are supportive of the designation of *Ursynovia* as a junior synonym of *Tetra* by Amrine *et al*. (2003). *Tetra* has 87 species (Amrine *et al*., 2003). These species have a distinctive body shape, with a broad middorsal furrow, and with prominantly long *sc*. The particularly long *sc* contributes towards the retrieval of these relationships.

26.) ***Abacarus*** **groups.**

26a.) ***Abacarus*** **group 26a:** *Abacarus acalyptus, A. hystrix, Porcupinotus* (Phyllocoptinae: Anthocoptini).

The 318taxEq tree: the group (node 320, Fig. 4.5) is supported by 11 homoplasies: *sc* on or near rear shield margin, *h1* present, frontal lobe present, front edge of frontal lobe blunt and rounded, but narrow, body elongated fusiform, wax secretion present in adults, and secreted from ridges, tibia longer than tarsus, but less than half the tarsus length longer, coxisternal plates II ornamented, genital coverflap entirely ornamented, and 6-rayed empodium. The latter four characteristics are usually used at the species level. The 318tax-k10 tree: the group (node 320, Fig. 4.17) is supported by one homoplasy: 6-rayed empodium.

26b.) ***Abacarus*** **group 26b:** *Abacarus hystrix*, *Porcupinotus* (Phyllocoptinae: Anthocoptini).

The 318tax-k20 tree: the group (node 325, Fig. 4.30) is supported by five homoplasies: body elongated fusiform, 8-rayed empodium, genital coverflap ornamented entirely, and wax secretion present in adults, secreted from ridges. Fifty *Abacarus* spp. are known (Amrine *et al*., 2003), most species occur on grasses (Amrine, 1996; Skoracka, 2009), and the genus may be monophyletic. *Porcupinotus* has two species, and the species included in the present study is a vagrant on the leaves of a *Cassia* sp. (Fabaceae) (Amrine *et al*., 2003). The possible reasons for the close relationships between *Abacarus* and *Porcupinotus* is not obvious, but they are morphologically similar, both have ridges on the body,

and wax secretion is present in the adults. The two *Abacarus* spp. being in one genus, and the classification of the three species in one higher taxon, are supported by the recovered relationships.

DIPTILOMIOPIDAE

4.5.3 Groups retrieved comprising largely Diptilomiopidae [*sensu* Amrine *et al.* (2003)] species

I. Diptilomiopidae groups (three groups)

27.) Diptilomiopidae groups and clades.

27a.) Diptilomiopidae clade – 318tax trees: all Diptilomiopidae species in the data set. The Diptilomiopidae were recovered as a clade in the 318tax-k10 and –k20 trees (Figs 4.6, 4.19, 4.26, 4.35). The 318tax-k10 tree: the clade (node 395, Fig. 4.20) is supported by two synapomorphies: gnathosoma with long form oral stylet, and chelicerae relatively long, large, and abruptly bent down at base (Figs 3.22b, d, e; 3.23). These are two characteristics of a complex of structures of the gnathosoma that differentiate the Diptilomiopidae from the Eriophyidae and Phytoptidae. The clade is also supported by one homoplasy: *l'* vertically on proximal third of tibia I. The 318tax-k20 tree: the clade (node 349, Fig. 4.36) is supported by the same two synapomorphies as in the 318tax-k10 tree, and additionally by three homoplasies: *sc* directed parallel or converging anteriad, 5- or 6-rayed empodium I, and genital coverflap smooth. The homoplasies are character states usually used at either the genus or the species level. The clade was not found by the 318tax analysis under equal weighting (Fig. 4.5), which recovered only a few smaller clades and groups of a subgroup of Diptilomiopidae species each. The clade was additionally not supported by a GF value of 50 or above (Fig. 4.24), or by a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree.

27b.) Diptilomiopidae clade – 18tax trees: all Diptilomiopidae species in the data sets. Only four species, two of the Rhyncaphytoptinae (*Rhyncaphytoptus* and *Rhinophytoptus*) and two of the Diptilomiopinae (*Diptacus* and *Diptilomiopus*) were included in the 18tax data sets. The four species were retrieved as a clade in all the 18correct, and 18modify analyses under all character weighting schemes, as well as in the trees found with equally weighted characters. The clade seems to be robust and even occurred in all the trees found by the analyses of the flawed data set of Hong & Zhang (1996a) (Fig. 4.3). The clade is always supported by one synapomorphy: the chelicerae abruptly curved downwards. This clade is not supported by symmetric resampling values; only the group with the two Diptilomiopinae species which is part of the clade, is supported by a GF value of 76 (Fig. 4.56a) and GC value of 72 (Fig. 4.56b) in the 18correct-k999 data tree.

27c.) **Diptilomiopidae groups – 66tax trees:** all Diptilomiopidae species in the data set, except *Catarhinus* and *Cheiracus*; or all Diptilomiopidae species, excluding *Rhyncaphytoptus* (Rhyncaphytoptinae) and including *Acamina* (Eriophyidae: Phyllocoptinae: Phyllocoptini).

The 66tax analyses did not recover the Diptilomiopidae as a clade under any of the weighting schemes. The 66tax-k999 and –k30 trees: most Diptilomiopidae species are in the same group (Fig. 4.43, and node 92, Fig. 4.45, respectively), except *Catarhinus-Cheiracus* which is a group positioned among largely Phyllocoptinae. The Diptilomiopidae group (node 92, Fig. 4.45) is supported by two homoplasies which were retrieved as synapomorphies in the 318tax analyses: long form oral stylet, and chelicerae relatively long, large, and abruptly bent down at the base (Figs 3.22b, d, e; 3.23). The 66tax-k20 tree: this tree is not a preferred tree, but as alternative hypothesis, in this tree (Fig. 4.54) the group includes all Diptilomiopidae species in the data set, except *Rhyncaphytoptus*, and it includes *Acamina*. It is supported by the two homoplasies which support the *Diptilomiopus* group in the other 66tax trees. Similar to the 318tax analysis under equal character weights, only some smaller groups with a few Diptilomiopidae species each were found by the 66taxEq analysis.

II. Two major parts within the Diptilomiopidae

Based on the interpretation of results from all the trees, and according to the framework of the classification of the Diptilomiopidae, one can tentatively divide the **Diptilomiopidae groups and clades (27)** of the 318tax and 66tax trees into two loosely defined parts:

28.) **"Rhyncaphytoptinae" part**: Part 2A in the 318tax-k10 tree (Figs 4.19, 4.20); 318tax-k20 tree (Figs 4.35, 4.36, 4.37); 66tax-k999 (Figs 4.43, 4.45); 66tax-k30 (Fig. 4.51); 66tax-k20 (Fig. 4.54).

The 318tax-k10 tree: all Rhyncaphytoptinae included in the 318tax data set (Table 4.1), except *Sakthirhynchus*, are in the **"Rhyncaphytoptinae" part**. It also contains 14 of the 40 non-*Diptilomiopus* Diptilomiopinae species included in the 318tax data set (Table 4.1), and no *Diptilomiopus* spp. This part is basal to the **"Diptilomiopinae" group (29)**, and was not found as a group at one node, but is part of **Diptilomiopidae clade – 318tax trees (27a)** at node 395 (Fig. 4.20). The 318tax-k20 tree: the part consists of the same species, and has more or less the same topology than in the 318tak-k10 tree. **Diptilomiopidae clade – 318tax trees (27a)** is at node 349 (Fig. 4.36) and the **"Rhyncaphytoptinae" part** is part of this clade, and part of it is basal (at node 348, Fig. 4.36) to the **"Diptilomiopinae" group (29)**, but some smaller groupings are at node 349 with unresolved relationships between themselves and the group at node 348. All the 66tax trees: the species of the **"Rhyncaphytoptinae" part** were not retrieved as a group with close relationships between the species, but all are outside the

"Diptilomiopinae" group (29), which was retrieved as a clade when the reduced number of species were analysed (see discussion of the **"Diptilomiopinae" group (29)** hereafter).

29.) "Diptilomiopinae" group: Parts 2B-2D in the 318tax-k10 tree (Figs 4.19, 4.21, 4.22, 4.23); 318tax-k20 tree (Figs 4.35, 4.37, 4.38, 4.39); 66taxEq tree (Figs 4.41, 4.42); 66tax-k999 tree (Figs 4.43, 4.45); 66tax-k30 (Fig. 4.51); 66tax-k20 (Fig. 4.54).

The 318tax-k10 tree: the group constitutes all the *Diptilomiopus* spp. included in the 318tax data set (Table 4.1), and the 26 non-*Diptilomiopus* Diptilomiopinae species not included in the **"Rhyncaphytoptinae" part (28)**. Only one species of the Rhyncaphytoptinae, *Sakthirhynchus*, is in this group. Apart from one species, *Diptilostatus* [see the discussion of the **One-Diptilomiopinae group (34)** further on] the **"Diptilomiopinae" group** is at node 20 (Fig. 4.21) supported by one homoplasy: the absence of *c2*. *Diptilostatus* may not be part of the **"Diptilomiopinae" group**. One species with *c2* absent, *Steopa*, is not within this group.

The 318tax-k20 tree: the **"Diptilomiopinae" group** (excluding *Diptilostatus*) is at node 342 (Fig. 4.37) supported by one synapomorphy, *c2* absent, and three homoplasies: *l''* on genu I absent, and coxisternal plates I and II unornamented. This group includes all the species found in the **"Diptilomiopinae" group** in the 318tax-k10 tree, but also *Steopa* which was in the **"Rhyncaphytoptinae" part (28)** in the latter tree. The position of *Steopa* is thus uncertain.

All the 66tax trees (including the 66taxEq tree): five exemplar species from the **"Diptilomiopinae" group** in the 318tax trees were included in the 66tax data set. They were recovered as an apparently robust clade [see the discussion of the **66-Diptilomiopinae clade (40)** later on] supported in all the 66tax trees by two synapomorphies: *c2* and its setal tubercle absent. The clade is also additionally supported by some homoplasies. The relationships between the species within this clade are resolved and seem to be robust.

Hong & Zhang (1997) found a clade in their phylogenetic study of the Diptilomiopinae, constituting all the genera which are part of the **"Diptilomiopinae" group** in the present study. The Diptilomiopinae genera which were largely (except for *Diptiloplatus*) found to be outside this clade in their study are part of the **"Rhyncaphytoptinae" part (28)** in the present study. This division of the Diptilomiopinae in roughly two groupings supports the "division" of the Diptilomiopinae species into the **"Rhyncaphytoptinae" part (28)** and **"Diptilomiopinae" group (29)** in the present study.

III. Groups and clades within the "Rhyncaphytoptinae" part (28) (Part 2a in the 318tax-k10 tree; Figs 4.19, 4.20)

30.) *Cheiracus* groups.

A ***Cheiracus* group** is present in all the 318tax trees. Only *Cheiracus*, of the species present in the ***Cheiracus* groups**, is included in the 66tax data set, and the robustness of the groups was thus not tested in the 66tax analyses.

30a.) ***Cheiracus* group 30a:** *Cheiracus*, *Brevulacus* (Rhyncaphytoptinae); *Acarhynchus* (Diptilomiopinae).

The 318taxEq tree: the group (node 325, Fig. 4.5) is supported by seven homoplasies, of which two were retrieved as synapomorphies supporting **Diptilomiopidae clade – 318tax trees (27a)**: long form oral stylet, and chelicerae bending down abruptly at the base. Two homoplasies concern body shape brought about by a more vagrant life-style: frontal lobe present, and dorsal annuli longer than ventral annuli. The remaining homoplasies are: *sc* directed converging or parallel anteriad, tibia longer than tarsus, but less than half tarsus length longer, and empodium I with numerous rays. The latter homoplasy is the most obvious morphological indication why these species were recovered as a group (discussed further on).

30b.) ***Cheiracus* group 30b:** *Cheiracus*, *Brevulacus*, *Stenarhynchus* (Rhyncaphytoptinae); *Acarhynchus* (Diptilomiopinae).

The 318tax-k20 tree: the group (node 352, Fig. 4.36) is supported by one homoplasy: 10-rayed empodium. It consists of ***Cheiracus* group 30a**, with the additional retrieval of *Stenarhynchus* (Rhyncaphytoptinae) as sister to the latter group (node 351) supported by one homoplasy: empodium I with numerous rays.

30c.) ***Cheiracus* group 30c:** *Cheiracus*, *Brevulacus*, *Stenarhynchus* (Rhyncaphytoptinae); *Steopa, Acarhynchus* (Diptilomiopinae).

The 318tax-k10 tree: *Steopa* is part of the ***Cheiracus* group** at node 400 (Fig. 4.20) supported by the same homoplasy supporting ***Cheiracus* group 30b**: empodium I with numerous rays. The group is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

The ***Cheiracus* groups (30)** are plausible. The central stems of the empodia from which the rays originate, are thickened and pad-like, in the species of the ***Cheiracus* groups (30)**, or when the empodia have not been specifically drawn and described as such, they probably have shape. These central empodial stems are usually relatively slender in other Eriophyoidea. The empodium of *Cheiracus* seems to be rounded and pad-like in its descriptive drawing, and was described as being pad-like, with no definite central stem, with about 16 rays around the margin, and much internal branching, and it is

not divided (Keifer, 1977a). The empodium of *Brevulacus* (Fig. 3.6m) consists mainly of bundles of rays basally, with normal apical rays which are faintly visible, depicted and described by Manson (1984a). He described the empodium as being divided, but Amrine (1996) regarded the empodium to be entire, based on the descriptive drawing by Manson (1984a) (Fig. 3.6m), and placed it in the Rhyncaphytoptinae. Although the depicted empodia of *Cheiracus* and *Brevulacus* differ, they may be more similar in reality, but drawn in different styles and probably on different focus levels. The empodium of *Acarhynchus* is depicted as a divided empodium with two pad-like stems (Fig. 3.6j) (Keifer, 1959b), and was described by him as a divided empodium which have the medium rays parallel for most of their length, rather than diverging. These three species, always present in the ***Cheiracus* groups (30)** under different weighting schemes, are morphologically relatively similar, in comparison different from the morphology of particularly Diptilomiopinae that belongs to the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. The morphology of *Stenarhynchus* is different in some structures from the three species just discussed, and the empodium is not described or depicted as particularly different in shape than the usual shape, and is only described as having 10 rays (Mohanasundaram, 1983c). The empodium is only drawn laterally, and its real shape can not be seen. Its inclusion in ***Cheiracus* group (30a)**, albeit weakly supported, causes doubt about the accuracy of the description. In contrast with the other ***Cheiracus* groups (30)** species, the morphology of *Steopa* is very similar to that of *Diptilomiopus* spp., and other species in the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. It also is the only species in the **"Rhyncaphytoptinae" part (28)** with *c2* absent (similar to all the species which are part of the **"Diptilomiopinae" group (29)**), with all the other species in the **"Rhyncaphytoptinae" part (28)** with *c2* present. The drawing of the empodium of *Steopa* is very schematic and without detail, and to do an exact comparison with the other empodia in question, is impossible. It is described as having broad branches and many rays on each branch (Chandrapatya & Boczek, 2001b). There are *Diptilomiopus* spp. with similar pad-like or broadened empodia (C. Craemer, *unpubl. data*), e.g., the empodium of *Diptilomiopus championi* (Huang, 1992). Although the author included a SEM image of the empodia, it is not clear, but the stems definitely seem broadened. The author did not mention about this in the text description. The same species (a junior synonym of *D. championi*) (Craemer *et al.*, 2005; Huang, 2005), is described again as *D. septimus* by Huang (2001c), and in this description and drawing nothing is visible and nothing is described in the text of the broadened stems of the empodium.

This account of the empodia of this group illustrates the importance of describing morphology of eriophyoid structures in detail and accurately and in such a way that they are comparable with similar structures that may be primary homologous in other taxa. To alleviate different interpretations and drawings of similar structures, ideally the original mite specimens themselves must be studied again to determine the exact morphology of structures in different species when compared by one person. The latter is unfortunately not always feasible or practically possible in the Eriophyoidea, because of the

sometimes rapid degradation and eventual loss of slide-mounted material (De Lillo *et al.*, 2010). Studying the morphology with techniques such as SEM (Chapter 3) will also aid in preventing different interpretations which frequently happens with descriptions from slide-mounted material. Some structures may also be distorted by slide-mounting (Chapter 3).

In their phylogenetic study of the Diptilomiopinae, Hong & Zhang (1997) included *Brevulacus* as part of the ingroup Diptilomiopinae probably on the basis of the placement of this genus in this subfamily by Manson (1984a). *Brevulacus* was found to be sister to the remainder of the Diptilomiopinae in their analysis supported by the presence of *bv* on leg I, and the absence thereof in the remainder of the Diptilomiopinae. These and the present results strongly support the placement of *Brevulacus* in the Rhyncaphytoptinae, and its exclusion from the **"Diptilomiopinae" group (29)** found in the present study.

This account about the ***Cheiracus* groups (30)** is a hypothesis, but it may illustrate the problems encountered with coding characters from descriptions for the present study, and the necessity for the improvement of accuracy and standardization of eriophyoid descriptions.

31.) Long-tibia groups.

31a.) Long-tibia group 31a: *Dialox, Neodialox* (Diptilomiopinae).

The 318tax-k10 tree: the group (node 516, Fig. 4.20) is supported by three homoplasies: wax secretion in adults, prosternal apodeme present, and tibia length (22 µm) in the category "very, very long" (Character 101), and it is even longer, category "exceptionally long" (30 µm or more), in *Dialox*. The 318tax-k20 and -Eq trees: the group (node 333, Fig. 4.5) is supported by 10 homoplasies, including the same character transformation of Character 101 found in this group in the 318tax-k10 tree, and additionally by the homoplasy, the tibia exceptionally longer than the tarsus, which is also based on the presence of a particularly long tibia. The other supportive homoplasies are: long form oral stylet, and chelicerae relatively long and abruptly bent at the base, empodium divided, 8-rayed empodium, *bv* on femur I absent, *l'* displaced to inner side of tibia, *1b* clearly further apart than *1a*, and adults with wax.

This group is feasible when evaluated on the similar morphology of these monospecific species, their distribution, habit and host plants, and the homoplasies supporting the group. *Neodialox* and *Dialox* both have distinctively long tibia, and they are vagrants on palms in the Oriental Region. They may even belong to the same genus, but are separated at couplet one of the key to Diptilomiopinae genera (Amrine *et al.*, 2003), because *sc* and its setal tubercles are absent in *Neodialox* (Mohanasundaram, 1983a), but present in *Dialox* (Keifer, 1962b). It is surprising that the group is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

31b.) Long-tibia group 31b: *Dialox, Neodialox*, *Diptacus pandanus* (Diptilomiopinae). In the 318tax-k10 and –k20 trees *Diptacus pandanus* is sister to **Long-tibia group 31a**. The 318tax-k10 tree: the group (node 517, Fig. 4.20) is supported by four homoplasies: 8-rayed empodium, tibia length (Character 101) "average long" (14–15 µm), but becoming longer in *Neodialox* and *Dialox* as discussed above, *h1*, and *l''* on genu II, present. The 318tax-k20 tree: the group (node 397, Fig. 4.37) is supported by six homoplasies: the four homoplasies supporting the group in the 318tax-k10 tree, and additionally *bv* on femur II present, and genital coverflap smooth with a change of the state in *Dialox*.

Diptacus has 43 species (Amrine *et al.*, 2003, Appendix A). Two *Diptacus* spp. were included in the 318tax data set, *D. pandanus*, and the type species, *D. sacramentae*. *Diptacus pandanus* was included because it previously belonged to *Diptilomiopus* and was re-assigned to *Diptacus* by Hong & Zhang (1997), but does not seem to belong in *Diptacus*, because it has *bv* present on femur II among other characteristics. Keifer (1962d) implied a close relationship between *Diptacus* and *Dialox*, because he differentiated *Dialox* from *Diptacus*. Although *Diptacus pandanus* was recovered in a group with *Dialox* and *Neodialox*, the type species *D. sacramentae* was not. The latter species is part of a group in the 318tax-k20 tree (node 379, Fig. 4.37) which is relatively closely related to the groups (node 345 and 344, Fig. 4.37) to which **Long-tibia group 31b** belongs. The three species of the **Long-tibia groups (31)** were not included in the 66tax and 18tax analyses for additional testing of the robustness of the groups.

32.) ***Apodiptacus*** **groups.**

32a.) ***Apodiptacus*** **group 32a:** *Apodiptacus*, *Asetadiptacus*, *Diptacus sacramentae*, *Duabangus*, *Pararhynacus*, *Trimeroptes* (Diptilomiopinae); *Asetacus*, *Konola* (Rhyncaphytoptinae).

The 318tax-k20 tree: the group (node 379, Fig. 4.37) is supported by four homoplasies: *sc* length average in relation to prodorsal shield length, wax secretion present in adults (with reversals in *Pararhynacus* and *Asetadiptacus*), tibia medium long (12-13 µm) (Character 101), but change to average (4–11 µm) in *Konola* and *Duabangus*, empodium I divided, but change to simple in the Rhyncaphytoptinae species, *Asetacus* and *Konola*. Within the group, *Pararhynacus* was recovered as a sister of *Asetadiptacus* (node 382) and *Diptacus sacramentae* as a sister of *Asetacus* (node 381).

The 318tax-k10 tree: ***Apodiptacus*** **group 32a** species is positioned at the base of **Diptilomiopidae clade – 318tax trees (27a)**, with close relationships between the species, but they were not recovered as a group at one node. *Pararhynacus* was again recovered as the sister of *Asetadiptacus* (node 483) supported by three homoplasies: *sc* absent, wax secretion in adults absent, and tibia more than half tarsus length longer than tarsus. *Trimeroptes* was found as the sister of *Apodiptacus* (node 474) supported by two homoplasies: *1a* ahead of *2a*, and body flattened fusiform. The relationship between

these two species was not resolved by the 318tax-k20 analysis. *Trimeroptes-Apodiptacus* is the sister group of *Pararhynacus-Asetadiptacus* (node 475), supported by one homoplasy: 5-rayed empodium.

The relatively close, but loose, relationships between the species of ***Apodiptacus* group 32a** are possible, although the group was found to be polymorphic. They are morphologically more similar to each other, than the species are to most other taxa in their respective subfamilies. The group, or part of the group, may be monophyletic, but the species belonging to such a clade will probably change with new information. Within ***Apodiptacus* group 32a**, *Trimeroptes*, *Apodiptacus*, *Asetacus* and *Konola* are morphologically roughly similar, based on their general shape, prodorsal shield shapes and ornamentations, and presence and shape of the frontal lobe. Although the characteristic was not included in the data set *per se*, all these species have some kind of indentation or notch (emarginated *sensu* Amrine *et al.*, 2003) medially in the frontal lobe. *Pararhynacus*, *Asetadiptacus*, *Duabangus* and *Diptacus* are morphologically more similar. The group's position within the **"Rhyncaphytoptinae" part (28)** of the 318tax-k10 tree is also more feasible, morphologically, than a position within the **"Diptilomiopinae" group (29)** which largely contains species that are more similar to *Diptilomiopus* spp., and are without *c2*.

The sister relationship found between the monospecific *Pararhynacus* described by Kuang (1986a) and *Asetadiptacus* described by Carmona (1970) (which has two species), and their retrieval outside the **"Diptilomiopinae" group (29)**, and thus the lack of a close relationship with *Diptilomiopus* and morphologically similar species, are feasible. They are morphologically similar in several characteristics, including: *sc* absent, but its tubercle present, and broadly similar, cell-like, dorsal shield patterns, which are not similar to the general dorsal shield cell-pattern of *Diptilomiopus* spp. Amrine (1996) synonymized *Pararhynacus* with *Asetadiptacus*, but Amrine *et al.* (2003) reversed the synonymy, and regarded *Pararhynacus* as a distinct, valid genus, because it is described as having a short median ridge behind the prodorsal shield, followed by a broad furrow (Kuang, 1986a), while the body of *Asetadiptacus* is evenly rounded (Carmona, 1970). They are differentiated from each other, on the basis of these different dorsal body shapes, in the same key couplet in Amrine *et al.* (2003). It is possible that the rounded body shape of *Asetadiptacus*, and/or the dorsal shape of *Pararhynacus* may be artefacts caused by slide-mounting.

The sister relationship found between *Trimeroptes* and *Apodiptacus* is plausible. They are morphologically similar, except for slight differences in the shape of their opisthosomal ridges. They are differentiated from each other in the same genus couplet in Amrine *et al.* (2003). The two species included in the analyses are both from North America (Amrine *et al.*, 2003).

32b.) ***Apodiptacus* group 32b:** *Apodiptacus*, *Diptacus sacramentae* (Diptilomiopinae); *Asetacus* (Rhyncaphytoptinae); *Acamina* (Eriophyidae, Phyllocoptinae, Phyllocoptini).

Three of the species in ***Apodiptacus* group 32a** were included in the 66tax data set, and they were recovered as a group, together with *Acamina*, under all character weighting schemes except equal weighting.

The 66tax-k999 tree: the group (node 89, Fig. 4.45) is supported by five homoplasies: adults secrete wax, tibia 12–13 µm or 14–15 µm long (these two homoplasies are also present in the homoplasies supporting ***Apodiptacus* group 32a**), *sc* directed parallel or converging anteriad, *h1* absent, and frontal lobe present. This group supports ***Apodiptacus* group 32a** retrieved by the 318tax analyses, and likewise was not recovered in the same group than species included from the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. This group, together with its sister species, *Hoderus*, is sister to **One-*Diptilomiopus* group** which will be discussed later.

The retrieval of *Acamina* (Phyllocoptinae) within this group may be wrong. It has been recovered as the sister of *Apodiptacus* (node 87, Fig. 4.45) supported by two homoplasies: opisthosomal ridges or furrows present, and 5-rayed empodium. If Diptilomiopidae are a monophyletic group supported by the synapomorphies that are characteristic of the gnathosoma of the Diptilomiopidae (Fig. 3.22b, d, e), the position of *Acamina* among the Diptilomiopidae is incorrectly retrieved by the 66tax analyses, except if the characteristics of the gnathosoma in the present data set were reversed in *Acamina*, which is unlikely. This characteristic is complex, and several homoplasious states can be identified from it. There is a possibility that *Acamina nolinae* may have the "typical" Diptilomiopidae gnathosoma. Its gnathosoma is quite robust (Keifer, 1939a), but so is the gnathosoma of some other Phyllocoptinae and Phytoptidae, but additionally on evaluation of the drawing of its gnathosoma (Keifer, 1939a) it may have a diptilomiopid-like gnathosoma. J. W. Amrine Jr. (*pers. comm.*) noted that this may be possible, and if *Acamina* belongs in the Diptilomiopidae, he will place it near *Asetacus madronae*. Another extrapolation from this position of *Acamina* could be that it indicates a close relationship between the Diptilomiopidae and the Phyllocoptinae. *Asetacus* is sister to *Apodiptacus-Acamina* in ***Apodiptacus* group 32b**. The group is also present in the 66tax-k30 (Fig. 4.51) and -k20 (Fig. 4.54) trees, but with a different topology in the –k20 tree.

The ***Apodiptacus* groups (32)** are not present in the 318taxEq and 66taxEq trees, and are not supported by any of the GF values of 50 or above (Figs 4.24, 4.49), or by a GC value of 20 or above (Figs 4.25, 4.50) in the 318tax-k10 and 66tax-k999 trees, respectively.

33.) *Rhyncaphytoptus* groups.

33a.) *Rhyncaphytoptus* group 33a: *Rhyncaphytoptus*, *Rhinophytoptus*, *Peralox* (Rhyncaphytoptinae).

The 318tax-k10 tree: the group (node 569, Fig. 4.20) is supported by three homoplasies: opisthosomal ridges or furrows absent (with a change in *Peralox* to the state "deep cleft behind shield"), and coxisternal plates I and II unornamented. The latter character is presently used for species differentiation. The relationships found between the species in this group are weak, with *Rhyncaphytoptus* sister to *Rhinophytoptus-Peralox*.

33b.) *Rhyncaphytoptus* group 33b: *Rhyncaphytoptus*, *Rhinophytoptus*, *Peralox*, *Rhinotergum*, *Hyborhinus* (Rhyncaphytoptinae).

The 318tax-k20 tree: the group (node 410, Fig. 4.36) is supported by five homoplasies: opisthosomal ridges or furrows absent, coxisternal plates I unornamented (these are two of the three homoplasies supporting ***Rhyncaphytoptus* group 33a**), body elongated fusiform, *1b* in line with *1a*, and *sc* directed divergently anteriad. In the 318tax-k10 tree *Hyborhinus* is sister to and basal to a group at node 393 (Fig. 4.20) consisting of the remainder of the Diptilomiopidae in the data set, except *Rhinotergum*, which is sister to and basal to *Hyborhinus*, and they are not in ***Rhyncaphytoptus* group 33a**.

Only *Rhyncaphytoptus* of the species in the **Rhyncaphytoptus groups (33)** was included in the 66-tax data set. *Rhyncaphytoptus* was not recovered in a group with any particular species in any of the 66tax analyses. The 66tax-k999 tree: it is included in a group (node 92, Fig. 4.45) with most of the Diptilomiopidae in the 66tax data set, and is sister to the remainder of the species in this group, and it is not part of the clade (node 118, Fig. 4.45) with the species sampled from the **"Diptilomiopinae" group (29)** in the 318tax-k10 tree. The 66tax-k30 tree has the same topology for these species. The 66tax-k20 tree: *Rhyncaphytoptus* is not part of a group with most of the Diptilomiopidae, but sister to all the Eriophyoidea in the tree apart from the **Phytoptinae and Sierraphytoptinae and *Pentasetacus*** group outside the larger Eriophyoidea group. The latter is not obviously feasible as a strong hypothesis, but it additionally indicates that the relationships of *Rhyncaphytoptus* with particularly other Diptilomiopidae species are uncertain. It is, however, probably part of a Diptilomiopidae clade in reality, similar to **Diptilomiopidae clade – 318tax trees (27a)** in the preferred 318tax-k10 tree, due to the characteristic and relatively complex gnathosomal morphology.

The ***Rhyncaphytoptus* groups** are not present in the 318taxEq tree (Fig. 4.5), and were not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree. Only *Rhyncaphytoptus* of the ***Rhyncaphytoptus* groups**' species were included in the 66tax data set (Table 4.1), and the robustness of the groups was thus not tested in the 66tax analyses. *Rhyncaphytoptus* and *Rhinophytoptus* were the only and all Rhyncaphytoptinae included in the 18tax

data sets. In the 18tax trees (Figs 4.55, 4.57, 4.58, 4.59, 4.60, 4.62) the relationship between *Rhyncaphytoptus* and *Rhinophytoptus* was not conclusive, but they are always part of a **Diptilomiopidae clade or group (27)** which includes the two Rhyncaphytoptinae species, and two Diptilomiopinae species.

With all evidence at hand it seems that the ***Rhyncaphytoptus* groups** are not well-supported and robust. *Rhyncaphytoptus*, which is part of these groups, is the type genus of the Rhyncaphytoptinae Roivainen, 1953 (Newkirk & Keifer, 1971), though, and I propose that it may eventually be part of a monophyletic group of species of which most are currently in the Rhyncaphytoptinae and some of the species in the Diptilomiopinae, such as *Bucculacus*. This group will probably exclude Rhyncaphytoptinae species that may eventually turn out to belong to other monophyletic groups, of which some possibly may correspond with e.g., the ***Cheiracus* groups (30)**, **Long-tibia groups (31)** and the ***Apodiptacus* groups (32).**

IV. Groups and clades within the "Diptilomiopinae" group (29) (Part 2a; Figs 4.19, 4.21, 4.22, 4.23)

34.) One-Diptilomiopinae group: *Diptilostatus*, *Thailandus*, *Prodiptilomiopus*, *Neorhynacus*, *Neoacarhis*, *Davisella*, *Acarhis lepisanthes*, *A. diospyrosis* (Diptilomiopinae); and the three species of ***Lithocarus* group (35)** which will be discussed later – *Mediugum*, *Lithocarus*, *A. siamensis* (Diptilomiopinae).

This group occurs in the 318tax-k10 (Figs 4.21, 4.22) and -k20 (Fig. 4.37) trees, but with different topologies. The 318tax-k10 tree: *Diptilostatus*, the remainder of the **One-Diptilomiopinae group**, and other **"Diptilomiopinae"group** species, are in one group (node 383, Fig. 4.21) supported by three homoplasies: prodorsal shield broadly oval, opisthosoma with dorsal annuli slightly longer than ventral annuli, and 5-rayed empodium I. The latter characteristic, particularly, is regarded as a species level character for the Eriophyoidea. **One-Diptilomiopinae group** (node 382, Fig. 4.21) is supported by one homoplasy: *c2* absent. Seta *c2* is absent in all species of this group, except *Diptilostatus*. Four species, including *Diptilostatus*, are at the base of the **One-Diptilomiopinae group** as well as the **"Diptilomiopinae" group (29)**. These are sister and basal to each other in the order: *Diptilostatus*, *Neorhynacus*, *Davisella*, and *Neoacarhis aglaiae* (Fig. 4.21). The remaining seven species of **One-Diptilomiopinae group** were recovered as a group (node 378, Fig. 4.22) supported by one homoplasy: *l''* on genu I absent. The latter group consists of two groups, namely ***Lithocarus* group (35)** (to be discussed further on); and *Thailandus* and *A. diospyrosae*, retrieved as sisters (node 375, Fig. 4.22) supported by two homoplasies: *sc* directed divergingly posteriad, and 6-rayed empodium I.

The 318tax-k20 tree: the group, and its subgroups, are also present in this tree (Fig. 4.37), but with a different topology. The topologies differ as follows: *Diptilostatus*, the remainder of the **One-Diptilomiopinae group** and the other **"Diptilomiopinae"group** species, were recovered as a group (node 343, Fig. 4.37), supported by three homoplasies: *l'* absent, prodorsal shield broadly oval, and frontal lobe absent. **One-Diptilomiopinae group** (except *Diptilostatus*) (node 342, Fig. 4.37) is supported by four homoplasies: *c2*, and *l''* on genu I, absent, and coxisternal plates I and II unornamented. The absence of *c2* may be one of the more important characteristics supporting this group, similar to the support of node 382 (Fig. 4.21) in the 318tax-k10 tree. Relationships between the species in the **One-Diptilomiopinae group** (except *Diptilostatus*) are unresolved, as well as the relationship between this group of species and the larger group at node 378, to which they are sister. *Diptilomiopus ervatamiae* was recovered together with the One-Diptilomiopidae species in this unresolved group, but in the present study the recovery of this species as part of the ***Africus* clade (38a)** (discussed further on) in the preferred 318tax-k10 tree, is favored.

The species of the **One-Diptilomiopinae group**, except *Davisella* and *Diptilostatus*, are from the Oriental Region (Taiwan, Thailand and India), and are morphologically similar, including similar body shapes, and broadly similar dorsal shield patterns. *Diptilostatus* and *Davisella*, more basal in the **One-Diptilomiopinae group**, are morphologically less similar, and a close relationship between them and the other species of the group is not particularly supported by their recovered positions within the group. Particularly *Diptilostatus*, with *c2* present, might eventually rather belong to the **"Rhyncaphytoptinae" part (28)**.

The sister relationship recovered between *Thailandus* and *A. diospyrosae* is feasible. *Acarhis diospyrosae* is wrongly placed in *Acarhis*, and may belong to *Thailandus*. Both species were collected in Thailand and are vagrants on the leaf under-surfaces of *Diospyros gracilis* (Chandrapatya & Boczek, 1997b) and *D. rhodacalyx* (Chandrapatya & Boczek, 1991c), respectively. They are morphologically similar, but must be re-examined due to unclear species descriptions with various mistakes, before their classification can be determined.

35.) ***Lithocarus* group:** *Lithocarus*, *Mediugum*, *Acarhis siamensis* (Diptilomiopinae).

This group is present in the 318taxEq (Fig. 4.5) and -k10 (Fig. 4.22) trees, but not in the 318tax-k20 tree. In the latter tree the species are part of the polytomy of **One-Diptilomiopinae group (34)** species (Fig. 4.37). The three species were not included in the 66tax and 18tax data sets.

The 318tax-k10 tree: the group (node 396, Fig. 4.22) is supported by four homoplasies: genu fused with femur in legs I and II, dorsal annuli with microtubercles only on ridges, and tibia shorter than half tarsus length. Although the latter can be quite subjective, these are relatively reliable characteristics.

The 318taxEq tree: the group (node 324, Fig. 4.5, Group E16) is supported by 19 homoplasies. The homoplasies include the four homoplasies supporting the group in the 318tax-k10 tree. The additional homoplasies include characters that are of importance at family and subfamily level: long form oral stylet, chelicerae abruptly bent down at the base (Fig. 3.22b, d, e), and divided empodium (Fig. 3.6h); at genus level: *c2* and its tubercle absent, and *bv* and *l''* absent on legs I and II; and normally differentiating species: *sc* short and short in relation to prodorsal shield length, coxisternal plates I and II unornamented, anterior coxae separated, 7-rayed empodium, and the prodorsal shield broadly oval. The relationships of this group with other eriophyoid taxa are not resolved in this tree.

This group is feasible. Its three species are morphologically similar, in particular, the genu is fused with the femur in legs I and II, and dorsally they have three longitudinal ridges, with microtubercles only present on the ridges. These detailed characteristics of the shape of the opisthosomal ridges were not included in the data set. *Acarhis siamensis* should not be in *Acarhis*, because its genu is fused with the femur in both legs I and II, while the genu is present in legs I and II in *Acarhis*. *Acarhis siamensis* keys out near *Acarhis* and/or *Suthamus* in the key of Amrine *et al*. (2003). Close relationships were not found between *A. siamensis* and the other two *Acarhis* spp. in the data set, although all three *Acarhis* spp. are part of the **One-Diptilomiopinae group (34)**. The absence of *l'* in *Mediugum* and *Lithocarus*, and its presence in *A. siamensis*, and the absence of *e* in *Mediugum*, are the most important morphological difference between them. The three species are leaf vagrants, and occur in the Oriental Region (Boczek & Chandrapatya, 2000; Chandrapatya & Boczek, 2000c; Huang, 2001d).

36.) *Dacundiopus* clade: *Dacundiopus*, *Lambella*, *Levonga papaitongensis* (Diptilomiopinae). This clade was recovered in the 318taxEq (Fig. 4.5) and 318tax-k10 (Fig. 4.21) trees, but not in the 318tax-k20 tree where they are part of a polytomy consisting mostly of *Diptilomiopus* spp. (Fig. 4.38). The three species were not included in the 66tax and 18tax data sets.

The 318taxEq tree: the clade (node 332, Fig. 4.5) is supported by one synapomorphy – the tarsus with two segments, and 15 homoplasies. Three of the homoplasies are characteristics placing them in the Diptilomiopidae and Diptilomiopinae. One homoplasy concerns their more vagrant bodies: dorsal annuli longer than the ventral annuli. The remainder of the homoplasies are coxae I being fused, and setal characters: *sc* present, directed anteriad, either parallel or convergent, *c2* and *1b*, as well as their tubercles absent, and *bv* on legs I and II, *l'* on leg I and *l''* on leg II absent. The relationships of this clade with other eriophyoid species and groups in this tree are unresolved. The 318tax-k10 tree: the clade (node 509, Fig. 4.21) is supported by the same synapomorphy as in the 318taxEq tree: tarsus with two segments. It is additionally supported by two homoplasies: *sc* present, and prodorsal shield sub-rectangular. The shield shape is an ambiguous character, scored on subjective interpretation. The clade

is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

The three species in the ***Dacundiopus*** **clade** were described from New Zealand by Manson (1984a). *Dacundiopus* and *Lambella* are monospecific, and *Levonga* has six species (Amrine *et al.*, 2003). The tarsus of five *Levonga* spp. (apart from the type species *Levonga papaitongensis*), is not divided into two segments, and some previously belonged to the genus *Pseudodiptacus* Chakrabarti *et al*., 1992. *Pseudodiptacus* has been assigned as a junior synonym of *Levonga* (Amrine *et al*., 2003). Three *Levonga* spp. have been included in the present study (Table 4.1) and only *Levonga papaitongensis*, with the tarsus divided into two segments, is part of the ***Dacundiopus*** **clade**. The tarsi may not be divided in reality, because sometimes in eriophyoid species it seems that the tarsus is divided because it has a deep indentation below *ft*. In the three ***Dacundiopus*** **clade** species, however, the tarsi may indeed be divided, because enlargements of the divided tarsi were included. Nevertheless, specimens of these taxa should be re-examined to confirm the characteristic. Specimens could not be obtained for the present study.

These results from the present study supports the close relationship between *Dacundiopus*, *Levonga* and *Lambella* (and *Pseudodiptacus*) found in the phylogenetic study of the Diptilomiopinae by Hong & Zhang (1997). Although their ingroup taxa were genera, and not exemplar species, they probably scored the characteristics of *Levonga* only from the type species, *L. papaitongensis*.

37.) Separate-coxae group: *Levonga litseae*, *Diptilomiopus guajavae*, *D. thangaveli* (Diptilomiopinae).

This group is present in the 318tax-k10 (node 537, Fig. 4.21) and -k20 (node 404, Fig. 4.39) trees. It is not present in the 318taxEq tree, and none of the species were included in the 66tax and 18tax data sets.

The 318tax-k10 tree: the group (node 537, Fig. 4.21) is supported by two homoplasies: *ft'* on tarsus II absent, and dorsal annuli with microtubercles. *Norma* is sister to the group. The 318tax-k20 tree: the group (node 404, Fig. 4.39) is supported by six homoplasies: genu present, and not fused with femur in legs I and II, *l''* on genu I present (change to genu fused with femur in legs I and II, and *l''* absent in *Diptilomiopus*), opisthosoma evenly rounded without ridges or furrows, dorsal annuli with microtubercles, and coxae I separated.

The recovered close relationships between these three species are not strongly supported, but they are morphologically similar, and the close relationship with each other and not with other *Diptilomiopus* spp. and/or *Levonga* spp., is feasible. *Diptilomiopus thangaveli* and *D. guajavae* do not belong in *Diptilomiopus* as the genus is currently diagnosed. The genu of legs I and II, and *l''* on genu I are

present in *D. thangaveli* (Mohanasundaram, 1983c). This species keys out to be *Vimola* in the key by Amrine *et al.* (2003). The description of *D. guajavae* is flawed. Mohanasundaram (1985) described the species as having a tibiotarsus in legs I and II (tibia fused with tarsus), but this is not likely, and in the drawing it seems that rather the genu is absent. If the latter is the case, *l'* is present in this species according to the descriptive drawing (*l'* is not present in *Diptilomiopus*). Apart from these ambiguities, there are also other inconsistencies in the description that need to be clarified. *Levonga litseae* previously belonged to *Pseudodiptacus*, but *Pseudodiptacus* was made a junior synonym of *Levonga* by Amrine & Stasny (1996) without an explanation. *Levonga litseae* keys out to be *Levonga* in the key by Amrine *et al.* (2003), but differs from the type species of *Levonga*, *L. papaitongensis*, among other characteristics, by having an entire and not a divided tarsus. It is proposed that close relationships between the species in the separated-coxae group, as well as between them and *Vimola* may exist.

38.) *Africus* group and clade.

38a.) *Africus* clade: *Africus*, *D. ervatamiae*, *Neodiptilomiopus* (Diptilomiopinae).

The 318tax-k10 tree: the clade (node 453, Fig. 4.23) is supported by one synapomorphy: *1a* absent. *Africus* and *Neodiptilomiopus* were recovered as sisters (node 452, Fig. 4.23), supported by two homoplasies: setal tubercle of *1a* absent (which is present in *D. ervatamiae*), and 5-rayed empodium I.

Africus is a monospecific genus described from South Africa (Meyer & Ueckermann, 1995) and *Neodiptilomiopus* is a monospecific genus described from India (Mohanasundaram, 1982b). They are morphologically broadly (particularly in shape, dorsal shield pattern, coxisternal plates and genital coverflap) similar, but have many differences, which are of importance at genus level, particularly in the legs and leg segments. *Diptilomiopus ervatamiae*, described from Thailand (Chandrapatya & Boczek, 1991a) does not belong in *Diptilomiopus*, particularly due to the presence of *1b* and absence of *1a*, but with the setal tubercles of *1a* present. With the traditionally accepted genus differentiations in the Eriophyoidea (Amrine *et al*., 2003) *D. ervatamiae* would probably be placed in a new genus. *Diptilomipus ervatamiae* is not morphologically particularly similar to either *Africus* or *Neodiptilomiopus*. The recovery of these three species in a clade is a relatively strong hypothesis in the present study, though, because it is supported by a synapomorphy in the preferred 318tax-k10 tree. Although the clade is feasible, it should be investigated further.

38b.) *Africus* group: *Africus*, *D. knorri* (Diptilomiopinae).

***Africus* clade (38a)** was not retrieved by the 318taxEq and –k20 analyses, where *Africus* was recovered as a sister to *D. knorri*. The 318taxEq tree: the group (node 326, Fig. 4.5) is supported by 20 homoplasies, which is a relatively high number of supportive homoplasies for one group in the present study. The most relevant (also excluding those characteristics supporting their placement in the Diptilomiopidae and Diptilomiopinae), are the absence of a suite of setae: palp *d*, *c2*, *1b*, *bv* and *l''* in

legs I and II, *l'*, and *ft'* on tarsus II, of which most traditionally position them in relatively close relationship with other *Diptilomiopus* spp. and with other species in the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. Additionally the homoplasies include: prodorsal shield broadly oval, coxisternal plates II ornamented, coxae I separated, and genital coverflap ornamented basally. The most important homoplasy is probably: genu partially, and not completely, fused with femur in legs I and II. The 318tax-k20 tree: the group (node 377, Fig. 4.39) is supported by six homoplasies, of which five is also supporting it in the 318taxEq tree: palp *d* absent, coxae I separated, genital coverflap ornamented basally, partial fusion of genu and femur of legs I and II, and additionally (not supporting the group in 318taxEq tree), 5-rayed empodium. *Diptilomiopus knorri* was described from Thailand.

The ***Africus* clade (38a)** and **group (38b)** found in the present study which includes *Africus*, were not found by Hong & Zhang (1997), possibly because they included the genus *Diptilomiopus* in their taxon sample and did not include individual *Diptilomiopus* spp. as was done in the present study. In their study *Africus* and *Diptilomiopus* were found to be positioned relatively close to each other in the same group which also included taxa which are in the ***Dacundiopus* clade (36)** of the present study. This result is not supported in the present study. In their study, however, *Neodiptilomiopus* was found to be sister to the group which includes *Africus* and *Diptilomiopus* and the close relationships between *Africus*, *Diptilomiopus* and *Neodiptilomiopus* found in the present study, support this relationship.

39.) SA *Diptilomiopus* group: *D. apobrevis* sp. nov., *D. apolongus* sp. nov., *D. faurius* sp. nov. (Diptilomiopinae, *Diptilomiopus*).

The three *Diptilomiopus* spp. from South Africa (SA) (Appendix M) were recovered as a group in all the 318tax trees, including the tree obtained under equal character weights. The group was also relatively strongly supported, in comparison with other eriophyoid groups found in the present study, by many homoplasies, and is supported by a GF value of 56 (Fig. 4.24), and a GC value of 52 (Fig. 4.25) in the 318tax-k10 tree. They were not included in the 66tax and 18tax analyses for additional testing of the robustness of the group.

The 318taxEq tree (Fig. 4.5): the group is part of the large Eriophyoidea clade (Fig. 4.4) at node 337 (Fig. 4.5), and is supported by 26 homoplasies. Some of these homoplasies are those characteristics supporting the suprageneric and generic placement of the three species: Diptilomiopidae (gnathosoma with long form oral stylet, with chelicerae relatively long and bent down at the base), Diptilomiopinae (empodium divided) and *Diptilomiopus* (*sc*, *c2*, *1b* and its setal tubercle, *bv*, *l''* on legs I and II, and *l'* absent, genu fused to femur in legs I and II). The other homoplasies are additional character states from the suite of characteristics differentiating *Diptilomiopus* spp., and some of these states are ambiguously described for *Diptilomiopus* spp. in general (see discussion below). The relationships of **SA *Diptilomiopus* group** with other eriophyoid species, groups and clades are unresolved in this tree.

The 318tax-k10 tree: the group (node 543, Fig. 4.23) is supported by four homoplasies: palp *d* absent, frontal lobe present, microtubercles on dorsal annuli absent in a central band, and 7-rayed empodium. The group is included in a group (node 454, Fig. 4.23) which largely consists of *Diptilomiopus* and some other Diptilomiopinae species. The relationships of the **SA *Diptilomiopus* group** with the other species and groups in this larger group are unresolved.

The 318tax-k20 tree (Fig. 4.35): the group (node 406, Fig. 4.39) is in a similar position than in the 318tax-k10 tree, supported by seven homoplasies including the four homoplasies supporting the group in the 318tax-k10 tree, and additionally: *h1* minute, frontal lobe anterior edge square with rounded corners, and genital coverflap ornamented basally. Apart from the genital coverflap ornamentation, the homoplasies which are supporting the 318tax-k10 and –k20 trees are also part of the series of homoplasies supporting the group in the 318taxEq tree, and particularly those that are species specific and which are probably ambiguous, as mentioned.

The closer relationship between the South African *Diptilomiopus* spp., which are the first *Diptilomiopus* spp. described from southern Africa, than their relationship with other *Diptilomiopus* spp. in the analyses, was not expected *a priori*. They were not morphologically clearly different from the remainder of most *Diptilomiopus* spp. when compared manually. The group might have been recovered and is relatively strongly supported, because some characters were described accurately for these three species in contrast to many other *Diptilomiopus* spp. in which these particular characters are frequently not described, thus scored "unknown" (e.g., the presence or absence of *ft'* and palp *d* which is not usually noted or described), or structures may be scored as absent, when they are actually present, or they may be described erroneously (e.g., the presence and shape of the frontal lobe, and a minute *h1*, which is hard to detect in slide-mounted specimens) (C. Craemer, *unpubl. data*). Seta *ft'* on tarsus II and palp *d* are absent, and *h1* is minute in the SA spp. The frontal lobe, which might have been wrongly recorded as absent in many *Diptilomiopus* spp., because it is so difficult to detect in slide-mounted specimens, is present in the SA species, and is thin and flexible, and the anterior edge is square with rounded corners. The description of the shape of the prodorsal shield was scored as broadly oval in the SA spp., but other shapes were also, subjectively, recorded for *Diptilomiopus* spp. These differences may be due to distortion of slide-mounted specimens, inaccurate drawings, and different subjective interpretations, and are ambiguous. The SA spp. have a 7-rayed empodium, but the number of empodial rays recorded for *Diptilomiopus* spp. is ambiguous, because it is difficult to count the empodial rays in slide-mounted specimens, since the rays are skew, and are partly overlapping (Chapter 4). Additionally, the number of empodial rays was not recorded for many *Diptilomiopus* spp. The remaining two species' characteristics supporting **SA *Diptilomiopus* group** are: microtubercles on dorsal annuli absent in a central band, and coxisternal plates II ornamented. Adding more species

specific characters to the data set, e.g., the prodorsal shield ornamentation, which has been done in a parallel study to the present study (C. Craemer, *unpubl. data*), improves the phylogenetic phylogenetic resolution and the reliability of clades and groups found in *Diptilomiopus*.

40.) **66-Diptilomiopinae clade:** *Rhynacus*, *Neorhynacus*, *Diptilomiopus averrhoae*, *D. assamica*, *D. jevremovici* (Diptilomiopidae: Diptilomiopinae).

These species, sampled as exemplar species from the **"Diptilomiopinae" group (29)** of the 318tax trees and included in the 66tax data set, were recovered as a clade (**66-Diptilomiopinae clade**). This clade is present in all the presented 66tax trees, and it supports the **"Diptilomipinae" group**.

The 66taxEq tree: the clade (node 75, Fig. 4.42) is supported by two synapomorphies, *c2* and its setal tubercle absent, and by three homoplasies: *l''* on genu II absent, tibia shorter than tarsus, but half or more of tarsus length, and empodium divided. The 66tax-k999 and –k30 trees: the clade (node 118, Figs 4.45 and 4.51, respectively) is supported by the same synapomorphies and homoplasies as in the 66taxEq tree, but the homoplasy, tibia shorter than the tarsus, is here replaced by the homoplasy *h1* minute. The 66tax-k20 tree: the clade is supported by the two synapomorphies supporting the clade in the other trees, and by homoplasies.

The phylogenetic phylogenetic resolution and topology within the clade is the same in all the 66tax trees, and the recovered groups are supported by the same synapomorphies and homoplasies. The relationships, with the 66tax-k999 tree as example, follow. *Diptilomiopus assamica* and *D. jevremovici* were recovered as a group (node 115, Fig. 4.45) supported by the synapomorphy, *ft'* absent on tarsus II, and by two homoplasies: coxisternal plates II ornamented, and prodorsal shield subtriangular. The homoplasies are characters used at the species level. Particularly the shape of the prodorsal shield is ambiguous in many descriptions, and prone to distortion by slide-mounting. *Diptilomiopus averrhoae* is sister to the *D. assamica-D. jevremovici* group, and this three-taxon clade is at node 116 (Fig. 4.45) supported by two synapomorphies, the genu fused to the femur in legs I and II, and by three homoplasies: *l''* on genu I, and *l'* absent, and dorsal annuli without microtubercles. *Neorhynacus* is sister to this clade at node 117 (Fig. 4.45) supported by two homoplasies: *sc* ahead of rear shield margin, and coxisternal plates I ornamented. *Rhynacus* is sister basally to *Neorhynacus*. *Neorhynacus* and *Rhynacus* were not recovered as a group or clade at one node and *Neorhynacus* is more closely related to the *Diptilomiopus* spp. than *Rhynacus*. Morphologically *Neorhynacus* is more similar to most *Diptilomiopus* spp. than *Rhynacus*, particularly the dorsal shield ornamentation.

4.6 RESULTS AND DISCUSSION: TWO MONOSPECIFIC GENERA WRONGLY CLASSIFIED

The analyses in the present study retrieved many relationships and placements of species that either confirmed doubts about their placement, wrong interpretation of structures, or "pointed out" species wrongly placed by error in the current classification. Two of the most certain and important are:

41.) *Prothrix aboula*

Amrine (1996) placed *P. aboula* in a new monospecific subfamily, Prothricinae (Phytoptidae), based on the presence of paired *vi* in addition to *ve* in *P. aboula*. When *vi* is present in other eriophyoid species, single *vi* is present in a mid-dorsal position. Due to the inclusion of *Prothrix* (Prothricinae) in the **Dorsal-rear-fused clade (7)**) together with sierraphytoptine species with single and paired *vi* absent, but a pair of *ve* present, *Prothrix* should be in the Sierraphytoptinae. The presumed pair of *vi* in *Prothrix* seems to be rather *sc* that moved far forward, as originally proposed by Keifer (1965a) when he described this species. Sierraphytoptinae contain species with and without *sc*. Prothricinae is thus a junior synonym of the Sierraphytoptinae (**new synonymy**). In future data sets for cladistic analyses, the absence of paired *vi* and presence of *sc* in a far forward position should be coded for this species and this may strengthen the support for the **Dorsal-rear-fused clade (7)**, and possibly even a closer and more robust relationship between this clade and the other sierraphytoptine species.

42.) *Palmiphytoptus oculatus*

Palmiphytoptus oculatus was tentatively placed in the Mackiellini of the Sierraphytoptinae by Navia & Flechtmann (2002), based on the presence of *ve* anteriorly on the prodorsum. They hypothesized that the genus belongs in the Phytoptidae, but regarded it as being similar to the Phytoptinae, as well as the Sierraphytoptinae. This species was included only in the 318tax data set. It was not found to have a close relationship with Phytoptidae taxa. It was in a group deeply imbedded in a large group of Eriophyidae taxa from various subfamilies and tribes. The 318tax-k10 tree: it was found to be sister to a *Cisaberoptus* group (node 500, Fig. 4.18), weakly supported by two homoplasies: minute *h1*, and frontal lobe present. This group is also in the 318tax-k20 tree, but it is not supported by the symmetric resampling values (Figs 4.24, 4.25). The relationship of *Palmiphytoptus* with other eriophyoid taxa is highly uncertain, and not resolved by the present analyses, but it does not seem to belong in the Phytoptidae. This supports the suggestion by Amrine *et al.* (2003) that *Palmiphytoptus* may belong to the Eriophyidae, and may possibly be an *Eriophyes* sp., and that the setae proposed to be *ve* by Navia & Flechtmann (2002) may be *sc* displaced far forward. *Palmiphytoptus* is re-assigned to the Eriophyinae.

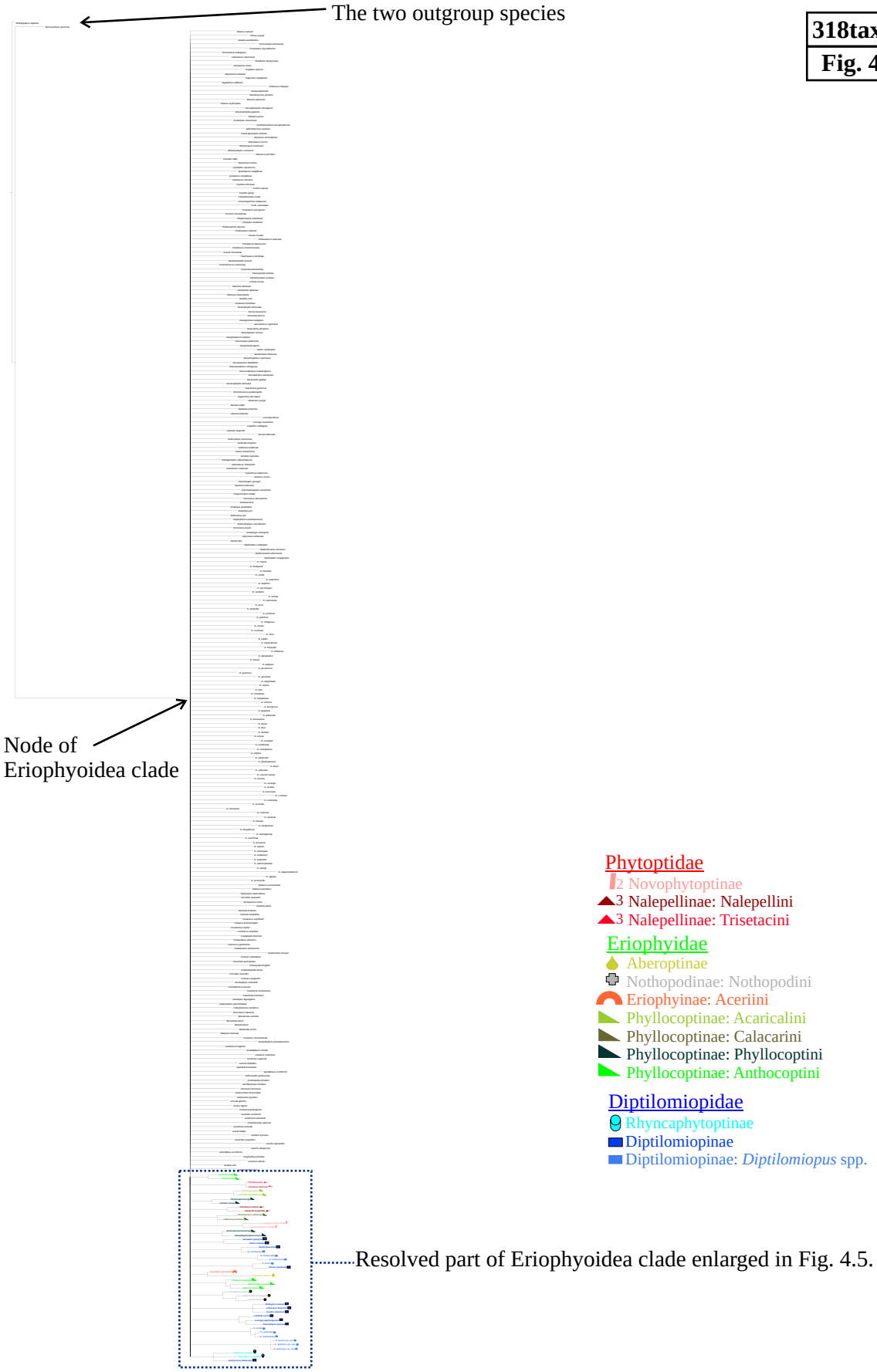


Fig. 4.4. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under equal weighting of characters in TNT: entire tree presented to show topology, and it is a metric tree. Total fit = 57.71; Adjusted homoplasy = 72.29; Total length = 5396; CI = 0.056; RI = 0.086. Uninformative characters included. Tree searched in and tree presented from TNT. Tree name is 318taxEq tree. Resolved part of Eriophyoidea clade enlarged in Fig. 4.5. The key to the classification of the terminal species is also applicable to Fig. 4.5.

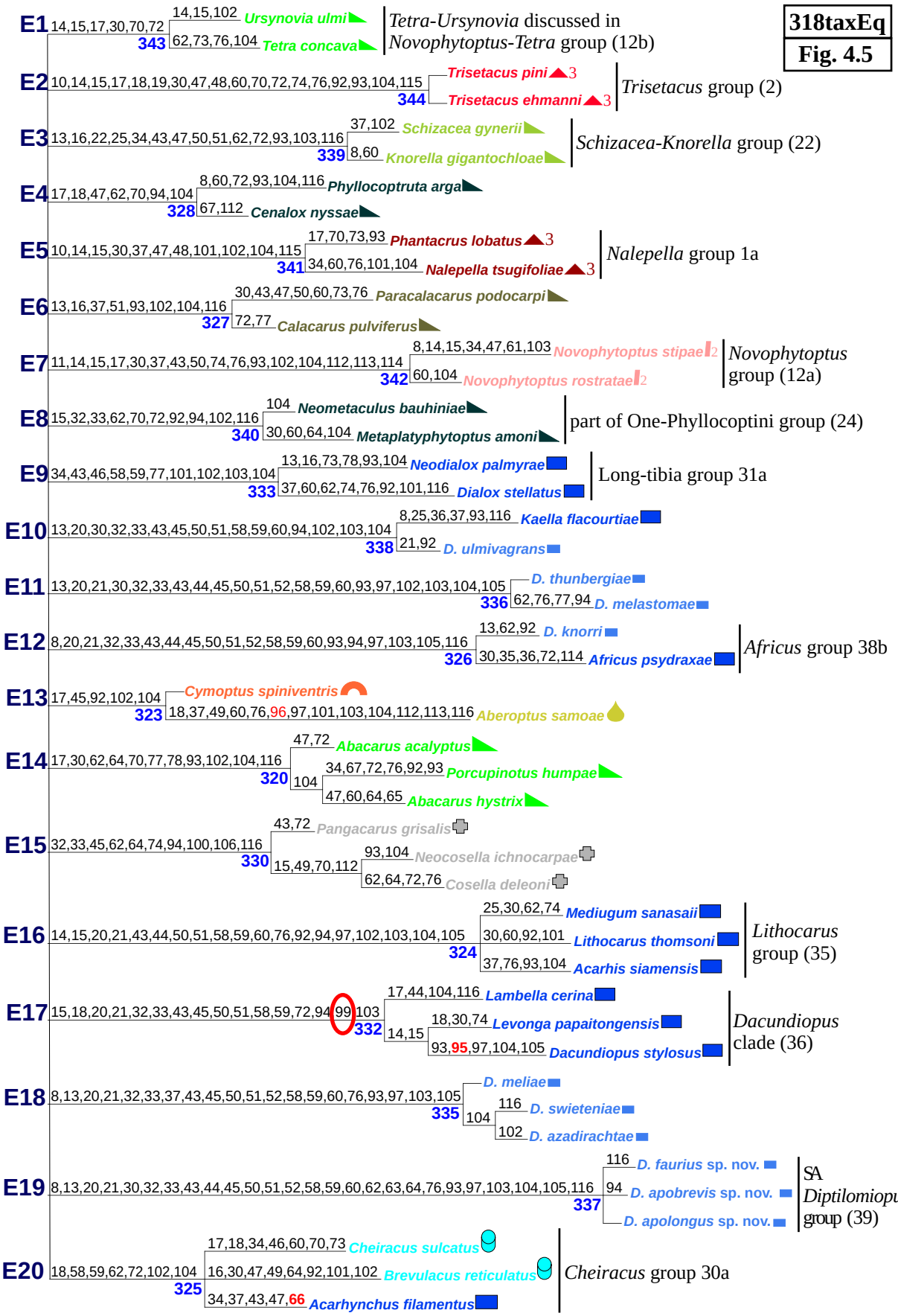


Fig. 4.5. Estimated consensus tree found with the analysis of the 318-taxon data matrix under equal weighting of characters in TNT (318taxEq tree, Fig. 4.4): enlarged resolved part of the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes, and those in red on terminal branches are autapomorphies. Blue numbers underneath the branches close to the nodes are the node numbers from TNT. Key to colours of and corresponding symbols following species names providing taxonomic classification are given in Fig. 4.4. Blue E-numbers on the left are reference numbers for groups found in tree, for indication of groups on other trees. Informal names of groups discussed in text are on the right.

Table 4.7. Character consistency indices (ci) and character retention indices (ri) of characters of the estimated consensus tree, found in TNT, of the 318 taxon data matrix under equal character weighting (Fig. 4.3, 4.4.). The indices in light grey are of characters which are uninformative regarding the relationships between ingroup taxa because they are autapomorphic for the Eriophyoidea, or the same for all taxa in the analysis (Characters 7 and 41), the indices within a block with a grey background are those of characters autapomorphic for a terminal ingroup taxon, and the indices in bold and in a block with thickened edges, are of homologous characters.

Character consistency indices (ci)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.108	1.000
10	0.250	0.063	1.000	0.009	0.096	0.048	0.063	0.019	0.051	0.077
20	0.010	0.020	0.063	--	1.000	0.050	--	1.000	1.000	1.000
30	0.013	1.000	0.009	0.018	0.034	0.333	0.600	0.045	0.500	1.000
40	1.000	--	--	0.007	0.011	0.008	0.222	0.063	0.154	0.417
50	0.008	0.008	0.018	1.000	1.000	--	1.000	0.500	0.008	0.015
60	0.093	0.500	0.019	0.080	0.094	0.571	--	0.070	1.000	1.000
70	0.065	1.000	0.043	0.099	0.052	0.400	0.091	0.083	0.313	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.020	0.026	0.063	1.000	--	0.037	--	**1.000**
100	0.222	0.109	0.039	0.079	0.035	0.024	0.200	1.000	1.000	1.000
110	--	--	0.111	0.118	0.167	0.286	0.027			

Character retention indices (ri)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.132	1.000
10	0.250	0.118	1.000	0.066	0.190	0.123	0.063	0.063	0.043	0.143
20	0.099	0.100	0.063	--	1.000	0.050	--	1.000	1.000	1.000
30	0.068	1.000	0.097	0.104	0.026	0.000	0.333	0.056	0.000	1.000
40	1.000	--	--	0.092	0.064	0.084	0.125	0.043	0.154	0.125
50	0.096	0.098	0.098	1.000	1.000	--	1.000	0.000	0.097	0.097
60	0.062	0.000	0.060	0.080	0.040	0.000	--	0.019	1.000	1.000
70	0.048	1.000	0.048	0.000	0.044	0.250	0.048	0.120	0.083	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.034	0.075	0.129	1.000	--	0.092	--	**1.000**
100	0.222	0.197	0.082	0.092	0.114	0.090	0.200	1.000	1.000	1.000
110	--	--	0.111	0.063	0.091	0.286	0.045			

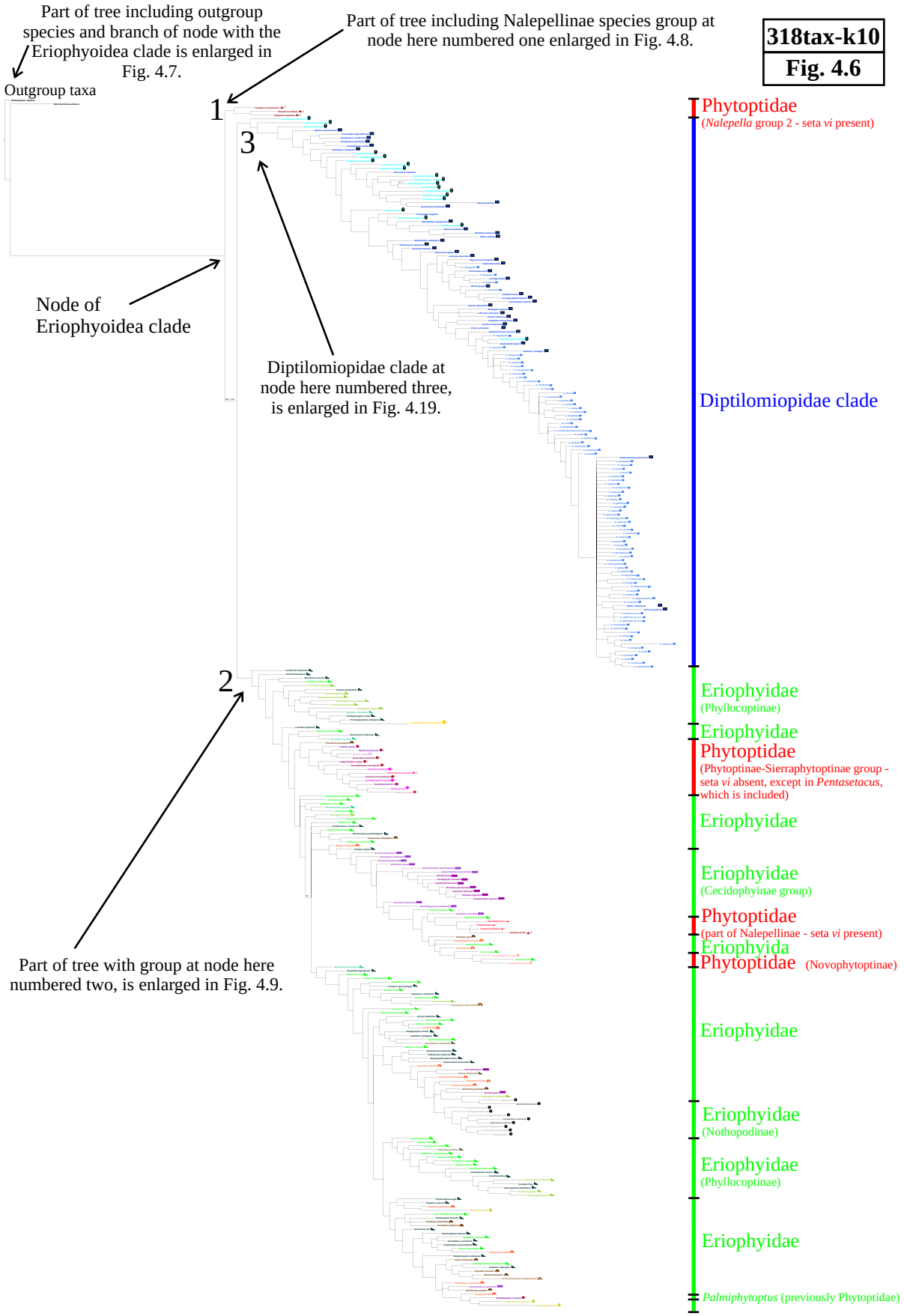


Fig. 4.6. Caption on next page.

318tax-k10
Fig. 4.7

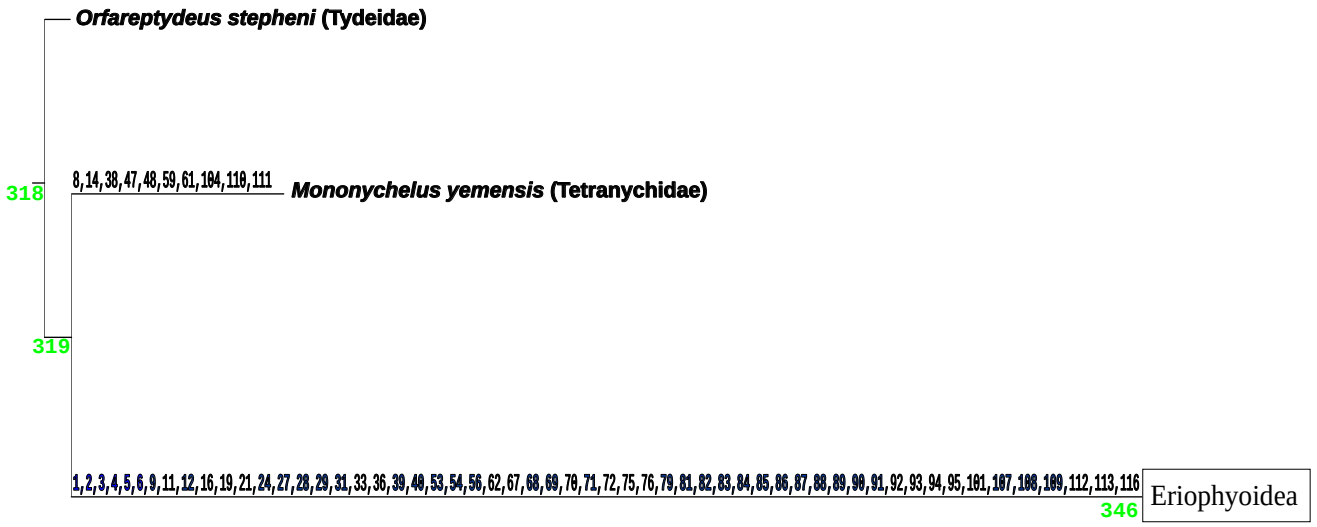
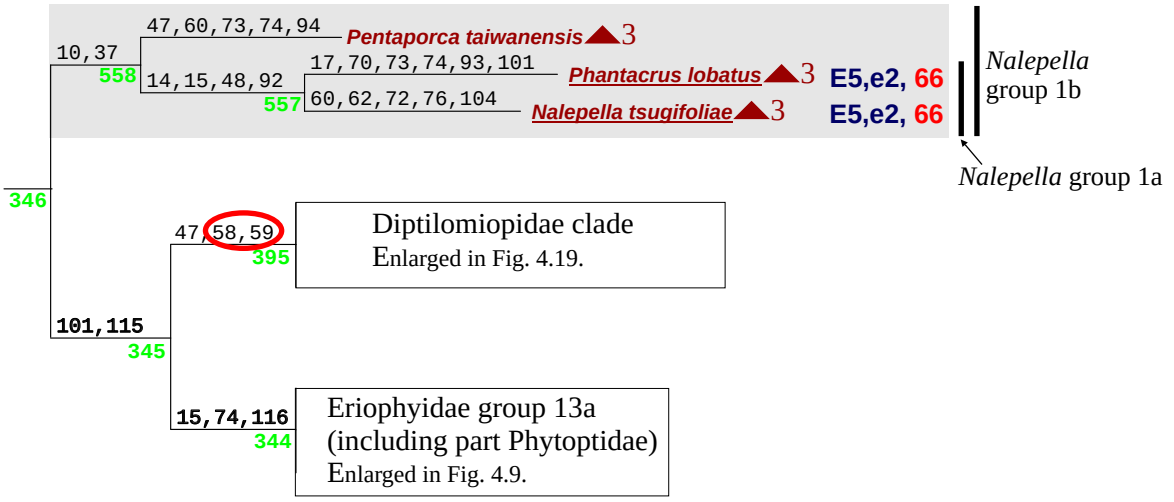


Fig. 4.6. (previous page). Strict consensus (Total fit = 72.29; Adjusted homoplasy = 57.71; Total length = 2402; CI = 0.125; RI = 0.623; Nodes = 255) of 32 most parsimonious trees (each - Total fit = 72.36; Adjusted homoplasy = 57.64; Total length = 2347; CI = 0.128; RI = 0.633; Nodes = 316) found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, with the best score hit 10 times, under implied weighting of characters with k=10. Uninformative characters were included. Unsupported branches were not collapsed. The entire tree is presented to show topology, and it is a metric tree. Tree presented from TNT. The tree name is 318tax-k10 tree. The bar on the right hand side indicate families and some notes on broad groups and clades. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between them, it doesn't always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node. The tree is divided into four parts, which are enlarged in Figs 4.7, 4.8, 4.9 and 4.19.

Fig. 4.7. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree including outgroup species and branch of node with the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies or homoplasious characters supporting the nodes, and those on the branch supporting node 346 (Eriophyoidea clade) in bold and dark blue are autapomorphies for the Eriophyoidea. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

318tax-k10
Fig. 4.8



▲3 Phytoptidae: Nalepellinae: Nalepellini

Node 558 :
setae vi (10): absent (2) --> one seta mid-anterior (1)
setae *1a* vs setae *2a* (37): ahead (0) –> slightly ahead (1)

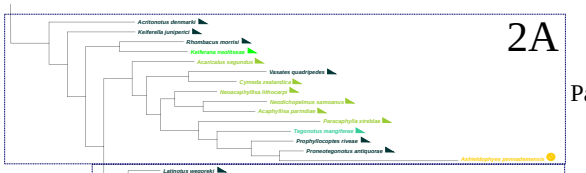
Node 345 :
leg 1 tibia length (101): very long (6) --> long (5)
spermathecal tubes (115): long (2) --> short (1)

Node 395 :
leg tibia 1 setae *l'* vertical position (47): distal third --> basal third
oral stylet (58): short form –> long form
chelicerae (59): short straight --> long bent

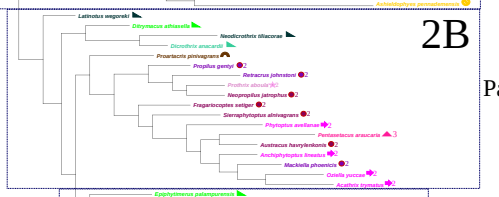
Node 344 :
sc length : prodorsal shield length (15): average length (3) --> short (4)
opisthosomal ridges or furrows (74): absent (0) --> present (1)
genital coverflap (116): smooth (1) --> ornamented basal distal area (5)

Fig. 4.8. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree including Nalepellinae species group at node numbered one in Fig. 4.6. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

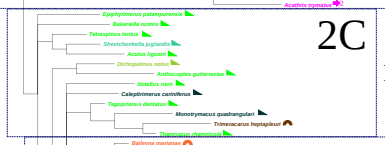
318tax-k10
Fig. 4.9



Part 2A is enlarged in Fig. 4.10.

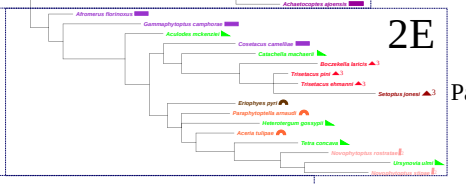


Part 2B is enlarged in Fig. 4.11.

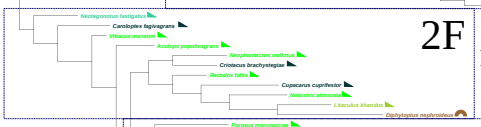


Part 2C is enlarged in Fig. 4.12.

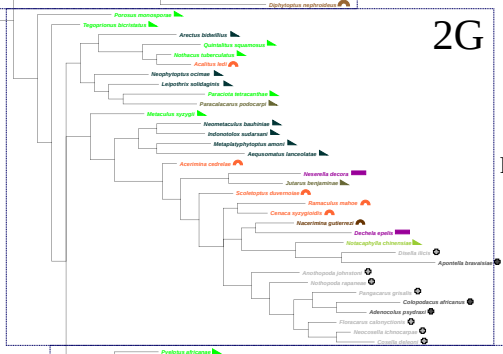
Part 2D is enlarged in Fig. 4.13.



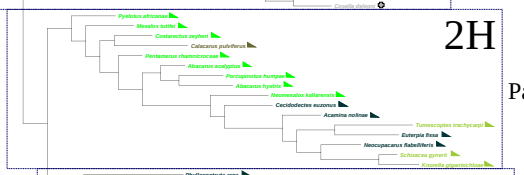
Part 2E is enlarged in Fig. 4.14.



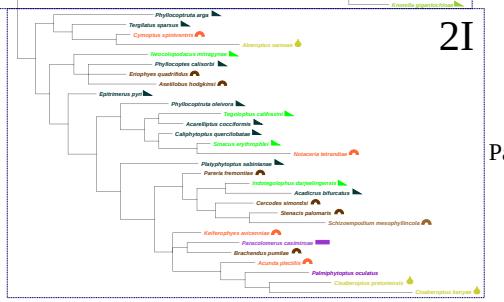
Part 2F is enlarged in Fig. 4.15.



Part 2G is enlarged in Fig. 4.16.



Part 2H is enlarged in Fig. 4.17.



Part 2I is enlarged in Fig. 4.18.

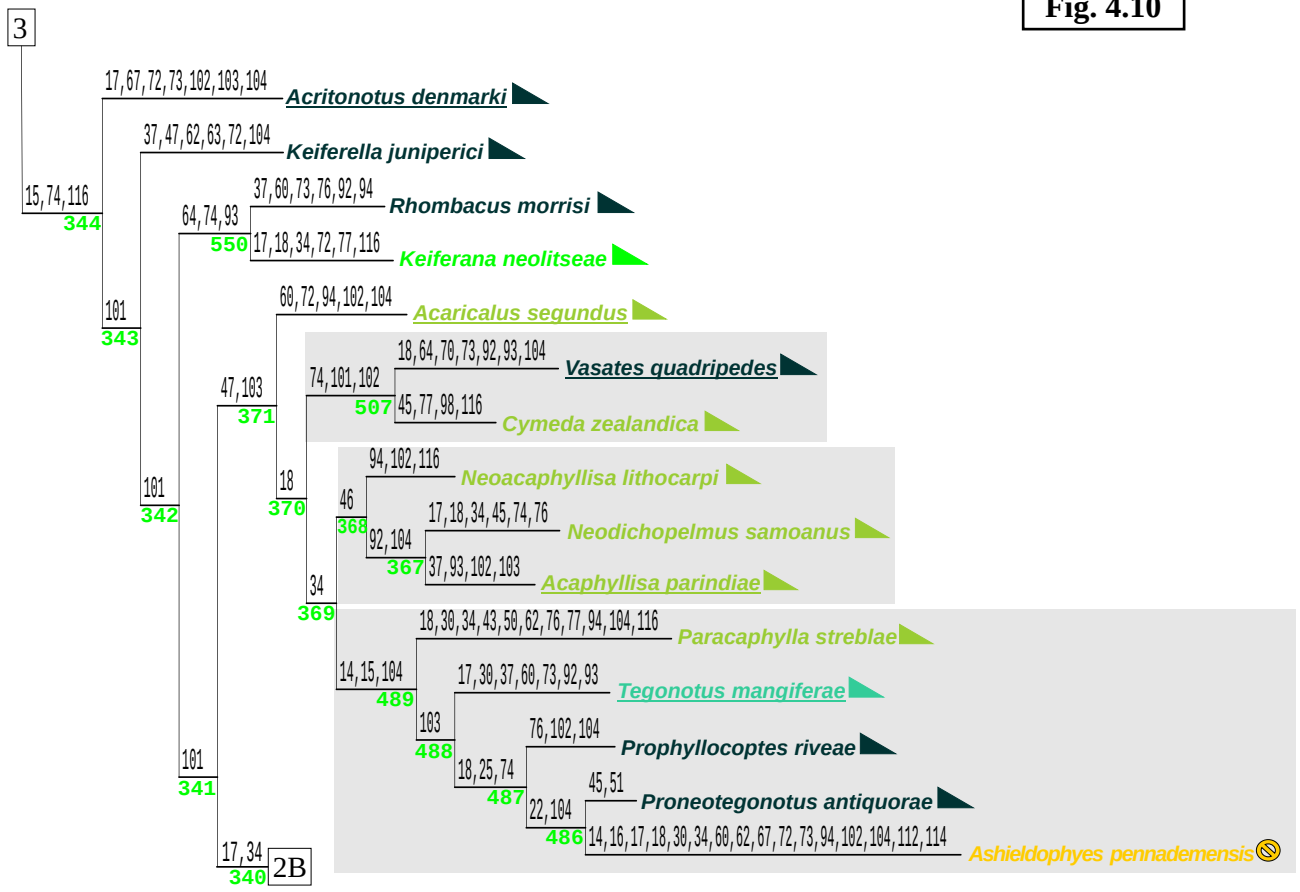
Eriophyidae
- Aberoptinae
- Nothopodinae: Colopodacini
- Nothopodinae: Nothopodini
- Ashieldophyinae
- Cecidophyinae: Cecidophyini
- Cecidophyinae: Colomerini
- Eriophyinae: Diphytoptini
- Eriophyinae: Eriophyini
- Eriophyinae: Aceriini
- Phyllocoptinae: Acaricalini
- Phyllocoptinae: Calacarini
- Phyllocoptinae: Tegonotini
- Phyllocoptinae: Phyllocoptini
- Phyllocoptinae: Anthocoptini

Phytoptidae
- ★2 Phytoptidae: Prothricinae
- 2 Phytoptidae: Novophytoptinae
- 3 Phytoptidae: Nalepellinae: Pentasetacini
- 3 Phytoptidae: Nalepellinae: Nalepellini
- 3 Phytoptidae: Nalepellinae: Trisetacini
- 2 Phytoptidae: Phytoptinae
- 2 Phytoptidae: Sierraphytoptinae: Sierraphytoptini
- 2 Phytoptidae: Sierraphytoptinae: Mackiellini

Fig. 4.9. Caption on next page.

Part 2A

318tax-k10
Fig. 4.10



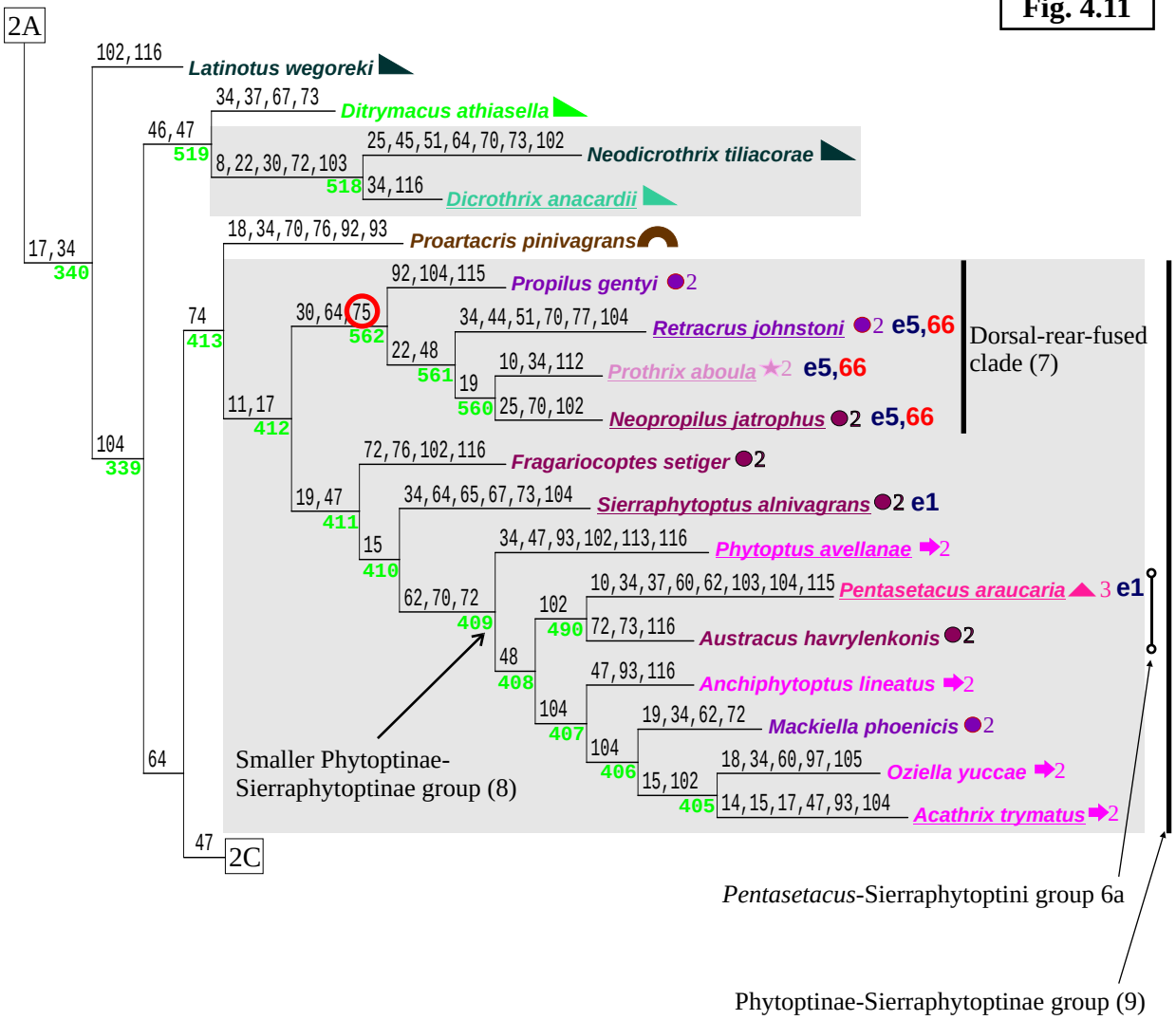
Eriophyidae: Ashieldophyinae
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.9. (previous page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree at node numbered two in Fig. 4.6, which includes the Eriophyidae and part of the Phytoptidae, to largely show topology. The tree is divided into parts 2A-2I which are enlarged in Figs 4.10-4.18.

Fig. 4.10. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66 taxon data matrix.

Part 2B

318tax-k10
Fig. 4.11

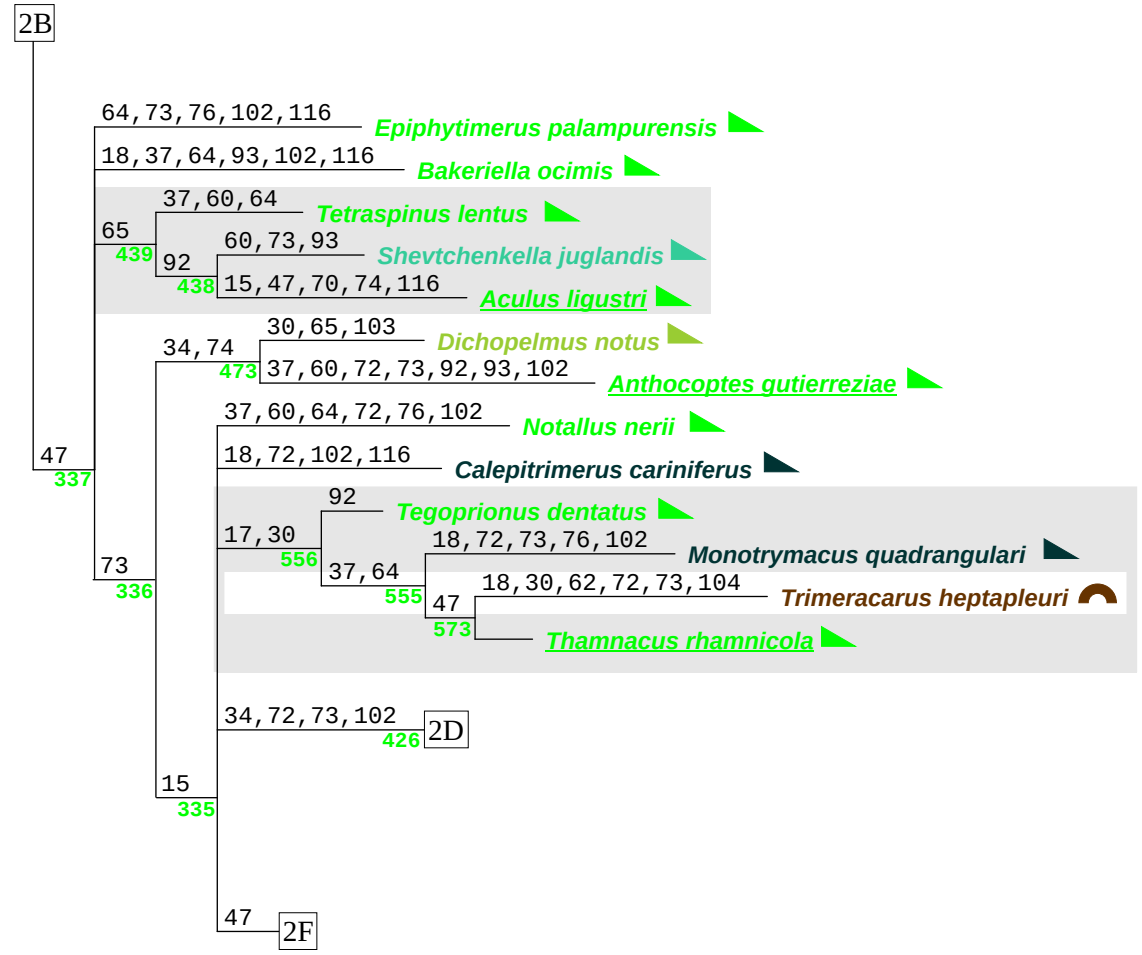


★2 Phytoptidae: Prothricinae
▲3 Phytoptidae: Nalepellinae: Pentasetacini
➡2 Phytoptidae: Phytoptinae
●2 Phytoptidae: Sierraphytoptinae: Sierraphytoptini
●2 Phytoptidae: Sierraphytoptinae: Mackiellini
Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.11. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right, and indicated with arrows. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2C

318tax-k10
Fig. 4.12



Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.12. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2C. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66-taxon data matrix.

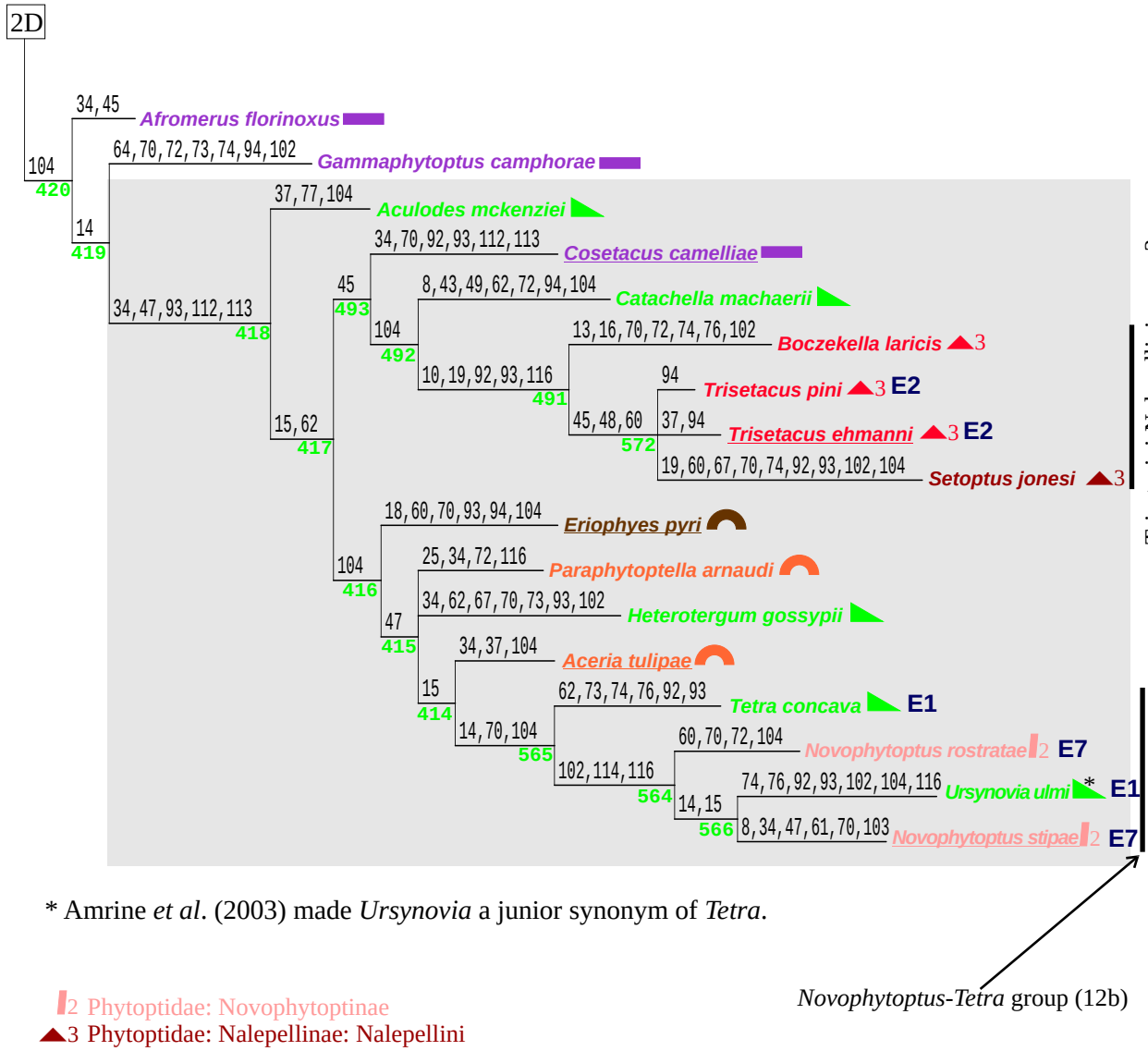
Part 2D

318tax-k10
Fig. 4.13

Fig. 4.13. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2D. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2E

318tax-k10
Fig. 4.14



* Amrine *et al*. (2003) made *Ursynovia* a junior synonym of *Tetra*.

2 Phytoptidae: Novophytoptinae
3 Phytoptidae: Nalepellinae: Nalepellini
3 Phytoptidae: Nalepellinae: Trisetacini
Eriophyidae: Cecidophyinae: Colomerini
Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Eriophyinae: Aceriini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.14. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2E. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of the groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2F

318tax-k10
Fig. 4.15

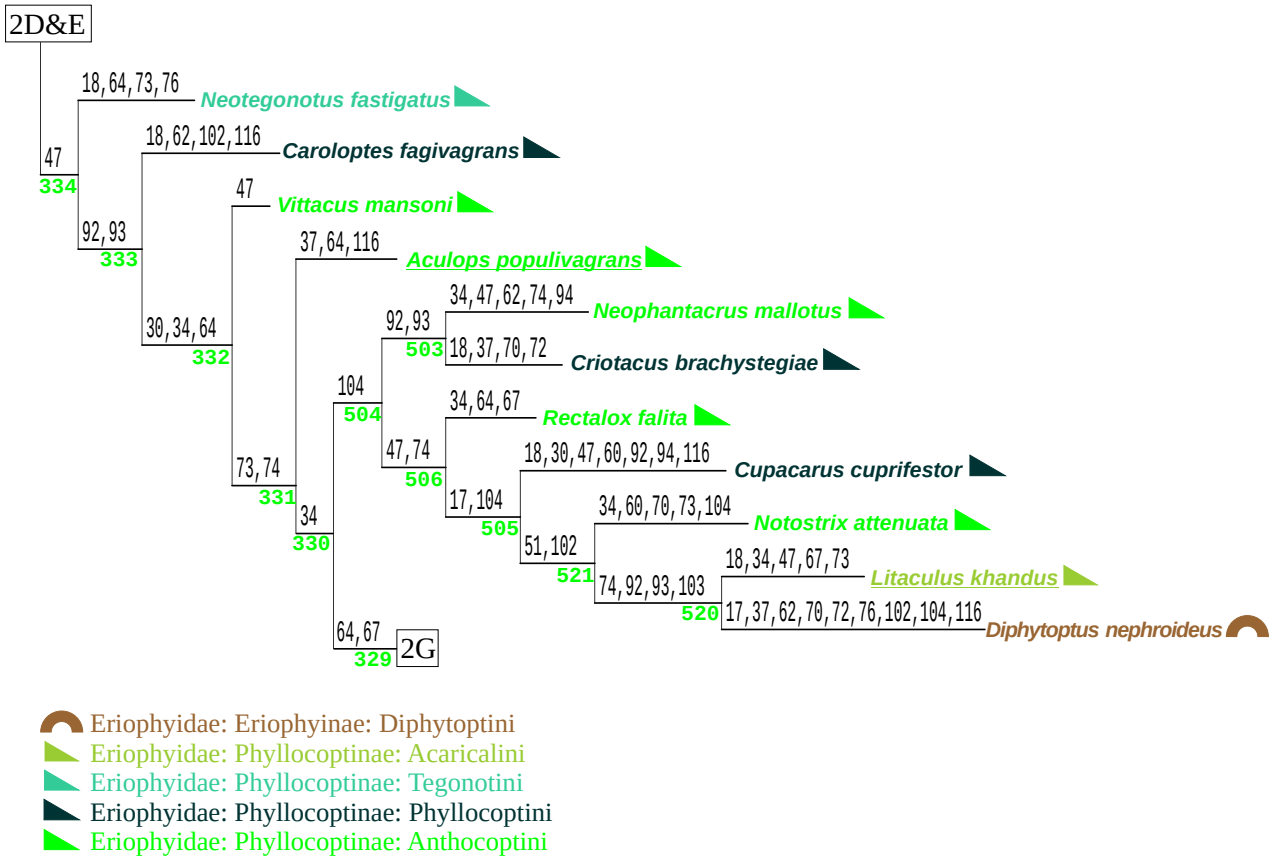


Fig. 4.15. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2F. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.16. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2G. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66-taxon data matrix.

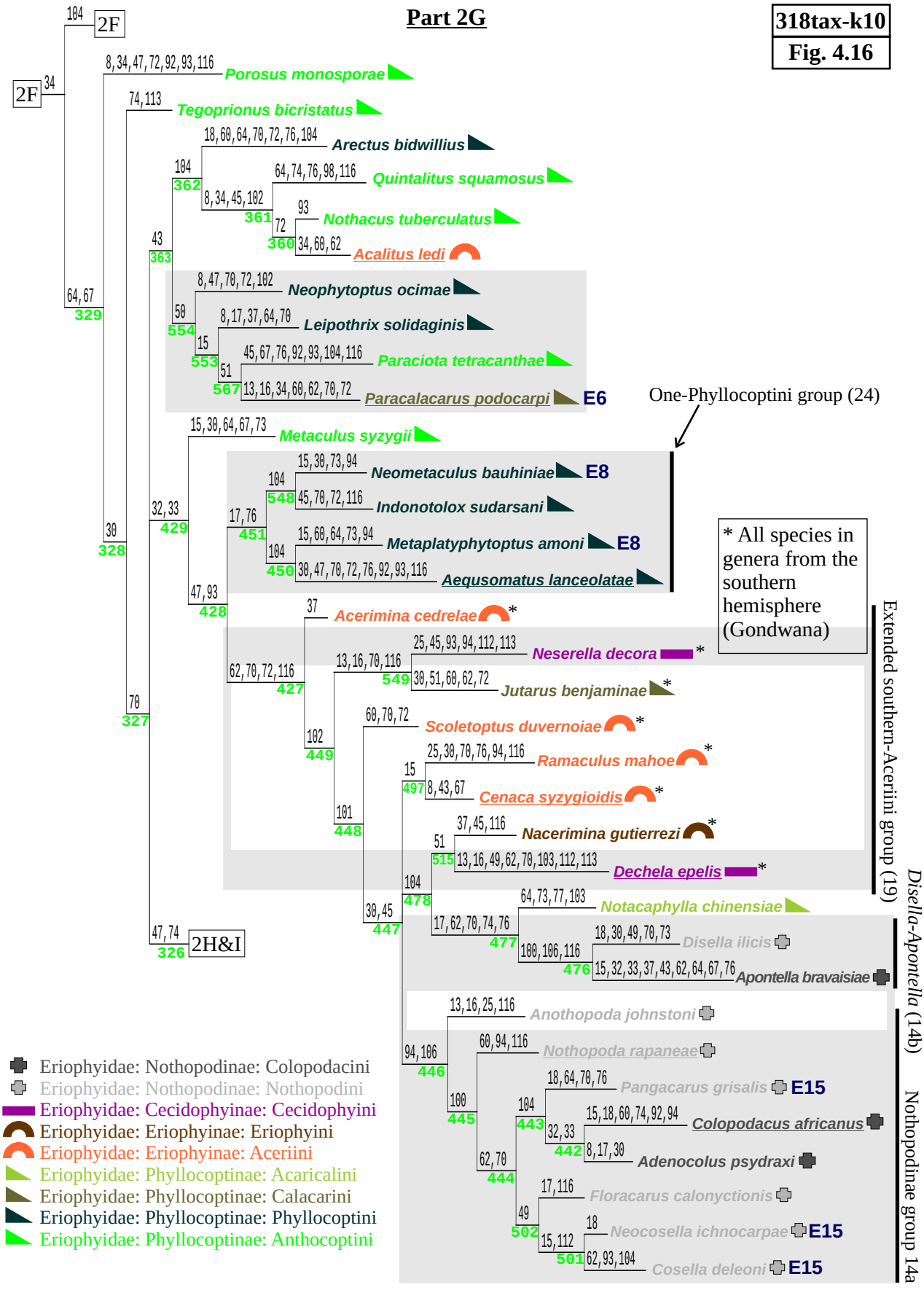


Fig. 4.16. Caption on previous page.

Part 2H

318tax-k10
Fig. 4.17

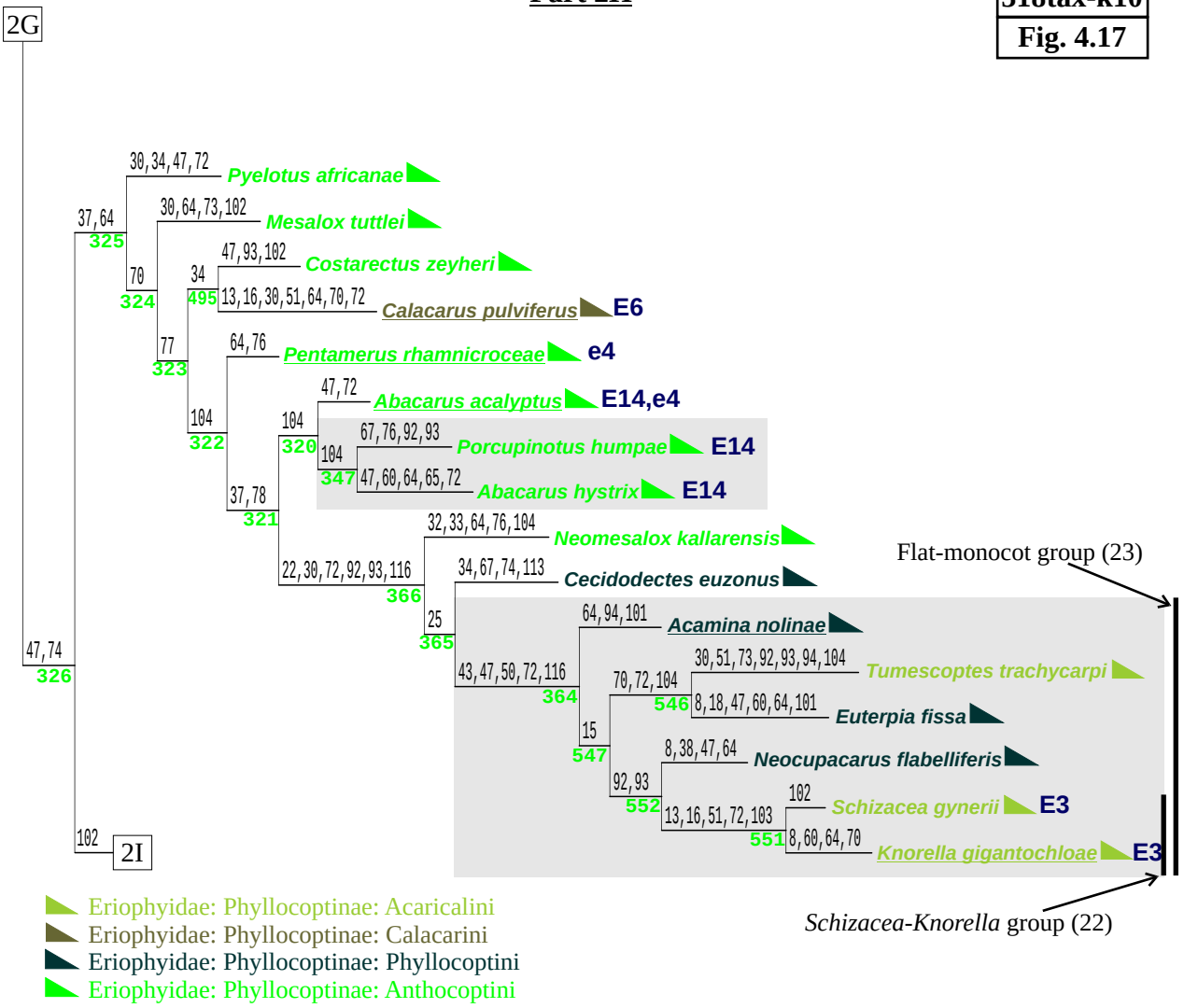


Fig. 4.17. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2H. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.18. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2I. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2I

318tax-k10
Fig. 4.18

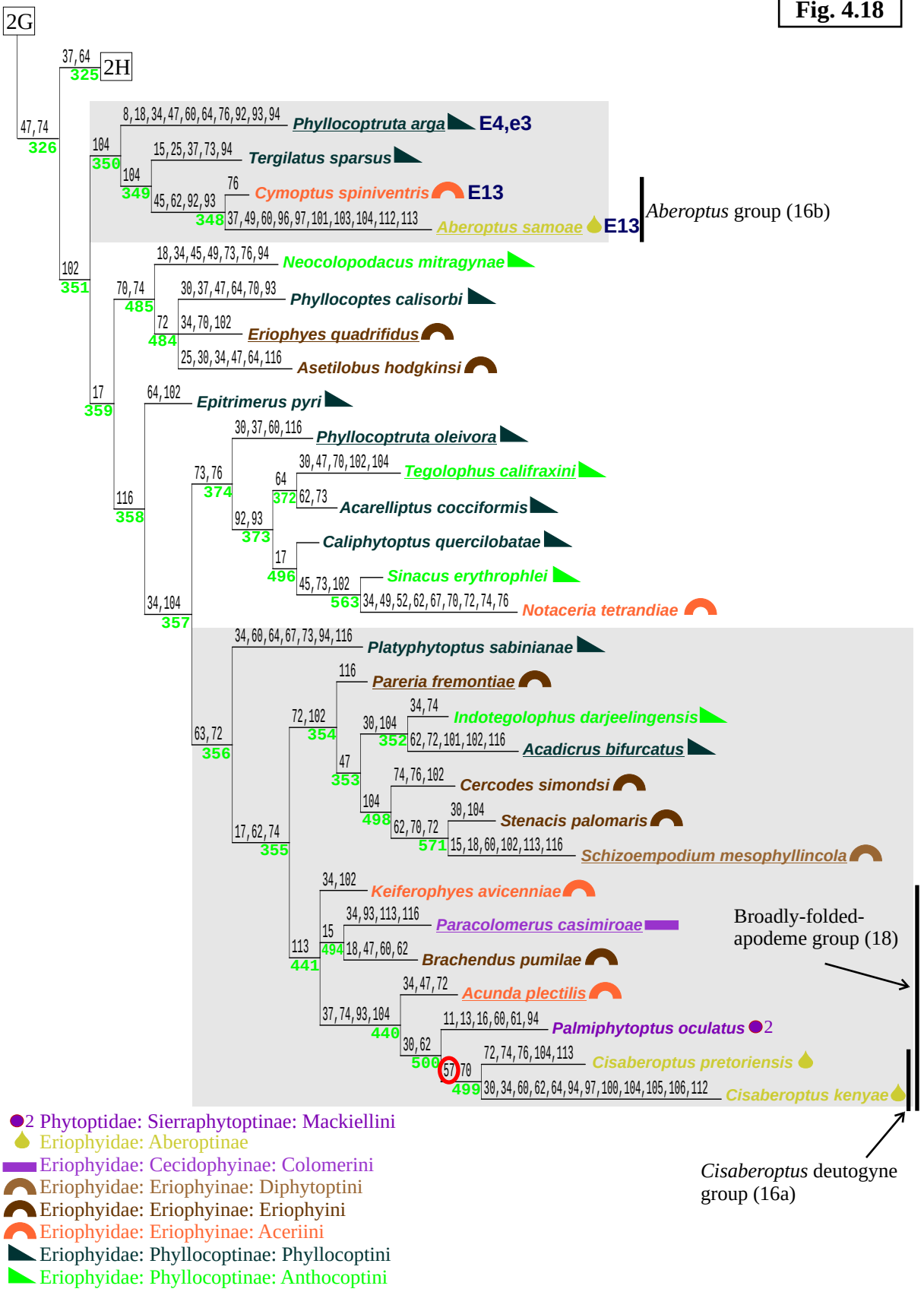


Fig. 4.18. Caption on previous page.

318tax-k10
Fig. 4.19

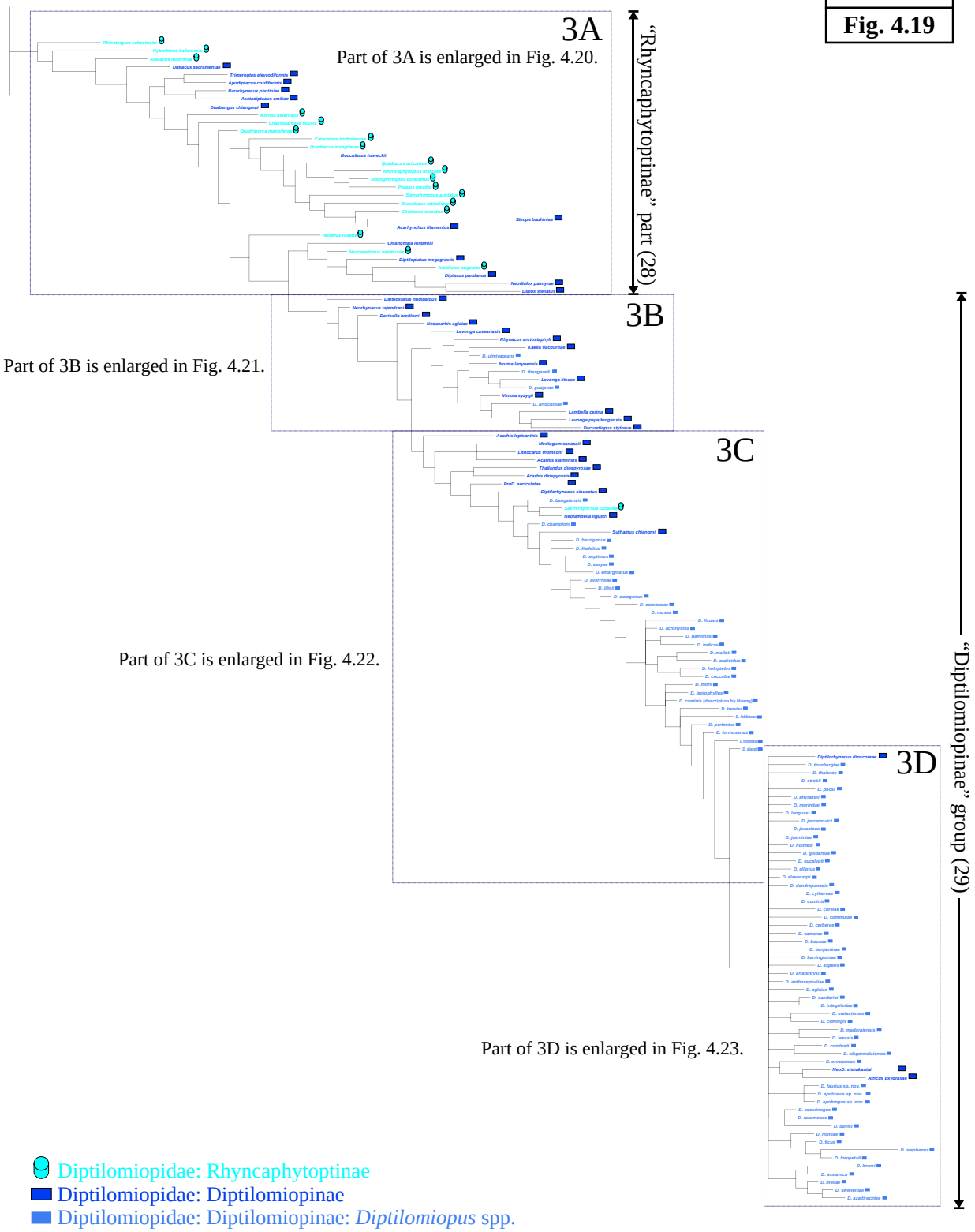


Fig. 4.19. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree at node numbered three in Fig. 4.6, which consists of the Diptilomiopidae clade, to largely show topology. The tree is divided into four parts 3A-3D which are enlarged in Figs 420-4.23.

Part 3A [”Rhyncaphytoptinae” part (28)]

318tax-k10
Fig. 4.20

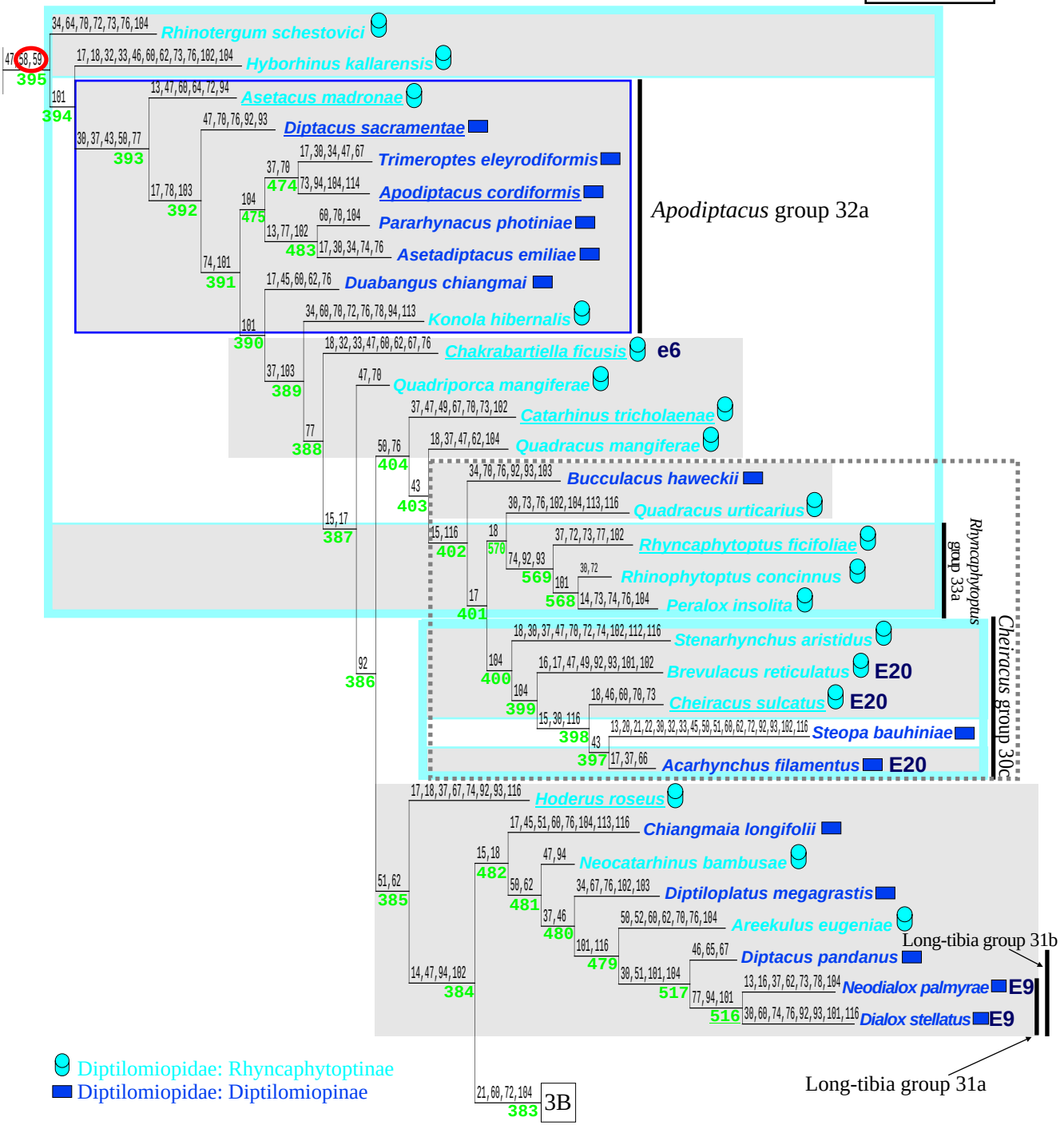


Fig. 4.20. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). The grey blocks with a thick light blue margin connecting them, are one larger group in Fig. 4.26 split up in two smaller groups in the tree above. The taxa included in the area margined by the grey stipple line, are positioned close together in the 318-taxon data matrix analysed under implied character weighting with k=20 (Fig. 4.36), excluding *Steopa* and including *Rhinotergum* and *Hyborhinus*. On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 3B

318tax-k10
Fig. 4.21

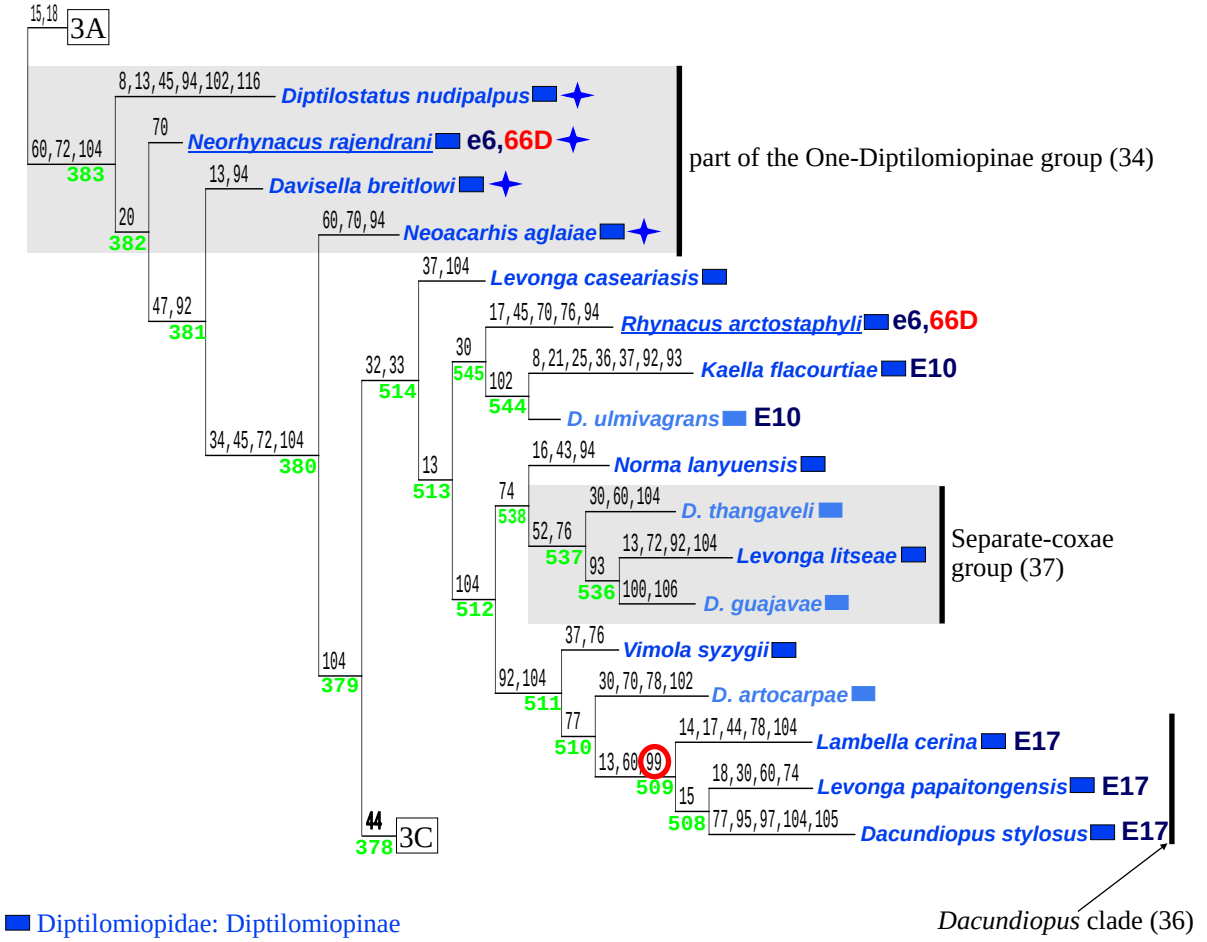


Fig. 4.21. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66-taxon data matrix.

Captions for figures (Figs 4.22, 4.23 which are on next two pages).

Fig. 4.22. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3C. Black numbers above branches are the character numbers of homoplasies supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.23. (page after next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3D. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 3C

318tax-k10
Fig. 4.22

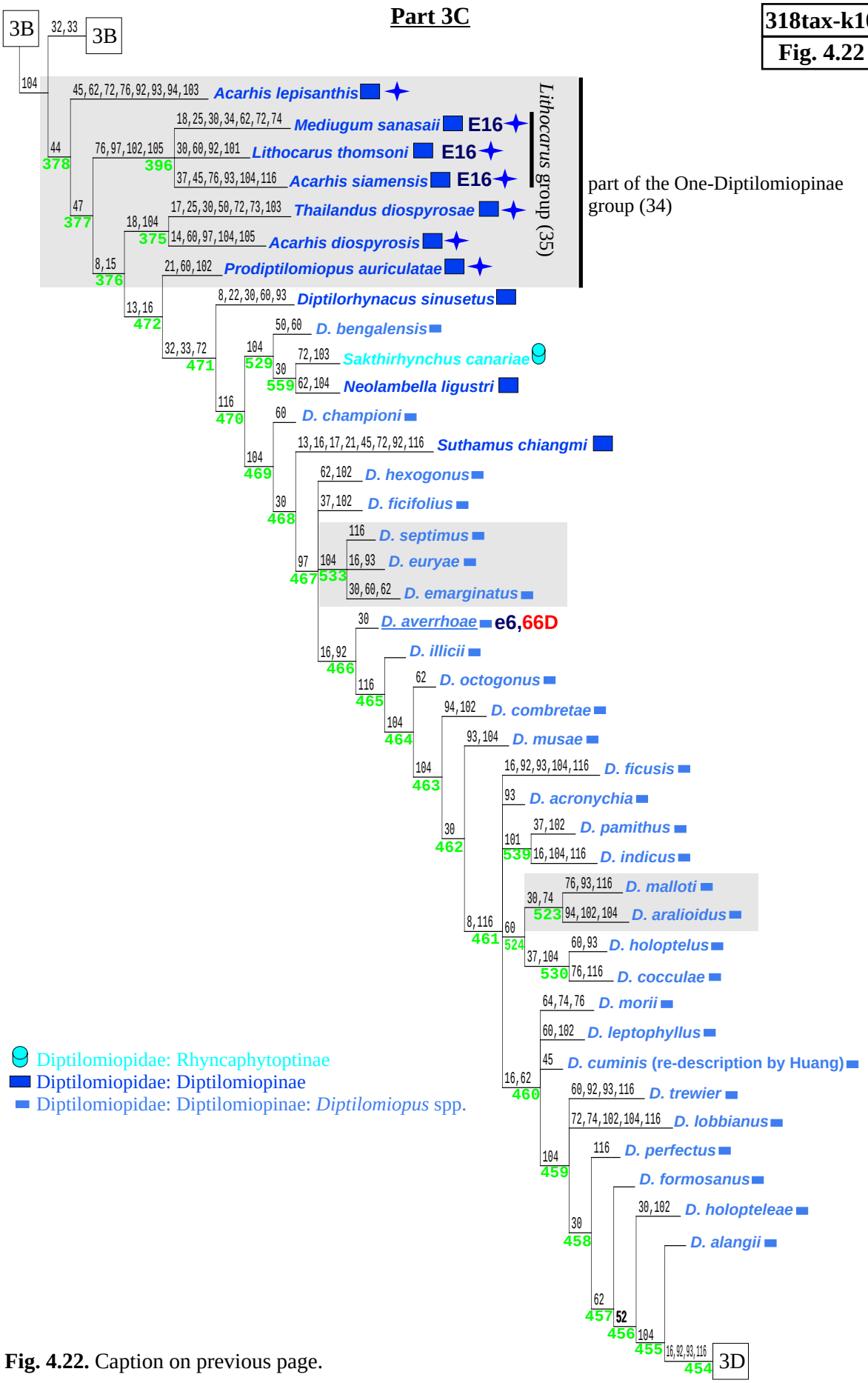


Fig. 4.22. Caption on previous page.

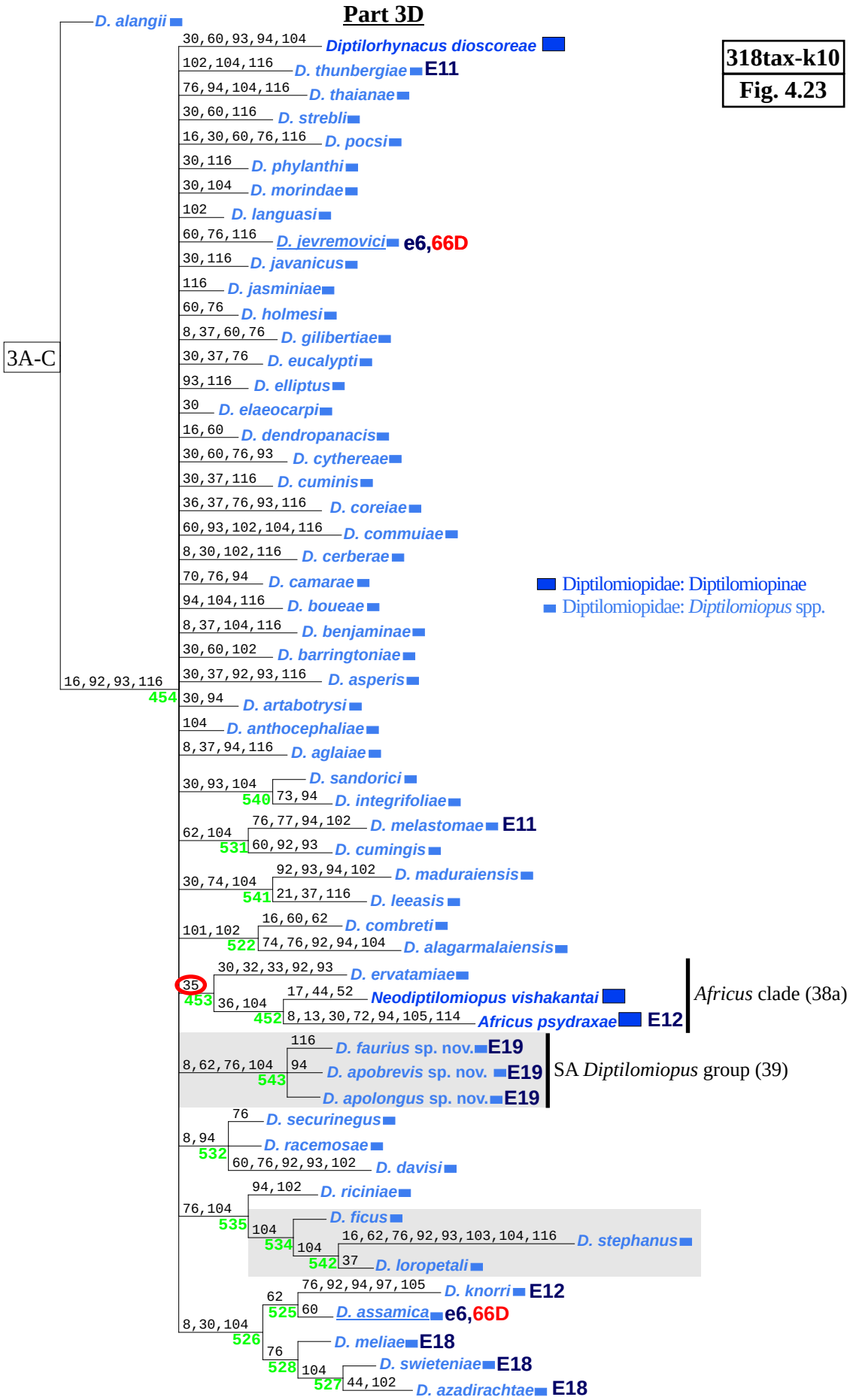


Fig. 4.22. Caption on page before previous page.

318tax-k10
Fig. 4.24

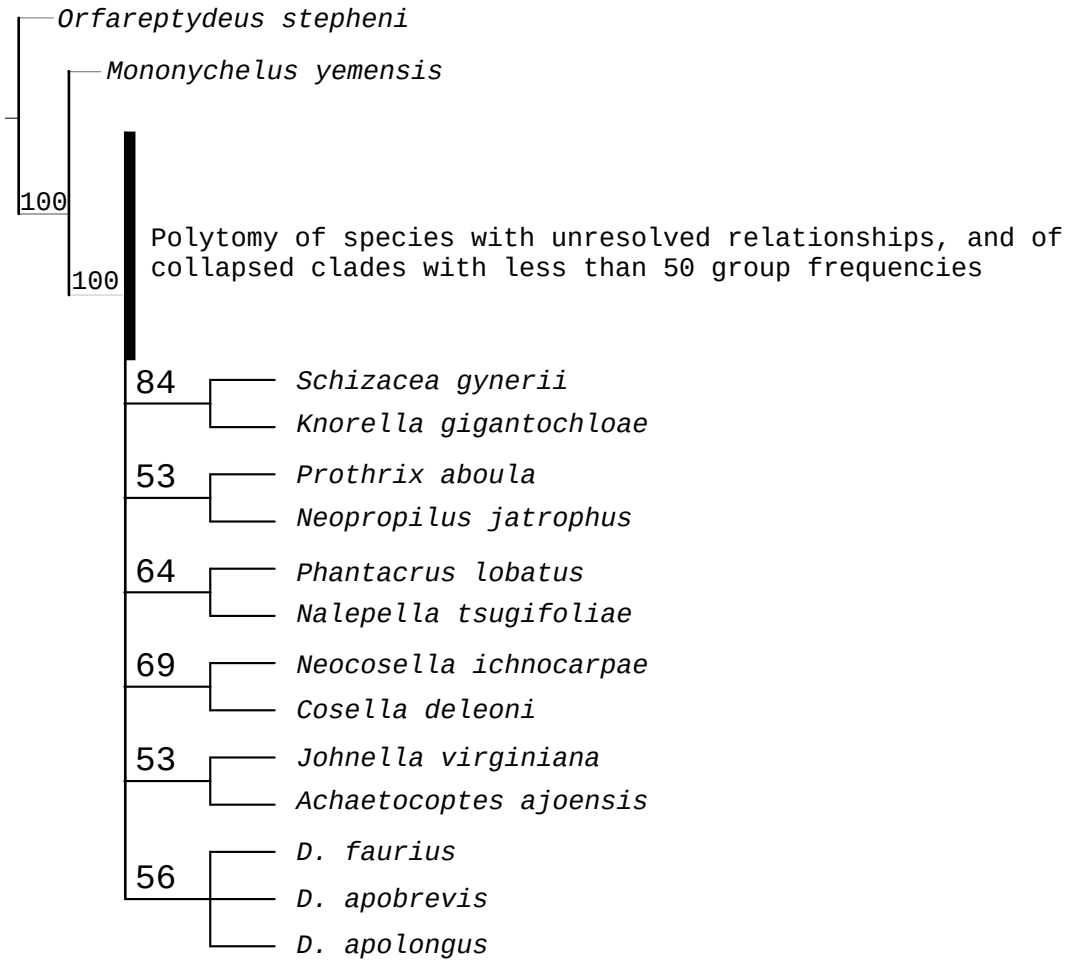
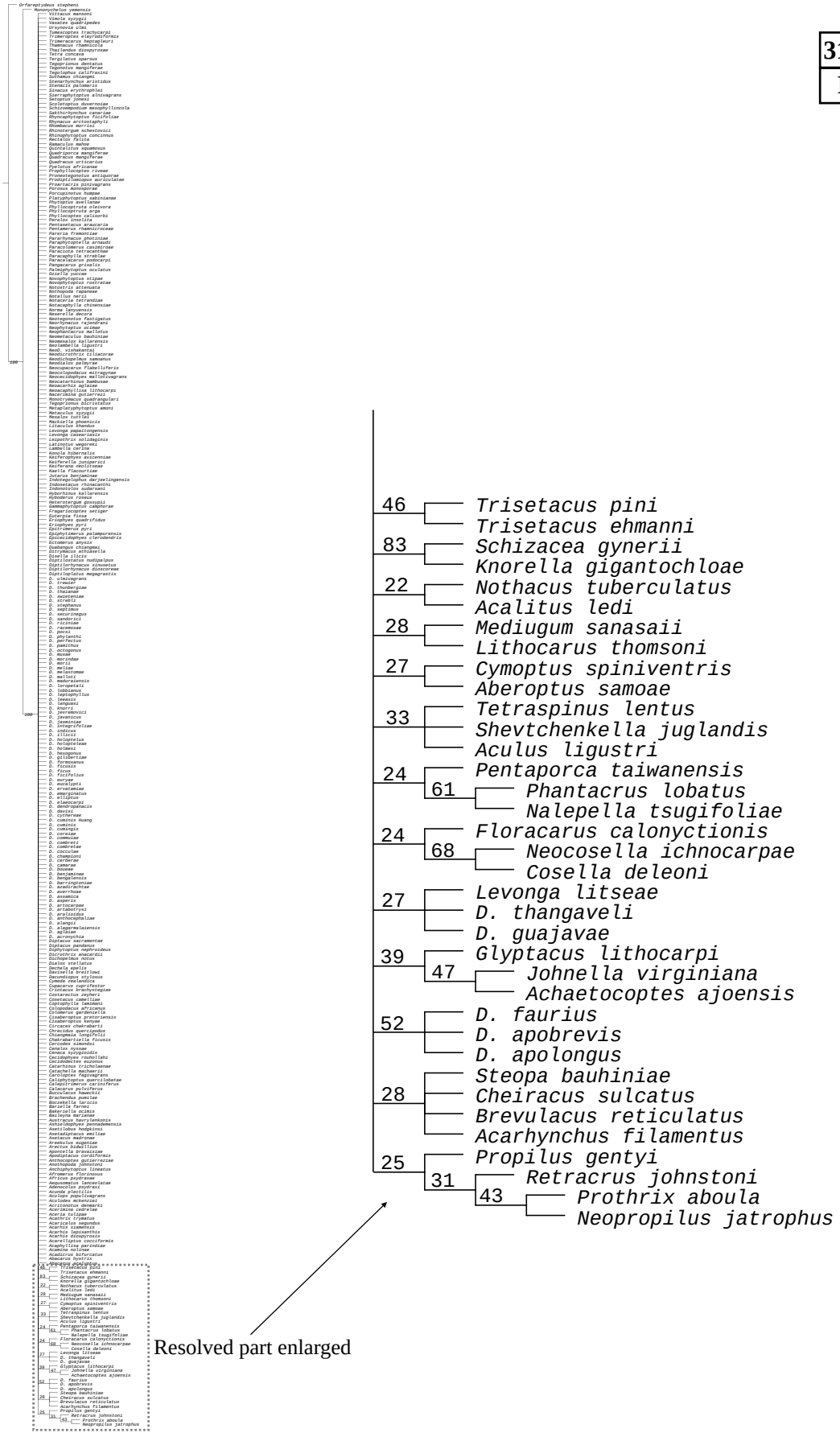


Fig. 4.24. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 318 taxon x 117 character data matrix, done in TNT with heuristic ("traditional" in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 50. Values are given above branches. Only those groupings which were not collapsed are presented, the taxa with unresolved relationships and the collapsed groups are substituted by the thick vertical bar.

318tax-k10
Fig. 4.25



Resolved part enlarged

Fig. 4.25. Symmetric resample group frequency differences (GC) values of symmetric resampling (P=33) of the 318-taxon data matrix done in TNT with heuristic (”traditional” in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 20. Values are given above branches. The resolved part of the tree with groups (supported by GC values of 20 or above) which did not collapse is enlarged on the right hand side.

Table 4.8. Character consistency indices (ci) and retention indices (ri) of characters in the strict consensus of 32 most parsimonious trees found with new technology searches in TNT under implied character weighting with k=10. A total of 117 characters are included in the data matrix, of which 52 are uninformative regarding the relationships between the ingroup (eriophyoid) taxa (the information for characters autapomorphic for the Eriophyoidea, and one character the same for all taxa in the analysis, are in grey, and the cell backgrounds of information for the characters autapomorphic for terminal taxa of the ingroup, are grey). Sixteen of the 65 informative characters are binary characters, and 49 are multistate characters. The number of character states for each character is listed in the column with the heading "state", 2 is a binary character and M is a multistate character followed by the number of character states. The characters with information in bold,are homologous for this tree.

Character	ci	ri	State
0	1.000	1.000	
1	1.000	1.000	
2	1.000	1.000	
3	1.000	1.000	
4	1.000	1.000	
5	1.000	1.000	
6	1.000	1.000	
7	-	-	
8	0.133	0.316	M5
9	1.000	1.000	
10	0.400	0.625	M3
11	0.200	0.765	2
12	1.000	1.000	
13	0.043	0.820	2
14	0.278	0.776	M7
15	0.156	0.763	M7
16	0.107	0.479	M4
17	0.043	0.604	M5
18	0.078	0.393	M8
19	0.167	0.643	2
20	0.500	0.991	2
21	0.286	0.955	M3
22	0.167	0.688	2
23	1.000	1.000	
24	1.000	1.000	
25	0.077	0.400	2
26	1.000	1.000	
27	1.000	1.000	
28	1.000	1.000	
29	1.000	1.000	
30	0.020	0.385	M3
31	1.000	1.000	
32	0.100	0.927	2
33	0.182	0.928	M3
34	0.046	0.278	M8
35	**1.000**	**1.000**	**2**
36	0.750	0.667	M4
37	0.055	0.233	M7
38	0.500	0.000	
39	1.000	1.000	
40	1.000	1.000	
41	-	-	
42	1.000	1.000	
43	0.071	0.914	2
44	0.200	0.957	2
45	0.033	0.797	2
46	0.333	0.500	M4
47	0.082	0.287	M8
48	0.400	0.769	M3
49	0.455	0.250	M6
50	0.083	0.919	2
51	0.063	0.887	2
52	0.200	0.934	2
53	1.000	1.000	
54	1.000	1.000	
55	1.000	1.000	
56	1.000	1.000	
57	**1.000**	**1.000**	**2**
58	**1.000**	**1.000**	**2**
59	**1.000**	**1.000**	**M3**
60	0.157	0.483	M16
61	0.500	0.000	M3
62	0.046	0.629	M4
63	0.667	0.960	M4
64	0.111	0.200	M13
65	0.800	0.667	M6
66	1.000	1.000	
67	0.103	0.352	M5
68	1.000	1.000	
69	1.000	1.000	
70	0.113	0.485	M12
71	1.000	1.000	
72	0.082	0.524	M9
73	0.108	0.094	M8
74	0.097	0.509	M7
75	**1.000**	**1.000**	**M3**
76	0.128	0.354	M16
77	0.118	0.400	M3
78	0.455	0.500	M8
79	1.000	1.000	
80	-	-	
81	1.000	1.000	
82	1.000	1.000	
83	1.000	1.000	
84	1.000	1.000	
85	1.000	1.000	
86	1.000	1.000	
87	1.000	1.000	
88	1.000	1.000	
89	1.000	1.000	
90	1.000	1.000	
91	1.000	1.000	
92	0.034	0.436	M4
93	0.043	0.438	M5
94	0.069	0.212	M6
95	1.000	1.000	
96	1.000	1.000	
97	0.300	0.920	M4
98	1.000	1.000	
99	**1.000**	**1.000**	**2**
100	0.500	0.778	M3
101	0.250	0.704	M9
102	0.057	0.371	M8
103	0.344	0.852	M13
104	0.070	0.573	M14
105	0.250	0.933	M3
106	0.500	0.800	M3
107	1.000	1.000	
108	1.000	1.000	
109	1.000	1.000	
110	1.000	1.000	
111	1.000	1.000	
112	0.214	0.593	M4
113	0.190	0.469	M5
114	0.286	0.545	M3
115	0.400	0.571	M3
116	0.040	0.359	M7

318tax-k20
Fig. 4.26

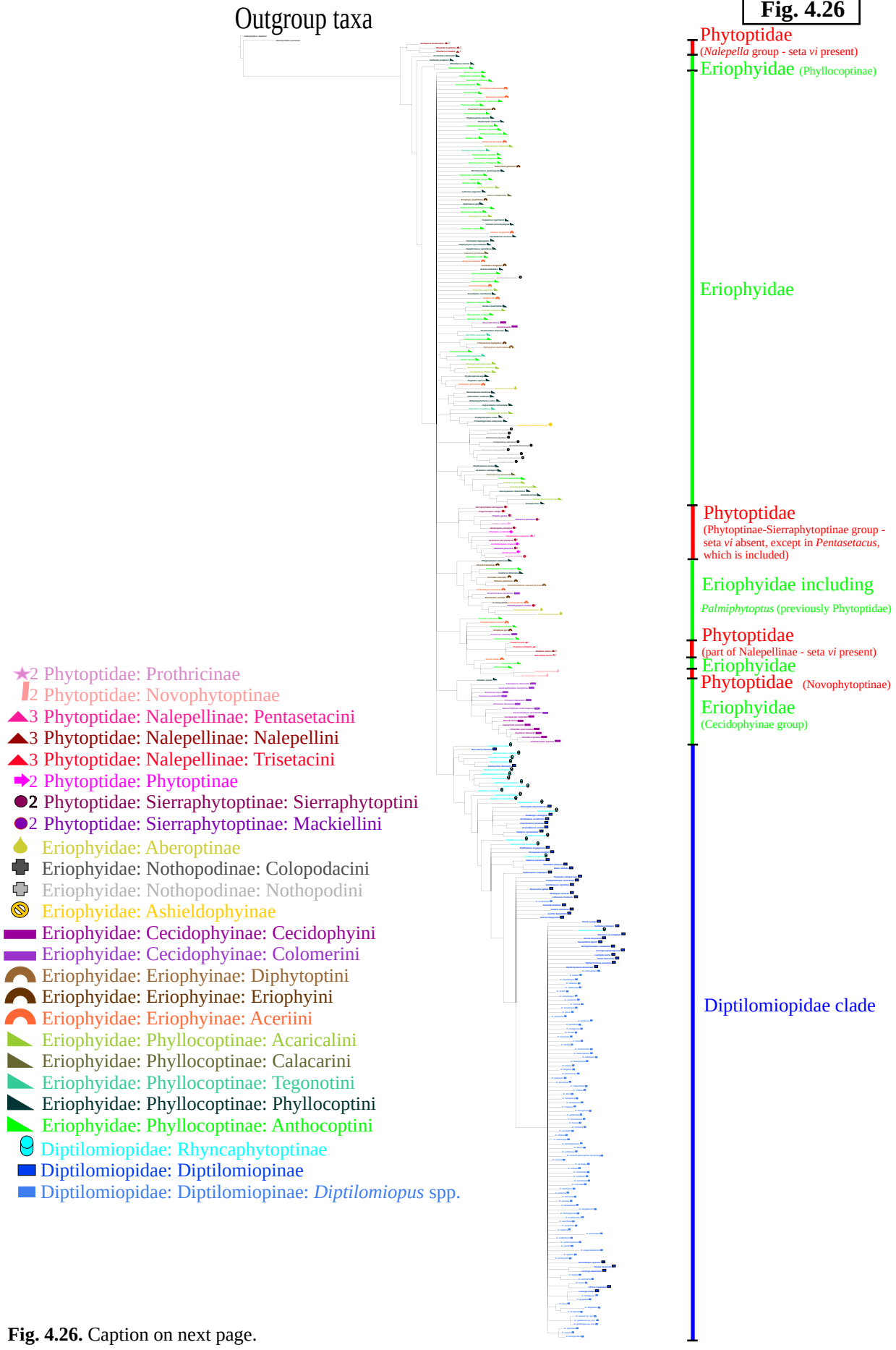


Fig. 4.26. Caption on next page.

318tax-k20
Fig. 4.27

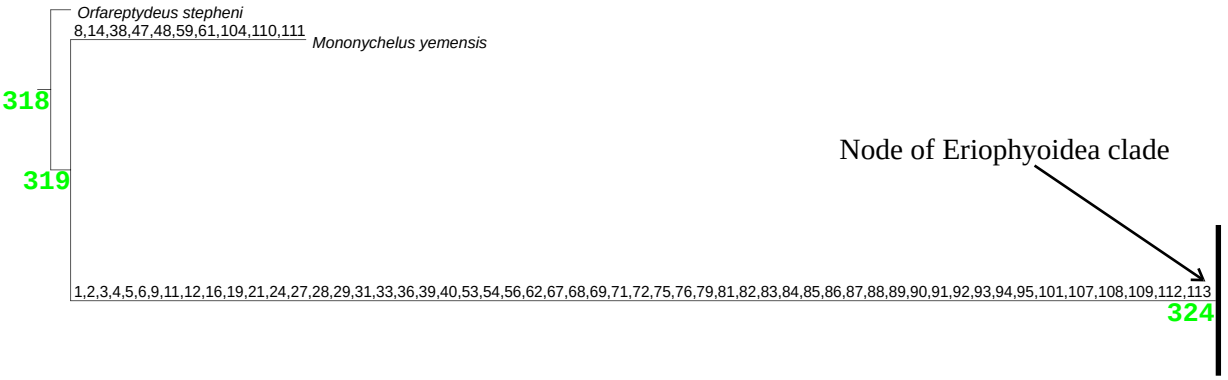


Fig. 4.26. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 in TNT. Total fit = 94.47; Adjusted homoplasy = 35.53; Total length = 2970; CI = 0.101; RI = 0.521; Nodes = 103. Uninformative characters were included. Unsupported branches were not collapsed. The entire tree is presented to show topology, and it is a metric tree. Tree presented from TNT. Tree name is 318tax-k20 tree. The bars on the right hand side indicate families and some notes on broad groupings and clades. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between them, it doesn't always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

Fig. 4.27. (this page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged part of tree including outgroup species and branch of node with the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies or homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

Fig. 4.28. (next page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): detail of basal part of tree enlarged; the group at node 320 divided into smaller groups (Groups 1-16, and the Diptilomiopidae clade) which are enlarged in Figs 4.29-4.35. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.29. (page after next page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged view of the polytomy of species with relationships between them unresolved and which are part of the group at node 320 (Fig. 4.28). Black numbers above the branches are the character numbers of the homoplasious characters supporting the terminal taxa.

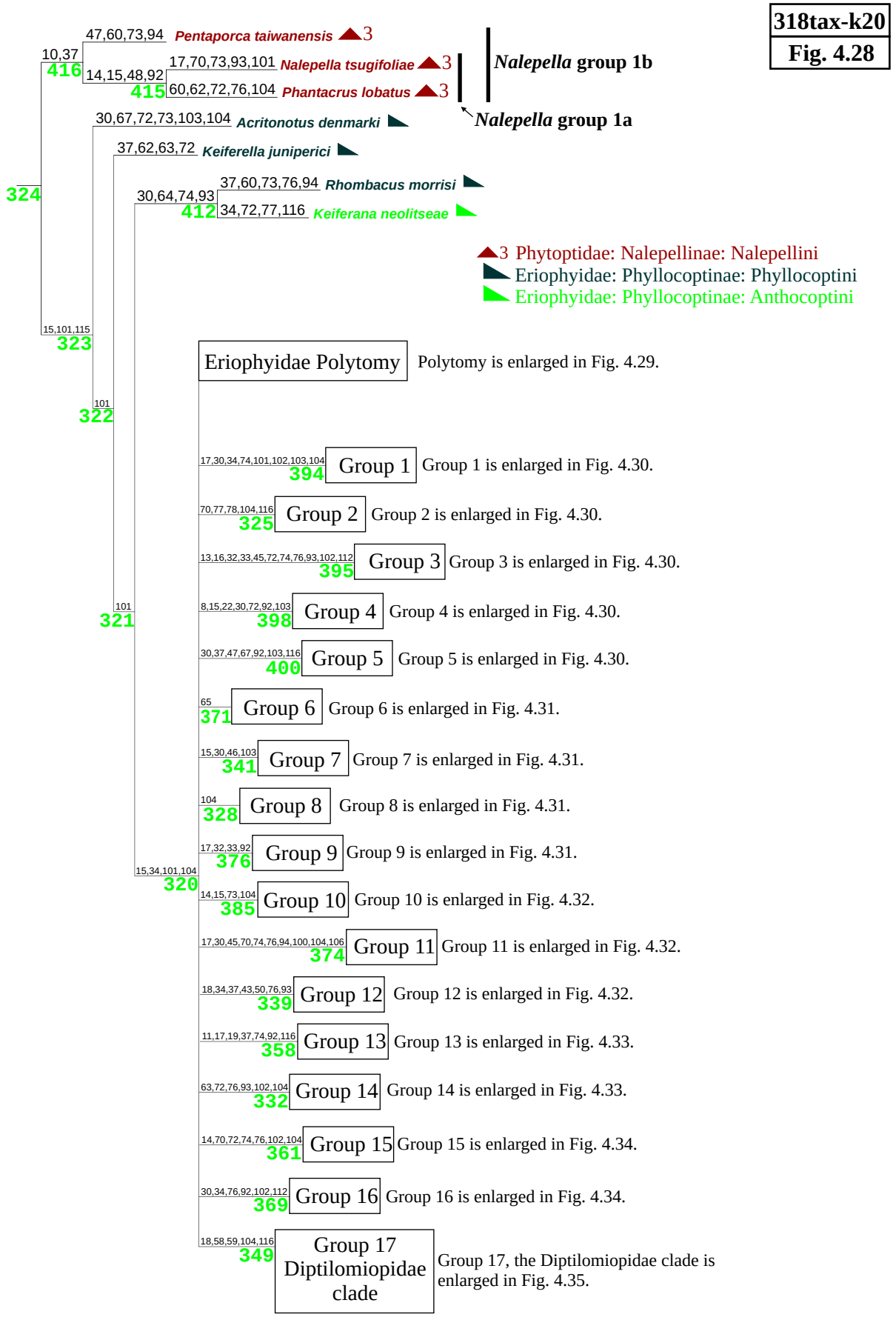


Fig. 4.28. Caption on previous page.

Eriophyidae Polytomy

318tax-k20
Fig. 4.29

Fig. 4.29. Caption on page before previous page.

318tax-k20
Fig. 4.30

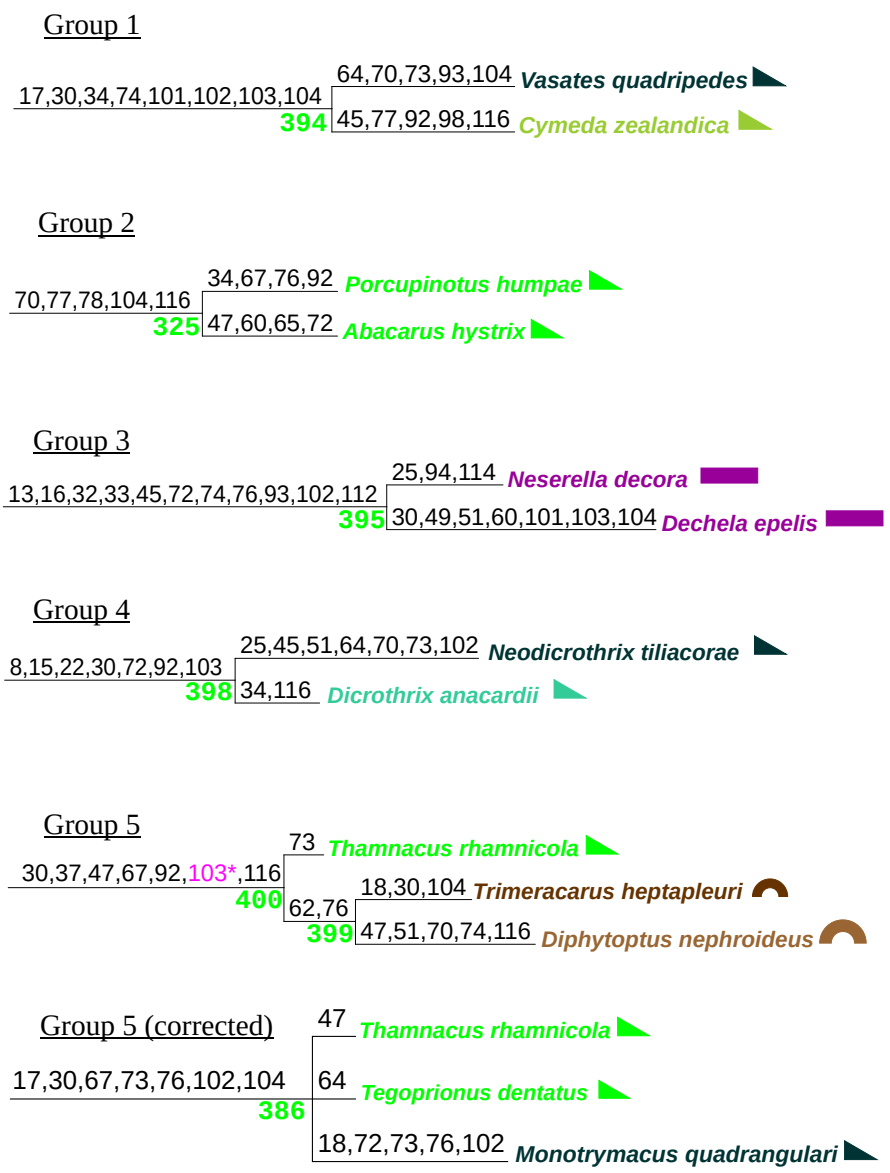
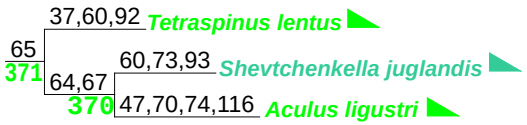


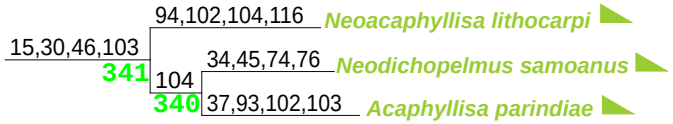
Fig. 4.30. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 1-5 of Fig. 4.28, and corrected Group 5. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The pink number marked with * on the branch of node 400 of Group 5 is the number of a character in the 318 taxon matrix that were accidentily wrongly coded for *Thamnacus rhamnicola* and *Trimeracarus heptapleuri* as 5 (shape of empodium on leg I divided); it should have been coded as 1 (shape of empodium simple). The data was corrected, and the estimated consensus under implied character weighting with k = 20, here presented, was re-analysed. In the tree with Character 103 coded wrongly, *Thamnacus* groups with *Trimeracarus* and *Diphytoptus*, partly supported by the empodium being divided (Character 103), and *Tegoprionus* and *Monotrymacus* are in the polytomy of this tree, in the tree of the corrected data, *Thamnacus* groups with *Tegoprionus* and *Monotrymacus*, and *Trimeracarus* and *Diphytoptus* are in the polytomy. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

318tax-k20
Fig. 4.31

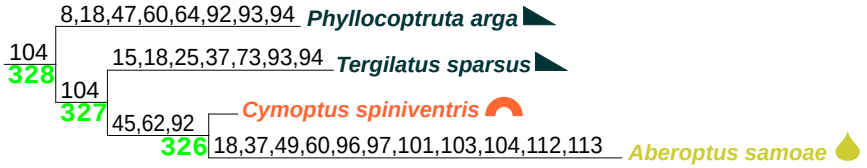
Group 6



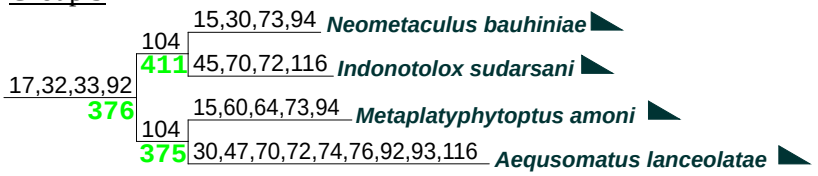
Group 7



Group 8



Group 9

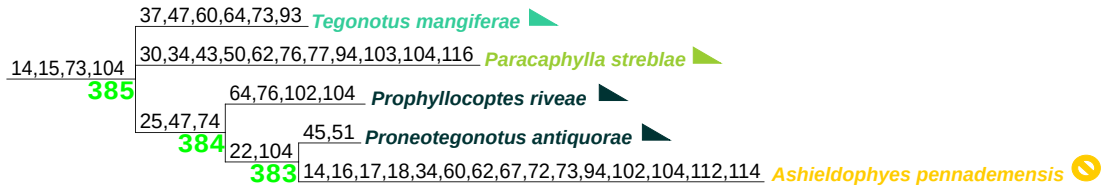


Eriophyidae: Aberoptinae
Eriophyidae: Eriophyinae: Aceriini
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

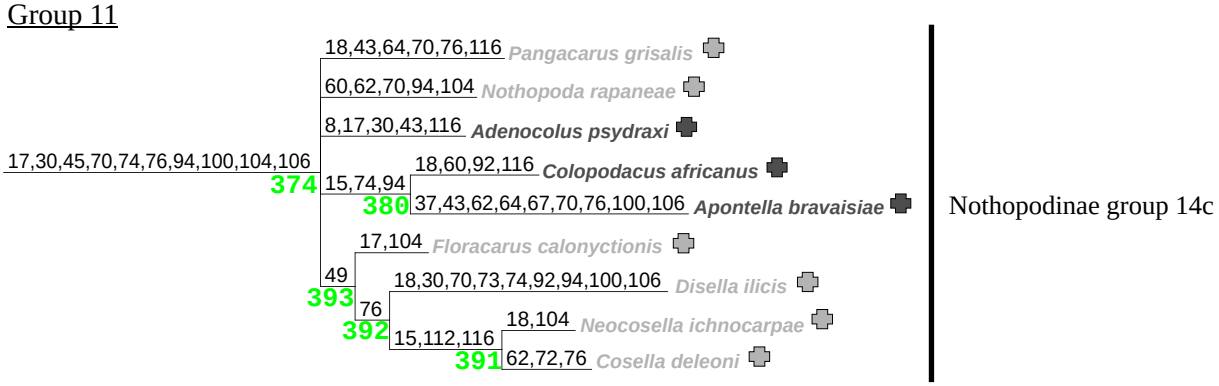
Fig. 4.31. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 6-9 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

318tax-k20
Fig. 4.32

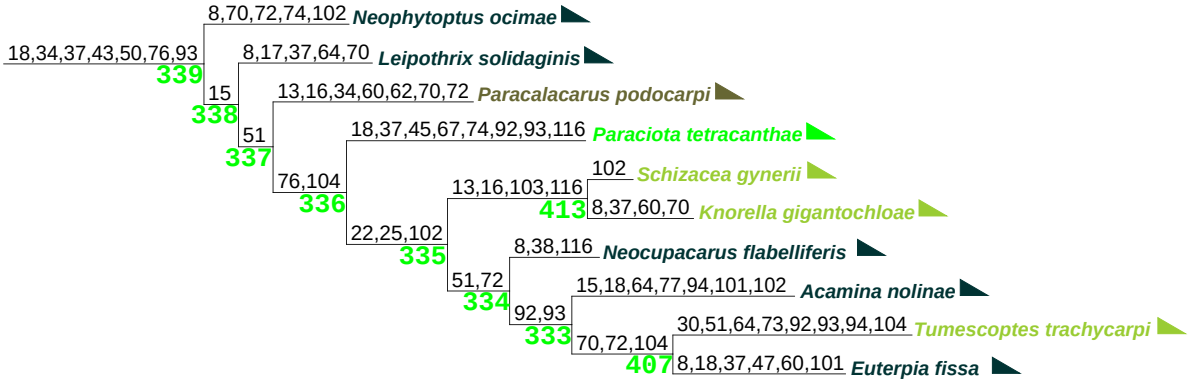
Group 10



Group 11



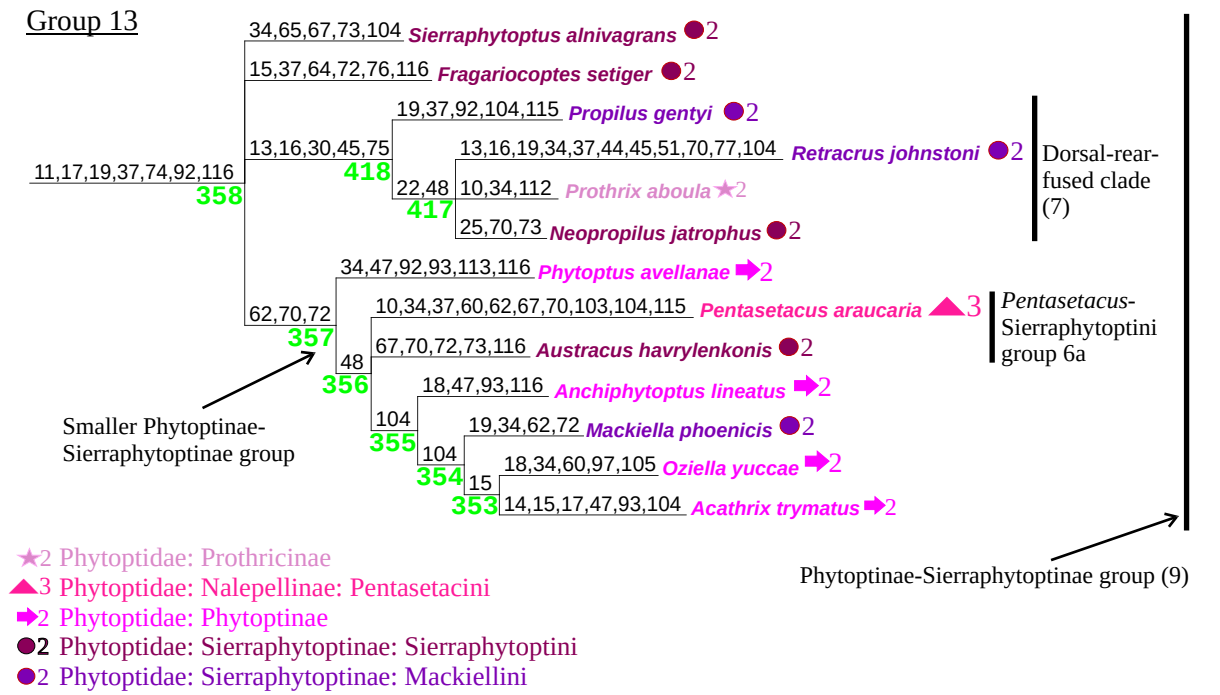
Group 12



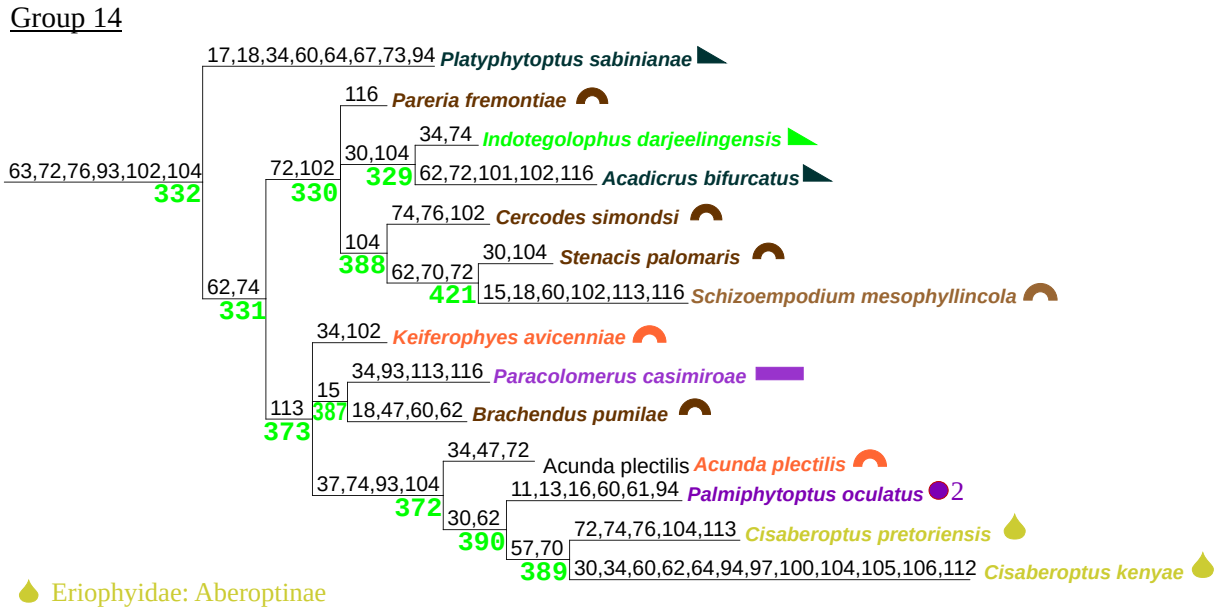
Eriophyidae: Nothopodinae: Colopodacini
Eriophyidae: Nothopodinae: Nothopodini
Eriophyidae: Ashieldophyinae
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Calacarini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini

Fig. 4.32. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 10-11 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

318tax-k20
Fig. 4.33



★2 Phytoptidae: Prothricinae
▲3 Phytoptidae: Nalepellinae: Pentasetacini
➡2 Phytoptidae: Phytoptinae
●2 Phytoptidae: Sierraphytoptinae: Sierraphytoptini
●2 Phytoptidae: Sierraphytoptinae: Mackiellini



Eriophyidae: Aberoptinae
Eriophyidae: Cecidophyinae: Colomerini
Eriophyidae: Eriophyinae: Diphytoptini
Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Eriophyinae: Aceriini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.33. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 13-14 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right, and some indicated with arrows.

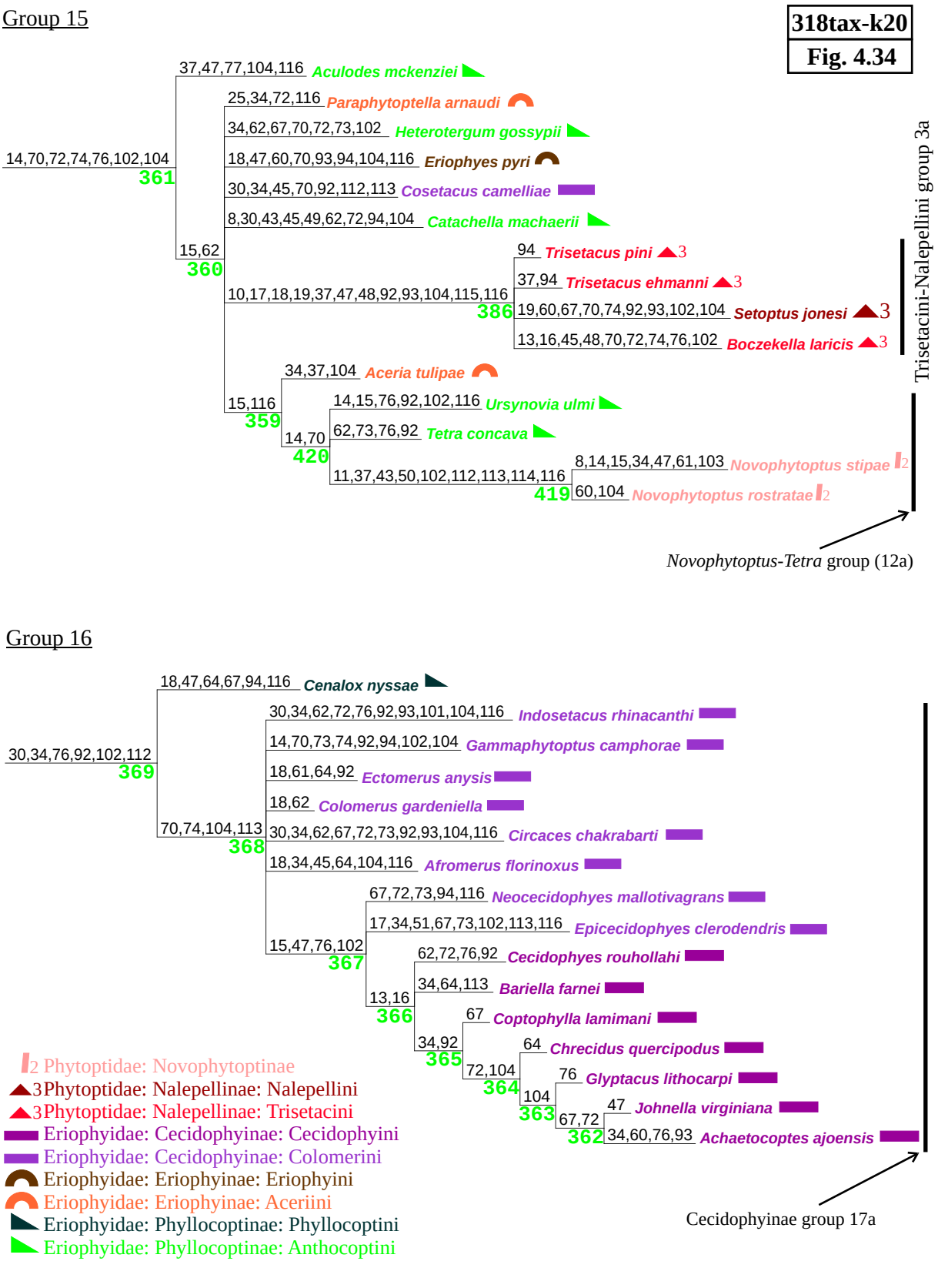


Fig. 4.34. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 15-16 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right, and some indicated with arrows.

318tax-k20
Fig. 4.35

Group 17
Diptilomiopidae clade

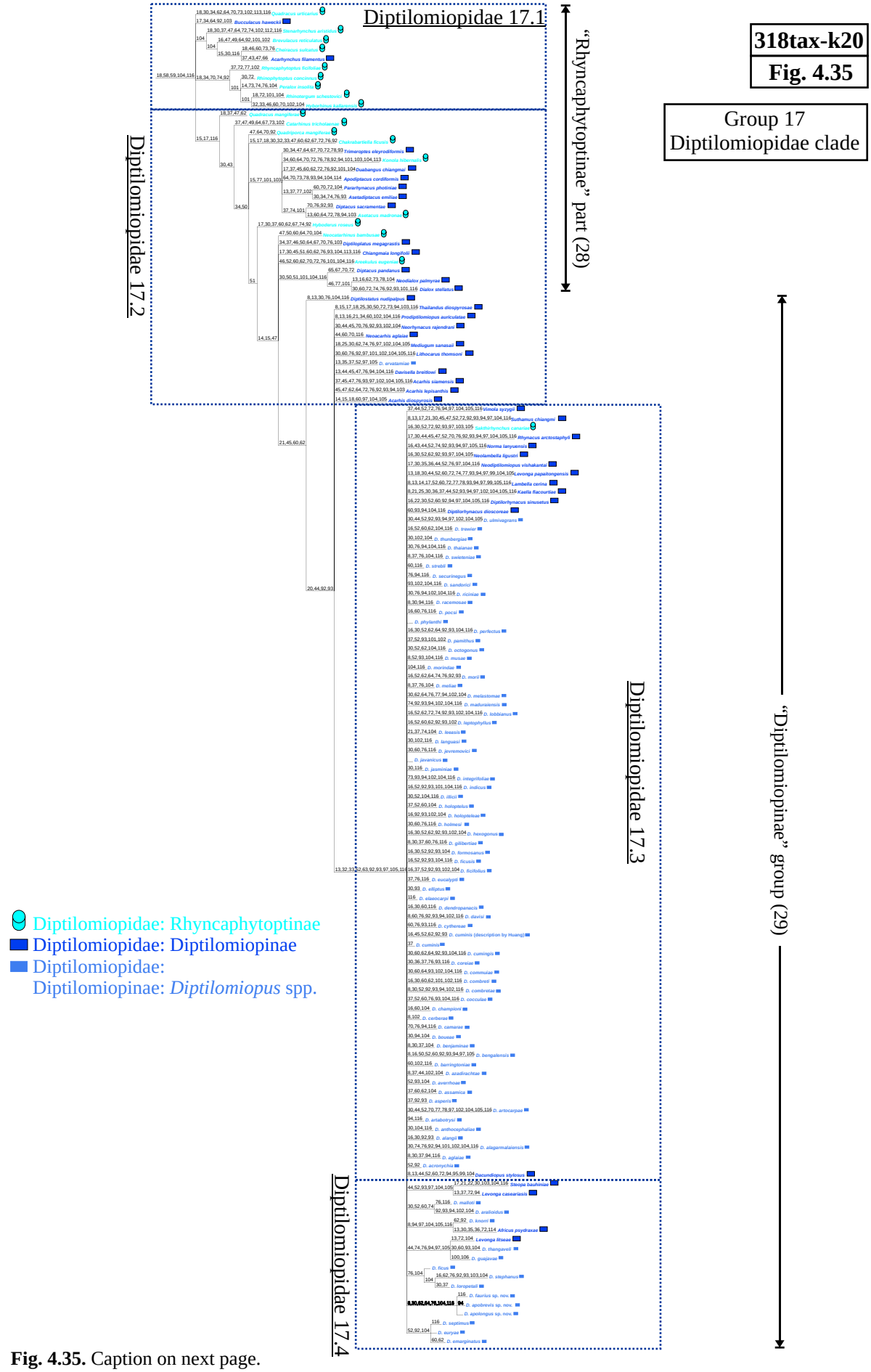


Fig. 4.35. Caption on next page.

318tax-k20
Fig. 4.36

Diptilomiopidae 17.1

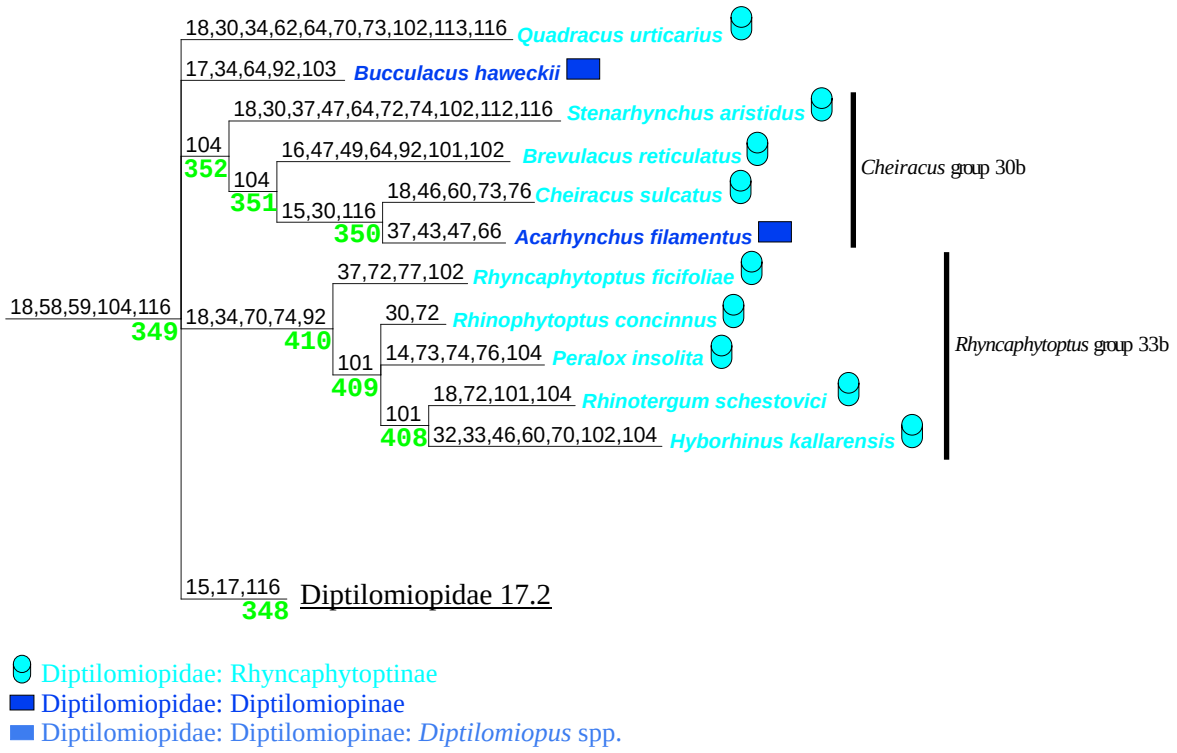


Fig. 4.35. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Group 17 (Diptilomiopidae clade) of Fig. 4.28. The clade in this figure and at this enlargement is largely presented to show topology and to divide the clade into four separate parts (Diptilomiopidae 17.1-17.4) which are enlarged in Figs 4.36-4.39. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.36. (this page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.1. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Diptilomiopidae 17.2

318tax-k20
Fig. 4.37

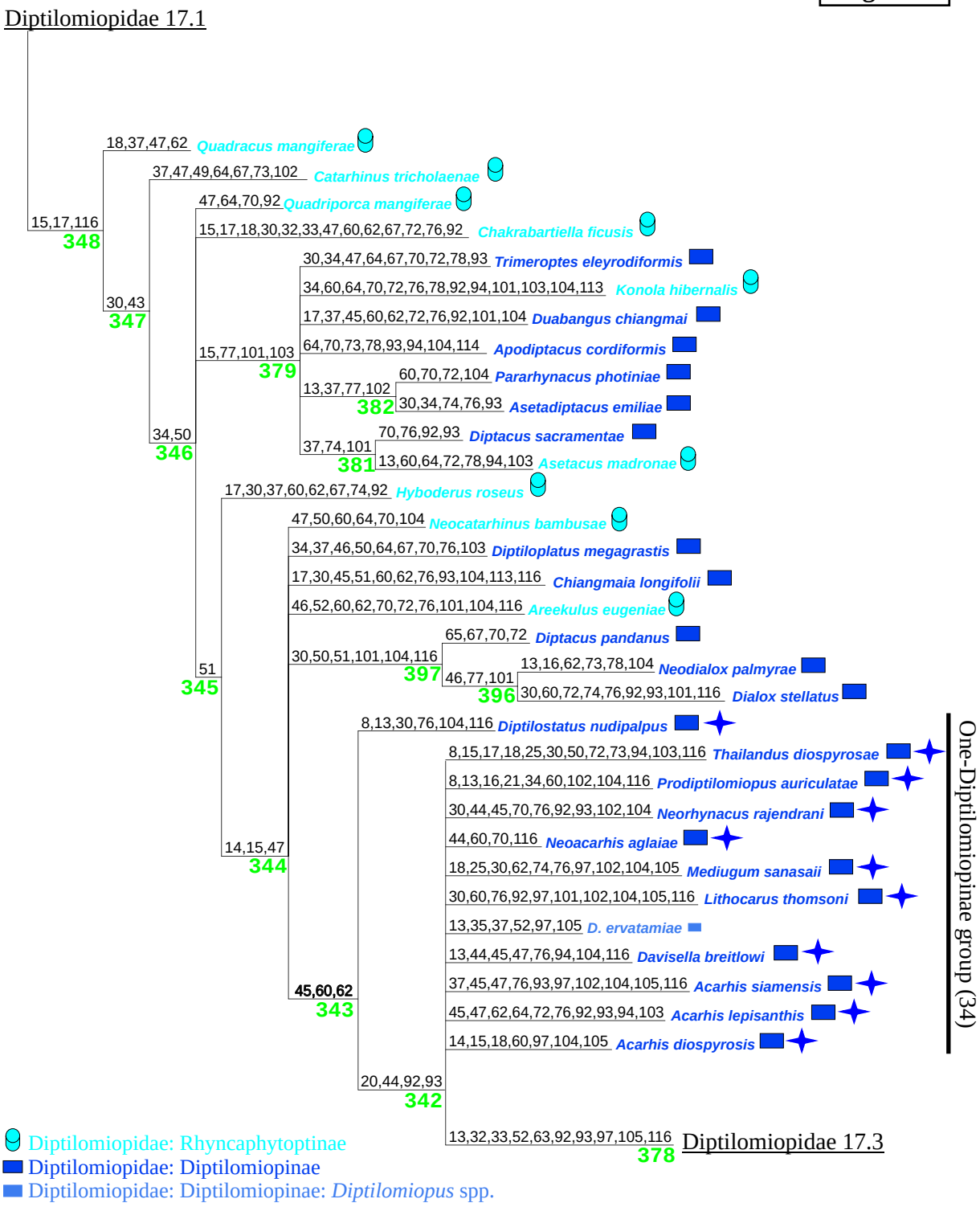


Fig. 4.37. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.2. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. The species marked with the blue crosses are part constitute the One-Diptilomiopinae group, and the blue crosses are mapped next to the same species in the 318tax-k10 tree (Figs 4.21-4.22). Informal name of group discussed in the text is on the right.

Diptilomiopidae 17.3

318tax-k20
Fig. 4.38

Diptilomiopidae 17.2 13,32,33,52,63,92,93,97,105,116

378

Diptilomiopidae 17.4

Diptilomiopidae: Rhyncaphytoptinae
Diptilomiopidae: Diptilomiopinae
Diptilomiopidae:
Diptilomiopinae: *Diptilomiopus* spp.

Fig. 4.38. Caption on next page.

Diptilomiopidae 17.4

318tax-k20
Fig. 4.39

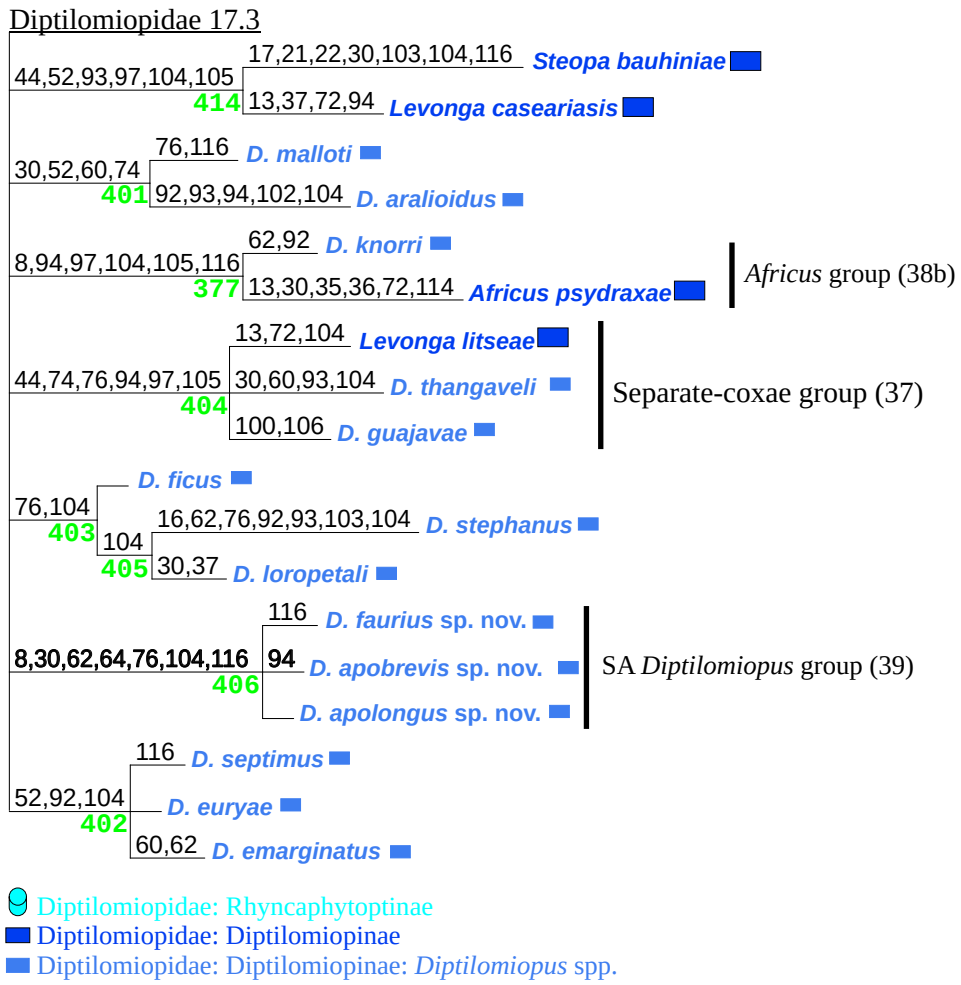


Fig. 4.38. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.3, which is a polytomy that is part of the group at node 378. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node number from TNT is the green number underneath the branch and close to the node.

Fig. 4.39. (this page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.4. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. The node numbers from TNT are the green numbers underneath the branches and close to the nodes. Informal names of groups discussed in the text are on the right.

Table 4.9. Character consistency indices (ci) and character retention indices (ri) of characters of the estimated consensus tree found with the analysis of the 318 taxon data matrix under implied weighting of characters with k=20 in TNT (Fig. 4.26). A total of 117 characters are included in the data matrix, of which 52 are uninformative regarding the relationships between the ingroup (eriophyoid) taxa (ci indices of characters autapomorphic for the Eriophyoidea, and one character the same for all taxa in the analysis are in grey, and the cell backgrounds of the ci indices of characters autapomorphic for terminal taxa of the ingroup, are grey). The characters with ci indices in bold are homologous for this tree.

Character consistency indices (ci)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.105	1.000
10	0.400	0.250	1.000	0.038	0.250	0.094	0.073	0.031	0.069	0.143
20	**1.000**	0.286	0.125	--	1.000	0.071	--	1.000	1.000	1.000
30	0.016	1.000	0.056	0.105	0.042	0.333	0.600	0.051	0.500	1.000
40	1.000	--	--	0.067	0.059	0.027	0.250	0.074	0.333	0.500
50	0.111	0.056	0.024	1.000	1.000	--	1.000	**1.000**	**1.000**	**1.000**
60	0.154	0.500	0.040	0.667	0.099	0.800	--	0.077	1.000	1.000
70	0.094	1.000	0.072	0.101	0.072	**1.000**	0.113	0.095	0.313	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.025	0.031	0.060	1.000	--	0.115	--	0.333
100	0.400	0.175	0.047	0.306	0.051	0.087	0.333	1.000	1.000	1.000
110	--	--	0.273	0.211	0.250	0.400	0.035			

Character retention indices (ri)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.105	1.000
10	0.625	0.824	1.000	0.795	0.741	0.579	0.208	0.432	0.308	0.571
20	**1.000**	0.955	0.563	--	1.000	0.350	--	1.000	1.000	1.000
30	0.242	1.000	0.863	0.864	0.200	0.000	0.333	0.178	0.000	1.000
40	1.000	--	--	0.908	0.830	0.748	0.250	0.202	0.692	0.375
50	0.941	0.872	0.328	1.000	1.000	--	1.000	1.000	**1.000**	**1.000**
60	0.469	0.000	0.569	0.960	0.090	0.667	--	0.111	1.000	1.000
70	0.365	1.000	0.449	0.031	0.325	**1.000**	0.252	0.240	0.083	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.201	0.212	0.071	1.000	--	0.736	--	0.000
100	0.667	0.535	0.233	0.824	0.395	0.764	0.600	1.000	1.000	1.000
110	--	--	0.704	0.531	0.455	0.571	0.251			

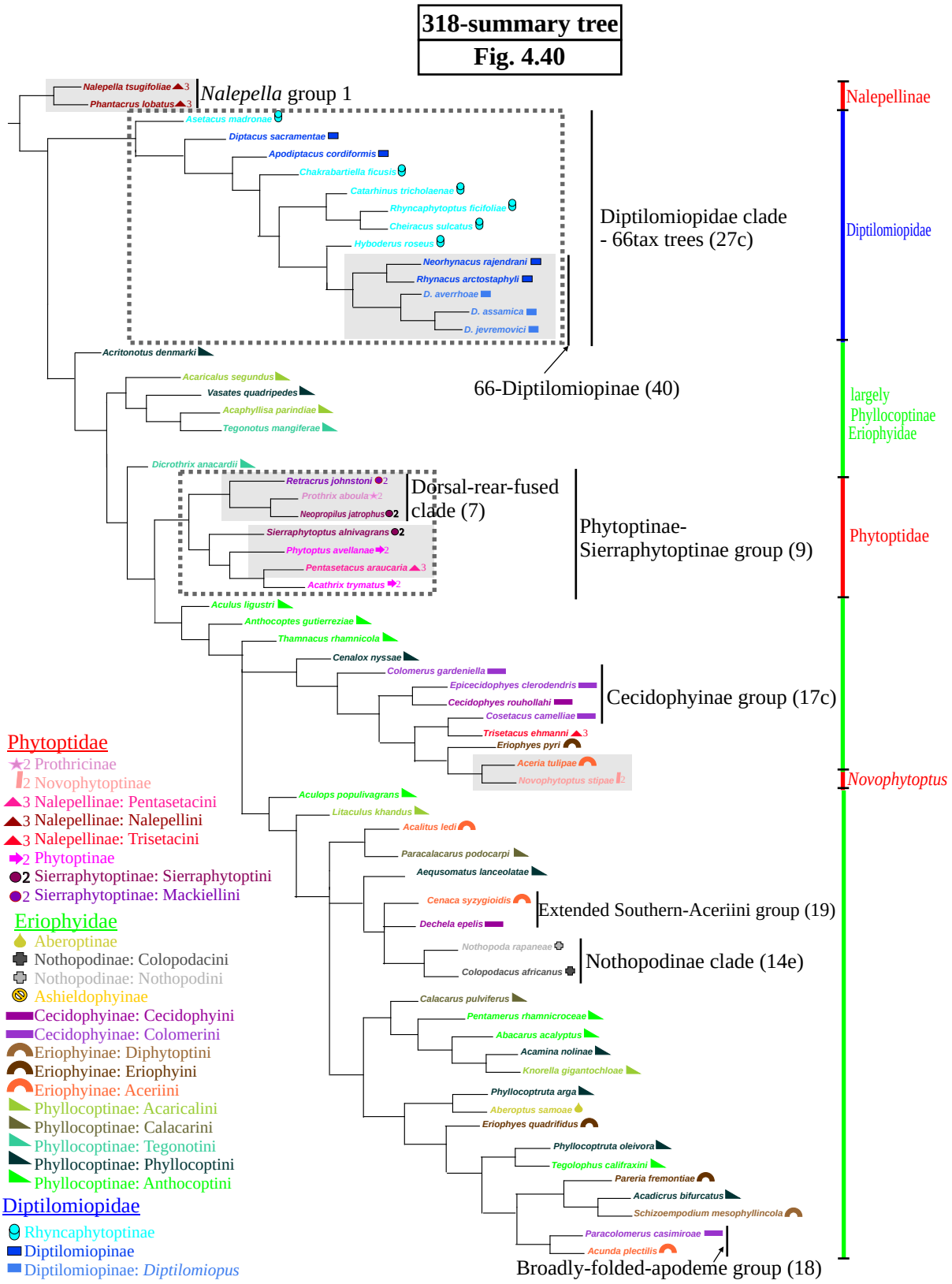


Figure 4.40. Summary (318-summary tree) of the 318tax-k10 tree (Fig. 4.6), constructed manually to schematically reflect the broad relationships between taxa from the 318-taxon data set which were included in the 66-taxon data set. It is a non-metric tree. It was literally done by eliminating those taxa not included in the 66-taxon analyses from the 318tax-k10 tree (Figs 4.6-4.23). The tree does not portray and should not be interpreted as literally sister group relationships found in the 318tax-k10 tree, but rather relative relationships and a hypothetical topology of what the topology of a 66-taxon tree in this study would be if it fully supported the relative relationships between taxa found in the 318tax-k10 tree. Parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43); parts of the tree blocked in stippled line block occur in the 66tax-k999 tree, but with different topologies.

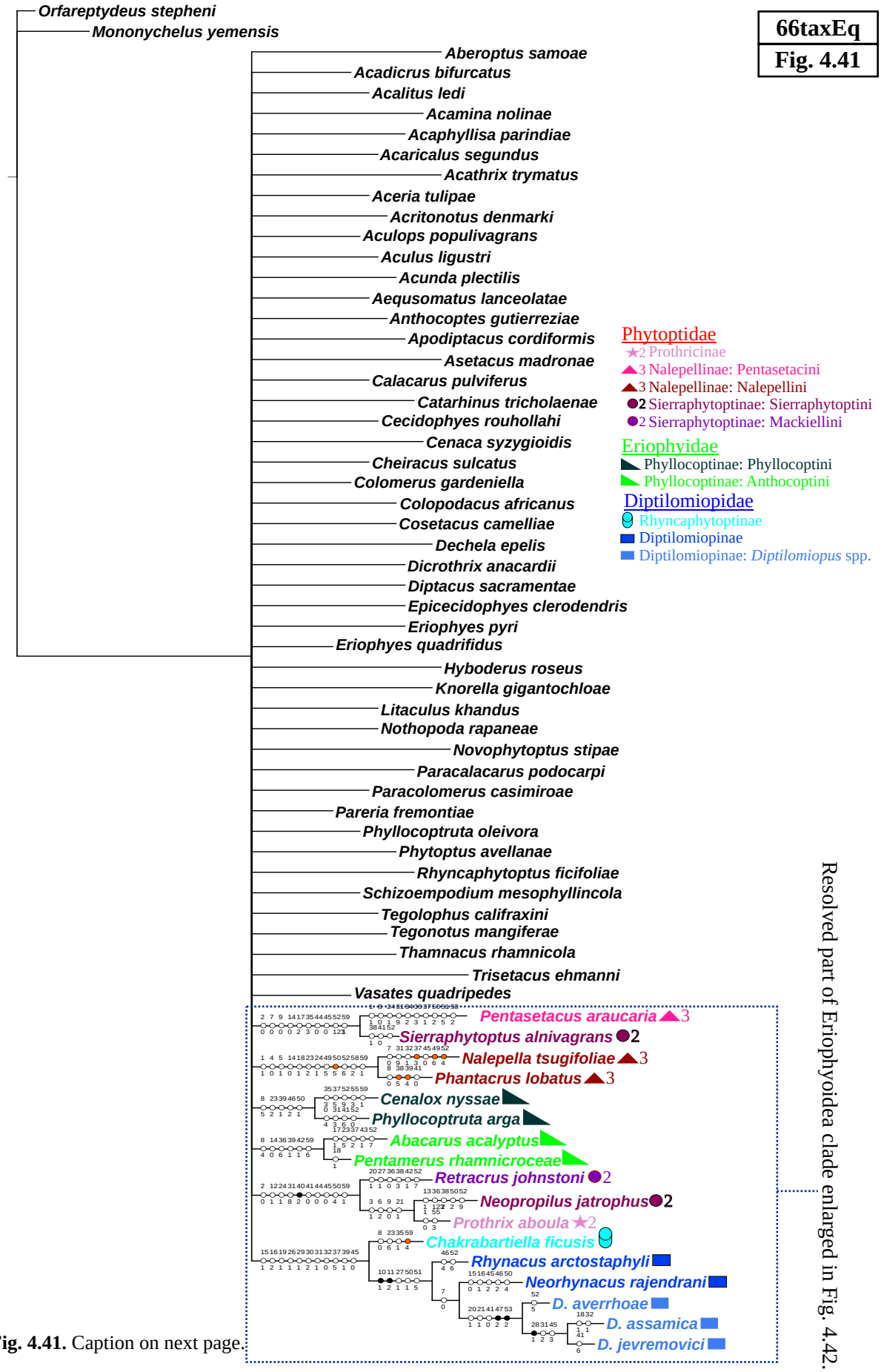


Fig. 4.41. Caption on next page.

66taxEq
Fig. 4.42

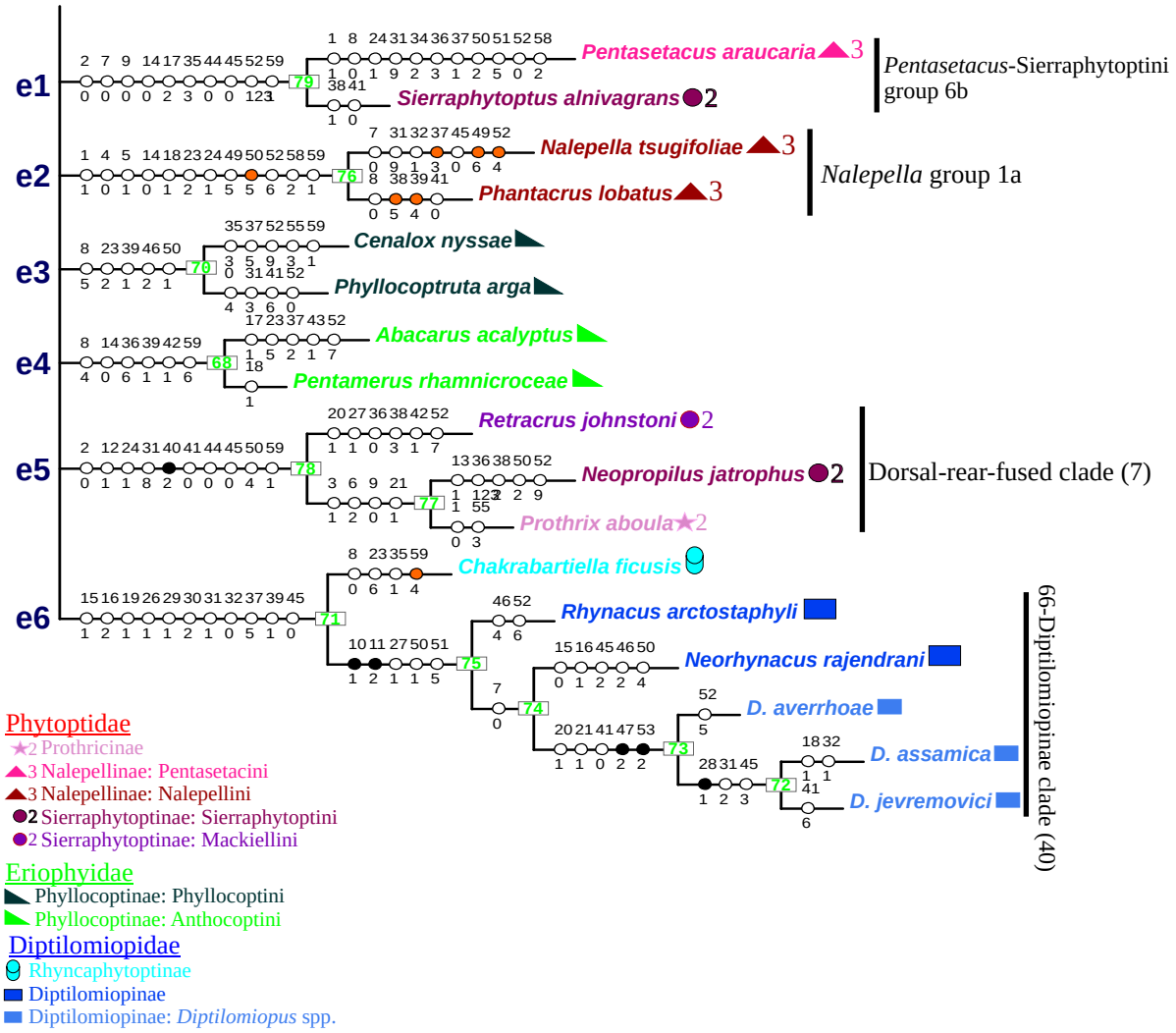


Fig. 4.41. (previous page). Strict consensus (Total fit = 38.91; Adjusted homoplasy = 47.09; Total length = 942; CI = 0.201; RI = 0.181) of 768 most parsimonious trees (each - Total fit = 44.20; Adjusted homoplasy = 41.80; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 207 times out of 7000 (replications overflowed), under equal character weights. Uninformative characters were excluded. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66taxEq tree. The resolved part of the tree is enlarged in Fig. 4.42. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character states below circles.

Fig. 4.42. (this page). Strict consensus of 768 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under equal character weights (66taxEq tree, Fig. 4.41): enlarged resolved part of the Eriophyoidea clade. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Blue e-numbers on left are reference numbers for groups found in tree, for indication of the groups on other trees. Informal names of groups discussed in text are on the right.

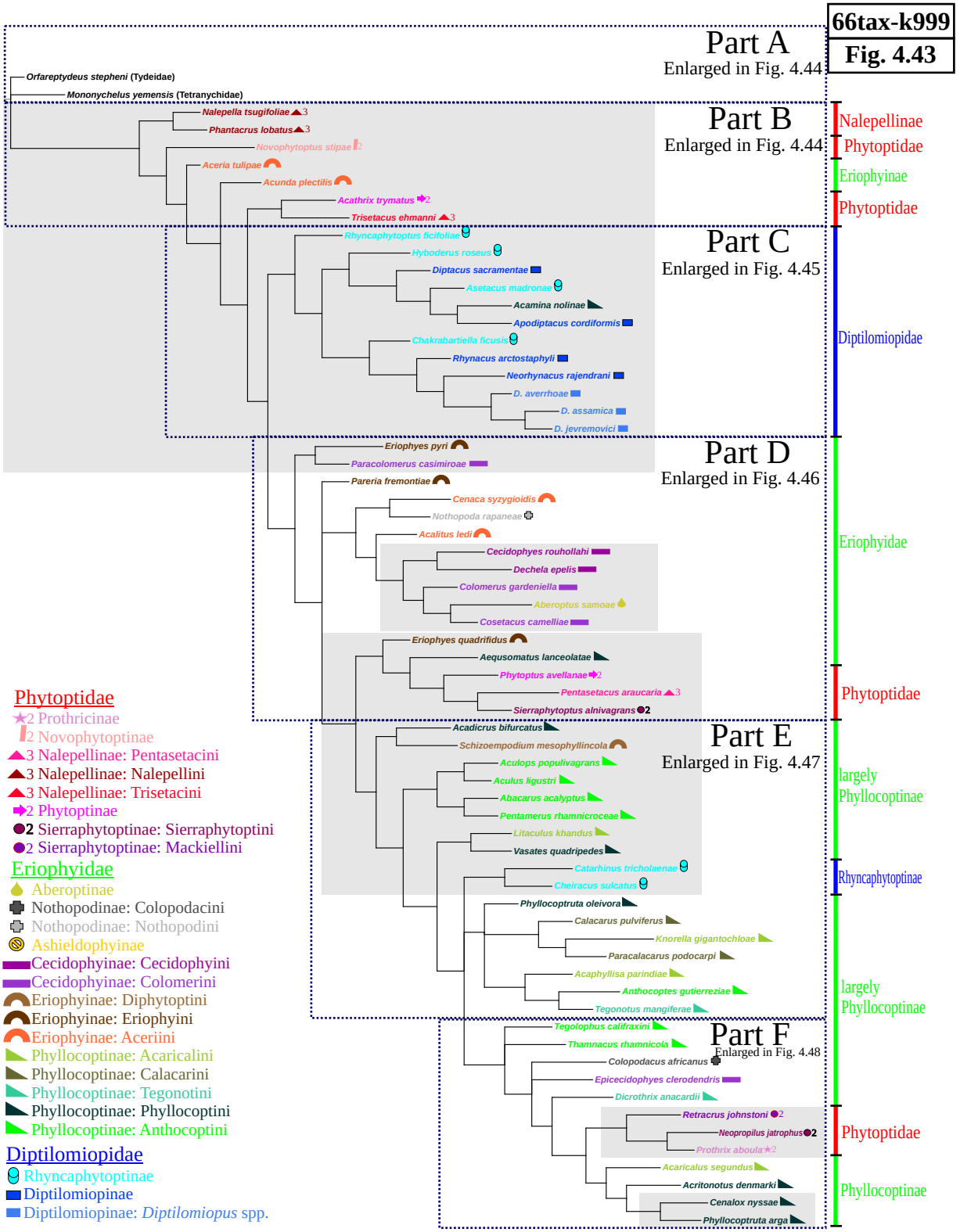


Fig. 4.43. Strict consensus (Total fit = 85.54; Adjusted homoplasy = 0.45; Total length = 649; CI = 0.291; RI = 0.501) of 3 most parsimonious trees (each - Total fit = 85.55; Adjusted homoplasy = 0.45; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 15 times out of 7000, 3 trees swapped with TBR branch-swapping, same 3 trees found, under implied character weighting with k=999, k=500, k=100, k=80, k=50 and k=40. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k999 tree. The bar on the right hand side indicate families and some notes on broad groupings. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between the, it does not always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node do not have "polarity" or "order" and can rotate around the node. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k30 tree (Fig. 4.51) which is one tree found with heuristic searches of the 66-taxon data matrix under implied character weighting with k=30. The tree is divided into six parts, which are enlarged in Figs 4.44-4.48.

66tax-k999
Fig. 4.44

Part A

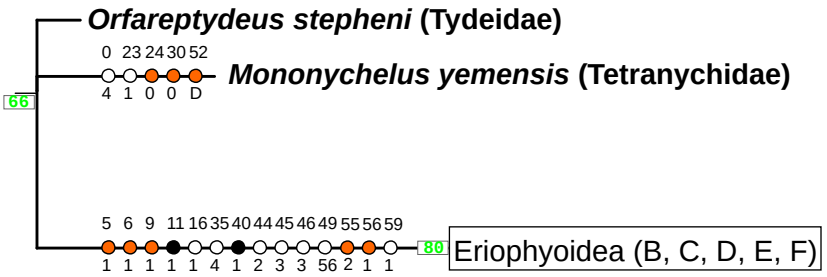


Fig. 4.44 Part A. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part A. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes.

Part B

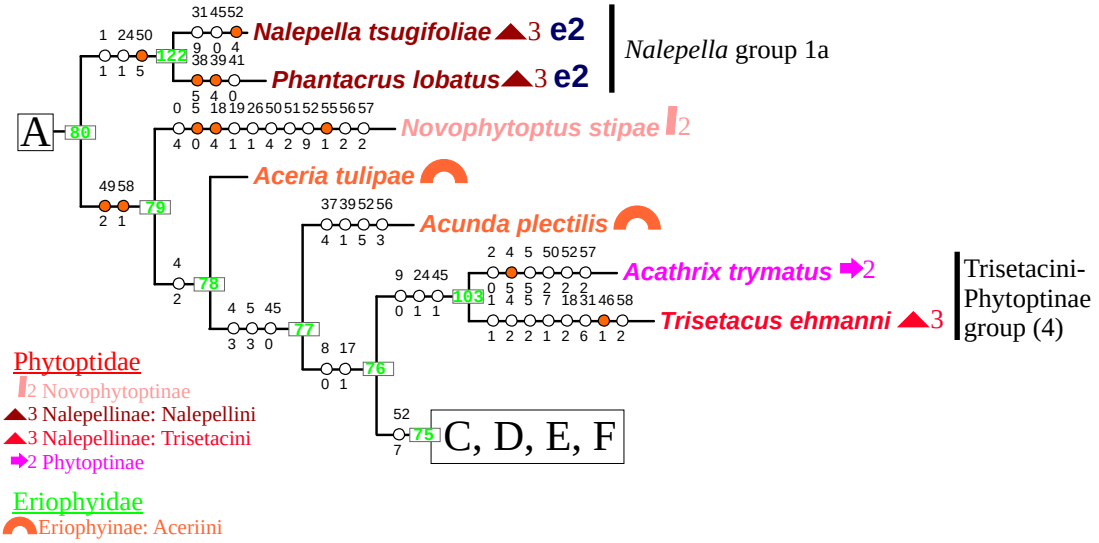


Fig. 4.44 Part B. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part B. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weights (Fig. 4.42).

Part C

66tax-k999
Fig. 4.45

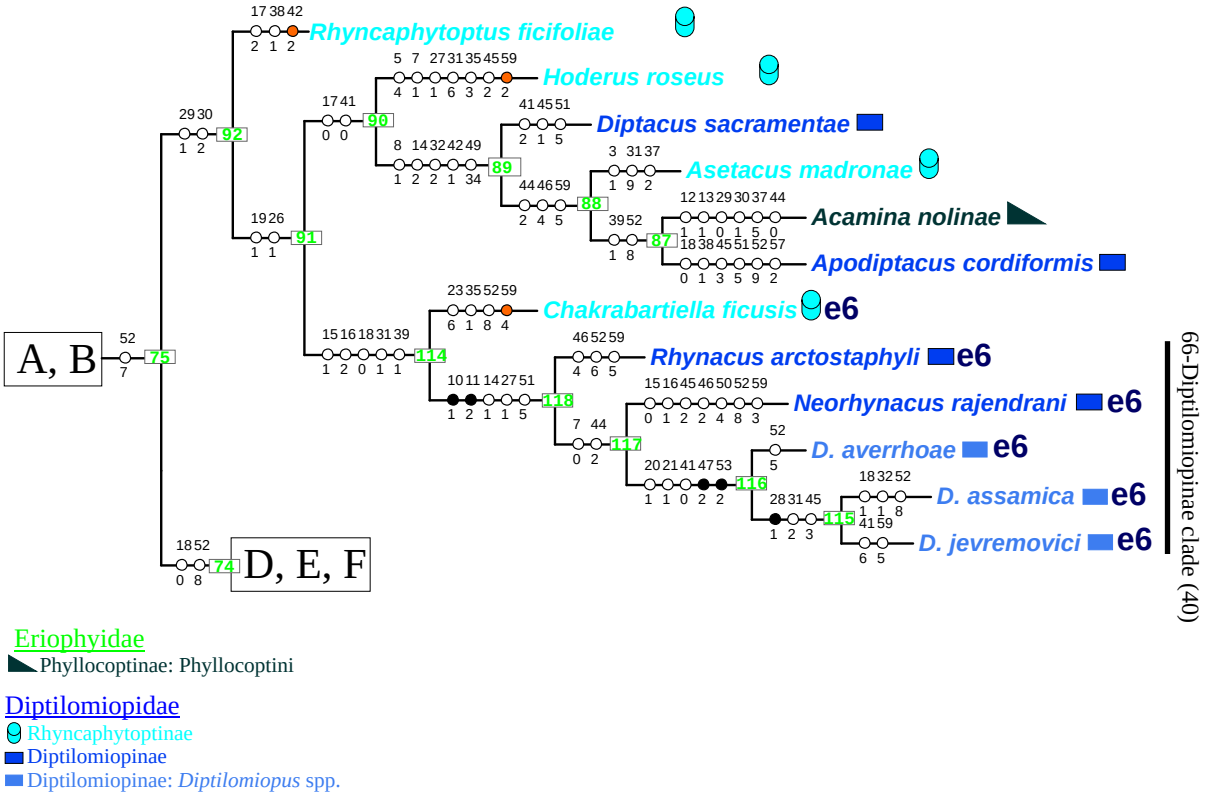
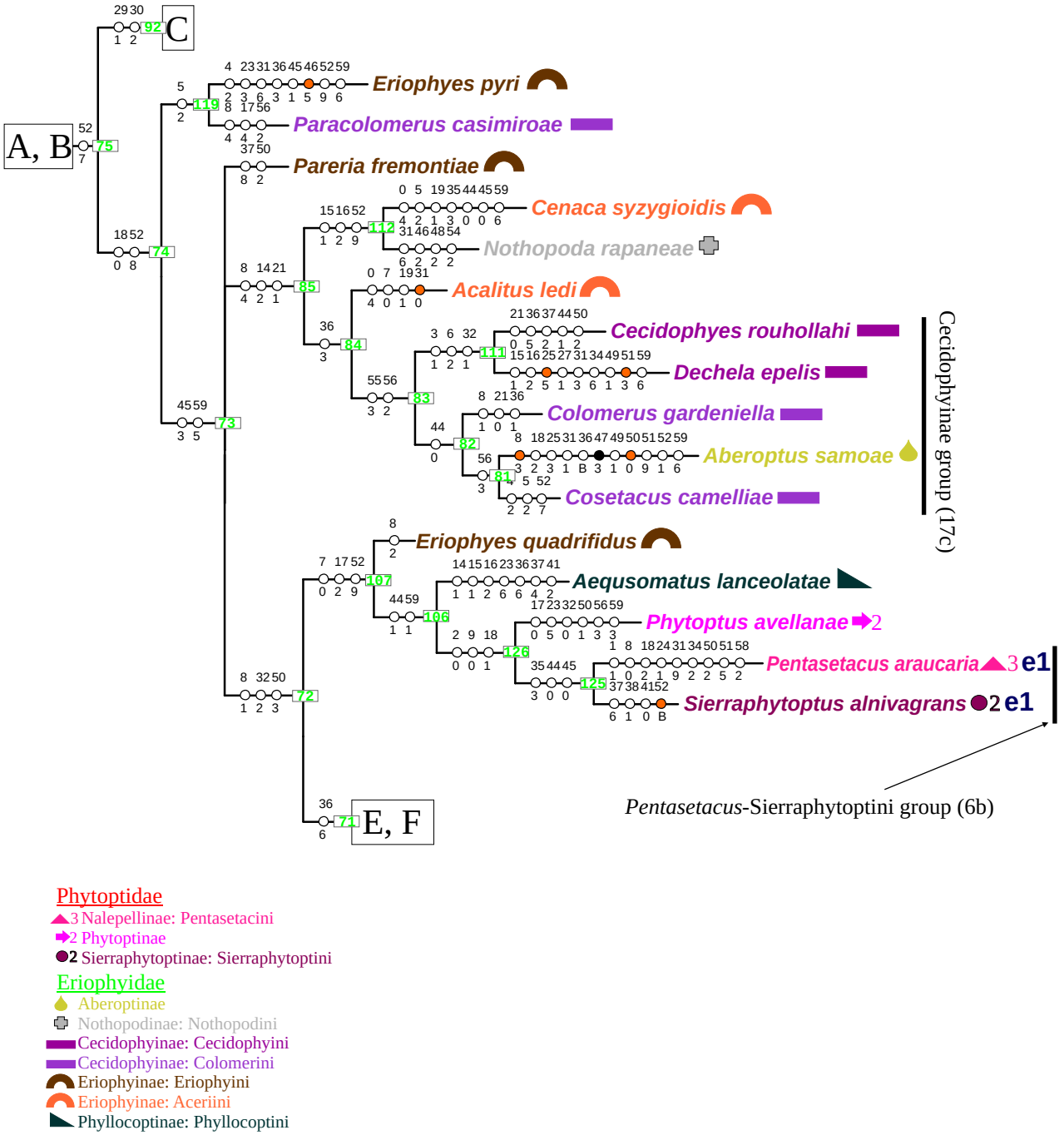


Fig. 4.45. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part C. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weights (Fig. 4.42).

Part D

66tax-k999
Fig. 4.46



Phytoptidae
▲3 Nalepellinae: Pentasetacini
➡2 Phytoptinae
●2 Sierraphytoptinae: Sierraphytoptini
Eriophyidae
Aberoptinae
Nothopodinae: Nothopodini
Cecidophyinae: Cecidophyini
Cecidophyinae: Colomerini
Eriophyinae: Eriophyini
Eriophyinae: Aceriini
Phyllocoptinae: Phyllocoptini

Fig. 4.46. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part D. Unsupported nodes were collapsed. Open circles are homoplasies, black circle an autapomorphy and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weights (Fig. 4.42).

Part E

66tax-k999
Fig. 4.47

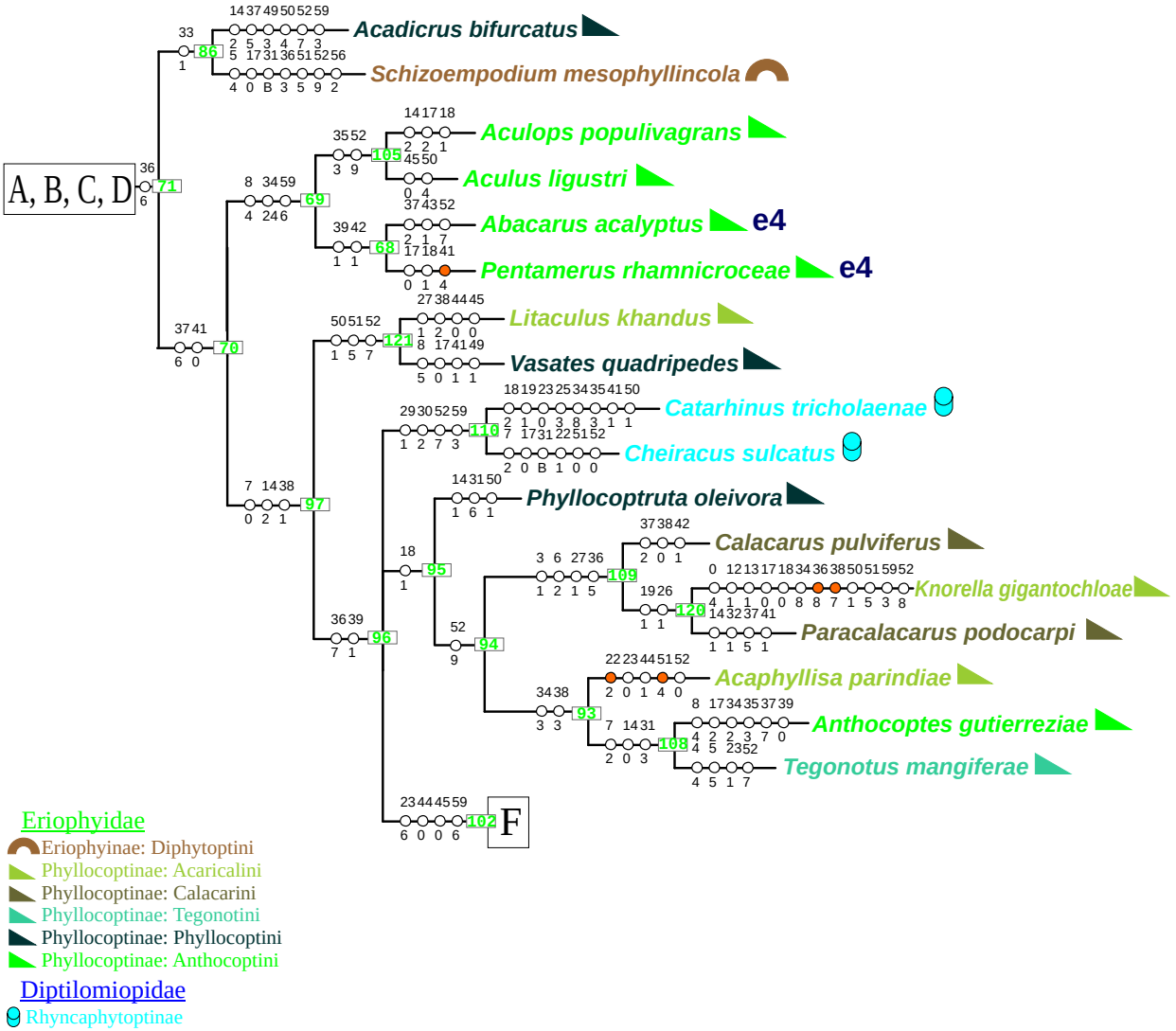
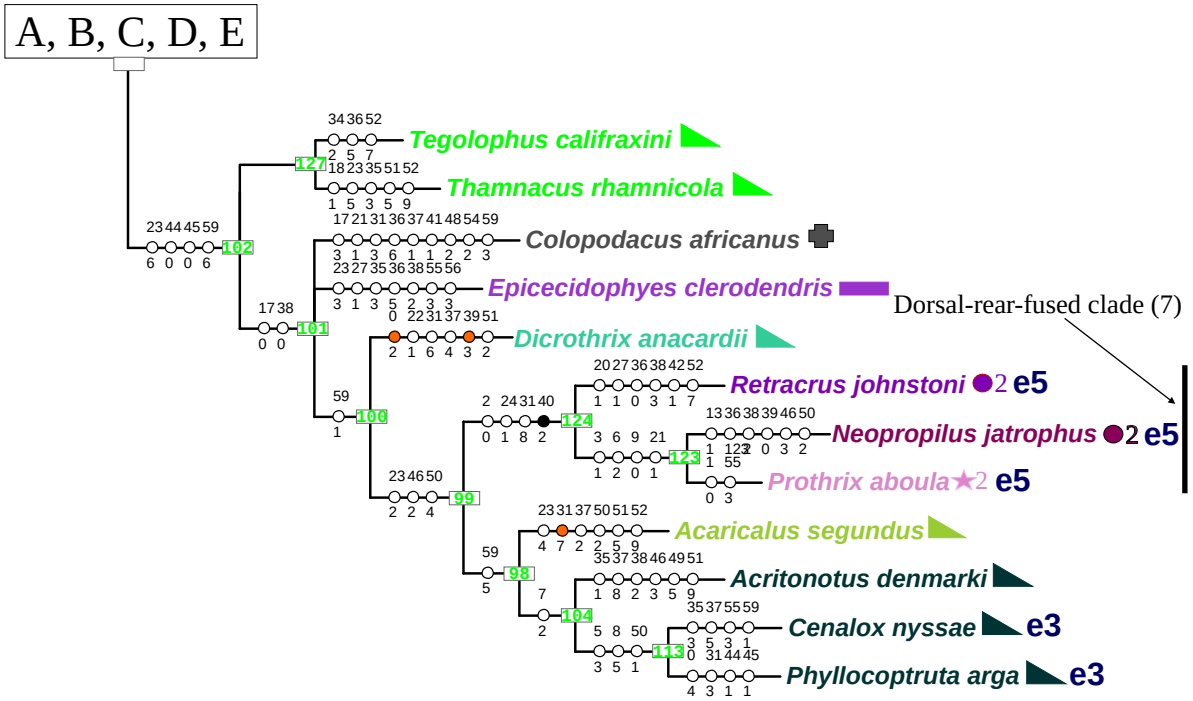


Fig. 4.47. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part E. Unsupported nodes were collapsed. Open circles are homoplasies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weights (Fig. 4.42).

Part F

66tax-k999
Fig. 4.48



Phytoptidae
★2 Prothricinae
●2 Sierraphytoptinae: Sierraphytoptini
●2 Sierraphytoptinae: Mackiellini

Eriophyidae
Nothopodinae: Colopodacini
Cecidophyinae: Colomerini
Phyllocoptinae: Acaricalini
Phyllocoptinae: Tegonotini
Phyllocoptinae: Phyllocoptini
Phyllocoptinae: Anthocoptini

Fig. 4.48. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part F. Unsupported nodes were collapsed. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right. Blue e-numbers on the right of terminal taxon names are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weights (Fig. 4.42).

66tax-k999
Fig. 4.49

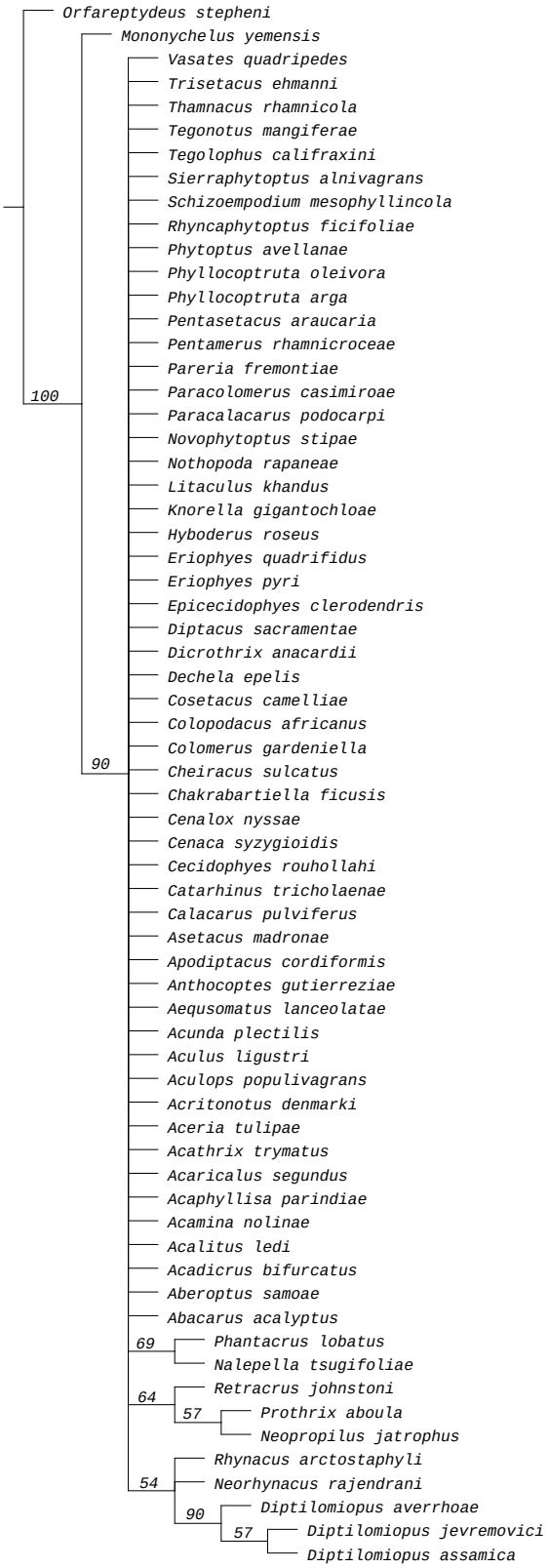


Figure 4.49. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic (”traditional” in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 50. Values are given above branches.

66tax-k999
Fig. 4.50

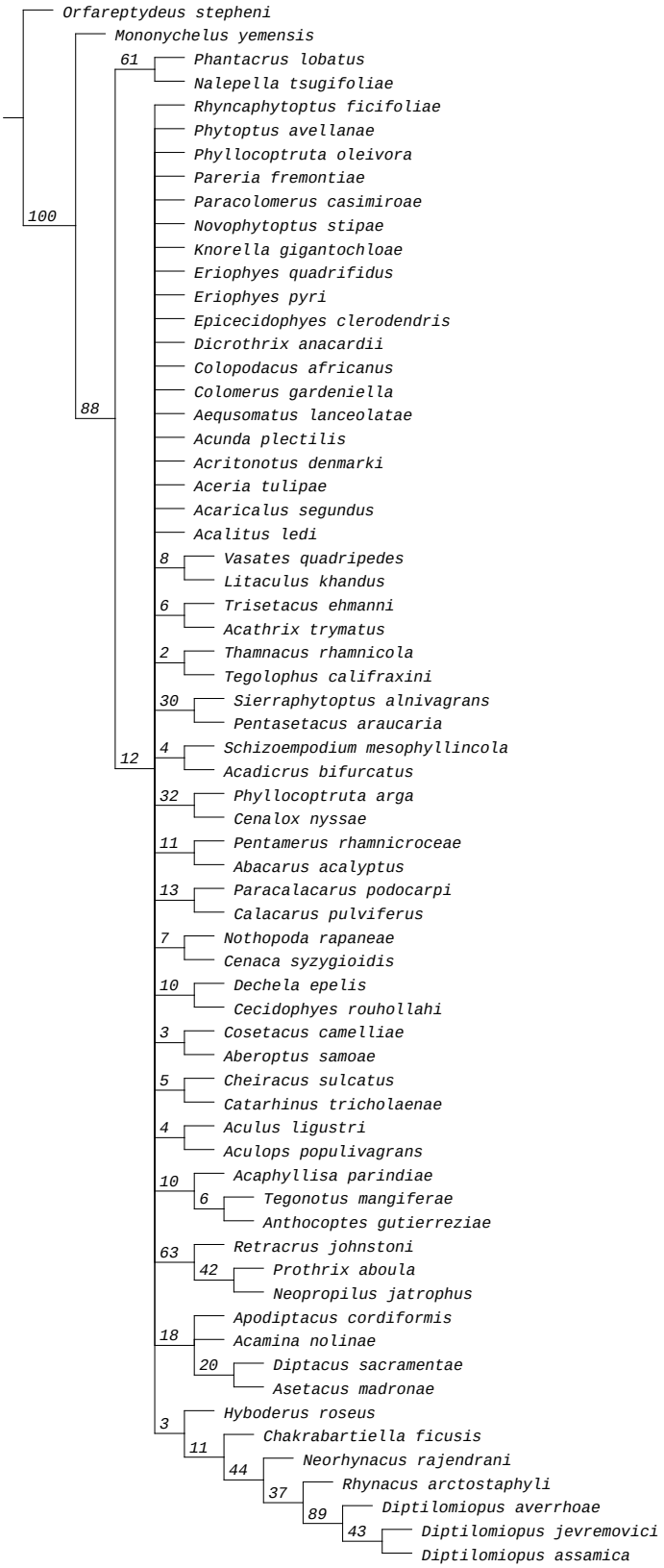


Figure 4.50. Symmetric resample group frequency difference (GC) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic (”traditional” in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 1. Only values of 20 or above were regarded as significant, and the other nodes were regarded as unsupported. Values are given above branches.

66tax-k30
Fig. 4.51

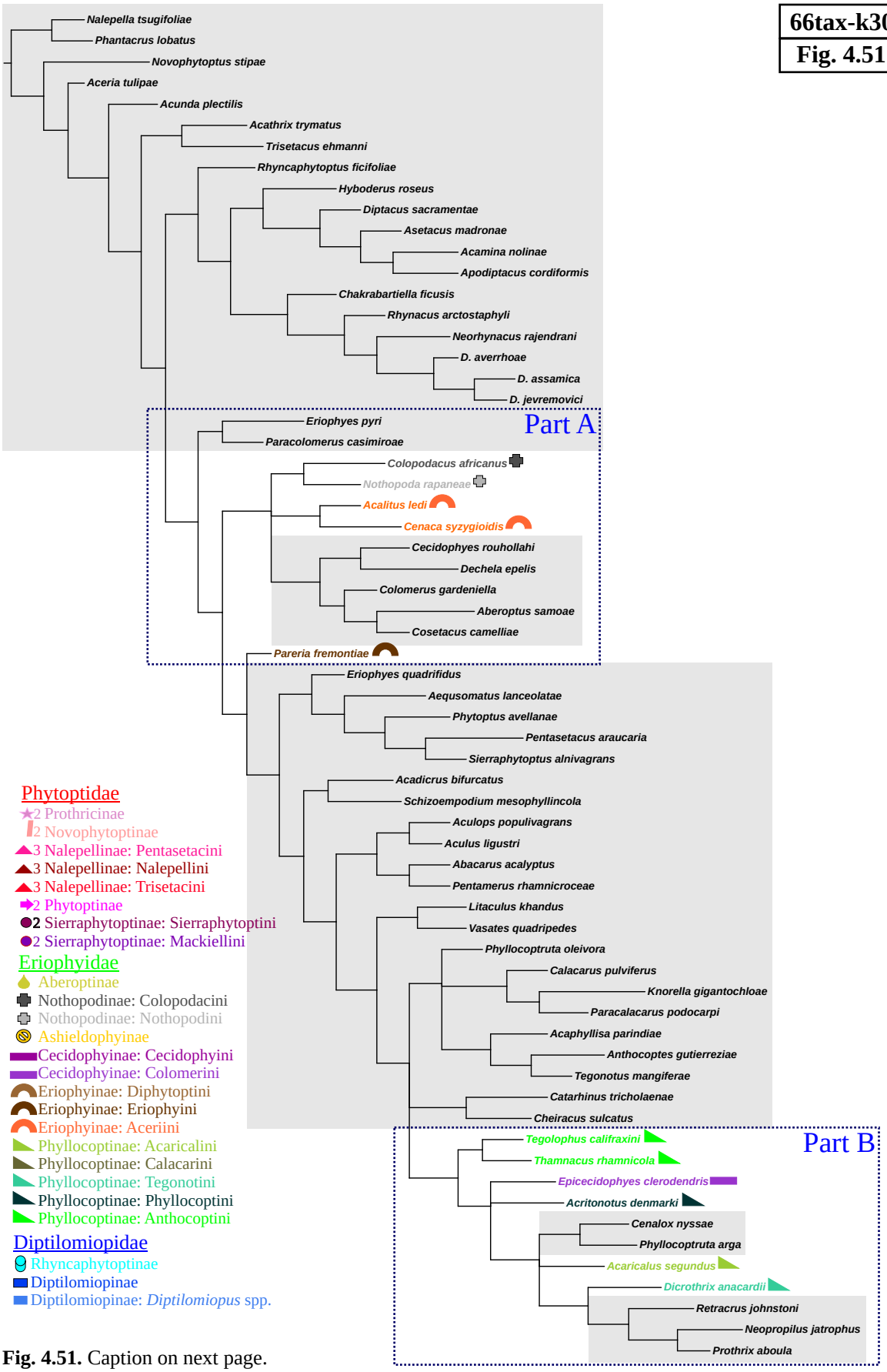


Fig. 4.51. Caption on next page.

Part A

66tax-k30
Fig. 4.52

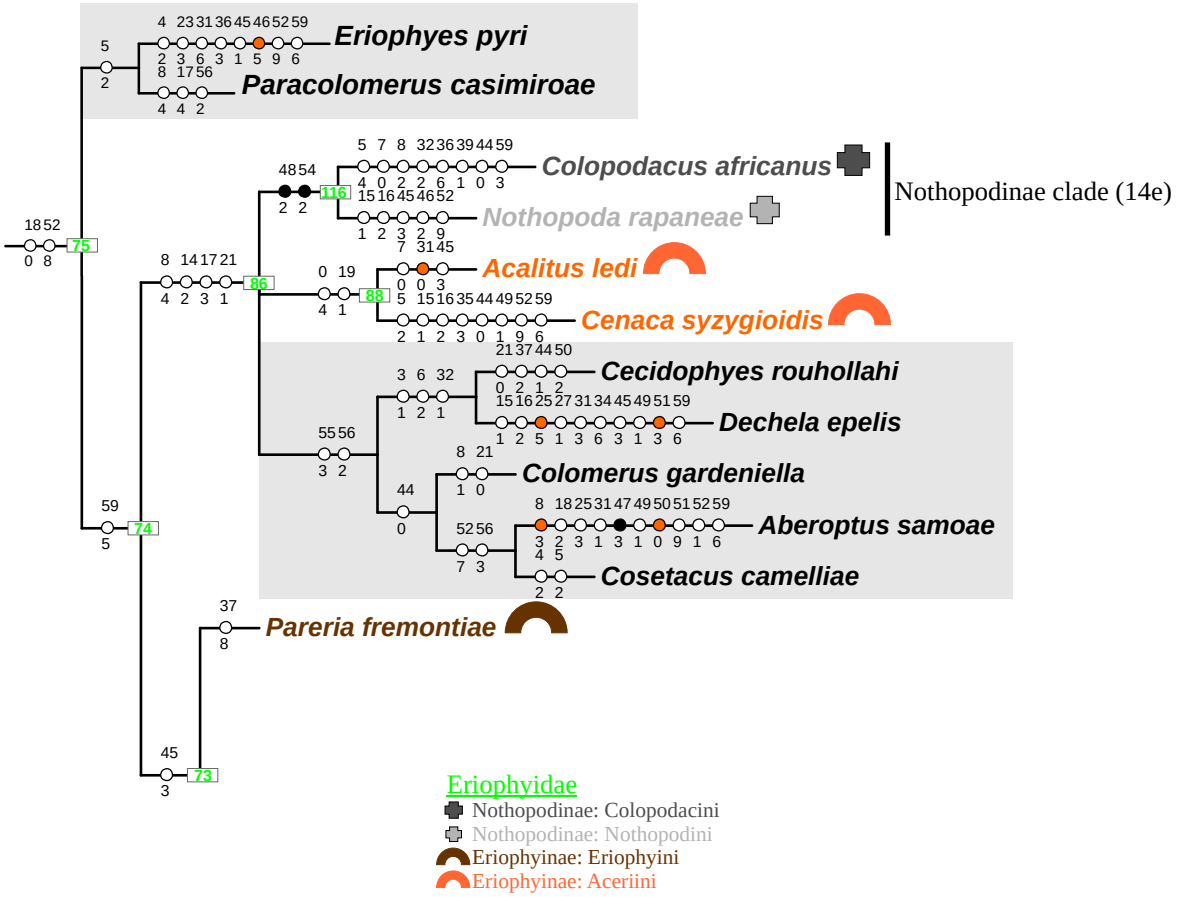


Fig. 4.51. (previous page) One most parsimonious tree (Total fit = 74.68; Adjusted homoplasy = 11.32; Total length = 651; CI = 0.290; RI = 0.497) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 2 times out of 7000, under implied character weighting with k=30. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k30 tree. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Only the two parts of the tree (Parts A and B) which partly differ in topology are enlarged in Figs 4.52 and 4.53, respectively.

Fig. 4.52. (this page) One most parsimonious tree found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied character weighting with k=30 (66tax-k30 tree, Fig. 4.51): enlarged Part A. Unsupported nodes were collapsed. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right.

Part B

66tax-k30
Fig. 4.53

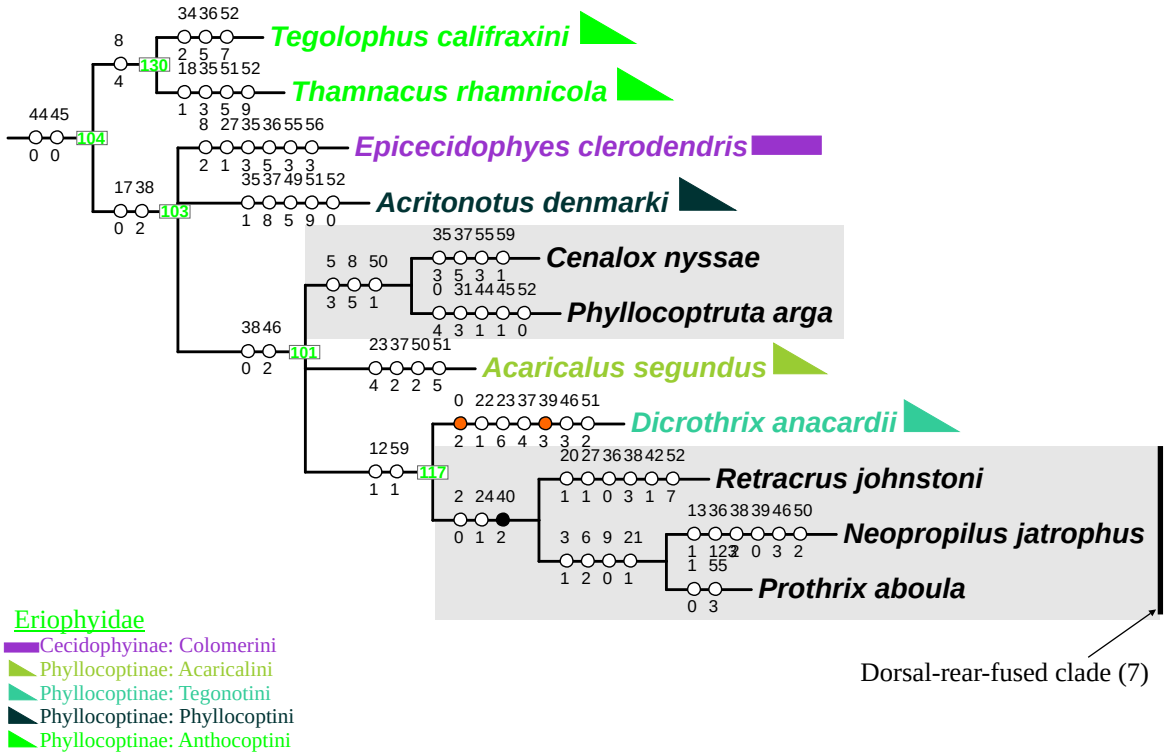


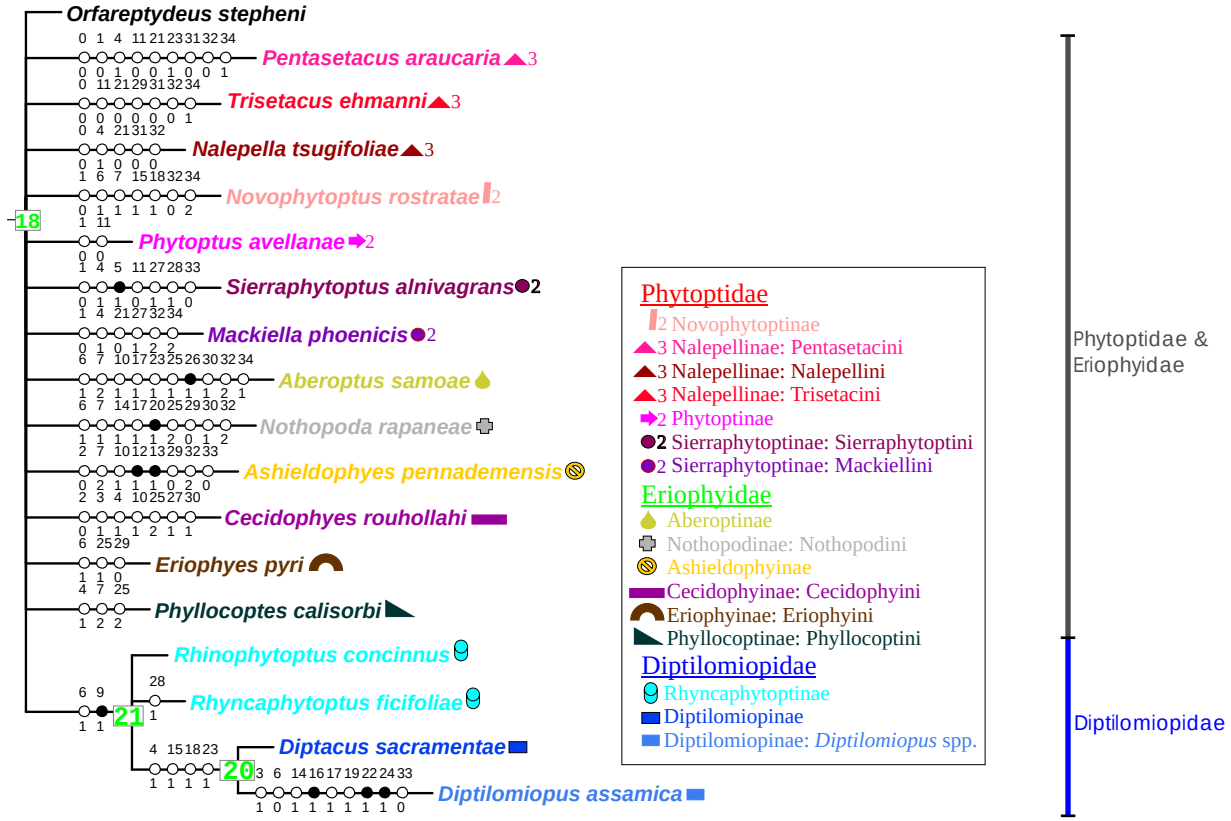
Fig. 4.53. (this page). One most parsimonious tree found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied character weighting with k=30 (66tax-k30 tree, Fig. 4.51): enlarged Part B. Unsupported nodes were collapsed. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. Open circles are homoplasies, black circles synapomorphies and orange circles character states which are not interrupted (not "homoplasious"). Character numbers above, and character state numbers below circles. The node numbers from TNT are the green numbers on the nodes. Informal names of groups discussed in the text are on the right.

Fig. 4.54. (next page) One most parsimonious tree (Total fit = 70.86; Adjusted homoplasy = 15.14; Total length = 659; CI = 0.287; RI = 0.489) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 1 time out of 7000, under implied character weighting with k=20. Uninformative characters were excluded. Unsupported nodes were collapsed. Tree plotted with Winclada. The entire tree is presented to show topology, and it is a metric tree. Tree name is 66tax-k20 tree. The parts of the tree blocked in grey also occur, with the same topology, in the 66tax-k999 tree (Fig. 4.43) which is a strict consensus tree of 3 most parsimonious trees found with heuristic search under implied character weighting of k=999. This tree is presented, although it is not the preferred tree, because it has an alternative topology to the other two trees presented, and seems to provide useful alternative hypotheses to be investigated. It provides another parameter "test" for the robustness of groups found in other trees, and gives an indication of the change in topology when weighting against homoplasy is slightly more significant than k=999 and 30 which have topologies very similar to one of the most parsimonious trees found under equal weighting. This tree is not discussed in such detail in the text than the other presented trees.

66tax-k20
Fig. 4.54

Fig. 4.54. Caption on previous page.

18correctEq
Fig. 4.55a



18correct-k999
Fig. 4.55b

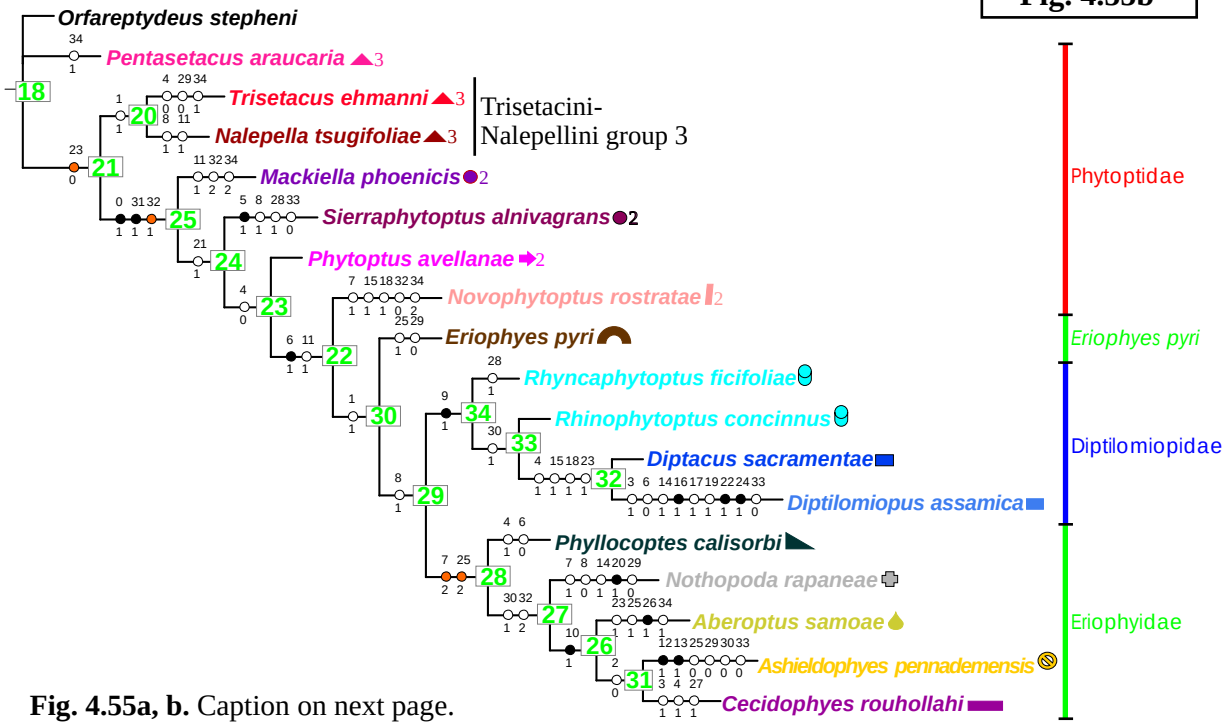


Fig. 4.55a, b. Caption on next page.

Fig. 4. 55. Corrected data matrix of Hong & Zhang (1996a) using taxa (but taxa are exemplar species, and not genera) characters and character states as defined by Hong & Zhang (1996a). I.) Preferred tree, implied weighting with k=999, implicit enumeration search resulted in one tree with L=85, ci=0.459, ri=0.483. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. II.) strict consensus (L=118, ci=0.331, ri=0.112) of 141 trees (each L=85, ci=0.459, ri=0.483), same data as for tree I above, analysed with implicit enumeration in TNT under equal weighting of characters. . The bars on the right hand side of the trees indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, the blue bars and text = Diptilomiopidae and the gray bar and text = mixture of Eriophyidae and Phytoptidae species. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

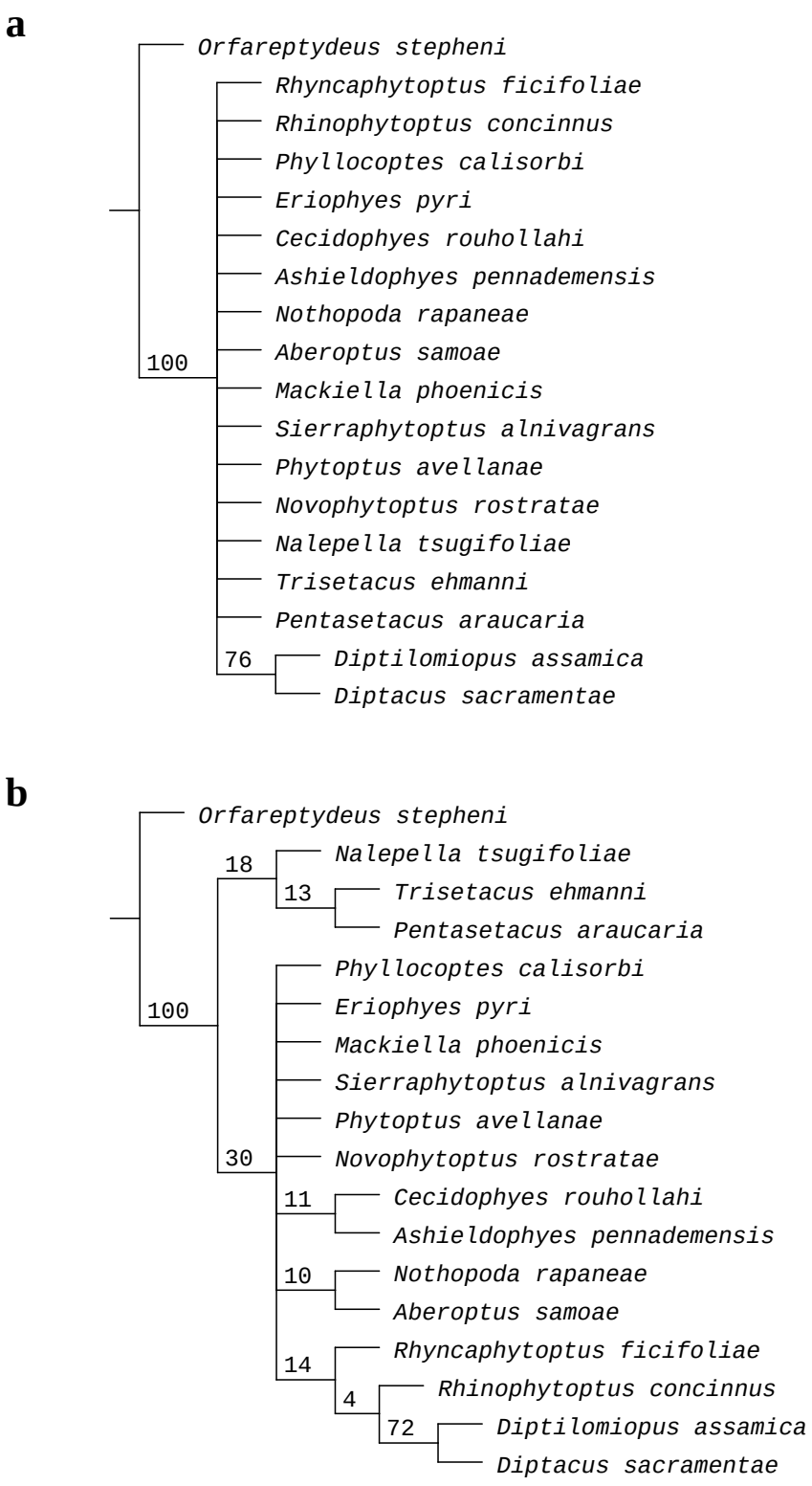


Fig.4.56. Symmetric resampling (P=33) with heuristic (”traditional” in TNT) searches of corrected Hong & Zhang (1996a) data set, 5000 replicates, done under implied weighting of characters with k=999 in TNT: **a)** group frequencies given above branches, branches with group frequency values of less than 50 are collapsed, average group support of 11; **b)** frequency differences (GC values) given above branches, branches with group frequency values of less than 1 are collapsed, average group support of 17.3.

18correct-k3
Fig. 4.57

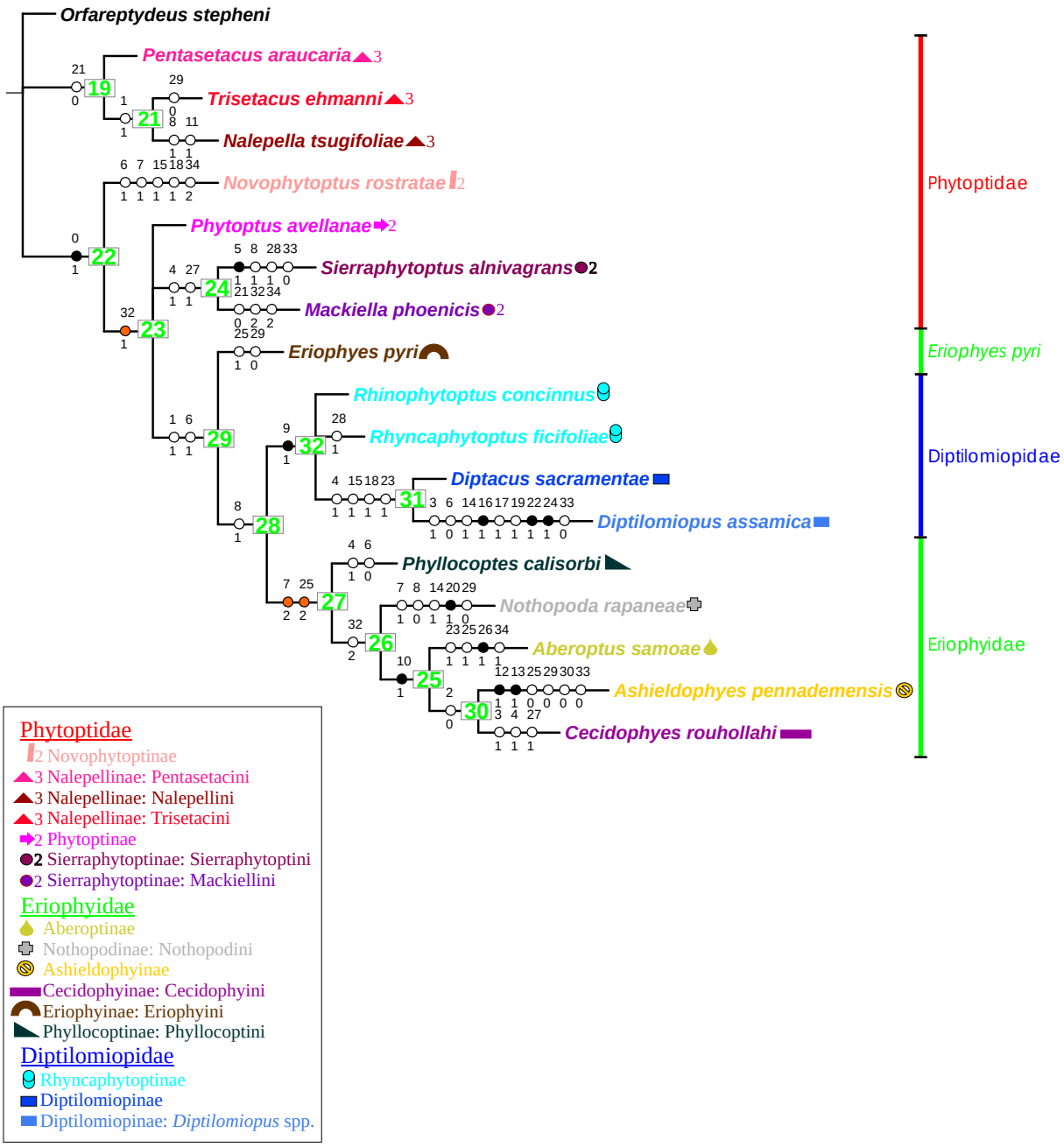


Fig. 4.57. Corrected data of Hong & Zhang (1996a) using characters and character states as defined by Hong & Zhang (1996a). Strict consensus (L=87, ci=0.448, ri=0.461) of 2 trees (each L=86, ci=0.453, ri=0.472), analysed with implicit enumeration in TNT under implied weighting of characters with k=3. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

18modifyEq
Fig. 4.58

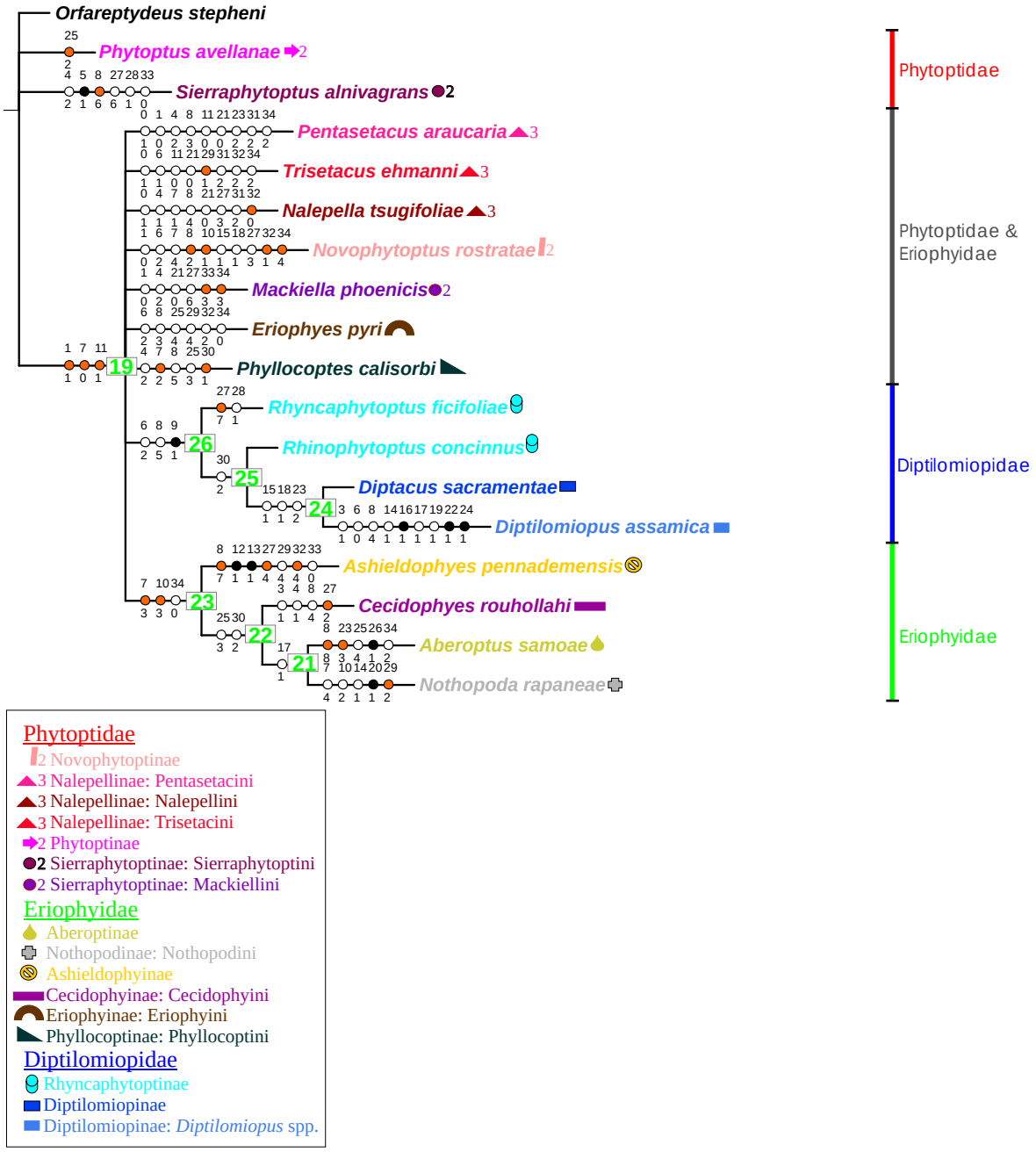


Fig. 4.58. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. I.) Strict consensus (L=132, ci=0.576, ri=0.309) of 10 trees (each L=117, ci=0.650, ri=0.494), analysed under equal weighting; II.) strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494) (a subcollection of 10 trees obtained under equal weighting). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, the blue bars and text = Diptilomiopidae, and the gray bar and text = a mixture of species of the Phytoptidae and Eriophyidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

18modify-k999
Fig. 4.59

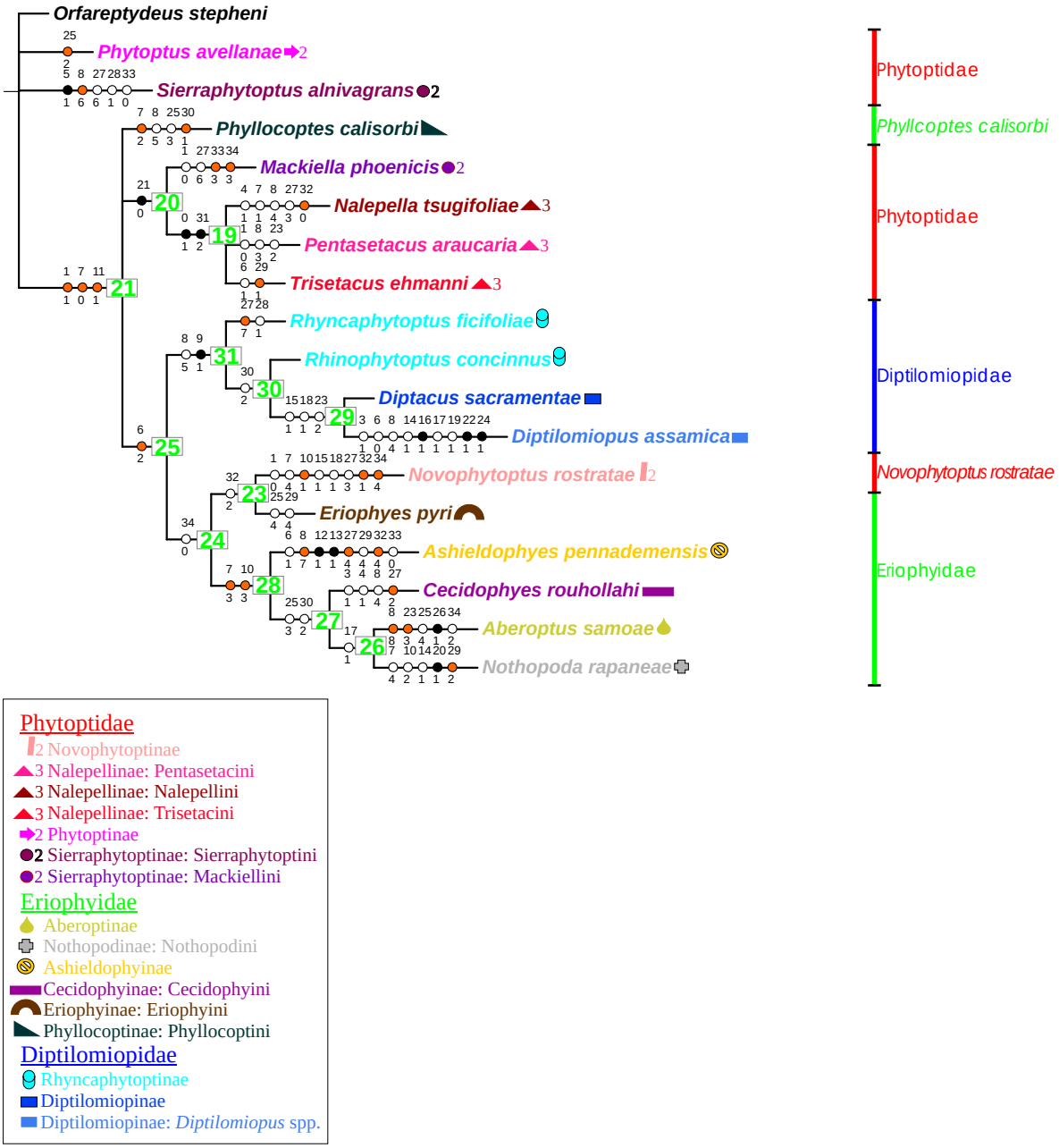


Fig. 4.59. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. Strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494), under implied weighting, k=100). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

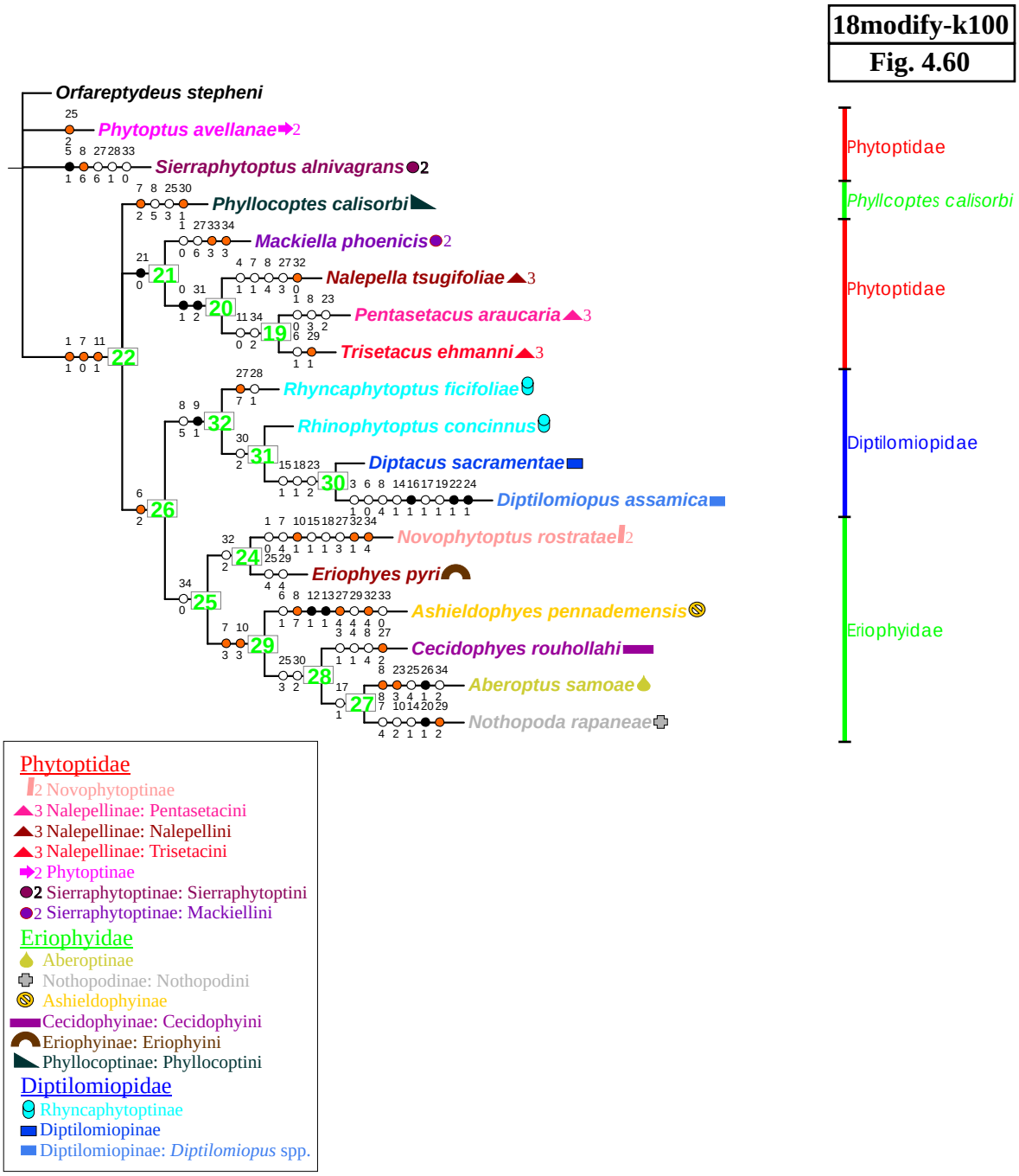


Fig. 4.60. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. Strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494), under implied weighting, k=100). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

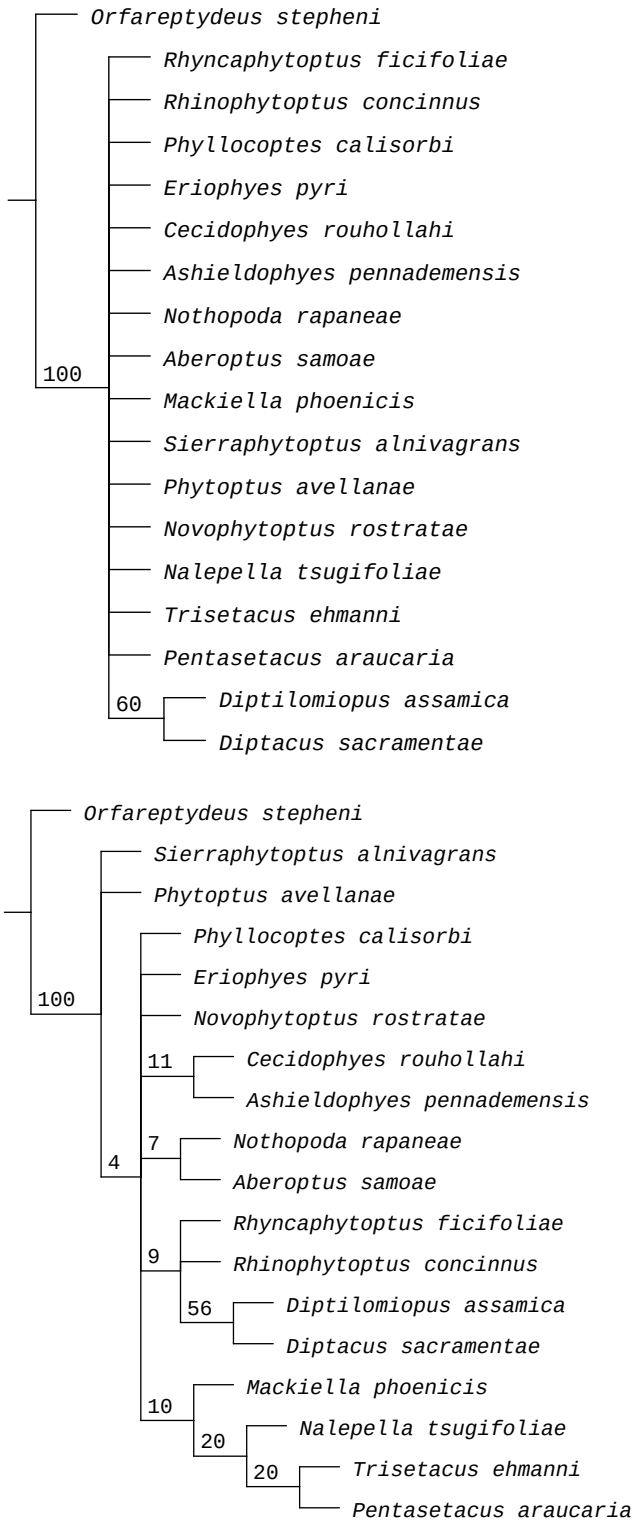


Fig.4.61. Symmetric resampling (P=33) with heuristic (”traditional” in TNT) searches of corrected Hong & Zhang (1996a) data set, with modified character states (this study), 5000 replicates, done under implied weighting of characters with k=100 in TNT: **a)** group frequencies given above branches, branches with group frequency values of less than 50 are collapsed, average group support of 10; **b)** frequency differences (GC values) given above branches, branches with group frequency values of less than 1 are collapsed, average group support of 15.

18modify-k3
Fig. 4.62

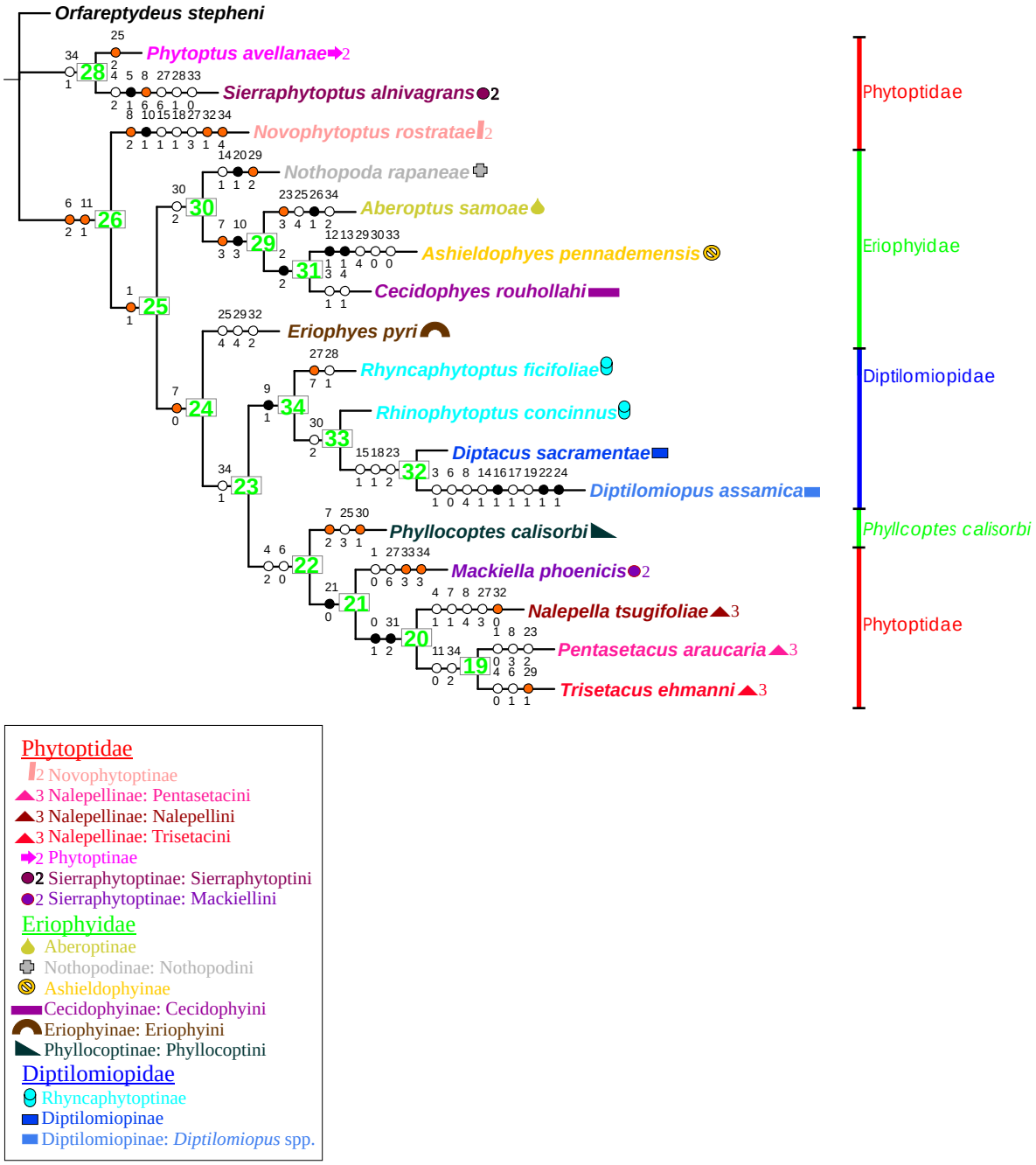


Fig. 4.62. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. One tree (L=118, ci=0.644, ri=0.481) resulted from implicit enumeration search in TNT under implied weighting, k=3. Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

4.7 RESULTS AND DISCUSSION: APPRAISAL OF THE MONOPHYLY OF ERIOPHYOIDEA SUPRAGENERIC TAXA OF THE CLASSIFICATION *sensu* Amrine *et al.* (2003)

This section largely concerns the assessment of the monophyly of the suprageneric taxa in the Eriophyoidea, and the first formal alternative classification partly based on empirical phylogenetic studies is proposed for the superfamily.

The trees obtained in the present study are the most parsimonious or approaching the most parsimonious and defendable hypotheses for the relationships and groups within the Eriophyoidea given the data sets analyzed. The best fit for the characters was also found by using implied weighting of characters. Most groupings are solely supported by homoplasies, though, and can not be regarded as monophyletic, although many groups make biological sense, and there is a chance that they may approach natural groupings. The groups are mostly not supported by resampling statistics, and the topology of the present results may change drastically in future, particularly when the character data are improved. Despite these shortcomings, useful hypotheses were obtained, even if just for consideration in decisions made according to traditional taxonomy within the Eriophyoidea. These should be done cautiously and keeping the lack of support for the results in consideration. The results indicate that the characters currently used for eriophyoid taxonomy are highly homoplasious anyway, and incorporating probably better hypotheses from the present phylogenetic study without disrupting the classification, will be an improvement. Groups and clades found by the different analyses and presented and discussed above are incorporated in this section by their names which are in bold and underlined, followed by their chronological number in brackets if the number is not inferred by the group name.

4.7.1 PHYTOPTIDAE

The Phytoptidae is one of three Eriophyoidea families (Table 1.1), and is regarded by some (e.g., Farkas, 1968b; Shevchenko, 1971; Sukhareva, 1994) as a key group in understanding the evolution of the Eriophyoidea. It is considered the earliest derived Eriophyoidea family, because they have characteristics which are regarded to be more primitive within the superfamily, and they additionally largely live on plants which are more primitive, including early derived Gymnospermae (Shevchenko, 1962; Das & Chakrabarti, 1989; Sukhareva, 1994; Lindquist & Amrine, 1996). The Phytoptidae *sensu* Keifer (1944, 1964a), Lindquist & Amrine (1996) and Amrine *et al*. (2003) are diagnosed by setae present anteriorly on the prodorsal shield: single or paired *vi* and/or *ve*. Shevchenko (1971, 1974a) did not regard the Phytoptidae *sensu* Amrine *et al*. (2003) as a monophyletic group. He divided this group of species into two of three superfamilies within the Tetrapodili which is the same taxon group

as the Eriophyidae *sensu* Nalepa (1929), and Eriophyoidea *sensu* Keifer (1964a), but at the suborder level. These superfamilies were: Trisetoidea (single *vi* present) which are the same grouping as Nalepellinae *sensu* Newkirk & Keifer (1971), and Phytoptoidea (single *vi* absent, *ve* present) which are the same grouping as Phytoptinae + Novophytoptinae + Sierraphytoptinae, taxa *sensu* Amrine & Stasny (1994). Shevchenko (1976) changed the two superfamilies, Trisetoidea and Phytoptoidea, to family level (Nalepellidae and Phytoptidae *sensu* Shevchenko, 1976), the same as in the classification presented by Boczek *et al.* (1989), but stressed that he still regards them as two separate, natural lineages. Shevchenko (in Boczek *et al.*, 1989) proposed a family rank taxon, Pentasetacidae (same group as Pentasetacini *sensu* Amrine & Stasny, 1994) for *Pentasetacus* Schliesske, 1985 (single *vi*, *ve* and *sc* present).

Species of all 21 Phytoptidae genera (Amrine *et al.*, 2003) were included in the present study. The Phytoptidae was never recovered as a clade, or as an exclusive group at one node, by any of the cladistic analyses under various parameters, and is proposed to be polyphyletic and partly paraphyletic [see for example the 318tax-k10 (Fig. 4.6) and –k20 (Fig. 4.26) trees]. These results do not support the classification presented in Amrine *et al*. (2003), but is more in accordance with the classification proposed by Boczek *et al.* (1989), although not entirely. The results also support the proposal that the Phytoptidae is not monophyletic by, among others, Lindquist (1996b) and Lindquist & Amrine (1996). They came to this conclusion because they regarded the diagnostic characters of the Phytoptidae as plesiomorphic character states within the Eriophyoidea, *a priori* phylogenetic analyses. This argumentation leads to the conclusion that the family is paraphyletic, which is also partly supported by the present study, since some Phytoptidae groups were recovered imbedded among the Eriophyidae.

Although the Phytoptidae was not retrieved as a monophyletic group in its entirety, it seems that classifying Phytoptidae subgroups as taxa largely exclusively with Phytoptidae species, is well-supported by the present results. Phytoptidae species were recovered in several relatively robust groups and clades under all parameters, and these groups, mostly, did not include Eriophyidae and never Diptilomiopidae species.

The Phytoptidae have five subfamilies (Amrine *et al*., 2003; Table 1.1), and the appraisal of their monophyly is as follows.

Prothricinae

This Phytoptidae *sensu* Amrine *et al*. (2003) subfamily is proposed to be a junior synonym of the Propilinae (new subfamily, Table 4.10), which is proposed to be a subfamily of the Phytoptidae *sensu* the present study (Table 4.10). See earlier discussion of the position of *Prothrix*. In his unpublished study (R. Ochoa, *pers. comm.*) *Prothrix* was also recovered in an exclusive group consisting of Sierraphytoptinae taxa, supporting the present proposal to include *Prothrix* in a subfamily of the Phytoptidae *sensu* the present study (Table 4.10).

Novophytoptinae

This subfamily comprises *Novophytoptus* spp., which have genitalia positioned much further away from the coxisternal area than usually found in the Eriophyoidea (Fig. 3.5g) (Roivainen, 1953: 85–86). Two of the six *Novophytoptus* spp. (Amrine *et al.*, 2003; Chetverikov & Sukhareva, 2007) were included in the 318tax data set, and were found to be sisters [***Novophytoptus* group (12a)**] under equal character weights, and the Novophytoptinae (or indeed the genus *Novophytoptus*) may be monophyletic. This supports the proposal by Lindquist & Amrine (1996) that the Novophytoptinae may be a clade, supported by one synapomorphy, the position of the genitalia. The position of the genitalia (Character 112, Appendices B & C), including the state "about 9-15 annuli removed from coxae, located posterior to c2" was always found to be homoplastic in the present study, though. When more phylogenetic phylogenetic resolution was found with implied weighting, the *Novophytoptus* spp. were found to be paraphyletic, and were recovered as sisters of some Phyllocoptinae species [***Novophytoptus-Tetra* group (12b)**], and when only one *Novophytoptus* sp. was included in a data set, it was sometimes recovered as sister of *Eriophyes* (Eriophyinae) [***Novophytoptus-Eriophyes* group (12c)**], but these relationships are weakly supported. The relationships of *Novophytoptus* spp. with each other and other Eriophyoidea taxa have not been resolved conclusively by the present study and are uncertain. It seems, though, that *Novophytoptus* probably have a closer relationship with some Eriophyidae than with Phytoptidae taxa. The subfamily is therefore assigned to the Eriophyidae (**comb. nov.**).

In Boczek *et al.* (1989) the Novophytoptinae is a subfamily of their more restricted Phytoptidae (which excludes species with single *vi* present), and not a subfamily on the same level with other subfamilies of the Phytoptidae *sensu* Keifer (1964a) which include subfamilies with single *vi* present. Boczek *et al.* (1989) thus implied the loss of single *vi* in *Novophytoptus* is earlier derived than the position of the genitalia. Neither of these classifications was supported by the present results, because the *Novophytoptus* spp. were not recovered in close relationships with other Phytoptidae species.

Table 4.10. A proposed new classification of suprageneric and genera of the Eriophyoidea, partly based on the phylogeny recovered in the present study. A priority was the preservation of the stability of the classification *sensu* Amrine *et al.* (2003), but with changes based on groups found with phylogenetic analyses in the present study, and which are proposed to render the classification more natural. Drastic changes, particularly to nomenclature and practicality (for classifying and identification), were regarded premature. The proposed classification is thus not entirely phylogenetic, purely based on the phylogeny found in the present study. The relationships and taxonomic positions of the genera are extrapolated from the relationships of the species (usually type species) found in the present study. This essentially assumes the monophyly of genera which is not necessarily true or implied. Where more than one species of a genus were included in the present study, they are included as separate species in the proposed classification. Many *Diptilomiopus* spp. were included in the analyses, but all remain in the Diptilomiopinae, and only the genus name is used.). The genera within a suprageneric taxon are listed alphabetically, and the order in which they are listed does not imply relationships. "*Comb. nov*." refers to the new position of the genus and not to a recombination of the species with another genus. Species and their genera not included in the present study, are not dealt with, and remain classified according to Amrine *et al.* (2003). The classificatory structure and position of the Phyllocoptinae and placement of its genera remain as presented in Amrine *et al*. (2003). Despite the inclusion of their presumably deutogyne females in the present phylogenetic study, *Aceria kenyae* (= *Cisaberoptus kenyae*) and *A. pretoriensis* (= *C. pretoriensis*) are not included in the classification proposed here, and they remain within *Aceria* (Eriophyidae: Eriophyinae) as proposed by Amrine *et al*. (2003).

Superfamily: Eriophyoidea Nalepa, 1898

Family: Nalepellidae Roivainen, 1953
= Nalepellinae Roivainen, 1953
= Trisetacini Farkas, 1968
= Nalepellini Roivainen, 1953

Boczekella **comb. nov.**
Nalepella
Pentaporca
Phantacrus
Setoptus **comb. nov.**
Trisetacus ehmanni **comb. nov.**
T. pini **comb. nov.**

Family: Pentasetacidae Shevchenko, 1989 (*in* Boczek, Shevchenko & Davis, 1989)
= Pentasetacini Shevchenko, 1989 *sensu* Amrine *et al.* (2003)

Pentasetacus

Family: Phytoptidae Murray, 1877
Subfamily: Phytoptinae Murray, 1877
= Sierraphytoptinae Keifer, 1944
= Phytoptini (= Sierraphytoptini Keifer, 1944)
= Mackiellini Newkirk & Keifer, 1971
Acathrix
Austracus
Fragariocoptes
Mackiella
Oziella
Phytoptus (= *Anchiphytoptus*) genus synonymy by Chetverikov *et al*. (2009)
Sierraphytoptus

Subfamily: Propilinae Keifer, 1975 **(new subfamily)**
Type genus/species: *Propilus gentyi* Keifer, 1975
= Prothricinae Amrine, 1996 **syn. nov.**

Diagnosis.
The fusion of dorsal annuli caudad *f*, is the synapomorphy supporting this subfamily, and distinguishing it from other Eriophyoidea. The body is fusiform, flattened dorsoventrally, with annuli differentiated into relatively narrow ventral annuli with microtubercles and fewer, broader dorsal annuli, without microtubercles, and when annuli are subequal dorsoventrally, the annuli are slightly broader than usually found in vermiform species, and the ventral annuli are without microtubercles. The prodorsal shield with a roughly similar shape in all species is broadly rounded or square, and anteriorly in lateral view characteristically dorsally elevated before the gnathosoma. Frontal lobe is present. Seta *ve* present, positioned anteriorly on the vertical prodorsum anterior edge, almost on the lateral angle of the broad prodorsal shield, and is projected anteriad. Single *vi* is absent. Seta *sc* as well as the scapular tubercle are present or absent. When present, *sc* may be positioned far forward, directed anteriad (e.g., *Prothrix*), or closer to the rear shield margin, and directed posteriad (e.g., *Retracrus*). Some species with wax. All species for which host plants were recorded, were collected from palms (Arecaceae).

Neopropilus Huang, 1992 **comb. nov.**
Propilus Keifer, 1975 **comb. nov.**
Retracrus Keifer, 1965 **comb. nov.**
Prothrix Keifer, 1965 **comb. nov.**

Family: Eriophyidae Nalepa, 1898
Subfamily: Novophytoptinae Roivainen, 1953 **comb. nov.**
Novophytoptus rostratae **comb. nov.**
Nov. stipae **comb. nov.**

Subfamily: Aberoptinae Keifer, 1966
Aberoptus

Subfamily: Nothopodinae Keifer, 1956
= Colopodacini Mohanasundaram, 1984
= Nothopodini Keifer, 1956
Adenocolus
Anothopoda

Apontella
Colopodacus\
Cosella
Disella
Floracarus
Neocosella
Nothopoda
Pangacarus

Subfamily: Ashieldophyinae Mohanasundaram, 1984
Ashieldophyes

Subfamily: Cecidophyinae Keifer, 1966
Tribe: Cecidophyini Keifer, 1966
Achaetocoptes
Bariella
Cecidophyes
Chrecidus
Coptophylla
Epicecidophyes **comb. nov.**
Glyptacus
Johnella
Neocecidophyes **comb. nov.**

Tribe: Colomerini Newkirk & Keifer, 1975
Afromerus
Circaces
Colomerus
Cosetacus
Ectomerus
Gammaphytoptus
Indosetacus

Subfamily: Eriophyinae Nalepa, 1898
= Diphytoptini Amrine & Stasny, 1994
= Eriophyini Nalepa, 1898
= Aceriini Amrine & Stasny, 1994
Acalitus
Aceria
Acerimina
Acunda
Asetilobus
Baileyna
Brachendus
Cenaca
Cercodes
Cymoptus
Dechela **comb. nov.**
Diphytoptus
Eriophyes pyri
E. quadrifidus
Keiferophyes
Nacerimina

Neserella **comb. nov.**
Notaceria
Palmiphytoptus **comb. nov.**
Paracolomerus **comb. nov.**
Paraphytoptella
Pareria
Proartacris
Ramaculus
Schizoempodium
Scoletoptus
Stenacis
Trimeracarus

Subfamily: Phyllocoptinae Nalepa, 1892
Classificatory structure remains as in Amrine *et al.* (2003)

Family: Diptilomiopidae Keifer, 1944
Subfamily: Diptilomiopinae Keifer, 1944
Acarhis diospyrosis
Acarhi. lepisanthis
Acarhi. siamensis
Africus
Dacundiopus
Davisella
Diptilomiopus
Diptilorhynacus dioscoreae
Diptilor. sinusetus
Diptilostatus
Kaella
Lambella
Levonga caseariasis
Le. litseae
Le. papaitongensis
Lithocarus
Mediugum
Neoacarhis
Neodiptilomiopus
Neolambella
Neorhynacus
Norma
Prodiptilomiopus
Rhynacus
Sakthirhynchus **comb. nov.**
Suthamus
Thailandus
Vimola

Subfamily: Rhyncaphytoptinae Roivainen, 1953
Acarhynchus **comb. nov.**
Apodiptacus **comb. nov.**
Areekulus
Asetacus
Asetadiptacus **comb. nov.**

Brevulacus
Bucculacus **comb. nov.**
Catarhinus
Chakrabartiella
Cheiracus
Chiangmaia **comb. nov.**
Dialox **comb. nov.**
Diptacus pandanus **comb. nov.**
Dipta. sacramentae **comb. nov.**
Diptiloplatus **comb. nov.**
Duabangus **comb. nov.**
Hoderus
Hyborhinus
Konola
Neocatarhinus
Neodialox **comb. nov.**
Pararhynacus **comb. nov.**
Peralox
Quadracus mangiferae
Quadra. urticarius
Quadriporca indicae
Quadri. mangiferae
Rhinophytoptus
Rhinotergum
Rhyncaphytoptus
Stenarhynchus
Steopa **comb. nov.**
Trimeroptes **comb. nov.**

Phytoptinae and Sierraphytoptinae

These are the two main Phytoptidae subfamilies with species with single *vi* absent, *ve* present, and the spermathecal tube moderately short. Seta *c1* is present in the Phytoptinae and present or absent in the Sierraphytoptinae (Keifer, 1944; Roivainen, 1953; Keifer, 1956, 1964a). Body shape differentiates the two subfamilies: Phytoptinae have a vermiform body shape with annuli subequal, and Sierraphytoptinae a fusiform body shape with dorsal annuli longer (Fig. 3.2b) than ventral annuli (Keifer, 1944). The Sierraphytoptinae have two tribes: the Sierraphytoptini (*c1* present) (Keifer, 1944; Roivainen, 1953; Keifer, 1956, 1964a; Channabasavanna, 1966; Newkirk & Keifer, 1971), and Mackiellini (*c1* absent) (Channabasavanna, 1966; Newkirk & Keifer, 1971).

Species of the Prothricinae (*Prothrix*), Sierraphytoptini (*Neopropilus*) and Mackiellini (*Propilus* and *Retracrus*) were recovered as a clade [**Dorsal-rear-fused clade (7)**] supported by one synapomorphy: fusion of rear dorsal annuli caudad *f*. This clade is proposed as a new subfamily, Propilinae, in the Phytoptidae *sensu* the present study, and the type genus and species is designated as *Propilus gentyi* Keifer, 1975 (Table 4.10). Morphologically, particularly in body shape, the species are roughly similar, and may also be defined as a new suprageneric taxon when evaluated according to conventional morphological criteria. There are, however, also differences between the genera which are conventionally regarded as being important at suprageneric and generic level, e.g., tibial solenidion, *c1*, *sc*, *l'*, *d*, and/or wax secretion is present or absent; and the shape of setal tubercles, dorsoventral differentiation in annuli, modifications such as ridges and lateral lobes, and detail in the coxigenital area, its position, and possibly shape of the internal genitalia vary between the taxa.

Under most parameters the Phytoptinae and Sierraphytoptinae as well as the two Sierraphytoptinae tribes, were found to be paraphyletic. All Phytoptinae, Sierraphytoptinae and the **Dorsal-rear-fused clade (7)**, and probably *Pentasetacus*, may constitute a clade. They were recovered as the **Phytoptinae-Sierraphytoptinae group (9)** (Fig. 4.11). When the majority of the species in this group are excluded from the smaller data sets, the **Phytoptinae-Sierraphytoptinae group (9)** is not supported in its entirety, although part of this group, the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (Fig. 4.11) is supported by the 66tax-k20 tree. In the smallest (18tax) data set, the Phytoptinae, and the Sierraphytoptinae tribes, Sierraphytoptini and Mackiellini, are each represented by one species. The two sierraphytoptine tribes particularly are again found to be paraphyletic, and were recovered as sisters [**Sierraphytoptinae group 11b**] under some parameters.

Lindquist & Amrine (1996) considered the Phytoptinae and Sierraphytoptini as monophyletic taxa problematic, because they are not supported by any synapomorphies. They regarded the Sierraphytoptinae to be supported by their fusiform body shape, which they regarded a homoplasious

apomorphy *a priori* phylogenetic analyses, and proposed that the Mackiellini may be monophyletic, supported by the homoplasious apomorphy, loss of *c1*.

In particular, the present results do not support the monophyly of the Sierraphytoptinae tribes, and they are not included in the proposed classification (Table 4.10). This partly supports the hypotheses by Lindquist & Amrine (1996), and it agrees with the classification proposed by Boczek *et al.* (1989) which did not include these tribes in their Eriophyoidea classification, implying they did not regard them to be monophyletic. Although not conclusively found by the present study, the indication that the Phytoptinae and Sierraphytoptinae may be paraphyletic was the strongest hypothesis, and the species that do not belong to the new subfamily, Propilinae, are all placed in the Phytoptinae, rendering the Sierraphytoptinae a junior synonym of this subfamily (Table 4.10). These are subfamilies of the Phytoptidae which constitutes all Phytoptidae species with single *vi* absent, but *ve* present, excluding the Novophytoptinae. The Phytoptinae is probably not a monophyletic taxon and the positions of particularly species of the Sierraphytoptinae *sensu* Amrine *et al*. (2003) are not certain. The Phytoptidae, or similar taxon, may eventually be subdivided into more clades, some of which may possibly also include Eriophyidae, and particularly the Sierraphytoptinae may be reinstated. The species is grouped in the same subfamily, though, until more conclusive results regarding the relationships between the Phytoptidae taxa *sensu* the present study, are found.

Nalepellinae

This subfamily comprises Phytoptidae species with single *vi* present anteromedially on the prodorsal shield, and with spermathecal tubes elongated. Seta *ve*, *sc* and *c1* are present or absent and the opisthosoma is vermiform with subequal annuli or fusiform with annuli differentiated dorsoventrally (Roivainen, 1953; Newkirk & Keifer, 1971; Lindquist & Amrine, 1996). The presence of single *vi* is correlated with long spermathecal tubes and with the Nalepellinae exclusively living on conifers. The Nalepellinae being a natural lineage deeply separated from other eriophyoid lineages with single *vi* absent was regarded by several eriophyoid systematists (e.g., Farkas, 1968b; Shevchenko, 1971) to be particularly important and well-supported. Lindquist & Amrine (1996) proposed the Nalepellinae might be monophyletic, and the elongated spermathecal tubes may be a synapomorphy for the subfamily.

The monophyly of the Nalepellinae is largely not supported by the present study, but the results were not conclusive. The Nalepellinae was recovered as a clade [see **Nalepellinae group and clade (5)**], when only one species of each of the three Nalepellinae tribes were included in the data set (the 18tax data set) and when character states from Hong & Zhang (1996a) were modified. This clade was supported by two synapomorphies: single *vi* present and spermathecal tubes long. When

more taxon and character data, and thus variation, were added in the larger data sets, however, the Nalepellinae species were not recovered as a monophyletic group anymore, and the latter results are more defendable.

The Nalepellinae *sensu* Amrine *et al*. (2003) comprise three tribes: Pentasetacini, Trisetacini (*c1* present), and Nalepellini (*c1* absent). Particularly the monospecific Pentasetacini was not recovered in the same clade or exclusive group with the remainder of the Nalepellinae, and will be discussed separately later on. The monophyly and relationships between the other Nalepellinae taxa are as follows.

The Nalepellinae tribes (Trisetacini and Nalepellini) were not recovered as monophyletic groups. Species from both tribes were recovered in broadly two groups. The one group comprises *Nalepella*, *Phantacrus* and *Pentaporca* of the Nalepellini [***Nalepella* groups (1)**]. Particularly when *Setoptus* (Nalepellini) was included in the data set, however, it was recovered in a group with the Trisetacini species [**Trisetacini-Nalepellini group 3a**], and when it was excluded, *Trisetacus* and the other Nalepellini species were recovered in the same group [**Trisetacini-Nalepellini groups 3b and 3c**]. The position of *Trisetacus* still remains particularly uncertain and plastic, though. Some analyses recovered it in a weakly supported sister relationship with *Acathrix* (Phytoptinae) [**Trisetacini-Phytoptinae group (4)**]. It, however, seems more likely that it has a close relationship with other Nalepellinae species [***Trisetacus* group (2)**, and **Trisetacini-Nalepellini groups (3)**], but its relationships with different Nalepellinae taxa are also uncertain. Overall, the groups with Nalepellinae species largely did not include Phytoptidae species with single *vi* absent.

In conclusion, the Nalepellinae, excluding *Pentasetacus*, may be monophyletic, the Trisetacini polyphyletic and the Nalepellini paraphyletic. The relationships between Trisetacini and Nalepellini species are not conclusive, and the amalgamation of the species of these two tribes (Table 4.10), is proposed pending more robust results regarding the relationships of the Nalepellidae taxa *sensu* the present study. These results partly support Lindquist & Amrine (1996) who proposed the Trisetacini may not be monophyletic, and that the Nalepellini is weakly supported by a homoplasious apomorphy: the loss of *c1*. The classification proposed in the present study (Table 4.10) agrees with the classification of Boczek *et al.* (1989) who did not divide their Nalepellinae (excluding *Pentasetacus*) in tribes.

Position of *Pentasetacus*

The Nalepellinae tribe Pentasetacini sensu Amrine *et al*. (2003) is monospecific, holding *Pentasetacus araucaria* described by Schliesske (1985), a species with five prodorsal setae (unpaired *vi*, *ve* and *sc*) – the maximum number of prodorsal setae in the Eriophyoidea, *c1*[1] present, a vermiform, but more vagrant-like body, with broad annuli subequal dorsoventrally, frontal lobe present, and divided empodium. It causes galling on an ancient relict coniferous species, *Araucaria araucana* (Araucariaceae), in the Chilean Andes of South America (Schliesske, 1985). *P. araucaria* is regarded to be the most primitive or early derived eriophyoid species (Sukhareva, 1994), and became central to most hypotheses regarding the phylogeny and evolution of the Eriophyoidea since its description, and the placement of this species is of particular importance.

The position and relationships of *Pentasetacus* could not be conclusively resolved by the present analyses. When its relationships with other eriophyoid taxa were resolved, *Pentasetacus* is found to be closely related to Phytoptidae, and not to Eriophyidae or Diptilomiopidae species. This relatively strongly supports its current placement in the Phytoptidae, or eventually in a subgroup exclusively with species that previously belonged to the Phytoptidae. In the 318tax- and 66tax trees, contrary to what one would expect, and current hypotheses regarding the species, it has a closer relationship with Phytoptidae with single *vi* absent, and in particular with the Sierraphytoptinae and Phytoptinae, than with Nalepellinae species [see ***Pentasetacus*-Sierraphytoptini groups (6)**, **Smaller-Phytoptinae-Sierraphytoptinae group (8)** and **Phytoptinae-Sierraphytoptinae group (9)**]. This does not support its placement within the Nalepellinae, and it seems from the homoplasies supporting these groups that the presence of *ve*, in combination with other characters, may be more important in determining the relationships of *Pentasetacus* than the presence of single *vi*.

In the 18modify analyses *Pentasetacus* was, however, recovered as part of the Nalepellinae when the subfamily was retrieved as a clade [see **Nalepellinae group and clade (5)**]. Although the trees obtained from data sets with a more comprehensive sampling of taxa and characters are preferred in the present study, the placement of *Pentasetacus* within the Nalepellidae can not be discarded as an alternative hypothesis.

Until evidence that is more conclusive is found regarding the position of *Pentasetacus*, I place it in its own family (Table 4.10) to retain stability of the Eriophyoidea classification in the mean time.

[1] *c1* have been wrongly reported as being absent in this genus by Amrine *et al.* (2003).

This coincides with Shevchenko (in Boczek *et al.*, 1989) who proposed a family rank taxon for *Pentasetacus* Schliesske, 1985, although his proposal was for a different reason. He argued that the family rank is dependent on the number of prodorsal shield setae. Sukhareva (1994) kept *Pentasetacus* in a family of its own, and proposed that it is more closely related to the Nalepellidae (*sensu* Shevchenko, 1976) than to the Phytoptidae (*sensu* Shevchenko, 1976), because it occurs on a conifer, and possesses *vi*. In the present study, it is rather proposed that *Pentasetacus* may be more closely related to the Phytoptidae *sensu* the present study, and may even be recovered to be in the same clade as the latter taxon.

4.7.1.1 A summary and discussion of the proposal to subdivide the Phytoptidae *sensu* Amrine *et al.* (2003) into three separate families (Table 4.10).

The distinction between Phytoptidae species with odd (with single *vi*) and those with even numbers (without single *vi*) of prodorsal setae was central in many arguments and studies regarding the evolution of the Eriophyoidea (e.g., Farkas, 1968b; Shevchenko, 1971, 1974a, 1976; Shevchenko *et al*., 1991). As previously mentioned, Shevchenko (1971, 1974a, b, 1976) and Boczek *et al.* (1989) argued strongly and pertinently that Phytoptidae species with odd and those with even numbers of prodorsal setae are two separate lineages within the Eriophyoidea. Farkas (1968b) and Shevchenko (1971, 1974a, 1976) pointed out that species with odd numbers of prodorsal setae occur exclusively on conifers [Gymnospermae], and those taxa with even numbers of prodorsal setae occurr on a wide range of hosts, including the more recently evolved Angiospermae. The long spermathecal tubes exclusively in species with single *vi* present, which may be another synapomorphy supporting the monophyly of the group (Shevchenko, 1971, 1974a, b, 1976). Lindquist (1996b) and Lindquist & Amrine (1996) also proposed that some Phytoptidae characteristics, such as the long spermathecal tubes and position of the solenidion on tibia I and median position of single *vi* present in some species, may be synapomorphic for clades within the Phytoptidae. On closer inspection, including studying the substructures in more detail, however, particularly the internal genitalia of *Pentasetacus* may not be entirely homologous to the genitalia of other Nalepellinae. The proposal by these authors that the Nalepellinae may be monophyletic is supported by strong arguments and evidence, and although it was not generally supported by the present study, it remains a strong hypothesis which has not been conclusively disputed by the present study.

The present study partly supports the arguments and proposals of the authors above. Generally the Phytoptidae with single *vi* present, and the Phytoptidae with single *vi* absent were found to be in separate clades or exclusive groups, but these two separate groups were generally not particularly

closely related. To express this lack of a close relationship between the two "lineages", they are proposed to be in separate families, Nalepellidae and Phytoptidae (Table 4.10). This agrees with the proposal of the superfamilies **Trisetoidea** and **Phytoptoidea by** Shevchenko (1971, 1974a), which were changed to family level Nalepellidae and Phytoptidae (Shevchenko, 1976; Boczek *et al*., 1989), expressing the proposal that they are two separate, natural lineages.

In the present study, the presence or absence of single *vi* was largely found to be homoplastic, though, and the two groups were not recovered as clades. The Nalepellidae *sensu* the present study, may be polyphyletic and in particular, *Boczekella*, *Setoptus* and *Trisetacus* may belong to other taxa, and possibly even as taxa of the Eriophyidae *sensu* Amrine *et al*. (2003). Even more likely, *Pentasetacus* may have a closer relationship with Phytoptidae without single *vi* than with those with single *vi* (discussed above). Additionally, *Acathrix* (Phytoptinae) and *Trisetacus* (Nalepellinae) were found to be sisters [**Trisetacini-Phytoptinae group (4)**] under some parameters, but as already discussed, this relationship is weakly supported and probably not natural. In the 18modify trees under implied weighting *Mackiella* was recovered as the sister to the **Nalepellinae clade (5)** to constitute the ***Mackiella*-Nalepellinae clade (11c)** and this relationship is supported by the synapomorphy: tibial solenidion *φ* present. If this monophyletic grouping eventually proves to be robust, the Mackiellini *sensu* Amrine *et al*. (2003) is polyphyletic, and the loss or retainment of single *vi* may be even more homoplastic than proposed in the present study.

4.7.1.2 The relationships of the Phytoptidae groups and clades with other eriophyoid taxa

Although some of the clades and groups within the Phytoptidae seem to be robust and stable, the relationships of the Phytoptidae groups and clades with other eriophyoid taxa in the present results are less certain and largely inconclusive. It can be proposed, though, that a large part of the Phytoptidae *sensu* Amrine *et al*. (2003) should be designated to the Eriophyidae or *vice versa*, depending on which taxa were found to be imbedded among the Eriophyidae. At least part of the Phytoptidae, however, is still positioned outside the remainder of the Eriophyoidea as a separate exclusive group or clade.

There are two main tree topologies regarding the Phytoptidae taxa excluded from, and possibly belonging to a separate lineage than the remainder of the Eriophyoidea. The analyses of taxon samples under most parameters recovered some or all Nalepellinae positioned outside a clade or exclusive group with the remainder of the Eriophyoidea including the remaining Phytoptidae (similar to the hypotheses of V.G. Shevchenko and others), and this is the preferred hypothesis. Under another set of parameters, alternatively, some vagrant Phytoptidae species (of the Sierraphytoptinae and Phytoptinae), sometimes including *Pentasetacus*, are positioned outside the remainder of the Eriophoidea, which consists of the Eriophyidae, Diptilomiopidae and a part of the Phytoptidae, including the Nalepellinae (sometimes including and sometimes excluding *Pentasetacus*). Either of these two different

Phytoptidae groups being excluded from the remainder of the Eriophyoidea is not well-supported and conclusive, however, because the group constituting the remainder of the Eriophyoidea was usually not well-supported [see **Eriophyidae groups and clades (13)**]. In general, it was found that *Pentasetacus* has a close relationship with, and is in exclusive groups including Phytoptinae and Sierraphytoptinae, and resultingly, based on the preferred hypotheses, *Pentasetacus* together with its closely related Phytoptidae could be designated to the Eriophyidae. This exclusive group (excluding part of the Nalepellinae) sometimes also includes the **Diptilomiopidae clade or group (27)** (Figs 4.9, 4.28, 4.33, 4.43, 4.51). The position of the Phytoptidae clades and exclusive groups among the Eriophyidae and Diptilomiopidae clades and groups in the different trees can be viewed in Figs 4.6, 4.26, 4.43, 4.55, 4.57, 4.58, 4.59, 4.60 and 4.62.

In conclusion, if a classification should be proposed mainly based on the preferred phylogeny recovered in the present study, the Phytoptidae, except *Nalepella*, *Phantacrus* and *Pentaporca*, should be designated to the Eriophyidae. This will cause a huge, probably premature, upset in the nomenclature and suprageneric concepts of the Eriophyoidea. With *Phytoptus* Dujardin, 1851 designated to the Eriophyidae, *Phytoptus* will take precedence over *Eriophyes* von Siebold, 1851 as the type species of the less restricted Eriophyidae, and resultantly Phytoptoidea and Phytoptidae Murray, 1877 will have precedence over Eriophyoidea and Eriophyidae. The Eriophyidae (possibly including the Diptilomiopidae) will be junior synonyms of the Phytoptidae. There may also be other implications which may leave the taxonomy of the Eriophyoidea unstable. Disrupting nomenclatural changes may be prevented, however, by applying to the Commission of the International Code for Zoological Nomenclature (ICZN) to overrule the Principle of Priority (Article 23.1) and give precedence to the taxon names currently in use to promote stability in the classification of the Eriophyoidea (Article 23.2) (ICZN, 1999). The diagnoses and concepts of most suprageneric taxa will, however, still change significantly. Most phylogenetic studies (e.g., Hong & Zhang, 1996a; present study) found that at least part of the Phytoptidae should be in the same clade with at least part of the Eriophyidae. The position, however, of, among others, *Phytoptus*, is still regarded to be uncertain. Taking all these aspects in regard, I propose that the Phytoptidae *sensu* Amrine *et al*. (2003), which should, according to the preferred phylogenetic groupings, be designated to the Eriophyidae, remain classified outside the Eriophyidae for the interim, pending more robust hypotheses. The Phytoptidae *sensu* Amrine *et al*. (2003) are classified into three taxa at the same taxon level as the Eriophyidae, namely the Phytoptidae, Pentasetacidae and the Nalepellidae (Table 4.10). The Novophytoptinae, however, are assigned to the Eriophyidae (Table 4.10). It is proposed that among these taxa, Phytoptidae and Pentasetacidae are closely related, possibly in the same clade, and the Phytoptidae-Pentasetacidae is more closely related to the Eriophyidae, than both are to the Nalepellidae. The reasons for subdividing the Phytoptidae *sensu* Amrine *et al*. (2003) in three families are discussed above.

4.7.2 ERIOPHYIDAE

Eriophyidae are species without anterior prodorsal setae – *ve* and paired or unpaired *vi*, and without the "diptilomiopid" gnathosoma. It is the largest family in the Eriophyoidea, and the classification of this family is in reality the most comprehensive hypothesis of the relationships between Eriophyoidea taxa. In contrast to the Phytoptidae, however, few phylogenetic and evolutionary hypotheses were specifically developed or discussed regarding the relationships between the Eriophyidae taxa, apart from the assumption that the Eriophyidae and most of its subgroupings are probably not monophyletic (including Lindquist & Amrine, 1996). Vagrant forms, living more exposed and tending to have broader host ranges than the non-vagrant species, are proposed to have developed repeatedly and homoplasiously from the usually more specialized non-vagrant species and *vice versa* (Das & Chakrabarti, 1989; Lindquist & Amrine, 1996). This brought about the general vermiform and fusiform body shapes found in the Eriophyoidea, including the Eriophyidae. The Eriophyidae live on a wide variety and range of host plant taxa, ranging from earlier derivitive Gymnospermae to the most recently derived plant taxa in the Angiospermae. It does not seem that there is a close relationship between the phylogeny of the host plants and the phylogeny of the Eriophyidae, similar to that proposed for the Phytoptidae.

The family Eriophyidae was not retrieved as a monophyletic group in any of the analyses and was found to be paraphyletic and possibly polyphyletic [see **Eriophyidae group and clades (13)**]. In the trees found with the 18tax analyses, the "Eriophyidae" clades are more supported (see e.g., **Eriophyidae clade 13e**) than the Eriophyidae groups or clades found by analyses of data sets with more characters and species. The 18tax tree **Eriophyidae clades (13)** include all the Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and all Phytoptidae except the Nalepellinae and are supported by the synapomorphies: single *vi* absent, and spermathecal tubes short. Alternatively, the clade includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and *Novophytoptus*, but excludes the other Phytoptidae, and the clade is supported by one synapomorphy, *sc* at or near the rear shield margin. The Eriophyidae (including the Diptilomiopidae) was retrieved as a separate group from all the Phytoptidae in one tree, but then the Eriophyidae group is supported by homoplasies. The hypotheses postulated from the 18tax trees can not be totally disregarded before further testing, but are not regarded as reliable, because the extremely small biased data set excluded a large amount of morphological evidence from other taxa in the Eriophyoidea. Results from 18tax analyses, however, are broadly similar to the results from the 318tax and 66tax analyses, as the Eriophyidae was found to be paraphyletic under most parameters, but it may also be polyphyletic, since some groups were only supported by homoplasies. To summarize results from the present study: the most supported recovered Eriophyidae groups or clades generally include all Eriophyidae taxa, include some of the Phytoptidae,

but exclude the ***Nalepella* groups (1)** or **Nalepellinae group or clade (5)** or, alternatively, exclude some of the **Phytoptinae-Sierraphytoptini groups (6),** and may also include the **Diptilomiopidae group or clade (27).** In other words, the **Eriophyidae group or clade (13)** in some trees can essentially be regarded as the same group of species as the monophyletic Eriophyoidea, except in all the trees a few species, usually Phytoptidae species, are not part of it. The **Eriophyidae groups or clades (13)** are not retrieved in analyses under equal weighting of characters, and is not supported by symmetric resampling values, and does not consist of the same species under all parameters, and can not be regarded as a robust grouping. The more restricted Eriophyidae *sensu* Amrine *et al*. (2003) are retained as a family separate from the Diptilomiopidae and Phytoptidae families *sensu* the classification proposed in the present study, largely to preserve the stability of the classification until more conclusive results can be obtained regarding the relationships of these family groupings (Table 4.10).

With the present data sets, less phylogenetic phylogenetic resolution and fewer and less robust groups were recovered from the Eriophyidae taxa, particularly those largely exclusively consisting of Eriophyidae species, than what were found in the Phytoptidae and Diptilomiopidae. It was found that many of the current suprageneric taxa in the Eriophyidae are most likely not monophyletic. Some subfamilies with specific body modifications, e.g., the Cecidophyinae with the genitalia appressed against the coxae, and the genital anterior apodeme folded up to appear as a thick line, and the Nothopodinae with reduced or fused tibiae, were found to be possibly monophyletic, or partly monophyletic, in the present study. Most Eriophyidae are, however, divided between non-vagrant forms (e.g., *Aceria*) (constituting the Eriophyinae) and vagrant forms (e.g., *Aculus*) (constituting the Phyllocoptinae) similar to the way Nalepa constructed the classification of the Eriophyoidea. None of these were found to be monophyletic.

The Eriophyidae have six subfamilies (Amrine *et al*., 2003; Table 1.1), and the appraisal of their monophyly is as follows.

Aberoptinae and Nothopodinae

The leg tibia of some Eriophyidae is entirely or partly fused with the tarsus, resulting in the reduction or apparent absence of the tibia. This is regarded as an important suprageneric character in the classification of the Eriophyidae, and is the key character differentiating the Nothopodinae and Aberoptinae from other Eriophyidae taxa, and additionally *l'* is always absent in these subfamilies (Keifer, 1956: 163; Lindquist & Amrine, 1996). The Aberoptinae is distinguished from the Nothopodinae by having spatulate or shovel-shaped projections on the tarsi (Amrine *et al.*, 2003).

The restricted Aberoptinae *sensu* Amrine *et al*. (2003) only comprise *Aberoptus* spp. In the present study, the subfamily was represented by an *Aberoptus* sp., and two *Cisaberoptus* spp. (Table 4.1).

Amrine *et al.* (2003) synonymized *Cisaberoptus* with *Aceria*, because the protogyne of *Cisaberoptus* spp. fits into the latter genus, and the generic concept of *Cisaberoptus* is based on the morphology of the supposed deutogyne females. Analyzing the data of *Cisaberoptus* spp. in the current data sets might be flawed, because the characteristics scored were from the supposed deutogyne females, while all other species in the data sets were scored from protogyne females. Nevertheless, the two *Cisaberoptus* spp. were found to be sisters, supported by the two homoplasies: apical palp ends spatulate or with triangular projections, and body flattened fusiform. They were not found to have a close relationship with *Aberoptus*. Lindquist & Amrine (1996) proposed the Aberoptinae might be monophyletic, supported by four synapomorphies: tarsi with projections, legs extraordinary stout, empodium II large with many rays, female genital coverflap abbreviated, and three to four times wider than long. The data set was not designed in such a way that the monophyly of the restricted Aberoptinae could be tested. The relationships of *Aberoptus* with other Eriophyoidea are uncertain. Under the different parameters, it was found to have close relationships with *Cymoptus* (Aceriini) and some Phyllocoptinae, or particularly with some Cecidophyinae species. The latter relationship is primarily supported by the position of its genitalia, and particularly in the small 18tax trees, *Aberoptus* is in the same clade as *Ashieldophyes*-*Cecidophyes*, supported by one synapomorphy: female genitalia appressed to coxae. It never was found to have a close relationship with the Nothopodinae. See the **Aberoptinae groups (16)** for further information. Since the relationships of the Aberoptinae could not be conclusively determined, the subfamily is retained as is (Table 4.10), but it is proposed that *Aberoptus* spp. may be closely related to some Cecidophyinae species.

Lindquist & Amrine (1996) proposed the Nothopodinae to be weakly supported by the reduced leg tibia, which they regarded as a homoplasious apomorphy. The monophyly of the Nothopodinae, although not conclusively, is supported more or less in most of the 318tax and 66tax trees under implied weighting [see the **Nothopodinae groups and clade (14)**]. In particular, in the 66tax-k30 tree, *Colopodacus* and *Nothopoda* are recovered as sister species (Fig. 4.52) well-supported by two synapomorphies: reduction of tibia, which is completely fused with tarsus in legs I and II. It seems that the Nothopodinae may be a well-supported clade, but it still needs testing.

The Nothopodinae are divided into the Colopodacini with *1b* present (Mohanasundaram, 1984; Amrine, 1996), and the Nothopodini with *1b* absent (Keifer, 1956; Amrine *et al*., 2003). The tribes, on the same taxonomic level, are not well-supported by the trees, and they each were found to be paraphyletic and polyphyletic, because the species of these tribes were recovered exclusively in the same groups and clades, and were not found to be separated in two groups that may support

the tribes. Boczek *et al.* (1989) did not include the taxon groups, Colopodacini and Nothopodini, *sensu* Amrine *et al.* (2003) in their classification.

Based on the present results, I do not recognize the new subfamily, Colopodacinae, proposed by Mohanasundaram (1984), and also not the subsequent division of the Nothopodinae into the tribes Colopodacini and Nothopodini by Amrine (1996). The Nothopodinae are potentially monophyletic, but is proposed not to be subdivided into smaller groupings at this stage (Table 4.10).

Ashieldophyinae

Mohanasundaram (1984) placed *A. pennadamensis* in its own monospecific family, Ashieldophyidae, largely based on his erroneous morphological description of the species (Amrine & Stasny, 1994; Amrine, 1996; Lindquist & Amrine, 1996; Amrine *et al.*, 2003) and Boczek *et al.* (1989) concurred with this placement, and retained the taxon for this species at family rank. Amrine & Stasny (1994) lowered the family to subfamily rank, and assigned the Ashieldophyinae to the Eriophyidae. *Ashieldophyes* has a particularly small prodorsal shield, encroached by dorsal annuli-like structures; a minute *sc* without a setal tubercle and located on the lateral prodorsal shield margin; coxisternal plates widely separated, without a prosternal apodeme, and external female genitalia between coxisternal plates II (Amrine & Stasny, 1994; Amrine, 1996; Lindquist & Amrine, 1996; Amrine *et al.*, 2003). Except for the size and position of *sc* and it being without a setal tubercle, the other characters are autapomorphic for this species (Lindquist & Amrine, 1996). The positions of *Ashieldophyes* recovered by the different analyses in the present study, were not well-supported, and its relationships are uncertain. It was recovered imbedded in the Eriophyidae and may be closely related to Phyllocoptinae or Cecidophyinae species. It should probably not be in its own subfamily, but it is retained therein (Table 4.10), since the relationships recovered are inconclusive.

Cecidophyinae

The Cecidophyinae are Eriophyidae species with female genitalia enlarged and the internal female anterior genital apodeme folded up, appearing as a broad line (Fig. 3.5c), in combination with the genitalia being pressed up against the coxisterna, separating the coxisternal plates more than usually found in the Eriophyoidea (Fig. 3.5a, b). In lateral view the genitalia is noticeably projecting from the ventral opisthosomal aspect. The longitudinal ridges on the female genital coverflap are usually in two ranks (Keifer, 1966d: 15, 17; Lindquist & Amrine, 1996; Amrine *et al.*, 2003).

The 19 Cecidophyinae species (Table 4.1) included in the present study, were never recovered as a clade, but strong affinities between most of the species were found, and they are largely positioned close to each other in the trees [see **Cecidophyinae groups (17)**], and an example of this group in the

318tax-k10 tree (Fig. 4.13). Some single species of the Cecidophyinae, however, were not recovered in close association with the bulk of the Cecidophyinae. One such species is *Paracolomerus* which was found in a group with *Keiferophyes*, *Acunda* and *Brachendus* (Eriophyinae), *Palmiphytoptus*, and *Cisaberoptus* deutogynes, constituting the **Broadly-folded-apodeme group (18)**. This group is largely supported by the anterior genital apodeme only broadly folded up, and not forming such a clear straight line as found in other Cecidophyinae, and it is a feasible grouping. *Neserella* and *Dechela* probably should also not be in the Cecidophyinae, but were rather found to have close relationships and may belong to a group of species from the southern hemisphere, including particularly some Eriophyinae [**Extended southern-Aceriini group (19)**]. In some of the 18tax trees, *Cecidophyes* (the only cecidophyine species included) was recovered in a clade with *Aberoptus* and *Ashieldophyes*, supported by the position of the genitalia, and a close relationship between these genera can be investigated.

Lindquist & Amrine (1996) proposed that the Cecidophyinae may be monophyletic, supported by one synapomorphy: enlarged genitalia appressed against coxae. In combination with this characteristic, the genital apodeme is folded up to form a thickened straight line (Fig. 3.5c). Based on the present results it is proposed that a large part of the Cecidophyinae may be monophyletic, but in its entirety, the subfamily was found likely polyphyletic and possibly paraphyletic. The phylogeny of the Cecidophyinae and possibly closely related species from other taxa may be better and more robustly resolved if the genitalia are studied in more exact detail. Descriptive drawings of the same internal genitalia and apodemes by different authors may differ considerably, e.g., the drawing of the internal genitalia of *Cecidophyes rouhollahi* by C. Craemer (Fig. 3.5c) and a drawing of the genitalia of the same species by H.H. Keifer (from his collection) (Craemer *et al*., 1999) as a less clear case. More detailed descriptions will facilitate the identification and more exact definition of primary homologies in the genitalia. The Cecidophyinae is retained, but *Paracolomerus*, *Neserella* and *Dechela*, is re-assigned to other subfamilies.

The Cecidophyinae have two tribes (conceived by Keifer, 1966b): the Cecidophyini with *sc* and its setal tubercle absent (Fig. 3.3), and the Colomerini with *sc* present (Keifer, 1966d; Newkirk & Keifer, 1975). Lindquist & Amrine (1996) did not regard either of these tribes as well-supported groupings. According to them, the Colomerini might not be monophyletic, because it is supported by a plesiomorphic character, and the Cecidophyini are weakly supported by one homoplasious apomorphy: the loss of *sc*.

In the present study, Cecidophyinae species were positioned close to each other in about two groupings coinciding with the tribes [see **Cecidophyinae groups (17)**], but neither formed a single grouping together at one node. They may be monophyletic groupings, being slightly paraphyletic or polyphyletic, e.g., *Neocecidophyes* and *Epicecidophyes* (Colomerini) may rather belong to the

Cecidophyini. Nothing conclusively about the monophyly of these two tribes was found in the present study and neither strongly support or negate the hypotheses. It seems generally more phylogenetic structure is present in the Cecidophyini than in the Colomerini. Boczek *et al.* (1989) only included Cecidophyini genera in the Cecidophyinae, and regarded the absence of *sc* and its setal tubercle as one of the diagnostic characteristics of the subfamily. They designated genera of the Colomerini *sensu* Keifer (1966d) and Newkirk & Keifer (1975) to the Eriophyinae and Phyllocoptinae. This classification is not supported by the present results. The Cecidophyinae tribes are retained (Table 4.10), pending more detailed analyses.

Eriophyinae and Phyllocoptinae

The largest Eriophyidae subfamilies – Eriophyinae and Phyllocoptinae – are essentially differentiated from each other by vagrant (Phyllocoptinae) and non-vagrant (Eriophyinae) body shape characteristics (Amrine *et al*., 2003). This division corresponds with the original division of the Eriophyoidea by Nalepa (1892, 1898b), which prevailed, despite the splitting of new taxa from these two major groupings. The Eriophyinae and Phyllocoptinae, and particularly their tribes, had the least phylogenetic signal of all the Eriophyoida suprageneric taxa, and none were recovered as monophyletic groupings in the present study. Particularly the Eriophyinae and Phyllocoptinae tribes were found to be highly polyphyletic. This supports Lindquist & Amrine (1996) who regarded these two subfamilies and their tribes as natural groupings problematic.

Eriophyinae

The Eriophyinae *sensu* Roivainen (1953), Newkirk & Keifer (1971) and Amrine *et al*. (2003) have a vermiform body, albeit sometimes slightly fusiform. The dorsal and ventral annuli are entirely or for most part of the opisthosoma subequal dorsoventrally, the prodorsal shield is typically without a frontal lobe, and if present, and particularly when it stretches across the gnathosoma, it is flexible and narrow and is present in combination with subequal annuli. Most species do not have body modifications, including ridges and furrows. This taxon is similar to the Eriophyinae defined by Nalepa (1898b: 5) but with the exclusion of species with a similar vermiform body shape now classified as the Aberoptinae, Nothopodinae, Cecidophyinae and Ashieldophyinae. The Eriophyinae body shape (Fig. 3.2a) is usually associated with non-vagrant[2] eriophyoid mites living a more sheltered life. They live in natural plant microhabitats e.g., in buds, underneath needle and leave sheaths, and between bulb scales (refuge-inhabiting[1] mites), or in microhabitats created by symptomatic growth caused by their feeding, such as galls (gall-inhabiting[1] mites). This life style and concurrent body shape probably developed homoplasiously and repeatly within the Eriophyoidea (Lindquist & Amrine, 1996). The present study supports this hypothesis, and characters describing body shape were found to be

[2] This terminology is used as it has been defined in Sabelis & Bruin (1996).

homoplastic, and were sometimes found as homoplasies, but never as synapomorphies, supporting clades.

The Eriophyinae are divided into three tribes: Diphytoptini (with divided empodia) (Amrine & Stasny, 1994), Eriophyini (scapular setal tubercles about ahead of the rear shield margin, with *sc* directed forward or up) (Fig. 3.3c), and the Aceriini (scapular setal tubercles on or very near the rear shield margin, with *sc* always directed to the rear) (Fig. 3.3b) (Amrine & Stasny, 1994; Amrine *et al.*, 2003). The tribes are thus differentiated by the empodial shape, and the position of *sc*, in combination with the direction into which *sc* is projected.

The species of the Eriophyinae and the Eriophyinae tribes are mostly scattered as single species in the trees found for the 318tax and 66tax data sets. Few supported groups and close relationships between them and other eriophyoid taxa were found by the analyses. Only one weakly supported group [**Extended Southern-Aceriini group (19)**] with an appreciable number of Eriophyinae species was identified from the recovered relationships. The positions and relationships of some of the single Eriophyinae species were, however, additionally evaluated to explore the type and quality of information that can be extracted from these. Some useful hypotheses can be proposed, and are presented and chronologically numbered: **Eriophyini species positions (20)** and **Aceriini species positions (21)**.

Lindquist & Amrine (1996) argued that the Diphytoptini and Aceriini might be supported by homoplasious apomorphies: divided empodium, and position and projection of *sc*, alternatively. They, however, proposed that the Eriophyini is probably not monophyletic, because it is not supported by any apomorphies. All three tribes were, however, found to be highly polyphyletic in the present study. Although the Eriophyinae was found to be polyphyletic as well, it has been decided for practical classification and identification, and for retaining the stability of the classification, to retain this subfamily pending more detailed analyses of particularly the large genera such as *Aceria*, and pending the recovery of improved, more robust monophyletic groupings in the Eriophyidae. It has been decided, based on the high polyphyly of the Eriophyinae tribes, to leave the Eriophyinae undivided (Table 4.10). It is believed this is the step in the right direction towards entirely restructuring and reclassifying the Eriophyidae according to the phylogeny of the group. Boczek *et al.* (1989) also did not recognize the tribes of the Eriophyinae, but they divided the Eriophyinae into two unnamed subgroups based on the presence of the frontal lobe, which is laterally thin and with a narrow base if present in the Eriophyinae. This subdivision is not supported by the present results either. The scoring of this character from slide-mounted

specimens is also difficult, subjective and ambiguous, and it is also not a good differentiating character in practical taxonomy.

Phyllocoptinae

The Phyllocoptinae *sensu* Newkirk & Keifer (1971) and Amrine *et al*. (2003) typically have a fusiform body, which is widened anteriorly. Their annuli are characteristically differentiated dorsoventrally with the dorsal annuli longer (length parallel to the body axis) than the ventral annuli, and they are usually smooth. The prodorsal shield generally has a rigid frontal lobe with a broad base (Nalepa, 1898b: 45; Roivainen, 1953). This general body shape (Fig. 3.2b) is usually associated with species living a more exposed life-style (vagrant[1] mites), e.g., on the leaf surface.

In the present study, the Phyllocoptinae was found to be polyphyletic and possibly also paraphyletic and agrees with Lindquist & Amrine (1996) which proposed that the Phyllocoptinae are not based on any apomorphy and are probably not monophyletic.
Farkas (1969) proposed that the Phyllocoptinae originated from two lineages, Eriophyinae species with *sc* on or near the rear shield margin, with these projected to the rear (e.g., *Vasates* originated from *Aceria*); and likewise *Phyllocoptes* originated from *Eriophyes*. This was not supported by the present study.

Newkirk & Keifer (1975) divided the Phyllocoptinae, which was perceived to have little classificatory structure, into five groups to simplify the identification and classification process. They noted it was for convenience, and that only some may indicate relationships. These informal groups were proposed as tribes by Amrine & Stasny (1994). Two of the phyllocoptine tribes (Acaricalini and Tegonotini) are defined by body structure shapes (empodia and annuli, respectively), while the others are largely defined by the presence, position or other characteristics of *sc* and its setal tubercle. Boczek *et al.* (1989) supported Newkirk and Keifer (1975) in creating subgroups for the Phyllocoptinae. They divided the Phyllocoptinae into ten subgroups with about the same morphological criteria than Newkirk & Keifer (1975), but subdivided the groups further on basis of the presence of the frontal lobe, and body shape in regard the presence of ridges and/or troughs.

The five Phyllocoptinae tribes, and the hypotheses of their monophyly by Lindquist & Amrine (1996), are as follows.

- The Acaricalini have a divided empodium (Newkirk & Keifer, 1975; Amrine & Stasny, 1994), which is a homoplasious apomorphy supporting the tribe.

- The Calacarini have *sc* vestigial or absent, and its setal tubercle may be present or absent (Newkirk & Keifer, 1975; Amrine & Stasny, 1994). This tribe is based on a homoplasious apomorphy: the loss of *sc*.
- The Tegonotini have lateral lobes or pointed projections from all or some opisthosomal annuli, or have a plate behind the prodorsal shield with lateral extensions (Newkirk & Keifer, 1975; Bagdasarian, 1978; Amrine & Stasny, 1994). This tribe is weakly supported by one homoplasious apomorphy: dorsoventral differentiation of opisthosomal annuli.
- The Phyllocoptini have *sc* present, with its setal tubercle ahead of rear shield margin, directing *sc* forward, up or medially. If the scapular setal tubercle is near the rear shield margin, the alignment of its base is longitudinal or diagonal to the body's long axis, and when the tubercle is subcylindrical it is bent forward (Newkirk & Keifer, 1975; Amrine & Stasny, 1994). The Phyllocoptini is not based on any apomorphy and is probably not monophyletic.
- The Anthocoptini have *sc* present, with its setal tubercle on or near the rear shield margin, directing *sc* to the rear. Alternatively, the tubercle is either subcylindrical, or the alignment of its base is transverse to the long axis of the body (Newkirk & Keifer, 1975; Amrine & Stasny, 1994).

In the present study, none of the Phyllocoptinae tribes were found to be monophyletic. The phylogenetic structure recovered for the group was meager and was weakly supported, but more structure was found than in the Eriophyinae. Some Phyllocoptinae were, however, positioned in proximity to each other, e.g., Figs 4.10, 4.12 and 4.15. Groups identified which can be proposed as potential monophyletic groupings pending further studies are: ***Schizacea-Knorella* group (22)** (Acaricalini); **Flat-monocot group (23)** (some Acaricalini and some Phyllocoptini); **One-Phyllocoptini group (24)** (some Phyllocoptini); ***Tetra-Ursynovia* group (25)** (some Anthocoptini); and ***Abacarus* groups (26)** (Anthocoptini and other taxa).

No robust alternative hypotheses for groupings within this family were retrieved in the present study, except for a few that are good hypothetical groupings to study. Additional analyses including more detailed characteristics of ridges and furrows and other modifications of the body may aid in the phylogenetic phylogenetic resolution of the Phyllocoptinae, but this is not sure. The entire classificatory structure of the Eriophyidae (apart from the Nothopodinae and Cecidophyinae) (particularly the Eriophyinae, the Phyllocoptinae and the tribes of both families) can, however, not be dissolved. It will make the classification awkward and development of keys and identification difficult. One could consider to dissolve the tribes of the Eriophyinae and not to subdivide this subfamily, to possibly group more related species together that are currently in the different tribes, but even this may be too preliminary and complicate identification. A team of researchers in the USA is currently

undertaking a phylogenetic analysis of the Eriophyoidea with molecular research, and included some species of the Eriophyidae, as well as more than one *Aceria* spp. This is a step in the right direction.

4.7.2.1 Conclusion: monophyly of the Eriophyidae

In conclusion, the Eriophyidae (without the Diptilomiopidae) being one clade is unlikely, but this aspect has not been resolved by the present analyses. It is broadly hypothesized the suprageneric taxa within the Eriophyidae are probably highly polyphyletic, including larger genera such as *Aceria*. The Cecidophyinae and Nothopodinae, may however, be more or less natural groupings, but the remainder of the Eriophyidae species will eventually "mix up" and be retrieved as totally new groups, different from the taxa in the existing Eriophyoidea classification.

4.7.3 DIPTILOMIOPIDAE

The diagnosis and delimitation of the Diptilomiopidae stayed more or less unchanged since its conception by Keifer (1944). The family is largely defined by the distinctive shape of the gnathosoma and its complex of structures (Keifer, 1944; Fig. 3.22), including strong and robust chelicerae projecting ahead and then abruptly downwards, and a "long-form" oral stylet (Fig. 3.22b, d, e) (Keifer, 1944; Roivainen, 1953; Keifer, 1964a). The Diptilomiopidae is probably a monophyletic taxon supported by synapomorphic gnathosomal characteristics (Lindquist & Amrine, 1996). It was also found as a monophyletic taxon in the empirical studies by Huang & Huang (1990) and Hong & Zhang (1996a). These studies included very few Diptilomiopidae species, but the Diptilomiopidae clades found were well-supported by one synapomorphy: chelicerae abruptly curved downwards.

The taxon sample from the Diptilomiopidae was significantly increased in the present study and species of 53 genera were included (Table 4.1), as well as 83 *Diptilomiopus* spp. The monophyly of the Diptilomiopidae was largely supported [see **Diptilomiopidae groups and clades (27)**], although not conclusively. Despite a complicated, and frequently ambiguous data set, with a very low characters:taxa ratio, and with obvious conflict and high levels of homoplasy, the congruence and phylogenetic information in the Diptilomiopidae taxa was robust enough for the group to be retrieved as a clade under some parameters [e.g., **Diptilomiopidae clade – 318tax trees (27a)**] after relatively light implied weighting against the influence of homoplasy and after finding the best overall fit for the characters. With all evidence in the present study it is again proposed that the Diptilomiopidae is monophyletic, despite lack of support by resampling methods, and analyses under equal weighting, and lack of consistent retrieval of the Diptilomiopidae as a single clade in the present study. Gnathosomal character states typical to the Diptilomiopidae remain the only synapomorphies supporting the group.

The gnathosoma is a complex organ in the Eriophyoidea and future data sets will be improved if its structure is studied in more detail, and smaller, independent gnathosomal substructures are proposed as

primary homologies. In this process, one should be cautious though, that character sampling for parsimony analyses should be random, and not to artificially weigh the importance of the exact same character. The variation in its complexity should not be masked either, though. This improvement may strengthen the robustness of the recovery of the Diptilomiopidae as a clade.

The structure and hierarchical position of the Diptilomiopidae proposed by Keifer (1944) and Roivainen (1953) and presented in Amrine *et al.* (2003) classifies the Diptilomiopidae on the same taxonomic level as the Phytoptidae and Eriophyidae, and they thus did not imply specific relationships between the families, apart from being part of one superfamily. Shevchenko (1971, 1974a), however, implied that the Eriophyidae are more closely related to the Diptilomiopidae than the Phytoptidae (Shevchenko, 1971) in his proposed classification. This has been supported in some of the preliminary empirical studies including Kuang *et al.* (1992) and Hong & Zhang (1996a). The close relationship between the Diptilomiopidae and Eriophyidae is also expressed in the classification proposed by Boczek *et al.* (1989) in which the Eriophyidae *sensu* Amrine *et al.* (2003) includes the Diptilomiopidae. Whether the Diptilomiopidae is a separate clade from the **Eriophyidae group or clade (13)**, or imbedded within the latter group in the present study, is inconclusive, but it was found to have a closer relationship with the extended Eriophyidae group, than with part of the Phytoptidae excluded from the latter group [see **Eriophyidae groups and clades (13)** and **Diptilomiopidae groups and clades (27)**].

The Diptilomiopidae have two subfamilies (Newkirk & Keifer, 1971: 9): Diptilomiopinae with a divided empodium (Keifer, 1944), and Rhyncaphytoptinae with a simple, undivided empodium (Roivainen, 1953). Lindquist & Amrine (1996) proposed Diptilomiopinae are weakly supported by the divided empodium, which they regarded a homoplasious apomorphy on which the subfamily is based, and Rhyncaphytoptinae are probably not monophyletic. These proposals are partly supported by the present study. Monophyly of the subfamilies was not retrieved, and they were found to be polyphyletic, and at the same time, particularly the Rhyncaphytoptinae, is probably also paraphyletic (Figs 4.19, 4.35 and 4.43). The character, the empodial shape and in particular, whether it is divided or not, differentiating the subfamilies, was found to be highly homoplasious within the Eriophyoidea.

The Diptilomiopidae species were recovered largely in two groupings, broadly corresponding to the Rhyncaphytoptinae [**"Rhyncaphytoptinae" part (28)**] and the Diptilomiopinae [**"Diptilomiopinae" group (29)**] (e.g., Figs 4.19, 4.35).

4.7.3.1 "Diptilomiopinae" group (29)

"Diptilomiopinae" group (29) was largely found to be monophyletic. It was retrieved as a group (318tax-k10 tree), and as a clade (318tax-k20). The monophyly of the group was supported by five exemplar species which were recovered as a relatively robust clade [**66-Diptilomiopinae clade (40)**] by all the 66tax analyses. When only two species of the Diptilomiopinae was included (the 18tax data set), they were recovered as sisters, although not as a clade. The **"Diptilomiopinae" group (29)** includes all *Diptilomiopus* spp. included in the respective data sets. It also includes species of about 65% of the genera currently in the Diptilomiopinae included in the 318tax data set, as well as one Rhyncaphytoptinae species, *Sakthirhynchus*.

Of the two parts, more phylogenetic structure was found in the **"Diptilomiopinae" group (29)** and it is also more robust. Several groups could be identified in the 318tax trees. Eleven Diptilomiopinae species were recovered as the **One-Diptilomiopinae group (34)**, where the species were positioned close to each other, but were not necessarily found as an exclusive group one node. These species are morphologically similar, except *Diptilostatus* and *Davisella* which may eventually be found not to be part of the group. Within the **One-Diptilomiopinae group (34)**, a smaller potential clade was recovered consisting of three morphologically similar Diptilomiopinae species from the Oriental Region [***Lithocarus* group (35)**]. Three species from New Zealand, with the tarsus divided into two segments, were recovered as a clade [***Dacundiopus* clade (36)**]. The **Separate-coxae group (37)** consists of three species (a *Levonga* and two *Diptilomiopus* spp.) that are not correctly placed in these genera [according to Amrine *et al*. (2003)], and this is only one of many examples where the present analyses retrieved groupings that confirms either mistakes in interpretation of structures, or obviously wrong generic placements of species. *Africus* is a monospecific genus described from South Africa (Meyer & Ueckermann, 1995). It had a close affinity with *Diptilomiopus* spp., and most definitely is correctly placed in the Diptilomiopinae. It was recovered in a clade with *Neodiptilomiopus* and *D. ervatamiae*, pending confirmation of the correctness of the description of the latter species. *Africus* may alternatively or additionally be closely related to *D. knorri* [see the ***Africus* group and clade (38)**]. Three new *Diptilomiopus* spp. are described from South Africa in the present study. They were retrieved as one group [**SA *Diptilomiopus* group (39)**] under many different parameters from the outset of the present study. The latter may be a case where correctness and detail of description (including SEM study) may have contributed to the recovery of the group, rather than real morphology and particularly the recovered relationships of these three *Diptilomipus* spp. may change with improved description of other *Diptilomiopus* spp., and additional data from molecular studies.

Very little phylogenetic resolution was found of the relationships between the *Diptilomiopus* spp., but this was expected, since the character sample was focused on including all characteristics used on suprageneric and generic level. Some species level characters were included, but possibly many

additional well-defined characters must be found on species level for the phylogenetic resolution of species in one Eriophyoidea genus. The little phylogenetic resolution in *Diptilomiopus* also confirms that the character sample was largely informative regarding genus and suprageneric groupings. A phylogenetic analysis of *Diptilomiopus* and closely related genera is in progress (C. Craemer, *unpubl. data*). In general, the *Diptilomiopus* spp. that were retrieved in relationships with species from other genera in the Diptilomiopinae in the present study were wrongly placed in *Diptilomiopus* according to the conventional classification and diagnosis of *Diptilomiopus*.

4.7.3.2 **"Rhyncaphytoptinae" part (28)**

"Rhyncaphytoptinae" part (28) (Figs 4.19, 4.20) as an exclusive grouping is not as robust as **"Diptilomiopinae" group (29)**, and was found to be paraphyletic, because it is at the base of the **Diptilomiopidae clade – 318tax trees (27a)** (Fig. 4.19) in an exclusive group at one node in the 318tax-k10 tree (not confirmed by the topology in the 318tax-k20 tree). The position of some species is uncertain, e.g., in the 66tax-k999 tree (Fig. 4.19) *Catarhinus* and *Cheiracus* were found as sisters, imbedded among the Phyllocoptinae, and outside the Diptilomiopidae group in the tree. Some groupings were, however, identified within **"Rhyncaphytoptinae" part (28)**. The position of the Diptilomiopinae which were recovered as part of this part is feasible and defendable. The ***Apodiptacus* groups (32)** largely constitute Diptilomiopinae species. They are generally morphologically different from the "general morphology" of the species in **"Diptilomiopinae" group (29)**. Species of the latter are morphologically more similar to *Diptilomiopus* spp. The phylogeny of the larger genera, such as *Diptacus*, in ***Apodiptacus* groups (32)** should be studied before one can propose strong hypotheses about their position. For example, *Diptacus gigantorhynchus* (Nalepa, 1892) (Keifer, 1952b), is morphologically more similar to *Diptilomiopus* spp., than some of the other *Diptacus* spp., including *Diptacus sacramentae*, are. The ***Apodiptacus* groups (32)** are not well-supported, but relationships between them and their placement in the Rhyncaphytoptinae are usable hypotheses. The other identified groupings within **"Rhyncaphytoptinae" part (28)** are ***Cheiracus* groups (30)**, **Long-tibia groups (31)**, and ***Rhyncaphytoptus* groups (33)** (Fig. 4.20) are all potential clades.

The monophyly of the Diptilomiopidae is likely. Although the family may be placed within the extended Eriophyidae *sensu* the present study, it is a relatively robust larger clade, and well-defined and differentiated from the remainder of the Eriophyoidea. It is retained as a separate family *on par* with the Eriophyidae (Table 4.10), but is proposed to have a close relationship with the extended Eriophyidae *sensu* the present study.

The Rhyncaphytoptinae are paraphyletic, and possibly polyphyletic, and the Diptilomiopinae is polyphyletic and paraphyletic, but a large part of the Diptilomiopinae *sensu* Amrine *et al*. (2003), may constitute a clade. The Diptilomiopidae subfamilies are currently defined and differentiated on the basis

of one character, having a divided or undivided empodium (Amrine *et al*., 2003). This character was found to be homoplasious within the Eriophyoidea and was not retrieved as a synapomorphy. It is quite conclusive that the Rhyncaphytoptinae and Diptilomiopinae are not monophyletic, and only confuse the real relationships within the Diptilomiopidae. It is proposed that the two subfamilies are retained (Table 4.10) pending more robust hypotheses about the Diptilomiopidae phylogenetic structure, but they are redefined in concordance with the two Diptilomiopidae groupings found in the present study implied by new combinations of the Diptilomiopidae species which were included in the present study. A series of phylogenetic analyses of smaller hypothetical potential clades, as well as the two larger groupings within the Diptilomiopidae are currently undertaken (C. Craemer, *in prep.*).

4.8 CONCLUSIONS

Phylogenetic analyses were undertaken to test the monophyly of suprageneric Eriophyoidea taxa. The analyses were designed to be exploratory, and a large number of taxa were included to sample variation at generic level comprehensively. Additional analyses under different parameters and of data matrices with fewer exemplar taxa were included to test the robustness of groups found, and to alleviate the problem of a small characters:taxa ratio. The hypothesis that the families, subfamilies and tribes of the Eriophyoidea are not monophyletic, with the possible exception of the Diptilomiopidae, was successfully appraised, but not conclusively proven to be true in all regards. Additionally, alternative feasible hypotheses about relationships between Eriophyoidea taxa, and some consequent changes to improve the suprageneric classification of the Eriophyoidea, were proposed. Previous phylogenetic analyses, and their results, were also appraised and compared with the results found in the present study.

The characters and character states for the analyses were scored and coded from published descriptions, and many descriptions were found to be faulty, and some characters were sometimes described in so little detail, that it was hardly possible to define primary homologies from them. Some of the chosen characters could not be scored for all species, or were scored ambiguously, because they were not included in all descriptions, although species descriptions were found to be largely standardized in content. It was confirmed that alpha taxonomic descriptions need to be improved and brought up to standard, otherwise both conventional and more comprehensive systematic studies will suffer the consequences.

The area primarily identified for future improvement in the systematics of the Eriophyoidea, is the improvement of morphological and other systematically useful character data. Descriptions should be standardized, and more systematically informative characters should be found, and this can mostly be achieved by incorporating more modern technologies, such as SEM and molecular studies more extensively and on a routine basis.

There is no doubt that the present phylogenetic study contributed a large amount of data that will be useful and improve the systematics of the Eriophyoidea, quantitatively and qualitatively superior to what a traditional, manual review of the classification would have been able to contribute. The study is also repeatable and testable, which places it on sound scientific ground. As result of the present study I became convinced that phylogenetic analyses should not be seen as a separate process from traditional taxonomy, but rather as a useful tool to be used concurrently with alpha taxonomy. The most important step in phylogenetic studies is the description of primary homologies in alpha taxonomic studies, and the preparation of a good quality data set for the analyses. This should also be the goal for traditional taxonomy, and should not entail extra, unnecessary work. The empirical analyses are used to test the taxonomist's hypotheses of primary homologies and classificatory placements and aid with the development of a natural classification as far as the data allow. Programs (e.g., TNT) are now freely available same as the know-how for undertaking phylogenetic analyses. It should be considered standard by eriophyoid systematists that description of new supraspecific taxa should incorporate phylogenetic analyses.

CHAPTER 5

GENERAL CONCLUSIONS

Central to the systematics of the Eriophyoidea is the need for alpha taxonomic descriptions of new species to address the huge short fall in our knowledge on their extant diversity and to obtain new information from the unknown taxon diversity for improving our understanding of and hypotheses on the phylogeny of the group. The description of new species and other taxa justifiably forms the bulk of systematic studies on the Eriophyoidea. During the present study it became increasingly clear that improvement in the systematics of the group should not be to the detriment of documenting the diversity, which is largely still unknown, but should be complimentary to it.

The descriptions of new taxa are relatively standardized and adhering to a certain quality and format, but particular shortcomings are persistent. These inadequacies include lack of detail in the description of minute morphology, over-simplified and schematic descriptive drawings, inaccurate and vaguely defined morphometric data, lack of needed improvement in the standardization, definition and delimitation of characters and character states, and additionally some descriptions include wrong and ambiguous data to the point where they become inadequate. The need for accurate and complete descriptions, and documenting of descriptive data, is exacerbated for these fragile mites, of which slide-mounted type material is not permanent and in time will be destroyed and lost to further study.

While capturing published descriptive data and attempting to structure it for a relational database including species sampled across the diversity of the Eriophyoidea, and eventually defining and scoring a data matrix for phylogenetic analyses during the present study, the shortcomings of the published descriptive data came to the forefront. It became clear that alpha taxonomic descriptions should be improved, particularly in detail, accuracy, standardization and definition of terminology. The definition and demarcation of characters and character states must be improved and when a species is described, it should be described rather in terms of hypothesizing primary homologies than merely describing a new taxon in a mechanical manner using repetitive formats and patterns. This may sound contradictory, but improving description does not necessarily entail diverging from a standardized format

entirely, but rather to improve within the framework, and still keep the descriptions complete and comparable. From the experience of the present study it is strongly proposed that the best way to do this would be to set up and master an electronic protocol and procedures where the descriptions can rather be done as structured data, from which natural language descriptions can be generated. It will be ideal, to develop such a structured definition of characters and character states collaboratively between practicing eriophyoid systematists. If such a descriptive structure could be collaboratively populated and primary descriptive data captured by each person describing a new taxon, the data would be available, without much extra work and to the detriment of describing new taxa, for developing interactive keys, monographs, catalogues and undertaking phylogenetic studies. It is by no means suggested that the autonomy and recognition of the research and data of each person, so necessary for building a career and securing funding, should be compromised, but rather that already published information be available in the same format and structure for larger collaborative studies on a worldwide scale. Unfortunately, there seems to still be technical difficulties and lack of general holistic software programs that can facilitate such an approach, but hopefully these will improve with time.

Eriophyoid mites are morphologically so simplified that there are relatively few additional characteristics from slide-mounted specimens, apart from those already utilized in taxonomy, to use for classifying and delimiting taxa and for inclusion in data matrices for phylogenetic analyses. This was somewhat confirmed by the present study. This restriction can be alleviated by adding molecular data, but it is crucial that morphological data should also be increased and improved. One way to increase comparative morphological data would be to study the morphology of these minute organisms in more detail and accuracy. The increased resolution of scanning electron microscopy (SEM) above light microscopy can serve to this end. Up to now SEM studies and images have contributed to our understanding of eriophyoid morphology, improvement of descriptions, and in a few cases added supplementary descriptive information. Generally, SEM studies remain infrequently and sporadically used in eriophyoid systematics, though, and when used, it is merely used to support descriptions from slide-mounted specimens, and not for additional morphological information. SEM studies are also not focused on specific body areas or structures, and the present study demonstrated with a comparative study of the gnathosoma between only a few species, that useful additional characters can be found in this way.

Not only can SEM studies contribute additional morphological information, but in the present study it was found that descriptive data from slide-mounted specimens may be seriously flawed by artefacts apart from the inability to study some structures sufficiently with light

microscopy. To improve the accuracy of descriptions and lessen artefacts, it is not sufficient to do any SEM study, but the best available SEM techniques should be incorporated to study the specimens in as real and natural way as possible to avoid introducing yet another set of artefacts. Incorporating SEM studies will not just contribute to data for phylogenetic studies, but will improve the descriptions and thus the taxonomy. It is also importance to improve slide-mounting of specimens, apart from incorporating new techniques like SEM as this will improve the quality of the descriptions for use in practical identification and classification.

The classificatory framework within which taxa are described, delimited, diagnosed, identified and classified is very important. The advantages of a natural classification, built with monophyletic groups, above an artificial classification are well-known and accepted. Before the present study it was generally proposed that the classification of the Eriophyoidea is largely artificial. Although a few preliminary small scale studies were undertaken to test the monophyly of suprageneric groupings of the present eriophyoid classification, the present study is the first attempt at a comprehensive phylogenetic study, incorporating a sample and analysis attaining a holistic exploratory study of the phylogeny of the Eriophyoidea. Although almost no unambiguous conclusions about the relationships between suprageneric eriophyoid taxa, and the monophyly of the groups in the present classification, it contributed a large amount of useful hypotheses in this regard, and tested previous hypotheses. Some of the results can be incorporated into the present classification and will improve it for practical taxonomic uses and base it on potentially more natural groupings than it is at the moment. It also showed areas in which research on phylogeny is particularly needed. With the summary above, incorporating phylogenetic studies as part of the everyday practical taxonomy will be to the advantage of improving the systematics theoretically and practically. It will also improve the scientific quality of eriophyoid systematics by incorporating empirical analyses.

The study set out to appraise some aspects of eriophyoid systematics. The families, subfamilies and tribes of the Eriophyoidea in the present classification, with the exception of the Diptilomiopidae, are shown not to be monophyletic. The present study did not prove this conclusively, but also did not find the groupings to be monophyletic, to the degree that it is proposed that some changes should be made to the presently accepted classification. Additionally, useful alternative hypotheses about relationships between taxa could be proposed, and it was again found that the characters currently used in eriophyoid taxonomy are highly homoplasious, but this could be probably attributed to high natural levels of homoplasy in the group. It was found that slide-mounted specimens contain artefacts and that these are incorporated in eriophyoid descriptions and classification, to a lesser or greater degree, depending on the quality of slide-mounting. Additional morphological data, more

than what was expected, were found by studying specimens using SEM. The definition and delimitation of characters and character states were found to be insufficient and problematic when structuring descriptive data for taxa across the Eriophyoidea and for use as primary homologies in phylogenetic analyses. With the correct and carefully constructed protocol for capturing primary descriptive data from the start, it should be possible to incorporate phylogenetic studies as part of alpha taxonomic endeavours and should be strongly advocated.

Finally, there is a need, for new technologies to be incorporated more extensively in the systematics of the Eriophyoidea. This may in some respects be a daunting task in practice, though, and the author will attempt to follow the conclusions found in this study, but there may be restrictions, such as infrastructure and funding, in attempting it. The quality and usefulness of systematic study of the Eriophyoidea by the author has already been improved as a result of the present study.

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APPENDIX A

Appendix A. The ingroup species (Eriophyoidea) and outgroup species (Tydeidae and Tetranychidae) included in the data sets in the present study of the phylogeny of the Eriophyoidea. All species are included in the 318 taxon data matrix. The number of species described in each genus mostly according to Amrine *et al.* (2003), or more recent, is listed in the column "Nu. spp."; Tydeidae - monotypic genus; Tetranychidae – according to Bolland *et al*. (1998).

Mite species	Classification	Nu. spp.	Articles from which characters were scored in the present study
Orfareptydeus stepheni Ueckermann & Grout, 2007	Tydeidae	1	Ueckermann & Grout, 2007
Mononychellus yemensis Meyer, 1996	Tetranychidae	29	Meyer, 1996
*Abacarus acalyptus (*Keifer, 1939)	Eriophyidae: Phyllocoptinae: Anthocoptini	50	Keifer, 1939d
Abacarus hystrix (Nalepa, 1896)	Eriophyidae: Phyllocoptinae: Anthocoptini	50	Nalepa, 1896; Keifer, 1952b
Aberoptus samoae Keifer, 1951	Eriophyidae: Aberoptinae	3	Keifer, 1951
Acadicrus bifurcatus Keifer, 1965	Eriophyidae: Phyllocoptinae: Phyllocoptini	3	Keifer, 1965b
Acalitus ledi Keifer, 1965	Eriophyidae: Eriophyinae: Aceriini	87	Keifer, 1965b
Acamina nolinae (Keifer, 1939)	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Keifer, 1939a
Acaphyllisa parindiae Keifer, 1978	Eriophyidae: Phyllocoptinae: Acaricalini	10	Keifer, 1978
Acarelliptus cocciformis Keifer, 1940	Eriophyidae: Phyllocoptinae: Phyllocoptini	4	Keifer, 1940b
Acarhis diospyrosis Chandrapatya, 1991	Diptilomiopidae: Diptilomiopinae	3	Chandrapatya & Boczek, 1991c
Acarhis lepisanthis Keifer, 1975	Diptilomiopidae: Diptilomiopinae	3	Keifer, 1975d
Acarhis siamensis Boczek & Chandrapatya, 2000	Diptilomiopidae: Diptilomiopinae	3	Boczek & Chandrapatya, 2000
Acarhynchus filamentus Keifer, 1959	Diptilomiopidae: Diptilomiopinae	5	Keifer, 1959b
Acaricalus segundus Keifer, 1940	Eriophyidae: Phyllocoptinae: Acaricalini	15	Keifer, 1940b
Acathrix trymatus Keifer, 1962	Phytoptidae: Phytoptinae	2	Keifer, 1962c
Aceria tulipae (Keifer, 1938)	Eriophyidae: Eriophyinae: Aceriini	900	Keifer, 1938a
Acerimina cedrelae Keifer, 1957	Eriophyidae: Eriophyinae: Aceriini	7	Keifer, 1957
Achaetocoptes ajoensis (Keifer, 1961)	Eriophyidae: Cecidophyinae: Cecidophyini	2	Keifer, 1961a
Acritonotus denmarki Keifer,1962	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Keifer, 1962d
Aculodes mckenziei (Keifer, 1944)	Eriophyidae: Phyllocoptinae: Anthocoptini	16	Keifer, 1944
Aculops populivagrans (Keifer, 1953)	Eriophyidae: Phyllocoptinae: Anthocoptini	158	Keifer, 1953
Aculus ligustri (Keifer, 1938)	Eriophyidae: Phyllocoptinae: Anthocoptini	248	Keifer, 1938a
Acunda plectilis Keifer, 1965	Eriophyidae: Eriophyinae: Aceriini	1	Keifer, 1965c
Adenocolus psydraxi Meyer & Ueckermann, 1997	Eriophyidae: Nothopodinae: Colopodacini	1	Meyer & Ueckermann, 1997
Aequsomatus lanceolatae Meyer & Ueckermann, 1995	Eriophyidae: Phyllocoptinae: Phyllocoptini	3	Meyer & Ueckermann, 1995
Africus psydraxae Meyer & Ueckermann, 1995	Diptilomiopidae: Diptilomiopinae	1	Meyer & Ueckermann, 1995
Afromerus florinoxus Meyer, 1990	Eriophyidae: Cecidophyinae: Colomerini	5	Meyer, 1990b
Anchiphytoptus lineatus Keifer, 1952	Phytoptidae: Phytoptinae	4	Keifer, 1952a
Anothopoda johnstoni Keifer, 1959	Eriophyidae: Nothopodinae: Nothopodini	5	Keifer, 1959d
Anthocoptes gutierreziae Keifer, 1962	Eriophyidae: Phyllocoptinae: Anthocoptini	50	Keifer, 1962c
Apodiptacus cordiformis Keifer, 1960	Diptilomiopidae: Diptilomiopinae	5	Keifer, 1960
Apontella bravaisiae Boczek & Nuzzaci, 1988	Eriophyidae: Nothopodinae: Colopodacini	1	Boczek & Nuzzaci, 1988
Arectus bidwillius Manson, 1984	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Manson, 1984a
Areekulus eugeniae Chandrapatya, 1998	Diptilomiopidae: Rhyncaphytoptinae	1	Boczek & Chandrapatya, 1998
Asetacus madronae Keifer, 1952	Diptilomiopidae: Rhyncaphytoptinae	7	Keifer, 1952a
Asetadiptacus emiliae Carmona, 1970	Diptilomiopidae: Diptilomiopinae	2	Carmona, 1970
Asetilobus hodgkinsi (Manson, 1965)	Eriophyidae: Eriophyinae: Eriophyini	1	Manson, 1965
Ashieldophyes pennadamensis Mohanasundaram, 1984	Eriophyidae: Ashieldophyinae	1	Mohanasundaram, 1984
Austracus havrylenkonis Keifer, 1944	Phytoptidae: Sierraphytoptinae: Sierraphytoptini	1	Keifer, 1944
Baileyna marianae Keifer, 1954	Eriophyidae: Eriophyinae: Aceriini	5	Keifer, 1954
Bakeriella ocimis Chakrabarti & Mondal, 1982	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Chakrabarti & Mondal, 1982
Bariella farnei De Lillo, 1988	Eriophyidae: Cecidophyinae: Cecidophyini	1	De Lillo, 1988a
Boczekella laricis Farkas, 1965	Phytoptidae: Nalepellinae: Trisetacini	3	Farkas, 1965a
Brachendus pumilae Keifer, 1964	Eriophyidae: Eriophyinae: Eriophyini	3	Keifer, 1964a
Brevulacus reticulatus Manson, 1984	Diptilomiopidae: Rhyncaphytoptinae	1	Manson, 1984a
Bucculacus kaweckii Boczek, 1961	Diptilomiopidae: Diptilomiopinae	2	Boczek, 1961
Calacarus pulviferus Keifer, 1940	Eriophyidae: Phyllocoptinae: Calacarini	41	Keifer, 1940b
Calepitrimerus cariniferus Keifer, 1938	Eriophyidae: Phyllocoptinae: Phyllocoptini	62	Keifer, 1938b
Caliphytoptus quercilobatae Keifer, 1938	Eriophyidae: Phyllocoptinae: Phyllocoptini	3	Keifer, 1938b
Caroloptes fagivagrans Keifer, 1940	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Keifer, 1940b
Catachella machaerii Keifer, 1969	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Keifer, 1969b
Catarhinus tricholaenae Keifer, 1959	Diptilomiopidae: Rhyncaphytoptinae	11	Keifer, 1959b
Cecidodectes euzonus Nalepa, 1917	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Meyer & Ueckermann, 1989b
Cecidophyes rouhollahi Craemer, 1999	Eriophyidae: Cecidophyinae: Cecidophyini	143	Craemer *et al*., 1999
Cenaca syzygioidis Keifer, 1972	Eriophyidae: Eriophyinae: Aceriini	3	Keifer, 1972
Cenalox nyssae Keifer, 1961	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Keifer, 1961b
Cercodes simondsi Keifer, 1960	Eriophyidae: Eriophyinae: Eriophyini	1	Keifer, 1960
Chakrabartiella ficusis (Chakrabarti, Ghosh & Das, 1992)	Diptilomiopidae: Rhyncaphytoptinae	1	Chakrabarti, Ghosh & Das, 1992
Cheiracus sulcatus Keifer, 1977	Diptilomiopidae: Rhyncaphytoptinae	4	Keifer, 1977a
Chiangmaia longifolii (Chandrapatya & Boczek, 2000)	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2000c
Chrecidus quercipodus Manson, 1984	Eriophyidae: Cecidophyinae: Cecidophyini	1	Manson, 1984a
Circaces chakrabartii Keifer, 1978	Eriophyidae: Cecidophyinae: Colomerini	4	Keifer, 1978
Cisaberoptus kenyae Keifer, 1966 (now jr. syn. of *Aceria*)	Eriophyidae: Aberoptinae	2	Keifer, 1966c (deutogyne)
Cisaberoptus pretoriensis Meyer, 1989 (now jr. syn. of *Aceria*)	Eriophyidae: Aberoptinae	2	Meyer, 1989a (deutogyne)
Colomerus gardeniella (Keifer, 1964)	Eriophyidae: Cecidophyinae: Colomerini	25	Keifer, 1964b

Colopodacus africanus Keifer, 1960	Eriophyidae: Nothopodinae: Colopodacini	14	Keifer, 1960
Coptophylla lamimani (Keifer, 1939)	Eriophyidae: Cecidophyinae: Cecidophyini	2	Keifer, 1939d
Cosella deleoni (Keifer, 1956)	Eriophyidae: Nothopodinae: Nothopodini	22	Keifer, 1956
Cosetacus camelliae (Keifer, 1945)	Eriophyidae: Cecidophyinae: Colomerini	2	Keifer, 1945
Costarectus zeyheri Meyer & Ueckermann, 1995	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Meyer & Ueckermann, 1995
Criotacus brachystegiae Keifer, 1963	Eriophyidae: Phyllocoptinae: Phyllocoptini	6	Keifer, 1963b
Cupacarus cuprifestor Keifer, 1943	Eriophyidae: Phyllocoptinae: Phyllocoptini	6	Keifer, 1943
Cymeda zealandica Manson & Gerson, 1986	Eriophyidae: Phyllocoptinae: Acaricalini	1	Manson & Gerson, 1986
Cymoptus spiniventris Keifer, 1946	Eriophyidae: Eriophyinae: Aceriini	4	Keifer, 1946
Dacundiopus stylosus Manson, 1984	Diptilomiopidae: Diptilomiopinae	1	Manson, 1984a
Davisella breitlowi (Davis, 1964)	Diptilomiopidae: Diptilomiopinae	6	Davis, 1964a
Dechela epelis Keifer, 1965	Eriophyidae: Cecidophyinae: Cecidophyini	1	Keifer, 1965a
Dialox stellatus Keifer, 1962	Diptilomiopidae: Diptilomiopinae	1	Keifer, 1962d
Dichopelmus notus, Keifer 1959	Eriophyidae: Phyllocoptinae: Acaricalini	4	Keifer, 1959c
Dicrothrix anacardii Keifer, 1966	Eriophyidae: Phyllocoptinae: Tegonotini	2	Keifer, 1966c
Diphytoptus nephroideus Huang, 1991	Eriophyidae: Eriophyinae: Diphytoptini	1	Huang, 1991
Diptacus pandanus (Boczek & Oleczek, 1988)	Diptilomiopidae: Diptilomiopinae	43	Boczek & Oleczek, 1988
Diptacus sacramentae (Keifer, 1939)	Diptilomiopidae: Diptilomiopinae	43	Keifer, 1939b
Diptilomiopus acronychia Chen, Wei & Qin, 2004	Diptilomiopidae: Diptilomiopinae	82	Chen, Wei & Qin, 2004
Diptilomiopus aglaiae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2002a
Diptilomiopus alagarmalaiensis Mohanasundaram, 1986	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1986a
Diptilomiopus alangii Mohanasundaram, 1982	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1982b
Diptilomiopus anthocephaliae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2002a
Diptilomiopus apobrevis sp. nov.	Diptilomiopidae: Diptilomiopinae	82	present study
Diptilomiopus apolongus sp. nov.	Diptilomiopidae: Diptilomiopinae	82	present study
Diptilomiopus aralioidus Huang, 2006	Diptilomiopidae: Diptilomiopinae	82	Huang, 2006
Diptilomiopus artabotrysi (Boczek, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991b
Diptilomiopus artocarpae Mohanasundaram, 1981	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1981b
Diptilomiopus asperis Ghosh & Chakrabarti, 1989	Diptilomiopidae: Diptilomiopinae	82	Ghosh & Chakrabarti, 1989a
Diptilomiopus assamica Keifer, 1959	Diptilomiopidae: Diptilomiopinae	82	Keifer, 1959c
Diptilomiopus averrhoae Wei & Feng, 1999	Diptilomiopidae: Diptilomiopinae	82	Wei & Feng, 1999
Diptilomiopus azadirachtae (Boczek, 1992)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1992b
Diptilomiopus barringtoniae (Chandrapatya, 1992)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1992b
Diptilomiopus bengalensis Chakrabarti & Mondal, 1979	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti & Mondal, 1979
Diptilomiopus benjaminae (Boczek & Chandrapatya, 2002)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 2002
Diptilomiopus boueae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2002a
Diptilomiopus camarae Mohanasundaram, 1981	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1981b
Diptilomiopus cerberae (Chandrapatya, 1998)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1998
Diptilomiopus championi (Huang, 1992)	Diptilomiopidae: Diptilomiopinae	82	Huang, 1992
Diptilomiopus cocculae Mohanasundaram, 1981	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1981b
Diptilomiopus combretae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2002a
Diptilomiopus combreti Wei & Lu, 2001	Diptilomiopidae: Diptilomiopinae	82	Wei & Lu, 2001
Diptilomiopus commuiae Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001b
Diptilomiopus coreiae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2002b
Diptilomiopus cumingis Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001a
Diptilomiopus cuminis Chakrabarti, Ghosh & Das, 1992	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti, Ghosh & Das, 1992
Diptilomiopus cuminis redescription by Huang (2001c)	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus cythereae (Chandrapatya, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991a
Diptilomiopus davisi Keifer, 1969	Diptilomiopidae: Diptilomiopinae	82	Keifer, 1969a
Diptilomiopus dendropanacis Chen, Wei & Qin, 2003	Diptilomiopidae: Diptilomiopinae	82	Chen, Wei & Qin, 2003
Diptilomiopus elaeocarpi (Boczek, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991a
Diptilomiopus elliptus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001d
Diptilomiopus emarginatus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus ervatamiae (Chandrapatya, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991a
Diptilomiopus eucalypti (Boczek, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991b
Diptilomiopus euryae Chen, Wei & Qin, 2003	Diptilomiopidae: Diptilomiopinae	82	Chen, Wei & Qin, 2003
Diptilomiopus faurius sp. nov.	Diptilomiopidae: Diptilomiopinae	82	present study
Diptilomiopus ficifolius (Boczek & Oleczek, 1988)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Oleczek, 1988
Diptilomiopus ficus Attiah, 1967	Diptilomiopidae: Diptilomiopinae	82	Attiah, 1967
Diptilomiopus ficusis Chakrabarti & Mondal, 1983	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti & Mondal, 1983
Diptilomiopus formosanus Huang, 2005	Diptilomiopidae: Diptilomiopinae	82	Huang, 2005
Diptilomiopus gilibertiae Kadono, 1984	Diptilomiopidae: Diptilomiopinae	82	Kadono, 1984
Diptilomiopus guajavae Mohanasundaram, 1985	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1985
Diptilomiopus hexogonus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus holmesi (Keifer, 1962)	Diptilomiopidae: Diptilomiopinae	82	Keifer, 1962c
Diptilomiopus holopteleae Abou-Awad & El-Banhawy, 1992	Diptilomiopidae: Diptilomiopinae	82	Abou-Awad & El-Banhawy, 1992
Diptilomiopus holoptelus Chakrabarti & Mondal, 1983	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti & Mondal, 1983
Diptilomiopus illicii Wei & Lu, 2001	Diptilomiopidae: Diptilomiopinae	82	Wei & Lu, 2001
Diptilomiopus indicus Chakrabarti & Pandit, 1996	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti & Pandit, 1996

Diptilomiopus integrifoliae Mohanasundaram, 1981	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1981b
Diptilomiopus jasminiae (Chandrapatya & Boczek, 2001)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2001a
Diptilomiopus javanicus Nalepa, 1916	Diptilomiopidae: Diptilomiopinae	82	Nalepa, 1916; Nalepa, 1918
Diptilomiopus jevremovici Keifer, 1960	Diptilomiopidae: Diptilomiopinae	82	Keifer, 1960
Diptilomiopus knorri Keifer, 1974	Diptilomiopidae: Diptilomiopinae	82	Keifer, 1974
Diptilomiopus languasi (Boczek, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991b
Diptilomiopus leeasis Chakrabarti, Ghosh & Das, 1992	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti, Ghosh & Das, 1992
Diptilomiopus leptophyllus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus lobbianus Huang & Cheng, 2005	Diptilomiopidae: Diptilomiopinae	82	Huang & Cheng, 2005
Diptilomiopus loropetali Kuang, 1986	Diptilomiopidae: Diptilomiopinae	82	Kuang, 1986a; Hong & Zhang, 1996c
Diptilomiopus maduraiensis Mohanasundaram, 1986	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1986a
Diptilomiopus malloti Wei & Feng, 1999	Diptilomiopidae: Diptilomiopinae	82	Wei & Feng, 1999
Diptilomiopus melastomae (Boczek & Chandrapatya, 2002)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 2002
Diptilomiopus meliae (Boczek, 1998)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1998
Diptilomiopus morii Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus morindae (Boczek, 1998)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1998
Diptilomiopus musae (Chandrapatya, 1998)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1998
Diptilomiopus octogonus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus pamithus (Boczek & Chandrapatya, 1989)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1989
Diptilomiopus perfectus Huang, 2001	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus phylanthi (Chandrapatya, 1992)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1992b
Diptilomiopus pocsi Farkas, 1967	Diptilomiopidae: Diptilomiopinae	82	Farkas, 1967
Diptilomiopus racemosae (Chandrapatya & Boczek, 2001)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 2001a
Diptilomiopus riciniae (Boczek & Chandrapatya, 2002)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 2002
Diptilomiopus sandorici (Chandrapatya, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991a
Diptilomiopus securinegus Boczek, 1992	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1992a
Diptilomiopus septimus Huang, 2001 (now jr. syn. of *D. championi*)	Diptilomiopidae: Diptilomiopinae	82	Huang, 2001c
Diptilomiopus stephanus Huang, 2005	Diptilomiopidae: Diptilomiopinae	82	Huang, 2005
Diptilomiopus strebli (Boczek, 1992)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 1992b
Diptilomiopus swieteniae (Chandrapatya, 1998)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1998
Diptilomiopus thaianae (Boczek, 1991)	Diptilomiopidae: Diptilomiopinae	82	Chandrapatya & Boczek, 1991a
Diptilomiopus thangaveli Mohanasundaram, 1983	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1983c
Diptilomiopus thunbergiae (Boczek & Chandrapatya, 2002)	Diptilomiopidae: Diptilomiopinae	82	Boczek & Chandrapatya, 2002
Diptilomiopus trewier Chakrabarti & Mondal, 1983	Diptilomiopidae: Diptilomiopinae	82	Chakrabarti & Mondal, 1983
Diptilomiopus ulmivagrans Mohanasundaram, 1984	Diptilomiopidae: Diptilomiopinae	82	Mohanasundaram, 1984
Diptiloplatus megagrastis Keifer, 1975	Diptilomiopidae: Diptilomiopinae	2	Keifer, 1975c
Diptilorhynacus dioscoreae Boczek & Nuzzaci, 1985	Diptilomiopidae: Diptilomiopinae	2	Boczek & Nuzzaci, 1985
Diptilorhynacus sinusetus Mondal, Ghosh & Chakrabarti, 1981	Diptilomiopidae: Diptilomiopinae	2	Mondal, Ghosh & Chakrabarti, 1981
Diptilostatus nudipalpus Flechtmann, 2003	Diptilomiopidae: Diptilomiopinae	2	Flechtmann & De Moraes, 2003
Disella ilicis (Keifer, 1965)	Eriophyidae: Nothopodinae: Nothopodini	12	Keifer, 1965a
Ditrymacus athiasella Keifer, 1960	Eriophyidae: Phyllocoptinae: Anthocoptini	3	Keifer, 1960
Duabangus chiangmai Chandrapatya & Boczek, 2000	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2000b
Ectomerus anysis (Keifer, 1970)	Eriophyidae: Cecidophyinae: Colomerini	4	Keifer, 1970
Epicecidophyes clerodendris Mondal & Chakrabarti, 1981	Eriophyidae: Cecidophyinae: Colomerini	2	Mondal & Chakrabarti, 1981
Epiphytimerus palampurensis Mohanasundaram, 1984 (now jr. syn. of *Abacarus*)	Eriophyidae: Phyllocoptinae: Anthocoptini	1?	Mohanasundaram, 1984
Epitrimerus pyri (Nalepa, 1891)	Eriophyidae: Phyllocoptinae: Phyllocoptini	151	Manson, 1984a
Eriophyes pyri (Pagenstecher, 1857)	Eriophyidae: Eriophyinae: Eriophyini	299	Manson, 1984b
Eriophyes quadrifidus Meyer & Ueckermann, 1989	Eriophyidae: Eriophyinae: Eriophyini	299	Meyer & Ueckermann, 1989a
Euterpia fissa Navia & Flechtmann, 2005	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Navia & Flechtmann, 2005
Floracarus calonyctionis Keifer, 1953	Eriophyidae: Nothopodinae: Nothopodini	18	Keifer, 1953
Fragariocoptes setiger (Nalepa, 1894)	Phytoptidae: Sierraphytoptinae: Sierraphytoptini	1	Roivainen, 1951; Boczek, 1964
Gammaphytoptus camphorae Keifer, 1939	Eriophyidae: Cecidophyinae: Colomerini	5	Keifer, 1939a
Glyptacus lithocarpi Keifer, 1953	Eriophyidae: Cecidophyinae: Cecidophyini	4	Keifer, 1953
Heterotergum gossypii Keifer, 1955	Eriophyidae: Phyllocoptinae: Anthocoptini	13	Keifer, 1955
Hoderus roseus (Keifer, 1975)	Diptilomiopidae: Rhyncaphytoptinae	2	Keifer, 1975d
Hyborhinus kallarensis Muhanasundaram, 1986	Diptilomiopidae: Rhyncaphytoptinae	1	Mohanasundaram, 1986a
Indonotolox sudarsani Ghosh & Chakrabarti, 1982	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Ghosh & Chakrabarti, 1982
Indosetacus rhinacanthi Ghosh & Chakrabarti, 1987	Eriophyidae: Cecidophyinae: Colomerini	1	Ghosh & Chakrabarti, 1987
Indotegolophus darjeelingensis Chakrabarti & Mondal, 1980	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Chakrabarti, Mondal & Roy, 1980
Johnella virginiana Keifer, 1959	Eriophyidae: Cecidophyinae: Cecidophyini	2	Keifer, 1959d
Jutarus benjaminae Boczek & Chandrapatya, 1989	Eriophyidae: Phyllocoptinae: Calacarini	2	Boczek & Chandrapatya, 1989
Kaella flacourtiae (Chandrapatya & Boczek, 2002)	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2002b
Keiferana neolitseae Channabasavanna, 1967	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Channabasavanna, 1967
Keiferella juniperici Boczek, 1964	Eriophyidae: Phyllocoptinae: Phyllocoptini	3	Boczek, 1964
Keiferophyes avicenniae Mohanasundaram, 1983	Eriophyidae: Eriophyinae: Aceriini	2	Mohanasundaram, 1983a
Knorella gigantochloae Keifer, 1975	Eriophyidae: Phyllocoptinae: Acaricalini	8	Keifer, 1975c
Konola hibernalis Keifer, 1979	Diptilomiopidae: Rhyncaphytoptinae	1	Keifer, 1979b
Lambella cerina (Lamb, 1953)	Diptilomiopidae: Diptilomiopinae	1	Manson, 1984a

Latinotus wegoreki Boczek, 1960	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Boczek, 1960
Leipothrix solidaginis Keifer, 1966	Eriophyidae: Phyllocoptinae: Phyllocoptini	12	Keifer, 1966c
Levonga caseariasis (Chakrabarti & Pandit, 1996)	Diptilomiopidae: Diptilomiopinae	6	Chakrabarti & Pandit, 1996
Levonga litseae (Chakrabarti, Ghosh & Das, 1992)	Diptilomiopidae: Diptilomiopinae	6	Chakrabarti, Ghosh & Das, 1992
Levonga papaitongensis Manson, 1984	Diptilomiopidae: Diptilomiopinae	6	Manson, 1984a
Litaculus khandus Manson, 1984	Eriophyidae: Phyllocoptinae: Acaricalini	6	Manson, 1984a
Lithocarus thomsoni Chandrapatya & Boczek, 2000	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2000c
Mackiella phoenicis Keifer, 1939	Phytoptidae: Sierraphytoptinae: Mackiellini	2	Keifer, 1939a
Mediugum sanasaii Huang, 2001	Diptilomiopidae: Diptilomiopinae	1	Huang, 2001d
Mesalox tuttlei Keifer, 1962	Eriophyidae: Phyllocoptinae: Anthocoptini	7	Keifer, 1962a
Metaculus syzygii Keifer, 1962	Eriophyidae: Phyllocoptinae: Anthocoptini	10	Keifer, 1962b
Metaplatyphytoptus amoni Hong & Kuang, 1989	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Hong & Kuang, 1989
Meyerella bicristatus (Meyer, 1989)	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Meyer, 1989b
Monotrymacus quadrangulari Mohanasundaram, 1982	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Mohanasundaram, 1982a
Nacerimina gutierrezi Keifer, 1979	Eriophyidae: Eriophyinae: Eriophyini	2	Keifer, 1979a
Nalepella tsugifoliae Keifer, 1953	Phytoptidae: Nalepellinae: Nalepellini	15	Keifer, 1953
Neoacaphyllisa lithocarpi Kuang & Hong, 1989	Eriophyidae: Phyllocoptinae: Acaricalini	1	Kuang & Hong, 1989
Neoacarhis aglaiae Kuang, 1998	Diptilomiopidae: Diptilomiopinae	1	Kuang, 1998
Neocatarhinus bambusae Kuang & Hong, 1990	Diptilomiopidae: Rhyncaphytoptinae	1	Kuang & Hong, 1990
Neocecidophyes mallotivagrans Muhanasundaram, 1980	Eriophyidae: Cecidophyinae: Colomerini	2	Mohanasundaram, 1980
Neocolopodacus mitragynae Mohanasundaram, 1980	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Mohanasundaram, 1980
Neocosella ichnocarpae Mohanasundaram, 1981	Eriophyidae: Nothopodinae: Nothopodini	2	Mohanasundaram, 1981d
Neocupacarus flabelliferis Das & Chakrabarti, 1985	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Das & Chakrabarti, 1985
Neodialox palmyrae Mohanasundaram, 1983	Diptilomiopidae: Diptilomiopinae	1	Mohanasundaram, 1983b
Neodichopelmus samoanus Manson, 1973	Eriophyidae: Phyllocoptinae: Acaricalini	1	Manson, 1973
Neodicrothrix tiliacorae Mohanasundaram, 1984	Eriophyidae: Phyllocoptinae: Phyllocoptini	4	Mohansundaram, 1984
Neodiptilomiopus vishakantai Mohanasundaram, 1982	Diptilomiopidae: Diptilomiopinae	1	Mohanasundaram, 1982b
Neolambella ligustri Lin & Kuang, 1997	Diptilomiopidae: Diptilomiopinae	1	Lin & Kuang, 1997
Neomesalox kallarensis Mohanasundaram, 1983	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Mohanasundaram, 1983a
Neometaculus bauhiniae Mohanasundaram, 1983	Eriophyidae: Phyllocoptinae: Phyllocoptini	4	Mohanasundaram, 1983a
Neophantacrus mallotus Mohanasundaram, 1981	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Mohanasundaram, 1981c
Neophytoptus ocimae Mohanasundaram, 1981	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Mohanasundaram, 1981a
Neopropilus jatrophus Huang, 1992	Phytoptidae: Sierraphytoptinae: Sierraphytoptini	1	Huang, 1992
Neorhynacus rajendrani Mohanasundaram, 1981	Diptilomiopidae: Diptilomiopinae	1	Mohanasundaram, 1981b
Neotegonotus fastigatus (Nalepa, 1892)	Eriophyidae: Phyllocoptinae: Tegonotini	5	Keifer, 1961a
Neserella decora Meyer & Ueckermann, 1989	Eriophyidae: Cecidophyinae: Cecidophyini	4	Meyer & Ueckermann, 1989b
Norma lanyuensis Huang, 2001	Diptilomiopidae: Diptilomiopinae	1	Huang, 2001a
Notacaphylla chinensiae Mohanasundaram & Singh, 1988	Eriophyidae: Phyllocoptinae: Acaricalini	3	Mohanasundaram & Singh, 1988
Notaceria tetrandiae Mohanasundaram & Muniappan, 1990 [emendation by Amrine *et al*. (2003) to *tetrandrae*]	Eriophyidae: Eriophyinae: Aceriini	1	Mohanasundaram & Muniappan, 1990
Notallus nerii Keifer, 1975	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Keifer, 1975c
Nothacus tuberculatus Manson, 1984	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Manson, 1984a
Nothopoda rapaneae Keifer, 1951	Eriophyidae: Nothopodinae: Nothopodini	10	Keifer, 1951
Notostrix attenuata Keifer, 1963	Eriophyidae: Phyllocoptinae: Anthocoptini	7	Keifer, 1963a
Novophytoptus rostratae Roivainen, 1947	Phytoptidae: Novophytoptinae	6	Roivainen, 1947
Novophytoptus stipae Keifer, 1962	Phytoptidae: Novophytoptinae	6	Keifer, 1962d
Oziella yuccae (Keifer, 1954)	Phytoptidae: Phytoptinae	2	Keifer, 1954; Amrine *et al*., 2003
Palmiphytoptus oculatus Navia & Flechtmann, 2002	Phytoptidae: Sierraphytoptinae: Mackiellini	1	Navia & Flechtmann, 2002
Pangacarus grisalis Manson, 1984	Eriophyidae: Nothopodinae: Nothopodini	1	Manson, 1984a
Paracalacarus podocarpi Keifer, 1962	Eriophyidae: Phyllocoptinae: Calacarini	1	Keifer, 1962d
Paracaphylla streblae Mohanasundaram, 1983	Eriophyidae: Phyllocoptinae: Acaricalini	2	Mohanasundaram, 1983b
Paraciota tetracanthae Mohanasundaram, 1984	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Mohanasundaram, 1984
Paracolomerus casimiroae Keifer, 1975	Eriophyidae: Cecidophyinae: Colomerini	2	Keifer, 1975c
Paraphytoptella arnaudi Keifer, 1959	Eriophyidae: Eriophyinae: Aceriini	2	Keifer, 1959b
Pararhynacus photiniae Kuang, 1986	Diptilomiopidae: Diptilomiopinae	1	Kuang, 1986a; Hong & Zhang, 1996c
Pareria fremontiae Keifer, 1952	Eriophyidae: Eriophyinae: Eriophyini	1	Keifer, 1952a
Pentamerus rhamnicroceae (Keifer, 1966)	Eriophyidae: Phyllocoptinae: Anthocoptini	5	Keifer, 1966a
Pentaporca taiwanensis Huang, 1996	Phytoptidae: Nalepellinae: Nalepellini	1	Huang & Boczek, 1996
Pentasetacus araucaria Schliesske, 1985	Phytoptidae: Nalepellinae: Pentasetacini	1	Schliesske, 1985
Peralox insolita Keifer, 1962	Diptilomiopidae: Rhyncaphytoptinae	3	Keifer, 1962b
Phantacrus lobatus Keifer, 1965	Phytoptidae: Nalepellinae: Nalepellini	1	Keifer, 1965c
Phyllocoptes calisorbi Keifer, 1965	Eriophyidae: Phyllocoptinae: Phyllocoptini	165	Keifer, 1965a
Phyllocoptruta arga Styer & Keifer, 1977	Eriophyidae: Phyllocoptinae: Phyllocoptini	23	Keifer, 1977b
Phyllocoptruta oleivora (Ashmead, 1879)	Eriophyidae: Phyllocoptinae: Phyllocoptini	23	Keifer, 1938a
Phytoptus avellanae Nalepa, 1889	Phytoptidae: Phytoptinae	38	Keifer, 1952b
Platyphytoptus sabinianae Keifer, 1938	Eriophyidae: Phyllocoptinae: Phyllocoptini	13	Keifer, 1938a
Porcupinotus humpae Mohanasundaram, 1984	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Mohanasundaram, 1984
Porosus monosporae Meyer & Ueckermann, 1995	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Meyer & Ueckermann, 1995
Proartacris pinivagrans Mohanasundaram, 1984	Eriophyidae: Eriophyinae: Eriophyini	3	Mohanasundaram, 1984

Prodiptilomiopus auriculatae Umapathy & Mohanasundaram, 1999	Diptilomiopidae: Diptilomiopinae	1	Umapathy & Mohanasundaram, 1999
Proneotegonotus antiquorae Mohanasundaram, 1983	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Mohanasundaram, 1983a
Prophyllocoptes riveae Mohanasundaram, 1984	Eriophyidae: Phyllocoptinae: Phyllocoptini	1	Mohanasundaram, 1984
Propilus gentyi Keifer, 1975	Phytoptidae: Sierraphytoptinae: Mackiellini	4	Keifer, 1975d
Prothrix aboula Keifer, 1965	Phytoptidae: Prothricinae	1	Keifer, 1965a
Pyelotus africanae Meyer, 1992	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Meyer, 1992c
Quadracus urticarius (Canestrini & Massalongo, 1893)	Diptilomiopidae: Rhyncaphytoptinae	5	Liro, 1941; Boczek & Kropczynska, 1965; Keifer, 1952b
Quadriporca samphramae (Boczek, 1997) (= *Q. indicae*, = *Kropczynella mangiferae*)	Diptilomiopidae: Rhyncaphytoptinae	3	Chandrapatya & Boczek, 1997a; Amrine & De Lillo, 2003
Quadriporca mangiferae Kuang & Cheng, 1991	Diptilomiopidae: Rhyncaphytoptinae	3	Hong & Zhang, 1996c
Quintalitus squamosus Meyer, 1989	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Meyer, 1989c
Ramaculus mahoe Manson, 1984	Eriophyidae: Eriophyinae: Aceriini	2	Manson, 1984b
Rectalox falita Manson, 1984	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Manson, 1984a
Retracrus johnstoni Keifer, 1965	Phytoptidae: Sierraphytoptinae: Mackiellini	2	Keifer, 1965c
Rhinophytoptus concinnus Liro, 1943	Diptilomiopidae: Rhyncaphytoptinae	14	Liro, 1943
Rhinotergum schestovici Petanovic, 1988	Diptilomiopidae: Rhyncaphytoptinae	4	Petanovic, 1988
Rhombacus morrisi Keifer, 1965	Eriophyidae: Phyllocoptinae: Phyllocoptini	7	Keifer, 1965b
Rhynacus arctostaphyli (Keifer, 1938)	Diptilomiopidae: Diptilomiopinae	3	Keifer, 1938b
Rhyncaphytoptus ficifoliae Keifer, 1939	Diptilomiopidae: Rhyncaphytoptinae	80	Keifer, 1939a
Sakthirhynchus canariae Umapathy & Mohanasundarm, 1999	Diptilomiopidae: Rhyncaphytoptinae	1	Umapathy & Mohanasundaram, 1999
Schizacea gynerii Keifer, 1977	Eriophyidae: Phyllocoptinae: Acaricalini	2	Keifer, 1977a
Schizoempodium mesophyllincola Oldfield, Hunt & Gispert, 1998	Eriophyidae: Eriophyinae: Diphytoptini	1	Oldfield, Hunt & Gispert, 1998
Scoletoptus duvernoiae Meyer, 1992	Eriophyidae: Eriophyinae: Aceriini	1	Meyer, 1992a
Setoptus jonesi (Keifer, 1938)	Phytoptidae: Nalepellinae: Nalepellini	14	Keifer, 1938a; Keifer, 1944
Shevtchenkella juglandis (Keifer, 1951)	Eriophyidae: Phyllocoptinae: Tegonotini	58	Keifer, 1951
Sierraphytoptus alnivagrans Keifer, 1939	Phytoptidae: Sierraphytoptinae: Sierraphytoptini	1	Keifer, 1939a
Sinacus erythrophlei Hong & Kuang, 1989	Eriophyidae: Phyllocoptinae: Anthocoptini	2	Hong & Kuang, 1989
Stenacis palomaris Keifer, 1970	Eriophyidae: Eriophyinae: Eriophyini	8	Keifer, 1970
Stenarhynchus aristidus Mohanasundaram, 1983	Diptilomiopidae: Rhyncaphytoptinae	1	Mohanasundaram, 1983c
Steopa bauhiniae (Chandrapatya & Boczek, 2001)	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2001b
Suthamus chiangmi Chandrapatya & Boczek, 2000	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 2000a
Tegolophus califraxini (Keifer, 1938)	Eriophyidae: Phyllocoptinae: Anthocoptini	52	Keifer, 1938b
Tegonotus mangiferae (Keifer, 1946)	Eriophyidae: Phyllocoptinae: Tegonotini	46	Keifer, 1946
Tegoprionus dentatus (Nalepa, 1894)	Eriophyidae: Phyllocoptinae: Anthocoptini	1	Keifer, 1961a
Tergilatus sparsus Meyer & Ueckermann, 1995	Eriophyidae: Phyllocoptinae: Phyllocoptini	2	Meyer & Ueckermann, 1995
Tetra concava (Keifer, 1939)	Eriophyidae: Phyllocoptinae: Anthocoptini	87	Keifer, 1939e
Tetraspinus lentus Boczek, 1961	Eriophyidae: Phyllocoptinae: Anthocoptini	8	Boczek, 1961
Thailandus diospyrosae Chandrapatya, 1997	Diptilomiopidae: Diptilomiopinae	1	Chandrapatya & Boczek, 1997b
Thamnacus rhamnicolus (Keifer, 1938)	Eriophyidae: Phyllocoptinae: Anthocoptini	7	Keifer, 1938b
Trimeracarus heptapleuri Farkas, 1963	Eriophyidae: Eriophyinae: Eriophyini	1	Farkas, 1963
Trimeroptes aleyrodiformis (Keifer, 1940)	Diptilomiopidae: Diptilomiopinae	3	Keifer, 1940b
Trisetacus ehmanni Keifer, 1963	Phytoptidae: Nalepellinae: Trisetacini	56	Keifer, 1963b
Trisetacus pini (Nalepa, 1887)	Phytoptidae: Nalepellinae: Trisetacini	56	Keifer, 1963b
Tumescoptes trachycarpi Keifer, 1939	Eriophyidae: Phyllocoptinae: Acaricalini	4	Keifer, 1939c
Ursynovia ulmi Boczek & Szymkowiak, 1997 (now jr. syn. of *Tetra*)	Eriophyidae: Phyllocoptinae: Anthocoptini	1?	Boczek & Szymkowiak, 1997
Vasates quadripedes Shimer, 1869	Eriophyidae: Phyllocoptinae: Phyllocoptini	27	Keifer, 1959b
Vimola syzygii Boczek, 1992	Diptilomiopidae: Diptilomiopinae	9	Boczek & Chandrapatya, 1992a
Vittacus mansoni Keifer, 1969	Eriophyidae: Phyllocoptinae: Anthocoptini	4	Keifer, 1969b

APPENDIX B

CHARACTERS CODED FOR PHYLOGENETIC ANALYSES: DEFINITION, DESCRIPTION AND DISCUSSION.

APPENDIX B

CHARACTERS CODED FOR PHYLOGENETIC ANALYSES: DEFINITION, DESCRIPTION AND DISCUSSION.

Only one complete character discussion was prepared. To facilitate the retrieval of the complete character discussion of each character, regardless of its different character numbers in the different data sets, an abbreviated character list and the character numbers of the three character data sets (for 318, 66 and 18 taxa) are listed in the same table, accompanied by two additional tables with the character numbers of the 66- and 18-taxon data sets in order (Appendix C).

The character marked *** is the same for all taxa in data set (ingroup and outgroup species), characters marked with * are autapomorphic to the Eriophyoidea, and characters marked with ** are autapomorphic for a terminal Eriophyoidea species. These characters did not provide information for determining relationships among the Eriophyoidea (ingroup) taxa in the analyses. Some character states and their terminology are illustrated in Figs 3.2-3.6, 3.22. Only one side of the organism is described, apart from the description of the prodorsal shield pattern (see Chapter 3 and 4: Material and Methods). Character states were scored from published descriptions, either from the text description and/or descriptive drawing accompanying it. Discrepancies and ambiguousness are noted.

GENERAL

***0. Life cycle:**

0 = four active immature instars
1 = three active immature instars
2 = two active immature instars

The life cycle of the Tydeidae, including *Orfareptydeus stepheni*, has four (larva, proto-, deuto- and tritonymph), and that of the Tetranychidae, including *Mononychellus yemensis*, three active immature instars (larva, deuto- and tritonymph) (Evans, 1992). The Eriophyoidea have two active immature instars [larva and nymph or proto- and deutonymph depending on the interpretation of the author (Lindquist, 1996a)].

Characters 1 - 5. The absence of a respiratory system with associated stigmata, an excretory system, cross-striated muscles, tonofibrillary muscle attachments, and absence of basal membranes around some organs (Lindquist, 1996b) are all autapomorphic character states for the Eriophyoidea in the present study. A priori phylogenetic analyses Lindquist (1996b) argued they may be ancestral (plesiomorphic) or derived (apomorphic) in the Eriophyoidea. If these states are primitive conditions rather than reversals, the Eriophyoidea may possibly be outside the Prostigmata or even outside the Acariformes, and the group may be an extremely ancient, independent group of very early chelicerate arthropodans (Lindquist, 1996b).

***1. Respiratory system with stigmata – presence:**

0 = present
1 = absent

A respiratory system, including tracheae and stigmata, with the stigmata located on the gnathosoma or on the dorsal and anterolateral surface of the prodorsum, is present in the Prostigmata (Evans, 1992). A Prostigmata type respiratory system is present in *O. stepheni* and *M. yemensis*.

A typical respiratory system is absent in the Eriophyoidea. Shevchenko & Silvere (1968) speculated that the motivator between the bases of the chelicerae is a modified relict of a tracheal system, and Krantz (1973) speculated that the pair of structures arising just posterior to the motivator may be tracheal trunks. Respiration in the eriophyoids is cuticular (Nuzzaci & Alberti, 1996), however, and no confirmed evidence exists of the contrary (Lindquist, 1996b).

***2. Excretory system – presence:**

0 = present
1 = absent, only with pervasive parenchymatous tissue

An excretory system, including an anus, is present in *O. stepheni* (Fig. 4.1) and in *M. yemensis* (Fig. 4.2), but is absent in the Eriophyoidea where the excretory system exists only of pervasive parenchymatous tissue (Lindquist, 1996b).

***3. Muscle striation:**

0 = cross-striated
1 = non-striated

The muscles of the Prostigmata, including *O. stepheni* and *M. yemensis*, are cross-striated (Lindquist, 1996b). The muscle cells of the Eriophyoidea are unique, not found in other arthropods (Nuzzaci & Alberti, 1996), and appear to be smooth (Lindquist, 1996b; Nuzzaci & Alberti, 1996). Some authors regard it to be a sign of primitiveness, but Nuzzaci & Alberti (1996) proposed that the non-striated muscle cells most likely derived secondarily from cross-striated cells, possibly because of miniaturization.

***4. Tonofibrillary muscle attachments – presence:**

0 = present
1 = absent

Tonofibrillary muscle attachments are present in the Prostigmata, including *O. stepheni* and *M. yemensis*, but are absent in the Eriophyoidea (Lindquist, 1996b).

***5. Basal membranes around organs, including salivary glands and central ganglion – presence:**

0 = present
1 = absent

Basal membranes are present around organs, such as the salivary glands and central ganglion of the Prostigmata, including *O. stepheni* and *M. yemensis*, but are absent around the organs of the Eriophyoidea (Lindquist, 1996b).

CHAETOTAXY

***6. Compliment of setae in immatures:**

0 = without all setae that are present in the adult
1 = with all setae that are present in the adult (except eugenital setae of male)

*****7. Chemical composition of setae:**

0 = setae without actinopilin
1 = setae with actinopilin, causing birefringence

F. Grandjean found that the majority of sensilli of the body and appendages in the Actinotrichida (to which the Prostigmata belong) are birefringent, an optical property, and this is due to a core or layer of anisotropic material termed actinopilin (Evans, 1992). Lindquist (1996b) argued that the presence of actinopilin in the setae of the Eriophyoidea, together with other character states, are evidence that the Eriophyoidea indeed belongs within the Acari, and particularly in the Actinotrichida. Actinopilin is present in all the species in the out- and ingroup of the present study. The character has been included in this character discussion, because it is regarded as important in the relationship of the Eriophyoidea with other arthropods and mites. Although it is not of use in studying the phylogeny of the taxa in this specific analysis, I regarded it as an important part of information to be added to the data matrix. The character states with similar evidence, including those listed by Lindquist (1996b), will be added to future data matrices expanding the matrix used in the present study.

Gnathosomal setae

8. Gnathosomal palp seta *d* – presence and shape:

0 = present, simple (e.g., Fig. 3.35)
1 = present, simple and prominent
2 = present, forked (Fig. 3.68)
3 = present, minute
4 = absent

A simple gnathosomal palpgenual seta (*d*) (named *dg* in the Tydeidae by André, 1981a), is present on the palpfemorogenu of *O. stepheni* (Fig. 4.1). In *M. yemensis* a seta is present on the palpgenu (*personal observation*), but according to Lindquist (1985) only a posterolateral seta (*l''* PGe), and not a dorsal seta, occurs on the palpgenu of all Tetranychidae, and the state "palp *d* absent" was assigned to *M. yemensis*. Within the Eriophyoidea, palp *d* [previously known as the subapical (Keifer, 1959a), antapical (Keifer, 1975a), or rostral seta (Ramsay, 1958)] is the only seta present on the segment that Lindquist (1996a) regards as the consolidated palptrochanter-femur-genu (Fig. 3.23). Based on its dorsodistal position, Lindquist (1996a) postulated it to be the palpgenual seta *d*.

Palp *d* is simple and tapering in most Eriophyoidea species, and additionally very prominent in *Neophytoptus ocimae* and minute in *Neocupacarus flabelliferis*. In five species in the present study (*Dicrothrix anacardii*, *Euterpia fissa*, *Leipothrix solidaginis*, *Neodicrothrix tiliacorae* and *Porosus monosporae*) (Eriophyidae: Phyllocoptinae), palp *d* is forked (e.g., Fig. 3.68). In *Vimola syzygii*, (Diptilomiopidae: Diptilomiopinae) palp *d* is strongly turned upwards distally (descriptive drawing

in Boczek & Chandrapatya, 1992a), but seemingly not with such a sharp corner that it can be regarded as a minute fork, as advised by Amrine (1996).

Particularly the shape of palp *d* is used in the classification and identification of the Eriophyoidea. Unfortunately, this seta is not routinely recorded, depicted and described in species descriptions, and this absence of published data renders it an ambiguous character for phylogenetic analyses if scored from published descriptions.

When palp *d* was recorded as present, but it was not depicted in the descriptive drawing (e.g., for *Paraciota tetracanthae*) (Mohanasundaram, 1984) the character state "present" was assigned and *vice versa*. When its presence was not described in the text and it was absent in the drawing [e.g., *Acarhis diospyrosis* (Chandrapatya & Boczek, 1991c) among many others], particularly found in earlier descriptions, the code "?" (unknown) was assigned. It was not regarded as absent, because the gnathosomal setae are generally not depicted, even when present.

The shape of palp *d* was determined from the text description and/or drawing, otherwise it is presumed the seta is simple if not otherwise recorded or depicted by the species author(s), because typically this seta is simple in the Eriophyoidea, and one can reasonably expect any other shape should have been recorded by the descriptor. The absence of palp *d* was not recorded for *Quintalitus squamosus* (Meyer, 1989c) and was determined on a SEM image of this species.

The character states scored for the following species, in particular, are ambiguous:

- *Cosella deleoni*, *Mackiella phoenicis* and *Diptilomiopus ficus* (Keifer, 1956; Keifer, 1939a; Attiah, 1967, respectively): presence of palp *d* was not recorded in the descriptive text, but a line or very short, vague line in the position where palp *d* is usually inserted, is an indication that it may be present, and character state "present" was assigned to these species;
- *Trisetacus pini*: although the presence of palp *d* was not recorded or depicted by Keifer (1963b) or Boczek (1969) it is presumed it is present and simple, similar to other known *Trisetacus* spp.;
- *Diptilomiopus camarae* and *Proneotegonotus antiquorae* (Mohanasundaram, 1981b; 1983a, respectively): palp *d* was described as thick; however, it was not depicted as such in the descriptive drawings. Character state "simple", without the inclusion of "thickness" as a state, was assigned to these species.

- *Acarhis diospyrosis* (Chandrapatya & Boczek, 1991c): palp *d* is absent in the drawing and not mentioned in the text. In this case *v* was depicted, and it is presumed the author would have depicted palp *d* if it was present. Character state "absent" was scored for this species.

It will be a better option to divide this character in future studies into at least two characters: palp *d* present or absent, and a second character to score the shape of the seta (including simple, simple and prominent, forked, and minute). The latter character can be further divided into length (e.g., long and minute) and shape (e.g., simple and forked). These options will increase "not applicable" scores, though.

***9. Solenidion on palptarsus – presence:**

0 = with solenidion *ω*
1 = without solenidion *ω*

Solenidion *ω* is almost consistently present on the palptarsus of Actinotrichida (Evans, 1992), and is also present on the palptarsus of *O. stepheni* (Fig. 4.1) and *M. yemensis* (Fig. 4.2), but it is absent in all Eriophyoidea species (Lindquist, 1996b).

Prodorsal setae

A compliment of four setae (on one side of the body) (or in other words: present as four pairs one on each side of the body for each seta) (Fig. 3.3d) are present on the prodorsum in many families of Prostigmata mites (Lindquist, 1996a). The maximum number of prodorsal setae in the Eriophyoidea is five setae (*ve* and *sc*, and single *vi*) in the monotypic *Pentasetacus* (Schliesske, 1985). The characteristics of the prodorsal setae (Fig. 3.3) form an integral part of the Eriophyoidea classification. In particular the presence of the setae anteriorly on the prodorsum (single or paired *vi*, and *ve*) distinguishes the family Phytoptidae (Fig. 3.3e–i), in which some or all these setae are present, from the Eriophyidae and Diptilomiopidae where these setae are absent in all species (Fig. 3.3j, k).

Characters 10 and 11. Lindquist (1996a) hypothesized that the loss of both *vi* and *ve* may have occurred once, in the common ancestors of the Eriophyidae and Diptilomiopidae, and the loss of *vi* and *ve* individually may have occurred once each in the family Phytoptidae.

10. Seta *vi* – presence, single or paired and position:

0 = one pair present
1 = one seta *vi* absent, position of remaining seta shifted to anteromedian position
2 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 108, Character 1: 0 = present; 1 = absent).

In the present analysis, paired *vi* is present in *O. stepheni* (Fig. 4.1) (similar to the generalized Tydeidae of Hong & Zhang, 1996a). Within the Tetranychidae paired *vi* is always absent in Tetranychinae species (Lindquist, 1985), including *M. yemensis* (Fig. 4.2). It is present or absent in the Bryobinae, or is rarely represented by single *vi* anteromedially (Lindquist, 1985), similar to Eriophyoidea species in the Nalepellinae.

In the Eriophyoidea classification this character is of importance at the family level. It is present as one seta anteromedially (single *vi*) (Fig. 3.3a, e–g) in species of the Nalepellinae (of which eight species are included in the present 318-taxon data set). Amrine (1996) proposed that the pair of setae anteromedially on the prodorsum of *Prothrix aboula*, is paired *vi* (Fig. 3.3h), and created a new subfamily, Prothricinae, for this species. In the original description of this species Keifer (1965a) regarded this pair as *sc* that moved far forward. *Prothrix aboula* is included in the present analysis, and the interpretation of Amrine (1996) that paired *vi* is present, is followed for scoring the character in the data matrix.

11. Seta *ve* – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 2: 0 = present; 1 = absent).

In the present analysis *ve* is present as a pair in *O. stepheni* (Fig. 4.1) and in *M. yemensis* (Fig. 4.2). When it is present, *ve* is always present as a pair (one seta on each side of the body) (Fig. 3.3d, e, h, i) in the Eriophyoidea. In the Eriophyoidea classification, most species of the Phytoptidae have *ve*, except Nalepellinae species, excluding *Pentasetacus*. In the present 318-taxon data set, 16 species with *ve* present are included. Seta *ve* is never present in the Eriophyidae or Diptilomiopidae.

***12. Prodorsal seta *sce* (*sc2*) – presence:**

0 = present
1 = absent

Seta *sce* is present as a pair in *O. stepheni* (Fig. 4.1) and in *M. yemensis* (Fig. 4.2), but is absent in all Eriophyoidea species.

Characters 13-18 (*sc*): according to the hypothesis of Lindquist (1996a) the paired posterolateral setae on the prodorsal shield of the Eriophyoidea (previously known as prodorsal or dorsal setae) are one of the two pairs of scapular setae (*sc*) found in other Prostigmata mites. He postulated that they are probably the internal scapular setae (*sci* or *sc1*). For scoring character states in the present study, it is presumed *sc* in Eriophyoidea is homologous to *sci* in other Prostigmata mites. The presence, position of and direction in which *sc* is projected (Fig. 3.3b, c), are used to typify Eriophyoidea genera (e.g., *Eriophyes* and *Aceria*) and tribes (e.g., Eriophyini and Aceriini).

13. Seta *sc* in Eriophyoidea (seta *sci* in other Prostigmata species) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 4: 0 = present; 1 = absent).

Seta *sci* is present as a pair in *O. stepheni* (Fig. 4.1) and in *M. yemensis* (Fig. 4.2). In the Eriophyoidea *sc* may be present (always in a pair) or absent. Lindquist (1996a) proposed that *sc* was lost repeatedly and independently within the Eriophyoidea, at least twice in both the Phytoptidae and Diptilomiopidae, and at least four times in the Eriophyidae. Indeed, within the taxa of the Eriophyoidea classification, and among the species included in the present study, species with and without *sc* co-occur in all three families and in some subfamilies: in the Phytoptidae: Nalepellinae, Phytoptinae and Sierraphytoptinae; Eriophyidae: Cecidophyinae, Nothopodinae and Phyllocoptinae and Diptilomiopidae: Diptilomiopinae and Rhyncaphytoptinae, as well as in some tribes, e.g., Phytoptinae: Acaricalini; Nalepellinae: Trisetacini; Sierraphytoptinae: Mackiellini and Nothopodinae: Nothopodini. Seta *sc* is absent in all *Diptilomiopus* spp.

The character states scored for the following species, in particular, are ambiguous:

- *Acarhis diospyrosis* (Diptilomiopidae): *sc* is recorded in the text as being absent, but *sc* is clearly depicted (Chandrapatya & Boczek, 1991c), and the authors placed the species in *Acarhis* in which, by definition, *sc* is present, and character state "present" was scored for this species.
- In some species (e.g., in the new *Diptilomiopus* spp., Appendix M) *sc* may seem absent, but on closer inspection, a remnant of *sc* might be present.

14. Seta *sc* length:

0 = exceptionally long (> 100 µm)
1 = very long (66 – 100 µm)
2 = long (31 – 65 µm)
3 = average (4 – 30 µm)
4 = short (1 – 3 µm)
5 = minute (not measurable, less than 1 µm long)

Seta *sc* is 30 µm (*n* = 1) long in *O. stepheni* (character state "average" assigned) and 103 µm (*n* = 1) in *M. yemensis* (character state "exceptionally long" assigned) (C. Craemer, *personal observations*). In the Eriophyoidea the lengths vary from exceptionally long to minute, but most lengths are in the average category (length data approximate normal distribution).

The length of *sc* of *Fragariocoptes setiger* was not reported in the original description by Nalepa (1894) and neither later in the redescription by Roivainen (1951), but was reported in the redescription by Boczek (1964) from which the character state was scored.

The character states scored for the following species, in particular, are ambiguous:

- *Acarhis diospyrosis* (Diptilomiopidae): *sc* is recorded to be absent, but character state "present" is assigned (see explanation with previous character) and in the descriptive drawing (Chandrapatya & Boczek, 1991c) *sc* is depicted extremely short, barely noticeable, and I deduced that it is probably less than 3 µm long and character state "short" was scored for this species.
- The length of *sc* of *Konola hibernalis* (Keifer, 1979b), *Bucculacus kaweckii* (shield length 26 µm) (Boczek, 1961) and *Catachela machaerii* (shield length 40 µm) (Keifer, 1969b) were not recorded, but the species were all assigned character state "average" based on the relative length of *sc* to the prodorsal shield in their drawings.

15. Seta *sc* length relative to prodorsal shield length:

0 = exceptionally long (> three times shield length)
1 = very long (< three, but > or equal to 1.5 shield length)
2 = long (< 1.5, but > or equal to one shield length)
3 = average length (< one, but > 0.2 shield length)
4 = short (< or equal to 0.2, but > 0.07 shield length)
5 = very short (< or equal to 0.07 shield length)

A character similarly defined, but the ratio between different characteristics than in the present study, was used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 115, Character 33: 0 = very long (longer than the distance between two tubercles); 1 = long (longer than half the distance between two tubercles); 2 = short (shorter than half the distance between two tubercles); 3 = absent).

In the present study *sc* length in relation to prodorsal shield length is experimentally included, to standardize length of *sc* with body size (for future studies it might be better to rather score *sc* length in relation to body length, if relationships are included in the data set). It was also included to have a character similar to that of the one in the previous analyses for comparative reasons, and to increase the number of characters for the present analyses. However, it is inadvisable to use relational data in phylogenetic analyses, and this character should probably be omitted in future analyses and data matrices for the Eriophyoidea.

Seta *sc* is 30 µm (n = 1) long and the prodorsal shield 75 µm (n = 1) long in *O. stepheni* (character state "average" assigned) and 103 µm (n = 1) and the prodorsal shield 145 µm (n = 1) long in *M. yemensis* (character state "average" assigned).

Fragariocoptes setiger: the length of neither the prodorsal shield nor *sc* was reported in the original description by Nalepa (1894) and neither later in the redescription by Roivainen (1951), but they were reported in the redescription by Boczek (1964) from which the character state was scored.

The character states scored for the following species, in particular, are ambiguous:

- *Acarhis diospyrosis* (Diptilomiopidae): *sc* is described to be absent, but it was scored as "present" (see explanation for Character 13). The relationship of *sc* with the prodorsal shield could be determined from the descriptive drawing (Chandrapatya & Boczek, 1991c), and I deduced that *sc* is very short in comparison with the prodorsal shield length.
- *Heterotergum gossypii* (Keifer, 1955), *Monotrymacus quadrangulari* (Mohanasundaram, 1982a), *Notacaphylla chinensiae* (Mohanasundaram & Singh, 1988), *Tegonotus mangiferae*

(Keifer, 1946), *Neoacarhis aglaiae* (Kuang, 1998) and *Levonga caseariasis* (Chakrabarti & Pandit, 1996): prodorsal shield length of these species was not recorded, however, for the present study, it was measured and determined from the original descriptive drawings and *sc* was "short" in relation to the shield length for the latter two species.

- *Acaphyllisa parindiae* (Keifer, 1978), *Acarhis diospyrosis* (Chandrapatya & Boczek, 1991c) and *Catachela machaerii* (Keifer, 1969b): *sc* length was not recorded for these species, and relative length to prodorsal shield length was determined by measuring these on the descriptive drawing, because the measurement ratios are well within the categories short, very short and long, respectively.

16. Scapular setal tubercle (Fig. 3.3b, c) – presence:

0 = primarily absent
1 = present
2 = secondarily absent
3 = prominent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 3: 0 = absent; 1 = present).

Setae of the Tenuipalpidae and the Tetranychidae are not usually, and particularly the setae of *O. stepheni* and *M. yemensis*, are not inserted on tubercles, with subsequent loss of the tubercles within the group. The absence of setal tubercles is regarded in these species as being "primarily absent" in the present study. In the Eriophyoidea most setae are usually inserted on tubercles and in some species a seta may be naturally absent (not broken off in specimens), while the setal tubercle is still present. For the present analysis it has been presumed *sc*, when it is present in the Eriophyoidea, is inserted on a setal tubercle. This may be ambiguous in some cases, but descriptive drawings and information generally are not detailed enough to determine the absence or presence of the setal tubercle when the seta is present.

The character states scored for the following species, in particular, are ambiguous:

- *Neolambella ligustri*: according to the original descriptive drawing (Lin & Kuang, 1997), it seems that the scapular setal tubercle is absent, and the species was assigned character state "absent" for the present study, but it may be present (there is a short diagonal line in the lateral area below the prodorsal shield pattern cells).
- *Prodiptilomiopus auriculatae*: the presence of scapular a setal tubercle is uncertain; character state "absent" is assigned to this species for the present study; structures depicted on the rear

shield margin (Umapathy & Mohanasundaram, 1999) may be tubercles, but they are not typical in the drawing.

- *Diptilomiopus* spp.: *sc* is always absent (the genus is currently defined as such), and according to Amrine *et al.* (2003) the scapular setal tubercle may be present or absent, within the genus. The presence of this tubercle is unknown for *D. javanicus*, the type species of *Diptilomiopus*, and the presence or absence of it in this species may have an influence on the definition and delimitation of *Diptilomiopus* and possibly whether *Vilaia* (it was wrongly differentiated from *Diptilomiopus* because it has the scapular setal tubercle present) may be regarded as a valid genus (Craemer *et al*., 2005). When the scapular setal tubercle is present in *Diptilomiopus* spp. it may be very small and can also be obscured by the ridges on the shield, and the presence in species for which it has been recorded as absent, is ambiguous and should be checked in future on type specimens if possible. Particularly the recorded absence for the following *Diptilomiopus* spp. may be ambiguous:
    - *championi* – structures, vaguely and obscurely visible in the scanning electron microscope image accompanying the original species description (Huang, 1992), may be the scapular setal tubercles;
    - *holopteleae* – depicted prodorsal shield (Abou-Awad & El-Banhawy, 1992) probably distorted and broken in this area, and determining the presence or absence of the scapular setal tubercle from the drawing is impossible;
    - *indicus* – Chakrabarti & Pandit (1996) recorded the absence of the scapular setal tubercle, but their drawing is too small to confirm;
    - *pocsi* – description and drawing (Farkas, 1967) generally in doubt;
    - and *ficus* – the presence or absence of the scapular setal tubercle was not described in the text, but structures which are probably these tubercles, are present in the drawing by Attiah (1967).

Characters 17 and 18. Position and direction of seta *sc*: In those Eriophyoidea species studied, with *sc* located on or near the rear shield margin in adults, directed posteriorly, this seta is located well ahead of the rear shield margin, and the seta is directed dorsoanteriorly in the larva. In the nymph of such species, *sc* generally is in a position and orientated intermediate between that of the larva and adult (Lindquist, 1996a). The larval state of *sc*, which may be retained in the adults of some species, was proposed to be ancestral or plesiomorphic by Lindquist (1996a) *a priori* phylogenetic analyses.

17. Seta *sc* and/or scapular setal tubercle position (Fig. 3.3b, c):

0 = ahead of rear shield margin (less than half of shield ahead)
1 = well ahead of rear shield margin (on half of shield or further anteriad)
2 = on rear shield margin, or slightly ahead of rear shield margin
3 = immediately caudad of rear shield margin

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 7: 0 = ahead of rear margin; 1 = at the rear margin).

The character states scored for the following species, in particular, are ambiguous:

- *Lithocarus thomsoni*: in the descriptive drawing of the dorsal view (Chandrapatya & Boczek, 2000c) it seems that *sc* is on or close to half of the dorsal shield length, and in the lateral view drawing further than half the shield length ahead (thus possibly "well ahead"), however, according to the reported measurements of the distance of *sc* from the rear shield margin in relation to the prodorsal shield length, *sc* is only about a third of the prodorsal shield length ahead of the rear shield margin (assigned character state "ahead").
- *Pararhynacus photiniae*: the scapular setal tubercle is just ahead of the rear shield margin in the descriptive drawing (Kuang, 1986a), but its position could not be confirmed in the Chinese text. The depicted position could have been caused by the prodorsal shield pressed down and to the back by the slide-mounting process (assigned character state "on rear shield margin, or slightly ahead of rear shield margin").
- *Steopa bauhiniae*: Chandrapatya & Boczek (2001b) described *sc* to be close to the rear shield margin, and it is just ahead of the rear shield margin in the dorsal view drawing. In the lateral view drawing, however, it seems to be ahead of the rear shield margin, thus dorsally it may have been pushed closer to the rear shield margin by the weight of the cover slip (assigned character state "on rear shield margin, or slightly ahead of rear shield margin").

18. Seta sc – direction of projection (Fig. 3.3b, c):

0 = anteriad, diverging
1 = anteriad: parallel, converging or up (Fig. 3.3c)
2 = medially
3 = up and to the outside
4 = posteriad, usually diverging (Fig. 3.3b)
5 = posteriad, converging
6 = no particular direction (i.e., in any direction)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 110, Character 8: 0 = forward; 1 = backward; 2 = upward or inward). They scored *sc* in Tydeidae as being directed forward. Seta *sci* of *O. stepheni* and of *M. yemensis* is not particularly directed in any direction (C. Craemer, *personal observations*). The direction in which

sc of the Eriophyoidea is projected corresponds with the position and/or the shape of its setal tubercle, and these characteristics in combination are used to differentiate between suprageneric Eriophyoidea taxa, for example, between Eriophyini and Aceriini.

The character states scored for the following species, in particular, are ambiguous:

- Although *sc* of *Acathrix trymatus* is too short to determine exactly in which direction it might be extended, it seems plausible that it will rather extend slightly divergently anteriad, than converging or parallel anteriad, when extrapolating the direction from the scapular tubercle as it is depicted by Keifer (1962c).
- It sometimes seems that a longer *sc* might have been directed medially if it was shorter, but because it is longer, it is directed about medially and then "turn" more anteriad and eventually, towards the tip of the seta, it diverges (e.g., *Eriophyes quadrifidus* Meyer & Ueckermann, 1989a); these cases were assigned character state "anteriad, diverging".
- The direction into which *sc* is directed in *Fragariocoptes setiger* is described and depicted in the original description by Nalepa (1894) and in the redescription by Boczek (1964) as being directed up and centrad, however, in the redescription by Roivainen (1951), it is described as being directed up, and in the drawing it is depicted as being directed divergently posteriorly, Amrine *et al.* (2003) interprets the situation in the couplet leading to the genus as "prodorsal shield with *sc* directed divergently forward or posteriorly". For the present study it has been decided to assign polymorphic character states: directed up and possibly pushing down in any of three directions, either anteriad diverging, anteriad converging or posteriad. This is ambiguous, and the descriptions may be of different species.
- It is not possible to determine solely on the only descriptive drawing of the lateral view (Liro, 1943) of *Rhinophytoptus concinnus* exactly in which direction *sc* is directed. It is clearly projecting anteriad, but it could either be converging or diverging. The descriptive drawing of *R. dudichi* is used in Amrine *et al.* (2003) to depict *Rhinophytoptus* and in this species, *sc* is directed diverging anteriad. Extrapolating from this, for the present study, the character state "diverging anteriad" was scored for *R. concinnus*.

Opisthosomal setae (Figs 3.2, 3.3a, 3.4)

Lindquist (1996a) homologized the setae found in the Eriophyoidea with that of other acariform mites. In the process, he also renamed them to the standard setal notation developed by F. Grandjean (references listed in Lindquist, 1996a). It is difficult to homologize the Eriophyoidea setae, especially the opisthosomal setae, with that of other acariform mites (Lindquist, 1996a). The

absence of cupules (lyrifissures) – a series of segmental remnants reflecting the ancestral segmentation – in the Eriophyoidea, contributes to this problem. Lindquist (1996a) based the setal homologies on the sequential arrangement of muscle sets in the Eriophyoidea opisthosoma, and on the suppression of anamorphosis also found in other Prostigmata groups. He regarded all opisthosomal setae in the Eriophyoidea as fundamental setae according to the concepts of F. Grandjean (references listed in Lindquist, 1996a), because all setae are already present in the larval instar. The larva is the first active life stage in most Prostigmata and plesiomorphically its hysterosoma (opisthosoma in Eriophyoidea mites) may have six transverse segments, according to F. Grandjean's (references listed in Kethley, 1990; Lindquist, 1996a) system anterior to posterior: C, D, E, F and H, and a segment consisting of the valves encompassing the anus designated as PS (pseudoanal) (Kethley, 1990; Lindquist, 1996a). Segment PS is typically reduced in size and occupies a ventrocaudal position (Lindquist, 1996a). Although the setal homologies and names for setae in the Eriophyoidea proposed by Lindquist (1996a) are based on his extensive and well recognized knowledge and experience with the morphology of acariform mites, the homologies stay ambiguous until they are empirically tested. Opisthosomal *d*, *e* and *f* were not specified as specific pairs of these setae present in other acariform mites (Lindquist, 1996a), but only that they occur on these segments. Lindquist (1996a) proposed that they are probably lateral elements of the dorsal setae on these segments. The maximum number of opisthosomal setae (seven pairs) occurs only in some Phytoptidae, and only *f* and *h2* are present in all Eriophyoidea species.

Table B.1. Opisthosomal setae (Figs 3.2, 3.3a, 3.4) (except *c1* and *h1*) absent in Eriophyoidea species included in the present study. Setae *f* and *h2* are never absent in the Eriophyoidea. Only species, with at least one of the opisthosomal setae absent, are included in the table. Absence of a setal pair is ticked x.

			c2	*d*	*e*
Phytoptidae:					
Prothricinae		*Prothrix aboula*		x	
Sierraphytoptinae:	Mackiellini:	*Retracrus johnstoni*		x	
	Sierraphytoptini:	*Neopropilus jatrophus*		x	x
Eriophyidae:					
Nothopodinae:	Nothopodini:	*Anothopoda johnstoni*			x
Eriophyinae:	Aceriini:	*Paraphytoptella arnaudi*			x
		Ramaculus mahoe			x
	Eriophyini:	*Asetilobus hodgkinsi*			x
Cecidophyinae	Cecidophyini:	*Neserella decora*			x
Phyllocoptinae:	Acaricalini:	*Knorella gigantochloae*		x	x
		Schizacea gynerii		x	x
		Tumescoptes trachycarpi		x	x
	Anthocoptini:	*Neomesalox kallarensis*		x	
	Calacarini:				
	Phyllocoptini:	*Acamina nolinae*		x	x
		Cecidodectes euzonus		x	x
		Euterpia fissa		x	x
		Neocupacarus flabelliferis		x	x
		Neodicrothrix tiliacorae		x	x
		Proneotegonotus antiquorae		x	x

		c2	*d*	*e*
	Prophyllocoptes riveae			x
	Tergilatus sparsus			x
Tegonotini:	*Dicrothrix anacardii*		x	
Ashieldophyinae	*Ashieldophyes pennadamensis*		x	x
Diptilomiopidae:				
Diptilomiopinae:	*Acarhis* spp. in the present study (3 spp.)	x		
	Africus psydraxae	x		
	Dacundiopus stylosus	x		
	Davisella breitlowi	x		
	Diptilomiopus spp. in the present study (86 spp.)	x		
	Diptilorhynacus dioscoreae	x		
	Diptilorhynacus sinusetus	x	x	
	Kaella flacourtiae	x		x
	Lambella cerina	x		
	Levonga spp. in the present study (3 spp.)	x		
	Lithocarus thomsoni	x		
	Mediugum sanasaii	x		x
	Neoacarhis aglaiae	x		
	Neodiptilomiopus vishakantai	x		
	Neorhynacus rajendrani	x		
	Norma lanyuensis	x		
	Prodiptilomiopus auriculatae	x		
	Rhynacus arctostaphyli	x		
	Steopa bauhiniae	x	x	
	Suthamus chiangmi	x		
	Thailandus diospyrosae	x		x
	Vimola syzygii	x		

Characters 19 and 20. Only *c1* and *c2* are present in the Tenuipalpidae (including in *O. stepheni*), named *d1* and *l1* by André (1981a) (Fig. 4.1). Setae *c1*, *c2* and *c3* are present in the Tetranychidae (Lindquist, 1985), and are also present in *M. yemensis* (Fig. 4.2). Setae *c3* are regarded as neotrichous (Lindquist, 1985).

19. Seta *c1* (Fig. 3.3a) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 12: 0 = present; 1 = absent).

The setae on the opisthosomal dorsum of the Tydeidae are very stable, and *c1* (named *d1* by André, 1981a) is present in all Tydeidae (André, 1981a) including *O. stepheni* (Fig. 4.1). Seta *c1* is present in all the instars of the Tetranychidae (Lindquist, 1985) including *M. yemensis* (Fig. 4.2). In the Eriophyoidea *c1* is only present in some members of the Phytoptidae, and absent in most Eriophyoidea species. It is significant in the Eriophyoidea classification at the subfamily and tribal

level. Thirteen Eriophyoidea species with *c1* [resorting in the Nalepellinae (Trisetacini, Pentasetacini), Phytoptinae, Prothricinae and Sierraphytoptinae (Sierraphytoptini)] are included in the present study.

20. Seta *c2* (Figs 3.2, 3.4) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 25: 0 = present; 1 = absent).

The setae on the opisthosomal dorsum of the Tydeidae are very stable, and *c2* (named *l1* by André, 1981a) is present in all Tydeidae (André, 1981a) including *O. stepheni* (Fig. 4.1). Seta *c2* is present in all the instars of the Tetranychidae (Lindquist, 1985) including *M. yemensis* (Fig. 4.2).

Within the species included in the present analyses, *c2* is only absent in species of the Diptilomiopinae (12 genera with and 22 genera, including *Diptilomiopus*, without *c2*) (Table B.1). Outside the Diptilomiopinae, *c2* is absent in *Thacra piperasia* Keifer, 1978 (Eriophyidae: Phyllocoptinae: Tegonotini) (Keifer, 1978; Amrine *et al.*, 2003). This species is not included in the present study. Lindquist (1996a) also reported it to be absent in *Cecidodectes* and *Acamina*, but it is present in the type species of these two genera (Meyer & Ueckermann, 1989b; Keifer, 1939a, respectively).

21. Setal tubercle of seta *c2* – presence:

0 = primary absent
1 = present
2 = secondary absent

Seta *c2* is not inserted on a tubercle in *O. stepheni* (Fig. 4.1) nor in *M. yemensis* (Fig. 4.2). To indicate that this tubercle is not usually present, with subsequent loss within the group, absent in these species is termed “primary absent”. When *c2* is present in the Eriophyoidea, it is presumed, for the present study, it is inserted on a setal tubercle. This is generally the case for Eriophyoidea species, but hasn’t been studied or described *per se* in most species. Seta *c2* is absent in all *Diptilomiopus* spp., but in an unusual occurrence, *D. leeasis* was described with *c2* absent, but the setal tubercle of *c2* present (Chakrabarti *et al.*, 1992).

Characters 22 – 24 (seta *d*). A maximum of two pairs of setae (*d1* and *d2*) occur on the dorsal opisthosomal transverse region D in the Prostigmata (Kethley, 1990). Seta *d2* is lost in most families of Anystina, Eupodoidea, Tydeoidea, Bdelloidea, Caligonellidae, Raphignathidae, and all Heterostigmata (Kethley, 1990). Only *d1* (*d2* in André, 1981a) is present in the Tydeoidea in this region (André, 1981a; André & Fain, 2000), except *Australotydeus* in which *d2* (*l2* in André, 1981a) is also present (André, 1981a; André & Fain, 2000). According to Ueckermann & Grout (2007) *d1* and *d2* are present in *O. stepheni* (Fig. 4.1). According to their naming of the setae they effectively proposed that one or more setae *ps* are absent, and both *d2* and *e2* is present, which would be an unusual case for a member of the Tydeidae. With alternative interpretation of the dorsal opisthosomal setae (C. Craemer, present study), *d2* may be absent in *O. stepheni*, and the seta currently named *d2* might rather be *e1*, André (1981a) mentioned that *e1* (*d3*) is the only seta that may migrate, and tend to move to fill the gap following the disappearance of *d2* (*l2*) and *e2* (*l3*). He adds, though, that it never goes beyond lyrifissure *im* and thus *e1* (*d3*) is always positioned behind this lyrifissure. The apparent position of this seta *O. stepheni* is, however, in the transverse area D (above lyrifissure *im* and more in the lateral region), and is problematic. Another hypothesis that might explain the dorsal setae in *O. stepheni* is that all setae of *e*, *f* or *h* may be entirely absent, but this does not seem likely. Further study, especially of the type specimens, is necessary to resolve the comparative homology of these setae, but falls beyond the scope of the present study.

Setae *d1*, *d2* and *d3* can be present in the Tetranychidae, *d3* is regarded as being neotrichous (Lindquist, 1985) or in other words, is considered secondary (Kethley, 1990). Only *d1* and *d2* are present in *M. yemensis* (Fig. 4.2).

This discussion on setal homologies, names and positions in the Tydeidae is so detailed, because for the outcome of the analysis, it is important to know which pair of the *d*-setae is homologous with *d* found in the Eriophyoidea. For the present study it is presumed the seta *d* homologous to *d* in the Eriophyoidea is present in *O. stepheni* and *M. yemensis* (i.e., *d1* or *d2*). A similar argument should be true for other outgroups and other setae (opisthosomal *e* and *f*) with less than the usual full complement of paired setae present per segment, if the specific pair can not be denoted as homologous to the pair present in the Eriophyoidea. This reasoning almost is kin to creating a hypothetical outgroup, where it is presumed the specific dorsal pair of setae were present plesiomorphologically, and that loss thereof is derived, regardless whether the specific homologous pair of setae is indeed

present in the outgroup species (be it a species from the Tydeidae, Tetranychidae or another Prostigmata group).

22. Seta *d* – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 13: 0 = present; 1 = absent).

Among Eriophyoidea species included in the present study *d* is absent in species belonging to all three families (Table B.1): in the Phytoptidae the three species with *d* absent are all fusiform with similar body shapes. Within the Eriophyidae, *d* is absent in members of the Phyllocoptinae, and they are also fusiform mites usually with an exposed life style, and in *Ashieldophyes pennadamensis*, also with an exposed life style (it is a leaf vagrant), albeit with a more vermiform body shape. Within the Diptilomiopidae *d* is absent in two species of the Diptilomiopinae, neither of them vermiform. One of the species not included in the present study, but reportedly with *d* absent (Mohanasundaram, 1986b) is the phyllocoptine species, *Hemiscolocenus rares*. However, in the drawing of this species it seems that *e* might be absent, with *d* present. Amrine *et al.* (2003) erroneously stated in their key that all opisthosomal setae are present in the latter genus. At first glance, it seems that *d* is lost particularly in species with a more fusiform body shape and exposed life style, and may have been lost at least three times homoplastically to account for its absence in all three families, if the classification *sensu* Amrine *et al.* (2003) are natural.

Of the 17 species in the present study without *d*, only *d* of the opisthosomal setae (except *c1* and *h1* which may also be absent) is absent in four species, the remainder also have either *c2* (in diptilomiopine species) or *e* (Phytoptidae and Eriophyidae species) absent (Table B.1).

The character states scored for the following species, in particular, are ambiguous:

- *Pararhynacus photiniae*: the presence of *d* could not be determined [ventral view not depicted and it could not be scored from the Chinese description by Kuang (1986a)]. It is presumed *d* is present, because the author stated that the new genus and species are similar to *Rhynacus*, and *Rhynacus* possesses *d*.
- *Steopa bauhiniae*: *d* was recorded as absent, and it seems that *d* is indeed absent according to the descriptive drawing (Chandrapatya & Boczek, 2001b), however, according to the position

of the seta, there is also a possibility that rather *e* is absent, and the seta present, now denoted *e*, may be *d*.

***23. Seta *d* – number of pairs:**

0 = more than one pair present
1 = only one pair present

Regardless of the precise homology of opisthosomal *d* between the Tetranychidae and Eriophyoidea, two pairs of opisthosomal *d* is present in *M. yemensis* (Fig. 4.2), and only one pair of *d* is present in the Eriophyoidea. The state of "more than one pair present" for *O. stepheni* is ambiguous, though. As interpreted by Ueckermann & Grout (2007) two pairs of opisthosomal *d* are present in *O. stepheni* (Fig. 4.1), but if alternative setal homologies are considered (C. Craemer, present study), only one pair of *d* may be present, similar to most other Tydeidae, including the genera from which it was differentiated (see discussion of alternative setal homologies above). The code "?" (unknown) is assigned to *O. stepheni*.

***24. Seta *d* – position:**

0 = dorsally
1 = displaced ventrolaterally

All setae *d* occur dorsally on the opisthosoma of the Tydeidae including *O. stepheni* (Fig. 4.1), and Tetranychidae including *M. yemensis* (Fig. 4.2). In the Eriophyoidea *d* occurs ventrolaterally. Lindquist (1996a) proposed that the ventral opisthosomal setae in the Eriophyoidea are setae of dorsolateral origin in other Prostigmata that moved to a ventral position.

Characters 25 – 27 (seta *e*). A maximum of two pairs of setae (*e1* and *e2*) occur on the dorsal opisthosomal transverse region E in the Prostigmata (Kethley, 1990). Seta *e2* is lost in most families of Anystina, Eupodoidea, Tydeoidea, Bdelloidea, Caligonellidae, Raphignathidae, and all Heterostigmata (Kethley, 1990). Only *e1* (*d3* in André, 1981a) is present in the Tydeoidea on this region (André, 1981a), and André (1981a) additionally regarded the presence of only *e1* (*d3*) [without *e2* (*l3*)] as the situation in the "dorsal idiosomal paleotaxy" (plesiomorphic or primitive state) of the Tydeidae. According to Ueckermann & Grout (2007) *e1* and *e2* (lengths of these setae were given in the text) are present in *O. stepheni* (Fig. 4.1). They did not comment on the significance of this in the Tydeidae. See the discussion of the presence of *d2* and possible alternative setal homologies for *O. stepheni* above. Setae *e1*, *e2* and *e3* can be present in the Tetranychidae,

e3 is regarded as being neotrichous (Lindquist, 1985) or in other words, is considered secondary (Kethley, 1990). Only *e1* and *e2* are present in *M. yemensis* (Fig. 4.2).

25. Seta *e* – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 14: 0 = present; 1 = absent).

Among Eriophyoidea species included in the present study, *e* is absent in species belonging to all three families (Table B.1). In the Phytoptidae, *e* is absent only in one species, *Neopropilus jatrophus*, and in this species, *d* is also absent (Huang, 1992). Within the Eriophyidae, *e* is absent in members of the Phyllocoptinae which are fusiform mites usually with an exposed life style, and in *Ashieldophyes pennadamensis*, also with an exposed life style (it is a leaf vagrant) (Mohanasundaram, 1984). In these species, *d* is usually also absent, except in two species of the Phyllocoptini, *Prophyllocoptes riveae* (Mohanasundaram, 1984) and *Tergilatus sparsus* (Meyer & Ueckermann, 1995) in which only *e* is absent. Different from Eriophyoidea species in which *d* is absent, *e* is also absent in members with a more vermiform body shape and mostly living a sequestered lifestyle in the Nothopodinae, Eriophyinae and Cecidophyinae (Table B.1). Only *e* (and not *c2* and *d*) is absent in these species. Within the Diptilomiopidae *e* is absent in three species of the Diptilomiopinae. In these three species *c2* is also absent (Table B.1).

The character states scored for the following species, in particular, are ambiguous:

- *Pararhynacus photiniae*: the presence of *e* could not be determined [ventral view not depicted and description by Kuang (1986a) in Chinese]. It is presumed *e* is present, because the authors stated that the new genus and species are similar to *Rhynacus*, and *Rhynacus* has *e* present.

***26. Seta *e* – number of pairs:**

0 = more than one pair present
1 = only one pair present

Regardless of the precise homology of opisthosomal *e* between the Tetranychidae and Eriophyoidea, two pairs of opisthosomal *e* are present in *M. yemensis* (Fig. 4.2), and only one pair of *e* is present in the Eriophyoidea.

The state of "more than one pair present" in the Tydeidae is ambiguous, though. As interpreted by Ueckermann & Grout (2007) two pairs of opisthosomal *e* are present in *O. stepheni* (Fig. 4.1), but if alternative setal homologies are considered, only one pair of *e* may be present in *O. stepheni*, similar to most other Tydeidae, including the genera from which it was differentiated or *e* may not even be present in *O. stepheni* (see discussion of alternative setal homologies above). The code "?" (unknown) is assigned to *O. stepheni*.

***27. Seta *e* – position:**

0 = dorsally
1 = displaced ventrolaterally

All setae *e* occur dorsally on the opisthosoma of the Tydeidae including *O. stepheni* (Fig. 4.1) and the Tetranychidae, including *M. yemensis* (Fig. 4.2). In the Eriophyoidea, they occur ventrolaterally. Lindquist (1996a) proposed that the ventral opisthosomal setae in the Eriophyoidea are setae of dorsolateral origin that have moved to a ventral position (similar to the situation for *d*).

***28. Seta *f* – number of pairs:**

0 = more than one pair present
1 = only one pair present

Setae *f1* and *f2* occur in the Prostigmata, but *f3* have been lost in all Prostigmata groups except in some Endeostigmata (Kethley, 1990). Regardless of the precise homology of opisthosomal *f* between the Tydeidae, Tetranychidae and Eriophyoidea, within the Tydeidae including *O. stepheni* (Fig. 4.1), and Tetranychidae including *M. yemensis* (Fig. 4.2), *f1* and *f2* (two setal pairs) are present. Seta *f* is never absent in the Eriophyoidea species known to date, but only one pair is present.

***29. Seta *f* – position:**

0 = dorsally
1 = displaced ventrolaterally

All setae *f* occur dorsally on the opisthosoma of the Tydeidae including *O. stepheni* (Fig. 4.1), and Tetranychidae including *M. yemensis* (Fig. 4.2). In the Eriophyoidea they occur ventrolaterally. Lindquist (1996a) proposed that the ventral opisthosomal setae in the Eriophyoidea are setae of dorsolateral origin that have moved to a ventral position.

30. Seta *h1* – presence and length:

0 = present
1 = minute or dot-like (2 µm or less)
2 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 115, Character 31: 0 = present; 1 = absent).

Setae *h1*, *h2* and *h3* may occur in the Prostigmata and of these, *h1* and *h2* occur in the Tydeidae (Kethley, 1990). With the plausible scenarios of setae homologies and names in *O. stepheni*, including the interpretation by Ueckermann & Grout (2007) (Fig. 4.1), both *h1* and *h2* are present in *O. stepheni* and neither is minute nor dot-like. In the Tetranychidae *h1* (that may possibly alternatively be *f3*) and *h2* and *h3* may occur (Lindquist, 1985). Seta *h1* is inserted dorsally, but *h2* and *h3* are smaller and inserted ventrocaudally, and *h3* may be a neotrichous seta (Lindquist, 1985). Setae *h1*, *h2* and *h3* occur in *M. yemensis* (Fig. 4.2) and are not either minute or dot-like.

Within the Eriophyoidea, conventionally, the presence or absence of *h1* is sometimes used to differentiate between species, but has not been used at a supraspecific level. Sometimes the length of *h1* is described as minute or dot-like. Unfortunately, in several cases, such as in *Diptilomiopus*, *h1* was described as being present, without any indication of length. In about all the taxa (families, subfamilies and tribes) all three states of *h1* are present, without a particular obvious pattern, except in the Diptilomiopinae, including all *Diptilomiopus* spp., where most species either have a very short or minute *h1*, or *h1* is absent. In contrast, most species in the Phytoptidae have *h1* present and it is longer than 2 µm, except in *Prothrix aboula* Keifer, 1965 (Keifer, 1965a) and some species in the Sierraphytoptinae.

The character states scored for the following species, in particular, are ambiguous:

- *Asetadiptacus emiliae*: Carmona (1970) recorded *h1* to be absent, with only small tubercles present. For the present analyses it is presumed *h1* is present, but minute in this species.
- As mentioned, the length of *h1* of many species was not recorded, e.g., for *Mediugum sanasaii* (Huang, 2001d) and *Schizoempodium mesophyllincola* (Oldfield, Hunt & Gispert, 1998), or the length of *h1* was recorded, but not available for the present study e.g., *Neolambella ligustri* (Lin & Kuang, 1997). Seta *h1* in these cases was assigned character state "present", but it may be "minute" for some of these species.
- *Prodiptilomiopus auriculatae* and *Sakthirhynchus canariae*: the presence or absence of *h1* was not recorded in the text (Umapathy & Mohanasundaram, 1999), however, these authors depicted and enlarged the lateral view of the caudum, and it is presumed they would have

depicted *h1* in these drawings if this seta was present, thus character state "absent" was scored for these two species for the present study.

***31. Opisthosomal setae *ps* – presence:**

0 = present
1 = absent

Setae *ps1*, *ps2* and *ps3* occur on the PS segment in the Prostigmata (Kethley, 1990). The *ps* series of setae are larval in origin. Some Prostigmata groups (Raphignathoidea, Cheyletoidea, Tetranychoidea, Eriophyoidea, Heterostigmata and Parasitengona) do not exhibit additions to the body chaetome beyond the larval *ps* series (Kethley, 1990).

André (1981a) proposed that only one pair of *ps* setae is present in the Tydeidae and these may be lost in some species. According to Kethley (1990) *ps1* and *ps2* occur in the Tydeidae. These are probably named *h1* and *h2* by André (1981a) in his interpretation of the setae. In *O. stepheni*, one pair of *ps* is regarded to be present, ventrally close to the anus (Ueckermann & Grout, 2007) (Fig. 4.1). Setae *ps*1, *ps*2 and *ps*3 occur in the Tetranychidae (Lindquist, 1985). Only *ps*1 and *ps*2 are present in *M. yemensis* (Fig. 4.2). Regardless of the precise homology of opisthosomal *ps* between the Tydeidae, and Tetranychidae, Lindquist (1996a) proposed that no *ps* setae are present in the Eriophyoidea.

Setae on coxisternal plates (Figs 3.4, 3.5)

The plesiomorphic number of coxisternal setae (presented in formulae) in all Tydeidae, on each of legs I-II is 3-1, respectively: *1a*, *1b* and *1c* on coxisternum I and *2a* on coxisternum II (André, 1981a), and this is also the case in *O. stepheni* (Fig. 4.1). In the Tetranychidae, the podosomal venter bears three pairs of prominent simple setae, known as ventral or intercoxal setae, of which only the anterior pair, *1a*, inserted between the bases of legs I and II and the second or middle pair, *3a*, between the bases of legs III, (Lindquist, 1985) are of concern in determining primary homologies between the Tetranychidae and the Eriophyoidea. These two pairs are already present in the larvae of tetranychid species (Lindquist, 1985). Seta *2a* is absent. On the coxisternal plates themselves, the primitive and maximum number of coxisternal setae (presented in formulae) on each of legs I-II is 2-2, respectively (Lindquist, 1985): *1b* and *1c* on coxisternum I and *2b* and *2c* on coxisternum II. In *M. yemensis*, this full compliment of intercoxal and coxisternal setae is present (Fig. 4.2).

In the Eriophyoidea the coxisternal plates characteristically have two pairs of setae (*1a* and *1b*) inserted on plates I and 1 pair (*2b*) on plates II, thus written in formula (not conventionally done for the Eriophyoidea) coxisternal I – coxisternal II is (2-1), and this is also the maximum number of these setae in this superfamily. The homologies of these setae with those in other acariform mites and their names were proposed by Lindquist (1996a). The relative position of the setae on the coxisternal plates in comparison with each other, in the Eriophyoidea, is stable intra-specifically (Hong & Zhang, 1996a), and has been described by some Eriophyoidea taxonomists such as Meyer (1990a).

32. Seta *1b* – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 15: 0 = present; 1 = absent).

Seta *1b* is present in *O. stepheni* and in *M. yemensis* (Figs 4.1, 4.2, and also see discussion above). Seta *1b* is generally shorter and weaker than *1a* and *2a* in the Eriophyoidea, and has been lost in some species in each of most subfamilies of the Eriophyidae and Diptilomiopidae, but not in any of the members of the Phytoptidae. The absence of *1b* is important at the generic level in the Eriophyoidea. It is especially of importance in keying to the tribes of the Nothopodinae (present in the Colopodacini, but absent in the Nothopodini), and is prominent in keying to and differentiating genera and generic groupings in the Diptilomiopinae and Aceriini (Amrine *et al.*, 2003). According to the key by Amrine *et al.* (2003) and recent diagnoses of the genus, *1b* is absent in all species assigned to *Diptilomiopus*. The presence or absence of *1b* in the type species (*D. javanicus*) is, however, not known. Nalepa (1918) described the position of the second pair of coxal setae (*1a*) in this species as "*die Hüftborsten des zweiten Paares vor den inneren Hüftwinkeln sitzend*", but did not mention the presence or absence of *1b*.

The character states scored for the following species, in particular, are ambiguous:

- *Neolambella ligustri*: in the descriptive drawing (reproduced in Amrine *et al.*, 2003), *1b* seems to be present, but according to T. Stasny (*pers. comm.*) the lines are folds in the coxal surface, and that this was confirmed with the species authors. For the present study this character is scored "absent" for this species.

- *Diptilomiopus ervatamiae*: *1b* is present (Chandrapatya & Boczek, 1991a) in only this one species of *Diptilomiopus*. When compared with the position of *1b* in this species, the presumably *1a* in some of the other *Diptilomiopus* spp. (e.g., *D. alagarmalaiensis*, *D. knorri* and *D. pocsi*) is situated so far ahead of the rear coxisternal margin in comparison with the length of coxisternal plates I, and the anterior approximation between them, that the seta may possibly be rather *1b* than *1a*, and *1a* may be absent. This is particularly the case in *Suthamus chiangmi*. Chandrapatya & Boczek (2000a) interpreted it as being *1a* with *1b* absent in this species, however, and it has been assigned as such for the present study. If *D. ervatamiae* (with *1b* present and only the tubercles of *1a* remaining) and the situation in single other diptilomiopine species were not known, this alternative hypothesis would have been regarded as unlikely, since *1a* seems to be much more stable and more rarely absent than *1b*, and usually when *1b* is absent, *1a* is also absent (also see Lindquist, 1996a).

33. Setal tubercle of *1b* – presence:

0 = primary absent
1 = present
2 = secondary absent

Seta *1b* is not primarily inserted on tubercles in the Tydeidae, including *O. stepheni* (Fig. 4.1), and the Tetranychidae, including *M. yemensis* (Fig. 4.2), and therefore has been assigned the state "primary absent" in these two species in the present study. The presence, size and shape of the setal tubercle on which *1b* is inserted is usually not described for Eriophyoidea species, and with most descriptive drawings being semi-schematic or the morphology not depicted so precisely, these details could, in most instances, not be determined from the drawings. It has thus been presumed, whenever *1b* is present, it is inserted on a setal tubercle, and presence of *1b* denotes presence of setal tubercle *1b*.

34. Distance between setae *1b* in comparison with distance between setae *1a*:

0 = *1b* clearly further apart than *1a*
1 = *1b* slightly further apart than *1a*
2 = *1b* longitudinally in line with *1a*
3 = *1b* slightly closer together than *1a*
4 = *1b* clearly closer together than *1a*

Setae *1b* are clearly further apart than *1a* in *O. stepheni* (Fig. 4.1) and *M. yemensis* (Fig. 4.2). The relation of the distance between setae *1b* to the distance between setae *1a* in the Eriophyoidea is frequently not measured or described in the text, but can be easily determined from a descriptive drawing of this area. The distance between *1b* in comparison with the distance between *1a* ranges from further apart to closer in both the Eriophyidae and Phytoptidae, but in the Diptilomiopidae it

generally seems to be further apart with only some species with states “slightly further” or “in line” or “slightly closer”. In none of the diptilomiopid species included in the present study are *1b* clearly closer together than *1a*. Within the Eriophyidae generally *1b* also rather seems to be further away or in line and sometimes closer, however, in the cecidophyine species included in the present study, *1b* mostly seems to be almost in line, in line or closer together than *1a* and never clearly further apart. Setae *1b* and *1a* usually seem in line or almost in line with each other in the Nalepellinae.

The assignment of character states for this character is subjective, and possible distortion of the coxisternal plates in slide-mounted specimens may cause the setae to be slightly pressed from their true position. Possible phylogenetic information in the character might additionally be obscured in the way the states were defined. The states where *1b* are slightly further or slightly closer together than *1a*, may be similar or the same as the setae being the same distance apart, or alternatively as being clearly further apart or closer together. Although the states are finely differentiated, they could be scored, and it was decided to experimentally keep the character states as they are for the present study. These relative positions of coxal setae to each other probably also inherently defines the shape of the coxae, and the latter may be a more realistic representation of these coxisternal plate characteristics.

35. Seta *1a* – presence:

0 = present
1 = absent

Seta *1a* is present in *O. stepheni* and in *M. yemensis* (Figs 4.1, 4.2), also see discussion above. Seta *1a*, in contrast to *1b*, is rarely absent in Eriophyoidea species. It is only absent in three species of the Diptilomiopinae: *Africus psydraxae*, *Diptilomiopus ervatamiae* and *Neodiptilomiopus vishakantai* (Meyer & Ueckermann, 1995; Chandrapatya & Boczek, 1991a; Mohanasundaram, 1982b, respectively). In *D. ervatamiae* the setal tubercle of *1a* is present, but *1a* is absent (*1b* is present in this species). This is quite an unusual state in the Eriophyoidea, since *1a* is rarely absent, and if absent, *1b* is absent as well (e.g., *A. psydraxae* and *N. vishakantai*). The absence of *1a* is autapomorphic for *D. ervatamiae* among *Diptilomiopus* spp. (also see discussion of Character 32).

The position of *1a* on the coxisternal plate may be of taxonomic and phylogenetic significance, but has not been scored in published descriptions. The variation of the position of *1a* from the rear proximal margin of coxisternal plate I was first noted in *Diptilomiopus* spp. in the present study. Seta *1a* of most *Diptilomiopus* spp. is situated quite close to the rear proximal margin of coxisternal plate I, and close to the approximation with coxisternal plate II. In some species,

however, this seta is inserted quite clearly further away from this position (e.g., in *D. bengalensis*, *D. dendropanacis*, *D. euryae*, *D. holoptelus*, *D. indicus*, *D. malloti*, *D. phylanthi*, *D. septimus*). The difference in position can be compared between *D. holmesi* (close to rear margin) and *D. jevremovici* (further away from rear margin), both described by H.H. Keifer (Keifer, 1962c; Keifer, 1960, respectively). The position of *1a* on the coxisternal plate was scored for *Diptilomiopus* spp. in the present study, and subsequently for some of the species in other genera, where distinguishing between "close to" or "ahead of" became less obvious. It turned out that the position of *1a* may vary continuously, without discrete gaps, and defining the states and subsequent scoring and coding is highly subjective at this stage, and it was decided not to include this character in the present study. Based on the absence of *1a* and presence of *1b* in *D. ervatamiae* (albeit the tubercle of *1a* is still present in this species), some of the setae, named *1a*, more ahead of the basal margin of coxisternal plate I may rather be *1b* (also see discussion of Character 32).

36. Setal tubercle of *1a* – presence and shape:

0 = primary absent
1 = present and shaped as usual (about rounded or cylindrical)
2 = present and elongated
3 = secondary absent

Seta *1a* is plesiomorphically not inserted on a tubercle in the Tydeidae including *O. stepheni* (Fig. 4.1) and Tetranychidae, including *M. yemensis* (Fig. 4.2), and therefore has been assigned the state "primary absent" in these two species in the present study.

For scoring the character states of this character for the Eriophyoidea, it is presumed the shape of the tubercle is normal, except when specifically mentioned or depicted otherwise in the species description. The setal tubercle of *1a* is different from the usual more rounded or cylindrical shape in only two species. Both species are in the Diptilomiopinae and the tubercle is elongated in both: in *Diptilomiopus coreiae* it is described as being long, and it is depicted markedly longer than usually found in the Eriophyoidea, in the accompanied drawings (Chandrapatya & Boczek, 2002b). Among *Diptilomiopus* spp. long tubercle *1a* is autapomorphic for *D. coreiae*. It is also elongated in *Kaella flacourtiae* (Chandrapatya & Boczek, 2002b). Unfortunately, the shape of these tubercles in Eriophyoidea species has generally not been described, and differences in shape, if present, may be subtle, and the descriptive drawings are probably mostly not reliable or specific in this regard.

The character states scored for the following species, in particular, are ambiguous:

- Farkas (1967) described the tubercle of *Diptilomiopus pocsi* as being "well developed" and Boczek & Chandrapatya (2002) described the tubercles of all coxal setae in *D. thunbergiae* as being large. However, the tubercles of these species, as well as those of some other species for which the tubercle was depicted as large in their drawings (e.g., *D. knorri*, *D. pamithus*, *D. securinegus*, and *D. thaianae*), although possibly larger or more pronounced than "normal" do not constitute a distinctly different state when compared between descriptive drawings, and were scored as "shaped as usual".

It will be a better option to divide this character in future studies into two characters: setal tubercle of *1a* present or absent, and a second character to score the shape of this tubercle, and for the latter character for those species with the setal tubercle absent, the score will be "not applicable".

37. Seta *1a* – position:

0 = ahead of *2a*
1 = slightly ahead of *2a*
2 = in line with *2a*
3 = slightly behind *2a*
4 = behind *2a*

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 115, Character 35: 0 = *1a* ahead of *2a*; 1 = *1a* same line as *2a*; 2 = *1a* behind *2a*).

Seta *1a* is clearly ahead of *2a* in *O. stepheni* (Fig. 4.1) and *2a* is absent in *M. yemensis* (Fig. 4.2), and "not applicable" was scored for the latter. Seta *1a* is ahead or slightly ahead of *2a* in the majority of the Eriophyoidea species included in the present study. In some of the species *1a* seems to be in line with *2a*, but this may be a consequence of schematic drawing, or the specimens may be slightly distorted due to slide-mounting, and these may also have *1a* slightly ahead of the *2a* or *vice versa*. Seta *1a* is slightly behind in three species [*Mackiella phoenicis*, *Propilus gentyi* (Sierraphytoptinae) and *Oziella yuccae* (Phytoptinae)] (Keifer, 1939a; 1975d; 1954, respectively) and clearly behind in two species [(*Novophytoptus rostratae* and *N. stipae* (Novophytoptinae)] (Roivainen, 1947l Keifer, 1962d, respectively), and all five species are in the Phytoptidae.

Similar to the distance between setae *1a* relative to the distance between setae *2a*, the character states are assigned subjectively, and the definition of states for this character may obscure phylogenetic information in the character, because it might have been defined into too many states with gaps between the states too small (e.g., slightly ahead, in line and slightly behind may essentially be the same character state). When studied carefully, the character states will probably

vary into each other without clear gaps, and may be more accurately portrayed by using actual measurements (which can be analysed in TNT). The character is probably also very prone to body distortion in slide-mounted specimens, albeit it is usually quite stable, and can be assigned to one state within a sample of specimens, but this will probably vary according to the quality of mounting. It may be better to take the measurements on SEM images of specimens that are orientated the same and at the same angles, depending on the robustness of variation tolerated. The character does have potential as a phylogenetically informative character. It is currently regarded as rather a species level character.

****38. Seta *2a* – presence:**

0 = present
1 = absent

Seta *2a* is present in *O. stepheni* (Fig. 4.1) and is absent in *M. yemensis* (Fig. 4.2). The homologies of these setae when the Tenuipalpidae and Tetranychidae are compared, may be suspect, and there is a possibility that *2a* may also be absent in the Tydeidae. Seta *2a* is present in all Eriophyoidea species included in the present study, except in *Neocupacarus flabelliferis* (Das & Chakrabarti, 1985) (Eriophyidae: Phyllocoptinae: Phyllocoptini), and its absence is thus autapomorphic for this species within the Eriophyoidea in the present study. Setae *1a* and *1b* are present in this species.

The character state scored for the following species, in particular, is ambiguous:

- *Diptilomiopus javanicus*: although the presence of *2a* has not been explicitly recorded by Nalepa (1916, 1918), most Eriophyoidea species, and all diptilomiopid species have these setae present, thus state "present" was scored for this species.

Setae associated with genitalia

Characters 39 – 42 are autapomorphic for the Eriophyoidea in the present analysis.

***39. Genital setae in adult – presence:**

0 = present
1 = absent

The maximum number of genital setae in the Tydeidae is six pairs but they are reduced or lost in some species (André, 1981a). Genital setae are not present in the larva of the Tydeidae, and is completely absent in tydeids of the Pronematinae (André, 1981a). Four pairs of genital setae are

present in the females and males of *O. stepheni* (Ueckermann & Grout, 2007). There are two pairs of genital setae in the females of the Tetranychidae (Lindquist, 1985) including *M. yemensis* (Fig. 4.2). No genital seta is present in the adults of the Eriophyoidea. The pair of setae flanking the posterior area of the external genitalia of females, males and all immatures, and termed the genital setae (*sensu* H.H. Keifer), rather represents the pair of coxisternal, or intercoxal setae, *3a* (Lindquist, 1996a) (Figs 3.4, 3.5).

***40. Aggenital setae in adult – presence:**

0 = present
1 = absent

The maximum number of aggenital setae in the Tydeidae is five pairs but is reduced in some species (André, 1981a). Some aggenital setae are already present in the larva of the Tydeidae (André, 1981a). Four pairs of aggenital setae are present in the males and females of *O. stepheni* (Ueckermann & Grout, 2007). Adult males and females of the Tetranychidae usually have one pair of aggenital setae, and one pair of aggenital setae is present in *M. yemensis* (Fig. 4.2). Aggenital setae are always absent in the Eriophyoidea.

Characters 41 and 42 (eugenital setae). Within the Actinotrichida eugenital setae are usually present in the adults of the Endeostigmata, a group considered most primitive of this superorder (Evans, 1992). Within the Eupodina, a suborder of the Prostigmata, eugenital setae may be present or absent (Evans, 1992).

The eugenital setae may be present and are eupathidia, and the maximum number is six pairs in the Eupodina (André, 1981a). The number is greatly reduced in most Tydeidae and they are always smaller in females than in males (André, 1981a). The female of *O. stepheni* do not have eugenital setae, and four pairs are present in the male (Ueckermann & Grout, 2007). Eugenital setae are absent in the Raphignatina, a suborder of the Prostigmata, which include the Tetranychidae (Evans, 1992) and also when extrapolated, in *M. yemensis*. In all Eriophyoidea species eugenital setae are absent in the females, and one pair of minute eugenital setae is present in the males (Lindquist, 1996a).

*****41. Eugenital setae in female – presence:**

0 = present
1 = absent

Eugenital setae are absent in the females of all species (including *O. stepheni* and *M. yemensis*) included in the present study (see discussion above).

***42. Eugenital setae in male – presence and number of pairs:**

0 = more than one pair present
1 = one pair of minute setae present
2 = absent

Four pairs of eugenital setae are present in the male of *O. stepheni* (Ueckermann & Grout, 2007), also see discussion above. No eugenital setae are present in the male of *M. yemensis* (see discussion above). One pair of minute eugenital setae is present in the males of possibly all Eriophyoidea species, but this need to be confirmed by further study (see discussion above).

Leg setae (Fig. 3.6a, b)

The leg cheatotaxy and ontogeny thereof are not generally described or recorded in detail in the description of tetranychid species, and have also not been described for *M. yemensis*, apart from the setal formula presented recording the number of setae, solenidia and duplicate setae on each segment of each leg (Meyer, 1996), and neither were the legs depicted. It falls beyond the scope of the present study and knowledge of the author to determine homology and to name each of the leg setae in *M. yemensis* from available specimens, and because Lindquist (1996a) homologized the leg setae in the Eriophyoidea with the basic setae (already present in the larva) of the Tetranychidae, and these should rarely be lost in the adults, the leg setae as depicted and named for a general adult female tetranychine spider mite in Lindquist (1985) have been used as if it is the leg setae present in *M. yemensis*.

Table B.2. Leg setae (except coxisternal setae) which are absent in Eriophyoidea species included in the data set. Where there are more than one species in a genus, only one species was included in the table, or if variation occur between species from the same genus, all such species with different absent setae were included. Only species with some leg setae absent are listed. Absence of a setal pair is ticked with x. Setae *bv* 1 is the seta on the femur of leg I, and *bv* 2 is the seta on the femur of leg II, likewise *l''* 1 is the seta on genu of leg I, and l'' 2 is the seta on genu of leg II. Seta *l'* is the seta on the tibia of leg I, and *ft'* 2 is seta *ft'* on the tarsus of leg II.

			bv 1	*bv* 2	*l''* 1	*l''* 2	*l'*	*ft'* 2
Phytoptidae:								
Nalepellinae	Trisetacini	*Boczekella laricis*					x	
Novophytoptinae		*Novophytoptus* spp. in the present study (2)	x	x				
Prothricinae		*Prothrix aboula*					x	
Sierraphytoptinae:	Mackiellini:	*Palmiphytoptus oculatus*					x	
		Propilus gentyi					x	
		Retracrus johnstoni			x	x		
	Sierraphytoptini:	*Neopropilus jatrophus*					x	
Eriophyidae:								
Aberoptinae		*Aberoptus samoae*					x	
		Cisaberoptus kenyae					x	
Nothopodinae:	Nothopodini:	*Anothopoda johnstoni*					x	
		Cosella deleoni					x	
		Disella ilicis					x	
		Floracarus calonyctionis					x	
		Neocosella ichnocarpae					x	
		Nothopoda rapaneae					x	
		Pangacarus grisalis	x				x	
	Colopodacini	*Adenocolus psydraxi*	x				x	
		Apontella bravaisiae	x				x	
		Colopodacus africanus					x	
Eriophyinae:	Aceriini:	*Acalitus ledi*	x				x	
		Cenaca syzygioidis	x				x	
		Cymoptus spiniventris					x	
		Notaceria tetrandiae					x	x
		Ramaculus mahoe					x	
	Diphytoptini	*Diphytoptus nephroideus*				x		
	Eriophyini:	*Nacerimina gutierrezi*				x		
Cecidophyinae	Cecidophyini:	*Dechela epelis*				x	x	
		Neserella decora					x	
	Colomerini	*Afromerus florinoxus*					x	
		Cosetacus camelliae					x	
		Epicecidophyes clerodendris				x		
Phyllocoptinae:	Acaricalini:	*Cymeda zealandica*					x	
		Knorella gigantochloae	x	x		x		
		Litaculus khandus				x		
		Neodichopelmus samoanus					x	
		Notacaphylla chinensiae					x	
		Paracaphylla streblae	x	x				
		Schizacea gynerii	x	x		x		
		Tumescoptes trachycarpi	x	x		x		
	Anthocoptini:	*Catachella machaerii*	x				x	
		Neocolopodacus mitragynae					x	
		Nothacus tuberculatus	x				x	
		Notostrix attenuata				x		
		Paraciota tetracanthae	x	x		x	x	
		Quintalitus squamosus	x				x	

		bv 1	*bv* 2	*l''* 1	*l''* 2	*l'*	*ft'* 2
	Sinacus erythrophlei					x	
Calacarini:	*Calacarus pulviferus*				x		
	Jutarus benjaminae				x		
	Paracalacarus podocarpi	x	x		x		
Phyllocoptini:	*Acamina nolinae*	x	x				
	Arectus bidwillius	x					
	Euterpia fissa	x	x				
	Indonotolox sudarsani					x	
	Leipothrix solidaginis	x	x				
	Neocupacarus flabelliferis	x	x				
	Neodicrothrix tiliacorae				x	x	
	Neophytoptus ocimae	x	x				
	Proneotegonotus antiquorae				x	x	
	Prophyllocoptes riveae						
	Tergilatus sparsus						
Tegonotini:	*Dicrothrix anacardii*						
Ashieldophyinae	*Ashieldophyes pennadamensis*						
Diptilomiopidae:							
Diptilomiopinae:	*Acarhis* spp. in the present study (2)	x	x	x	x		
	Acarhis diospyrosis	x	x	x	x	x	
	Acarhynchus filamentus	x					
	Africus psydraxae	x	x	x	x	x	x
	Apodiptacus cordiformis	x	x				
	Asetadiptacus emiliae	x	x				
	Chiangmaia longifolii	x	x			x	
	Dacundiopus stylosus	x	x		x	x	
	Davisella breitlowi	x	x		x		
	Dialox stellatus	x					
	Diptacus pandanus	x					
	Diptacus sacramentae	x	x				
	24 of *Diptilomiopus* spp. in the present study*	x	x	x	x	x	
	54** of *Diptilomiopus* spp. in the present study*	x	x	x	x	x	x
	Diptilomiopus artocarpae	x	x		x		
	Diptilomiopus azadirachtae	x	x		x		x
	Diptilomiopus bengalensis	?			x		
	Diptilomiopus cuminis Huang	x	x	x	x		
	Diptilomiopus guajavae	x	x		x		x
	Diptilomiopus thangaveli	x	x		x		x
	Diptilomiopus ulmivagrans	x	x		x		
	Diptiloplatus megagrastis	x			x		
	Diptilorhynacus sinusetus	x	x	x	x	x	
	Diptilorhynacus dioscoreae	x	x	x	x	x	x
	Diptilostatus nudipalpus	x	x		x	x	
	Duabangus chiangmai	x	x			x	
	Kaella flacourtiae	x	x		x	x	
	Lambella cerina	x	x	x	x	x	
	Levonga spp. in the present study (2)	x	x		x	x	
	Levonga litseae	x	x		x	x	x
	Lithocarus thomsoni	x	x	x	x	x	
	Mediugum sanasaii	x	x	x	x	x	

		bv 1	*bv* 2	*l''* 1	*l''* 2	*l'*	*ft'* 2
	Neoacarhis aglaiae	x	x		x	x	
	Neodialox palmyrae	x					
	Neodiptilomiopus vishakantai	x	x		x	x	
	Neolambella ligustri	x	x	x	x	x	
	Neorhynacus rajendrani	x	x		x		
	Norma lanyuensis		x		x	x	
	Pararhynacus photiniae	x	x				
	Prodiptilomiopus auriculatae	x	x	x	x	x	
	Rhynacus arctostaphyli	x	x		x		
	Steopa bauhiniae	x	x		x	x	
	Suthamus chiangmi	x	x	x	x		
	Thailandus diospyrosae	x		x	x	x	
	Trimeroptes eleyrodiformis	x	x				
	Vimola syzygii	x	x		x	x	
Rhyncaphytoptinae	*Areekulus eugeniae*	x	x		x		x
	Asetacus madronae	x	x				
	Catarhinus tricholaenae	x					
	Chakrabartiella ficusis	x	x				
	Hoderus roseus	x	x		x		
	Konola hibernalis	x	x				
	Neocatarhinus bambusae	x			x		
	Quadriporca mangiferae	x	x				
	Sakthirhynchus canariae	x	x	x	x	x	

* *D. championi* excluded – presence of *bv* on femur I and II, *l''* on genu I and II, *l'* on tibia, and *ft'* on tarsus II unknown.
** *D. pocsi* and *D. sandorici* – presence of *l'* unknown.

43. Leg I: seta *bv* (Fig. 3.6a, b) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 16: 0 = present; 1 = absent).

Seta *bv* originally belonged to the more basal of the two femoral segments of the legs in more plesiomorphic acariform mites, and it is the only ventral fundamental seta found on the femora of legs I and II in acariform mites (Lindquist, 1996a). Lindquist (1996a) proposed that the ventral femoral seta in the Eriophyoidea is homologous with seta *bv* in acariform mites.

In the Tydeidae the maximum number of setae occurring on femur I and II respectively is six and four, and the minimum on these two segments is two on each (André, 1981b). The proximoventral seta, *pv*, in the Tydeidae is amongst the strongest setae on the leg femur of legs I and II (André, 1981b). The position of this seta on the femur is similar to that of *bv''* in the Tetranychidae and represents the fundamental seta *bv* in acariform mites. This seta is present in *O. stepheni* (C.

Craemer, own observation). The femur in legs I and II in the larval and protonymphal instars of the Tetranychidae have three setae of which one is seta *bv''*, a seta in a proximoventral position, homologous to the fundamental seta *bv* in acariform mites. Seta *bv''* is present in legs I and II of adult females of the Tetranychidae (Lindquist, 1985), and is also regarded to be present in *M. yemensis.*

Seta *bv* on femur I is present or absent in Eriophyoidea species (Table B.2). Among species in the present study it is absent in some species in all three families. In the Phytoptidae it is absent in the two *Novophytoptus* spp. (Novophytoptinae). In the Eriophyidae it is absent in relatively few (five) species: of the Nothopodinae (three species) and Eriophyinae (two species in the Aceriini), and *bv* on femur II is not absent in any of these. In the Phyllocoptinae, with more exposed living forms, *bv* on femur I is absent in several species of most tribes of this subfamily, and frequently this seta on femur II is also absent in these species. Within the Diptilomiopidae, *bv* on femur I is absent in all species of the Diptilomiopinae, except in two species not belonging to *Diptilomiopus*, and two *Diptilomiopus* spp. for which the presence is unknown. Within the Rhyncaphytoptinae about half of the species are with and the other half without *bv* on femur I. In the majority of Diptilomiopidae species, *bv* on femur II is also absent when *bv* on femur I is absent.

The character state scored for the following species, in particular, is ambiguous:

- *Pararhynacus photiniae*: the presence of *bv* on femur I could not be determined [ventral view not depicted and text description by Kuang (1986a) in Chinese]. It is presumed *bv* is absent, because the authors stated that the new genus and species is similar to *Rhynacus*, and this seta is absent in *Rhynacus*.

44. Leg I: seta *l''* (Fig. 3.6a, b) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 112, Character 17: 0 = present; 1 = absent).

The maximum number of setae on the genua of the Tydeidae is four. There is no other reference point on this segment to evaluate the setae, and there is no variation during ontogeny, and determining the homology of these setae with setae on this segment in the acariform mites is difficult and ambiguous (André, 1981b). The number of setae on genu I in the Tydeidae ranges from four to one (André, 1981b). Three setae are present on genu I of *O. stepheni* (Ueckermann &

Grout, 2007), and based on the setal positions in comparison with the labeled setae on leg I of *Meyerella marshalli* (André, 1980), *l''* are present, as well as *v'* and *l'* (Fig. 4.1).

In the larva and protonymph of the Tetranychidae, four setae is the standard number of setae on genua I and II, namely *l'*, *l''*, *v'*, and *v''*, and in the Tetranychinae *d* is added on genua I and II in the deutonymphs (Lindquist, 1985) and in the tetranychine adults these five setae are present (Lindquist, 1985). Seta *l''* is part of the basic larval-protonymphal complement, and it is not conceivable that it will be lost in *M. yemensis*, and it is extrapolated for the present study that *l''* is present on genu I of *M. yemensis*.

In the Eriophyoidea *l''* on the genu may be present or absent (Table B.2). Among the species included in the present study, it is present in all Phytoptidae [apart from *Retracrus johnstoni* (Sierraphytoptinae) where seta *l''* is absent from genu I and II (Keifer, 1965c)] and Eriophyidae, and is only absent in members of the Diptilomiopidae, and particularly of the Diptilomiopinae [among the Rhyncaphytoptinae it is only absent in *Sakthirhynchus canariae* (Umapathy & Mohanasundaram, 1999)]. Within the Diptilomiopinae it is absent in all *Diptilomiopus* spp. and in species of about 11 other Diptilomiopinae genera. Seta *l''* of genu I is present in some species currently in *Diptilomiopus* (*D. artocarpae*, *D. azadirachtae*, *D. guajavae*, *D. thangaveli* and *D. ulmivagrans*) (Mohanasundaram, 1981b; Boczek & Chandrapatya, 1992b; Mohanasundaram, 1985; 1983c; 1984, respectively), but these species should probably not be in *Diptilomiopus*. Seta *l''* on genu I is much more stable, and is lost in less species than *l''* on genu II. In species in the present study, *l''* is also absent from genu II when it is absent from genu I (Table B.2).

The character states scored for the following species, in particular, are ambiguous:

- *Diptilomiopus azadirachtae*: the presence of *l''* in leg I is ambiguous. Its presence is not mentioned in the text by Boczek & Chandrapatya (1992b), and the drawing seems to be wrong: the legs are depicted with 4 segments (excluding coxae), but the way the setae are positioned, it seems that the tibia may be absent, and not the genu. The segment proximally of the tarsal segment is relatively long, with a very strong seta (similar to a genual seta in other Eriophyoidea species). This can not be the tibia, firstly because in the text it is explicitly mentioned that the tibial seta *l'* is absent, and the seta is much longer and stronger than what seta *l'* usually is. The depiction of the second pair of legs has the same mistakes as the first leg, and the tibia of leg II never has a seta in the Eriophyoidea, and a similar strong seta is depicted dorsally on the segment just proximal of the tarsus. The most plausible explanation is that the genua (and *l''*) are present in this species, and that the distal margin of the tibiae was

not depicted, creating a "tibiotarsus". There is an unusually long space basally of *ft'* and *ft''*. Seta *l''* was scored as present, however, this score is ambiguous.

- The presence or absence of *l''* in *Diptilomiopus* spp. is not described in the text or reliably depicted in the drawings in many cases, however, if the absence of genu I is clearly described or depicted, it is presumed *l''* is also absent, if not mentioned or depicted otherwise. This decision is supported by the definition of *Diptilomiopus* with *l''* absent and leg I and II, and presumably authors should not have assigned species to *Diptilomiopus* if it was otherwise.

45. Leg I: seta *l'* (Lindquist, 1996a) or *l* (proposed in the present study, for future investigation) (Fig. 3.6a, b) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 18: 0 = present; 1 = absent).

The hypothesized plesiomorphic setal compliment on the tibia of the Tydeidae includes five setiferous setae (*d*, *l'*, *l''*, *v'* and *v''*) of which one may be eupathidial, a famulus *k''* and solenidion *φ* (André, 1981b). In *Tydeus*, a genus relatively closely related to *Orfareptydeus*, only three setiferous setae are present on tibia I, and these are *l'*, *l''*, and *v'*; seta *l''* moved into the position of *d* (André, 1981b). Similar only these three setae are present on tibia I in *O. stepheni* (Fig. 4.1). Within the Pronematinae of the Tydeidae most species also have only three setae, *l'*, *l''*, and *v'*, in the case of these species though, *l'* moved into the position of the absent *d* (André, 1981b). The latter setal arrangement is not proposed for *O. stepheni* in the present study.

In the Eriophyoidea a single tibial setiferous seta may be present dorsally on tibia I, and tibia II is always without any setae. Lindquist (1996a) compared this seta with the tibial setae in the Tydeidae, and came to a conclusion that it may either be *d* or *l'*, but because *l'* is more stable than *d* in the Tydeidae, (*d* is replaced by *l'* in tibia II of the Tydeidae [*sic*]), he proposed that the tibial seta in the Eriophyoidea is seta *l'*. He commented, though, that the homology of this seta is problematic. One should, however, rather compare tibiae I with each other, than tibia I with tibia II. As discussed above, *d* may be lost and replaced by either seta *l'* or seta *l''* in tibia I of the Tydeidae (André, 1981b). In some Eriophyoidea species the tibial seta is displaced to the inner (paraxial) aspect of the tibia, and this may possibly indicate that the tibial seta is rather *l'*, however, in some other species it is displaced to the outer (antaxial) aspect of the tibia, and an

argument can be made that this may indicate that the tibial seta is rather *l''*. In the present study the name *l' sensu* Lindquist (1996a) is still used, but I propose that the tibial seta in the Eriophyoidea may be homologous to a lateral seta (*l*), but that it can not be denoted as being the antaxial (*l''*) or paraxial (*l'*) lateral seta. This may have implications for determining primary homologies between the Eriophyoidea and other mite groups.

In the larva and protonymph of the Tetranychidae the basic setation of tibia I is five setae (*d*, *l'*, *l''*, *v'*, *v''*) and one solenidion (Lindquist, 1985). The setae on tibia I of adults of the Tetranychinae are not very variable and are 9 setae, and one solenidion *φ*, with addition of setae to the basic setation (Lindquist, 1985). It is extrapolated for the present study that *l'* and *l''* is present on the tibia of *M. yemensis*.

Seta *l'* can be present or absent in the Eriophyoidea (Table B.2). It is absent in a wide variety of taxa from all three Eriophyoidea families. In the Phytoptidae it is absent in members of the Nalepellinae, Prothricinae and Sierraphytoptinae. In the Eriophyoidea it is absent in all members of the Aberoptinae and Nothopodinae, partly defining these two subfamilies, but it is also widely absent in the Eriophyinae, Cecidophyinae and Phyllocoptinae. In the Diptilomiopidae it is absent in most members, including most *Diptilomiopus* spp., but within the Rhyncaphytoptinae it is absent in only *Sakthirhynchus canariae* (Umapathy & Mohanasundaram, 1999).

The character states scored for the following species, in particular, are ambiguous:

- *Boczekella laricis*: the presence of *l'* is not recorded, however, this seta is absent in the descriptive drawing of the species (Farkas, 1965a) and because the *l'* is normally depicted when present, it is presumed *l'* is absent, for the present study.
- *Scoletoptus duvernoiae*: *l'* is recorded as being absent in the original description (Meyer, 1992a), however, on close inspection this seta seems to be present. It is extremely fine and not clearly visible. The specimens available for study were in bad condition and additional newly collected specimens will have to be studied to confirm the presence of these setae. The character state "present" is scored for this species in the present study.

46. Leg I: seta *l'* – position:

0 = dorsal on tibia
1 = displaced to the inner (paraxial) side of tibia
2 = displaced to the outer (antaxial) side of tibia

If it is assumed that the tibial seta in the Eriophyoidea is either seta *d*, or one of the lateral setae that shifted to the dorsal position originally occupied by the absent seta *d*. The position of these

setae is dorsally on the tibia of both *O. stepheni* (Fig. 4.1) and *M. yemensis* (see discussion of Character 45 above). For determining the position of the seta homologous to the tibial seta in the Eriophyoidea in other mite groups, it becomes very important to determine the real homology of the seta, and in having trouble doing so, it renders the character ambiguous. Several scenarios are possible in which the state for the character in the outgroup taxa, may either be dorsal or lateral (paraxial or antaxial), depending whether the tibial seta *l'* (as denoted by Lindquist, 1996a) represents *d*, *l'*, or *l''* in the outgroup taxa.

In the Eriophyoidea, when *l'* is present, it is usually inserted dorsally on the tibia. Among species included in the present study, *l'* is positioned on the paraxial aspect of the tibia in the Diptilomiopidae (Diptilomiopinae: *Dialox stellatus*, *Diptiloplatus megagrastis* and *Neodialox palmyrae*, and Rhyncaphytoptinae: *Areekulus eugeniae* and *Cheiracus sulcatus*) (Keifer, 1962d; 1975c; Mohanasundaram, 1983b; Boczek & Chandrapatya, 1998; Keifer, 1977a, respectively). In the Phyllocoptinae it is positioned on the paraxial aspect in the Anthocoptini (*Ditrymacus athiasella*), and in the Tegonotini (*Dicrothrix anacardii*) (Keifer, 1960; 1966c, respectively), and on the antaxial or outer aspect of three species: *Hyborhinus kalarensis* (Rhyncaphytoptinae) (Mohanasundaram, 1986) and *Acaphyllisa parindiae* and *Neoacaphyllisa lithocarpi* (Phyllocoptinae: Acaricalini) (Keifer, 1978; Kuang & Hong, 1989, respectively).

The character states scored for the following species, in particular, are ambiguous:

- *Areekulus eugeniae*: it clearly seems as if *l'* is on the paraxial side of the tibia in the descriptive drawing (Boczek & Chandrapatya, 1998), however, this displacement is not mentioned in the descriptive text. For the present study the character state "displaced to the inner side of tibia" is assigned to this species, but it may be based on a drawing error.
- *Acarhynchus filamentus*: particularly in the enlarged drawing of the legs, it seems that *l'* might either be on the paraxial or antaxial aspects of the tibia (Keifer, 1959b), however, this is not mentioned in the text, and the character state "dorsal on tibia" was assigned to this species for the present study.
- *Hyborhinus kallarensis*: it clearly seems as if *l'* is on the antaxial side of the tibia in the drawing (depending on the aspect of the drawing facing towards the reader), however, this is not mentioned in the descriptive text of Mohanasundaram (1986). For the present study the character state "displaced to the outer side of tibia" is assigned to this species, but it may be based on a drawing error.
- *Neoacaphyllisa lithocarpi*: Kuang & Hong (1989) described *l'* as being on the mesal surface of the tibia. This might indicate that the seta is on the inner or "middle" surface of the tibia, but in

the drawing it seems that it might be on the antaxial or outer aspect of the tibia, and because this species is reportedly close to *Acaphyllisa*, in which this seta is inserted on the antaxial aspect, the state "displaced to the outer side of the tibia" is assigned to this species for the present study.

47. Leg I: seta *l'* – vertical position:

0 = near apical (distal) margin (less than quarter tibial length from distal margin)
1 = at about distal quarter
2 = at distal third
3 = on about middle (half) of tibia
4 = at basal third
5 = at basal quarter
6 = near proximal (basal) margin (less than a quarter from basal margin)

In *O. stepheni* (Fig. 4.1) and *M. yemensis* the tibial seta in the position of seta *l'* and *d* respectively is on the distal half of the tibia. In this case it is very important to determine the real homology of the setae, and in having trouble doing so, it renders the character ambiguous. In the Eriophyoidea the position of *l'* along the length of the tibial segment varies from near the apical (distal) margin to near the proximal (basal) margin of the segment. The states are probably too finely divided, but it was not clear where the division between different states should be. In future, real distances from one of the margins should be used. Apart from determining this position from the descriptive drawings, it is also frequently described in the text. The text description of this character got priority in the present study. In the few Diptilomiopinae species where *l'* is present, it is mostly inserted on the distal half of the tibia with single species with the seta on the basal third. Within the Rhyncaphytoptinae it is present in varying positions along the tibial length, but mostly at the basal third, and even near the basal margin. In the majority of Eriophyidae in the present study *l'* is on about the middle of the tibia (half) and on the basal half. It is in the distal half only in a few single species, except in the Phyllocoptini where it is in the distal half for slightly more species (eight species). Within the Phytoptidae, the position is more in the middle and in the distal half within the Nalepellinae, and in the remainder of the Phytoptidae it tends to be more in the middle and in the basal half of the tibia.

48. Leg I: tibial solenidion *φ* – presence and position:

0 = present, about mid-tibial antaxial position
1 = present, in ventrodistal position
2 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 22: 0 = present; 1 = absent). Hong & Zhang (1996a) erroneously

scored this solenidion to be present in their general Tydeidae, however, it is absent in some species, such as *O. stepheni* (Ueckermann & Grout, 2007).

The hypothetical plesiomorphic condition or archetype of the Tydeidae includes only one solenidion on tibia I, namely solenidion *φ* (André, 1981b). No solenidion is present on tibia I of *O. stepheni* (Ueckermann & Grout, 2007) (Fig. 4.1). In larval and protonymphal Tetranychidae and eventually in adults of the Tetranychinae, similarly, only one solenidion, solenidion *φ*, is present on tibia I of females, however, more solenidia may be added on tibia I of males after the protonymphal stage (Lindquist, 1985). The solenidion in these species is inserted on the antaxial side of the tibia, about in the middle of the tibia.

Lindquist (1996a) proposed that the solenidion sometimes present on the tibia of Eriophyoidea mites represents solenidion *φ*, but commented that a fundamental solenidion in this almost ventral position is not present in any other Acariformes. The tibial solenidion *φ* in the Eriophyoidea is inserted ventrally and apically (distally) on the tibia. This solenidion is present only in the Phytoptidae, and in most members of all the subfamilies, except the Novophytoptinae, where it is absent in all members.

49. Leg I: tarsal solenidion *ω* – position:

0 = antaxial, about distal third of tarsus
1 = dorsal, about mid-tarsus
2 = dorsal, close to and above empodium
3 = lateral, close to empodium, on outer side of tarsus
4 = lateral, close to empodium, on inner side of tarsus
5 = ventrad of empodium

The hypothetical plesiomorphic condition or archetype of the Tydeidae includes only one solenidion on tarsus I, namely solenidion *ω* (André, 1981b). Solenidion *ω* is present about middorsally on tarsus I of *O. stepheni* (Ueckermann & Grout, 2007) (Fig. 4.1). In larval and protonymphal Tetranychidae generally only one solenidion, solenidion *ω''*, is present on tarsus I, and is autapomorphic for the Tetranychidae within the Tetranychoidea in its position closely beside seta *ft''*, to form a set of "duplex setae" (Lindquist, 1985). In the Tetranychinae three tarsal solenidia is present on tarsus I of females (Lindquist, 1985). Solenidion *ω''* is already present in the larva, and is thus the basic seta, and *ω* in the Eriophyoidea probably represents *ω''* in the Tetranychidae. Solenidion *ω''* is in a more antaxial position on the tarsus slightly distally of the middle of the tarsus (Lindquist, 1985).

Immature instars and adults of all Eriophyoidea species have a prominent solenidion, *ω*, on the tarsus of legs I and II, which is usually slightly curved, but may also be straight, and frequently is slightly enlarged apically to form a knob-like apical end. Within the Eriophyoidea the tarsal solenidion *ω* is usually inserted apically and dorsally, very close to and dorsal of the empodium. Within the following species included in the present study, it is inserted in another position: in one species, *Notaceria tetrandriae* (Eriophyinae: Aceriini) it is inserted dorsally, but proximally of the middle of the tarsus, and away from the empodium (Mohanasundaram & Muniappan, 1990), more similar to the position of solenidion *ω* in *O. stepheni*, than the other positions here recorded. In three species, *Aberoptus samoae* (Eriophyidae: Aberoptinae) and *Brevulacus reticulatus* and *Catarhinus tricholaenae* (Diptilomiopidae: Rhyncaphytoptinae), tarsal solenidion *ω* is inserted close to, but laterad (antaxial) of the empodium (Keifer, 1951; Manson, 1984a; Keifer, 1959b, respectively). In five species, *Cosella deleoni*, *Disella ilicis*, *Floracarus calonyctionis* and *Neocosella ichnocarpae* all from the Nothopodinae, and *Neocolopodacus mitragynae* in the Phyllocoptinae, tarsal solenidion *ω* is inserted close to, but laterad (paraxial) of the empodium (Keifer, 1956; 1965a; 1953; Mohanasundaram, 1981d; 1980, respectively). In two species, *Catachela machaerii* (Phyllocoptinae) and *Dechela epelis* (Cecidophyinae), tarsal solenidion *ω* is inserted close to, but ventrad of the empodium (Keifer, 1969b; 1965a, respectively).

50. Leg II: seta *bv* (Fig. 3.6a, b) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 19: 0 = present; 1 = absent).

The homology of *bv* on femur II and presence thereof in the Tydeidae including *O. stepheni* and in the Tetranychidae including *M. yemensis*, is similar to the homology for *bv* on femur I presented above, and it is present in *O. stepheni* and *M. yemensis*. Seta *bv* on femur II is present or absent in the Eriophyoidea (Table B.2). Among the Eriophyoidea species in the present study the loss of *bv* on femur II follows about the same pattern as the loss of *bv* on femur I, and they are absent in some species in all three families. Mostly when *bv* on femur I is lost, *bv* on femur II is also absent, and this is the case in species of the Novophytoptinae (Phytoptidae), Phyllocoptinae (Eriophyidae) and Diptilomiopidae. In the Nothopodinae and Eriophyinae *bv* is absent on femur I in only a few species, and in these *bv* on femur II is still present.

The character state scored for the following species, in particular, is ambiguous:

- *Pararhynacus photiniae*: the presence of *bv* on femur II could not be determined [ventral view not depicted and description by Kuang (1986a) in Chinese]. It is presumed this seta is absent, because the authors stated that the new genus and species are similar to *Rhynacus*, and seta *bv* is absent on femur II of *Rhynacus*.

51. Leg II: seta *l''* (Fig. 3.6a, b) – presence:

0 = present
1 = absent

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 20: 0 = present; 1 = absent).

Determining the homology of genual setae in the Tydeidae with setae on this segment in the Acariformes mites is difficult and ambiguous (André, 1981b, and see treatise of *l''* on genu I above). The number of setae on genu II in the Tydeidae ranges from four to none (André, 1981b). Two setae are present on genu II of *O. stepheni* (Ueckermann & Grout, 2007), and based on the setal positions in comparison with the labeled setae on leg I of *Meyerella marshalli* (André, 1980), *v'* and *l'* are present, with *l''* absent (Fig. 4.1). In Tetranychinae adults five setae are present on genu II (similar to genu I – also see discussion of *l''* on genu I above): *l'*, *l''*, *v'*, *v''* and *d* (Lindquist, 1985). By extrapolation these (and especially seta *l''* being one of the basic larval-protonymphal setae) are also present on genu II of *M. yemensis*.

In the Eriophyoidea *l''* on genu II may be present or absent (Table B.2). Among the species included in the present study *l''* on genu II is less stable, and is lost in more species in a wider range of taxa than *l''* on genu I. Seta *l''* is sometimes absent from genu I when it is absent from genu II, but in many species only *l''* on genu II is absent (Table B.2). Similar to *l''* on genu I, this seta on genu II is absent in a relatively large group of the Diptilomiopidae: in the Diptilomiopinae it is absent in all *Diptilomiopus* spp. and in species of about half of the remaining genera, and in the Rhyncaphytoptinae it is absent in four genera. It further is absent in one species of the Phytoptidae, *Retracrus johnstoni* (Sierraphytoptinae), where *l''* is absent from genu I and II (Keifer, 1965c). Seta *l''* on genu I is not absent in any of the Eriophyidae included in the present study, but *l''* on genu II is absent in some species in the Eriophyinae (*Diphytoptus nephroideus* and *Nacerimina gutierrezi*), in the Cecidophyinae (*Dechela epelis*) (Huang, 1991; Keifer 1979a; 1965a, respectively) and several species and genera in the Phyllocoptinae.

The character state scored for the following species, in particular, is ambiguous:

- *Areekulus eugeniae*: *l''* on genu II is absent in the descriptive drawing, but its absence was not mentioned in the descriptive text by Boczek & Chandrapatya (1998). It was scored "present" in the present study.

52. Leg II: seta *ft'* (Fig. 3.6a, b) – presence:

0 = present
1 = absent

The homologies of setae on the tarsi of adult Tydeidae are easy to establish, because each setiform structure retains a fixed position (André, 1981b). Seta *ft'* and *ft''* are present in the setal compliment of tarsus I and II of the Tydeidae (André, 1981b), and both setae are present in *O. stepheni* (Ueckermann & Grout, 2007) (Fig. 4.1). Setae *ft'* and *ft''* are also present in the basic tarsal setation of tarsus I and II of the Tetranychidae, and in their adults *ft'* and *ft''* may be closely associated with *ω'* and *ω''* respectively to form duplex setae (Lindquist, 1985). It is extrapolated that *ft'* and *ft''* are present on tarsus I and II of *M. yemensis*.

In the Eriophyoidea the presence of *ft'* on tarsus II is rarely recorded in the descriptive text, however, whenever it was missing in the descriptive drawing, and if the drawing could be trusted to be reasonably accurate, it was scored as "absent", in order to increase the information of this character in the present study by reducing unknowns (Table B.2). I suspect that this seta may be absent in many *Diptilomiopus* spp. and it may be of use in recovering clades within *Diptilomiopus*, or should at least be part of the diagnosis of the genus.

The character states scored for the following species, in particular, are ambiguous:

- *Neolambella ligustri* and *Areekulus eugeniae*: ft' is absent in the descriptive drawings (Lin & Kuang, 1997; Boczek & Chandrapatya, 1998, respectively) and the state "absent" was scored for these species, but the accuracy of the drawings is not certain and absence was not recorded in the descriptive text. This is the situation in most of the *Diptilomiopus* spp.

GNATHOSOMA

Presence of unique gnathosomal autapomorphies for the Eriophyoidea in comparison with all Acari and as evidence for the hypothesized monophyly of the Eriophyoidea are listed by Lindquist (1996b) and these are included as Characters 53–56.

***53. Gnathosomal stylets – presence of infracapitular (auxiliary) stylets:**

0 = without a pair of styletlike structures (infracapitular stylets) additional to and flanking styletlike chelicerae
1 = with a pair of styletlike structures (infracapitular stylets) additional to and flanking styletlike chelicerae

The infracapitular (auxiliary) stylets are flanking the cheliceral stylets ventrolaterally in all Eriophyoidea and they appear to channel secretions from salivary glands (Keifer, 1975a; Lindquist, 1996a; Nuzzaci & Alberti, 1996). Determining the homology of the infracapitular stylets with gnathosomal structures in other non-Eriophyoidea mites are problematic (Lindquist, 1996a). Similar stylets do not appear in any non-Eriophyoidea species, including *O. stepheni* and *M. yemensis*, and their presence was listed by Lindquist (1996b) as a unique autapomorphy for the Eriophyoidea in comparison with all Acari and he proposed it as evidence for the monophyly of the Eriophyoidea.

***54. Motivator between cheliceral bases – presence:**

0 = not with a motivator between the cheliceral bases activating movement of cheliceral digits
1 = with a motivator between the cheliceral bases activating movement of cheliceral digits

A small knob or motivator lies between the cheliceral bases of the Eriophyoidea and activates alternate back-and-forth boring motions of the cheliceral stylets during feeding (Keifer, 1975a; Lindquist, 1996a; Nuzzaci & Alberti, 1996). The motivator is a structure unique (autapomorphic) to this superfamily (Lindquist, 1996b), and a homologous structure is absent in non-Eriophyoidea species, including *O. stepheni* and *M. yemensis*.

***55. Apical ends of palpi – structure:**

0 = palp-claw complex
1 = simple and linear
2 = blunt and truncated

The palpi, including the apical ends, are simple and linear in the Tydeidae (André, 1981a; Evans, 1992) and likewise in *O. stepheni* (Fig. 4.1). In the Tetranychidae (including *M. yemensis*) the two distal palp segments are modified into a palp-claw complex, with an enlarged tibial seta which forms a terminal claw-like structure and a tarsus displaced to a ventral position relative to the tibia (Evans, 1992). Distally the palpi of the Eriophyoidea are blunt and truncated with a disc-like lip facilitating an adhesive function (Fig. 3.19).

***56. Palpi – shape:**

0 = free limb-like appendages somewhat below and flanking the chelicerae
1 = enfolding and supporting the cheliceral and other gnathosomal stylets

The palpi of most Acari are free limb-like appendages (Evans, 1992). In the Eriophyoidea they are enfolding and supporting the gnathosomal stylets (Nuzzaci, 1979), which is an autapomorphic character state for the Eriophyoidea (Lindquist, 1996b).

57. Modification of palp apical ends – presence:

0 = not spatulate and without triangular projections
1 = strengthened, spatulate or with triangular projections

The apical segments of the palpi of the proposed deutogyne females of *Cisaberoptus kenyae* are fused, strengthened and spatulate (Keifer, 1966c). Likewise the distal ends of the palpi of the proposed deutogyne females of *C. pretoriensis* are strengthened with triangular projections (Meyer, 1989a). Amrine *et al*. (2003) strongly proposed that the deutogyne form of the female should not influence the generic concepts of the Eriophyoidea, and they synonymized *Cisaberoptus* with *Aceria*. Including and scoring the morphology of deutogyne females in the data sets of the present study is not strictly correct. Only protogyne females of the other Eriophyoidea species were included, and thus the same form of the females are not compared. However, these projections and strengthening of the palpi are unique for these two species, and didn't influence the retrieval of relationships for other species in the analyses, apart from potentially retrieving these two species as being closely related, as well as their relationships with other Eriophyoidea species in the analyses.

58. Gnathosoma, oral stylet form:

0 = short form (Fig. 3.22a)
1 = long form (Fig. 3.22b)

All Diptilomiopidae species have the long form oral stylet, and this may be a synapomorphy for this family (Lindquist & Amrine, 1996). The character is very clearly demarcated and easily distinguishable in specimens, and published descriptive data of this character are probably in general not ambiguous.

59. Gnathosoma, cheliceral shape:

0 = greatly elongated, strongly recurved basally within a stylophore, deeply retractable
1 = relatively straight and short in comparison with palpi (Figs 3.2a, 3.22a)
2 = abruptly bent down near base and relatively long in comparison with palpi (Figs 3.2b, 3.22b)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 110, Character 10: 0 = evenly curved; 1 = abruptly curved). They scored the Tydeidae as having evenly curved chelicerae.

This character has the same character state distribution in the Eriophyoidea than the oral stylet form, but it is an entirely separate part of a complex of gnathosomal structures. If the gnathosoma is studied in more detail, both morphologically and anatomically, a suite of characters, which may not necessarily be linked, may be found and may have phylogenetic signal (also see the comparative morphological study of the gnathosoma in Chapter 3). The movable digits of the Tydeidae chelicerae are stylet-like (Nuzzaci & Di Palma, 2002) and mostly straight and shorter than the palpi, and although their detail morphological structures were not homologized with the same structures in the Eriophyoidea for the present study, they are broadly morphologically more similar than to those of the Tetranychidae. The chelicerae of the Tetranychidae are very different from those of the Eriophyoidea and the Tydeidae, consisting of relatively greatly elongated chelicerae with the bases fused to form a stylophore within which the cheliceral stylets can retract (Lindquist, 1985).

PRODORSUM

Prodorsal shield

60. Prodorsal shield shape:

0 = prodorsal shield almost absent
1 = broadly oval (shorter than wide)
2 = triangular or subtriangular, sometimes with rounded sides or more semicircular
3 = subtriangular with bulging sides
4 = subtriangular and broad
5 = inverted subtriangular
6 = circular or subcircular
7 = diamond-shaped
8 = subquadrate
9 = sub-rectangular
a = elongate oval
b = elongate triangular
c = with a prominent transverse division
d = roughly pentagonal
e = broadly T-shaped
f = about mushroom-shaped (e.g., *Cisaberoptus kenyae*)

The prodorsum of the Eriophyoidea is always covered or partly covered by a prodorsal shield. The shield shape can be broadly divided into being subcircular or subtriangular. The prodorsal shield

shape varies more than these two states, and a more variable character state definition could be constructed. The species could be scored fairly accurately, but it was difficult to define primary homologies between the shapes. The prodorsal shield shape is usually described or depicted in species descriptions, and sometimes used in the classification and differentiation of species. It is not a very reliable and accurate character, however, because the states are delineated and determined subjectively, and it may additionally be influenced by distortion caused by slide-mounting. In particular it is not always clear whether the shape of the frontal lobe also influences the evaluation of the shield shape (see descriptions of *Diptilomiopus* spp.). The character is included in the present study, because it is usually described, and sometimes used to differentiate genera.

The number of character states was restricted to 16 in the present study (the default setting in TNT). Sometimes additional character states may improve the delimitation of character states, for example for this character, the state "no shield present on the prodorsum" would have been more accurate for coding the outgroup species than the state "prodorsal shield almost absent" scored for the outgroup species as well as for *Ashieldophyes* in the present study. The character states for this character should be improved in future studies, either by increasing or decreasing states, or redefining the character and the character states entirely.

The character states scored for the following species, in particular, are ambiguous:

- *Davisella breitlowi*: the shield shape was scored code "?" (unknown), because the measurements of the shield is given as 35 µm long and 70 µm wide (twice as wide as long), but in the drawing the shield seems to be as long as, or slightly longer than wide (Davis, 1964a).
- *Neoacaphyllisa lithocarpi* and *Dicrothrix anacardii*: although there is a unique extension at the rear margin of the prodorsal shield of *N. lithocarpi* (Kuang & Hong, 1989), the shape of the anterior or "main" part of the prodorsal shield is subtriangular, and the character state "subtriangular" was assigned. The rear extension can be regarded as a separate character, but it was not scored for the present analysis because it is autapomorphic for *N. lithocarpi*, and would not be informative for retrieving relationships between Eriophyoidea taxa in the analyses. Similarly the shape of the prodorsal shield of *D. anacardii* was assigned character state "semi-circular" despite an extensive extension at the rear shield margin (Keifer, 1966c).
- *Keiferella juniperici*: the character state "subtriangular" was assigned, despite a deeply convex (towards the posterior end) rounded rear shield margin (Boczek, 1964). A similar shape is also

present in other species and was assigned as such. These states should be re-evaluated and probably re-scored.

61. Ocelli or ocellar-like areas on the prodorsal shield – presence, number and shape:

0 = present, two well delineated ocelli on each side
1 = absent, or not visible on surface cuticle
2 = present, one or two ocellar-like areas laterally on prodorsal shield

The primitive number of ocelli on the prosoma of the Actinotrichida is three pairs (Evans, 1992). Two pairs of lateral ocelli are frequently present in the Prostigmata (Evans, 1992), and in the Tetranychidae (including *M. yemensis*) two pairs of ocelli are consistently present laterally on the prodorsum (Lindquist, 1985). In the Tydeidae (including *O. stepheni*) no ocellus-like differentiated surface cuticle is visible, but so-called ocelli in the form of aggregates of pigment granules in the integument are present (Evans, 1992).

Eriophyoidea mites are characterized as being without eyes (Lindquist, 1996a). There are, however, sometimes one or two ocellus-like structures present on each posterolateral area of the prodorsal shield that may be light-receptive organs (Keifer, 1975a; Lindquist, 1996a). For the present study it is presumed the ocellus-like structures in the Eriophyoidea and the ocelli in the Tetranychidae are homologous. In the Eriophyoidea classification (Amrine *et al*., 2003) a systematic pattern in the species with these ocellus-like structures is not apparent and they occur in several species of different genera in the Phytoptidae and the Eriophyidae (Flechtmann *et al.*, 1995; Lindquist, 1996a). Among the Eriophyoidea species included in the present study, three species have ocellus-like structures: *Ectomerus anysis* (Eriophyidae: Cecidophyinae) (Keifer, 1970), *Novophytoptus stipae* (Phytoptidae: Novophytoptinae) (Keifer, 1962d) and *Palmiphytoptus oculatus* (Phytoptidae: Sierraphytoptinae) (Navia & Flechtmann, 2002). It will be an improvement to divide this character in future studies into two or more characters: ocelli or ocellar-like areas present or absent, and a second character to score the shape of these, and another character to score the number of ocelli present. For the latter two characters for those species with these structures absent, the score will be "not applicable".

Characters 62-66. The prodorsal shield may have an anteromedian extension "frontal lobe", "anterior lobe" or "prodorsal shield lobe" (the term "frontal lobe" was preferred by Amrine (1996) and is used in the present study). The presence or absence of the frontal lobe, together with other frontal lobe and opisthosomal characteristics, is significant at the subfamily, tribe and genus level of the present Eriophyoidea classification (Lindquist & Amrine, 1996; Amrine *et al.*, 2003). A well-developed frontal lobe may provide rigid

support for the gnathosoma of free-living eriophyoids which feed on more exposed and thick-walled cells than species living in protected areas like galls (Shevchenko, 1970). Some characteristics of the frontal lobe, e.g., the presence of spines or other processes, defining genera, are regarded as being trivial by some authors (Lindquist & Amrine, 1996). The definition and scoring of all characters regarding the frontal lobe should be improved in future studies.

62. Frontal lobe (Figs 3.2, 3.4) – presence and shape:

0 = absent
1 = short or indistinct (not reaching across cheliceral bases)
2 = present
3 = absent, shield with deep invagination

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 5: 0 = absent; 1 = present). They scored the frontal lobe as being absent in the Tydeidae.

Interpretation, delimitation of character states, scoring and subsequent coding is highly subjective and ambiguous for this character. In practical taxonomy (description, classification and identification) of Eriophyoidea the frontal shield lobe is considered present when it is extending across the motivator or bases of the chelicerae (Amrine *et al*., 2003; Amrine, *pers. comm*.). For determining homologies this is an artificial delimitation, because some *Aceria* and *Diptilomiopus* spp., and species of many other genera described and even depicted without a frontal lobe, clearly possesses a structure that is homologous with other conventionally recognized frontal lobes, particularly when studied with SEM (see Chapter 3).

The frontal lobes of species scored as character state “short or indistinct” actually groups two types of frontal lobes which are not homologous: a thin, apparently flexible lobe e.g., in *Diptilomiopus*, *Aceria* and *Eriophyes* spp. and a short but more thick and rigid lobe, e.g., in *Cecidophyes* spp. They have the characteristic in common that their frontal lobes are not extending across the cheliceral bases and motivator. Additionally the differentiation of this state from the state where the frontal lobe is present is subjective. This character must be carefully redefined, using e.g. SEM studies to determine true primary homologies between the frontal lobe characteristics.

The character states scored for the following species, in particular, are ambiguous:

- *Davisella breitlowi*: in the text, the frontal lobe is described as being absent (“dorsal shield not projecting over rostral base”), and a frontal lobe does not seem to be present in the

drawing of the lateral aspect, however, in the dorsal view drawing (Davis, 1964a), it seems that the prodorsal shield may overhang the gnathosoma anteriorly. The frontal lobe is scored "absent" for this species in the present study.

- Although *Hyborhinus kallarensis* is described as having a short projection of the shield over the gnathosomal base (Mohanasundaram, 1986) similar to *Catarhinus*, in the dorsal view drawing the anterior edge of the shield and its possible frontal lobe does not resemble that of *Catarhinus*, and seems more similar to *Hoderus roseus*, in which the frontal lobe was described as being absent. The frontal shield is scored as "absent" for this species in the present study.
- The recorded presence of the frontal lobe in *Rhinophytoptus concinnus* and *Rhyncaphytoptus ficifoliae* (Liro, 1943; Keifer, 1939a, respectively) is ambiguous and particularly based on subjective interpretation. Laterally it seems that no appreciable lobe is present, however, dorsally, and in line with the robustness of the body, it seems that the prodorsal shield is extending across the cheliceral bases. It was scored as being "present" for these two species in the present study.

63. Frontal lobe – flexibility:

1 = thin and flexible
2 = rigid
3 = absent, shield with deep invagination

This character of the frontal lobe is taxonomically important, but as defined here it overlaps somewhat with the previous character. The character definition should be improved. The frontal lobe is usually more thin and flexible in non-vagrant species, and it is this type of frontal lobe that is frequently recorded as absent, when it is present. For example, when a frontal lobe was recorded or depicted as being present in a *Diptilomiopus* sp. it is presumed to be thin and flexible, similar to the three new species from South Africa, where the lobes are barely visible studying slide-mounted specimens, but clearly present in SEM images (Appendix M). There is a possibility that all *Diptilomiopus* spp. may have a frontal lobe similar to the three new species, but that it was not detected by the authors. A more rigid and extensive frontal lobe is usually present in vagrant species, e.g., in the Phyllocoptinae. The scoring is highly ambiguous for this character.

64. Frontal lobe – shape of apical edge:

1 = blunt and rounded
2 = blunt and rounded, but narrow in shape (e.g., when lobe is more triangular)
3 = blunt and rounded with irregular edge
4 = sharply pointed
5 = spine-like

6 = square with rounded corners
7 = rectangular anterior lobe with indentation
8 = acuminate, but not sharply pointed
9 = small indentation
a = broad, clear indentation with broad lobes
b = fine, slender lateral extensions
c = short, bilobed with small central triangle

Similar to previous characters of the frontal lobe, this character is also subjectively and ambiguously described and scored. In the present study the state was usually determined on the descriptive drawings. It is used in the Eriophyoidea classification usually at genus level, for example, the frontal lobe is sharply pointed in *Aculops* spp., and more rounded in *Aculus* spp. (both of the Phyllocoptinae), and this is essentially the only characteristic differentiating these two genera (Amrine *et al*., 2003). The character has potential to be phylogenetically informative, but its definition should be improved, primarily by studying frontal lobes more carefully, and in their true and natural state as far as possible.

65. Frontal lobe or shield – presence and number of spines on anterior edge:

0 = absent
1 = one spine present
2 = two spines present
3 = three spines present
4 = four spines present
5 = with several tooth-like projections on apex

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 109, Character 6: 0 = absent; 1 = present).

It is uncertain whether each spine present in one species is homologous with a spine present in another species at the level of preciseness of morphological study generally undertaken for taxonomy. A more reliable determination of primary homology might be possible incorporating careful comparative morphological, anatomical and ontological study. This character is thus ambiguous, but it is used as such in Eriophyoidea taxonomy.

****66. Frontal lobe – presence of one slender projecting filament:**

0 = absent
1 = present

The anterior edge of the frontal lobe of *Acarhynchus filamentus* (Diptilomiopinae) has a filament curving down in front of the gnathosoma (Keifer, 1959b), and this character state is autapomorphic

for this species in the present analyses. It is used in the key to Eriophyoidea genera (Amrine *et al*., 2003) to key to this genus and species.

Prodorsal shield ornamentation

The prodorsum is the dorsal surface of the anterior region or prosoma of mite bodies. The prodorsum in the Eriophyoidea is easily distinguishable from the opisthosoma (Figs 3.2, 3.3) because it lacks the transverse annuli or other transverse partitions of the opisthosoma and is always covered by a shield, named the "shield", "dorsal shield", "cephalothoracic shield", "propodosomal shield" and "anterior shield" in the Eriophyoidea literature (Lindquist, 1996a).

67. Prodorsal shield ornamentation – presence:

0 = prodorsal shield similar to that of the Eriophyoidea absent
1 = ornamentation absent (prodorsal shield essentially smooth)
2 = absent centrally, ornamented along edges
3 = faint, obscure or virtually unornamented
4 = ornamentation present

A prodorsal shield similar to that in the Eriophyoidea is not present in *O. stepheni* (Fig. 4.1) and *M. yemensis* (Fig. 4.2). Their prodorsums are covered with striae similar to striae on the remainder of the body.

The prodorsal shield in the Eriophyoidea may be smooth or nearly smooth, or it may be ornamented (Figs 3.3a–c) with various markings and ridges forming an essentially species distinctive pattern, although it may have more or less intraspecific variation, depending on the species. It may lend itself to be regarded as the "finger print" of a species (J.W. Amrine Jr., *pers. comm*.). These markings may in part reflect the pattern or position of muscle insertions (Lindquist, 1996a), and may also provide a framework of strength to the shield (Shevchenko, 1970). The scoring of this character was subjective, particularly when the prodorsal shield is smooth or nearly smooth, in comparison with faintly or sparsely ornamented.

IDIOSOMA

***68. Opisthosomal lyrifissures (cupules or slit organs) – presence:**

0 = present
1 = absent

Opisthosomal lyrifissures are widely distributed in the Arachnida, and are mechanoreceptors measuring strains or loads induced by muscular activity, substrate vibrations and haemolymph pressure (Evans, 1992). The distribution of cuticular organules like lyrifissures and setae are often used as indicators of segmentation (Evans, 1992). Lyrifissures are present in the Tydeidae, including *O. stepheni*, and in the Tetranychidae, including *M. yemensis*, but are absent in the Eriophyoidea.

***69. Opisthosoma of female caudal rear end – shape:**

0 = rounded and without adhesive anal structure
1 = acuminate with adhesive anal structures

The opisthosoma of the Eriophyoidea is more or less acuminate caudally and the rear ends in two adhesive lobe-like structures (Fig. 3.2).

Opisthosomal shape and microtuberculation

70. Body shape:

0 = varying from rounded to oval (e.g., Tetranychidae)
1 = vermiform (worm-like) (e.g., *Phytoptus* and *Aceria* spp.)
2 = cylindrical (e.g., *Austracus havrylenkonis* and *Novophytoptus rostratae*)
3 = vermiform, elongated (e.g., *Cecidodectes euzonus* and *Pentasetacus araucaria*)
4 = vermiform, extremely elongated (e.g., *Novophytoptus stipae* and *Scoletoptus duvernoiae*)
5 = fusiform, medium thick to "fat", with or without narrower rear end (e.g., *Africus psydraxae*, *Arectus bidwillius* and most *Diptilomiopus* spp.)
6 = fusiform, elongated, medium thick (e.g., *Aculus* and *Abacarus* spp.)
7 = fusiform, flattened (e.g., *Anthocoptes gutierreziae* and *Calepitrimerus cariniferus*)
8 = fusiform, extremely flattened (e.g., *Setoptus jonesi* and *Tergilatus sparsus*)
9 = fusiform, very long (e.g., *Notostrix attenuata* and *Ashieldophyes pennadamensis*)
a = fusiform, broad anteriorly, very narrow tail (e.g., *Nothacus tuberculatus*)
b = fusiform, flattened, narrow tail (e.g., *Aberoptus samoae*)

This character was previously used in analyzing the phylogeny of the Eriophyoidea [Hong & Zhang, 1996a, p. 110, Character 9: 0 = worm-like; 1 = fusiform (spindle-shaped)]. They scored the character in the Tydeidae as being worm-like, which is incorrect.

Similar to most mite species, the body shape of the Tenuipalpidae (including *O. stepheni*) and the Tetranychidae (including *M. yemensis*) is about rounded to oval (Figs 4.1, 4.2). Eriophyoidea mites by and large have a worm-like shape due to their elongated opisthosoma (Fig. 3.2). The

more specific body shape of species, genera or higher groupings is generally described as vermiform (worm-like) (Fig. 3.2a) or fusiform (spindle-shaped) (Fig. 3.2b). Vermiform species have a more elongated, flexible body and is more characteristic of non-vagrant species living in sheltered spaces (e.g., in buds, galls, erinea and under leaf sheaths). Fusiform species have a less elongated body, can be arched dorsally, and often with fewer, thicker and less flexible annuli and other structures dorsally, and is more associated with vagrant species occupying exposed habitats. In some aspects body shape is thus probably heavily influenced by the habitat a species occupies.

When the body shapes are more closely scrutinized and compared, however, many more subgroups of shapes can be distinguished than the two main shapes mentioned above. In the present study body shape has been divided in ten states for the Eriophyoidea, but this is a very preliminary definition of the character, and it should be studied more closely to properly define and demarcate states. For example, states vermiform, elongated vermiform and extremely elongated vermiform may be homologous in shape to each other and rather differentiated in body length (another character), however, there is a difference in shape due to difference in length, thus they were coded separately.

Although quite accurate in the extreme shapes, determining body shape is subjective. The problem of objectivity and standardization is further exacerbated by distortion of body shape in slide-mounted specimens. When determining states from published descriptions, schematic or semi-schematic drawings may not truly portray body shape, and interpretation of shape by the descriptor is also subjective. e.g., *Phyllocoptruta oleivora*: in the descriptive drawing by Keifer (1938a) one may describe the shape from dorsal and lateral views as “fusiform fat”, and later in additional drawings of the lateral view of this species (Keifer, 1952b) the shape could be scored as “fusiform flat”.

Body shape, together with other body characteristics, however, is presently an important character in the higher classification of the Eriophyoidea and it is included in the present study, despite the subjectivity and ambiguity, also to evaluate the phylogenetic signal in the character.

The character states scored for the following species, in particular, are ambiguous:

- *Bakeriella ocimis*: body shape is somewhat similar to that of *Diptilomiopus* spp. (“fusiform, medium thick to fat”) with a more rounded body in transverse section with a broad anterior part narrowing quite steeply to the rear in lateral view (Chakrabarti & Mondal, 1982), however, the dorsal aspect is fairly rigid and flatter than in e.g., *Diptilomiopus* spp. and

character state "fusiform, flattened", has been assigned to this species. The ventral aspect of the body depicted, could be expanded more, away from the dorsum, than natural, due to slide-mounting. A new state could possibly be considered in future for this shape.

- *Pentaporca taiwanensis*: body shape is described as spindle-form (Huang & Boczek, 1996), but it is impossible to determine the exact fusiform shape from the descriptive drawings. For the present study it has been decided to score it as "fusiform, medium thick to fat", because in the parts depicted, the mite seems to be more rounded.
- *Pararhynacus photinae*: this species was scored the state "fusiform, broad anteriorly, very narrow tail", but it could possibly be the style of the drawing by Kuang (1986a), and the shape may be "fusiform fat", similar to many species in the Diptilomiopinae, including most of the *Diptilomiopus* spp.
- *Euterpia fissa*: body shape is described as "fusiform" (Navia & Flechtmann, 2005), but based on the body composition (as depicted in the drawing of the ventral aspect) being similar to that of *Tergilatus sparsus*, particularly in the extension of the lateral areas alongside the ventral annuli, this species may be extremely flattened, and the state "fusiform, extremely flattened" was assigned to it.
- *Neolambella ligustri*: body shape in lateral view was not depicted by Lin & Kuang (1997), but it is presumed to be more "fat" than flattened, because this group of mites in possibly closely related genera all seem to have in general about the same body shape than most *Diptilomiopus* spp.
- *Fragariocoptes setiger*: body shape was depicted in the original description by Nalepa (1894) as being elongated fusiform, but in the redescription by Boczek (1964) and Roivainen (1951), it was depicted as closer to short fusiform and slightly flattened dorsoventrally. To allow for both shapes until the exact shape and variation therein has been sorted out, the states "fusiform, elongated, medium thick" and "fusiform, flattened" were assigned to it.
- *Diptilomiopus camarae*: body shape was described as "worm-like" (Mohanasundaram, 1981b), however, based on the descriptive drawings, the shape rather seems to be fusiform, but additionally elongated, and the state "fusiform, elongated, medium thick" was assigned to it.

***71. Opisthosoma – presence of annuli:**

0 = without annuli
1 = with annuli

The body surface of the Tenuipalpidae (including *O. stepheni*) and the Tetranychidae (including *M. yemensis*) is striated (Figs 4.1, 4.2), but does not have annuli homologous with the series of transverse superficial rings or annuli present in all active instars of Eriophyoidea mites. These

annuli in the Eriophyoidea encircle the body entirely (Fig. 3.2). In the present study this is an autapomorphic character state for the Eriophyoidea, but similar annuli are found in two other mite groups living in minute spaces, namely the Demodicidae (living in hair follicles and similar habitats on mammalian hosts) and the Nematalycoidea (living in tightly confined spaces in the soil) (Krantz, 1978). Lindquist (1996b) attributed the presence of similar annuli, as well as some other characteristics that are similar between these three groups as convergent or parallel development of characters in response to miniaturization and living in extremely small, confined spaces.

72. Opisthosoma dorsoventral differentiation; annuli presence, number and appearance (Fig. 3.2):

0 = annuli absent
1 = subequal and similar in appearance, dorsally and ventrally (Fig. 3.2a)
2 = subequal, differentiated in appearance dorsally and ventrally
3 = subequal, numerous, and visibly narrower than usually found in the Eriophyoidea
4 = subequal or equal in count, but broader than usually found in the Eriophyoidea
5 = differentiated into slightly broader dorsal annuli and narrower ventral annuli
6 = clearly differentiated into broader dorsal annuli and narrower ventral annuli (Fig. 3.2b)
7 = dorsal annuli extremely broader than ventral annuli
8 = variably different (e.g., *Paraphytoptus*)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 114, Character 28: 0 = absent; 1 = differentiates into broader dorsal annuli [tergites] and narrower ventral annuli [sternites]).

The body surface of the Tenuipalpidae (including *O. stepheni*) and the Tetranychidae (including *M. yemensis*) does not have annuli homologous with the annuli present in all active instars of all Eriophyoidea mites (see Character 71), and were scored “annuli absent”. Annuli in the immature stages (larva and nymph) of the Eriophyoidea are usually numerous, similar in form from anterior to posterior body regions, and is very little, if at all, differentiated in shape and number dorsally and ventrally (Lindquist, 1996a). In adults the annuli shapes can be divided in about two major forms that are mostly strongly correlated with the habitat and living conditions of the mites (Lindquist, 1996a). The species living in more sheltered and enclosed spaces e.g., in galls, usually retain a more vermiform body, with relatively numerous annuli differentiated very little or not at all from the anterior to the posterior end of the body, and annuli are subequal in number and not differentiated in shape dorsally and ventrally (Fig. 3.2a). The group of species living exposed on e.g., leaf surfaces, or more fusiform mites, usually has a relatively shorter body, with annuli differentiated dorsoventrally to varying degrees with broader, fewer, more robust, thicker and less

flexible dorsal annuli (previously named tergites), with the ventral annuli (previously named sternites) remaining narrower and more flexible (Fig. 3.2b). A conspicuous example of these two different forms can be seen in *Paraphytoptus* spp. which lives with the front end sheltered in erineum, and the rear end usually exposed outside the erineum. In this genus the front end is similar to a vermiform mite, and the rear end similar to the exposed or fusiform mites (Keifer, 1975a).

On closer inspection the differentiation of annuli can be divided in more states than merely the two major groups. In the present study the character has seven states for the Eriophyoidea, but this is only a preliminary division, and the states should be scrutinized and their definition and demarcation should be improved. Especially the state "variably different" is not defining a specific morphological change in morphology, but rather is a category where all shapes that can not be defined by the other states, are "dumped".

The character states scored for the following species, in particular, are ambiguous:

- *Neolambella ligustri*: the dorsoventral differentiation of the annuli was not described, neither specifically depicted in the description of this species by Lin & Kuang (1997), but based on the group of mites to which this species is similar (*Diptilomiopus*-like species in the Diptilomiopinae) and the relative width of the annuli in the partial dorsal and ventral view drawings, it was scored "differentiated into slightly broader dorsal annuli and narrower ventral annuli".
- *Neodiptilomiopus vishakantai*: dorsal and ventral annuli may be subequal, rather than differentiated. There are only 5 more ventral than dorsal annuli (Mohanasundaram, 1982b). The species was scored "differentiated into slightly broader dorsal annuli and narrower ventral annuli".
- *Pararhynacus photiniae*: the differentiation between the dorsal and ventral annuli could not be determined from the description, Kuang (1986a), however, stated that *Pararhynacus* is similar to *Rhynacus*, and the annuli are slightly differentiated in *Rhynacus* and was scored as such for *Pararhynacus*.
- *Indonotolox sudarsani*: the annuli of *Indonotolox* were described to have the dorsal annuli broader than ventral annuli; however, in the type species of the genus, *Indonotolox sudarsani*, described in the same article, the annuli were described as being equal in number dorsally and ventrally. In the lateral view drawing the annuli seem broader than generally found in the Eriophyoidea with subequal annuli dorsoventrally, and in the ventral view drawing the annuli

seem to be narrower (Ghosh & Chakrabarti, 1982). The annuli for this species were scored as "subequal or equal in count, but broader than usually found in the Eriophyoidea".

73. Lateral extensions on opisthosomal dorsal annuli – presence and shape:

0 = without lateral extensions or lobes
1 = very slight lateral projection (no demarcation line laterally)
2 = with slight lateral projection (in lateral view, dorsal annuli separated from ventral annuli by some sort of demarcation); the extend of lateral projection not always clear, some of these species are not in Tegonotini
3 = with clear lateral extensions or lobes (currently defining state for Tegonotini)
4 = small spine-like lobes on margin between dorsal and ventral annuli
5 = extensive lateral lobes, also present dorsally
6 = ventro-lateral ridges forming grooves
7 = lateral lobes uneven, extending more from some annuli

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 114, Character 29: 0 = not extended laterally; 1 = extended laterally or with indentations).

Particularly in species living exposed and with the body more fusiform and dorsal annuli broader and more rigid than ventral annuli, the dorsal annuli may be differentiated into various structures. Some of these modifications are the extension of some or all dorsal annuli laterally into lobes of various shapes, thickenings and the consolidation of some dorsal annuli into plates (Lindquist and Amrine, 1996), and these types of modifications presently largely define the tribe Tegonotini (Eriophyidae: Phyllocoptinae) (Lindquist and Amrine, 1996). I found the distinction between the presences or absences of lateral lobes unclear and subjective, e.g., compare *Acarelliptus cocciformis* (Phyllocoptini) (Keifer, 1940b) with *Tegonotus mangiferae* (Tegonotini) (Keifer, 1946). The lateral lobes of some *Tegonotus* and *Shevtchenkella* spp. are even less pronounced than in the latter two species. The scoring of this character is subjective, and influenced by the interpretation of various descriptors, and additionally the character should be redefined.

The character state scored for the following species, in particular, is ambiguous:

- *Neopropilus jatrophus*: presence of lateral lobes in the species was not mentioned in the description by Huang (1992), and the presence thereof in the SEM images provided with the description, and descriptive drawings by Amrine *et al.* (2003) are not conclusive, however, the dorsal annuli seem to extend somewhat laterally, and the state "with slight projection" was scored for this species in the present study.

74. Opisthosoma: ridge(s) and/or furrow(s) – presence and some shapes:

0 = absent
1 = present
2 = absent, except for some rear dorsal annuli which are higher than the others
3 = some anterior dorsal annuli fused into elaborate dorsal structures
4 = with large lobes dorsally
5 = dorsal annuli undulate, forming about regular rows of lobes, or "ridges"
6 = deep cleft behind prodorsal shield, first two dorsal anterior annuli raised

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 23: 0 = absent; 1 = present).

The dorsal annuli of the Eriophyoidea may have various forms of ridges, lobes and troughs, and similar to Character 73 (lateral extensions or lobes) it largely occurs in species living exposed and with the body more fusiform and with dorsal annuli broader and more rigid than ventral annuli. The presence and shape of dorsal ridges and troughs or furrows are used very predominantly in the classification of the Eriophyoidea to define particularly genera. Evaluation and very detailed, precise demarcation of these modifications in separate discrete states and homologous structures may not be so important in classical classification and identification, but is crucial for studying phylogenetic relationships. Particularly in this character as defined here, a large amount of variation is grouped and masked within a relatively few states of one character. The detailed variation of these body modifications is thus largely ignored in the present study. It was decided not to score the different types of ridges and furrows and other body modifications in detail, because the definition of homologies and states is complex, subjective and ambiguous, and I didn't want to complicate the data set with ambiguous data any more than it already is.

Ridges and troughs are very susceptible to distortion in slide-mounted species, however, and particularly when the ridges or troughs are less pronounced (weak), they may be overlooked or interpreted wrongly. For example in some *Diptilomiopus* spp. (like *Diptilomiopus aralioidus*, *D. alagarmalaiensis*, and *D. malloti*) (Huang, 2006; Mohanasundaram, 1986; Wei & Feng, 1999, respectively) the presence of ridges or troughs are neither described nor depicted, however, for the present study it is presumed ridges are present in *Diptilomiopus*, since they are so weak and subtle, that they could easily have been overlooked. However, in a parallel study in progress (C. Craemer, *unpubl. data*) including phylogenetic analyses of *Diptilomiopus* spp., the ridges and furrows are described and coded in more detail, and some of the problems with interpretation, and state definition and scoring are discussed there.

The character states scored for the following species, in particular, are ambiguous:

- *Asetadiptacus emiliae*: ridges and furrows were scored as "absent", and this decision is substantiated by the couplet decision which key out to this species, "dorsal opisthosoma evenly rounded" (Amrine *et al*., 2003). The species was specifically described as having the opisthosoma without any ridges or furrows; and this state was used by Carmona (1970) to differentiate *Asetadiptacus* from *Diptacus*. In the descriptive drawings (Carmona, 1970), however, it seems that a slight middorsal ridge, subdorsal furrows and sublateral ridges may be present, similar to those in most *Diptilomiopus* spp.
- *Duabangus chiangmai*: only two weak lateral ridges are present low down on the body in the descriptive drawing by Chandrapatya & Boczek (2000b), but the dorsum is rather evenly rounded. The species was scored to have ridges, but it is ambiguous.
- The body shape, regarding presence of ridges and/or troughs, is not described for *Diptilomiopus maduraiensis* and *D. thangaveli* and in the descriptive drawing the body seems to be evenly rounded without any ridges or troughs (Mohanasundaram, 1986a; 1983c, respectively). However, the species may have a slight middorsal ridge possibly flanked by troughs forming lateral ridges, similar to most other *Diptilomiopus* spp.; these may have been obscured by the mounting process. Ridges and troughs in these two species were scored to be absent. Similarly, the body shape regarding presence of ridges and/or troughs was not described in the text description of *Diptilomiopus ulmivagrans* but in the drawing the body seems to have a slight middorsal ridge (Mohanasundaram, 1984); this is similar to what is found in most other *Diptilomiopus* spp. The latter species was scored as if it has a ridge.

In their phylogenetic analysis of the Diptilomiopinae Hong & Zhang (1997) coded ridges or furrows (troughs) on the opisthosoma present for the genus *Diptilomiopus*. It may not be that all species currently assigned to *Diptilomiopus* have ridges and/or furrows. Furthermore, the shape and presence of ridges and furrows of *Diptilomiopus* spp. vary, and if sufficiently studied and described in more detail, differences may define different groupings within the genus that may even be similar to genus level groupings in other Eriophyoidea taxa. These differences are usually very subtle, though, and one might only be able to score the character states from SEM images.

75. Fusion of rear dorsal annuli – presence:

0 = without annuli
1 = not fused
2 = fused

The annuli and microtubercles in the rear portion of the opisthosoma, from the opisthosomal *f* to the anal lobes, in most species are different from the remainder of the opisthosoma, but in some species they are the same. The microtubercles ventrally on the annuli in this area are distinct,

elongated and rib-like in most species (Keifer, 1966d). Keifer (1966d) named this part of the opisthosoma the telosome for descriptive purposes, but the use of the term is discouraged (Amrine *et al*., 2003). Although the telosome is an artificial region (Lindquist, 1996a), the term is useful in descriptions. For the present study it is presumed there is not a region homologous with the telosome in the Tenuipalpidae (including *O. stepheni*) and the Tetranychidae (including *M. yemensis*).

The dorsal annuli beyond *f* up to the anal lobes are characteristically fused in a few species in the Phytoptidae, and four of these are included in the present study: *Neopropilus jatrophus*, *Propilus gentyi* and *Retracrus johnstoni* in the Sierraphytoptinae and *Prothrix aboula* in the Prothricinae (Huang, 1992; Keifer, 1975d; 1965c; 1965a, alternatively). When this opisthosomal region is not described neither depicted for a species, it is presumed the annuli are not fused, because they are not usually fused within the Eriophyoidea. If they were fused, it is presumed the author(s) would have recorded it, because it is a conspicuous character state.

76. Microtubercles on dorsal annuli – presence:

0 = without microtubercles (mostly smooth)
1 = entirely microtuberculated
2 = entire but mostly obscure or faint
3 = smooth with few scattered microtubercles in sparse clumps (laterally and/or middorsally) (see *Chiangmaia longifolii*) or with clumps or spots with microtubercles (see *Duabangus chiangmai*)
4 = smooth with microtubercles on ridges: lateral (see *D. stephanus*); relatively large spines on ridges (see *Pentamerus rhamnicroceae*)
5 = faint but clear on lateral ridges (see *Notallus nerii*)
6 = with central area smooth, and microtuberculated laterally
7 = mostly smooth with few microtubercles laterally and caudally (see *D. knorri*)
8 = with faint or no microtubercles anteriorly, clearly microtuberculated towards rear (see *D. davisi*)
9 = microtuberculated anteriorly, rear annuli smooth (see *Indosetacus rhinacanthi*, *Arectus bidwillius*) or smooth with microtubercles mediodorsally on anterior annuli
a = smooth with microtubercles on the first few anterior and posterior annuli (see *Scoletoptus duvernoiae*)
b = elongated or near elongated microtubercles aligned in longitudinal rows
c = punctuate becoming smoother towards rear (see *Porosus monosporae*)
d = punctuate dorsally, elongated ridges laterally, intercepted by smooth annuli (see *Cymeda zealandica*)
e = crossed by fine broken lines (see *Peralox insolita*)
f = elongated fissures (see *Rhinotergum schestovici*)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 115, Character 34: 0 = absent; 1 = present). Hong & Zhang (1996a) simply coded the dorsal annuli as smooth or with microtubercles present. The presence or absence of

microtubercles are more complex, though, ranging from dorsal annuli entirely without microtubercles ("smooth") to the dorsal annuli entirely with microtubercles.

Microtubercles are rounded, ridge-, spine-like or other shaped protuberances usually in single rows on or along the annuli margins when present in Eriophyoidea species. They usually occur on the ventral annuli about uniformly, but may be sparser, of a different shape or absent on the dorsal annuli. The presence and other characteristics, including shape and position, of the microtubercles are usually used at species level. Similar to many other characteristics of the body, the presence and density of microtubercles on mainly the dorsal annuli correspond with the lifestyle of the species. More vermiform, non-vagrant species, generally have numerous and well-developed microtubercles, also dorsally, and more fusiform vagrant species, tends to have less or no microtubercles, especially dorsally. Microtubercles are probably correlated with water loss and mobility (Lindquist, 1996a).

The homology between the microtubercles found in the Eriophyoidea and the lobes occurring on the striae of the Tenuipalpidae (including *O. stepheni*) and the Tetranychidae (including *M. yemensis*) could not be researched in depth for the present study, but superficially it seemed that they may possibly be homologous, and character states were assigned as such. Thus microtubercles were designated as being present on the entire dorsal surface of *O. stepheni* and *M. yemensis*.

Similar to most of the more complex characters of the Eriophyoidea, the definition of this character, particularly for use in phylogenetic analyses, needs to be improved. It was initially defined with more than 16 states, but 16 were eventually chosen to be the maximum number of states, and some states had to be combined with others. The states are thus not optimally differentiated. The definition of these characteristics might be improved by first dividing the dorsum into homologous regions, and treating each region as a separate character with defined character states.

The character states scored for the following species, in particular, are ambiguous:

- *Proneotegonotus antiquorae*: the character was initially scored as "smooth, faint longitudinal lines on first enlarged dorsal annulus", but for the analyses the number of states for this character had to be reduced, and the state for this species was changed to "without microtubercles; mostly smooth". Although longitudinal lines occur on the first enlarged dorsal annulus (Mohanasundaram, 1983a), these longitudinal lines are probably not microtubercles.

- *Diptilomiopus azadirachtae*, *D. guajavae*, *D. riciniae* and *D. swieteniae*: dorsal annuli were described as smooth, respectively by Boczek & Chandrapatya (1992b), Mohanasundaram (1985), Boczek & Chandrapatya (2002), and Chandrapatya & Boczek (1998). In all or at least one of the descriptive drawings of each of these species, however, microtubercles are clearly depicted on the dorsal annuli, and species were scored to have microtuberculated dorsal annuli.
- *D. coreiae* and *D. melastomae*: dorsal annuli were described as being smooth (Chandrapatya & Boczek, 2002b; Boczek & Chandrapatya, 2002, respectively), but a few scattered microtubercles were clearly depicted laterally on the dorsal annuli, and the species were scored as "smooth with few scattered microtubercles in sparse clumps (laterally and/or middorsally)".
- The dorsal annuli were recorded in the descriptive text as smooth (Mohanasundaram, 1981b) in *D. camarae*, however, fine tubercles are depicted dorsally on caudal annuli, and plausibly also for the lower lateral parts of the dorsal annuli, and it was scored "mostly smooth with few microtubercles laterally and caudally" similarly to *D. knorri*.
- The character was not described for *Diptilomiopus aralioidus*, *D. commuiae*, *D. cumingis*, *D. elliptus*, *D. maduraiensis*, *D. perfectus*, and *D. championi* (description of *D. septimus*) (Huang, 2006; 2001b; 2001a; 2001d; Mohanasundaram, 1986; Huang, 2001c, respectively), but the dorsal annuli were depicted without microtubercles in the accompanying descriptive drawings, and the microtubercles were scored as absent. Drawings are not always accurate regarding the presence of microtubercles, since some detail, including microtubercles, are not always included in semi-schematic drawings, particularly when presented at a small scaled size.
- The dorsal annuli were described as smooth for *D. securinegus*; however, in the descriptive drawings and accompanying SEM images (Boczek & Chandrapatya, 1992a), microtubercles are clearly present on the lateral areas of the dorsal annuli, and the species was scored "with central area smooth, and microtuberculated laterally".
- *Lithocarus thomsoni*: dorsal annuli were described as smooth (Chandrapatya & Boczek, 2000c), however, in the accompanying descriptive drawing some microtubercles were depicted on some of the dorsal ridge lobes. The species was scored "smooth with microtubercles on ridges".
- Dorsal annuli of *Chiangmaia longifolii* were described in the text as smooth; however, in the descriptive drawings a few scattered microtubercles are present (Chandrapatya & Boczek, 2000c). The species was scored for the present study as "smooth with few scattered microtubercles in sparse clumps (laterally and/or middorsally)".

Secretions

77. Wax secretion – presence:

0 = absent
1 = present in adults
2 = present only in immatures

Wax, secreted by them, occurs on the bodies of some Eriophyoidea species. The wax probably adds protection against desiccation and may possibly be a deterrent against predators. The presence of other secretions e.g., a liquid globule covering the body of *Hoderus globulus* (Mohanasundaram, 1981) (Mohanasundaram, 1981e) and *Rhyncaphytoptus constrictus* (Hodgkiss, 1913) (Hodgkiss, 1930; Baker *et al*., 1996) probably with the same function as wax, was not included in the present study, but should be included in future studies. Twenty-seven of the Eriophyoidea species in the present study secrete wax, and it occurs on the adults, except in one species, *Rhyncaphytoptus ficifoliae*, where the wax is only present on the immatures (Keifer, 1939a). The wax secreting species occur in all three families, but especially in species that have a more exposed, vagrant lifestyle. The species with wax are listed in Table B.3, including the structures from which the wax is probably secreted. Extrapolated from the Eriophyoidea classification it seems that the ability to secrete wax possibly developed homoplasiously (parallel evolution) in at least three lineages.

Table B.3. List of Eriophyoidea species with wax, including their classification and structures from which the wax is probably secreted, or on which it occurs. The data were obtained from the original descriptions of the mites.

Classification		**Species**	**Structures etc.**
Phytoptidae			
Sierraphytoptinae	Mackiellini	*Retracrus johnstoni*	tubercles
Eriophyidae			
Phyllocoptinae	Acaricalini	*Cymeda zealandica*	rim
		Notacaphylla chinensiae	tubercles
		Paracaphylla streblae	covered
	Anthocoptini	*Abacarus acalyptus*	ridges
		Abacarus hystrix	ridges
		Aculodes mckenziei	powdery
		Costarectus zeyheri	tubercles
		Keiferana neolitseae	covered
		Neomesalox kallarensis	ridges
		Pentamerus rhamnicroceae	tubercles
		Porcupinotus humpae	ridges
	Calacarini	*Calacarus pulviferus*	tubercles
	Phyllocoptini	*Acamina nolinae*	ridges
Diptilomiopidae	Diptilomiopinae	*Apodiptacus cordiformis*	ridges
		Dialox stellatus	tubercles
		Diptacus sacramentae	tubercles
		Diptilomiopus artocarpae	patches
		Diptilomiopus melastomae	covered

		Duabangus chiangmai	tubercles
		Lambella cerina	ridges
		Levonga papaitongensis	covered
		Neodialox palmyrae	ridges
		Trimeroptes eleyrodiformis	ridges
	Rhyncaphytoptinae	*Asetacus madronae*	covered
		Konola hibernalis	powdery
		Rhyncaphytoptus ficifoliae	immatures

In the present study, when no wax secretion or presence of wax were reported or depicted for a species, it is presumed no wax secretions are present. The data for this character are probably riddled with errors, especially in cases where wax may be present, but has been washed off by the slide-mounting process (see Chapter 3).

The character state scored for the following species, in particular, is ambiguous:

- *Suthamus chiangmi* is described as lacking wax (Chandrapatya & Boczek, 2000a), in contrast with the wax secretion found (Manson, 1984a) in the genus *Lambella*, from which it has been differentiated. The ridges of *S. chiangmi* are depicted with thickened edges (Chandrapatya & Boczek, 2000a), and there is a possibility that the ridges may secrete wax similar to *Lambella*.

78. Wax type and secreting structures:

1 = present, thickened wax bearing ridges
2 = present, wax from tubercles
3 = broad wax rim around shield, large wax plates along body margin
4 = body covered with wax
5 = sparse wax patches
6 = wax secreting pores on dorsal body surface
7 = covered with white powdery wax

The origin and nature of wax secretions are usually not studied and described in detail to facilitate reliable hypotheses on homologies. Two features of wax secretions can be broadly defined: the origin, or organs or structures secreting wax; and the nature of the wax itself. In order to commence with some sort of analysis, it was decided to take the available information and code it into states including both or either of origin and structure, and separating e.g., a broad definition like “body covered with wax” to more detailed “wax produced from tubercles”. This is not a scientifically sound character definition, because two aspects, which may constitute two separate characters, were grouped into one character, but it is hoped that it serves as a starting point for data to be refined and added in future, with improvement of the character definition.

The character state scored for the following species, in particular, is ambiguous:

- Although the detail of wax body coverage or wax secretion was not described for *Duabangus chiangmai* by Chandrapatya & Boczek (2000b), the microtubercles in separate groups suggest that the wax may be secreted from these, and the state "wax from tubercles" was scored for this species, however, "sparse wax patches" may also be applicable.

LEGS, INCLUDING COXISTERNAL PLATES AND STERNAL AREA

Many characteristics of the legs are autapomorphic for the Eriophyoidea. It is, for example, the only mite group with only two pairs of legs in all the life stages. Some of these characters are here included.

***79. Larva with:**

0 = legs III present
1 = legs III absent

***80. Larva with:**

0 = legs IV present
1 = legs IV absent

***81. Nymphal instar(s) with:**

0 = legs III present
1 = legs III absent

***82. Nymphal instar(s) with:**

0 = legs IV present
1 = legs IV absent

***83. Adults with:**

0 = legs III present
1 = legs III absent

***84. Adults with:**

0 = legs IV present
1 = legs IV absent

***85. Legs I:**

0 = with true (paired) claws
1 = without true (paired) claws

***86. Legs II:**

0 = with true (paired) claws
1 = without true (paired) claws

***87. Legs I:**

0 = with empodia not well-developed "feather-claws"
1 = with empodium a well-developed "feather-claw"

***88. Legs II:**

0 = with empodia not well-developed "feather-claws"
1 = with empodium a well-developed "feather-claw"

***89. Coxisternal plates I:**

0 = clearly separate and not contiguous or fused medially
1 = slightly separate or contiguous or fused medially

***90. Coxisternal plates I:**

0 = not basally contiguous with coxisternal plates II
1 = contiguous basally with coxisternal plates II

***91. Larval instar:**

0 = with urstigmata between coxisternal plates I and II
1 = without urstigmata between coxisternal plates I and II

Ornamentation on coxisternal plates (Figs 3.4, 3.5)

The coxae in the Prostigmata are immovably fused to the ventral aspect of the body (Kethley, 1990). The coxal remnants are represented by coxal fields (or coxisternal plates *sensu* Lindquist, 1996a, followed in the present study) delineated by internal apodemes from which intrinsic coxal musculature originates. Usually in Eriophyoidea literature, the coxisternal plates are merely referred to as coxae, or coxal plates (Amrine *et al*., 2003).

The presence and morphology of ornamentation on coxisternal plates I and II are extensively used within the Eriophyoidea to distinguish between species. The ornamentation is frequently described in combination, without distinguishing the differences between coxisternal plates I and II, e.g., merely describing the coxisternal ornamentation as "coxae granulated". The ornamentation on coxisternal plates I and II is frequently the same type of ornamentation, but often the ornamentation is sparser on the latter, and/or a smaller area of them are covered. This causes problems and errors when the ornamentation of the two pairs of coxisternal plates is homologized

and scored as separate characters. Ornamentation on the coxisternal plates is usually described very vaguely and with disregard of true structures and detail. A line depicted on particularly coxisternal plates II can for example be either an internal apodeme, a ridge on the surface, or a folding line caused by slide-mounting. It is usually impossible to distinguish between these types of characters, both from the text description and the descriptive drawing. It is also frequently difficult to distinguish between small, rounded tubercles, and slightly elongated microtubercles, which may rather be defined as dashes. The type of detail found in ornamental structures necessary for accurate determination of homologies, e.g. on the coxisternal plates, are most accurately observable in SEM studies (Chapter 3), in combination with information from slide-mounted specimens.

92. Coxisternal plates I ornamentation – presence:

0 = unornamented (mostly smooth) (also scored when described as "virtually unornamented")
1 = faintly or slightly ornamented
2 = ornamented
3 = body striations extended on legs, including coxisternal plates

The character states scored for the following species, in particular, are ambiguous:

- The coxisternal plates of *Kaella flacourtiae* were described to have some broken lines, however, coxisternal plates I were depicted to be smooth, and the broken lines were only depicted on coxisternal plates II (Chandrapatya & Boczek, 2002b). Usually in the Eriophyoidea, coxisternal plates I are ornamented more strongly or more densely than coxisternal plates II, and it is presumed the drawing might be wrong, and coxisternal plates I and II for this species were scored "ornamented".
- The coxisternal plates of *Lithocarus thomsoni* were described to be smooth, however, in the descriptive drawing some tubercles were depicted basally on particularly coxisternal plates I (Chandrapatya & Boczek, 2000c). Coxisternal plates I was scored "slightly ornamented".
- The coxisternal plates of *Steopa bauhiniae* were described to be smooth, however, in the descriptive drawing some slight tubercles and possibly dashes are depicted on particularly coxisternal plates I (Chandrapatya & Boczek, 2001b). Coxisternal plates I was scored "slightly ornamented", and coxisternal plates II, "smooth". The description and scoring of *Suthamus chiangmi* (Chandrapatya & Boczek, 2000a) are similar.
- A score of unornamented (smooth) for coxisternal plates I and/or II of the following species is ambiguous: *Acarhis diospyrosis* (coxisternal plates described to be smooth, but single lines were depicted on them in the descriptive drawing) (Chandrapatya & Boczek, 1991c); and coxisternal plates I of *A. siamensis* were described as smooth, however, in the descriptive

drawing, one solid line was depicted about diagonally across the upper right corner of coxisternal plates I and II (Boczek & Chandrapatya, 2000).

93. Coxisternal plates II ornamentation – presence:

0 = unornamented (smooth), including virtually unornamented
1 = faintly ornamented
2 = sparsely ornamented
3 = ornamented
4 = body striations extended on legs, including coxisternal plates

The ornamentation on coxisternal plates II is frequently fainter, sparser and less defined than on coxisternal plates I, and it has generally been described less carefully and correctly than for coxisternal plates I. As previously mentioned, there are also frequently folds or underlying apodemes that may be drawn on coxisternal plates II, but which are not necessarily ornamentation on the surface. *Diptilomiopus* spp. were more extensively scored for coxisternal plate ornamentation in a phylogenetic analyses of this genus parallel to the present study, and the plates were subdivided into smaller potentially homologous parts (C. Craemer, *unpubl. data*).

The character states scored for the following species, in particular, are ambiguous:

- *Acarhis diospyrosis*: coxisternal plates were described as smooth, but single lines and dashes are unclearly depicted on the plates in the descriptive drawing (Chandrapatya & Boczek, 1991c). The character was nevertheless scored as "smooth" in the present study.
- *Diptilorhynacus dioscoreae*: the ornamentation of the coxisternal plates was described as "coxae with ornamentation of granules", however, in the descriptive drawing coxisternal plates II are unornamented, and thus without granules (Boczek & Nuzzaci, 1985), and was scored as unornamented in the present study.
- *Lithocarus thomsoni*: the coxisternal plates are described as smooth, however, in the descriptive drawing some tubercles are depicted basally on particularly coxisternal plates I (Chandrapatya & Boczek, 2000c), and the description is thus erroneous, but the ornamentation of coxisternal plates II was nevertheless scored as unornamented.
- Ornamentation on coxisternal plates II was scored as present for the following *Diptilomiopus* and other Diptilomiopinae species, because there were some marks depicted on these plates in the descriptive drawings, but the coxisternal plates may be unornamented in reality:

  D. artabotrysi
  D. assamica
  D. boueae
  D. jasminiae
  D. racemosae
  D. elaeocarpi

D. jevremovici
D. knorri
D. strebli
D. thunbergiae
Acarhis siamensis
Africus psydraxae

94. Prosternal apodeme between coxae I (Figs 3.4, 3.5) – presence:

0 = coxisternal plates I more widely separated than in the Eriophyoidea, prosternal apodeme not present, "normal' ventral area extended between coxae
1 = widely separated (see *Davisella breitlowi*, *Neocecidophyes mallotivagrans*, *Palmiphytoptus oculatus* and *Trisetacus ehmanni*)
2 = separated
3 = coxae I touching, usually with sternal apodeme clearly present
4 = sternal apodeme visibly broader than usually found in the Eriophyoidea (see *Rhynacus arctostaphyli*)
5 = totally fused centrally (or prosternal apodeme may be present but effaced – not visible as sternal line in slide-mounted specimens)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 114, Character 30: 0 = absent; 1 = present).

The prosternal apodeme (called "sternal line" in most Eriophyoidea descriptions) is an internal structure (Lindquist, 1996a). The character state definitions and scoring of this character are subjective and ambiguous. For example, the states "widely separated", "separated" and "sternal apodeme broad" may be confused in different descriptions, and may in reality be broadly the same homologous structure and state, interpreted or observed differently by different authors. For example, the approximation between coxae I of *Acarhis lepisanthis* was described by Keifer (1975d) as a "strong ridge between forecoxae", and it is probably an elevation or ridge on the surface between the coxal plates. Another example is *Asetacus madronae*: Keifer (1952a) described and depicted the approximation between coxae I as "anterior coxae with a sharp ridge between". Whether there is an internal apodeme associated with this ridge is not known, but for the present study the presence of a ridge is regarded as the presence of the prosternal apodeme. These descriptions together with the depiction thereof were interpreted, and the states were scored in the present study as "sternal apodeme visibly broader than usually in the Eriophyoidea". In *Acarhis siamensis*, however, coxae I are described as being "separated, not forming a sternum" (Boczek & Chandrapatya, 2000). One can not deduce from the descriptions and drawings whether the latter and the previous two species have strong, broad sternal apodemes or whether the coxae are separated and without an internal sternal apodeme, and whether the structures are homologous.

Trisetacus ehmanni is another example of uncertainty; Keifer (1963b) described "anterior coxae well separated by a low indistinct ridge". In the drawing the coxae seem to be separated and this

character of the species was scored in the present study as "widely separated", but the state might rather be "sternal apodeme visibly broader than usually found in the Eriophyoidea". These two states describe two different structures which are not primarily homologous. The "broad sternal apodeme" describe the presence of a certain type of sternal apodeme, while "separated coxae not touching each other" describes the absence of a sternal apodeme, with the inner margins of the coxae separated for an appreciable distance from each other. Sometimes the latter state ("separated") was interpreted in the present study as if the inner coxal margins are touching, even if for a small distance, but the presence of an internal sternal apodeme is not clear or certain e.g., in *Acathrix trymatus* (Keifer, 1962c).

Another example of possible ambiguity: when coxae I are connate medially, but no sternal apodeme is present, or apparently present, e.g., as described for *Leipothrix solidaginis* (Keifer, 1966c), no distinction was made between this state where coxae I may be merely touching without a sternal apodeme, and those species with a sternal apodeme present. These descriptions of this area were scored as "coxae I touching, usually with sternal apodeme clearly present". This mingling of possibly different structures in one state was unavoidable because the presence of an internal apodeme or not, is not well described and distinguished in a bulk of the descriptions, and can not be deduced from the descriptive drawings either. This state should be separated into more states, if the real structures are not homologous.

****95. Coxae I: sternal region – presence of lobes:**

0 = no region homologous to anterior edge of coxisternal plates in the sternal region of the Eriophyoidea
1 = anterior edge of coxisternal plates in sternal region without four lobes
2 = anterior edge of coxisternal plates in sternal region with four lobes

Four finger-like lobes are present on the anterior edge of the coxisternal region (Manson, 1984a) of *Dacundiopus stylosus*, and this character states is autapomorphic for this species. The state is used in the genus key (Amrine *et al.*, 2003) to differentiate *Dacundiopus*.

LEGS (excluding coxae) (Fig. 3.6)

****96. Tarsi of legs – presence of shovel-shaped projections:**

0 = without shovel-shaped projections on legs
1 = with shovel-shaped projections on legs

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 114, Character 27 (shovel-shaped projections on legs or triangular projections on palp apical ends): 0 = absent; 1 = present).

The shovel-shaped projections occur on the tarsi of *Aberoptus* spp., of which only *A. samoae* was included, and the character state is autapomorphic for this species in the present study. The legs of this genus are generally modified. They are stout, with shortened segments, and the empodia on legs II are large with numerous rays (Keifer, 1951).

97. Leg I – femur and genu articulation – whether fused:

0 = normally articulated
1 = division weak, almost fused
2 = not articulated, totally fused
3 = genu present, but "fused" to femur

The character states scored for the following species, in particular, are ambiguous:

- *Diptilorhynacus dioscoreae*: the fusion of the genu with the femur was not recorded in the text description, and furthermore the genu of legs I and II is present in *Diptilorhynacus*, although *l''* is absent on both legs. The genu is fused with the femur in legs I and II in the descriptive drawing (Boczek & Nuzzaci, 1985), however, and was scored as such in the present study.
- The legs of *Lithocarus* were described as six segmented, however, in the descriptive drawing of *Lithocarus thomsoni*, the type species of the genus, the femur and genu were depicted as fused (genu absent) (Chandrapatya & Boczek, 2000c). Amrine *et al*. (2003) corrected the error and the monospecific genus keys out in there key to genera by their five segmented legs, with the genu absent. The genu was scored in the present study as being fused with the femur in both legs I and II.
- Manson (1984a) described the genu and femur to be "almost fused" in *Dacundiopus*, however, in the type species (*D. stylosus*) these segments were described to be "fused" (Manson, 1984a), and in the descriptive drawing it seems that the fusion is complete. The character for this species was scored "totally fused".

****98. Leg I – division of femur:**

0 = undivided
1 = inconspicuously divided
2 = clearly divided

A divided femur is regarded to be plesiomorphic in the Acariformes (Lindquist, 1996a). The femur of *Cymeda zealandica* is clearly divided into two segments (Manson & Gerson, 1986). The femur

of *Quintalitus squamosus* was described to be inconspicuously divided (Meyer, 1989c). In the present study, states one and two are autapomorphic for each particular species. In future one could compare the homology of the divisions of the femur, and possibly amalgamate them in one state.

99. Leg I – division of tarsus – presence:

0 = undivided
1 = divided

Only three species of the Diptilomiopinae were described with tarsus I divided: *Dacundiopus stylosus, Lambella cerina* and *Levonga papaitongensis* and the character state may be a synapomorphy for these species. They were described or redescribed by Manson (1984a). Tarsus I of *Levonga caseariasis* and *L. litseae* (Chakrabarti & Pandit, 1996; Chakrabarti *et al*., 1992, respectively), both from India, is apparently not divided, however, neither of the latter two species are particularly accurately described or depicted, and the real morphology is uncertain.

100. Leg I – tibia presence, or whether fused with tarsus:

0 = present
1 = partly fused to tarsus
2 = completely fused to tarsus (absent)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 113, Character 21: 0 = normal; 1 = reduced or fused).

The character state scored for the following species, in particular, is ambiguous:

- *Lithocarus thomsoni*: legs of the genus *Lithocarus* are described in the text to be six segmented (no leg segments fused), further on in the same description (Chandrapatya & Boczek, 2000c), the measurement of a tibiotarsus in leg I was recorded for *L. thomsoni*, implicating that the tibia is fused with the tarsus in this species. In the descriptive drawing of *L. thomsoni*, however, the femur and genu are depicted as fused (genu absent). For the present study the tibia of this species is regarded to be present, separate from the tarsus.

101. Leg I – tibia length:

1 = short (2-3 micron)
2 = average (4-11 micron)
3 = medium long (12-13 micron)
4 = average long (14-15 micron)
5 = long (16-17 micron)
6 = very long (19-20 micron)
7 = very, very long (22 micron)

8 = exceptionally long (30 micron or more)

The tibial lengths were plotted on a graph. They essentially had a normal distribution (C. Craemer, *unpubl. data*). There were no particular large gaps between the lengths for allowing more objective determination of categories. The categories of lengths were determined by categorizing all the species with length within the standard deviation to be "average", and species with a tibial length lower or higher than "average" were divided into 2 µm increasing or decreasing categories as coded above. The length of the tibia of some species for which the length was not recorded, were usually deduced and scored from the descriptive drawing. The categories, and some lengths included, of this character are consequently subjective and probably ambiguous.

The character states scored for the following species, in particular, are ambiguous:

- The tibial length of leg I was not recorded, but was recorded for the tibia of leg II in *Lithocarus thomsoni* and *Diptilomiopus integrifoliae* (Chandrapatya & Boczek, 2000c; Mohanasundaram, 1981b, respectively). The tibial lengths of legs I and II seemed to be similar in the accompanying descriptive drawings, and it was extrapolated that the tibia of leg I is about the same length as that recorded for the tibia of leg II.
- Tibial length was not recorded for the following species, but in their descriptive drawings the tibiae seemed to be neither exceptionally long nor short, and their lengths were scored "average":

  Norma lanyuensis
  Diptilomiopus alagarmalaiensis
  D. aralioidus
  Diptilomiopus camarae
  D. commuiae
  D. cumingis
  D. cuminis (redescription by Huang, 2001c)
  D. dendropanacis
  D. elliptus
  D. emarginatus
  D. euryae
  D. formosanus
  D. hexogonus
  D. leptophyllus
  D. lobbianus
  D. loropetali (Kuang, 1986a; description in Chinese)
  D. maduraiensis (length was recorded for "tibiotarsus")
  D. morii
  D. octogonus
  D. perfectus
  D. stephanus
  Prodiptilomiopus auriculatae
  Sakthirhynchus canariae
  Vasates quadripedes (redescription by Keifer, 1959b)

Levonga casearias
Norma lanyuensis
Aberoptus samoae
Cisaberoptus pretoriensis
Shevtchenkella juglandis
Fragariocoptes setiger

102. Leg I – tibial length in relation to tarsal length:

0 = tibia shorter than half of tarsus length
1 = tibia shorter than tarsus, half or more of tarsus length
2 = tibia length equal to tarsus length
3 = tibia longer than tarsus, but less than half the length of tarsus longer
4 = tibia longer than tarsus, half or more, but less than twice the tarsus length
5 = tibia about twice as long as tarsus
6 = tibia exceptionally longer than tarsus (three or four times the tarsus length)

Relational data should ideally not be used for phylogenetic analyses (Thiele, 1993). It was decided to include this relational character, though, in an attempt to increase the number of characters, because it is used as such in many descriptions, and due to the explorative nature of the present study.

The character states scored for the following species, in particular, are ambiguous:

- Characteristics of leg I (including tibial and tarsal lengths) were not recorded for *Diptilomiopus integrifoliae*, and the measurements of leg II (Mohanasundaram, 1981b) were used for this character.
- The tarsal lengths were not recorded for *Aceria tulipae*, *Aculus ligustri* and *Catarhinus tricholaenae* in their original descriptions (Keifer, 1938a; 1959b), and the relation between the length of the tibia and tarsus was determined by measuring these segments on the descriptive drawings, and although these drawings by Keifer are reliable, they are semi-schematic and may be inaccurate for such detail.
- The tibial and tarsal lengths were not recorded for the following species, but were scored from the descriptive drawings, and the scoring is highly ambiguous, because it is not certain whether the drawings are accurate:

  Aberoptus samoae
  Aceria tulipae
  Catarhinus tricholaenae
  Diphytoptus nephroideus
  Diptilomiopus alagarmalaiensis
  D. aralioidus
  D. camarae
  D. commuiae
  D. cumingis
  D. cuminis (redescription by Huang, 2001c)
  D. dendropanacis

D. elliptus
D. emarginatus
D. euryae
D. formosanus
D. hexogonus
D. leptophyllus
D. lobbianus
D. loropetali Kuang, 1986a (description in Chinese)
D. maduraiensis [length was recorded for "tibiotarsus" by Mohanasundaram (1986a)]
D. morii
D. octogonus
D. perfectus
D. septimus
D. stephanus
Fragariocoptes setiger
Levonga caseariasis
Mediugum sanasaii
Neopropilus jatrophus
Norma lanyuensis
Pararhynacus photiniae
Phyllocoptruta oleivora (redescription by Keifer, 1938a)
Prodiptilomiopus auriculatae
Platyphytoptus sabinianae
Sakthirhynchus canariae
Setoptus jonesi
Shevtchenkella juglandis
Vasates quadripedes (redescription by Keifer, 1959b)

103. Leg I – empodial shape (Fig. 3.6):

0 = pad-like with numerous rays (tenent rays or non-tenent rays or hair) (Fig. 4.1)
1 = simple (Fig. 3.6c, d)
2 = simple, distally elongated (Fig. 3.6e)
3 = simple, rays asymmetrical (more rays on one side than the other)
e.g., *Dechela epelis* (Fig. 3.6f)
4 = partly divided (Fig. 3.6g)
5 = divided (Fig. 3.6g)
6 = divided, stems unequal (Fig. 3.6i)
7 = divided, stems pad-like with numerous rays (Fig. 3.6j)
8 = divided, with central stem (Fig. 3.6k)
9 = palmate (Fig. 3.6l)
a = basal rays finely branched, hair-like (e.g., *Brevulacus reticulatus*) (Fig. 3.6m)
b = reduced to a bristle (Fig. 3.6n)
c = distal part splitting into six hairs, hairs not tenent shaped (Fig. 4.2)

This character was previously used in analyzing the phylogeny of the Eriophyoidea [Hong & Zhang, 1996a, p. 113, Character 24: 0 = simple (normal); 1 = not normal (divided, palm-shaped etc.)]. The shape of the empodium is used to differentiate Eriophyoidea taxa at the genus level, and sometimes at the subfamily level (e.g., Diptilomiopinae and Rhyncaphytoptinae). Taxa with

divided empodia are present in all three Eriophyoidea families, and the character seems to be homoplasious.

The character state scored for the following species, in particular, is ambiguous:

- The empodium of *Diptilomiopus stephanus* was described as "divided" (Huang, 2005); however, in the accompanying drawing it seems that the two stems of the empodium may be pad-like (Huang, 2005). It was scored as being pad-like for the present study.

104. Leg I – number of empodial rays:

0 = numerous rays (can not count with ease)
1 = 16-rayed or more
2 = 11-12 rayed
3 = 10-rayed
4 = 9-rayed
5 = 8-rayed
6 = 7-rayed
7 = 6-rayed
8 = 5-rayed
9 = 4-rayed
a = 3-rayed
b = 2-rayed
c = reduced to a bristle (no rays)
d = six hairs splitting from one point

The number of empodial rays is extensively used to differentiate between Eriophyoidea species. It may vary within a species, and the character should be scored cautiously. Despite its own problems, it is relatively one of the clearer, easily observable and concise Eriophyoidea characters, though, and Meyer (*unpubl. data*) commenced with a key to the *Aceria* spp. of South Africa using the number of rays as the initial character to divide the genus into groups.

The character states scored for the following species, in particular, are ambiguous:

- The empodium of *Dechela epelis* is asymmetrical with the inside 5-rayed and the outside 7-rayed (Keifer, 1965a; Fig. 3.6f). To accommodate this difference in rays, ideally the number of empodial rays should be divided into two characters: the number of rays on the inner side of the empodium and the number of rays on the outer side of the empodium. This is usually not recorded in Eriophyoidea descriptions, though. The two states were coded as a polytomy in the present study. This is erroneous, but in my opinion a better option than scoring the code "?" (unknown).
- The number of rays on the empodium of *Acarhis lepisanthis* was described as "with 6-7 rays on outer fork and fewer on inner", in the accompanying drawing there seems to be about 2-3

rays on the inner branch and 7 rays on the outer branch (Keifer, 1975d; Fig. 3.6i). In the lateral view drawings this distinction between the inner and outer branch is not clearly depicted. The state was scored as polymorphic, namely 6 or 7 rays, because there is a slight chance that Keifer may have viewed the one branch dorsally and the other laterally. This is probably an erroneous interpretation by me and should be investigated.

- The empodium of *Diptilomiopus holmesi* was described by Keifer (1962c) as having about 6 rays, indicating that there is a variation in number of rays, or that he was not sure about the number. It was scored as 6-rayed.
- The empodium of *Diptilomiopus racemosae* was recorded as 6-rayed, however, in the descriptive drawing, the empodium is depicted with 7 rays (Chandrapatya & Boczek, 2001a). It was scored as 6-rayed.
- The number of empodial rays of the following species was not recorded in the text, and was counted on their descriptive drawings. Counting number of empodial rays on descriptive drawings may be very ambiguous, e.g., in *Chiangmaia longifolii* the number of empodial rays was recorded as 9, however, in the descriptive drawing of this species only 5 rays is depicted in the enlarged view of the empodium (Chandrapatya & Boczek, 2000c).

Acarhis diospyrosis
Diptilomiopus aglaiae
D. anthocephaliae
D. artabotrysi (one stem 5-rayed the other 6-rayed, coded as if it is a polymorphism – either 5- or 6-rayed)
D. azadirachtae
D. barringtoniae
D. benjaminae
D. boueae
D. cerberae
D. cythereae
D. elaeocarpi
D. ervatamiae
D. eucalypti
D. languasi
D. melastomae
D. meliae
D. morindae
D. musae
D. pamithus
D. pocsi
D. riciniae
D. sandorici
D. strebli
D. swieteniae
D. thaianae
D. thunbergiae
Lambella cerina
Lithocarus thomsoni

Neolambella ligustri
Prodiptilomiopus auriculatae
Sakthirhynchus canariae

105. Leg II: femur and genu articulation – whether fused:

0 = normally articulated
1 = division weak, almost fused
2 = not articulated, totally fused

The character state scored for the following species, in particular, is ambiguous:

- The legs of *Lithocarus* are described as being six segmented, however, in the descriptive drawing of *Lithocarus thomsoni*, the type species of the genus, the femur and genu are depicted as being fused (genu absent). For the present study, the genu and femur were scored as being totally fused.

106. Leg II: tibia presence, or whether fused with tarsus:

0 = present
1 = partly fused to tarsus
2 = completely fused to tarsus (absent)

The character state scored for the following species, in particular, is ambiguous:

- Similar problems found with *Lithocarus thomsoni* for Character 100 (presence of tibia in leg I) are also experienced with the presence of tibia in leg II, and the species was also scored here with the tibia present, separate from the tarsus.

GENITALIA (Figs 3.4, 3.5)

Several of the characteristics of the Eriophyoidea genitalia are either hypothetically synapomorphic or are autapomorphic for the superfamily (Lindquist, 1996b) and some of these are included here. In general characters of the genitalia, particularly internal genitalia, are regarded to be informative regarding the phylogeny of groups. Internal genitalia are less exposed to the environment and therefore probably less influenced by environmental and niche changes. For example, characters of the genitalia are extensively used in the systematics of spiders (A.S. Dippenaar-Schoeman, *pers. comm.*). The internal genitalia of the Eriophyoidea vary significantly, but unfortunately, they are frequently difficult to study, because they are easily destroyed during slide-mounting of specimens, and can not be studied with the SEM. Even though the morphology of the internal genitalia of females are frequently briefly described (usually only the shape of the anterior apodeme), and depicted, the description of fine detail is not included. It is probably partly

due to the extremely tiny size of these structures, which are obscured by other body structures. De Lillo *et al*. (2010) suggested that the genitalia should be dissected out of the body to be studied, but this is technically difficult and precise work. There are also many species for which character states of the internal genitalia are unknown, because they were, or could not be described. The external morphology and position of the genitalia of females, but not the males, are generally described and used in Eriophyoidea taxonomy.

***107. Post-larval instars – presence of genital acetabula:**

0 = with genital acetabula
1 = without genital acetabula

***108. Nymphal instar – presence of progenital opening and chamber:**

0 = with progenital opening and chamber
1 = without progenital opening and chamber

***109. Genital opening of female – presence of flap:**

0 = not covered by an anteriorly hinged flap
1 = covered by an anteriorly hinged flap

***110. Sperm transfer type:**

0 = with spermatophores deposited on substrate
1 = directly with aedeagus

***111. Aedeagus – presence:**

0 = present
1 = absent

112. External genitalia – position:

0 = caudally (Figs 4.1, 4.2)
1 = about 9-15 annuli removed from coxae, located posterior to *c2* (Fig. 3.5g)
2 = close to, but not appressed to coxae (Fig. 3.5d)
3 = appressed to coxae (Fig. 3.5a, b)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 110, Character 11: 0 = not appressed to coxae II; 1 = appressed to coxae II).

This character is particularly of importance in defining the genus *Novophytoptus* (with the genitalia removed relatively far from the coxae) (Fig. 3.5g), and the subfamily Cecidophyinae (with the genitalia appressed against the coxae) (Fig. 3.5a, b). The position of the genitalia may be distorted by the slide-mounting process, for example the genitalia of *Cisaberoptus kenyae* are

drawn against the coxae, and those of *C. pretoriensis*, slightly away. In this regard also compare Fig. 3.5a with 3.5b.

The character state scored for the following species, in particular, is ambiguous:

- *Cosella deleoni*: the genitalia were not described as being appressed against the coxae (a characteristic partly defining the Cecidophyinae) (Keifer, 1956). It is coded as appressed to the coxae, because the genitalia seems to be pressed up against the coxae in the descriptive drawing of the species, with no space or annuli between the genitalia and coxae II, with the genitalia partly situated between coxae II.

113. Female, internal genital apodeme – shape:

0 = internal genital apodeme similar to that of the Eriophyoidea absent
1 = moderately extended to front ("normal") (Fig. 3.5e, i)
2 = folded up, appearing like a thick transverse line (Fig. 3.5c)
3 = folded up, but appearing slightly broader than a transverse line
4 = folded up, with special structure, consisting of about three transverse areas

The main diagnostic character of the subfamily Cecidophyinae is the shape of the internal female anterior genital apodeme which is folded up, appearing like a transverse line (Fig. 3.5c). However, if studied and compared in more detail, other characteristics of this apodeme also vary (e.g., although it is not a good example, compare Fig. 3.5c with 3.5f). In the present study the shape of this apodeme was scored "normal", except when otherwise noted or depicted, and even when the internal genitalia were not described or depicted, and especially when the external genitalia were not appressed to the coxae.

The character state scored for the following species, in particular, is ambiguous:

- *Aberoptus samoae*: the internal genitalia were not described nor depicted (Keifer, 1951), however, externally it looks very similar to those of *Cisaberoptus kenyae* (Keifer, 1966c) and it is presumed the internal genitalia of these two species may also be very similar, and in the present study they were scored to be the same.

114. Spermathecae – shape:

0 = spermathecae similar to Eriophyoidea and Tetranychidae absent
1 = round or ovalish (Fig. 3.5c, e)
2 = elongated (Fig. 3.5f)

I find it notoriously difficult to see the spermathecae in the slide-mounted specimens of most species, and dissecting the genitalia from the body will probably help in studying them (as proposed by De Lillo *et al*., 2010, see above). The spermathecae of the Eriophyoidea are usually

round (Fig. 3.5c, e) or slightly more oval. Among the species included in the present study, they are elongated in largely Phytoptidae species, [*Novophytoptus rostratae*, *N. stipae* (Novophytoptinae), *Acathrix trymatus*, *Anchiphytoptus lineatus*, *Oziella yuccae*, *Phytoptus avellanae* (Phytoptinae), *Austracus havrylenkonis*, *Sierraphytoptus alnivagrans* (Sierraphytoptinae)] (Roivainen, 1947; Keifer, 1962d; 1962c; 1952a; 1954; 1952b; 1944; 1939a, respectively) excluding the Nalepellinae. They are also elongated in *Africus psydraxae* (ambiguous) and *Apodiptacus cordiformis* (Diptilomiopinae) and *Ashieldophyes pennadamensis* (Ashieldophyinae) (Meyer & Ueckermann, 1995; Keifer, 1960; Mohanasundaram, 1984, respectively). The shape of the spermathecae of the latter three species is not exactly the same as the long spermathecae in the Phytoptidae, and they may not be homologous character states. It is detail like this that needs to be sorted out.

115. Spermathecal tube length:

0 = spermathecal tubes similar to that in the Eriophyoidea and Tetranychidae absent
1 = relatively short to very short (normal) (Fig. 3.5c, e, f)
2 = long (Fig. 3.5i)

This character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 115, Character 32: 0 = long; 1 = short).

Long spermathecal tubes are present only in Nalepellinae species, and may be a synapomorphy for this subfamily (Lindquist & Amrine, 1996). They have also been depicted as elongated in *Pentasetacus araucaria* of this subfamily, but the tubes of the latter species is not the same shape as in the other Nalepellinae. It has been scored as "long" in the present study, though.

116. Female genital coverflap ornamentation:

0 = absent
1 = entirely unornamented (Fig. 3.5h, g)
2 = entirely unornamented, but divided into a basal and distal area (e.g., *Hoderus roseus*)
3 = basally ornamented, distally unornamented (smooth)
4 = basally unornamented (smooth), distally ornamented
5 = entirely ornamented, divided in basal and distal area (possibly coverflap of *Cecidophyes* – Fig. 3.5a, b)
6 = entirely ornamented, not divided in basal and distal area (Fig. 3.5d)

A similar character was previously used in analyzing the phylogeny of the Eriophyoidea (Hong & Zhang, 1996a, p. 114, Character 26 (ridges of the female genital coverflap): 0 = absent; 1 = one longitudinal row; 2 = two longitudinal rows or transverse lines).

Characteristics of the external female genitalia are usually described and used in Eriophyoidea taxonomy. In particular the ornamentation on the female genital coverflap is extensively used in differentiating species. Detail of the type of ornamentation was not included in the data set of the present study. Defining characters and character states was attempted, but it turned out to be too ambiguous and uncertain, both in determining homologous areas of the coverflap (e.g., precisely determining the basal and distal area of the coverflap for comparison), and in the accuracy with which it was described. More detail of the ornamentation was, however, included in a parallel study of *Diptilomiopus* and closely related species (C. Craemer, *unpubl. data*).

For example, the distinction between an entirely ornamented genital flap, without distinction between a basal and distal area, and an entirely ornamented flap of which the ornamentation is divided between a basal and distal area, is not clear in published descriptions. For example, the coverflap ornamentation for *Costarectus zeyheri* is described as being "coverflap of gonopore with 11 longitudinal markings" (Meyer & Ueckermann, 1995), however, in the drawing it seems that there may be one or two transverse lines, of which the basal is centrally interrupted, basally to the longitudinal lines. This can be regarded as constituting a basal area, but although it has been depicted in this species, it has not been recorded in the text description. In the published descriptions of many other species with similar ornamentation, this basal area may not even be depicted. In the present study, *Costarectus zeyheri* was scored as entirely ornamented without a basal and distal area.

I will go as far as to suggest that many Eriophyoidea species descriptions where the genital coverflap was depicted, described and coded as entirely ornamented, but with the ornamentation not divided in a basal and distal area, may be inaccurate. In these species the ornamentation may be similar to e.g., *Costarectus zeyheri* (discussed above) and *Pentamerus rhamnicroceae* where there actually may be a basal area, but may be very thin and inconspicuous (descriptive drawing in Keifer, 1966a).

Many discrepancies and incorrect descriptive data regarding the shape and ornamentation of the female genital coverflap are present in the descriptions of Eriophyoidea species. The character states scored for the following species, in particular, are ambiguous:

- *Acarhis diospyrosis*: Chandrapatya & Boczek (1991c) described the ornamentation of the female genital coverflap as "genital coverflap with granules", however, the exact area on which these granules occur, was not described. The area could not be determined from the descriptive drawing, because the granules can be on the basal area, or the flap could be pushed

up and open, with granules on the entire area of the flap, however, according to the scanning electron images of the species it seems that the granules are only on the basal area. Unfortunately, the SEM images on the photocopied reprint are of very bad quality, and the original copies could not be obtained, and the state remains ambiguous.

- *Diphytoptus nephroideus*: the coverflap ornamentation was described as "about 7 short longitudinal lines" (Huang, 1991). The state was scored in the present study as "distally ornamented and basally smooth or unornamented", because the lines are described as short, and it could be similar to that of *Davisella breitlowi* (Davis, 1964a), however, this could not be confirmed on the descriptive drawing, because the coverflap is distorted.
- *Quadriporca mangiferae*: the genital coverflap ornamentation could not be determined from the original Chinese description (Kuang *et al*., 1991). In the descriptive drawing a row of short longitudinal ridges is present, however, it can not be determined whether these ridges only occurs basally on the flap, or distally on the flap, since the flap is distorted and unclear. The ornamentation was scored to occur distally, similar to some of the other morphologically similar Rhyncaphytoptinae.
- *Diptilomiopus illicii*: the female genital flap ornamentation was described as "coverflap with basal faint lines and granules on either side" and was depicted as such in the descriptive drawing (Wei & Lu, 2001). Granules on the lateral areas of the coverflap is unusual, and do not occur in any other Eriophyoidea species. For the present study the state was scored as if ornamentation only occurs on the basal area.
- *Diptilomiopus loropetali*: the coverflap was described as "coverflap with a W-shaped design" (Kuang, 1986a). According to the shape and position of this ornamentation it seems that the author might have confused the interior apodemes and structures of the internal genitalia with ornamentation that may occur on the surface of the coverflap. The coverflap may be smooth, but for the present study, it was decided to stand with the author's interpretation, and the coverflap ornamentation was scored as "present on the entire coverflap".
- *Diptilomiopus phylanthi*: the coverflap was described as "coverflap with few longitudinal striae", however, in the drawing some tubercles are depicted on the base of the coverflap (Boczek & Chandrapatya, 1992b).
- *Diptilomiopus swieteniae*: the coverflap was described as "smooth" (Chandrapatya & Boczek, 1998), however, in the descriptive drawing of the ventral aspect, the flap was clearly depicted ornamented with tubercles or granules, and in the lateral view drawing it seems to be smooth. For the present study it is scored as "entirely ornamented".
- *Lambella cerina*: the coverflap was described as "smooth" (Lamb, 1953) in the original description. In the redescription by Manson (1984a) the coverflap was described as

ornamented “with fine granules”, without reference to the state in the original description. The coverflap was scored “entirely ornamented” in the present study.

- *Vimola syzygii*: the coverflap ornamentation was described to be on the distal part of the flap (Boczek & Chandrapatya, 1992a); however, in the drawing it seems to be similar to the usual ornamentation which occurs basally on the coverflap. It was scored “basally ornamented, distally unornamented (smooth)” in the present study.
- *Keiferana neolitseae*: the coverflap ornamentation was described as “coverflap with no particular design” (Channabasavanna, 1967); however, in the drawing the ornamentation is strangely shaped and may include parts of the underlying internal genitalia. The shape and ornamentation of the flap is not clear. For the present study, the flap ornamentation is scored “entirely unornamented”.

APPENDIX C

List of characters included in analyses, with different character numbers as used in data matrices.

APPENDIX C.

	Character numbers		
	318tax set	66tax set	18tax set
Characters			
GENERAL			
*Immature stages: number of	0		
*Respiratory: presence stigmata	1		
*Excretory system: presence	2		
**Muscles, cross-striated or smooth	3		
**Tonofibrillary muscle attachments: presence	4		
**Organs, basal membranes: presence	5		
CHAETOTAXY: General			
*Immatures: what seta present	6		
***Setal morphology: presence actinopilin	7		
CHAETOTAXY: Gnathosomal setae			
Palp seta *d* : presence and shape	8	0	
*Palp tarsus: presence of solenidion	9		
CHAETOTAXY: Prodorsal setae			
seta vi: presence	10	1	0
seta ve: presence	11	2	1
*Seta *sc2* : presence	12		
Seta *sc1* (*sc* in Eriophyoidea): presence	13	3	3
Seta *sc* : length	14	4	32
Seta *sc* , length relative to shield length	15	5	
Seta *sc* , length relative to distance between them			
Scapular setal tubercle, presence and shape	16	6	2
Seta *sc* and/or its tubercle, position	17	7	6
Seta *sc* , direction of projection	18	8	7
CHAETOTAXY: Opisthosomal setae			
Seta *c1* , presence	19	9	11
Seta *c2* , presence	20	10	24
Setal tubercles *c2* , presence	21	11	
Seta *d* , presence	22	12	12
*seta *d* , number of pairs present	23		
*seta *d* , position	24		
seta e, presence	25	13	13
*seta e, number of pairs present	26		
*seta e, position	27		
*seta f, number of pairs present	28		
*seta f, position	29		
seta h1, presence	30	14	30
*seta ps, presence	31		
CHAETOTAXY: Coxisternal plate setae			
seta 1b, presence	32	15	14
Setal tubercles *1b* , presence	33	16	
1b -*1b* :*1a* -*1a* , relationship of distance between setae	34	17	
seta *1a* , presence	35		
Setal tubercle *1a* , presence and shape	36		
seta *1a* , position in relation to seta 2a	37	18	34
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*Genital setae, presence in adult	39		
*Aggenital setae, presence	40		
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Leg I genu, seta l'', presence	44	20	16
Leg I tibia, seta l', presence	45	21	17
Leg I tibia, seta l', position	46	22	
Leg I tibia, seta l', vertical position	47	23	
Leg I tibia, solenidion φ, presence and position	48	24	21
Leg I tarsus, solenidion ω, position	49	25	
Leg II femur, seta bv, presence	50	26	18
Leg II genu, seta l'', presence	51	27	19
Leg II tarsus, seta ft', presence	52	28	
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**Cheliceral bases, presence of motivator	54		
**Apical ends of palpi, shape	55		
**Palpi, shape and position	56		
Oral stylet: form	57	29	
Chelicerae: shape and position	59	30	9
PRODORSUM: Prodorsal shield			
Prodorsal shield: shape	60	31	
Ocelli or ocellar-like areas: presence, position, shape	61		
Frontal lobe: presence and general shape	62	32	4
Frontal lobe: shape	63	33	
Frontal lobe apical edge: shape	64	34	
Frontal lobe, shield anterior edge: presence of spines	65		5
Frontal lobe: presence of one slender filament	66		
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*Lyrifissures: presence	68		
*Opisthosoma rear end: shape in female	69		
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Body: shape	70	36	8
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Opisthosomal annuli: dorsoventral differentiation	72	37	27
Dorsal annuli lateral extensions or lobes: presence, shape	73	38	28
Opisthosomal shape: presence ridges and furrows	74	39	22
"Telosomal" dorsal annuli: whether fused	75	40	
Dorsal annuli microtubercles: presence and position	76	41	33
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APPENDIX D.

Data matrix for 318-taxon analyses. Data matrix of morphological characters for 316 eriophyoid species and two outgroup species (*Orphareptydeus* and *Mononychelus*) for the 318tax analyses. ? = uncertain or unknown character states, - = inapplicable states. Codes in light grey are of autapomorphic characters, codes in black and bold are homologous characters.

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Orfareptydeus stepheni	0000000100	0000330060	000?00?000	0000000000	0100000221	0100010**0–1**	–10––00000	0000001**0**–0	1000000000	0034000000	0810000000	1100000
Mononychelus yemensis	1000000140	2000030060	0000000000	000000**0**–10	0120000100	0000000**0–0**	–00––00000	0000001**0**–0	1000000000	0034000000	081cd00000	0000120
Abacarus acalyptus	21111111?1	2110331241	0101101111	0101101001	1110000522	0001121**001**	2122200411	6120110111	1111111111	1123310000	0231700111	1121116
Abacarus hystrix	2111111101	2110331241	0101101111	0101101001	1110000322	0001121**001**	b122810411	6150110111	1111111111	1123310000	0231500111	1121116
Aberoptus samoae	21111111?1	2110331231	0101101111	2101201201	111001––23	0001121**001**	110––00411	b1100110–1	1111111111	1100311300	0109c00111	1133116
Acadicrus bifurcatus	2111111101	2110331211	0101101111	2101101001	1110000522	0001121**001**	2121b00411	6150011**0**–1	1111111111	1123310000	0341700111	1121113
Acalitus ledi	2111111141	2110331041	0101101111	2101301001	111101––22	0001121**001**	a10––00411	3110011**0**–1	1111111111	1123310000	0211800111	1121115
Acamina nolinae	2111111101	2110331011	0111111111	2101001101	1111000322	1001121**001**	2122600411	7150110111	1111111111	1100410000	0331800111	1121115
Acaphyllisa parindiae	2111111101	2110?41021	0101101111	2101101101	1110002022	0001121**001**	2122300411	7163110–1	1111111111	1113310000	0224a00111	1121115
Acarelliptus cocciformis	21111111?1	2110331011	0101101111	0101101001	1110000422	0001121**001**	2112200411	7162110–1	1111111111	1100310000	0211800111	1121116
Acarhis diospyrosis	21111111?1	2110551041	1201101111	2101001001	111111––22	1101121**012**	710––00411	5160110–1	1111111111	1100310100	0215810111	1121??3
Acarhis lepisanthis	2111111101	2110441011	1201101111	2101001001	1111100322	1101121**012**	1112600411	5120111[12]0–1	1111111111	1111410000	0216[67]00111	1121113
Acarhis siamensis	2111111101	2110441011	1201101111	2101001101	1111100222	1101121**012**	110––00411	5160111**0**–1	1111111111	1103210200	0205[45]20111	1121??5
Acarhynchus filamentus	2111111101	2110341011	0101101111	2101201201	1111000022	0001121**012**	2122101411	5160111**0**–1	1111111111	1123310000	0237000111	1121113
Acaricalus segundus	2111111101	2110341011	0101101111	2101001001	1110000422	0001121**001**	7122100411	7120110**0**–1	1111111111	1100210000	0225900111	1121115
Acathrix trymatus	2111111101	2010551200	0101101111	0101101101	1110000312	0001121**001**	210––00411	1110011**0**–1	1111111111	1111310000	0221200111	1121211
Aceria tulipae	2111111101	2110211241	0101101111	0101001101	1110000422	0001121**001**	210––00411	1110011**0**–1	1111111111	1123310000	0211600111	1121116
Acerimina cedrelae	2111111101	2110331241	0101101111	0112–01101	1110000422	0001121**001**	210––00411	1110011**0**–1	1111111111	1100310000	0231900111	1121116
Achaetocoptes ajoensis	2111111101	2111––2––1	0101101111	2101101001	1110000322	0001121**001**	d122200311	7173112**0**–1	1111111111	1123310000	0221[56]00111	1132116
Acritonotus denmarki	2111111101	2110341211	0101101111	2101001001	1110000222	0001121**001**	2122100111	7182110**0**–1	1111111111	1100310000	0549a00111	1121115
Aculodes mckenziei	2111111101	2110231241	0101101111	0101101101	1110000322	0001121**001**	2122400411	1110011171	1111111111	1123310000	0211600111	1121116
Aculops populivagrans	2111111101	2110331241	0101101111	2101201101	1110000522	0001121**001**	2122400311	6160012**0**–1	1111111111	1123310000	0231900111	1121116
Aculus ligustri	2111111101	2110331241	0101101111	0101101001	1110000522	0001121**001**	2122220311	6160012[02]0–1	1111111111	1120310000	0241900111	1121116
Acunda plectilis	2111111101	2110331241	0101101111	0101001101	1110000222	0001121**001**	210––00411	1140111**0**–1	1111111111	1110310000	0211500111	1123116
Adenocolus psydraxi	2111111141	2110331241	0101101111	1101401001	111101––22	0001121**001**	2122100411	6160011**0**–1	1111111111	1123510000	2–1[78]02111	1121111
Aequsomatus lanceolatae	2111111101	2110331011	0101101111	1112–01001	1110000622	0001121**001**	2122100411	6140012**0**–1	1111111111	1113310000	0231a00111	1121??1
Africus psydraxae	2111111141	2110451021	1201101111	0112–13–01	111111––22	1111121**012**	110––00411	5120116**0**–1	1111111111	1123210100	0215810111	1121213
Afromerus florinoxus	2111111101	2110331201	0101101111	2101201001	111001––22	0001121**001**	2122400411	1110011**0**–1	1111111111	1100310000	0211700111	1132??6
Anchiphytoptus lineatus	21111111?1	2010331010	0101101111	0101101101	1110000312	0001121**001**	210––00411	111001b**0**–1	1111111111	1113310000	0231800111	1121213
Anothopoda johnstoni	21111111?1	2111––2––1	0101111111	2112–01001	111001––22	0001121**001**	210––00411	1110011**0**–1	1111111111	1123510000	0101902111	1121113
Anthocoptes gutierreziae	2111111101	2110341241	0101101111	0101201101	1110000422	0001121**001**	3122200311	7173010**0**–1	1111111111	1123310000	0221900111	1121115
Apodiptacus cordiformis	2111111101	2110331211	0101101111	2101001001	1111000422	1001121**012**	2122900411	7161110111	1111111111	1123410000	0335900111	1121215
Apontella bravaisiae	2111111101	2110341041	0101101111	2101001101	111101––22	0001121**001**	2112200311	7150112**0**–1	1111111111	1123310000	1––1801111	1121??5
Arectus bidwillius	2111111101	2110331011	0101101111	0101001001	1111000522	0001121**001**	9122600411	5150019**0**–1	1111111111	1123510000	0231700111	1121115
Areekulus eugeniae	2111111101	2110451021	0101101111	2101?01?01	1111001022	1111121**012**	1112100411	a150111**0**–1	1111111111	11??210000	0341800111	1122??1
Asetacus madronae	21111111?1	2111–10–1	0101101111	2101001101	1111000322	1001121**012**	9122700411	5120010141	1111111111	1120410000	0431700111	1121115
Asetadiptacus emiliae	21111111?1	2111–10–1	0101101111	1101101101	1111000322	1001121**012**	2112100411	5160011**0**–1	1111111111	1123310000	0345800111	1121113
Asetilobus hodgkinsi	2111111101	2110331021	0101111111	2101301001	1110000322	0001121**001**	2122200411	5110011**0**–1	1111111111	1123310000	0211[89]00111	1121?16
Ashieldophyes pennademensis	2111111101	2110552131	0111111111	0101201001	1110000322	0001121**001**	110––00111	9140010**0**–1	1111111111	1100510000	0241900111	1131211
Austracus havrylenkonis	2111111101	2010331000	0101101111	0101101101	1110000412	0001121**001**	210––00111	2161010**0**–1	1111111111	1100310000	0221900111	1121212
Baileyna marianae	2111111101	2110331241	0101101111	0101301001	1110000422	0001121**001**	210––00111	1150112**0**–1	1111111111	1100310000	0211900111	1121115

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Bakeriella ocimis	2111111101	2110341251	0101101111	0101101101	1110000422	0001121001	2122800311	7160110−1	1111111111	1101310000	0221900111	1121116
Bariella farnei	2111111101	2111−−2−−1	0101101111	2101401001	1110000322	0001121001	2122600411	7160110−1	1111111111	1100310000	0221800111	1134115
Boczekella laricis	211111117?1	1111−−2−−0	0101101111	0101?01?01	111001−−22	0001121001	210−200411	5150110−1	1111111111	1111310000	0221[56]00111	1121??1
Brachendus pumilae	2111111101	2110321201	0101101111	0101101001	1110000322	0001121001	d111100411	1110011−1	1111111111	1123310000	0211800111	1123116
Brevulacus reticulatus	2111111101	2110333011	0101101111	0101101001	1110000623	0001121012	2122a00411	5160111−1	1111111111	1100310000	034ª000111	1121111
Bucculacus haweckii	2111111101	2110331011	0101101111	0101301001	1110000422	0001121012	2122200411	7160110−1	1111111111	1100310000	0235700111	1121??1
Calacarus pulviferus	2111111101	2111−−2−−1	0101101111	2101101101	1110000422	0101121001	2122100411	5120110121	1111111111	1123310000	0231900111	1121115
Calepitrimerus cariniferus	211111117?1	2110331221	0101101111	0101101001	1110000422	0001121001	2122200311	7151110−1	1111111111	1100310000	0221900111	1121116
Caliphytoptus quercilobatae	2111111101	2110331221	0101101111	0101101001	1110000422	0001121001	2122100411	7161110−1	1111111111	1100310000	0211800111	1121116
Caroloptes fagivagrans	211111117?1	2110331201	0101101111	0101101001	1110000522	0001121001	2112200311	7161110−1	1111111111	1123310000	0211900111	1121114
Catachella machaerii	2111111141	2110221241	0101101111	2101101001	111101−−25	0001121001	2112200411	1120011−1	1111111111	1123510000	0211[345]00111	1121115
Catarhinus tricholaenae	211111117?1	2110341011	0101101111	2101101201	1111000023	0001121012	2122800311	7161110−1	1111111111	1123310000	0211700111	1121113
Cecidodectes euzonus	2111111101	2110331001	0111111111	2101201001	1110000422	0001121001	2122200111	3140010−1	1111111111	1100310000	0211800111	1122111
Cecidophyes rouhollahi	2111111101	2111−−2−−1	0101101111	2101301001	1110000322	0001121001	2112100411	5120011−1	1111111111	1110310000	0221800111	1132115
Cenaca syzygioidis	2111111141	2110321241	0101101111	2112−0101001	111101−−22	0001121001	210−−00311	1110011−1	1111111111	1100310000	0111900111	1121116
Cenalox nyssae	2111111101	2110331251	0101101111	2101301001	1110000222	0001121001	2122400311	7150111−1	1111111111	1100210000	0211900111	1131111
Cercodes simondsi	2111111101	2110331201	0101101111	0101201001	1110000522	0001121001	210−−00411	1180219−1	1111111111	1123310000	0211900111	1121116
Chakrabartiella ficusis	2111111101	2110331201	0101101111	0112−0101001	1111000622	1001121012	110−−00111	5150111−1	1111111111	1100310000	0231800111	1121114
Cheiracus sulcatus	2111111101	2110341251	0101101111	2101001001	1110001422	0001121012	b122100411	7161110−1	1111111111	1123310000	0230000111	1121113
Chiangmaia longifolii	2111111101	2110451221	0101101111	1101101001	111101−−22	1001121012	510−−00411	5160113−1	1111111111	1120210000	0215400111	1123116
Chrecidus quercipodus	2111111101	2111−−2−−1	0101101111	2101201001	1110000322	0001121001	2122800411	5150010−1	1111111111	1120310000	0221700111	1132115
Circaces chakrabarti	2111111101	2110331241	0101101111	0101201001	1110000422	0001121001	210−−00311	1181011−1	1111111111	1111310000	0211900111	1132116
Cisaberoptus kenyae	2111111101	2110331241	0101101111	2101301101	111001−−22	0001121101	f111c00111	7110111−1	1111111111	1100210200	1−−1121111	1133116
Cisaberoptus pretoriensis	2111111101	2110331241	0101101111	1101101101	1110000422	0001121101	2121200111	7120019−1	1111111111	1100310000	0211600111	1121??1
Colomerus gardeniella	2111111101	2110331211	0101101111	2101301001	1110000422	0001121001	210−−00411	1110011−1	1111111111	1100310000	0211800111	1132115
Colopodacus africanus	2111111101	2110341021	0101101111	2101301001	111001−−22	0001121001	3122100411	6110111−1	1111111111	1100310000	2−−1802111	1121113
Coptophylla lamimani	211111117?1	2111−−2−−1	0101101111	2101201001	1110000322	0001121001	2122200111	6161010−1	1111111111	1120310000	0221800111	1132116
Cosella deleoni	2111111101	2110341041	0101101111	2112−0101001	111001−−24	0001121001	2112900411	6140018−1	1111111111	1120510000	2−−1802111	1131116
Cosetacus camelliae	2111111101	2110221241	0101101111	2101401001	111001−−22	0001121001	210−−00411	3110011−1	1111111111	1100310000	0211700111	1133115
Costarectus zeyheri	2111111101	2110331241	0101101111	0101101101	1110000522	0001121001	2122200411	6160110121	1111111111	1120310000	0241900111	1121116
Criotacus brachystegiae	2111111101	2110331201	0101101111	2101001101	1110000522	0001121001	2122800311	3140011−1	1111111111	1100310000	0221800111	1121111
Cupacarus cuprifestor	2111111101	2110331021	0101101111	0101001001	1110000222	0001121001	d122800311	6160110−1	1111111111	1113210000	0221700111	1121113
Cymeda zealandica	2111111141	2110341021	0101101111	2101001001	111001−−22	0001121001	2122100411	7160010d131	1111111111	1100310020	0115800111	1121111
Cymoptus spiniventris	2111111101	2110331241	0101101111	2101301001	111001−−22	0001121001	210−−00411	1120510−1	1111111111	1100310000	0201b00111	1121?11
Dacundiopus stylosus	2111111141	2110451011	1201101111	2112−0101001	111101−−22	1101121012	910−−00411	5160110−1	1111111111	1123520201	0215b20111	1121??1
Davisella breitlowi	211111117?1	2111−10−1	1201101111	2101101001	1111000322	1101121012	110−−00411	5150111−1	1111111111	1100110000	0215800111	1121??4
Dechela epelis	2111111101	2111−−2−−1	0101101111	2112−0101001	111001−−25	0101121001	3112600411	3110011−1	1111111111	1123310000	0113[68]00111	1132116
Dialox stellatus	2111111101	2110551001	0101101111	1101001101	1111001422	0001121012	c122a00411	5130011121	1111111111	1100310000	0865500111	1121116
Dichopelmus notus	2111111101	2110341241	0101101111	2101201001	1110000422	0001121001	2122250311	7161010−1	1111111111	1100310000	0234900111	1121??5
Dicrothrix anacardii	2111111121	2110341011	0111101111	2101001001	1110001622	0001121001	6122100411	7140310−1	1111111111	1100310000	0232900111	1121111
Diphytoptus nephroideus	2111111101	2110331241	0101101111	2101001101	1110000322	0101121001	210−−00311	1110011−1	1111111111	1100310000	0235900111	1121114

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Diptacus pandanus	2111111101	2110451021	0101101111	0101101101	1111000322	0001121012	2122130111	7150110–1	1111111111	1123210000	0455500111	1121111
Diptacus sacramentae	2111111101	2110331211	0101101111	2101001101	1111000022	1001121012	2122100411	6160012121	1111111111	1111310000	0435700111	1121111
Diptilomiopus acronychia	211111??1	2111–10–1	1201101111	2112–0101	111111––22	1101121012	110––00411	5150110–1	1111111111	1103310200	0215720111	1121111
D. aglaiae	2111111141	2111–10–1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123510200	0215720111	1121116
D. alagarmalaiensis	2111111101	2111–10–1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150011–1	1111111111	1103210200	0105920111	1121113
D. alangii	2111111101	2111––2––1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1100310200	0215720111	1121111
D. anthocephaliae	2111111101	2111–10–1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123310200	0215820111	1121113
D. aralioidus	2111111101	2111–10–1	1201101111	1112–0101	111111––22	1101121012	210––00411	5150010–1	1111111111	1100510200	0205820111	1121111
D. artabotrysi	2111111101	2111–10–1	1201101111	2112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123210200	0215[78]20111	1121113
D. artocarpae	2111111101	2111–10–1	1201101111	1112–0101	111101––22	1101121012	110––00411	7150110151	1111111111	1123310000	0255800111	1121115
D. asperis	2111111101	2111–10–1	1201101111	2112–0111	111111––22	1111121012	110––00411	5150110–1	1111111111	1100310200	0215720111	1121111
D. assamica	211111??1	2111–10–1	1201101111	2112–0111	111111––22	1111121012	2111100411	5150110–1	1111111111	1123310200	0215820111	1121111
D. averrhoae	211111??1	2111–10–1	1201101111	2112–0101	111111––22	1101121012	110––00411	5150110–1	1111111111	1120310200	0215520111	1121111
D. azadirachtae	2111111141	2111–10–1	1201101111	2112–0111	111101––22	1111121012	110––00411	5150112?0–1	1111111111	1123310200	0225920111	1121111
D. barringtoniae	2111111101	2111–10–1	1201101111	2112–0101	111111––22	1111121012	210––00411	5150110–1	1111111111	1123310200	0225720111	1121113
D. bengalensis	2111111141	2111––2––1	1201101111	2112–0101	111?11––22	0101121012	210––00411	5150110–1	1111111111	1100210000	0215700111	1121111
D. benjaminae	2111111141	2111–10–1	1201101111	1112–0111	111111––22	1111121012	110––00411	5150110–1	1111111111	1123310200	0215620111	1121111
D. boueae	2111111101	2111–10–1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123510200	0215820111	1121111
D. camarae	2111111101	2111–10–1	1201101111	[12]1112–01001	111111––22	1111121012	110––00411	6150117–1	1111111111	1123510200	0215720111	1121113
D. cerberae	2111111141	2111–10–1	1201101111	2112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123310200	0225720111	1121111
D. championi	211111??1	2111––2––1	1201101111	2112–01?01	111?????22	???1121012	710––00411	5150110–1	1111111111	11???10???	0??55?0111	1121111
D. cocculae	211111??1	2111–10–1	1201101111	2112–0111	111111––22	1101121012	210––00411	5150111–1	1111111111	1120310200	0215620111	1121113
D. combretae	2111111141	2111–10–1	1201101111	1112–0101	111111––22	1101121012	110––00411	5150110–1	1111111111	1100210200	0205720111	1121113
D. combreti	211111??1	2111––2––1	1201101111	1112–0101	111111––22	1111121012	4111–00411	5150110–1	1111111111	1123310200	0105720111	1121113
D. commuiae	211111??1	2111–10–1	1201101111	1112–0101	111111––22	1111121012	410–200411	5150110–1	1111111111	1120310200	0225620111	1121116
D. coreiae	2111111101	2111–10–1	1201101111	1112–0210	111111––22	1111121012	110––00411	5150113–1	1111111111	1120310200	0215720111	1121116
D. cumingis	211111??1	2111–10–1	1201101111	1112–0101	111111––22	1111121012	2111600411	5150110–1	1111111111	1100310200	0215620111	1121116
D. cuminis	2111111101	2111–10–1	1201101111	2112–0111	111111––22	1111121012	110––00411	5150110–1	1111111111	1123310200	0215720111	1121111
D. cuminis Huang	211111??1	2111––2––1	1201101111	2112–0101	1111100022	1101121012	1111100411	5150110–1	1111111111	1100310200	0215720111	1121111
D. cythereae	211111??1	2111–10–1	1201101111	2112–0101	111111––22	1111121012	210––00411	5150111–1	1111111111	1122310200	0215720111	1121113
D. davisi	2111111141	2111–10–1	1201101111	2112–0101	111111––22	1111121012	410––00411	5150118–1	1111111111	1111210200	0205720111	1121113
D. dendropanacis	211111??1	2111––2––1	1201101111	1112–0101	111111––22	1111121012	210––00411	5150110–1	1111111111	1123310200	0215720111	1121113
D. elaeocarpi	2111111101	2111–10–1	1201101111	2112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1123310200	0215720111	1121113
D. elliptus	211111??1	2111–10–1	1201101111	1112–0101	111111––22	1111121012	110––00411	5150110–1	1111111111	1120310200	0215720111	1121111
D. emarginatus	211111??1	2111––2––1	1201101111	2112–0101	111111––22	1101121012	4111100411	5150110–1	1111111111	1100310200	0215420111	1121111
D. ervatamiae	2111111101	2111–10–1	1201101111	2101111101	111111––22	1111121012	110––00411	5150110–1	1111111111	1100310200	0215720111	1121113
D. eucalypti	2111111101	2111–10–1	1201101111	2112–0111	111111––22	1111121012	110––00411	5150111–1	1111111111	1123310200	0215720111	1121113
D. euryae	211111??1	2111–10–1	1201101111	1112–0101	111111––22	1101121012	110––00411	5150?100–1	1111111111	1103310200	0215420111	1121111
D. ficifolius	211111??1	2111––2––1	1201101111	?112–0111	111111––22	1101121012	110––00411	5150110–1	1111111111	1100310200	0225520111	1121111
D. ficus	2111111101	2111–10–1	1201101111	2112–0101	111111––22	1111121012	110––00411	5150111–1	1111111111	1123310200	0215520111	1121113
D. ficusis	2111111101	2111––2––1	1201101111	2112–0101	111111––22	1101121012	110––00411	5150110–1	1111111111	1112310200	0215620111	1121115

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
D. formosanus	21111111?1	2111––2––1	1201101111	1112–**0**1001	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1100310200	0215820111	1121111
D. gilibertiae	2111111141	2111–10–1	1201101111	1112–**0**1101	111111––22	1111121**012**	210––004**1**1	5150**1**110–1	1111111111	1123310200	0215720111	1121113
D. guajavae	2111111101	2111–10–1	1201101111	2112–**0**1001	111101––22	1111121**012**	110––004**1**1	5150**1**?0–1	1111111111	1103210000	2––5702111	1121111
D. hexogonus	21111111?1	2111––2––1	1201101111	1112–**0**1001	111111––22	1101121**012**	1111100**1**11	5150**1**100–1	1111111111	1100310200	0245520111	1121111
D. holmesi	21111111?1	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	410––004**1**1	5150**1**110–1	1111111111	1123310200	0215720111	1121113
D. holopteleae	2111111101	2111––2––1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1100310200	0235820111	112111[16]
D. holoptelus	2111111101	2111–10–1	1201101111	2112–**0**1101	111111––22	1101121**012**	410––004**1**1	5150**1**100–1	1111111111	1123310200	0215620111	112111[16]
D. illicii	21111111?1	2111–10–1	1201101111	1112–**0**1001	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1123310200	0215520111	1121113
D. indicus	21111111?1	2111––2––1	1201101111	2112–**0**1001	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1100310200	0115620111	1121114
D. integrifoliae	21111111?1	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5151**1**100–1	1111111111	1122510200	0235820111	1121113
D. jasminiae	2111111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1123310200	0215720111	1121116
D. javanicus	21111111?1	2111––??–1	1201101111	21???**0**1?01	111111––2?	1111121**012**	?1???004**1**1	5150**1**100–1	1111111111	11???10200	0?15720111	1121111
D. jevremovici	21111111?1	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	210––004**1**1	5150**1**160–1	1111111111	1123310200	0215720111	1121115
D. knorri	2111111141	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	1111600**1**11	5150**1**170–1	1111111111	1103210100	0215810111	1121113
D. languasi	2111111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1123310200	0235720111	1121113
D. leeasis	2111111101	2111–10–1	1101101111	2112–**0**1101	111111––22	1111121**012**	110––004**1**1	5150**0**100–1	1111111111	1123310200	0215820111	1121111
D. leptophyllus	21111111?1	2111––2––1	1201101111	2112–**0**1001	111111––22	1101121**012**	2111100**1**11	5150**1**100–1	1111111111	1100310200	0225720111	1121111
D. lobbianus	21111111?1	2111––2––1	1201101111	2112–**0**1001	111111––22	1101121**012**	1111100**1**11	5120**0**100–1	1111111111	1100310200	0235920111	1121116
D. loropetali	21111111?1	2111–10–1	1201101111	1112–**0**1101	111111––22	1111121**012**	110––004**1**1	5150**1**110–1	1111111111	1123310200	0215420111	1121113
D. maduraiensis	2111111101	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**0**100–1	1111111111	1100210200	0205820111	1121113
D. malloti	21111111?1	2111–10–1	1201101111	1112–**0**1001	111111––22	1101121**012**	210––004**1**1	5150**0**110–1	1111111111	1123310200	0215720111	1121116
D. melastomae	2111111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	1111900**1**11	5150**1**3141	1111111111	1123510200	0205620111	1121111
D. meliae	2111111141	2111–10–1	1201101111	2112–**0**1101	111111––22	1111121**012**	110––004**1**1	5150**1**110–1	1111111111	1123310200	0215820111	1121111
D. morii	21111111?1	2111––2––1	1201101111	2112–**0**1001	111111––22	1101121**012**	1111800**1**11	5150**0**110–1	1111111111	1100310200	0215720111	1121111
D. morindae	21111111?1	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1123310200	0215820111	1121113
D. musae	2111111141	2111–10–1	1201101111	2112–**0**1001	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1122310200	0215920111	1121113
D. octogonus	21111111?1	2111–10–1	1201101111	1112–**0**1001	111111––22	1101121**012**	1111100**1**11	5150**1**100–1	1111111111	1123310200	0215620111	1121113
D. pamithus	21111111?1	2111–10–1	1201101111	2112–**0**1101	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1120310200	0105720111	1121111
D. perfectus	21111111?1	2111––2––1	1201101111	1112–**0**1001	111111––22	1101121**012**	1111200**1**11	5150**1**100–1	1111111111	1100310200	0215820111	1121113
D. phylanthi	21111111?1	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1123310200	0215?20111	1121111
D. pocsi	21111111?1	2111––2––1	1201101111	2112–**0**1001	11111???22	1111121**012**	210––004**1**1	5150**1**110–1	1111111111	1123310200	0215720111	1121116
D. racemosae	2111111141	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1123210200	0215720111	1121116
D. riciniae	2111111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**110–1	1111111111	1123210200	0205620111	1121113
D. sandorici	2111111101	2111–10–1	1201101111	2112–**0**1001	11111???22	1111121**012**	110––004**1**1	5150**1**100–1	1111111111	1122310200	0205820111	1121113
D. securinegus	21111111?1	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	110––004**1**1	5150**1**160–1	1111111111	1123210200	0215?20111	1121116
D. septimus	21111111?1	2111––2––1	1201101111	1112–**0**1001	111111––22	1101121**012**	110––004**1**1	5150**1**100–1	1111111111	1100310200	0215420111	1121113
D. apolongus sp. nov.	2111111141	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	1121600**1**11	5150**1**160–1	1111111111	1123310200	0215[56]20111	1121113
D. apobrevus sp. nov.	2111111141	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	1121600**1**11	5150**1**160–1	1111111111	1123510200	0215[56]20111	1121113
D. faurius sp. nov.	2111111141	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	1121600**1**11	5150**1**160–1	1111111111	1123310200	0215[56]20111	1121116
D. stephanus	21111111?1	2111––2––1	1201101111	2112–**0**1001	111111––22	1111121**012**	1111200**1**11	5150**1**140–1	1111111111	1100310200	0217220111	1121111
D. strebli	21111111?1	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	410––004**1**1	5150**1**100–1	1111111111	1123310200	0215720111	1121116

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
D. swieteniae	211111141	2111–10–1	1201101111	2112–**0**1101	111111––22	1111121**012**	110––00411	51501**1**10–1	1111111111	1123310200	0215920111	1121113
D. thaianae	211111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––00411	51501**1**10–1	1111111111	1123210200	0215820111	1121115
D. thangaveli	21111111?1	2111–10–1	1201101111	1112–**0**1001	111101––22	1111121**012**	210––00411	51500**1**10–1	1111111111	1100210000	0215800111	1121113
D. thunbergiae	211111101	2111–10–1	1201101111	1112–**0**1001	111111––22	1111121**012**	110––00411	51501**1**00–1	1111111111	1123310200	0205620111	1121111
D. trewier	211111101	2111––2––1	1201101111	2112–**0**1001	111111––22	1101121**012**	411110**0**411	51501**1**00–1	1111111111	1123310200	0215820111	1121115
D. ulmivagrans	211111101	2111–10–1	1201101111	1112–**0**1001	111101––22	1101121**012**	110––00411	51501**1**00–1	1111111111	1100210000	0205[56]00111	1121111
Diptiloplatus megagrastis	211111101	2110451021	0101101111	2102**0**1101	1111001022	0101121**012**	2122200311	7160**1**120–1	1111111111	1123210000	0238700111	1121113
Diptilorhynacus dioscoreae	211111101	2111–10–1	1201101111	2112–**0**1001	111111––22	1111121**012**	610––00411	51501**1**00–1	1111111111	1120210200	0215620111	1121113
Diptilorhynacus sinusetus	211111101	2111––2––1	1211101111	0112–**0**1001	111111––22	1101121**012**	910––00411	51501**1**00–1	1111111111	1103210000	0215600111	1121116
Diptilostatus nudipalpus	211111141	2111–10–1	0101101111	1101**1**01001	111101––22	1101121**012**	110––00411	51501**1**20–1	1111111111	1123510000	0205800111	1121115
Disella ilicis	211111101	2110331051	0101101111	1112–**0**1001	111001––24	0001121**001**	2122100411	5151**1**100–1	1111111111	1100310000	1––1801111	1121115
Ditrymacus athiasella	211111101	2110341241	0101101111	0101201101	1110001622	0001121**001**	2122100311	7163**1**100–1	1111111111	1100310000	0231900111	1121115
Duabangus chiangmai	211111101	2110331111	0101101111	2101**0**1101	111101––22	1001121**012**	410––00411	5150**1**13121	1111111111	1100310000	0235[456]00111	1121??3
Ectomerus anysis	211111101	2110331201	0101101111	2101**3**0100**1**	1110000422	0001121**001**	2222800411	11100**1**10–1	1111111111	1120310000	0211800111	1132115
Epicecidophyes clerodendris	211111101	2110341021	0101101111	2101**0**0100**1**	1110000322	0101121**001**	2122100311	5162**1**100–1	1111111111	1100310000	0231800111	1133116
Epiphytimerus palampurensis	211111101	2110341241	0101101111	0101**1**01001	1110000422	0001121**001**	2122900411	7162**1**10–1	1111111111	1100310000	0241900111	1121116
Epitrimerus pyri	211111101	2110331021	0101101111	0101**0**0100**1**	1110000422	0001121**001**	2122200411	7160**1**10–1	1111111111	1123310000	0221900111	1121116
Eriophyes pyri	211111101	2110221201	0101101111	0101**1**01001	1110000322	0001121**001**	610––00411	3110**0**110–1	1111111111	1121510000	0211900111	1121?16
Eriophyes quadrifidus	211111101	2110331021	0101101111	0101**2**01001	1110000422	0001121**001**	2122100411	11100**1**10–1	1111111111	1123310000	0231900111	1121115
Euterpia fissa	211111121	2110341031	0111111111	2101**0**0100**1**	1111000222	1001121**001**	6122100411	8120**1**100–1	1111111111	1100310000	0111a00111	1122???
Floracarus calonyctionis	211111101	2110331241	0101101111	2112–**0**1001	111001––24	0001121**001**	2122100411	6110**0**110–1	1111111111	1123510000	2––1902111	1121115
Fragariocoptes setiger	211111101	20103410[014]	**0**0101101**1**1	1010**1**10100	1111000042	2000112**100**	1212220041	1[67]**1**500120–	1111111111	1110031000	0022190011	1121??6
Gammaphytoptus camphorae	211111101	2110231241	0101101111	2101**3**0100**1**	1110000422	0001121**001**	2122100411	5161**5**110–1	1111111111	1110510000	0221700111	1132115
Glyptacus lithocarpi	21111111?1	2111––2––1	0101101111	2101**2**0100**1**	1110000322	0001121**001**	2122100411	6151**1**110–1	1111111111	1110310000	0211600111	1132116
Heterotergum gossypii	211111101	2110221241	0101101111	0101**2**0100**1**	1110000422	0001121**001**	2122400311	6162**0**110–1	1111111111	1120310000	0221800111	1121115
Hyboderus roseus	211111101	2110341101	0101101111	0101**0**01101	1111000422	1101121**012**	610––00311	5160**0**100–1	1111111111	1112310000	0231[67]00111	1121112
Hyborhinus kallarensis	211111101	2110331101	0101101111	0112–**0**1001	1110002422	0001121**012**	610––00411	5161**0**160–1	1111111111	1100310000	0441600111	1121111
Indonotolox sudarsani	211111101	2110331001	0101101111	0112–**0**1001	111001––22	0001121**001**	2122100411	a1401**1**00–1	1111111111	1100310000	0231700111	1121111
Indosetacus rhinacanthi	211111101	2110331241	0101101111	0101**4**0100**1**	1110000422	0001121**001**	210––00411	1180019**0**–1	1111111111	1123310000	0111900111	1132111
Indotegolophus darjeelingensis	211111101	2110331241	0101101111	2101**4**0100**1**	1110000522	0001121**001**	210––00411	5180**1**110–1	1111111111	1123310000	0221700111	1121116
Johnella virginiana	21111111?1	2111––2––1	0101101111	2101**2**0100**1**	1110000422	0001121**001**	2122200311	7173**0**100–1	1111111111	1110310000	0211600111	1132115
Jutarus benjaminae	211111101	2111––2––1	0101101111	2112–**0**1001	1110000222	0101121**001**	1122700411	5150**0**110–1	1111111111	1110310000	0211900111	1121??3
Kaella flacourtiae	211111141	2111–10–1	1201111111	1112–**0**2101	111101––22	1101121**012**	110––00411	5150**1**100–1	1111111111	1122210000	0205600111	1121??6
Keiferana neolitseae	211111101	2110341241	0101101111	2101**2**0100**1**	1110000122	0001121**001**	2122300411	6140**0**1014**1**	1111111111	1103310000	0351800111	1121??1
Keiferella juniperici	21111111?1	2110341011	0101101111	0101**0**01101	1110000322	0001121**001**	2133–00411	5130**1**100–1	1111111111	1100310000	0431600111	1121??5
Keiferophyes avicenniae	211111101	2110331241	0101101111	0101**2**0100**1**	1110000422	0001121**001**	210––00411	11100**1**10–1	1111111111	1123310000	0231800111	1123116
Knorella gigantochloae	211111141	2111––2––1	0111111111	2101**0**0100**1**	1111000322	1101121**001**	8122800411	8167**1**100–1	1111111111	1123310000	0215800111	1121113
Konola hibernalis	211111101	2110331211	0101101111	2101**2**0100**1**	1111000422	1001121**012**	a122a00411	6120**1**16171	1111111111	1100210000	0231600111	1123115
Lambella cerina	211111141	2110341111	1201101111	2112–**0**1001	111111––22	1101121**012**	910––00411	5160**1**0111	1111111111	1120510001	0215700111	1121116
Latinotus wegoreki	211111101	2110341201	0101101111	0101**1**01001	1110000222	0001121**001**	2122100411	7160**1**100–1	1111111111	1100310000	0241800111	1121116
Leipothrix solidaginis	211111121	2110341021	0101101111	0101**0**01201	1111000522	1001121**001**	2122200411	6160**1**110–1	1111111111	1123310000	0231900111	1121115

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Levonga caseariasis	2111111101	2110441011	1201101111	2112–0101	111101––22	1101121012	110––00411	5160110–1	1111111111	1100210000	0215400111	1121?11
Levonga litseae	2111111101	2110441011	1201101111	2112–0101	111101––22	1111121012	110––00411	5110011–1	1111111111	1123210000	0215600111	1121113
Levonga papaitongensis	2111111101	2110451021	1201101111	0112–0101	111101––22	1101121012	210––00411	5160010141	1111111111	1120510001	0215800111	1121??1
Litaculus khandus	2111111101	2110331011	0101101111	2101101001	1110000422	0101121001	2122300411	6162010–1	1111111111	1100310000	0215700111	1121?15
Lithocarus thomsoni	2111111101	2110441011	1201101111	1101001001	111111––22	1101121012	410––00411	5160114–1	1111111111	1110210200	0105620111	1121116
Mackiella phoenicis	2111111101	2010331001	0101101111	0101301301	1110000412	0001121001	2122600411	116001b0–1	1111111111	1100310000	0231600111	1121?11
Mediugum sanasaii	211111117?1	2110441041	1201111111	0101101001	111111––22	1101121012	112––00411	5150014–1	1111111111	1100210200	0?05620111	1121??3
Mesalox tuttlei	2111111101	2110331241	0101101111	2101001101	1110000422	0001121001	2122804111	6161110–1	1111111111	1123310000	0221900111	1121115
Metaculus syzygii	2111111101	2110341241	0101101111	1112–0101	1110000522	0001121001	2122303111	7161011–1	1111111111	1123310000	0231900111	1121115
Metaplatyphytoptus amoni	211111117?1	2110341011	0101101111	0112–0101	1110000422	0001121001	3122200411	7166110–1	1111111111	1100510000	0231a00111	1121??5
Tegoprionus bicristatus	2111111101	2110331241	0101101111	0101001001	1110000522	0001121001	2122100411	6160414–1	1111111111	1123310000	0231900111	1123115
Monotrymacus quadrangulari	2111111101	2110331051	0101101111	2101101101	1110000422	0001121001	3122100311	7182114–1	1111111111	1100310000	0241900111	1121115
Nacerimina gutierrezi	2111111101	2110341201	0101101111	2112–0101	1110000322	0101121001	810––00411	1110011–1	1111111111	1123310000	0111600111	1121115
Nalepella tsugifoliae	211111117?1	1110011011	0101101111	0101201101	1110000212	0001121001	9112200411	5130011–1	1111111111	1120310000	0651400111	1121121
Neoacaphyllisa lithocarpi	211111117?1	2110341021	0101101111	2101101001	1110002422	0001121001	2122200411	7160110–1	1111111111	1100510000	0215800111	1121??6
Neoacarhis aglaiae	211111117?1	2110441011	1201101111	2101001001	111101––22	1101121012	610––00411	7160110–1	1111111111	1100310000	0215700111	1121??1
Neocatarhinus bambusae	211111117?1	2110451021	0101101111	2101001001	1111000222	0101121012	6122200411	6160110–1	1111111111	1123310000	0241[56]00111	1121??3
Neocecidophyes mallotivagrans	2111111101	2110341231	0101101111	2101301001	1110000322	0001121001	2122100111	1143110–1	1111111111	1100110000	0221800111	1132111
Neocolopodacus mitragynae	2111111101	2110331051	0101101111	0101101001	111001––24	0001121001	2122100411	5162010–1	1111111111	1123510000	0211900111	1121115
Neocosella ichnocarpae	2111111101	2110341031	0101101111	2112–0101	111001––24	0001121001	2122200411	6150010–1	1111111111	1123510000	2––1902111	113???6
Neocupacarus flabelliferis	2111111131	2110341221	0111111111	2101001–11	1111000422	1001121001	2122100411	7150110–1	1111111111	1123310000	0211800111	1121114
Neodialox palmyrae	2111111101	2111––2––1	0101101111	0101001001	1111001422	0001121012	210––00411	5161110111	1111111111	1123310000	0765300111	1121111
Neodichopelmus samoanus	2111111101	2110341241	0101101111	2101201001	111001––22	0001121001	2122300411	7162011–1	1111111111	1110310000	0235a00111	1121??5
Neodicrothrix tiliacorae	2111111121	2110341131	0111111111	2101101001	111001––22	0101121001	8122300411	a1420100–1	1111111111	1100310000	0222900111	1121115
Neodiptilomiopus vishakantai	2111111101	2111–11–1	1201101111	1112–1301	111101––22	1101121012	110––00411	5150111–1	1111111111	1123310000	0215820111	1121113
Neolambella ligustri	211111117?1	2111––2––1	??0111???11	0112–0101	111111––22	1101121012	111––00411	5150110–1	1111111111	1100310000	0??5800111	1121??1
Neomesalox kallarensis	2111111101	2110331241	0111101111	2112–0101	1110000422	0001121001	2122804111	6140116111	1111111111	1100310000	0231900111	1121??1
Neometaculus bauhiniae	2111111101	2110341001	0101101111	2112–0101	1110000422	0001121001	2122100411	7162110–1	1111111111	1100510000	0231700111	1121115
Neophantacrus mallotus	2111111101	2110331241	0101101111	2101301001	1110000422	0001121001	210––00311	6160411–1	1111111111	1100510000	0231800111	1121?16
Neophytoptus ocimae	2111111111	2110331221	0101101111	0101001101	1111000422	1001121001	2122100411	1150011–1	1111111111	1123310000	0221900111	1121115
Neopropilus jatrophus	211111117?1	2011––2––0	0111111111	2101101101	111001––12	0001121001	8122100411	b1620200–1	1111111111	11??310000	0221900111	1121??1
Neorhynacus rajendrani	2111111101	2110441[12]1	1201101111	1101101001	1111000022	1101121012	110––00411	6150111–1	1111111111	1122210000	0245800111	1121113
Neotegonotus fastigatus	2111111101	2110331251	0101101111	0101101001	1110000522	0001121001	2122400311	6162116–1	1111111111	1100310000	0231900111	1121115
Neserella decora	2111111101	2111––2––1	0101111111	0112–0101	111001––22	0001121001	210––00411	5110011–1	1111111111	1123510000	0211900111	1133213
Norma lanyuensis	211111117?1	2111––2––1	1201101111	2112–0101	111001––22	1101121012	110––00411	5150010–1	1111111111	1100510000	0215700111	1121??5
Notacaphylla chinensiae	2111111101	2110331041	0101101111	2112–0101	111001––22	0001121001	2122800411	7162110121	1111111111	1100310000	0105800111	1121116
Notaceria tetrandiae	2111111101	2110331241	0101101111	0101401001	111001––21	0011121001	210––00111	1110011–1	1111111111	1100310000	0221800111	1121116
Notallus nerii	2111111101	2110331241	0101101111	0101101101	1110000422	0001121001	6122800311	7181115–1	1111111111	1100310000	0221900111	1121115
Nothacus tuberculatus	211111114?1	2110331041	0101101111	2101401001	111101––22	0001121001	2122100411	a1100110–1	1111111111	1121210000	0211800111	1121115
Nothopoda rapaneae	2111111101	2110331241	0101101111	2112–0101	111001––22	0001121001	610––00411	1110011–1	1111111111	1123210000	2––1902111	1121115
Notostrix attenuata	2111111101	2110331041	0101101111	2101201001	1110000322	0101121001	b1224003 11	9161110–1	1111111111	1123310000	0211600111	1121115

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Novophytoptus rostratae	2111111101	2010111241	0101101111	0101101401	1111000422	1001121001	b10--00411	2130011 0–1	1111111111	1123310000	0241[ab]00111	1112211
Novophytoptus stipae	211111114 1	2010001241	0101101111	0101001401	1111000522	1001121001	220--00411	4110011 0–1	1111111111	1123310000	0242900111	1112211
Oziella yuccae	2111111101	2010341050	0101101111	0101001301	1110000412	0001121001	610--00411	1110011 0–1	1111111111	1120310100	0221[56]10111	1121211
Palmiphytoptus oculatus	2111111101	2011--2--1	0101101111	1101101101	111001--22	0001121001	d221200211	1110111 0–1	1111111111	1100110000	0211500111	1123111
Pangacarus grisalis	2111111101	2110331031	0101101111	2112–01001	111101--22	0001121001	2122200411	5160010 0–1	1111111111	1120510000	2--1802111	1121116
Paracalacarus podocarpi	2111111101	2111--2--1	0101101111	1101101101	1111000122	1101121001	6112100411	5151111 0–1	1111111111	1123310000	0231900111	1121115
Paracaphylla streblae	2111111101	2110451011	0101101111	1101301001	1111000422	1001121001	210--00411	7162111141	1111111111	1100210000	0235[56]00111	1121113
Paraciota tetracanthae	2111111101	2110341241	0101101111	2101001001	111101--22	1101121001	2122100111	7162010 0–1	1111111111	1100310000	0231800111	1121116
Paracolomerus casimiroae	2111111101	2110321241	0101101111	0101401001	1110000422	0001121001	210--00411	1110011 0–1	1111111111	1120310000	0211800111	1122111
Paraphytoptella arnaudi	211111113 1	2110221241	0101111111	0101301001	1110000422	0001121001	210--00411	1180011 0–1	1111111111	1123310000	0211800111	1121113
Pararhynacus photiniae	211111113 1	2111–12–1	0101101111	2101001101	1111000122	1001121012	610--00411	a150110 0–1	1111111111	1120310000	0?45900111	1121??5
Pareria fremontiae	211111113 1	2110331201	0101101111	0101101001	1110000422	0001121001	210--00411	1180011 0–1	1111111111	1123310000	0221800111	1121115
Pentamerus rhamnicroceae	2111111101	2110331241	0101101111	0101001101	1110000422	0001121001	2122400411	6160114121	1111111111	1123310000	0231800111	1121116
Pentaporca taiwanensis	211111113 1	1110131001	0101101111	0101301101	1110000022	0001121001	7122100411	5161110 0–1	1111111111	1100210000	0651600111	1121??1
Pentasetacus araucaria	2111111101	1010331000	0101101111	0101201201	1110000412	0001121001	9122200311	3110011 0–1	1111111111	1100310000	0225a00111	1121?21
Peralox insolita	2111111101	2110231201	0101101111	0101201001	1110000422	0001121012	2122900411	6164611e0–1	1111111111	1100310000	0331600111	1121111
Phantacrus lobatus	2111111101	1110011201	0101101111	0101101101	1110000212	0001121001	2122800411	6165410 0–1	1111111111	1123310000	0551600111	1121121
Phyllocoptes calisorbi	2111111101	2110331021	0101101111	1101001101	1110000222	0001121001	2122800411	6110011 0–1	1111111111	1121310000	0211900111	1121115
Phyllocoptruta arga	211111114 1	2110331251	0101101111	2101401001	1110000222	0001121001	3122800411	7160116 0–1	1111111111	1111210000	0211a00111	1121115
Phyllocoptruta oleivora	2111111101	2110331021	0101101111	1101101101	1110000422	0001121001	6122100411	7161110 0–1	1111111111	1123310000	0211800111	1121115
Phytoptus avellanae	2111111101	2010331010	0101101111	0101001101	1110000522	0001121001	210--00411	1110011 0–1	1111111111	1113310000	0211[89]00111	1123213
Platyphytoptus sabinianae	2111111101	2110331021	0101101111	0101201001	1110000422	0001121001	e1216003 11	8116111 0–1	1111111111	1123210000	0211800111	1121113
Porcupinotus humpae	2111111101	2110331241	0101101111	0101001001	1110000422	0001121001	2122200111	6160116111	1111111111	1111310000	0231500111	1121116
Porosus monosporae	211111112 1	2110331241	0101101111	2101101001	1110000022	0001121001	2122100411	6140011c0–1	1111111111	1100310000	0231900111	1121111
Proartacris pinivagrans	2111111101	2110341221	0101101111	0101001001	1110000222	0001121001	2122200411	6160011 0–1	1111111111	1123310000	0231900111	1121114
Prodiptilomiopus auriculatae	211111114 1	2111--2--1	1101101111	2101201001	111111--22	1101121012	410--00411	5160110 0–1	1111111111	1100310000	0235600111	1121116
Proneotegonotus antiquorae	2111111101	2110451051	0111111111	2101101001	111001--22	0101121001	2122100411	a162010 0–1	1111111111	1100310000	0231800111	1121115
Prophyllocoptes riveae	2111111101	2110451051	0101111111	2101101001	1110000322	0001121001	2122200411	7162016 0–1	1111111111	1100310000	0221600111	1121111
Propilus gentyi	2111111101	2011--2--1	0101101111	2101101301	111001--22	0001121001	6122100411	7163020 0–1	1111111111	1120310000	0201a00111	1121121
Prothrix aboula	2111111101	0011--2--0	0111101111	2101301101	111001--12	0001121001	8122100111	7160120 0–1	1111111111	1100210000	0241800111	113??11
Pyelotus africanae	2111111101	2110331241	0101101111	1101201101	1110000622	0001121001	2122200411	7180115 0–1	1111111111	1123310000	0231900111	1121??5
Quadracus urticarius	2111111101	2110331201	0101101111	2101001001	1110000422	0001121012	2112600411	9163110 0–1	1111111111	1123310000	0211800111	1123116
(Kropczynella) mangiferae	2111111101	2110341021	0101101111	0101101101	1110000322	0001121012	210--00411	5160111 0–1	1111111111	1123310000	0231800111	1121??3
Quadriporca mangiferae	211111113 1	2110341011	0101101111	2101001001	1111000222	1001121012	2122200411	a160110 0–1	1111111111	1100310000	0231800111	1121??4
Quintalitus squamosus	211111114 1	2110331241	0101101111	1101401001	111101--22	0001121001	2122800411	7160110 0–1	1111111111	1123510010	0211800111	1121??6
Ramaculus mahoe	2111111101	2110321241	0101111111	0112–01001	111001--22	0001121001	210--00411	6110019 0–1	1111111111	1123510000	0111[89]00111	1121114
Rectalox falita	2111111101	2110331241	0101101111	2101101001	1110000322	0001121001	2122600111	6160110 0–1	1111111111	1123310000	0221800111	1121115
Retracrus johnstoni	2111111101	2010341041	0111101111	2101001201	1110100212	0101121001	8122100111	a163120121	1111111111	1100210000	0241700111	1121111
Rhinophytoptus concinnus	211111113 1	2110331201	0101101111	2101?01?01	1110000422	0001121012	?1121004 11	6110011 0–1	1111111111	1123110000	0331700111	1121???1
Rhinotergum schestovici	2111111101	2110331011	0101101111	0101301001	1110000422	0001121012	2122200411	6152011f0–1	1111111111	1100310000	0531900111	1121111
Rhombacus morrisi	2111111101	2110341011	0101101111	2101001101	1110000022	0001121001	3122300411	a162011 0–1	1111111111	1123510000	0341800111	1121115

318-taxon data matrix											1	1
	0	1	2	3	4	5	6	7	8	9	0	1
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
Rhynacus arctostaphyli	21111111?1	2111–12–1	1201101111	1112–**0**1001	1111000422	1101121**012**	110––004**1**1	61501**1**10–1	1111111111	1100410000	0215600111	1121115
Rhyncaphytoptus ficifoliae	21111111?1	2110331201	0101101111	0101201101	1110000422	0001121**012**	2122600411	61710**1**12–1	1111111111	1100310000	0221700111	1121111
Sakthirhynchus canariae	21111111?1	2111––2––1	1201101111	0112–**0**1001	111111––22	1101121**012**	110––00411	51601**1**00–1	1111111111	1100310000	0211700111	1121??1
Schizacea gynerii	2111111101	2111––2––1	0111111111	2101001101	1111000322	1101121**001**	2122200411	71621**1**00–1	1111111111	1123310000	0205800111	1121113
Schizoempodium mesophyllincola	2111111101	2110341211	0101101111	0101001001	1110000522	0001121**001**	b12180411	31100**1**10–1	1111111111	1123310000	0235900111	1122115
Scoletoptus duvernoia	2111111101	2110331–41	0101101111	0112–**0**1001	1110000122	0001121**001**	a10––00[14]11	41400**1**[1a]0–1	1111111111	1100310000	0111900111	1121116
Setoptus jonesi	2111111101	1110221101	0101101111	0101101101	1110000312	0001121**001**	510––00311	81101**1**10–1	1111111111	1123310000	0231300111	1121121
Shevtchenkella juglandis	21111111?1	2110341241	0101101111	0101101001	1110000422	0001121**001**	3122220311	71631**1**00–1	1111111111	1123310000	0211900111	1121115
Sierraphytoptus alnivagrans	2111111101	2010331010	0101101111	0101201101	1110000422	0001121**001**	2122110311	71610**1**00–1	1111111111	1100310000	0231b00111	1121211
Sinacus erythrophlei	21111111?1	2110331241	0101101111	0101101001	111001––22	0001121**001**	2122100411	71601**1**00–1	1111111111	1100310000	0221800111	1121??6
Stenacis palomaris	2111111101	2110331201	0101101111	1101301001	1110000522	0001121**001**	2121[689]00411	31100**1**10–1	1111111111	1123310000	0222a00111	1121116
Stenarhynchus aristidus	2111111101	2110331231	0101101111	1101101101	1110000322	0001121**012**	2122800411	31100**1**10–1	1111111111	1123310000	0221300111	1111116
Steopa bauhiniae	2111111101	2111–12–1	1011101111	1112–**0**1001	111101––22	1101121**012**	110––00411	51501**1**00–1	1111111111	1110310000	0217000111	1121??5
Suthamus chiangmi	211111114 1	2110451111	1001101111	1112–**0**1001	1111100222	1101121**012**	110––00411	51601**1**00–1	1111111111	1110210000	0215520111	1121??6
Tegolophus califraxini	2111111101	2110331041	0101101111	2101101001	1110000622	0001121**001**	2122200411	51611[01]0–1	1111111111	1100310000	0231700111	1121116
Tegonotus mangiferae	2111111101	2110451221	0101101111	0101101101	1110000122	0001121**001**	3122300411	71631**1**00–1	1111111111	1123310000	0231700111	1121115
Tegoprionus dentatus	2111111101	2110331041	0101101111	2101101001	1110000422	0001121**001**	3122200311	71611**1**00–1	1111111111	1120310000	0231900111	1121??6
Tergilatus sparsus	2111111101	2110341221	0101111111	0101001101	1110000422	0001121**001**	2122100411	81621**1**10–1	1111111111	1123510000	0251b00111	1121115
Tetra concava	2111111101	2110111241	0101101111	0101101001	1110000422	0001121**001**	2122800411	71611**1**20–1	1111111111	1110310000	0211900111	1121116
Tetraspinus lentus	21111111?1	2110341241	0101101111	0101101101	1110000422	0001121**001**	1122120411	71601**1**00–1	1111111111	1100310000	0231900111	1121115
Thailandus diospyrosae	211111114 1	2110451241	1201111111	1101101001	111111––22	0101121**012**	110––00411	51811**1**00–1	1111111111	1100510000	0211700111	1121??6
Thamnacus rhamnicola	21111111?1	2110331041	0101101111	2101101101	1110000522	0001121**001**	2122100311	71611**1**00–1	1111111111	1100310000	0231900111	1121??6
Trimeracarus heptapleuri	21111111?1	2110331001	0101101111	1101?01?01	1110000522	0001121**001**	210––00311	71501**1**10–1	1111111111	11??310000	0231800111	1122??6
Trimeroptes eleyrodiformis	2111111101	2110331011	0101101111	1101101001	1111000222	1001121**012**	2122700111	715011**0**111	1111111111	1123310000	0335800111	1121113
Trisetacus ehmanni	2111111101	1110221100	0101101111	0101101201	1110000312	0001121**001**	610––00411	11100**1**10–1	1111111111	1111110000	0211600111	1121121
Trisetacus pini	2111111101	1110221100	0101101111	0101101101	1110000312	0001121**001**	610––00411	11100**1**10–1	1111111111	1111210000	0211600111	1121121
Tumescoptes trachycarpi	2111111101	2110341221	0111111111	0101001101	1111000322	1101121**001**	2122200411	81211**1**00–1	1111111111	1111210000	0211b00111	1121115
Ursynovia ulmi	2111111101	2110001241	0101101111	0101101001	1110000422	0001121**001**	210––00411	71601**1**00–1	1111111111	1100310000	0231800111	1121??3
Vasates quadripedes	21111111?1	2110––1051	0101101111	2101001001	1110000422	0001121**001**	2122800411	61610**1**10–1	1111111111	1123310000	0115700111	1121115
Vimola syzygii	2111111101	2111–10–1	1201101111	2112–**0**1101	111101––22	1101121**012**	110––00411	51601**1**10–1	1111111111	1123210000	0215800111	1121??3
Vittacus mansoni	2111111101	2110331241	0101101111	2101201001	1110000622	0001121**001**	2122800311	61611**1**40–1	1111111111	1123310000	0231900111	1121115

APPENDIX E.

List of morphological characters and character states in 66 taxon data set used in analyses. All characters were analyzed unordered, except characters 4, 5, 49, and 52 which were ordered. Except for the ordered characters, no transformation series are implied by the character state numbers. The characters and character states are sub-samples of the characters used in the analyses of the 318 taxon data set, and see Chapter 4 for a complete discussion, and source, of the characters. Some of the character states not applicable for the taxon sample for the 66 taxon data set were omitted, but the characters could not be renumbered in time, and those in between state applicable, were left in. These didn't have an influence on the analyses, and the states will be renumbered, and those inapplicable will be excluded in the data sets for publication in peer reviewed journals.

CHAETOTAXY

Gnathosomal setae

0. Gnathosomal palpal setae *d*
- 0 = present, simple
- 1 = present, forked
- 2 = absent

Prodorsal setae

1. Setae *vi*
- 0 = pair present
- 1 = one seta absent, position of remaining seta shifted to mid-anterior
- 2 = absent

2. Setae *ve*
- 0 = present
- 1 = absent

3. Setae *sc* (presume setae *sc* in the Eriophyoidea are setae *sci* (*sc*1))
- 0 = present
- 1 = absent

4. Setae *sc* relative length
- 0 = exceptionally long (> 100)
- 1 = very long (66 – 100)
- 2 = long (31 – 65)
- 3 = average (4 – 30)
- 4 = short (1 – 3)
- 5 = minute (not measurable, less than 1 long)

5. Setae *sc* length relative to prodorsal shield
- 0 = exceptionally long (> three shield length)
- 1 = very long (< three, but > or equal to 1.5 shield length)
- 2 = long (< 1.5, but > or equal to one shield length)
- 3 = average length (< one, but > 0.2 shield length)
- 4 = short (< or equal to 0.2, but > 0.07 shield length)
- 5 = very short (< or equal to 0.07 shield length)

6. Scapular setal tubercles (dorsal tubercles)
- 0 = primary absent
- 1 = present
- 2 = secondary absent

7. Setae *sc*, and/or *sc* setal tubercles position
- 0 = ahead of rear shield margin (ahead, but less than half of shield ahead)
- 1 = well ahead of rear shield margin (on half of shield or further anteriad)
- 2 = on rear shield margin, or slightly ahead of rear shield margin

8. Direction of projection of setae *sc*
- 0 = anteriad, diverging
- 1 = anteriad: parallel, converging or up
- 2 = medially
- 3 = up and to the outside
- 4 = posteriad, usually diverging
- 5 = posteriad, converging
- 6 = any direction

Opisthosomal setae

9. Setae *c1* (subdorsal setae)
0 = present
1 = absent

10. Setae *c2* (lateral setae)
0 = present
1 = absent

11. Setal tubercles of setae *c2* (lateral setae)
0 = primary absent
1 = present
2 = secondary absent

12. Setae *d* (1st ventral setae)
0 = present
1 = absent

13. Setae *e* (2nd ventral setae)
0 = present
1 = absent

14. Setae *h1* (accessory setae)
0 = present
1 = minute or dot-like (2 µ or less)
2 = absent

Coxal plates setae

15. Setae *1b*
0 = present
1 = absent

16. Setal tubercles of setae *1b*
0 = primary absent
1 = present
2 = secondary absent

17. Distance between setal tubercles of setae *1b* in comparison with distance between setal tubercles of setae *1a*
0 = *1b* clearly further apart than *1a*
1 = *1b* slightly further apart than *1a*
2 = *1b* longitudinally in line with *1a*
3 = *1b* slightly closer together than *1a*
4 = *1b* clearly closer together than *1a*

18. Setae *1a*
0 = ahead of setae *2a*
1 = slightly ahead of setae *2a*
2 = in line with setae *2a*
3 = slightly behind setae *2a*
4 = behind setae *2a*

Leg setae

19. Leg I: basiventral femoral setae (*bv*)
0 = present
1 = absent

20. Leg I: setae *l''* (antaxial genual setae)

0 = present
1 = absent

21. Leg I: setae *l'* (paraxial tibial setae)
0 = present
1 = absent

22. Leg I: setae *l'* (paraxial tibial setae) position
0 = dorsal on tibia
1 = displaced to inner side of tibia
2 = absent

23. Leg I: setae *l'* (paraxial tibial setae) vertical position
0 = close to apical (distal) margin (less than quarter tibial length from distal margin)
1 = at about distal quarter
2 = at distal third
3 = on about half of tibia
4 = at basal third
5 = at basal quarter
6 = near basal margin (less than a quarter from basal margin)

24. Leg I: tibial solenidion φ
0 = present, in "normal" position
1 = present, in ventrodistal position
2 = absent

25. Leg I: tarsal solenidion ω position
0 = antaxial, on distal third of tarsus
1 = dorsal, about mid-tarsus
2 = dorsal, close to and above empodium
3 = lateral, close to empodium, on outer side of tarsus
4 = lateral, close to empodium, on inner side of tarsus
5 = ventrad of empodium

26. Leg II: setae *bv* (basiventral femoral setae)
0 = present
1 = absent

27. Leg II: setae *l''* (antaxial genual setae)
0 = present
1 = absent

28. Leg II: paraxial, fastigial, tarsal setae (*ft'*)
0 = present
1 = absent

GNATHOSOMA

29. Gnathosoma: oral stylet
0 = of short form (Fig. 3.22a)
1 = of long form (Fig. 3.22b)

30. Gnathosoma: chelicerae
0 = very long and recurved in stylophore
1 = relatively straight and relatively short in comparison with palpi (Fig. 3.22a)
2 = abruptly bent down near base and relatively long in comparison with palpi (Fig. 3.22b)

PRODORSUM

Prodorsal shield

31. Prodorsal shield shape
- 0 = almost absent
- 1 = broadly oval (shorter than wide)
- 2 = triangular or subtriangular, sometimes with rounded sides or more semicircular
- 3 = subtriangular with bulging sides
- 4. = subtriangular and broad
- 5 = inverted subtriangular
- 6 = circular or subcircular
- 7 = diamond-shaped
- 8 = subquadrate
- 9 = sub-rectangular
- A = elongate oval
- B = elongate triangular

32. Prodorsal shield frontal lobe
- 0 = absent
- 1 = short or indistinct (not reaching across cheliceral bases)
- 2 = present

33. Prodorsal shield frontal lobe
- 0 = absent
- 1 = present, thin and flexible
- 2 = present, rigid

34. Apical edge of frontal lobe
- 0 = lobe absent
- 1 = blunt and rounded
- 2 = blunt and rounded, but narrow in shape (e.g. when lobe is more triangular)
- 3 = blunt and rounded with irregular edge
- 4 = sharply pointed
- 5 = spine-like
- 6 = square with rounded corners
- 7 = rectangular anterior lobe with indentation
- 8 = acuminate, but not sharply pointed
- 9 = small indentation
- A = broad, clear indentation with broad lobes
- B = fine, slender lateral extensions

Prodorsal shield ornamentation

35. Prodorsal shield ornamentation (Eriophyoidea)
- 0 = shield absent
- 1 = ornamentation absent
- 2 = absent centrally, ornamented along edges
- 3 = faint, obscure or virtually unornamented
- 4 = ornamentation present

IDIOSOMA

Opisthosoma shape and microtuberculation

36. Body shape
- 0 = varying from rounded to oval
- 1 = vermiform (similar to *Phytoptus* and *Aceria* spp.)
- 2 = cylindrical
- 3 = vermiform, elongated
- 4 = vermiform, extremely elongated

5 = fusiform, medium thick to more "fat" (similar to *Diptilomiopus* spp.), with or without narrow rear end
6 = fusiform, elongated, medium thick (similar to *Aculus* or *Abacarus* spp.)
7 = fusiform, flattened
8 = fusiform, extremely flattened
9 = fusiform, very long
A = fusiform, broad anteriorly, very narrow tail
B = fusiform, flattened, narrow tail (e.g. *Aberoptus samoae*)

37. Opisthosoma dorsoventral differentation: annuli
0 = annuli absent
1 = subequal and similar in appearance, dorsally and ventrally
2 = subequeal, differentiated in appearance dorsally and ventrally
3 = subequal, numerous, and visibly narrower than "normal"
4 = subequal or equal in count, but broader than "normal"
5 = differentiated into slightly broader dorsal annuli and narrower ventral annuli
6 = clearly differentiated into broader dorsal annuli and narrower ventral annuli
7 = dorsal annuli extremely broader than ventral annuli
8 = variably different

38. Opisthosomal dorsal annuli
0 = without lateral extensions or lobes
1 = very slight lateral projection (no demarcation line laterally)
2 = with slight lateral projection (in lateral view, dorsal annuli separated from ventral annuli by some sort of demarcation); the extend of lateral projection not always clear, some of these species not assigned to Tegonotini
3 = with clear lateral extensions or lobes (currently defining state for Tegonotini)
4 = small spine-like lobes on margin between dorsal and ventral annuli
5 = extensive lateral lobes, also present dorsally
6 = ventro-lateral ridges forming grooves
7 = lateral lobes uneven, extending more from some annuli

39. Opisthosoma: ridge(s) and/or furrow(s)
0 = absent
1 = present
2 = absent, except for some rear dorsal annuli which are higher than the others
3 = some anterior dorsal annuli fused into ellaborate dorsal structures
4 = with large lobes dorsally

40. Dorsal annuli of telosome
0 = annuli absent
1 = not fused
2 = fused

41. Dorsal annuli
0 = without microtubercles (mostly smooth)
1 = entirely microtuberculated
2 = entire but mostly obscure or faint
3 = smooth with few scattered microtubercles in sparse clumps (laterally and/or middorsally) (e.g. *Chiangmaia longifolii*) or with clumps or spots with microtubercles (see *Duabangus chiangmai*)
4 = smooth with microtubercles on ridges: lateral (see *D. stephanus*); relatively large spines on ridges (see *Pentamerus rhamnicroceae*)
5 = faint but clear on lateral ridges (see *Notallus nerii*)
6 = with central area smooth, and microtuberculated laterally

Secretions

42. Wax secretion
0 = absent
1 = present in adults

2 = only present in immatures

43. Wax type and secreting structures
0 = absent
1 = present, thickened wax bearing ridges
2 = present, wax from tubercles
3 = broad wax rim around shield, large wax plates along body margin
4 = body covered with wax

LEGS, COXAL PLATES AND STERNAL AREA

Ornamentation on coxal plates andmorphology of sternal area

44. Coxal plates I
0 = unornamented (mostly smooth) (also including described as "virtually unornamented")
1 = faintly or slightly ornamented
2 = ornamented
3 = continuation of body striae

45. Coxal plates II
0 = unornamented (smooth), including virtually unornamented
1 = faintly ornamented
2 = sparsely ornamented
3 = ornamented
4 = continuation of body striae

46. Prosternal apodeme: coxae I
0 = more widely separated than found in the Eriophyoidea, prosternal apodeme not present, "normal' ventral area extended between coxae
1 = widely separated (see *Davisella breitlowi*, *Neocecidophyes mallotivagrans*, *Palmiphytoptus oculatus* and *Trisetacus ehmanni*)
2 = separated
3 = coxae I touching, usually with sternal apodeme present
4 = sternal apodeme visibly broader than usually in the Eriophyoidea (see *Rhynacus arctostaphyli*)
5 = totally fused centrally (or prosternal apodeme may be present but effaced – not "visible" as sternal line)

LEGS (excluding coxae)

47. Leg I: femur and genu articulation
0 = normally articulated
1 = division weak, almost fused
2 = not articulated, totally fused
3 = genu present, but "fused" to femur

48. Leg I: tibia presence
0 = present
1 = partly fused to tarsus
2 = completely fused to tarsus (absent)

49. Leg I: tibia length
*1 = short (2-3 micron)
2 = average (4-11 micron)
3 = medium long (12-13 micron)
4 = average long (14-15 micron)
5 = long (16-17 micron)
6 = very long (19-20 micron)
7 = very, very long (22 micron)

8 = exceptionally long (30 micron)

* character state numbers start at 1, and not at 0, because 0 (absent) was replaced with "-" (not applicable) in the final matrix that was analysed (Appendix E)

50. Leg I: length of tibia in relation to length of tarsus
0 = tibia shorter than half of tarsus length
1 = tibia shorter than tarsus, half or more of tarsus length
2 = tibia length equal to tarsus length
3 = tibia longer than tarsus, but less than half the length of tarsus longer
4 = tibia longer than tarsus, half or more, but less than twice the tarsus length
5 = tibia about twice as long as tarsus

51. Leg I: empodium
0 = pad-like with numerous rays
1 = simple
2 = simple, distally elongated
3 = simple, rays unsymmetrical (more rays on one side than the other) e.g. *Dechela epelis*
4 = partly divided
5 = divided
6 = divided, stems unequal
7 = divided, stems pad-like with numerous rays
8 = divided, with central stem
9 = palmate
A = basal rays finely branched, hair-like (e.g. *Brevulacus reticulatus*)
B = reduced to a bristle
C = six tenent hairs basally and centrally attached

52. Leg I: number of empodial rays.
0 = numerous rays (can not count)
1 = 16-rayed or more
2 = 11-12 rayed
3 = 10-rayed
4 = 9-rayed
5 = 8-rayed
6 = 7-rayed
7 = 6-rayed
8 = 5-rayed
9 = 4-rayed
A = 3-rayed
B = 2-rayed
C = reduced to a bristle (no rays)
D = six tenent hairs

53. Leg II: femur and genu articulation
0 = normally articulated
1 = division weak, almost fused
2 = not articulated, totally fused

54. Leg II: tibia presence
0 = present
1 = partly fused to tarsus
2 = completely fused to tarsus (absent)

GENITALIA

55. Location of genital area
0 = caudally
1 = about 9-15 annuli removed from coxae, located posterior to setae *c2*
2 = close to, but not appressed to coxae
3 = appressed to coxae

56. Form of female internal genital apodeme
- 0 = homologous structure to eriophyoid female genital apodeme absent
- 1 = moderately extended to front (“normal”)
- 2 = folded up, appearing like a thick transverse line
- 3 = folded up, but appearing slightly broader than a transverse line

57. Shape of spermathecae
- 0 = spermathecae homologous to the eriophyoid spermathecae absent
- 1 = round or ovalish
- 2 = elongated

58. Spermathecal tubes
- 0 = spermathecal tubes similar to those in the Eriophyoidea absent
- 1 = relatively short to very short (normal)
- 2 = long

59. Female genital coverflap
- 0 = absent
- 1 = entirely unornamented
- 2 = entirely unornamented, but divided into a basal and distal area (e.g. *Hoderus roseus*)
- 3 = basally ornamented, distally unornamented (smooth)
- 4 = basally unornamented (smooth), distally ornamented
- 5 = entirely ornamented, divided in basal and distal area
- 6 = entirely ornamented, not divided in basal and distal area

APPENDIX F.

Data matrix of morphological characters for 64 eriophyoid species and two outgroup species (*Orphareptydeus* and *Mononychelus*) for the 66tax analyses. ? = uncertain or unknown character states, - = inapplicable states.

APPENDIX F.

	0 0123456789	1 0123456789	2 0123456789	3 0123456789	4 0123456789	5 0123456789
Orfareptydeus stepheni	0000330060	0000000000	0002210102	1?0??00000	010?340008	1000000000
Mononychelus yemensis	2200030060	000000002?0	0001000002	0?0??00000	010?340008	1CD0000120
Abacarus acalyptus	?210331241	0100001100	0005220000	1222246201	1011233002	3170021116
Aberoptus samoae	?210331231	0100201220	01??230000	110??4B100	110?003301	09C0033116
Acadicrus bifurcates	0210331211	0100201100	0005220000	1221B46500	110?233003	4170021113
Acalitus ledi	2210331041	0100201301	01??220000	1A0??43100	110?233002	1180021115
Acamina nolinae	0210331011	0111201011	0003221000	1222647501	1011004003	3180021115
Acaphyllisa parindiae	0210?41021	0100201110	0020220000	1222347631	100?133002	24A0021115
Acaricalus segundus	0210341011	0100201000	0004220000	1722147201	100?002002	2590021115
Acathrix trymatus	0200551200	0100001110	0003120000	120??41100	110?113002	2120021211
Aceria tulipae	0210211241	0100001010	0004220000	120??41100	110?233002	1160021116
Acritonotus denmarki	0210341211	0100201000	0002220000	1222117821	100?003005	49A0021115
Aculops populivagrans	0210331241	0100201210	0005220000	1222436600	120?233002	3190021116
Aculus ligustri	0210331241	0100001100	0005220000	1222236600	1[02]0?203002	4190021116
Acunda plectilis	0210331241	0100001010	0002220000	120??41401	110?103002	1150023116
Aequsomatus lanceolatae	0210331011	0100112?00	0006220000	1222146400	120?133002	31A0021??1
Anthocoptes gutierreziae	0210341241	0100001210	0004220000	1322237730	100?233002	2190021115
Apodiptacus cordiformis	0210331211	0100201001	0004221001	2222947611	1011234003	3590021215
Asetacus madronae	?211??10?1	0100201011	0003221001	2922745200	1014204004	3170021115
Calacarus pulviferus	0211???2??1	0100201110	0004220100	1222145201	1012233002	3190021115
Catarhinus tricholaenae	?210341011	0100201121	0000230001	2222837611	110?233002	1170021113
Cecidophyes rouhollahi	0211???2??1	0100201300	0003220000	1212145200	110?103002	2180032115
Cenaca syzygioidis	2210321241	0100212?01	01??220000	120??31100	110?003001	1190021116
Cenalox nyssae	0210331251	0100201300	0002220000	1222437501	110?002002	1190031111
Chakrabartiella ficusis	0210331201	0100012?01	0006221001	210??15501	110?003002	3180021114
Cheiracus sulcatus	0210341251	0100201000	0014220001	2B22147611	100?233002	3000021113
Colomerus gardeniella	0210331211	0100201300	0004220000	120??41100	110?003002	1180032115
Colopodacus africanus	0210341021	0100201300	01??220000	1322146101	110?00302?	?180221113
Cosetacus camelliae	0210221241	0100201400	01??220000	120??43100	110?003002	1170033115
Dechela epelis	0211???2??1	0100212?00	01??250100	1312643100	110?233001	13[678]0032116
Dicrothrix anacardii	1210341011	0110201000	0016220000	1622147403	100?003002	3290021111
Diptacus sacramentae	0210331211	0100201011	0000221001	2222146600	1212113004	3570021111
Diptilomiopus assamica	?211??10?1	1200212?11	11??221111	2211145501	100?233202	1582021111

	0 0123456789	1 0123456789	2 0123456789	3 0123456789	4 0123456789	5 0123456789
Diptilomiopus averrhoae	?211??10?1	1200212?01	11??221101	210??45501	100?203202	1552021111
Diptilomiopus jevremovici	?211??10?1	1200112?01	11??221111	220??45501	160?233202	1572021115
Epicecidophyes clerodendris	0210341021	0100201000	0003220100	1222135621	100?003002	3180033116
Eriophyes pyri	0210221201	0100001100	0003220000	160??43100	110?215002	1190021?16
Eriophyes quadrifidus	0210331021	0100001200	0004220000	1222141100	110?233002	3190021115
Hyboderus roseus	0210341101	0100001011	0004221101	260??35600	100?123002	31[67]0021112
Knorella gigantochloae	2211???2??1	0111201001	0003221100	1822848671	100?233002	1580021113
Litaculus khandus	0210331011	0100201100	0004220100	1222346620	100?003002	1570021?15
Nalepella tsugifoliae	?110011011	0100001210	0002120000	1912245300	110?203006	5140021121
Neopropilus jatrophus	?201???2??0	0111201110	01??120000	182214B620	200???3002	2190021??1
Neorhynacus rajendrani	02104410[12]1	1200101101	0000221101	210??46501	110?222002	4580021113
Nothopoda rapaneae	0210331241	0100212?00	01??220000	160??41100	110?23202?	?190221115
Novophytoptus stipae	2200001241	0100001041	0005221000	120??44100	110?233002	4290012211
Paracalacarus podocarpi	0211???2??1	0100101111	0001221100	1612145511	110?233002	3190021115
Paracolomerus casimiroae	0210321241	0100001400	0004220000	120??41100	110?203002	1180022111
Pareria fremontiae	?210331201	0100001100	0004220000	120??41800	110?233002	2180021115
Pentamerus rhamnicroceae	0210331241	0100001010	0004220000	1222446601	1412233002	3180021116
Pentasetacus araucaria	0100331000	0100001220	0004120000	1922233100	110?003002	25A0021?21
Phantacrus lobatus	0110011201	0100001110	0002120000	1222846654	100?233005	5160021121
Phyllocoptruta arga	2210331251	0100201400	0002220000	1322847601	160?112002	11A0021115
Phyllocoptruta oleivora	0210331021	0100101110	0004220000	1622147611	100?233002	1180021115
Phytoptus avellanae	0200331010	0100001010	0005220000	120??41100	110?133002	11[89]0023213
Prothrix aboula	0001???2??0	0110201310	01??120000	1822117601	200?002002	418003??11
Retracrus johnstoni	0200341041	0110201020	1002120100	182211A631	2012002002	4170021111
Rhynacus arctostaphyli	?211??12?1	1200112?01	0004221101	210??46501	110?004002	1560021115
Rhyncaphytoptus ficifoliae	?210331201	0100001210	0004220001	2222646710	112?003002	2170021111
Schizoempodium mesophyllincola	0210341211	0100001000	0005220000	1B21843100	110?233002	3590022115
Sierraphytoptus alnivagrans	0200331010	0100001210	0004220000	1222137610	100?003002	31B0021211
Tegolophus califraxini	0210331041	0100201100	0006220000	1222245611	1[01]0?003002	3170021116
Tegonotus mangiferae	0210451221	0100001110	0001220000	1322347631	100?233002	3170021115
Thamnacus rhamnicola	?210331041	0100201110	0005220000	1222137611	100?003002	3190021??6
Trisetacus ehmanni	0110221100	0100001120	0003120000	160??41100	110?111002	1160021121
Vasates quadripedes	?210??1051	0100201000	0004220000	1222846610	110?233001	1570021115

APPENDIX G

Appendix G.1. List of characters and character states from unchanged data set of Hong & Zhang (1996a). Some terminology was changed.

Appendix G.2. List of modified characters and character states of Hong & Zhang (1996a) to coincide with the data set defined for the present study.

Appendix G.1. List of characters and character states from unchanged data set of Hong & Zhang (1996a). Some terminology was changed.

0. Setae *vi*: (0) present; (1) absent.
1. Setae *ve*: (0) present; (1) absent.
2. Scapular setal tubercles: (0) absent; (1) present.
3. Setae *sc*: (0) present; (1) absent.
4. Frontal lobe (naso): (0) absent; (1) present.
5. Spine(s) on frontal lobe: (0) absent; (1) present.
6. Location of *sc*: (0) ahead of shield rear margin; (1) at shield rear margin.
7. Direction of *sc*: (0) anteriad; (1) posteriad; (2) upward or inward.
8. Body shape: (0) vermiform (worm-like); (1) fusiform (spindle-shaped).
9. Cheliceral curvature: (0) evenly curved; (1) abruptly curved downwards.
10. Location of genital area: (0) not appressed to coxae II; (1) appressed to coxae II.
11. Opisthosomal setae *c1*: (0) present; (1) absent.
12. Opisthosomal setae *d*: (0) present; (1) absent.
13. Opisthosomal setae *e*: (0) present; (1) absent.
14. Coxal setae *1b* on coxae I: (0) present; (1) absent.
15. Seta *bv* on femur I: (0) present; (1) absent.
16. Seta *l″* on genu I: (0) present; (1) absent.
17. Seta *l′* on tibia I: (0) present; (1) absent.
18. Seta *bv* on femur II: (0) present; (1) absent.
19. Seta *l″* on genu II: (0) present; (1) absent.
20. Tibia: (1) separate segment (“normal”); (1) reduced or fused.
21. Solenidion on tibia I: (0) present; (1) absent.
22. Ridge(s) or through(s) on opisthosoma: (0) absent; (1) present.
23. Empodium: (0) simple (“normal”); (1) divided, palm-shaped etc. (not “normal”).
24. Opisthosomal setae *c2*: (0) present; (1) absent.
25. Ridges on the female genital coverflap: (0) absent; (1) one longitudinal row; (2) two longitudinal rows or transverse lines.
26. Spatulate or shovel-shaped projections on legs: (0) absent; (1) present.
27. Lateral opisthosomal differentiation: (0) absent; (1) differentiated into broader dorsal and narrower ventral annuli.
28. Extensions on dorsal annuli: (0) not extended laterally; (1) extended laterally or with indentations.
29. Prosternal apodeme (sternal line): (0) absent; (1) present.
30. Opisthosomal setae *h1*: (0) present; (1) absent.
31. Spermathecal tubes in female: (0) long; (1) short.
32. Length of setae *sc*: (0) very long; (1) long; (2) short; (3) absent.
33. Microtubercles on dorsal annuli: (0) absent; (1) present.
34. Comparison between locations of coxal setae *1a* and *2a*: (0) *1a* ahead of *2a*; (1) *1a* in line with *2a*; (3) *1a* behind *2a*.

Appendix G.2. List of modified characters and character states of Hong & Zhang (1996a) to coincide with the data set defined for the present study.

0. Setae *vi*: (0) pair present; (1) one seta mid-anteriorly; (2) absent.
1. Setae *ve*: (0) present; (1) absent.
2. Scapular setal tubercles: (0) primary absent; (1) present; (2) secondary absent.
3. Setae *sc1*: (0) present; (1) absent.
4. Frontal lobe (naso): (0) absent; (1) very short or indistinct; (2) present.
5. Spine(s) on frontal lobe: (0) absent; (1) one spine; (2) three spines.
6. Location of *sc*: (0) ahead of shield rear margin; (1) well ahead of shield rear margin; (2) on or near shield rear margin.
7. Direction of *sc*: (0) anteriad diverging; (1) anteriad parallel or converging; (2) medially; (3) to outside; (4) posteriad diverging; (5) any direction.
8. Body shape: (0) rounded to oval; (1) vermiform (worm-like); (2) cylindrical; (3) vermiform-elongated; (4) fusiform-fat; (5) fusiform-elongated; (6) fusiform-flattened; (7) fusiform-very-long; (8) flattened-narrow-tail.
9. Cheliceral curvature: (0) recurved in stylophore; (1) evenly curved or straight; (1) abruptly curved downwards.
10. Location of genital area: (0) caudally; (1) 9-15 annuli removed from coxae II; (2) near coxae II; (3) appressed to coxae II.
11. Opisthosomal setae *c1*: (0) present; (1) absent.
12. Opisthosomal setae *d*: (0) present; (1) absent.
13. Opisthosomal setae *e*: (0) present; (1) absent.
14. Coxal setae *1b* on coxae I: (0) present; (1) absent.
15. Seta *bv* on femur I: (0) present; (1) absent.
16. Seta *l″* on genu I: (0) present; (1) absent.
17. Seta *l′* on tibia I: (0) present; (1) absent.
18. Seta *bv* on femur II: (0) present; (1) absent.
19. Seta *l″* on genu II: (0) present; (1) absent.
20. Tibia: (1) separate segment (“normal”); (1) reduced or fused with tarsus.
21. Solenidion on tibia I: (0) present in ventrodistal position; (1) absent.
22. Ridge(s) or through(s) on opisthosoma: (0) absent; (1) present.
23. Empodium on tarsus I: (0) pad-like with numerous unbranched rays; (1) simple (“normal”); (2) divided; (3) palmate.
24. Opisthosomal setae *c2*: (0) present; (1) absent.
25. Ridges on the female genital coverflap: (0) genital coverlap absent; (1) smooth; (2) ornamented basally; (3) entirely ornamented with basal and distal area; (4) entirely ornamented.
26. Spatulate or shovel-shaped projections on leg tarsi: (0) absent; (1) present.
27. Lateral opisthosomal differentiation: (0) annuli absent; (1) subequal and similar; (2) subequal and differentiated; (3) subequal and narrow; (4) subequal and broad; (5) differentiated into slightly broader dorsal than ventral annuli; (6) differentiated into broader dorsal than ventral annuli; (7) differentiated into extremely broader dorsal annuli than ventral annuli.
28. Extensions on dorsal annuli: (0) not extended laterally; (1) with slight lateral extensions.
29. Prosternal apodeme (sternal line): (0) present, very wide; (1) absent; (2) absent, coxae widely separated; (3) separated; (4) apodeme present (coxal inner margins touching); (5) coxae fused.
30. Opisthosomal setae *h1*: (0) present; (1) minute; (2) absent.
31. Spermathecal tubes in female: (0) eriophyoid-type spermathecal tubes absent; (1) short; (2) long.
32. Length of setae *sc*: (0) exceptionally long; (1) very long; (2) long; (3) average; (4) very short.
33. Microtubercles on dorsal annuli: (0) absent; (1) present; (2) obscure; (3) elongated, in rows.
34. Comparison between locations of coxal setae *1a* and *2a*: (0) *1a* ahead of *2a*; (1) *1a* slightly ahead of *2a*; (2) *1a* in line with *2a*; (3) *1a* slightly behind *2a*; (4) *1a* behind *2a*.

APPENDIX H (H.1, H.2, H.3)

APPENDIX H.1. Original data matrix (Hong & Zhang, 1996a) of morphological characters for 17 eriophyoid species and one outgroup Tydeidae for the 18-original analyses. ? = uncertain or unknown character states or inapplicable states.

APPENDIX H.2. Data matrix of morphological characters for 17 eriophyoid species and one outgroup species (*Orphareptydeus*) for the 18-correct analyses. ? = uncertain or unknown character states, - = inapplicable states.

APPENDIX H.3. Data matrix of morphological characters for 17 eriophyoid species and one outgroup species (*Orphareptydeus*) for the 18-modify analyses. ? = uncertain or unknown character states, - = inapplicable states.

APPENDIX H.1. Original data matrix (Hong & Zhang, 1996a) of morphological characters for 17 eriophyoid species and one outgroup Tydeidae for the 18-original analyses. ? = uncertain or unknown character states or inapplicable states.

	0 0123456789	1 0123456789	2 0123456789	3 01234
Tydeidae	0000000000	0000000000	0000000000	00000
Pentasetacus	0010100000	0000000000	0001000001	00011
Trisetacus	0110000000	0000000000	000000000?	00010
Nalepella	0110100010	0100000000	000000010?	000?0
Novophytoptus	1010001100	0100010010	0100000001	00012
Phytoptus	1010000000	0000000000	0000000001	00010
Sierraphytoptus	1010110210	0000000000	0100000111	00200
Mackiella	1010100000	0100000000	0000000101	00001
Aberoptus	1110001110	1100000100	1101011100	11111
Nothopoda	1110000100	0100100100	1100000000	11210
Ashieldophyes	110000?200	1111100000	0100000000	01200
Cecidophyes	110110??10	1100000000	0100020100	11310
Eriophyes	1110000?00	0100000000	01000?000?	?1110
Phyllocoptes	1110100210	0100000000	01000?0101	?11?0
Diptacus	1110100011	0100010010	01110?0101	?12?0
Diptilomiopus	1111100?11	0100011111	0111100010	?13?0
Rhinophytoptus	1110100011	0100000000	0100000101	?12?0
Rhyncaphytoptus	1110100011	0100000000	01?00?0101	?11?0

APPENDIX H.2. Data matrix of morphological characters for 17 eriophyoid species and one outgroup species (*Orphareptydeus*) for the 18-correct analyses. ? = uncertain or unknown character states, - = inapplicable states.

	0 0123456789	1 0123456789	2 0123456789	3 01234
Orfareptydeus_stepheni	0000000--0	0000000001	0101000000	0-010
Pentasetacus_araucaria	0010100000	0000000000	0001000001	00011
Trisetacus_ehmanni	0110000000	0000000000	0000000000	00011
Nalepella_tsugifoliae	0110100010	0100000000	0000000001	00010
Novophytoptus_rostratae	1010001100	0100010010	0100000001	01012
Phytoptus_avellanae	1010000000	0000000000	0100000001	01110
Sierraphytoptus_alnivagrans	1010110010	0000000000	0100000111	01100
Mackiella_phoenicis	1010100000	0100000000	0000000101	01212
Aberoptus_samoae	1110001210	1100000100	0101011001	11211
Nothopoda_rapaneae	1110001100	0100100100	1100020000	11210
Ashieldophyes_pennademensis	1100000210	1111000000	0100000000	01200
Cecidophyes_rouhollahi	110110--10	1100000000	0100020101	11-10
Eriophyes_pyri	1110001000	0100000000	0100010000	01?10
Phyllocoptes_calisorbi	1110100210	0100000000	0100020001	01110
Diptacus_sacramentae	1110101011	0100010010	0101000101	11110
Diptilomiopus_assamica	1111100-11	0100111111	0111100101	11-00
Rhinophytoptus_concinnus	1110001011	0100000000	0100000001	1??1?
Rhyncaphytoptus_ficifoliae	1110001011	0100000000	0100000111	01110

APPENDIX H.3. Data matrix of morphological characters for 17 eriophyoid species and one outgroup species (*Orphareptydeus*) for the 18-modify analyses. ? = uncertain or unknown character states, - = inapplicable states.

	0 **0123456789**	**1** **0123456789**	**2** **0123456789**	**3** **01234**
Orfareptydeus_stepheni	0000000500	0000000001	0100000000	00310
Pentasetacus_araucaria	1010200030	2000000000	0002010103	02312
Trisetacus_ehmanni	1110001010	2000000000	0001010101	02212
Nalepella_tsugifoliae	1110100140	2100000000	0001010303	02011
Novophytoptus_rostratae	2010002420	1100010010	0101010303	01114
Phytoptus_avellanae	2010000110	2000000000	0101020103	01311
Sierraphytoptus_alnivagrans	2010210160	2000000000	0101010613	01301
Mackiella_phoenicis	2010200010	2100000000	0001010603	01333
Aberoptus_samoae	2110002380	3100000100	0103041103	21312
Nothopoda_rapaneae	2110002410	2100100100	1101030102	21310
Ashieldophyes_pennademensis	2120001370	3111000000	0101010404	01400
Cecidophyes_rouhollahi	212110--40	3100000000	0101030203	21-10
Eriophyes_pyri	2110002030	2100000000	0101040104	01210
Phyllocoptes_calisorbi	2110200250	2100000000	0101030103	11311
Diptacus_sacramentae	2110202051	2100010010	0102010603	21321
Diptilomiopus_assamica	2111100-41	2100111111	0112110503	21-01
Rhinophytoptus_concinnus	2110002051	2100000000	0101010103	2?31?
Rhyncaphytoptus_ficifoliae	2110002051	2100000000	0101010713	01311

APPENDIX I

Glossary.

Appendix I. Glossary. Definition of selected terms used in the dissertation.

Term	Definition	Source
apomorphy	Derived character or character state.	Kitching *et al*. (1998)
arrhenotokous	Males hatching from haploid (unfertilized), and females from diploid (fertilized) eggs	
artificial group/taxon	Polyphyletic or paraphyletic group or taxon (not monophyletic).	
character	An observable feature or attribute of an organism, which may or may not have alternative manifestations (character states) which can be used to distinguish between different organisms.	Modified from Kitching *et al*. (1998)
character state	One of two or more alternative manifestations of a character.	Kitching *et al*. (1998)
characteristic, feature	Used as an alternative term for character state. See definition of character state.	
ci (consistency index)	Measure of the fit of a character to a tree. It is calculated by the minimum number steps a character will have on any cladogram (e.g., for a binary character this will be 1), divided by the minimum number of steps a character has on a particular cladogram.	Kitching *et al*. (1998); Lipscomb (1998)
CI	Average fit of all characters to a tree or in other words it measures the relative amount of homoplasy in a tree.	Kitching *et al*. (1998)
clade	Alternative term for monophyletic group (see monophyletic group for definition).	Kitching *et al*. (1998)
EM	Electron microscopy or electron microscope, depending on the context.	
erineum	abnormal plant hair growth	
gall-inhabiting eriophyoid mites	Non-vagrant eriophyoid mites living in plant microhabitats created by symptomatic growth caused by their feeding, such as galls, erineum and blisters.	Sabelis & Bruin (1996)
homologize	**1.** To make homologous. **2.** To show to be homologous.	
metric tree	Cladogram in which the length of each branch is proportional to the amount of character changes that occurs along it.	Kitching *et al*. (1998)
monophyletic group	Group which contains the most recent common ancestor plus all and only all its descendants. The group is diagnosed as monophyletic by the discovery of shared homologies (synapomorphies). This group is also known as a clade.	Definition by Hennig in Kitching *et al*. (1998), wording modified
monophyletic, monophyly	See monophyletic group	
node	Point in a cladogram where three or more branches meet to form a group.	Modified from Kitching *et al*. (1998)
non-vagrant eriophyoid mites	Eriophyoid mites living a more sheltered life: in natural plant microhabitats e.g., in buds, underneath needle and leave sheaths, and between bulb scales (refuge-inhabiting mites), or in microhabitats created by symptomatic growth caused by their feeding, such as galls (gall-inhabiting mites).	Sabelis & Bruin (1996)
organule	Association of small numbers of integumental cells which perform some specific function different from that of the general population of epidermal cells, eg.,	Lawrence (1966)

	setae, scales, dermal glands and lyrifissures.	
over-resolved cladogram	"A cladogram with spurious resolution due to the presence of one or more zero-length branches."	Kitching *et al*. (1998)
paraphyletic group	A group of which one or more parts were removed. If these parts are added to the paraphyletic group, it will be monophyletic. (Can also be defined as group recognized by symplesiomorphies.)	Definition by Hennig in Kitching *et al*. (1998), wording modified
polyphyletic group	A group that does not include the most recent common ancestor of all its members. It is also defined as a goup based on homoplastic (homoplasious) assumed to have been absent in the most recent common ancestor of all its members. Groups based on convergent characters are also regarded as being polyphyletic.	Definition by Hennig in Kitching *et al*. (1998), wording modified and added on by Kitching *et al.* (1998) and author
refuge-inhabiting eriophyoid mites	Non-vagrant eriophyoid mites living in natural plant microhabitats e.g., in buds, underneath needle and leave sheaths, and between bulb scales, and not in symptomatic growth caused by their feeding.	Sabelis & Bruin (1996)
retention index (ri)	A measure of the fit of a character to a tree. It measures the relative amount of homoplasy required by a character to fit a cladogram.	Kitching *et al*. (1998); Lipscomb (1998)
SEM	Scanning electron microscope or scanning electron microscopy, depending on the context.	
sister group / taxon	Two taxa that are more closely related to each other than either is to a third taxon	Kitching *et al*. (1998)
stepwise addition	The sequence by which taxa are added to a developing cladogram during the initial building phase of an analysis.	Kitching *et al*. (1998)
synapomorphy	Shared apomorphy, which is not homoplasious, that unites two or more taxa into a monophyletic group; also known as homology. It can also be defined as a secondary homology, depending on the definition of homology.	Modified from Kitching *et al*. (1998)
tree	Alternative term for cladogram, generally used in cladistics, and in the present dissertation.	
unweighted tree	A tree (cladogram) found under equal weighting of characters.	

APPENDIX J

Published abstracts.

J.1. Craemer, C. & Hall, A.N. 2003. The use of low-temperature scanning electron microscopy for studying eriophyoid mites (Acari: Eriophyoidea). p. 76 In: *Proceedings of the Microscopy Society of Southern Africa* 33.

J.2. Craemer, C. 2006. Morphology of eriophyoid mites (Eriophyoidea) as elucidated by scanning electron microscopy: trivial pursuit or valuable systematic contribution? p. 45 In: Bruin, J. (Ed.). *Abstract Book.* 12th International Congress of Acarology, 21-26 August 2006, Amsterdam, The Netherlands.

THE USE OF LOW-TEMPERATURE SCANNING ELECTRON MICROSCOPY FOR STUDYING ERIOPHYOID MITES (ACARI: ERIOPHYOIDEA)

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Mites of the superfamily Eriophyoidea are entirely phytophagous, generally host-specific, and may occur on the majority of perennial higher plant species, with some causing conspicuous deformities or diverse symptoms. Some species are economically important plant pests in agriculture, while others are beneficially used in the control of weeds.

The diversity of eriophyoid mites is virtually unknown. Approximately 3 700 species are known world-wide[3], which accounts for a scant estimated 1% or less of extant species. Therefore the most important requirement in the systematics of this group remains the description of new taxa. An exact study of morphology is a prerequisite for the adequate description of a taxon, and for hypotheses of homology for phylogenetic studies.

Eriophyoids are a morphologically unique group of mites with elongated, annulated bodies, and four legs in all life stages. They are soft bodied and microscopic, on average about 100-200 µm long and 30 µm wide. During recent years conventional scanning electron microscope (SEM) studies have been sporadically used to supplement light microscope studies of these mites, and this has contributed towards the understanding of their morphology, but it has not been routinely and widely used. Unfortunately conventional SEM preparation methods are associated with artifacts, and particularly for the preparation of eriophyoid mites. Low-temperature SEM, as one of the alternative methods[1,4,5] seems to be the most successful in obtaining highly magnified, largely artifact-free images of these mites[2]. Based on this information, the latter method was chosen to undertake the current study on eriophyoid mites of South Africa. In this study a JEOL 840 SEM with a cryo stage was used. After plunge-freezing in nitrogen slush, specimens were etched for ca. 30 minutes to remove surface condensed water vapor and then sputter coated with gold palladium.

The frozen specimens remained turgid and the form of the mites remained mainly unaltered. The mechanical damage caused by preparatory manipulation to delicate structures, including wax secretions (Fig. 1), was largely prevented. In addition mites could be studied *in situ* in galls and on plant material, facilitating observations on their biology (Fig. 2). Useful data on the morphology was obtained which will be incorporated in the taxonomy of these mites. However, results were not always satisfactory: surface ice could not always be entirely removed; material often degraded after prolonged examination; and some mites intact on plant pieces were washed off[4] during sample preparation. The use of a field emission SEM with cryo-attachment[5] will enhance results, especially for the resolution of fine structure on e.g. specialized setae, but this option was not available.

We strongly recommend that SEM studies should be incorporated in the systematics of eriophyoid mites.

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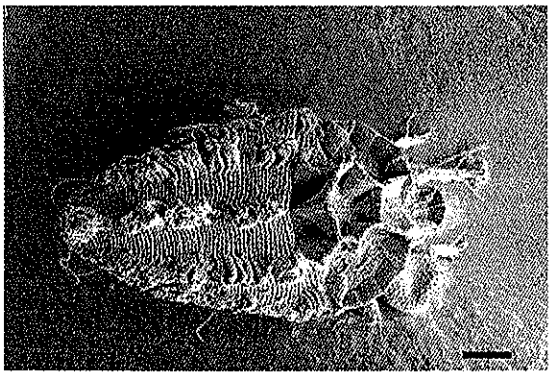

Fig. 1. Dorsal view of a *Calacarus* sp. showing intact wax secretions. Bar = 10 µm.

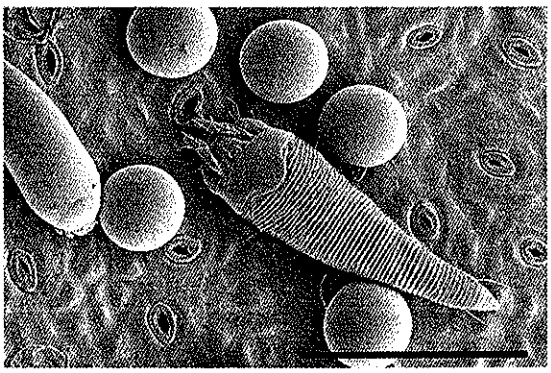

Fig. 2. *Cisaberoptus* sp. on a leaf, e = egg. Bar = 100 µm.

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Morphology of eriophyoid mites (Eriophyoidea) as elucidated by scanning electron microscopy: trivial pursuit or valuable systematic contribution?

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Eriophyoids are the smallest of all mites. Their morphology is unique, and their relatively soft bodies are simplified. Despite many characters available for taxonomy, some are not clearly delimited or readily discernible, and too few are available for phylogenetic studies.

Light microscopic studies of cleared, slide mounted specimens are almost exclusively used for studying the taxonomy of these mites using morphology. This method is still the simplest and the most practical. However, artifacts caused by slide mounting and inefficient resolution of detailed morphology may be detrimental to eriophyoid taxonomy. Scanning electron microscope (SEM) studies have been used only sporadically to supplement conventional descriptions of eriophyoid mites. This has contributed towards the understanding of their morphology, but it has not been routinely used. The conventional SEM preparation methods commonly used may also cause artifacts in specimens. Low-temperature SEM seems to be the most successful in obtaining highly magnified, largely artifact-free images of these mites. In this study, the latter method was utilized to study *ca.* 30 eriophyoid species from South Africa. The frozen specimens remained turgid and the shape of the mites remained largely unaltered, and mechanical damage to delicate structures, including wax secretions, was prevented.

Although results were not always satisfactory, partly due to the quality of equipment available, useful morphological data was obtained. Discrepancies between species descriptions from slide mounted specimens and the SEM images were found. This included body form, interpretation of structures and the presence of secretions. Additional morphological characters were found in the detailed morphology not generally used in the conventional taxonomy such as on the gnathosoma and legs.

The general incorporation and reliance on information from SEM studies in the classification and identification of these mites remain a problem: it is time consuming, expensive, requires additional suitable material; and inaccessibility of electron microscope facilities. SEM studies are also not able to replace the datasets obtained from slide mounted specimens and the investigator's interpretation thereof in morphological illustrations. Furthermore, with printing and subsequent photocopying of publications, the quality of SEM images, in many cases, lose their degree of clarity.

Despite these, the usefulness of SEM studies to mite morphology cannot be disputed, and the contribution of taxonomically useful morphology is clearly demonstrated for the Eriophyoidea. The possible incorporation of artifacts in the description and classification of the group by studying slide mounted specimens should not be ignored. It is also clear that SEM studies can contribute additional characters needed for systematic studies. More importantly, the incorporation of SEM images provides additional information to type material, especially where the type specimens have either deteriorated or were destroyed over time. Eriophyoid taxonomists should thus ideally plan for and enhance their studies with high quality SEM studies.

APPENDIX K

Published article. Craemer, C.; Amrine, J.W. Jr.; De Lillo, E. & Stasny, T.A. 2005. Nomenclatural changes and new synonymy in the genus *Diptilomiopus* Nalepa, 1916 (Acari: Eriophyoidea: Diptilomiopidae). *International Journal of Acarology* 31: 133–136.

NOMENCLATURAL CHANGES AND NEW SYNONYMY IN THE GENUS *DIPTILOMIOPUS* NALEPA, 1916 (ACARI: ERIOPHYOIDEA: DIPTILOMIOPIDAE)

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ABSTRACT - The concept of the genus *Diptilomiopus* Nalepa, 1916 is re-examined. Several species in *Vilaia* Chandrapatya and Boczek, 1991a, a junior synonym, are reassigned to *Diptilomiopus*, namely *aglaiae* Chandrapatya and Boczek, 2002a, *anthocephaliae* Chandrapatya and Boczek, 2002a, *benjaminae* Boczek and Chandrapatya, 2002, *boueae* Chandrapatya and Boczek, 2002a, *cerberae* Chandrapatya, 1998, *combretae* Chandrapatya and Boczek, 2002a, *coreiae* Chandrapatya and Boczek, 2002b, *jasminiae* Chandrapatya and Boczek, 2001, *melastomae* Boczek and Chandrapatya, 2002, *meliae* Boczek, 1998, *morindae* Boczek, 1998, *musae* Chandrapatya, 1998, *racemosae* Chandrapatya and Boczek, 2001, *riciniae* Boczek and Chandrapatya, 2002, *swieteniae* Chandrapatya, 1998, and *thunbergiae* Boczek and Chandrapatya, 2002. *Diptilomiopus septimus* Huang, 2001 is a junior synonym of *Rhynacus championi* Huang, 1992, which is transferred to *Diptilomiopus*.

Key words - New combinations, new synonymy, Acari, Eriophyoidea, Diptilomiopidae, Diptilomiopinae, *Diptilomiopus*, *Vilaia*.

INTRODUCTION

This is the first in a series of articles on the Diptilomiopidae Keifer, 1944. Nalepa (1916) described the then monotypic genus, *Diptilomiopus* with *Diptilomiopus javanicus* type species by original designation; the genus was placed at that time in the Phyllocoptinae. His original description reads: "*Dorsalseite des Abdomens von zwei seichten, nach hinten verstreichenden Längsfurchen durchzogen. Keine Patella, Beine daher fünfgliedrig. Prätarsus (Fiederklaue) gegabelt. Beinglieder mit Ausnahme des Tarsus borstenlos*". ["Dorsal surface of the abdomen with two shallow (weak) longitudinal furrows, extending to the rear. No patella (genu), legs therefore five segmented. Pretarsus (featherclaw = empodium) forked (divided). Leg segments, with the exception of the tarsus, without setae."] An additional description of this genus, probably meant by Nalepa to be the original description, was received by the publisher in November 1916, but not published until 20 January 1918 (Nalepa, 1918) (Newkirk, 1984). The latter description reads: "*Abdomen ungleichartig geringelt, Rückenhalbringe breiter als die Bauchhalbringe. Beinglied 3 fehlend, Beine daher fünfgliedrig. Schaft der Fiederklaue gegabelt*". ["The abdomen unequally ringed (annulated), dorsal half rings (dorsal annuli) broader than the ventral half rings (ventral annuli). Leg segment three (genu) absent, legs therefore five segmented. Shaft of the featherclaw (empodium) forked (divided)."] Lamb (1953) also translated the 1918 description to English.

Chandrapatya and Boczek (1991a) described *Vilaia*, with type species *Rhynacus pamithus* Boczek and Chandrapatya, 1989, differentiating this new genus from the diptilomiopine genera *Asetadiptacus* Carmona, 1970 and *Neodiptilomiopus* Mohanasundaram, 1982, but not from *Diptilomiopus*.

In their study on the systematics of the Diptilomiopinae, Hong and Zhang (1997) concluded that *Vilaia* is a junior synonym of *Diptilomiopus* based on a comparison of the character states of *Diptilomiopus* and *Vilaia* spp. The confusion may have been created by the fact that the definition of *Diptilomiopus* by Keifer (1975) and later, the generic keys of Boczek *et al.* (1989) and Amrine (1996) implied that *Diptilomiopus* species do not have

scapular setal tubercles; however, many *Diptilomiopus* species do possess scapular setal tubercles (Hong and Zhang, 1997). Although the scapular setae are described as being absent in the type species of *Diptilomiopus* (*D. javanicus*) (Nalepa, 1916, 1918), the presence or absence of the scapular tubercles is not mentioned. No figures of *Diptilomiopus javanicus* are available, and it should be noted that the drawings published by Boczek *et al.* (1989) (page 182, plate 190) are of *Diptilomiopus jevremovici* Keifer, 1960, and not of *D. javanicus* as wrongly indicated.

Hong and Zhang (1997) acted on the synonymy of *Vilaia* with *Diptilomiopus* by transferring the 13 *Vilaia* species (Chandrapatya and Boczek, 1991a, b; Boczek and Chandrapatya, 1992) known at that time to *Diptilomiopus*.

Since the synonymy of *Vilaia* by Hong and Zhang (1997), 16 additional *Vilaia* species have been described (Boczek and Chandrapatya, 1998; Chandrapatya and Boczek, 1998; Chandrapatya and Boczek, 2001, 2002a, b; Boczek and Chandrapatya, 2002), without any indication whether the authors accepted or rejected the synonymy. An attempt should be made to study specimens of *D. javanicus* for the presence or absence of the scapular setal tubercles in the type species of *Diptilomiopus*, which may influence the synonymy of *Vilaia* with *Diptilomiopus*; *Diptilomiopus javanicus* was described as an inquiline in 2-mm pouch-like galls caused by *Aceria hemigraphidis* (Nalepa, 1916) on the upper surfaces of leaves of *Hemigraphis confinis* (Nees) T. Anders (Acanthaceae), collected by W. Docters van Leeuwen-Reijvaan in 1914 in Semarang, Java (Nalepa, 1916, 1918). At this time we concur with the synonymy proposed by Hong and Zhang (1997), and hereby transfer *Vilaia* species in question to *Diptilomiopus*.

We also assign a new species synonymy within *Diptilomiopus*.

Diptilomiopus Nalepa, 1916

Diptilomiopus Nalepa, 1916: 283; Nalepa, 1918: 228-230; Keifer, 1938: 305; Lamb, 1953: 369; Keifer, 1975: 521; Newkirk and Keifer, 1975: 585; Chakrabarti and Mondal, 1983: 299; Amrine and Stasny, 1994: 173; Boczek *et al.*, 1989: 25, 182 (plate 190 not of *D. javanicus*, but of *D. jevremovici*); Kuang, 1995: 168; Amrine, 1996: 111, 140; Hong and Zhang, 1996: 71; Hong and Zhang, 1997: 321; Amrine *et al.*, 2003: 137, 195-196.

Sectipes Keifer, 1962a: 18-19; Keifer, 1962b: 19, **synonym**; Newkirk and Keifer, 1975: 585.

Vilaia Chandrapatya and Boczek, 1991a: 427-428; Boczek and Chandrapatya, 1989: 139-140; Amrine and Stasny, 1994: 311-312; Amrine, 1996: 114, 141; Hong and Zhang, 1997: 321, **synonym**; Amrine *et al.*, 2003: 137, 215.

Type species - *Diptilomiopus javanicus* Nalepa, 1916, by original designation.

NEW COMBINATIONS

***Diptilomiopus aglaiae* (Chandrapatya and Boczek, 2002), n. comb.**

Vilaia aglaiae Chandrapatya and Boczek, 2002a: 129-131, fig. 3.

***Diptilomiopus anthocephaliae* (Chandrapatya and Boczek, 2002), n. comb.**

Vilaia anthocephaliae Chandrapatya and Boczek, 2002a: 126-129, fig. 2.

***Diptilomiopus benjaminae* (Boczek and Chandrapatya, 2002), n. comb.**

Vilaia benjaminae Boczek and Chandrapatya, 2002: 25-27, fig. 1.

***Diptilomiopus boueae* (Chandrapatya and Boczek, 2002), n. comb.**

Vilaia boueae Chandrapatya and Boczek, 2002a: 123-126, fig. 1.

***Diptilomiopus cerberae* (Chandrapatya, 1998), n. comb.**

Vilaia cerberae Chandrapatya, 1998, *in* Boczek and Chandrapatya, 1998: 37-38, fig. 4.

***Diptilomiopus combretae* (Chandrapatya and Boczek, 2002), n. comb.**

Vilaia combretae Chandrapatya and Boczek, 2002a: 132-134, fig. 4.

***Diptilomiopus coreiae* (Chandrapatya and Boczek, 2002), n. comb.**

Vilaia coreiae Chandrapatya and Boczek, 2002b: 135-138, fig. 1.

***Diptilomiopus jasminiae* (Chandrapatya and Boczek, 2001), n. comb.**

Vilaia jasminiae Chandrapatya and Boczek, 2001: 96-99, fig. 3.

***Diptilomiopus melastomae* (Boczek and Chandrapatya, 2002), n. comb.**

Vilaia melastomae Boczek and Chandrapatya, 2002: 31-33, fig. 3.

***Diptilomiopus meliae* (Boczek, 1998), n. comb.**

Vilaia meliae Boczek, 1998, *in* Boczek and Chandrapatya, 1998: 35-36, 38, fig. 3.

***Diptilomiopus morindae* (Boczek, 1998), n. comb.**

Vilaia morindae Boczek, 1998, *in* Boczek and Chandrapatya, 1998: 32, 34-35, fig. 2.

***Diptilomiopus musae* (Chandrapatya, 1998), n. comb.**

Vilaia musae Chandrapatya, 1998, *in* Chandrapatya and Boczek, 1998: 45-46, fig. 4.

***Diptilomiopus racemosae* (Chandrapatya and Boczek, 2001), n. comb.**

Vilaia racemosae Chandrapatya and Boczek, 2001: 99-101, fig. 4.

***Diptilomiopus riciniae* (Boczek and Chandrapatya, 2002), n. comb.**

Vilaia riciniae Boczek and Chandrapatya, 2002: 31, 34-36, fig. 4.

***Diptilomiopus swieteniae* (Chandrapatya, 1998), n. comb.**

Vilaia swieteniae Chandrapatya, 1998, *in* Chandrapatya and Boczek, 1998: 43-44, fig. 3.

***Diptilomiopus thunbergiae* (Boczek and Chandrapatya, 2002), n. comb.**

Vilaia thunbergiae Boczek and Chandrapatya, 2002: 28-31, fig. 2.

NEW COMBINATION AND NEW SYNONYM

***Diptilomiopus championi* (Huang, 1992), n. comb.**

Rhynacus championi Huang, 1992: 226, 232, figs. 5-8 (SEM images); Amrine and Stasny, 1994: 274; Hong and Zhang, 1996: 72; Hong and Zhang, 1997: 326.

Diptilomiopus septimus Huang, 2001: 67-68, fig. 67, **new synonym.**

REMARKS - Huang (2001) redescribed *Rhynacus championi* Huang, 1992 (Huang, 1992) as a new species, *Diptilomiopus septimus* Huang, 2001, without mentioning that the two mites are the same. The fourth author (T. Stasny) uncovered the problem and Huang (pers. comm., 2002) commented that *R. championi* will now be *Diptilomiopus septimus*. As stated by article 23.1 of the International Code for Zoological Nomenclature (ICZN, 1999) the valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission. *Rhynacus championi* is thus the valid name, and *championi* is hereby transferred to *Diptilomiopus* based on the redescription as given for *D. septimus*.

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APPENDIX L

Published article. De Lillo, E.; Craemer, C.; Amrine, J.W. Jr. & Nuzzaci, G. 2010. Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). *Experimental and Applied Acarology* 51: 283–307. DOI 10.1007/s10493-009-9311-x

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Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata)

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Abstract Methods used for sample storage, specimen clearing, slide mounting, species illustration and morphometric description in alpha-taxonomic studies are essential for the Eriophyoidea. Eriophyoid mites are very tiny and delicate, for which truly permanent specimen slides currently cannot be prepared, resulting in eventual loss of material, including type specimens. Often, published descriptions and drawings have not achieved the required level of quality, and thus many relevant taxonomic details have been permanently lost or neglected. These shortcomings can make certain identifications impossible and cause significant confusion. Consequently, there is a considerable need for accurate and uniform descriptive and illustrative data for the Eriophyoidea. Based on their expertise on this topic, the authors provide guidelines and advices, assisted also by illustrations, of the main critical aspects in managing eriophyoid mites in order to supplement and improve techniques for handling and preparation of specimens, and for improving their taxonomic study. The effects of the short- and long-term preservation methods (i.e., fresh, dried and liquid preservative choices) on digesting the internal tissues of the mites are discussed. Clearing and mounting procedures are analyzed, and special tips are suggested for handling mites and designing tools needed during these steps. Methods for recovering specimens from unsuitable slides (i.e., undercleared and overcleared specimens) are proposed and described. Techniques and tricks to produce descriptive line drawings of good

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quality are highlighted, and the content to include in plates is stressed. Finally, detailed instructions for standardization of measurements are given.

Keywords Eriophyoidea · Storage · Clearing · Mounting · Illustrations · Descriptions

Introduction

As for other mites, eriophyoid systematics depends on the quality of studied specimens and morphological description. Conversely, the microscopic size and ultra fine structural details of these tiny and fragile mites make their morphological study more difficult. Furthermore, the accuracy and correctness of descriptions and associated drawings depend on the methods used in processing, mounting and studying the mites.

Several comprehensive accounts (e.g., Nalepa 1906; Hassan 1928; Keifer 1952, 1975; Amrine and Manson 1996) are available on methods for sample preservation and storage, specimen clearing and mounting, drawing, descriptive arrangements and other activities related to taxonomic/systematic investigations/publications. Hassan (1928) extensively described preservation and mounting methods, eventually mounting mites in Canada balsam (miscible with 100% xylene) or euparal (miscible with 95% ethanol). Hassan's material has not been found by the authors, so it is unknown how long such specimens can remain in useable conditions. Amrine mounted mites, including eriophyoids, in both Euparol® and balsam (Permount®) media. In all cases, the mites were slowly dehydrated through a graded series of ethanol solutions (passing at 5% ethanol intervals usually from 60 to 100%) for Euparol®, or they were transferred from 100% ethanol to xylene for Permount®. Despite careful processing, mounted specimens were always badly crumpled and deformed and no useful descriptions could be made.

Keifer experimented with several methods and chemicals for clearing and mounting, and set an excellent standard for making illustrations and taxonomic descriptions of eriophyoids during his career ranging from 1938 to 1991 (see Baker et al. 1996, for a compendium of Keifer's descriptions of species from the USA, including drawings not published before). However, even in 1975, he commented about the general lack of standards for describing eriophyoids. His particular style and high standards for accuracy is conveyed in his reply (Fig. 1) to Nuzzaci who, novice eriophyoidologist, had sent him microscope slides, a draft description and line drawings of a new eriophyoid mite for his assessment and advice. Since Keifer's publications, the major contributions to the interpretation of the external morphology of eriophyoid mites were by Lindquist (1996). Besides, Amrine and Manson (1996) gave a further contribution on the preparation, mounting and descriptive methods of study of these mites; their main intent was to strongly urge "authors to achieve greater uniformity in presenting descriptive, illustrative and biological data" and this seems to have been partially accomplished in the past decade.

However, today many descriptions and drawings still often do not achieve the required standard and quality, even as set by Keifer, and many relevant taxonomic details may be permanently lost or obscured as a result. These shortcomings can lead to incorrect classification, sometimes making certain identifications impossible, or misinterpretation (for example, the prodorsal shield, scapular setae *sc* and coxal setae *1b* and *1a* of *Ashieldophyes* were not clearly described in Mohanasundaram 1984) which can cause considerable confusion. These inadequacies cannot be justified considering the quality of the

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However, I take most direct exception with the correctness and adequacy of your drawings. Admittedly all drawings of these mites are but diagrams, but one must ask - how clearly do the delineations show the precise features of the species in question? Are the diagrams bare, or do they convey specificity? Drawings of these mites are in no sense art. But they must be done with precise recognition of line direction, of relative size of the parts, and they must also include angles and points, when they are present. To do a good job on such depictions takes practice and study.

You have done the usual thing in regard to drawings - produced rather bare diagrams. We have too many of such being continually published. If I can get you to rise above bare delineations or diagrams, and show specific features of these mites I will have accomplished something worthwhile. Dr. Nuzzaci, what I'm trying to do is get you started correctly. All of this takes practice and study. Actually the study of eriophyids is a full time job, and if you dilute your time with publications on other mites your efforts on eriophyids will more or less suffer.

Sincerely H. H. Keifer

Fig. 1 Letter by Keifer commenting on slides, description and descriptive drawings of a new species by Nuzzaci

microscopes and cameras available today. Moreover, a method universally accepted and used for preparing and mounting mites is not available and those methods commonly applied fail to give permanent slides.

Appropriately, Lindquist (2001) emphasized the importance of optimizing the quality of description of mites, including Eriophyoidea. Therefore, standardized descriptions are always imperative and must be continuously promoted, especially in view of the current high rate of description of new eriophyoid genera and species (de Lillo and Skoracka 2009), and also because the best slide mounted specimens rarely last very long and frequently become opaque or precipitated, or too transparent for study (Amrine and Manson 1996). Keifer's slide collection at the US National Museum of Natural History, in Beltsville, Maryland, USA, is a sad example of these shortcomings (Fig. 2). In addition, it should be emphasized that proper interpretation of morphological details certainly support systematic studies, but they are also required for many non-systematic investigations including plant-mite relationships and pest control, identification for quarantine purposes, vectored pathogens, and biological control of weeds.

The present paper provides guidelines and recommendations for techniques that researchers should employ when preparing, studying and describing eriophyoids that supplement techniques previously presented in other articles (e.g., Keifer 1975; Amrine and Manson 1996).

Preservation

Temporary preservation

When working with fresh, mite-infested plant samples, the researcher needs to prevent damage caused by desiccation or fungal degradation.

Fig. 2 Slides in the original eriophyoid collection of Keifer at the US National Museum of Natural History, Beltsville, Maryland, USA. Many slides cannot be used any more because they appear to be completely dark or the mounting medium is dried out

Fresh samples should be brought to the laboratory as soon as possible. They should not be exposed to heat and, therefore, they should be contained in plastic bags and stored in a cooler. Similarly, fresh plant material shipped by courier should be kept cold in a thermally insulated package with a frozen fluid pack or dry ice pack during extended shipment. Mites on plant samples not properly packed and shipped in luggage usually do not survive high altitude aircraft flights or ground transport because of excessive low or high temperatures during transport. Live mites can be extracted from plant samples using a washing solution (Monfreda et al. 2007) and can be stored in water containing a few drops of a commercial surfactant (household detergent or polisorbate as Tween®). Eriophyoids preserved in this manner were able to survive the shipment and stayed alive for 3–4 weeks in a refrigerator at about 4°C. Finally, live mites were successfully collected directly in the field by washing bunches of grapes without cutting them from the plant (de Lillo et al. 2005).

When fresh plant samples with live mites are returned to the laboratory, the mites must be processed within a short time after field collecting. In order to keep the material fresh, the sample can be wrapped in damp (not wet) paper towel, or other paper-like material, then sealed in a plastic bag, preventing it from drying out, and stored in a cold place (e.g., a refrigerator, climate controlled room or cabinet) without freezing the material. Fine holes can be punched in the plastic bag to reduce humidity if necessary (S. Ozman-Sullivan, pers. comm.). Depending on the type of sample and its quality, live mites can still be collected from the plant samples even after a month's, or as in the case of filbert big bud mites (*Phytoptus avellanae* Nalepa), 2 months' storage (S. Ozman-Sullivan, pers. comm.).

Permanent preservation as dried samples

In addition to slide mounted specimens, there is a requirement for additional long term preservation of mite-infested plant material or of mites themselves. Permanent preservation

may be necessary because mite specimens cannot always be processed and slide mounted before being stored or accessed in a collection (also see Keifer 1975), and additional material can be used when slide mounted specimens deteriorate or become totally destroyed, or are lost.

For practical convenience, mainly related to sample transportation, handling and storage, mite samples are often permanently preserved and managed as dried (mummified) specimens on leaves and other plant organs. Particular care must be taken on how the plant sample is dried out. In case of improper desiccation, the mite body may be destroyed or nearly completely invaded by fungi (Fig. 3). As a consequence, morphological details can be obscured, making mite identification frequently difficult or impossible. Therefore, plant samples should be dried out as soon as possible after field collecting and prepared as herbarium specimens for sending to specialists for mite identification or for deposition in a dry specimen collection (i.e., a zoo-cecidotheca). Dehydration of plant material should be carried out applying all possible techniques to prevent fungal infection of the mites (e.g., use of desiccating papers, frequent paper change, sample pressing between absorbent pads, slight warming in sunlight or in an oven). The properly dried samples should afterwards be enclosed in an envelope (letter envelope, transparent paper envelope, transparent plastic specimen bag, etc.) and labeled with all relevant data. A repellent or a deterrent compound (PDB, thymol, etc.) or other protective methods should be applied for preventing museum beetle attacks and deterioration over time. Trotter and Cecconi, authors of the *Cecidotheca Italica* (Fig. 4), were familiar with this method (Trotter 1904) and their dried specimens are still well suited for the identification of species after about one century, as demonstrated by Boczek and Nuzzaci (1988), and Petanović et al. (1993).

Well dried and properly preserved specimens, similarly to freshly collected mites, need usually only a few minutes in a mounting or clearing medium on a hot plate in order to become perfectly cleared and to return to their original shape and size.

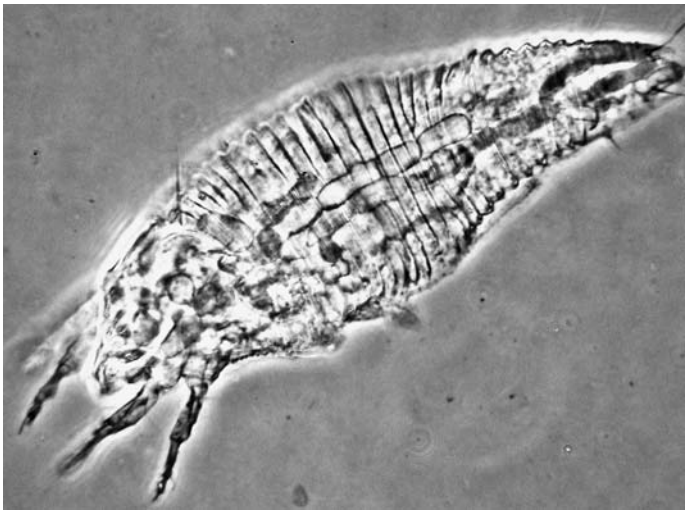

Fig. 3 A *Metaculus* specimen completely invaded by fungi obscuring its morphological details

Fig. 4 *Cecidotheca Italica*: front page of a publication by Trotter and Cecconi (1902) (on the *left*); original sample of *Geranium sanguineum* L. from which specimens of *Aceria dolichosoma* (Canestrini) were slide mounted and re-described by Petanović et al. (1993) (on the *right*)

Permanent preservation in liquid preservatives

In contrast with the general good and relatively quick results of clearing fresh and dried specimens, the digestion of non-cuticular structures of specimens preserved and fixed for years in alcoholic solutions (60–70% ethanol in water) requires much more time. This difficulty increases proportionally with length of preservation, and the results are often poor or insufficient for an exhaustive and reliable identification and description (Keifer 1975). Moreover, the alcoholic solutions tend to evaporate, and specimens usually become completely dried out (Fig. 5). Amrine needed to prepare a few specimens of the genus *Phytoptochetus* from a sample preserved in a vial, originally containing ethanol, for about 70 years and belonging to Nalepa's collections (Amrine and Manson 1996; Amrine et al. 2003). A few specimens were found after careful examination of a yellow powder; clearing took a period of 2 months and needed particularly careful and extensive processing. Specimens were heated at about 90°C in a few drops of Keifer's booster (Amrine and Manson 1996) for a few days. Then they were washed in water and transferred to a few drops of lactic acid, heated for a few days, washed in water once more, and hereafter transferred back to Keifer's booster again. This entire procedure was repeated many times. Eventually a collection of suitable mite fragments were found to correctly illustrate the shield, the coxi-genital region, the legs and the opisthosoma to make adequate drawings to define the essential characteristics of *Phytoptochetus.* On the contrary, notwithstanding similar attempts, the re-description of *Aceria sonchi* (Nalepa) from original powder remnants of dried ethanol preserved material was not possible (D. Knihinicki, pers. comm.).

Fig. 5 Original vials from Nalepa's collection containing ethanol preserved *Galium cruciata* (L.) Scop. and associated mites

Usually, the addition of glycerol to the preservatives (as in AGA and Oudeman's solution) makes the tissues softer and less rigidly fixed, allowing them to be more susceptible to the clearing agents. Glycerol also prevents the specimens from completely drying out, as usually happens when other solvents evaporate over time.

In addition, Keifer (1975) found that a mixture of thin sorbitol syrup in a 25% solution of isopropyl alcohol kept the eriophyoids well preserved and suitable for slide preparation. Craemer commonly uses this fluid, composed by 25% solution of propan-2-ol in water to D-sorbitol powder (e.g., add about 4 ml propan-2-ol diluted with 12 ml water to 30 g D-sorbitol powder) until forming a thin syrup with the consistency of heated honey, at most. When the liquid is added to the powder, the mixture is milky white and after a few hours it dissolves properly, becoming clear and slightly thick. At warm and humid environmental conditions, a very small amount of potassium iodide and an iodine crystal should be added to the mixture to prevent mould growth. The mixture should be kept in a sealed and well closed container, because it quickly becomes too thick and crystallizes when exposed to air. Mites are very easily transferred to and from a small amount of this "sorbitol fluid". S. Neser (pers. comm.) uses a novel way to collect and transport mites in this fluid also facilitating easy recovery. A small droplet of this solution is placed inside the lid of a polypropylene micro centrifuge tube (Fig. 6). About 100 specimens can easily be collected in this droplet, and when the vessel is closed, it can be safely transported and mailed. The droplet becomes very sticky, dries out over time and it can be re-hydrated by breathing over it. Otherwise, the entire droplet, even when crystallized, can be added to the clearing medium and processed as normal. The suitability of the mites to be slide mounted over extended periods of preservation in sorbitol has not been tested yet, but the mites are well suited if mounted within a few months.

Alternatively and for populations of a few dozen to a few hundred specimens, eriophyoids can also be kept on work slides (Amrine and Manson 1996). Unfortunately, high

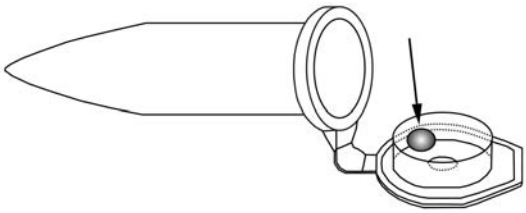

Fig. 6 A small droplet of "sorbitol fluid" into which eriophyoid specimens can be collected (*arrow*), positioned in the side corner of the lid of a 1.5 ml micro centrifuge tube

environmental humidity and temperature can reduce the quality of the specimen preservation on these work slides.

Finally, specimens can be preserved in ATL buffer (a buffer containing edetic acid and sodium dodecyl sulphate) stored in a refrigerator some time before DNA isolation according to Dabert et al. (2008). After the DNA extractions, the mite exoskeleton can be mounted and its morphology can be efficiently studied (Skoracka and Dabert 2009).

Handling eriophyoids and tools

Mites are usually found on plant samples with the aid of a stereo dissecting microscope, and can be picked up using pin-like or other tools, even if the plant material is deformed. The moistening of the tip of the tool with water or other media can enhance the ease with which the mites are picked up. When mites are rare on the plant sample or the plant organs are severely modified and architecturally intricate, especially when dried, finding and collecting eriophyoids can become time-consuming and inefficient. Then, collecting can be greatly improved by concentrating the mites (Monfreda et al. 2009). In the case of dried material, mites can be easily recovered as described by Amrine and Manson (1996), or by soaking part of the sample overnight in a water solution with a few drops of a surfactant and bleach at room temperature (Monfreda et al. 2009). Hereafter the suspension is stirred and sieved: the specimens can be more easily detected, because of their restored shape, and picked up from a filter paper or from a filtered sediment (through a 20–25 μm sieve) poured into a Petri dish using water plus a small amount of a surfactant (Monfreda et al. 2007).

Commercially available laboratory needles are usually too thick and robust to be used in picking up, transferring and generally handling eriophyoid mites. Several types of apparatus can be specifically made for this purpose, and each laboratory usually has its own design. Some of these tools are mentioned in the materials and methods of many articles concerning Eriophyoidea. They include an eyelash, or several kinds of fine needles or pins, attached to or stuck into some sort of pen-like rod or wooden dowel in different ways (Fig. 7; Keifer 1975; Amrine and Manson 1996).

Insect mounting pins are suitable for constructing an eriophyoid handling tool. These come in different sizes and materials and stainless steel is recommended. Keifer (1975) proposed a size 00 insect pin for "needling" mites from solution to solution and slide to slide. A pair of size 3 insect pins in wooden dowels is useful for dissecting galls and unrolling leaf margins. These needles can be sharpened as needed on Arkansas soap-stones or other fine grindstones. They are commonly used for mounting delicate insect specimens such as microlepidoptera and small flies. Stainless steel micro-pins, known as Austerlitz® minutens or minuten pins, headless, 0.1 mm in diameter and about 12 mm long, with one sharpened end, can be particularly recommended. They do not chemically react with the preserving, clearing, and mounting media, and they can be manipulated to suit a

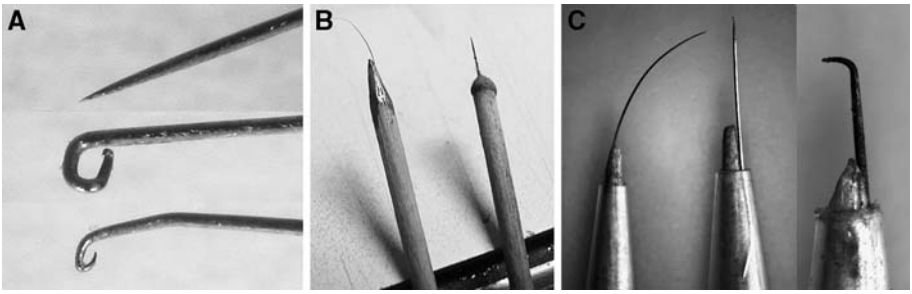

Fig. 7 Handling tools for eriophyoid mites: **A** details of variously shaped micropins; **B** details of an eyelash held in place with nail polish (on the *left*) and short minuten pin held in place with epoxy (on the *right*); **C** eyebrow hair (on the *left*), micropin (on the *center*) and bent pin (on the *right*) inserted into the narrow end of a micropipette and held in place by inserting a toothpick from the other end

researcher's needs, and their physical properties allow them to be dipped into reagents without being altered. These needle probes should be personally prepared by each researcher for making specimen handling comfortable and convenient. They can be mounted on wood or plastic handles. In particular, exhausted fine- or medium-tip markers can be re-cycled, and the blunt end of the micro-pin can be inserted into their felt-tip and fixed to it by a drop of a cyanoacrylic glue which hardens the felt. If preferred or needed, the sharp end of the pin can be curved or bent into a loop for producing a sort of spoon (Fig. 7A), using tweezers or micropliars under a dissecting microscope. Pointed and looped pins are suitable for transferring individuals without injuring or damaging them.

Disposable plastic micropipette tips (1 ml or c. 60 mm long × 8 mm diameter) can also be used for making a variety of handling tools (S. Neser, pers. comm.). A firm, pointed short hair (e.g., from an eyebrow), or micro-pins as above can be inserted into the narrow end and held in place by inserting a toothpick, or other probes of appropriate length from the other end (Fig. 7C). Alternatively root canal files (size 30, c. 0.3 mm in diameter, or thinner) as discarded by dentists, or available from dentist tool suppliers, may be inserted into holders as above.

Comprehensive information on equipment (hot plates, coverslips, plain and cavity slides, tweezers, etc.) and other useful facilities and supplies can be found in Keifer (1975), and Amrine and Manson (1996).

Clearing

An historical review of this aspect is in Keifer (1975), and in Amrine and Manson (1996) in which they underlined the difficulties in preparing adequately cleared specimens on slides.

Currently, many researchers have developed and improved a preferred medium on the basis of the personal experience and convenience, sometimes changing method over time. Eriophyoidologists have been applying the following media with satisfactory results: Heinze's medium (A. Skoracka, S.-G. Wei, pers. comm.), F-medium with Booster medium plus phenol according to Keifer (1975) (C. Craemer, P. Natchev, S. Ozman-Sullivan, pers. comm.), lactic acid (M. Lewandowski, P. Natcheff, R. Petanovic, C.-Q. Wang, pers. comm.), modified Berlese's medium (J.W. Amrine Jr., A. Chandrapatya, pers. comm.),

modified Keifer's Booster solution including water saturated phenol (E. de Lillo, E. Denizhan, R. Monfreda, G. Nuzzaci, pers. comm.), Nesbitt's medium (C.-Q. Wang, pers. comm.), and a stained mixture of Nesbitt's medium with lactophenol (Faraji and Bakker 2008). The applied clearing procedure should always be reported in publications.

A modified Berlese's medium was described by Amrine and Manson (1996). To about 15 ml of freshly made medium, 10–20 drops of glacial acetic acid, ca 100 mg of metallic iodine crystals and 100 mg of potassium iodide powder are added. This medium is placed on a hot plate at 90°C for about 30 min to dissolve the metallic iodine (or left from overnight to 48 h at room temperature). Iodine, included also in Keifer's medium, stains the fine sculptured details of the cuticle, the microtubercles and other cuticular structures, especially the internal apodemes and genitalia (Keifer 1975). Consequently, the brown color often enhances the contrast of fine or delicate features.

A further improvement of the image quality can be offered by digital cameras on microscopes. They can be adjusted to correct the 'white balance' or intensity and contrast adjustments to obtain excellent micrographs, even though the specimen may appear too dark or too pale at first glance.

When the medium used for digesting the mite internal tissue serves also for mounting (e.g., Heinze's medium), most eriophyoids can be placed directly into a small, shallow drop of medium on the slide. Live mites will right themselves and orient in proper position as they attempt to crawl in the thin film to leave the medium; this will not happen if they are immersed or are previously killed. Their orientation can be adjusted by stroking with the sharp tip of a micropin; the opisthosoma can be stroked several times to "right" a lateral mite into dorso-ventral orientation. In some cases, the uncovered slide with adjusted mites can be put on the hot plate margin for a few moments to thicken the medium and hold specimens in proper position. A small drop of the final medium can be added to a clean coverslip. A drop of glacial acetic acid can be added to this drop (e.g., modified Berlese's medium) which is stirred on the coverslip. Then, the coverslip is placed over the uncovered mounted specimen, using the tips of the forceps to guide specimen orientation and position as the coverslip settles. This step allows more rapid spread of the medium (eliminating air bubbles), keeps the orientation of the mites, and aids more rapid and complete clearing of the mites. The fresh slide is then placed on the edge of a hot plate at about 80–90°C to clear within about 30 min. Most live mites can be prepared in this way to make excellent slides in about 1 h. The boiling of the slide must be avoided because it moves the mites from the center to the margin of the coverslip where they cannot be studied.

In case the medium used for clearing is different from that used for mounting, (e.g., mounting in F-medium, after clearing with Keifer's booster medium with added phenol) cavity slides can be used for the clearing process. Mites can be placed directly into a drop of clearing medium and the slide can be heated until the mites are cleared. The mixture must not boil or become too viscous or hard. When the mite body is sufficiently cleared, drops of water or fresh medium can be added to the mixture to make it fluid enough for further passages. Then, mites are transferred to the mounting medium by means of micropins and a coverslip is added.

A few modifications to clearing procedures are used by eriophyoidologists: live mites are cleared, or alternatively are killed in a preserving solution before clearing; mites are cleared at room temperature taking a long time (days or weeks); mites in the clearing medium are heated carefully over an open alcohol flame, or they are kept in an oven or on a hot plate set at 40–60°C.

Overheating and overclearing can easily occur and are the major sources of error. If the covered slide is placed on a spot of the hot plate that is too hot for too long (about 1 h or more), numerous small air bubbles can develop and cannot be removed. These can often obliterate fine details needed for descriptions or photographs. Using new infrared thermometers, the researcher can carefully map the temperatures on a hot plate and know exactly where to place the slide(s) for best results.

For species difficult to clear using this technique, slides can be left in a cooler portion of the hot plate at about 70°C overnight or for 24–48 h. If your hot plate is too hot at the lowest setting, a thick thermal glass can be placed on the plate and will drop the surface temperatures for several degrees. Alternatively, the temperature of the hot plate can also be regulated by means of a rheostat between the receptacle and the hot plate (be sure to match wattage of the rheostat to that of the hot plate).

These methods are tedious, but they allow a researcher to routinely make excellent slides from which type specimens can be selected. This part of specimen preparation represents 90% of quality control for professional preparation of eriophyoid specimens, and a successful method needs to be learnt well. Amrine and de Lillo have prepared slides using the above methods as early as 1987, and these slides are still well suited for microscopic studies.

Mounting

For the final mounting, eriophyoidologists have also been applying different water based mixtures such as Heinze's medium (R. Petanovic, A. Skoracka, C.-Q. Wang, S.-G. Wei, pers. comm.), F-medium according to Keifer (1975) (C. Craemer, E. de Lillo, E. Denizhan, R. Monfreda, P. Natchev, G. Nuzzaci, R. Petanovic, S. Ozman-Sullivan, pers. comm.), modified Berlese's medium (J. W. Amrine Jr., A. Chandrapatya, M. Lewandowski, A. Skoracka, pers. comm.), and a stained Hoyer's medium (Faraji and Bakker 2008). The applied mounting procedure should always be reported in publications.

Most researchers add more or less mounting medium to alter the amount of pressure of the coverslip on the specimens. A few short fibers can be also mounted underneath at the borders of the coverslip to support it above the mite specimens, according to Keifer (1975). The diameter of the fibers can be chosen according to the thickness and width of the specimens to be mounted. Following Keifer's advice, de Lillo and Nuzzaci have selected three different fibers with different thicknesses cut into short lengths: fiberglass (about 10 μm in diameter), kapok (about 20 μm in diameter) and "wool" used for aquariums (about 40 μm in diameter). The main aim in using these fibers is to avoid excessive specimen flattening (Keifer 1975) which can alter feature proportions and the general shape of the mite. For example, ridges and furrows on the dorsal side of the opisthosoma, especially when they are slight, can be often "lost" during examination of flattened specimens. Moreover, the addition of fibers allows the coverslip to be moved more easily on the slide face by pushing one side of the coverslip with a pin or tweezers; of course, the coverslip must not be sealed and the medium must be fluid. In this way the mite can be rolled around its longitudinal axis, allowing observations and descriptions of a species from a single holotype specimen (Amrine and Manson 1996). However, even when fibers have not been added under the coverslip, if the mounting medium is still fluid and the slide has not been sealed yet, the coverslip can be moved changing the mite position, as reported by Nalepa (1906).

It is more difficult, and sometimes impossible, however, to study (draw and photograph) fine details (e.g., prodorsal shield features, female internal genitalia and the ray arrangement of particularly fine empodia presenting intricate details) on specimens that have not been flattened to some extent. It is probably most advisable to mount some specimens without and others with fibers. This will not always be feasible, depending on the specimens and time available. If important, and of consequence, it should also be mentioned in the description which method was used to obtain the particular morphological aspects described, because these can differ considerably, as in the example of the dorsal shield patterns in *Aceria angustifoliae* (Denizhan et al. 2008). It may even be arguable which method will render the best results for identification and comparative purposes. Both methods are difficult to standardize, and likely will vary depending on the mounting medium and amount used, the degree of clearing, and the skill of the worker.

Information on labeling and sealing methods is in Amrine and Manson (1996).

Overcleared slides

In the case of overcleared specimens, slide sealing can be carefully removed by a large pin, scalpel, razor or by other means. Then the coverslip can be loosened using water and heat on a hotplate, and excess water removed. A drop of medium containing iodine stain (preferably using the same medium originally used to prepare the slide) can be placed to one side of the coverslip. An absorbent paper can be held against the other side of the coverslip while the slide is heated to boiling very briefly. In this way, the iodine stained medium is drawn over the mites and fills the coverslip, while the excess medium is removed by blotting. As result, the freshly stained mites can be observed, drawn and photographed. This may not work with very old slides, difficult media such as polyvinyl alcohol, or overly faded specimens; but if the slide is not usable, this technique is worth a try.

Dismounting specimens from slides

Slides can be dismounted when specimens are undercleared or overcleared, or are at the coverslip edges, or when the researcher might need to view a different aspect of a mite, or would apply a different microscopic technique, as Nuzzaci and de Lillo did for the study by scanning electron microscopy of *Aceria caulobia* (Nalepa) and *P. avellanae* (Nuzzaci et al. 1991).

After removing the slide sealant, the water-based media can be made less viscous by addition of water and/or heating, such as in the procedures previously described, or by leaving the slide under a high humidity glass dome for a few hours at room temperature. These media are hygroscopic, absorbing water from the air at the coverslip margin and eventually becoming quite fluid, allowing the coverslip to slide freely, so that it can be propped up by insertion of a small pin from one side so that it can be lifted and removed with a forceps.

Line drawings

Adequately descriptive line drawings of good quality are not easy to produce and appear to be one of the weak points in eriophyoid systematics. The importance of this part of a

description was highlighted by Keifer (1975) and Amrine and Manson (1996), but even stronger emphasis should be made.

Slide mounted eriophyoid specimens, including type material, usually deteriorate over time, and are eventually not adequate for study, and may ultimately be totally destroyed. This deterioration can be caused by several factors, including: the water-based mounting media which may dry out rather quickly, air may penetrate under the coverslip, and, under certain conditions, specimens may continue to be cleared by the chemicals in the mounting medium, and fade away. Other representations of the original type series, including digital images of slide mounted specimens and electron microscope images, should also be archived in addition to slide mounted specimens and they have a support value, as previously mentioned by Amrine and Manson (1996). In the absence of type material, however, the original description and, particularly the drawings, become critically important, usually being the only representation of the described species. In many cases, drawings presented in the original description become the nearest equivalent of a holotype.

Moreover, drawings are rather clearly understood by everyone, and they are useful for a primary comparison whatever language is utilized, and regardless of the interpretation of characters in the text description. Certainly, line drawings in the style of Keifer (Fig. 8) are permanent and universally understandable. They are the core of each description and must be the best basic representation of an eriophyoid species (Keifer 1975; Amrine and Manson 1996).

The adequacy and value of drawing depends largely on the skill and experience of the researcher and on the quality of the slide mounted specimens.

Edward Baker and Richard Newkirk (pers. comm.) observed Keifer working and both related that the researcher made his final drawings directly using a drawing tube (=camera lucida) device with extraordinary care and accuracy. In some cases, Keifer drew freehand from the eyepiece using no drawing aids. But Keifer's talent was certainly unique!

Because of the minute size of these mites and their features, when studying, drawing and describing them, the researcher should always use a good-quality, phase contrast light microscope equipped with an oil immersion 100× objective at a large numerical aperture (one of the best is a fluorite objective with 1.30 numerical aperture or higher), and a drawing tube. A zoom lens on the microscope or drawing tube is very helpful. A 2× objective can additionally be mounted on some drawing tubes to allow the enlargement of very small details to prevent their obstruction by the pencil's point. In addition Amrine employs a chemical apparatus clamp to hold a reversed binocular at the appropriate position and angle to form a small field visible through the drawing tube (Fig. 9). Very detailed structures such as of the empodia (Fig. 9), male genitalia, female genital apodemes, etc. can be drawn using this method.

The illustrator should try to prepare an image eventually on a lower plane than that of the microscope-base level: in this way the illustrator can sketch a larger preliminary draft, and the much larger drawing scale usually helps in reducing the visibility of mistakes and irregular lines when reduced for the final plate. The drawing plane should be illuminated by a table lamp adjustable for light direction and intensity in order to clearly and concurrently see the pencil marks superimposed below the cuticular structures of the mite, both with good contrast. It is advisable for the aspiring illustrator to be taught by an experienced researcher using these techniques if at all possible.

The microscope stage and the slide mounted specimen should be oriented on the horizontal plane in such a way as to make the outlines of the specimen well suited to the illustrator's drawing technique (usually, lines on a paper are more easily drawn when the

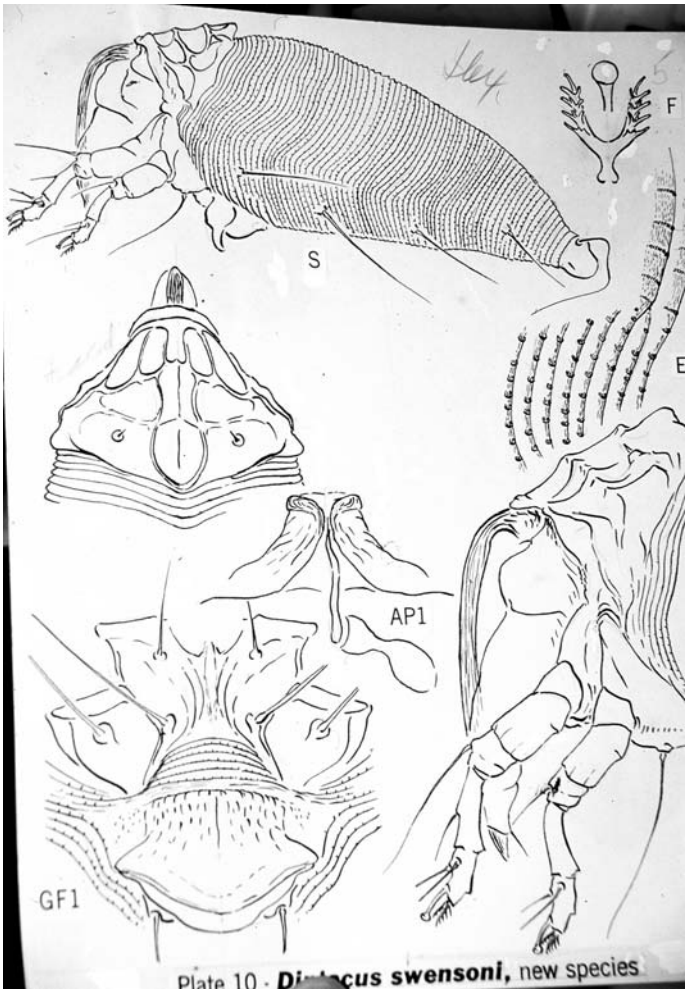

Fig. 8 *Diptacus swensoni* Keifer: original inked line drawings by Keifer at the US National Museum of Natural History, Beltsville, Maryland, USA

hand moves from left below to right above for right-handed people). An initial focus plane on the slide is chosen, and the illustrator draws the visible cuticular details in that plane on the paper. The illustrator can then focus on a higher or lower plane and add more details to the original drawing. Progressively, plane by plane, the illustrator can portray all the morphological features critical to the identity of the mite.

During drawing, one can cover the tube opening by one's hand to reduce the external light noise on the slide and to increase the contrast of specimen details. One can additionally cover the field diaphragm by the hand to obscure the mite and see just the sketch through the tube. The repeated, fast alternate movement of the hands facilitates detection of the presence or absence of some details on the line drawing by alternately flashing the two superimposed images.

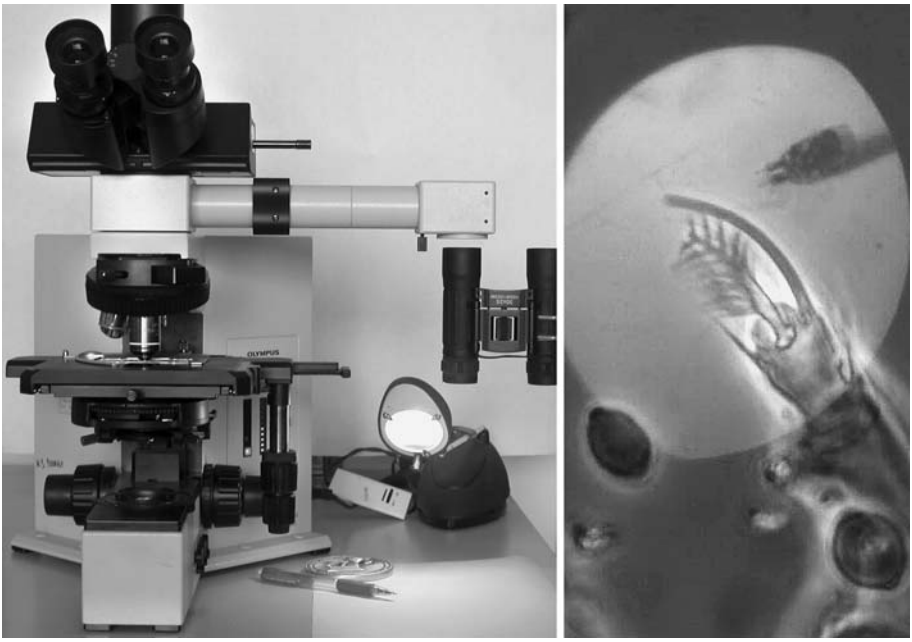

Fig. 9 Apparatus for drawing fine details: inverted binocular placed under the drawing tube opening (on the *left*) to decrease the size of the pencil or pen relative to small structures, such as empodia (on the *right*)

Descriptive drawings are usually semischematic, but they should be sufficiently detailed to portray the real morphology of the holotype specimen as closely as possible, and care should be taken not to "correct", "exaggerate" or interpret the features too much, so that some information is altered (see Keifer's recommendations in Fig. 1). The drawings should show the typical deviation from bilateral symmetry, and drawing one half, then copying the flip side of it to the other side becomes a fabrication, not science. Very often one specimen is not enough to get satisfactory information and additional specimens must be drawn, or even their features can be combined within one plate. This depends on the clearness, orientation and integrity of the specimen, contrast of the cuticle with the mounting media, and, of course, on the ability of the illustrator. This procedure also allows confirmation of some details.

In addition to the holotype specimen, other specimens should be studied to determine intraspecific variation in morphological features, at least in this one sample. Systematically important variations may be depicted in additional drawings if necessary.

Content that should be included in eriophyoid descriptive drawings

Often the content of eriophyoid plates can differ slightly depending on whether the depicted mite belongs to the Phytoptidae, Eriophyinae (Fig. 10), Phyllocoptinae or Diptilomiopidae (Fig. 11).

Amrine and Manson (1996) listed the most important body parts that should be illustrated by line drawings. Attempting to standardize the figure layout will make it

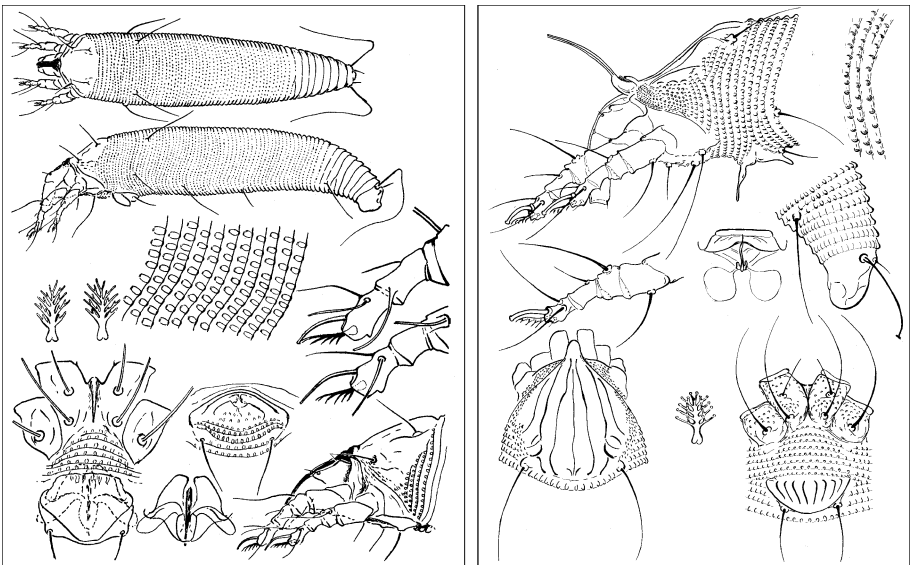

Fig. 10 Line drawings of a phytoptid (*Phytoptus corniseminis* Keifer-redrawn; on the *left*) and an eriophyid mite (*Aceria ficus* [Cotte], drawing by E. de Lillo; on the *right*)

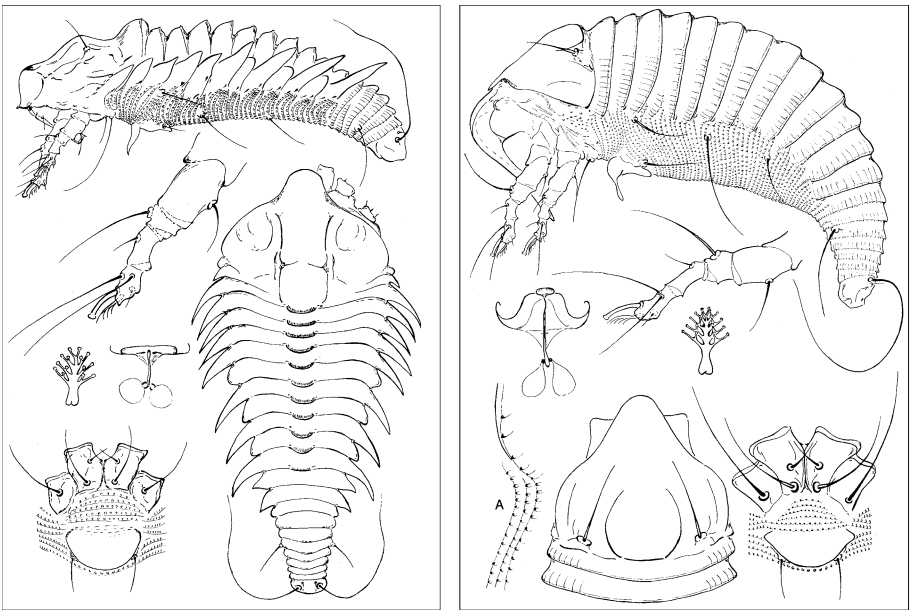

Fig. 11 Line drawings of a phyllocoptid (*Tegonotus heptacanthus* [Nalepa]; on the *left*) and a diptilomiopid mite (*Rhynchaphytoptus ficifoliae* Keifer; on the *right*) (drawings by E. de Lillo)

easier to compare the depiction of different species with each other, and for finding particular details in a drawing. Additional information to enhance their list is provided below.

Scanning electron microscopy pictures can assist in the understanding and perception of all features included in a table, but should never be used to the exclusion of line drawings, light microscopy, or other illustrations.

Prodorsal shield

The prodorsal shield must be depicted dorsally, including all ornamentations such as ridges, lines, granules, dots, cells, frontal lobe, anterior (*vi* and *ve*) and scapular (*sc*) setae and their tubercles, paying attention to the shape and size of these parts. The description of complex prodorsal shield ornamentation is almost always obscure if it is not accompanied by quality line drawings which are a fundamental requirement for a species' description, discrimination and identification although intraspecific variations may occur. Particular care should also be taken in depicting the frontal lobe margin and its shape. This lobe is frequently obscured by underlying gnathosomal and prodorsal elements, and may additionally be very thin and almost translucent, and its presence and margin may be very difficult to detect. It may help to study several specimens in this regard. Additionally, the illustrator must watch out for extremely tiny or obscure features like spines and extensions that may occur on the anterior edge of this lobe.

Coxal area and genitalia

The coxal and genital regions have to be carefully drawn on the ventral view position of the specimen. When illustrating these structures, coxal ornamentation should be studied in detail (e.g., ornamentations on coxae I may differ from that on coxae II) and care should be taken to determine whether lines are internal apodemes (e.g., near the base of coxae II) or surface lines or ridges. The following information should also be depicted: presence, shape and position of coxal tubercles, coxal seta robustness and length, shape and length of the internal coxisternal apodeme (sternal line), number of coxi-genital semiannuli or other structures set between coxae II and female or male external genitalia, and number and shape of microtubercles on these semiannuli. Regarding the genital region, the following features should be depicted: female and male (if found) external genitalia, particularly including details of the female genital coverflap, whether the coverflap seems to be divided in more than one region (e.g., basal and distal region), the ornamentation on these regions, ornamentation just anteriad of the coverflap and whether it is part of the area between coxae II. The length of setae *3a* should also be depicted accurately.

The genital apodemes, and softer parts like the spermathecae, are often difficult to observe and draw because of their size and their internal position and variability. Dissecting a clarified specimen at the level of the coxae or just posterior to the genital region is recommended, in order to have fewer disturbing elements (Keifer 1975). The length of the spermathecal tube and the size of the anterior part of the apodemes should be carefully observed, too.

Legs

For legs in lateral view, the ornamentations (e.g., spines, ridges) along the segments and at the level of the articulations, size of solenidia and shape of its tip, presence, position, and length of all leg setae must be depicted.

Concerning the empodium, particular care is needed in distinguishing the central shaft shape (whether divided or simple), the number of rays, and eventually the shape of branch tips.

Dorso-ventral view of the Diptilomiopidae

The large gnathosoma of the diptilomiopidae usually makes it difficult to have specimens oriented in true dorso-ventral position. In this case, the distal part of their large gnathosoma can be carefully removed or cut by a pin. Even though this is a tedious process, a bit of practice will allow the illustrator to get good results. A sharpened insect pin or fine dissecting scalpel should be used.

Lateral view drawings

With regard to the anterior part of the body, the illustrator needs to represent the lateral view of the gnathosoma, legs, prodorsal shield with its frontal lobe and setae (when present), lateral seta, first annuli after the prodorsal shield, and genital area. When printed, the anterior part of the mite should preferably be oriented to the left of the drawing. Particular care must be paid to the gnathosomal details, including the presence and shape of the palp coxal seta (*ep*), dorsal palp genual seta (*d*) and subapical palp tarsal seta (*v*), shape and size of the prodorsal shield, and any other surface detail (e.g., ornamentation on the pedipalp segments).

The anal lobes and the annuli up to the setae *f* have to be drawn in lateral view taking care to depict microtubercles, setae and any other detail. The posterior part of the anal lobes should preferably be orientated to the right side of the drawing.

Moreover, a few annuli need to be drawn trying to elucidate the shape and the size of the microtubercles (elliptical, roundish, pointed, etc.), their distribution, orientation, size of dorsal and ventral semiannuli, and details of lateral lobes, if they are present. These should be portrayed in lateral view to show the possible contrast between dorsal and ventral opisthosomal arrangement. Usually, the area chosen to be depicted is between the annuli at the level of opisthosomal setae c_2 and *d*.

For species with large dorsal semiannuli (e.g., Phyllocoptinae and some Diptilomiopidae) it might be better to draw the whole specimen in dorsal and/or in lateral view; using particular care to point out ridges, furrows, and lateral lobes on the opisthosoma. If the illustrator draws the specimen in lateral view, the body should be horizontally placed in the plate and the anterior part should preferably be directed to the left. In case of the dorsal view, the body should be orientated in the vertical plane of the table and it should have the anterior part placed near the top of it.

Preparation of the final plate

An initial draft with many notes and details is the result of the work at the drawing tube. The draft might be redrawn by pencil with special attention to the fine details. It should be compared at the microscope with mounted specimens without the light interference of the drawing tube in order to get more contrast and richness in details seen on the slide mounted specimen. Comparison of several specimens will allow you to note details of possible variation of key elements; this information can be presented in the description, or in some cases, a second drawing may be necessary.

After checking the initial draft, a smooth tracing paper can be put over the line drawing and final inking done on it, and not directly on the line drawing itself. For a better result, a large light table can be used for illuminating the draft and the final drawings to increase the line perception. Some researchers draw the final drawing by means of a technical pen (i.e., the well known rapidograph line pens, Rotring™ and Steadtler™ pens). Nuzzaci and de Lillo prefer metal nibs with pointed tips, of at least two sizes, mounted on a holder without an ink reservoir. The nib needs to be repeatedly refilled with a small amount of ink while drawing. Actually, nibs have the advantages of being easier to clean and to preserve than the tips of technical pens, and for making the size of the line variable by simply changing the pressure applied to the nib tip on the paper. Moreover, the dorsal, ventral and lateral parts of the nibs can be used according to the needed thickness of the line. Opaque black Indian ink is adequate and any mistaken and imperfect line can be removed from the tracing paper using a razor blade. Alternatively, mistakes can be removed from drawings after digitization using appropriate software applications.

The illustrator can initially prepare a large plate, with the drawings arranged on it, generally 42 cm wide and 58 cm high (an A2 sheet size). This large canvas allows the illustrator to reduce or mask defects such as those caused by a trembling hand, line imperfections, dirty marks, wrong lines, corrections, and so on. The large size of the drawing may be a problem for the printer. A scanner can be used to digitize the drawings (also single drawn body parts, if necessary), combine the plate, and to reduce their size keeping the high resolution required for printing. In preparing the final plate, the proportions of the single details should be carefully considered. Usually, the first leg and the microtubercle details are two times larger, and the empodium is four times larger than the other parts. Finally scale bars should be added, too.

Line drawings can be also made on a computer (Li et al. 2006; Wei et al. 2007; Wang et al. 2007) using a digitizer tablet with a digital pen. Drawing digitally can replace the inking process of the initial pencil draft as described above, but first of all it still remains of utmost importance to accurately interpret critical detailed morphology. It should theoretically be possible to take digital images of the slide mounted specimen, and electronically draw directly on the image. However, this procedure is limited by the tiny and intricate morphology of Eriophyoidea and by the need of high magnifications with limited field depth. Images can be stacked, but it has not been tested whether the final image will be sufficiently detailed and contrasted to replace the carefully made initial pencil draft and final inked drawings.

Measurements

Measurement instructions for typical descriptive features of Eriophyoidea were described by Amrine and Manson (1996). Figures demarcating the positions of features that may cause confusion or need better definition or standardization are surely more helpful and will overcome any linguistic misinterpretation (Figs. 12, 13, 14, 15).

Many interpretative doubts on the measurements of some features came out during the present authors' experiences and several of these have relevant importance, especially for phylogenetic studies on the Eriophyoidea. Most of them require a careful consideration about the standardization and correct definition of homologies between taxa.

However, each group, genus or species will present different problems and one precise solution will not fit all. Therefore, the author of a new mite must be flexible and able to

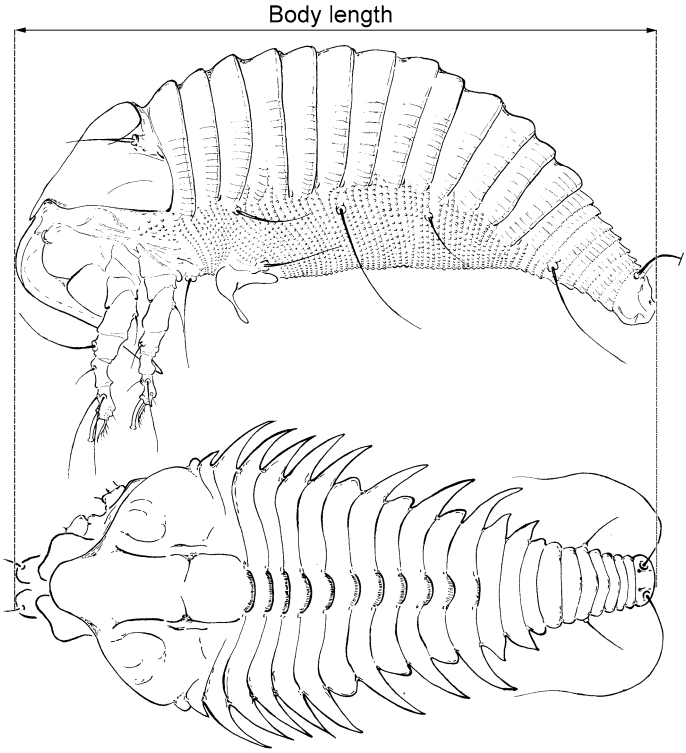

Fig. 12 Body length: from the rear end of the anal lobe to the maximum extent of the gnathosoma (above for *Rhyncaphytoptus ficifoliae* Keifer) or from the rear end of the anal lobe to the tip of the pedipalps (below for *Tegonotus heptacanthus* [Nalepa]; de Lillo's original drawings)

adapt and see the unique characteristics of the specimen at hand. This means, also, that the description paper should give note to the views and ways the measurements were taken.

A stage micrometer slide is used to calibrate the eyepiece reticule. Then, to make measurements of the specimen, the calibrated reticule is simply superimposed over any image viewed through the light path of the microscope and the linear dimensions (length and width) of a specimen feature can be measured. When making many measurements, the researcher often finds tedious, tiring and time consuming all the little movements and rotations needed with the microscope stage and with the eyepiece for matching the reticule scale with the features to be measured, especially when the morphological details are very fine and short.

To alleviate the tedium, the stage micrometer slide is used to draw a scale paper strip through the drawing tube for each objective lens. Then, the operator can measure more details of the same specimen by just re-positioning the scale strip and without changing the position of the slide or of the eyepiece. This technique saves time and makes measurements much more convenient.

Measurements can also be taken with an electronic image analysis set up. A digital camera is mounted on the microscope, and images are captured and transferred to a computer. Then, they are viewed and manipulated on screen to various angles and levels, and details are measured using different techniques, depending on the digital image

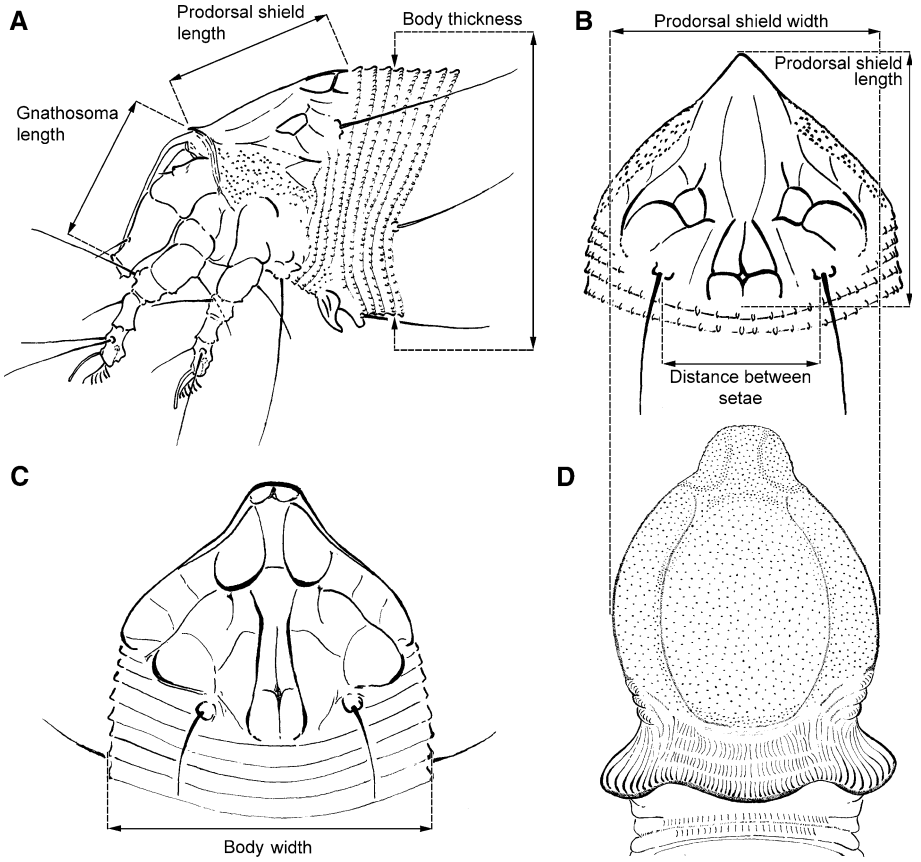

Fig. 13 **A**, **B** *Aceria novellae* Denizhan, Monfreda, Cobanoglu and de Lillo, **C** *Aculops pelekassi* (Keifer), **D** *Bariella farnei* de Lillo. Gnathosoma length: from the proximal margin of the cheliceral bases to the midpoint of the pedipalp tips. Prodorsal shield length: from the most anterior margin (of the prodorsal shield or frontal lobe) to the anterior margin of the first complete annulus posterior to the shield. Prodorsal shield width: from side to side at the level of the first distinct lateral annulus or at the widest level if the shield margins are protruded. Body width: from side to side at the level of setae *c2* or widest dimension if *c2* is absent. Body thickness: from dorsal to ventral aspect of the opisthosoma at the level of setae *c2*, if present. Distance between setae *sc*: from the inside margins of the setal bases. Distance between tubercles of setae *sc*: from the inside margins of the tubercles (de Lillo's original drawings)

software application used. Care should be taken that the system has been correctly calibrated by comparing with a set of *manual* measurements, and that the digital images are clear and have sufficient contrast to show each minor detail to be measured completely (e.g., very fine setae). Craemer conducted more accurate measurements *on live/video* images (where the image can still be focused up and down on the screen), rather than on a captured images, which may not be able to capture the entire structure to be measured at once, even when using different stacking methods.

Concerning measurements of the holotype, de Lillo measures selected specimens of a population and chooses the holotype within this group as the specimen with closest measurements to the average value for the greatest number of details.

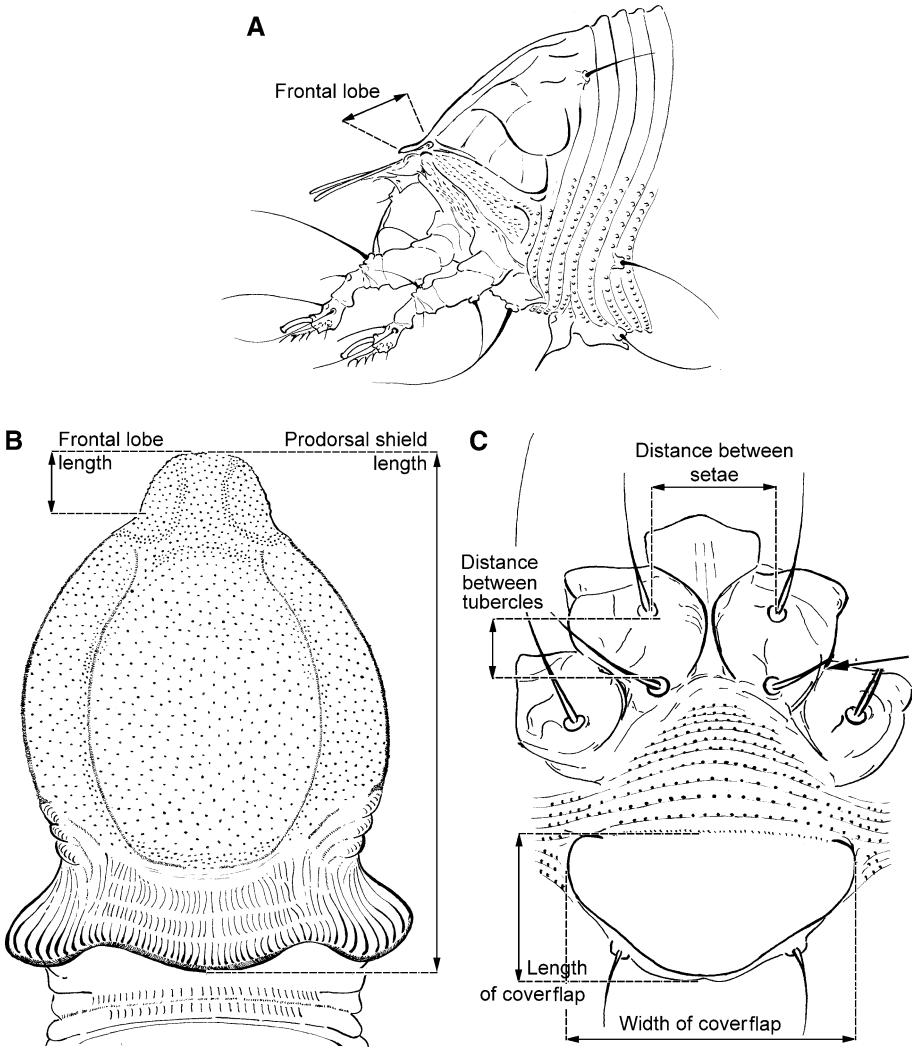

Fig. 14 **A** *Aculops pelekassi* (Keifer), **B** *Bariella farnei* de Lillo, **C** *Diptacus gigantorhynchus* (Nalepa). Distance between coxal setae: from the inside margins of the setal bases. Distance between tubercles of coxal setae: from the inside margins of the tubercles. *Arrows* indicate the short apodeme exactly where the two legs come together, at their contact, or where they pivot; the apodeme is usually quite distinctive and the anterior edge of this apodeme is used as a reference point for measuring both leg I and leg II length in ventral-dorsal view. Prodorsal shield length: from the most anterior margin (of the prodorsal shield or frontal lobe) to the anterior margin of the first complete annulus posterior to the shield. Frontal lobe length: from the motivator (gnathosomal base) to the anterior edge of the frontal lobe. Genital coverflap width: from its lateral margins. Coverflap length: from the transverse line anteriorly placed to the rear line of the coverflap (de Lillo's original drawings)

Finally, when taking many measurements of many specimens, a spreadsheet such as Microsoft Office's Excel® is very convenient for taking averages and ranges of values for each characteristic; properly designed, the files can be printed as tables to support the description.

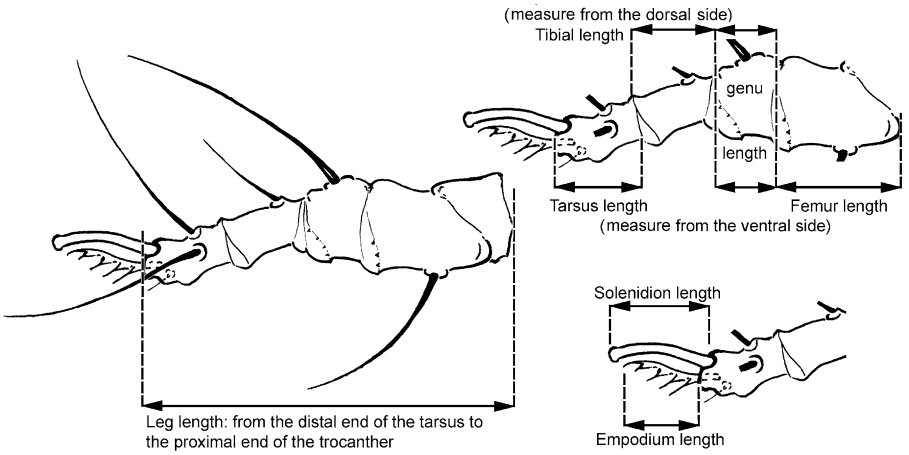

Fig. 15 *Aceria ficus* (Cotte). Length of legs from the trochanter proximal margin to the distal margin of the tarsus excluding the empodium and solenidion. Femur and tarsus length: measured ventrally. Tibial length: measured dorsally. Genu length: measured dorsally or ventrally. Solenidion and empodium lengths: from the pigmented base where inserted to the distal tip (de Lillo's original drawings)

Language

Every researcher is free to choose to publish eriophyoid taxonomic papers in the author's mother tongue. Fortunately, taxonomic articles published in English have been increasing considerably in the past decade, allowing for a wider and more convenient dissemination of information. Nevertheless, many older papers need to be translated because the drawings are often incomplete and cannot show data usually indicated in the morphometric description, and the English abstracts usually lack needed and detailed information. One particular language is not more important than another but, in the scientific environment, English is so widespread and most often understood that it is worth while to have an abstract which contains an English translation, taking care that it should be as complete as possible in order to be useful for identification purposes and morphological comparisons.

Considering the costs of having a paper translated, or of obtaining interlibrary loans, a shared web archive should be arranged and promoted within the copyright rules. The electronic information facilities of public institutions should be preferably used to ensure non-profit designations. This can allow researchers to upload/download translated and other papers in a sort of peer to peer network. Such a network would greatly facilitate sharing important biological and descriptive data, or key publications, and ultimately to promote greater advances in eriophyoid research. Many authorities provide digital copies of their key publications on their web sites, which is enormously helpful.

Completeness of descriptions

Strong recommendations were given by Keifer (1975) and Amrine and Manson (1996) about the need to include knowledge on the host plant identification, mite habit and host plant relationships. Particular care should be taken in finding and collecting males; their morphology often helps to understand the female status as protogyne/deutogyne mites.

Often, in literature, many species are described based on a small population and/or without the male. Such descriptions often have very limited biological data and lack information about the intraspecific morphometric variability. A new species should ideally be described based on widely dispersed samples in order to avoid describing an accidental presence of a mite on an improper host.

Considering the general availability of GPS devices, collection localities should also include latitude and longitude data at least to the level of minutes.

The rules of the International Code of Zoological Nomenclature (ICZN 1999), currently on line at http://www.iczn.org/iczn/index.jsp, must always be followed for nomenclature decisions, name assignment and for gender agreement between genus and species name. Often, patronymic and locality names are assigned after their latinization. Researchers should try to avoid applying genus and species names characterized by a series of contiguous consonants or vowels in order to reduce typing mistakes when these names are listed in tables, indexes and catalogues, as sometimes happens.

Finally, in order to reduce confusion in eriophyoid systematics, species identity should be clearly established when biological observations are specifically carried out, and publications of unnamed or unidentified species should be avoided, such as recently happened for an *Acalitus* sp. of *Carpinus tschonoskii* Maxim (Kawashima and Amano 2004).

Concluding remarks

The information and recommendations given in this article may seem overly demanding and meticulous at first glance. However, these come from our collective and shared experience in studying Eriophyoidea for systematic purposes. It is not meant to be a text book recipe, but hopefully it will spur new ideas and techniques in attaining proper and exact descriptions that will add value and stability in eriophyoid systematics and reduce confusion which is currently prevalent in some groupings.

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APPENDIX M

New characters from scanning electron microscopy improve Eriophyoidea descriptions, illustrated by the description of three new species of *Diptilomiopus* Nalepa, 1916 (Acari: Diptilomiopidae: Diptilomiopinae) from South Africa.

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New characters from scanning electron microscopy improve Eriophyoidea descriptions, illustrated by the description of three new species of *Diptilomiopus* Nalepa, 1916 (Acari: Diptilomiopidae: Diptilomiopinae) from South Africa

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Abstract

Three new *Diptilomiopus* species associated with indigenous trees from South Africa are described and illustrated. Two of the descriptions are significantly enhanced with morphological information from low temperature (cryo) scanning electron microscopic (LT-SEM) studies which provide novel characteristics. Morphology obtained from slide-mounted specimens, containing artefacts, is compared with SEM images. The new species are in the subfamily Diptilomiopinae of the family Diptilomiopidae: *Diptilomiopus faurius* **sp. nov.** from *Faurea rochetiana* (A. Rich.) Pic. Serm. (Proteaceae), and *Diptilomiopus apobrevis* **sp. nov.** and *Diptilomiopus apolongus* **sp. nov.** from *Apodytes dimidiata* E.Mey. ex Arn. (Icacinaceae). The species are vagrants on the leaf under-surfaces of their host plants, causing no apparent damage. The genus *Diptilomiopus* is re-diagnosed and re-described, and the generic assignments of some species currently in *Diptilomiopus*, are discussed. A key to the Diptilomiopidae species known from South Africa is provided.

Key words: Acari, Trombidiformes, Prostigmata, *Diptilomiopus*, plant-feeding mites, South Africa, taxonomy, morphology, scanning electron microscopy, new descriptive characters

Introduction

Eriophyoidea are obligatory plant-feeding mites. They have a cosmopolitan distribution, and occur on a vast range of plant families of most groups of land-living multicellular plants, but the majority of species are generally regarded to be very host-specific (Oldfield, 1996). About 4 000 Eriophyoidea species are known worldwide (De Lillo & Skoracka, 2010). This probably represents only a tiny proportion of extant species. It is conservatively estimated that the world extant eriophyoid fauna may range from 35 000 to 50 000 species (Amrine *et al*., 2003), and indicates that less than 8 to 11 % (depending on the country and area) may be known. In South Africa, and the remainder of the Afrotropical Region in particular, the diversity is largely unknown. The description of new eriophyoid species are thus of primary importance to address the short fall of the knowledge on the diversity of these mites.

The Eriophyoidea are morphologically distinct among mites. They are minute (on average 150–250 µm long), with elongated, worm-like and annulated bodies, and are unique in having all instars of both sexes with two pairs of similarly developed legs anteriorly (Keifer, 1975a). Their minute, soft bodies and ultra-fine structures cause challenges for their morphological study and preparation for such study (De Lillo *et al.*, 2010). Eriophyoid morphology for systematic use is almost exclusively studied on cleared and slide-mounted specimens, which are not permanent (De Lillo *et al*., 2010), using phase contrast light microscopy. Eriophyoid descriptions still largely follow the standard and format set by Keifer (Nuzzaci & De Lillo, 1996; De Lillo *et al.*, 2010). Amrine & Manson (1996) reviewed taxonomic characters and their use, and proposed what should be included in an eriophyoid species description. These standard descriptions are still the simplest and the most practical, and form the basis of the classification and identification of the Eriophyoidea.

Identification keys to the genera of the Eriophyoidea worldwide by Amrine (1996) and Amrine *et al.* (2003) are generally accepted, and identification, description and differentiation of eriophyoid taxa at all levels are more or less satisfactory. In practice, however, many descriptions and drawings do not achieve the required standard and in particular do not always convey exact taxonomically important detailed characteristics (Amrine & Manson, 1996; De Lillo *et al.*, 2010). Some of the factors causing it are problems with the quality and standardization of slide-mounted specimens (Amrine & Manson, 1996; De Lillo *et al.*, 2010), and the resultant standardization and quality of their description. Artefacts inherently caused by slide mounting and inefficient resolution of detailed morphology are contributing to the problem and may be detrimental to eriophyoid taxonomy. Additionally, some taxonomic characters are not well-defined and demarcated, and this presents problems for practical taxonomy and the determination of primary homologies for phylogenetic analyses. It is further evident that there are not enough morphological characters documented and available for phylogenetic analyses, and most of these were found to

be highly homoplasious by phylogenetic studies (Hong & Zhang, 1996a, b, 1997; C. Craemer, *in preparation*).

Many of these systematic problems can be rectified or improved on by the discovery of additional new systematically informative characters, apart from those characters that might be obtained from the discovery of new species. There is, however, not much such additional information available from slide-mounted specimens. The characters are already obtained from the entire body (Lindquist & Amrine, 1996; Amrine *et al.*, 2003), and most easily observable and taxonomically useful characters are already utilized. The degree of morphological diversity is also limited by the lack of observed ontogenetic diversity in characters (characters have the same states throughout all life stages), and the lack of distinctive characters in the male (Lindquist & Amrine, 1996). There is furthermore a need for the morphological study of eriophyoids in a more natural, artefact-free condition, to determine the types of artefacts caused by slide-mounting, and standardization of these for taxonomic practices.

Electron microscopy (EM), which facilitates higher resolution than light microscopy and renders three-dimensional images, is largely superior to light microscopy for studying the morphology of minute organisms with ultra-fine structures. Electron microscopy already contributed more information on the external and internal morphology of eriophyoid mites, and our understanding of and knowledge on their morphology have been improved (Nuzzaci & De Lillo, 1996). Scanning electron microscope (SEM) images are, however, sporadically, and not routinely, incorporated in eriophyoid taxonomic articles. They are moreover largely used to enhance and confirm descriptions of Eriophyoidea from slide-mounted specimens. When they are included in articles it is normally without particular comment or focus on them. The SEM-images probably contributed to the correctness and detail of the descriptions wherein they were used (e.g., Keifer *et al.*, 1982; Boczek & Nuzzaci, 1985; Schliesske, 1985; De Lillo, 1988; Chandrapatya & Boczek, 1991a,b; Boczek & Chandrapatya, 1992; Amrine *et al.*, 1994; De Lillo, 1994; Huang & Wang, 2004; Menon *et al*., 2011), essentially no additional morphological or descriptive information were defined or discussed from them, except Menon *et al*. (2011) who described spines occurring on leg segments largely from SEM images.

Low-temperature SEM (cryo-SEM), with an integrated high vacuum freezing and sputter unit, seems to be the most successful in obtaining highly magnified, largely artefact-free images of eriophyoid mites, particularly minimizing shrinkage (Sutherland & Hallett, 1987; Duffner *et al.*, 1998; Wergin *et al.*, 2000; Achor *et al.*, 2001).

Three new *Diptilomiopus* spp. are described here.[1] The descriptions are more detailed than the norm for Eriophyoidea species descriptions, and the description of two of the species include

[1] This is the second paper in a series of articles on the Diptilomiopidae Keifer, 1944. The previous article (Craemer *et al*., 2005) entailed species recombinations and a new synonymy in *Diptilomiopus*.

characters described from SEM images, which are not visible or distinguishable in slide-mounted specimens. The SEM images are additionally compared with the slide-mounted specimens to determine the amount of artefacts and loss of information caused by slide-mounting. Differentiation of the species, however, includes characters available from slide-mounted specimens. The morphometric information of the descriptions is provided statistically more structured than usually found in eriophyoid descriptions in an effort to improve the quality and usefulness of morphometric data in descriptions for phylogenetic analyses. It is now possible to utilize continuous morphometric data, without gap coding, in phylogenetic analyses in the program TNT© (Tree Analysis Using New Technology) (Goloboff *et al*., 2008).

The new species are the first *Diptilomiopus* spp. (Diptilomiopidae: Diptilomiopinae) recorded from South Africa. The only record of the Diptilomiopidae from this country is *Africus psydraxae* Meyer & Ueckermann, 1995, a genus and species described from *Psydrax livida* (Hiern) Bridson (Rubiaceae) (Meyer & Ueckermann, 1995).

Diptilomiopus, the type genus of the Diptilomiopidae, was described by Nalepa (1916) to accommodate the type species, *D. javanicus*, an inquiline in galls on the upper leaf surface of *Hemigraphis confinis* (Nees) T. Anders (Acanthaceae) in Java (Nalepa, 1916). Since 1916, and before the present study, 90 *Diptilomiopus* spp. have been described, with the majority from the Indomalayan Ecozone (Oriental Region) (Thailand – 31, India – 19, Taiwan – 16, China – 16, Philippines – 1, Japan – 1, Java – 1) (Hong & Zhang, 1997; Craemer *et al*., 2005; Hong *et al*., 2010), and one species from Australia (Keifer, 1969) in the Australasian Ecozone. Three species are known from the Afrotropical Ecozone (Sub-Saharan Region) and these are: *D. ficifolius* (Boczek & Oleczek, 1988) from *Ficus sur* Forssk. (= *F. capensis* Thunb.) (Moraceae) in Nigeria (Boczek & Oleczek, 1988); *D. holopteleae* Abou-Awad & El-Banhawy, 1992 from a *Holoptelea* Planch. sp. (Abou-Awad & El-Banhawy, 1992) (possibly *Holoptelea grandis* Mildbr.) (Ulmaceae) in Kenya; and *D. jevremovici* Keifer, 1960 from *Coffea arabica* L. (Rubiaceae) in the Democratic Republic of the Congo (Keifer, 1960). One species – *D. ficus* Attiah, 1967 from Egypt – is known from the Palearctic Ecozone. It, however, was collected on "fig trees" (Attiah, 1967), presumably the cultivated fig, *Ficus carica* L., which is believed to have originated in western Asia and later spread to the Mediterranean (Tous & Ferguson, 1996). *Diptilomiopus ficus* probably originated with its host in western Asia. It seems as if *Diptilomiopus* may have originated in the Indomalayan Ecozone, and may be restricted to the subtropical and tropical areas of this and the Australasian and Afrotropical Ecozones.

Diptilomiopus is re-diagnosed and re-described, based on a review of the genus. The classification of some *Diptilomiopus* spp. is discussed, and some of these are re-assigned to other genera. A key to the Diptilomiopidae species from South Africa is included.

Materials and methods

Specimens were collected by hand from plant material using a stereo microscope mostly at 40x to 80x magnification, and were prepared and slide-mounted according to a modified version of Keifer's media and method (Keifer 1975a; De Lillo *et al*. 2010). The SEM images are of specimens prepared and studied with a modified version of the low-temperature (cryo) fixation technique described by Echlin *et al*. (1970), using a conventional JEOL JSM 840 SEM with a cryo-stage. The figures presented in this paper, consist of realistic line drawings of slide-mounted specimens, and SEM images of specimens studied by above technique.

The terminology and setal notation in the descriptions are largely based on Lindquist's (1996) system. In the text and figure captions (not tables), largely setae and solenidia are referred to by their alphabetic name in italics, without the term "seta" or "solenidion" before them. Only one side of the body is described and measured. Measurements and counts are rounded to the nearest integer, are in micrometers (µm), and are presented in Tables 2–4.

All types of the new species are preserved as slide-mounted specimens. The type material is deposited in the National Collection of Arachnida: Acari, Biosystematics Building, Roodeplaat, ARC–Plant Protection Research Institute, P/Bag X134, Pretoria Queenswood, 0121 South Africa, and one slide, with paratypes, of each new species will be deposited in the Insect and Mite Collection, National Museum of Natural History (NMNH), Smithsonian Institution, Washington D.C., USA. The Mite Collection is housed at USDA, ARS, SEL, Beltsville, Maryland, USA. The scanning electron microscope images will be archived and kept in the collection in Pretoria in addition to the type material.

Systematics

Key to the Diptilomiopidae of South Africa

1. Seta *sc* present, but minute; *1a* absent ……...…….. ……. *Africus psydraxae* Meyer & Ueckermann, 1995
-- Seta *sc* absent; *1a* present ……..... 2
2. Ridge m2 (dividing cells B1L and B1R) (Figs 1A,B; 3D,E) of the dorsal shield pattern present, and the prosternal apodeme anteriorly with a diamond-shaped part (Fig. 6A) …….. ……. *Diptilomiopus faurius* sp. nov.
-- Ridge m2 (dividing cells B1L and B1R) (Figs 1A,B) of the dorsal shield pattern absent, or invisible in slide-mounted specimens, and the prosternal apodeme without a diamond-shaped part or prosternal apodeme effaced or absent ……. 3
3. Cells D1L and D1R at base of dorsal shield pattern (Figs 1A; 12A,D) present, number of opisthosomal microtubercles mid-ventrally about 12–18 / 20 µm, approximate setal lengths: *d* 10–13, *e* 8–12, *3a* 6–9 (Table 1) ……... *Diptilomiopus apobrevis* sp. nov.

-- Cells D1L and D1R at base of dorsal shield pattern (Figs 1A; 21A,G) absent, number of opisthosomal microtubercles mid-ventrally about 8–13 / 20 µm, approximate setal lengths: *d* 53–63, *e* 47–59, *3a* 10–13 (Table 1) …….... *Diptilomiopus apolongus* sp. nov.

Table 1. Measurements and counts of the three new *Diptilomiopus* spp., and *D. gilibertiae*.

	faurius			*apobrevis*			*apolongus*			*gilibertiae*		
	mean	min	max	**mean**	min	max	**mean**	min	max	**mean**	min	max
body length (pedipalpi included)	**272**	222	322	**222**	188	265	**280**	232	311	**251**	206	291
seta *v* (apico-ventral seta) length	**4**	3	4	**5**	5	6	**6**	5	6			
chelicerae length	**77**	70	82	**74**	68	77	**85**	81	98			
prodorsal shield length	**33**	28	37	**38**	32	41	**38**	35	42	**34**		
prodorsal shield width	**62**	56	69	**73**	65	80	**72**	63	80	**75**		
scapular tubercles distance apart	**24**	22	28	**27**	23	32	**28**	25	30	**27**		
number of ventral microtubercles / 20 µm	**10**	7	12	**15**	12	18	**10**	8	13			
seta *d* length	**48**	40	56	**12**	10	13	**58**	53	63	**12**		
seta *e* length	**40**	32	52	**10**	8	12	**53**	47	59	**8**		
setae *e* distance apart	**33**	27	38	**27**	22	31	**34**	30	36	**29**		
seta *f* length	**38**	35	41	**44**	40	48	**46**	43	48	**34**		
coxal seta *1a* (2nd coxal seta) length	**36**	29	40	**37**	28	46	**45**	36	55	**28**		
coxal seta *2a* (3rd coxal seta) length	**52**	50	59	**55**	47	61	**61**	53	68	**39**		
Leg I length (from base of trochanter)	**40**	37	43	**42**	37	45	**49**	45	57	**61**		
Leg I tarsus length (excluding extremities)	**13**	11	14	**11**	10	14	**15**	14	17	**12**		
Leg I empodium number of rays	**7**	7	8	**7**	7	8	**7**	7	8	**6**		
Leg II length (from base of trochanter)	**36**	33	39	**37**	34	42	**43**	39	47	**50**		
Leg II tarsus length (excluding extremities)	**11**	10	12	**11**	10	11	**14**	12	14	**10**		
Leg II seta *ft''* (lateral tarsal seta) length	**36**	32	39	**33**	32	35	**41**	39	45			
seta *3a* (genital seta) length	**11**	8	12	**7**	6	9	**12**	10	13	**6**		

***Diptilomiopus* Nalepa, 1916**

Diptilomiopus Nalepa, 1916: 283; Nalepa, 1918: 228–230; Keifer, 1938: 305; Keifer, 1975b: 521; Newkirk & Keifer, 1975: 585; Chakrabarti & Mondal, 1983: 299; Amrine & Stasny, 1994: 173; Boczek *et al*., 1989: 25, 182 (plate 190 not of *D. javanicus*, but of *D. jevremovici*); Kuang, 1995: 168; Amrine, 1996: 111, 140; Hong & Zhang, 1996c: 71; Hong & Zhang, 1997: 321; Amrine *et al*., 2003: 137, 195–196; Craemer *et al*., 2005: 133–134.

Sectipes Keifer, 1962a: 18–19; Keifer, 1962b: 19, **syn**.; Newkirk & Keifer, 1975: 585.

Vilaia Chandrapatya & Boczek, 1991a: 427–428; Boczek & Chandrapatya, 1989: 139–140; Amrine & Stasny, 1994: 311–312; Amrine, 1996: 114, 141; Hong & Zhang, 1997: 321, **syn**.; Amrine *et al*., 2003: 137, 215; Craemer *et al*., 2005: 133–135.

Type species: *Diptilomiopus javanicus* Nalepa, 1916, by original designation.

RE-DIAGNOSIS. This diagnosis is a compilation and modification of the diagnoses by Nalepa (1916, 1917), Hong & Zhang (1997) and Amrine *et al.* (2003). *Diptilomiopus* has the typical diagnostic characteristics of the Diptilomiopidae and Diptilomiopinae, and is distinguished from other genera in the Diptilomiopinae by the following combination of character states: dorsal annuli slightly more than ventral annuli; legs I and II 5-segmented with the genu seemingly absent, probably fused with the femur, with *bv*, *l''*, and *l'* absent; coxisternal plates I with *1b* absent; opisthosoma with *c2* absent, and *d*, *e*, *f*, *h2*, *1a*, *2a* and *3a* present; *sc* absent.

RE-DESCRIPTION. This description is an expansion and modification of the genus descriptions by Nalepa (1916, 1917), Keifer (1938), but here including morphological variation within the genus, and new insight and information from a review and compilation of descriptive data of *Diptilomiopus* spp. worldwide. It does not include the family (Diptilomiopidae), subfamily (Diptilomiopinae) and diagnostic generic characteristics given above.

FEMALE (typifies the genus).

Idiosoma – fusiform to somewhat elongated fusiform (e.g., Figs 2; 11A,B); relatively thick in lateral and dorsal view, broadest at the prodorsum, tapering towards the rear end, sometimes sharply, with the rear end slanting downwards. Many species described to be light to dark amber (orangey) when alive.

Opisthosoma – evenly rounded; usually with a longitudinal middorsal ridge, which may be slight, flanked by a shallow trough on each side which sometimes, together, form a v-shape with narrow

end towards the rear, and each is frequently flanked on the outside by a very slight, barely discernable subdorsal ridge (e.g., Fig. 2D). These ridges and furrows fade towards the rear, until they are absent. All or some of these ridges and furrows are described as being absent in some species, but these cases need confirmation. Wax secretions not present, except in *D. artocarpae* (wax patches) and *D. melastomae* (covered with wax), but *D. artocarpae* do not belong in *Diptilomiopus* (see below).

Dorsal annuli entirely without microtubercles in most species, but in some species they are covered with microtubercles, which may occasionally be sparse or scattered, or may be restricted to certain areas, e.g., absent in a central band, which is flanked by microtubercles on each side, or only on rear dorsal annuli. Ventral annuli covered with microtubercles in all species.

Seta *h1* absent or present, when present always minute (e.g., Fig. 2C), the recorded absence in some species may be ambiguous, because its presence might have been missed due to the tiny size of the seta.

Gnathosoma – palp *d* present or absent, but presence or absence usually not recorded; *ep* and *v* probably always present, but are rarely recorded or described. Some ornamentation and structures may be present on palpi as illustrated in SEM images (e.g., Fig. 4) of the new species here described, but are most probably largely not visible in slide-mounted specimens, and were not previously described for *Diptilomiopus* spp.

Prodorsal shield – usually broadly oval, with width much broader then the length of the relatively short shield, with characteristic convex shape with declivitous rear area (e.g., Fig. 3A). It has been described as sub-triangular or diamond-shaped in some species, and the shape was sometimes used to differentiate between species. Evaluation and depiction of prodorsal shield shape is highly subjective, and may be ambiguous due to distortion of slide-mounted specimens.

Prodorsal shield pattern prominent, consisting of ridges in a roughly typical cell-like pattern, of which a more complete version is schematically depicted in Fig. 1A. This complete typical expression of the ridge-pattern consists broadly of three rows of cells named as follows: 12 cells (A1L–A6L and A1R–A6R) in anterior row, six cells (B1L–B3L and B1R–B3R) in second row and two cells (C1L and C1R) in basal row; two open cell-like areas, D1L and D1R are formed at the base of the shield pattern on the declivitous basal part of the shield (Figs 1A; 3A,D,E) and may be regarded as a fourth cell row. Due to the compression of this area on the slides, if present, D1L and D1R are not always clearly present on the slide-mounted specimens (e.g., Fig. 12B). Alongside D1L and D1R three cell-like areas may be present, D4L, D3L, D2L and D2R, D3R, D4R, which sometimes seem like an extension of the basal row (C1L and C1R). More prominent variations of the dorsal shield ornamentation between species are: presence or absence of sections of the median line (e.g., ridge/line between cells A1L and A1R, B1L and B1R, C1L and C1R, and between D1L and D1R) or of the other transverse or longitudinal ridges, dividing or forming cells, as well as the

relative larger and smaller size or difference in shape of cells in comparison with the "complete" and "typical" shield pattern depicted in Fig. 1A. Sub-shield lateral area usually with granules.

Scapular setal tubercles present or absent – absence or presence of these tubercles was not described, and is still unknown, for some species, including the type species. Scapular tubercles when present and described as such, are relatively small, rounded and ahead of rear shield margin (e.g., Figs 3A–D). They may be obscured by the ridges on the shield, and recorded absence in species is ambiguous and should be confirmed.

A frontal lobe might be present in all or most species, but was recorded and depicted as absent in most species, because it is inconspicuous in slide-mounted specimens, as demonstrated by the new species described here (e.g., Figs 3D; 12B; 21A). In the new species, however, a transversely broad but longitudinally narrow frontal lobe with a slight, broad indentation of the anterior margin is unambiguously present when viewed with SEM (e.g., Figs 3A,B; 12A). The frontal lobe, when present, is probably thin and flexible and not overhanging the basal parts of the chelicerae, and is subjectively not classified as a frontal lobe when evaluated for use in descriptions and diagnoses of taxa, and the keys to genera and species in the Eriophyoidea. The presence or absence of the frontal lobe is used to differentiate supra-generic taxa.

Legs – tibia of average length in comparison with other Eriophyoidea genera, and usually shorter than, or sometimes equal in length to tarsus. It is longer than tarsus (but not twice the tarsal length) only in a few species: *D. hexogonus*, *D. holopteleae*, *D. integrifoliae*, *D. languasi*, and *D. lobbianus* (Huang, 2001; Abou-Awad & El-Banhawy, 1992; Mohanasundaram, 1981; Chandrapatya & Boczek, 1991b; Huang & Cheng, 2005, respectively). Shape and structures of tibiae I and II are well discernable in SEM images, and may entail ridges in the length, dorsally terminating in well developed spines (e.g., Fig. 7B); these are less discernable in slide-mounted specimens (e.g., Figs 7C,D). The shape of the tibia may be of systematic use in *Diptilomiopus* spp., but is not described.

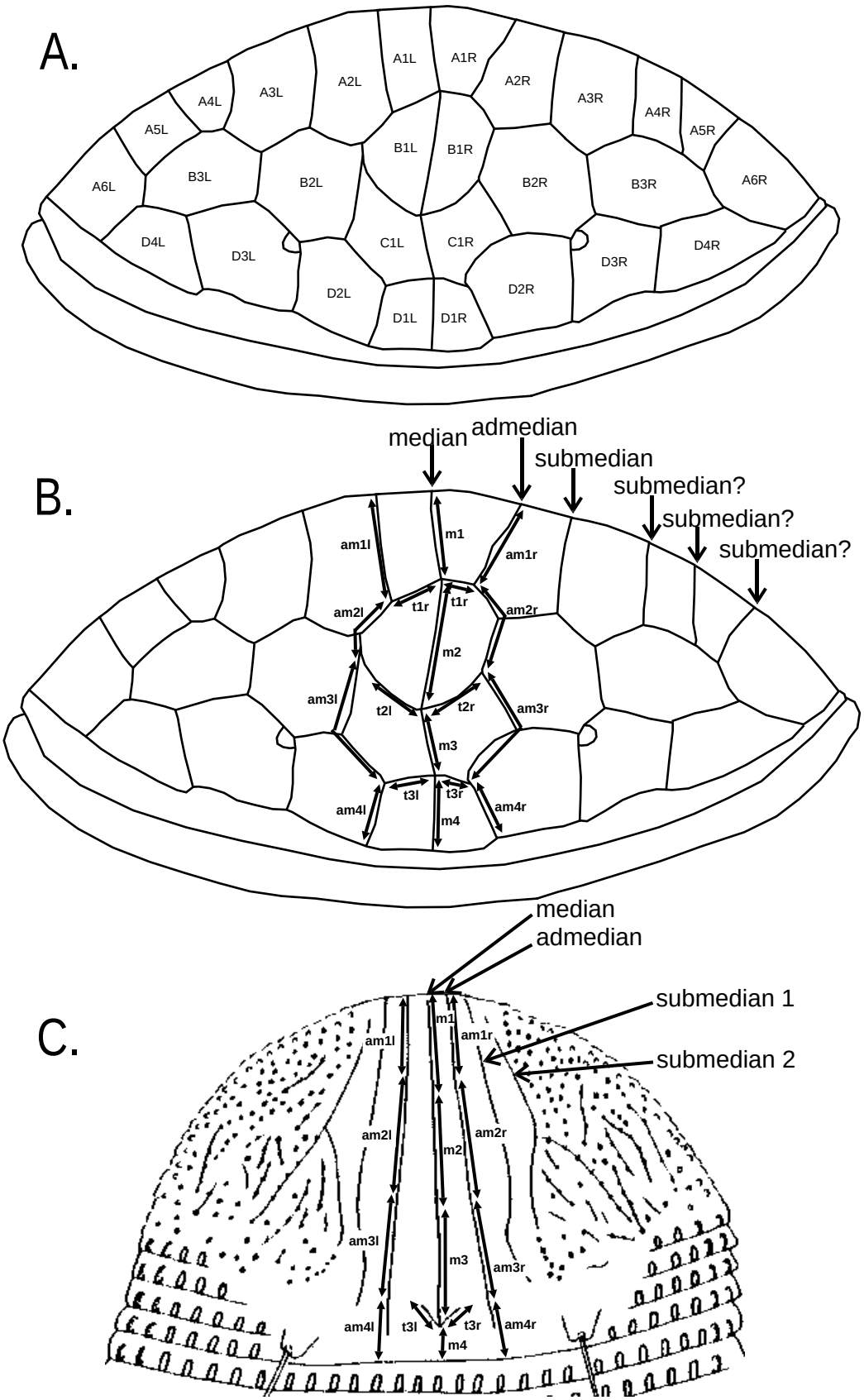

Figure 1. Prodorsal shield ornamentations. A. Cell names of "*Diptilomiopus*"-like schematic prodorsal shield network; **B**. line or ridge names of "*Diptilomiopus*"-like schematic prodorsal shield network; **C**. line or ridge names of dorsal shield pattern of *Aceria barbertoni* Meyer & Ueckermann, 1992, reproduced from Meyer & Ueckermann (1992), with frontal lobe deleted to facilitate clearer labeling of lines.

Seta *ft'* on tarsus of leg II is present or absent, but presence or absence was rarely described. Both setae *ft* in legs I and II are usually simple and tapering, but in *D. eucalypti*, *D. ficifolius*, *D. musae* and *D. sandorici* these setae have a small sub-branch or spike near the bases of the setae (Chandrapatya & Boczek, 1991b; Boczek & Oleczek, 1988; Chandrapatya & Boczek, 1998, 1991a, respectively). In the diagnosis of *Vilaia*, a new genus described by Chandrapatya & Boczek (1991a), the tarsal setae are described "with short perpendicular spike at the base". The tarsal setae of the designated type species of *Vilaia*, *Diptilomiopus pamithus* (= *Rhynacus pamithus*, = *Vilaia pamithus*) are not described in the text, however, and are depicted as simple (without spikes) (Boczek & Chandrapatya, 1989). *Vilaia* was designated a junior synonym of *Diptilomiopus* (Hong & Zhang, 1997), but might be a valid, monophyletic genus, supported by the possible synapomorphy, presence of spikes on the tarsal setae, but this should be recovered by phylogenetic analyses. Seta *u'* in legs I and II might be curved or sharply bent in some species (e.g., Figs 8A,B).

Typical ornamentation may be present on the leg surfaces, e.g., on the coxae, trochanters and femorogenua, of all or some *Diptilomiopus* spp. as illustrated by the ridges and tubercles present on the legs of the new species. These ornamentations, which may have systematic value, are not described, though, because it may be invisible or inconspicuous in slide-mounted specimens, but are clearly discernable in some SEM images (e.g., Figs 7G,H).

Deeply divided empodium with rays of sub-branches which generally slant towards the front and against the central stems (e.g., Fig. 8C), ranging approximately from 4- to 9-rayed, except *D. stephanus* with 11–12 rays. Possibly due to some difficulty in counting the rays, their number is not reported for many species, and the range given here was partly determined from counting the rays in descriptive drawings.

Tarsal solenidion ω always above and close to empodium.

Coxae and genitalia (Figs 7 & 8) – Coxisternal plates I and II may be smooth (unornamented) or ornamented, usually with rounded to short dash-like tubercles, usually almost covering coxisternal plates I entirely, and covering smaller areas of coxisternal plates II; inner margins of coxae I in most species touch and form a prosternal apodeme (sternal line), but sometimes the coxisternal plates are fused with the prosternal apodeme effaced, and in some species the coxisternal plates are separated, and inner margins present, but not forming a prosternal apodeme.

Setae *1a* and *2a* "normal" (simple and tapering), and *1a* positioned slightly or clearly ahead of an imaginary line through tubercles of *2a,* and never in line or behind *2a.*

Internal anterior genital apodeme extending forward, and spermathecae round or slightly ovalish with relatively short spermathecal tubes, as usually found in the Eriophyoidea (e.g., Fig. 14B); genital coverflap entirely smooth (unornamented), only ornamented on the basal area (e.g., Figs 6A,D), or entirely ornamented, sometimes with ornamentation clearly divided in a basal and distal area; ornamentation usually tubercles (granules), sometimes combined with dashes, when

ornamentation only on basal area, the ornamentation may loosely be divided into two separate subcircular areas (e.g., Fig. 6D); other types of ornamentation only present in a few species, e.g., one rank of longitudinal ridges in *D. artocarpae*, and semi-circular transverse lines in *D. ulmivagrans*. Genital coverflap ornamentation frequently vaguely and ambiguously described.

Based on this re-diagnosis and –description of *Diptilomiopus*, particularly the following species might not resort within the genus, and are dealt with or discussed, their eventual classificatory positions pending their relationships and the monophyly of the genus recovered by phylogenetic analyses:

1. ***Vimola artocarpae*** (Mohanasundaram, 1981) **comb. nov.**

Diptilomiopus artocarpae Mohanasundaram, 1981, Mohanasundaram (1981): 45–46. Although the presence of the genu is not mentioned in the text description of *D. artocarpae*, legs I and II are depicted with six segments and the genu clearly present (Mohanasundaram, 1981), and *D. artocarpae* should thus not be in *Diptilomiopus*. There are additionally other characteristics of the species which differ from most *Diptilomiopus* spp., and which support its exclusion from *Diptilomiopus*: genu I with *l'* present; the dorsal shield pattern is different from the general cell-pattern (Fig. 1A) of other *Diptilomiopus* spp.; the tibia is twice the length of the tarsus, while the tibia is shorter, equal or only slightly longer than the tarsus in most *Diptilomiopus* spp.; and it has wax patches, while wax secretions are not present in *Diptilomiopus* spp., except in *D. melastomae*. The species keys out to *Vimola* Boczek, 1992 with the key to genera by Amrine *et al.* (2003).

2. ***Vimola thangaveli*** (Mohanasundaram, 1983) **comb. nov.**

Diptilomiopus thangaveli Mohanasundaram, 1983, Mohanasundaram (1983): 177–178. The genu is present in legs I and II of *D. thangaveli* – depicted and mentioned in the differential diagnosis (Mohanasundaram, 1983), and genu I with *l'* present; and thus *D. thangaveli* does not belong to *Diptilomiopus*. The species keys out to *Vimola* Boczek, 1992 with the key to genera by Amrine *et al.* (2003).

3. ***Vimola ulmivagrans*** (Mohanasundaram, 1984) **comb. nov.**

Diptilomiopus ulmivagrans Mohanasundaram, 1984, Mohanasundaram (1984): 265, 282. Although the presence of the genu is not mentioned in the text description of *D. artocarpae*, legs I and II are depicted with six segments and the genu clearly present and genu I with *l'* present (Mohanasundaram, 1984), and *D. ulmivagrans* thus do not belong in *Diptilomiopus*. The species keys out to *Vimola* Boczek, 1992 with the key to genera by Amrine *et al.* (2003).

4. ***Diptilomiopus bengalensis*** Chakrabarti & Mondal, 1979, Chakrabarti & Mondal (1979): 47–49.

The description of *D. bengalensis* by Chakrabarti & Mondal (1979) is ambiguous, but it clearly does not belong in *Diptilomiopus*. The presence of *bv* is ambiguous, because the length of *bv* is recorded for legs I and II, but these setae are absent in the descriptive drawings (Chakrabarti & Mondal, 1979). Although *l'* is absent, the genu is present, in legs I and II – described in the text and depicted (Chakrabarti & Mondal, 1979), and the species should thus not be in *Diptilomiopus*. This is supported by the dorsal shield pattern of *D. bengalensis* which is different from the general cell-pattern (Fig. 1A) of other *Diptilomiopus* spp. The species keys out to *Vimola* Boczek, 1992 with the key to genera by Amrine *et al.* (2003). The species keys out close to *Neolambella* Lin & Kuang, 1997, with the key to genera by Amrine *et al.* (2003), but *D. bengalensis* differs from *N. ligustri* Lin & Kuang, 1997 in the absence of *1b*, and the possible presence of *bv* in the former species. *Diptilomiopus bengalensis* may belong to a new genus, but this decision pending the correct description of the species, and results from phylogenetic analyses.

5. ***Diptilomiopus ervatamiae*** (Chandrapatya, 1991)

Vilaia ervatamiae Chandrapatya, 1991, Chandrapatya & Boczek (1991a): 430–431. *Diptilomiopus ervatamiae* keys out close to *Diptilomiopus* in the key by Amrine *et al*. (2003), but *1b* is present in the species, and it does not belong in *Diptilomiopus* as the genus is currently diagnosed, and might belong to a new genus, pending results of phylogenetic analyses. Seta *1b* is present in *D. ervatamiae*, and *1a* is absent, but setal tubercle of *1a* present (Chandrapatya & Boczek, 1991a). This is quite an unusual state in the Eriophyoidea, since *1a* is rarely absent, in contrast to *1b*, and if absent, *1b* is also absent. The presence of *1b* and absence of *1a* is autapomorphic for *D. ervatamiae* among *Diptilomiopus* spp. The probable exclusion of *D. ervatamiae* from *Diptilomiopus* is supported by the difference of the dorsal shield pattern of *D. bengalensis* from the general cell-pattern (Fig. 1A) of other *Diptilomiopus* spp.

6. ***Diptilomiopus guajavae*** Mohanasundaram, 1985, Mohanasundaram (1985): 23–25.

The text description and depiction of the legs of *D. guajavae* by Mohanasundaram (1985) are highly ambiguous, among other discrepancies in this description. The length of a tibiotarsus is recorded for legs I and II (Mohanasundaram, 1985). This description in comparison with the depiction of the legs by Mohanasundaram (1985) can be interpreted in four ways, if some corrections are presumed, with corresponding generic placement in brackets:

- Genu absent in legs I and II, *l''* absent (*Diptilomiopus*);
- Genu absent (tarsus and tibia present), *l''* present (possibly new genus, because *l''* is not present in *Diptilomiopus*);

- Tibiotarsus present and thus tibia absent, and genu present, in legs I and II, *l'* present on genu I (possibly new genus). It is highly unlikely that a tibiotarsus might be present in any species of the Diptilomiopinae.
- Tarsus, tibia and genu present as separate segments in legs I and II, *l'* present on genu I (*Vimola*).

The correct generic placement requires re-description of the species and results of phylogenetic analyses.

Species descriptions (exclude diagnostic generic characters described above)

The new *Diptilomiopus* spp. from South Africa are differentiated from each other, and from *D. gilibertiae* Kadono, 1984 (Kadono, 1984), because the three new *Diptilomiopus* spp. from South Africa were found as a group which may be monophyletic, and *D. gilibertiae* was found to be a potential sister species of the South African species group, with preliminary parsimony analyses (C. Craemer, *in preparation*). The similarities between these four species include: broadly the same prodorsal shield ornamentation of ridges in a cell-like pattern; scapular setal tubercles present, small and rounded, positioned anterior of prodorsal shield rear margin; coxisternal plates I largely covered with granules, and coxisternal plates II with granules anteriad of *2a*; the number of dorsal and ventral annuli about the same; palp *d*, and *ft'* on tarsus II, absent; minute *h1* present; female genital coverflap with granules on the basal area, and smooth distally; female internal genitalia broadly similar.

***Diptilomiopus faurius* sp. nov.**

DIFFERENTIAL DIAGNOSIS.

Diptilomiopus faurius sp. nov. is differentiated from the other new *Diptilomiopus* spp. from South Africa in the key to Diptilomiopidae of South Africa (above). Differences between this new species and *D. gilibertiae* include: dorsal annuli of *D. faurius* sp. nov. with microtubercles absent in a central band, flanked by microtubercles on each side, and the empodium with 7–8 rays; while the dorsal annuli are entirely covered with microtubercles in *D. gilibertiae*, and its empodium has 6 rays. Setae *d* and *e* (about 48 and 40 µm, respectively) of *D. faurius* sp. nov. much longer than these in *D. gilibertiae* (about 12 and 8 µm, respectively). A hump middorsally behind rear shield margin (Fig. 10B,D) in the nymph which might be unique to *D. faurius*.

Measurements and counts in Table 2.

FEMALE (Figs 2–5; 6A–F; 7; 8A–C)

Idiosoma – Fusiform to somewhat elongated fusiform (Figs 2A,B,D; 5B,E); light to dark amber (orangey) in life.

Gnathosoma (Fig. 4) – Shape and structures determined largely on SEM images: about basal half of palpcoxal base directed anteriad in the same direction as the long axis of the body, where after palpi and gnathosomal stylets bend ventrad, perpendicularly to the long body axis, basal part with an approximately oval depression (Figs 4A,D,E) varying in size and depth; part of margin between palpcoxal base and trochanter-femur-genu interrupted by a smooth area (Fig. 4A); a conspicuous, rounded, dorsally somewhat flattened lobe-like structure enclosed by a ridge antero-laterally is situated just proximal of or at the distal margin of the trochanter-femur-genu (Figs 4A,C,E); a short ridge probably present dorsally on palptibia on the inner margin bordering the stylet sheath (Fig. 4D); palptibia with a convex hump distally on the ventral side (Figs 4A,B).

Infracapitular guides are conspicuous, apparently freely projecting processes originating at the level of the distal margin of the trochanter-femur-genu, interlocked or lying close together and appearing as one elongated triangular structure in the ventral view of the gnathosoma of slide-mounted specimens (Fig. 5B).

Palpi with palp *d* absent; *ep* present, lying or standing in a shallow groove, with a ridge on the outer and inner side (Figs 4A,D,E); *v* present, inserted on a small raised area ventrally and distally on the palptarsus (Fig. 4B).

Table 2. Measurements and counts *Diptilomiopus faurius* sp. nov.

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (n=12) (rounded)						♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		median	mean	SD	min	max	CV*				
BODY SIZE											
body length (pedipalpi included)	256	268	272	36	222	322	13.40		227	167	228
idiosomal length (gnathosoma excluded)	207	223	225	38	163	283	17.19	239	181	135	188
body width just behind prodorsum	86	81	82	4	78	90	5.45		67	58	67
body width at level of setae *f*	47	41	42	3	38	47	7.72		35	24	28
body thickness (just below genital flap)								89			
GNATHOSOMA											
length (dorsal) excluding stylets	49	49	51	7	42	64	13.04		44	29	45
length (lateral) excluding stylets								58			
seta *ep* (basal seta) length	3	3	3	0	3	3	0		3	2	2
seta *d* (antapical seta)	absent	absent						absent	absent	absent	absent
seta *v* (apico-ventral seta) length	4	4	4	0	3	4	10		4	3	3
chelicerae length	78	77	77	4	70	82	4.84	74	69	49	55

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (n=12) (rounded)						♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		median	mean	SD	min	max	CV*				
PRODORSAL SHIELD											
length	36	33	33	3	28	37	9.17		29	28	31
width	63	62	62	4	56	69	6.90		55	33	49
***sc* setal tubercles (dorsal tubercles)**											
distance apart	25	24	24	2	22	28	6.75		20	24	26
length	1	1	1	0	1	2	36.94		1	1	2
base width	2	2	2	0	1	2	15.38		2	1	2
distance ahead of rear shield margin	10	9	9	2	6	12	25.05		5	10	10
OPISTHOSOMA											
number of dorsal microtubercles / 20 µm	0 (smooth)								0	7	0
number of ventral microtubercles / 20 µm	11	11	10	1	7	12	14.15		11	8	9
position seta *d* (first ventral seta)	31	32	32	2	29	36	6.80		26	15	21
number of microtubercles between setae *d*	26	24	24	3	20	29	11.09		15	8	14
seta *d* length	53	49	48	5	40	56	10.13		35	25	37
setae *d* distance apart	51	53	52	5	45	58	8.94		40	30	43
position setae *e* (second ventral setae)	50	50	51	3	47	57	6.17		42	21	31
number of microtubercles between setae *e*	15	15	15	3	11	20	18.27		10	7	9
seta *e* length	37	40	40	5	32	52	13.43		39	15	35
setae *e* distance apart	32	32	33	4	27	38	11.39		28	22	30
position setae *f* (third ventral setae)	71	70	71	4	64	78	6.11		61	32	47
position setae *f* from rear	11	11	11	1	10	12	6.23		11	6	8
number of microtubercles between setae *f*	24	22	22	3	18	27	13.38		17	11	18
seta *f* length	40	38	38	2	35	41	5.58		37	19	27
setae *f* distance apart	35	33	33	2	30	37	6.73		29	21	24
seta *h2* (caudal seta) length	67	59	56	10	36	69	18.13		35	24	31
seta *h1* (accessory seta) length	2	1	1	0	1	2	37.70		1	1	1
number of dorsal annuli lateral to shield	4	3	3	1	2	5	23.69		2?	0	4
number of dorsal annuli	66	65	64	4	58	72	6.21		57	45	51
number of annuli clearly forming central ridge	36	35	35	6	19	42	17.65		30	0	7
total number of dorsal annuli	70	69	68	4	61	75	6.23		59	45	55
total number of ventral annuli	81	79	81	5	74	89	5.74		71	37	54
COXAL AREA											
sternal line length	7	7	7	2	4	9	25.65		8	absent	absent
coxal seta *1a* (2nd coxal seta) length	40	37	36	3	29	40	9.04		29	12	23
coxal setae *1a* distance apart	10	10	10	1	9	11	8.03		9	6	7
coxal seta *2a* (3rd coxal seta) length	50	51	52	3	50	59	5.36		47	26	30

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (n=12) (rounded)						♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		median	mean	SD	min	max	CV*				
coxal setae *2a* distance apart	32	31	31	2	27	34	7.47		28	18	24
Distance setae *1a* to *2a*	7	7	7	1	5	8	14.21		8	5	4
number of complete annuli in coxi-genital region	4	4	4	0	4	5	7.22		5	8	11
number of half annuli in coxi-genital region	2	2	2	0	2	3	14.15		2	0	0
total number of annuli in coxi-genital region	6	6	6	1	5	8	11.22		7	8	11
LEGS I											
length (including coxa) including extremities	77	73	73	2	70	77	3.04		65	45	57
length (including coxa) excluding extremities	70	65	65	2	62	70	3.67		58	40	52
length (from base of trochanter)	41	41	40	2	37	43	5.64	40	37	21	32
trochanter length (dorsal)	4	5	5	1	4	6	14.89	7	4	2	5
femur-genu length	16	17	17	2	15	19	9.62	17	17	7	12
tibia length	10	9	9	0	9	10	4.99	9	7	5	6
tarsus length (excluding extremities)	13	13	13	1	11	14	6.43	12	10	7	8
seta *ft''* (lateral tarsal seta) length	43	42	42	2	40	46	4.11		40	24	31
seta *ft'* (dorsal tarsal seta) length	41	41	40	2	38	44	4.48		37	23	20
seta *u'* (mesal seta) length	5	6	6	1	5	7	10.26		5	3	4
solenidion ω (tarsal solenidion) length	9	9	9	1	8	10	7.95	8	8	5	7
em (tarsal empodium) length	12	11	11	1	10	12	5.44	12	10	8	8
LEGS II											
length (including coxa) including extremities	61	59	59	2	55	62	3.89		54	35	45
length (including coxa) excluding extremities	52	51	50	2	45	53	4.34		46	31	41
length (from base of trochanter)	35	36	36	2	33	39	4.59	35	32	21	25
trochanter length (dorsal)	6	6	6	1	3	7	21.40	6	4	4	4
femur-genu length	16	15	14	2	11	16	13.32	13	13	8	8
tibia length	8	8	8	1	7	8	7.11	6	7	4	5
tarsus length (excluding extremities)	11	11	11	1	10	12	6.84	10	10	6	8
seta *ft''* (lateral tarsal seta) length	37	35	36	2	32	39	5.82		33	18	26
seta *ft'* (dorsal tarsal seta) length	absent								absent	absent	absent
seta *u'* (mesal seta) length	5	5	5	1	5	7	12.47		5	3	3
solenidion ω (tarsal solenidion) length	9	8	8	1	8	9	6.25		8	5	6
em (tarsal empodium) length	11	10	10	1	8	11	9.73	12	9	6	7
EXTERNAL GENITALIA											
genital coverflap width	31	31	31	1	29	33	3.50				
genital coverflap length	16	17	17	1	16	19	5.13				
male genitalia width									20		
male genital area length									17		
seta *3a* (genital seta) length	11	11	11	1	8	12	9.72		8	5	7
setae *3a* distance apart	22	22	22	1	20	24	6.37		19	7	12

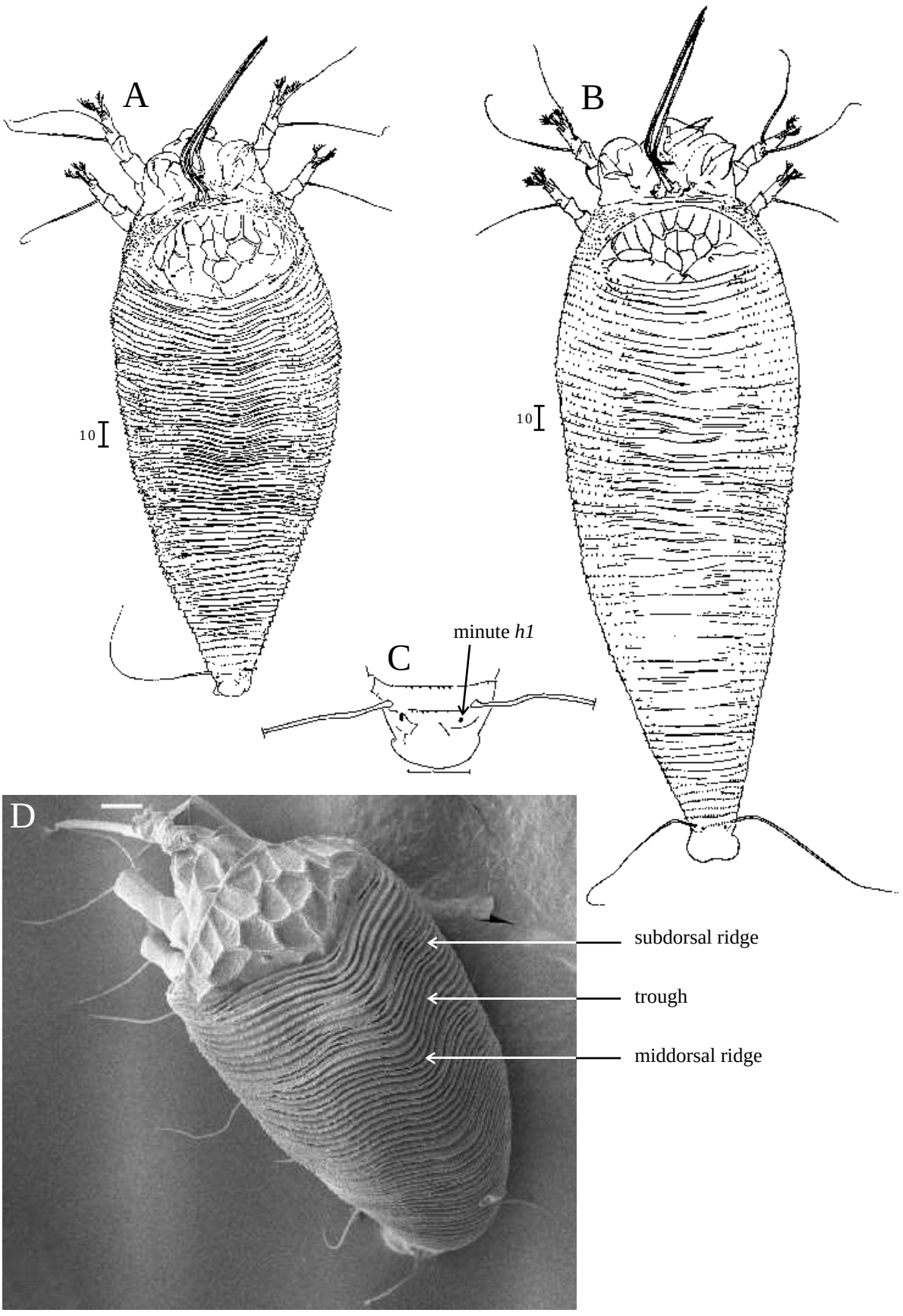

Figure 2. ***Diptilomiopus faurius*** **sp. nov., female, dorsal views**. **A**. smaller specimen; **B**. larger specimen probably more flattened and distorted than specimen A in this figure; **C**. enlarged rear (caudal) area; **D**. clearly with middorsal ridge flanked by a shallow trough and a subdorsal ridge on each side.

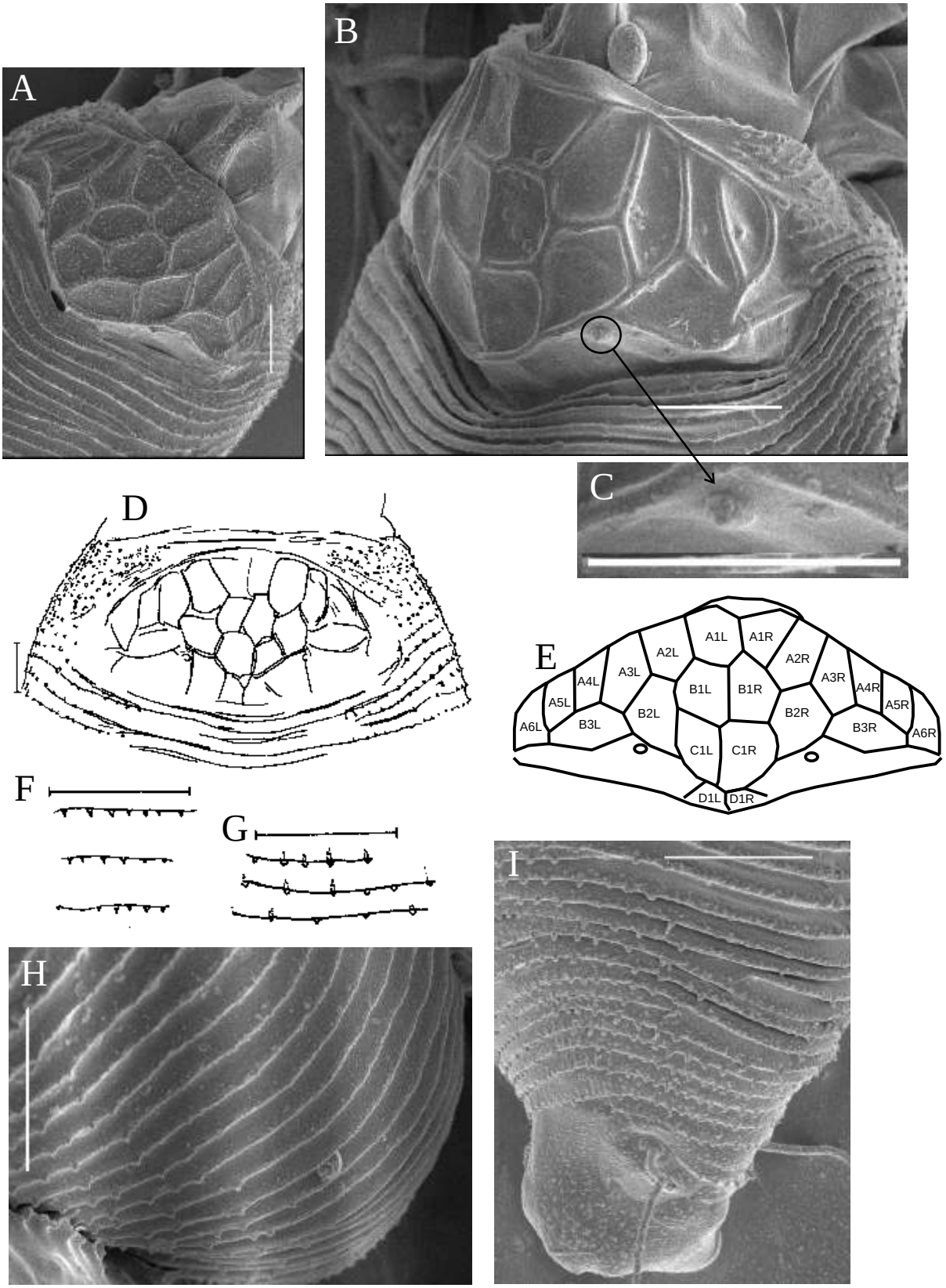

Figure 3. ***Diptilomiopus faurius*** **sp. nov., female**. **A**, **B**, **D**. dorsal view of prodorsum; **C**. enlargement of scapular tubercle; **E**. schematic, labeled version of prodorsal shield; opisthosomal microtubercles: **F**. middorsally just beyond setae *f* (caudal region); **G**. in lateral area of about middorsum; **H**. dorso-laterally; **I**. caudal area (oblique view).

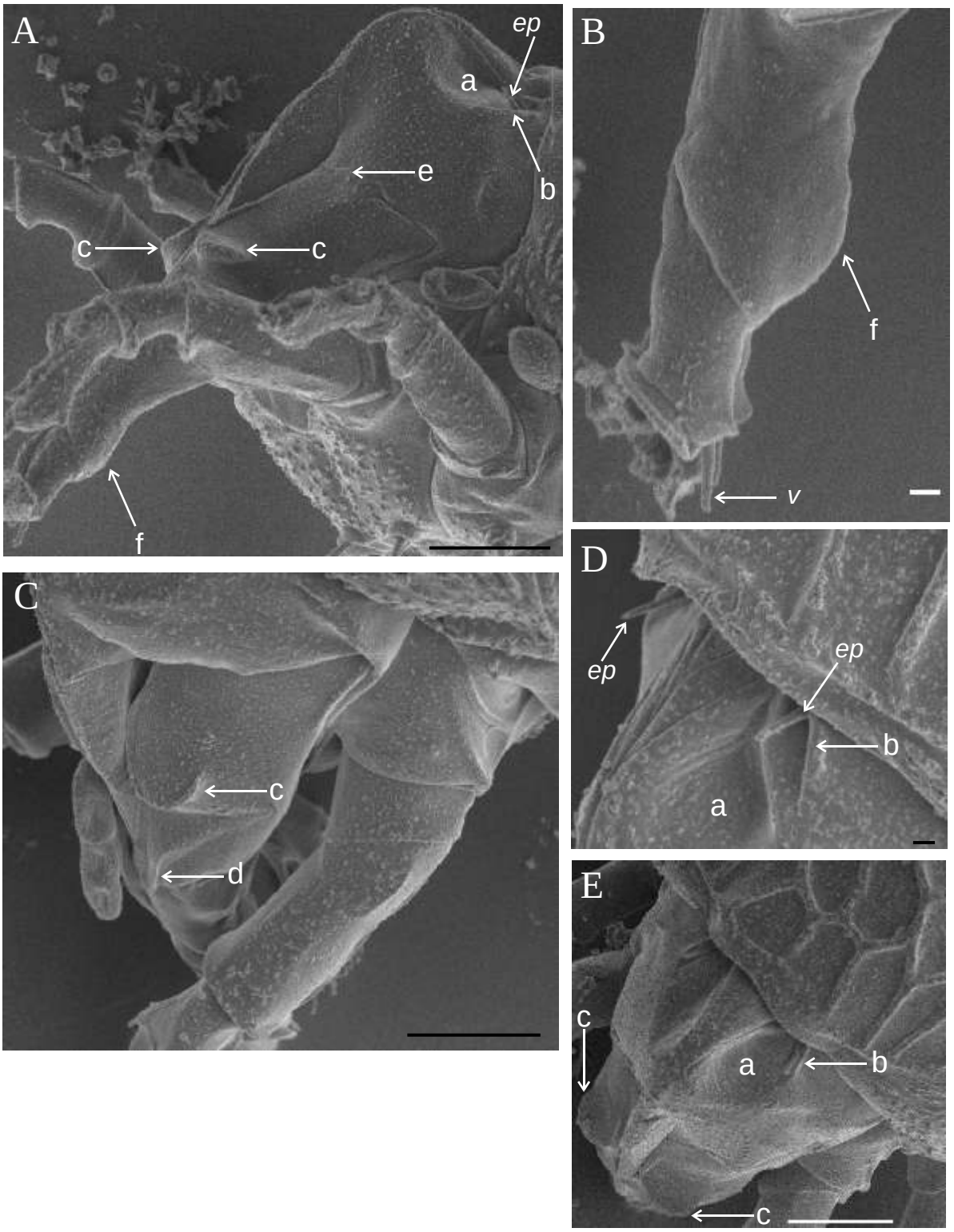

Figure 4. ***Diptilomiopus faurius*** **sp. nov., female gnathosoma. A**. lateral view; **B**. lateral view of tibia and tarsus; **C**. dorso-lateral view; **D**. dorso-lateral view of basal part of palpcoxal base; **E**. dorsal view of palpcoxa and trochanter-femur-genu. **a.** oval depression at base of palp coxa (varies between specimens in size and depth); **b.** ridge on outside of seta *ep*; **c.** round, flattened lobe, with ridged margin anteriorly, apically on trochanter-femur-genu; **d.** short ridge on inner margin of palp tibia bordering the stylet sheath; **e.** smooth area interrupting margin between palp coxal base and trochanter-femur-genu; **f.** convex bulged area ventrally and distally on palp tibia; *ep*. seta *ep* at the base of the palp coxa, lying in a groove; ***v.*** seta *v* inserted on a raised area distally on the palp tarsus.

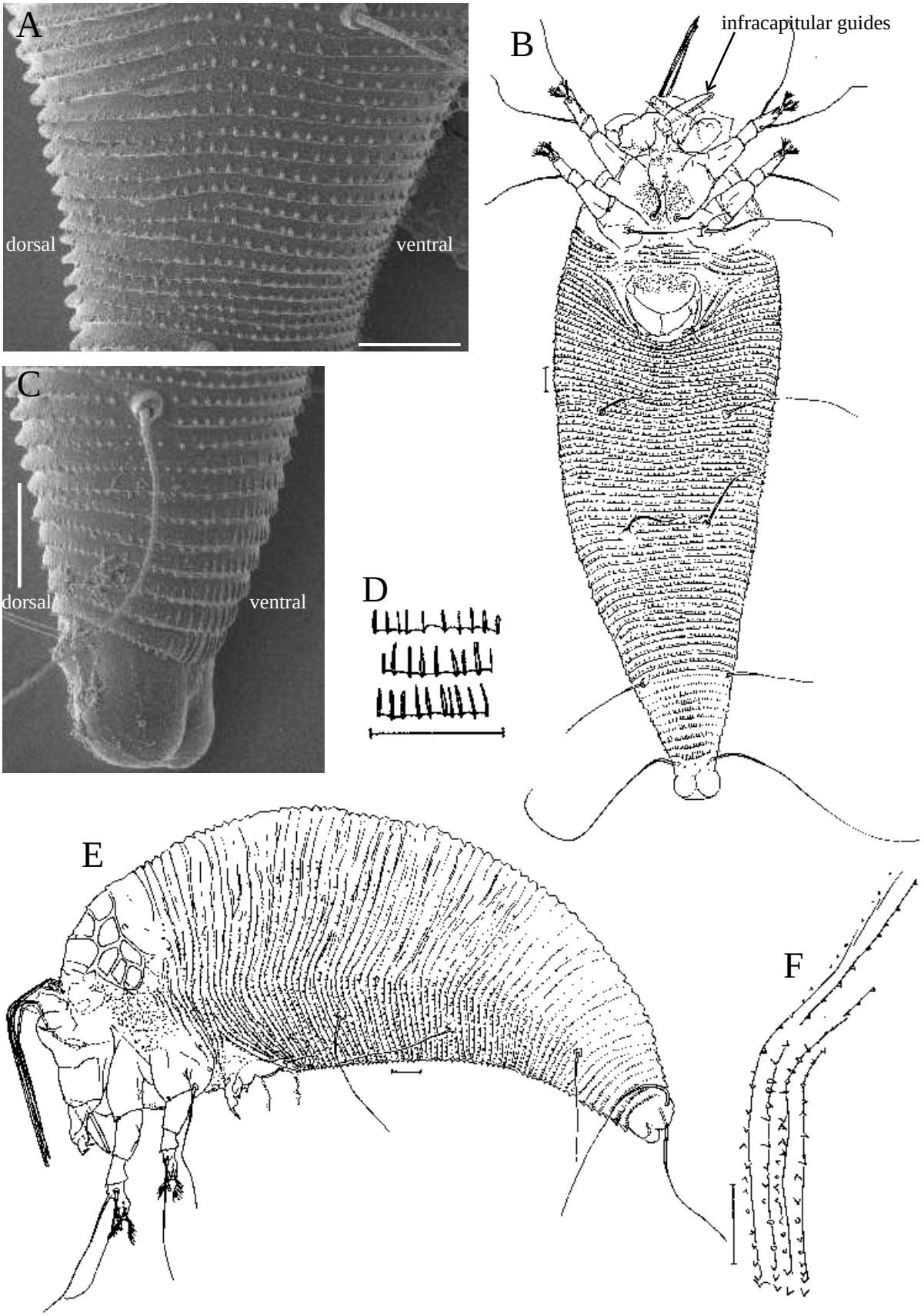

Figure 5. ***Diptilomiopus faurius*** **sp. nov., female**. **A**. opisthosomal microtubercles on the annuli between setae *e* and *f*; **B**. ventral view; **C**. opisthosomal microtubercles on the rear annuli; **D**. opisthosomal microtubercles on rear three caudal annuli; **E**. lateral view; **F**. opsithosomal microtubercles in lateral view at about the level of seta *d*.

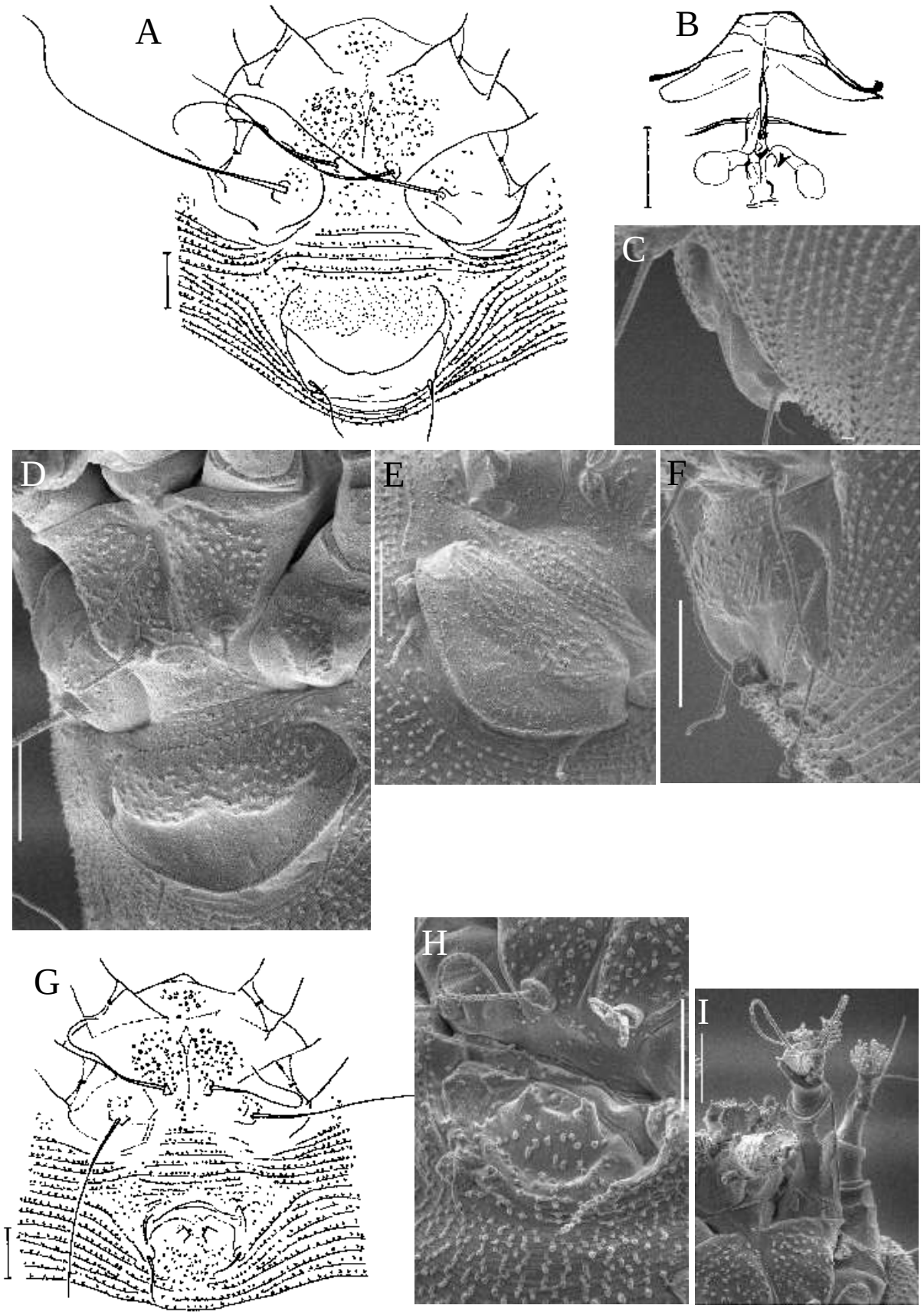

Figure 6. ***Diptilomiopus faurius*** **sp. nov.** F**emale**. **A**, **D**. coxi-genital area; **B**. internal genitalia; **C**. external genitalia to show the three dimensional profile in lateral view; **E**, **F**. genital coverflap. **Male. G**, **H**. coxi-gential area; **I**. ventral view of legs, gnathosoma, and anterior part of coxi-sternal area.

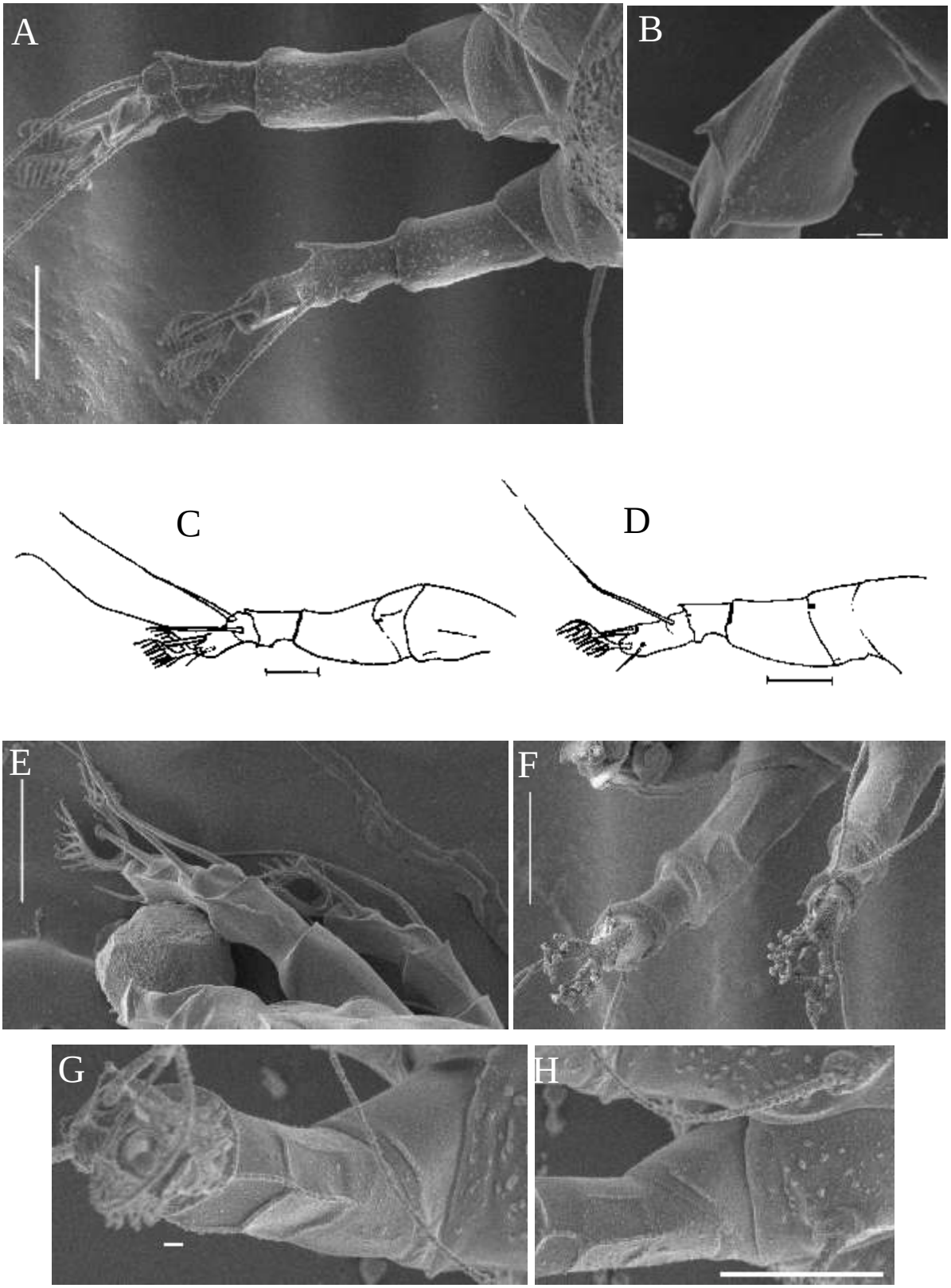

Figure 7. ***Diptilomiopus faurius*** **sp. nov., female**. **A**. lateral view of leg I (above) and II (below); **B**. oblique view of tibia; **C**. lateral adaxial view of leg I; **D**. lateral adaxial view of leg II. **E**. dorsal view of leg I (left) and II (right); **F**. ventral view of leg I (left) and II (right) to illustrate the pattern of ridges on femur-genu I and II, ridges more pronounced on femur-genu I than on femur-genu II; **G**. most complete ridge pattern on femur-genu I; **H**. ridge pattern on femur-genu II more pronounced in comparison with leg II in F of this figure.

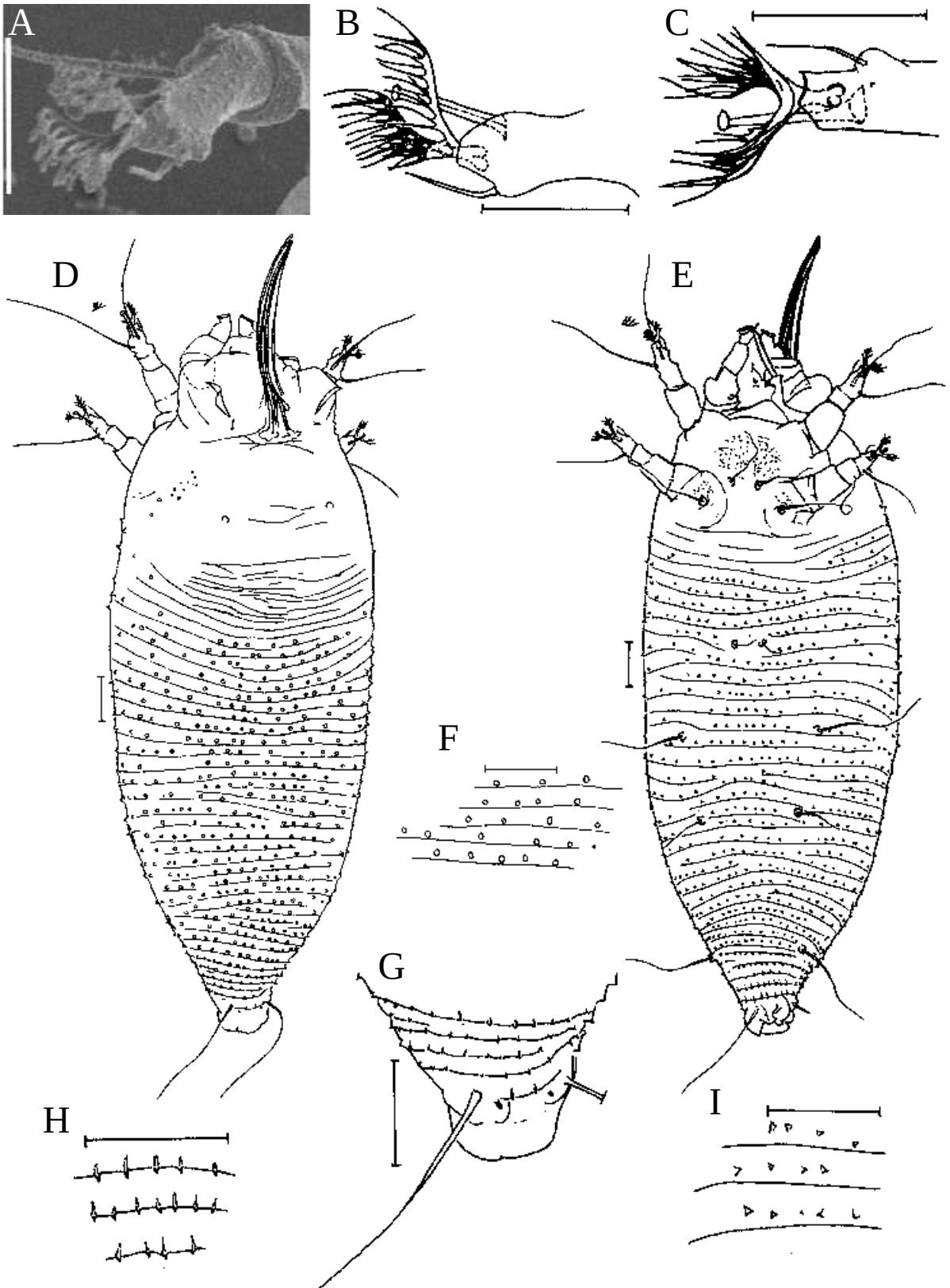

Figure 8. ***Diptilomiopus faurius*** **sp. nov. Female empodium. A.** oblique view of tarsus of leg I; **B**. distal part of tarsus I with empodium, solenidion ψ and seta *u*', empodium seems to be 7-rayed, but may have an unbranched basal 8th ray; **C**. distal part of tarsus I, note the difficulty in counting the number of rays particularly when the empodium lies in a dorso-ventral position. L**arva**. **D**. dorsal view; **E**. ventral view; **F**. opisthosomal microtubercles in mid-dorsal area; **G**. dorsal view of caudum; **H**. opisthosomal microtubercles ventrally beyond setae *f*; **I**. opisthosomal microtubercles mid-ventral area; .

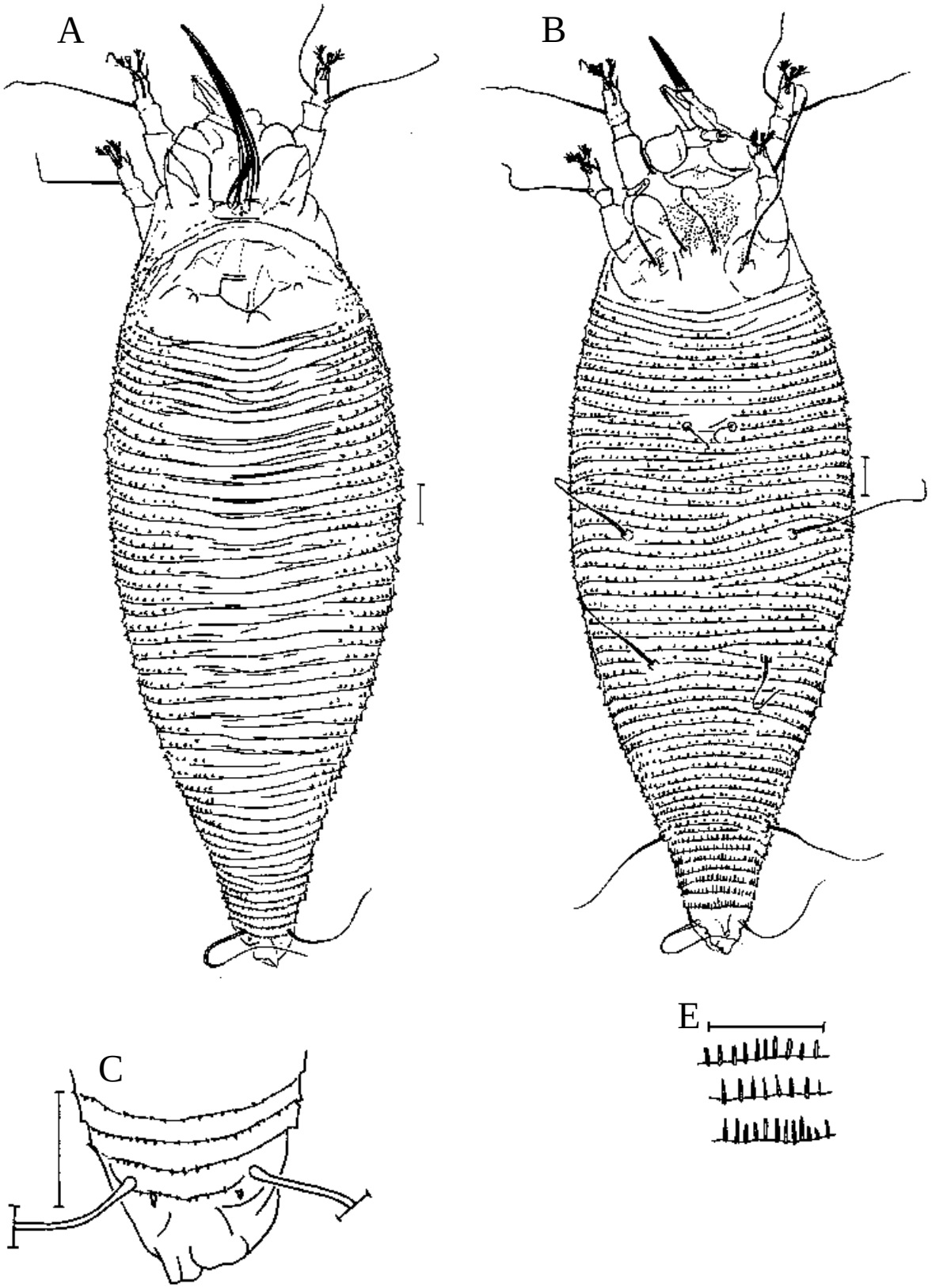

Figure 9. ***Diptilomiopus faurius*** **sp. nov., nymph**. **A**. dorsal view; **B**. ventral view; **C**. dorsal view of caudal region; **D**. opisthosomal microtubercles in lateral area of middorsal region on the level of setae *d*; **E**. opisthosomal microtubercles ventrally on last three caudal annuli; **F**. opisthosomal microtubercles ventrally between setae *d*.

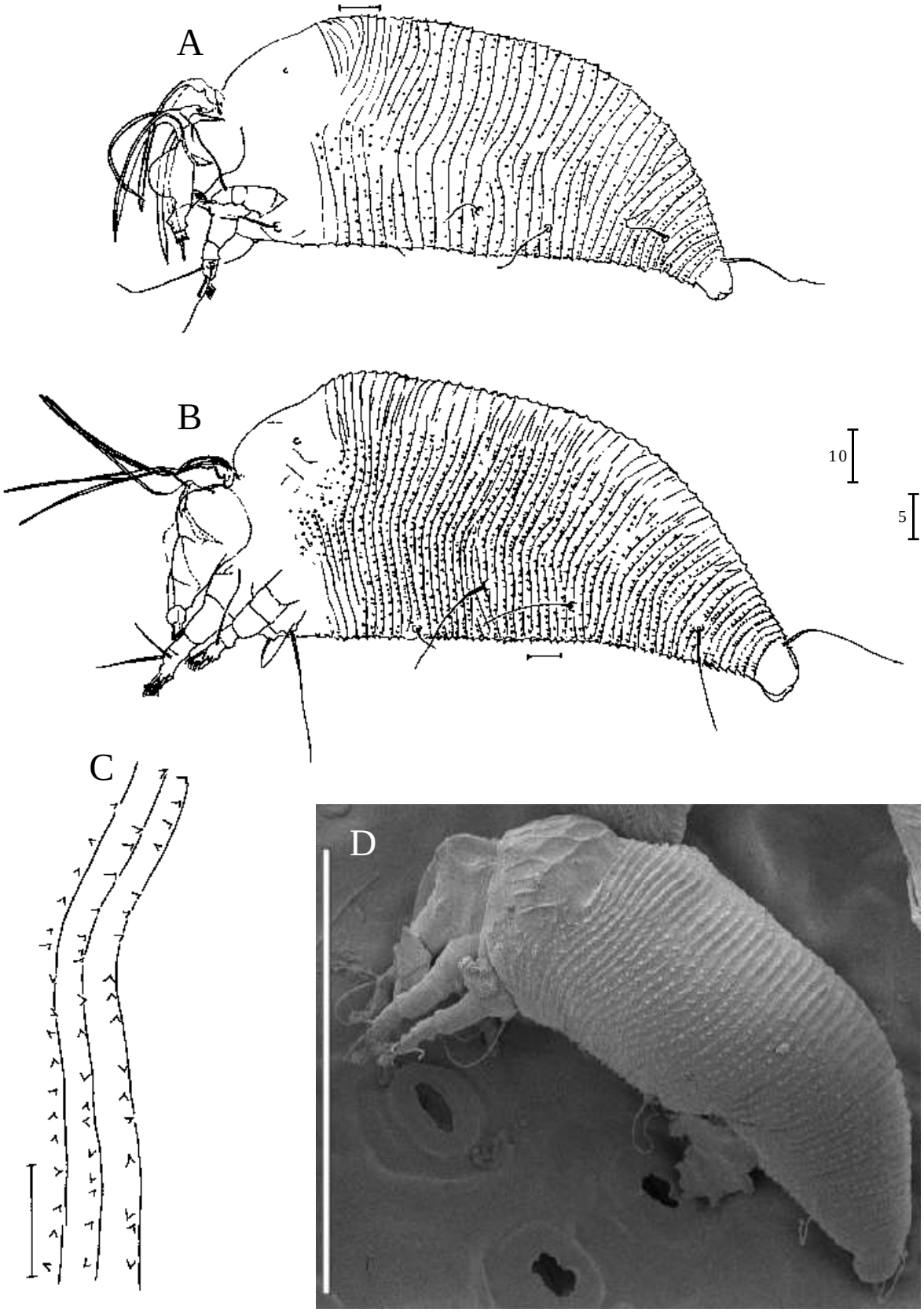

Figure 10. ***Diptilomiopus faurius*** **sp. nov., larva**. **A**. lateral view, **nymph**. **B**. lateral view; **C**. opisthosomal microtubercles in area between setae *d* and *e* of specimen in lateral view; **D**. oblique view.

Prodorsal shield (Figs 3A–E) – broadly oval and short, with the characteristic convex shape with declivitous rear area, of other *Diptilomiopus* spp. (Fig. 3A). Shield ornamentation is formed by ridges in a cell-like pattern (Figs 3A,B,D) consisting broadly of three rows of cells numbered here as follows: 12 cells (A1L–A6L and A1R–A6R) in anterior row, six cells (B1L–B3L and B1R–B3R) in second row and two cells (C1L and C1R) in basal row; two open cell-like areas, D1L and D1R are formed at the base of the shield pattern on the declivitous basal part of the shield (Fig. 3E). Due to the compression of this area on the slides, D1L and D1R are not always clearly present on the slide-mounted specimens (Fig. 2A). Although all cells are typically present in all specimens, the shield pattern is not exactly symmetrical around the middle and cell shapes varies in different specimens (compare cells of Figs 3A,B,D). Sub-shield lateral area with granules somewhat arranged in lines (Fig. 3B), sometimes forming a loose circular pattern in an area more towards the legs and just above the coxae.

Frontal lobe present (Fig. 3A), but not overhanging the basal parts of the chelicerae which is necessary for regarding the frontal lobe as being present as required by the keys to genera and species in the Eriophyoidea, and additionally will probably be regarded by most authors as being absent, similar to other published *Diptilomiopus* spp. descriptions, because it is almost completely inconspicuous in slide-mounted specimens (Figs 2A,B; 3D; 5E). In SEM images a transversely broad but longitudinally narrow and probably thin and flexible frontal lobe with a slight, broad indentation of the anterior margin is unambiguously present (Figs 3A,B; 4E).

Scapular setal tubercles are present, relatively small, rounded and ahead of rear shield margin (Figs 2A,B,D; 3A–D; 5E). In some slide-mounted specimens it seemed as if there is a slight bump or slightly darker spot in the center of the tubercles. This could not be conclusively determined to be a bump on the tubercle, or distortion of the tubercle by the slide mounting process, or possibly a remnant of *sc*. Although indications of this “bump” are present in some SEM images (Fig. 3C), the exact nature of this feature cannot be conclusively determined here either, because resolution is too poor, and presence or possible presence of ice crystals obscures and confuses the detailed morphology. With evidence at hand and for practical reasons I regard *sc* absent.

Opisthosoma – Evenly rounded with a shallow, central ridge, flanked by shallow troughs and a barely discernable subdorsal ridge on either side, all fading towards the rear, absent from about annulus 44 onwards. In some of the slide-mounted specimens the ridges and troughs are barely visible (Fig. 2B), and the outer ridges are mostly undetectable, and in SEM imaged specimens they are more conspicuous to various degrees (Fig. 2D).

Ventral annuli on average about 13 annuli more than dorsal annuli (Table 2). Microtubercles on dorsal annuli: absent in a central band, flanked by microtubercles on each side (Figs 2A,B,D; 3H). Dorsolateral opisthosomal microtubercles, smaller, more sparsely spaced than on ventral annuli (Figs 5A,E), and situated on the rear annulus margins (Fig. 3G). In slide-mounted specimens these dorsal microtubercles appears more elongated with the proximal part beneath the dorsal surface, lightly coloured, with the apical point exposed on the rear annulus margin (Fig. 3G), the elongated submerged part becoming shorter and vaguer towards the rear. The last few rear dorsal annuli entirely covered with triangular, pointed microtubercles (Figs 3F,I). Opisthosomal microtubercles on ventral annuli pointed, about triangularly shaped in slide-mounted specimens, close to the rear edges of the annuli, becoming progressively elongated ridges from about the level of *f* (on the rear about 10 ventral annuli) (Figs 5A,C,D,F).

Seta *c2* absent; *d*, *e*, *f*, *h1* and *h2* present. Setae *d*, *e*, *f* and *h2* relatively long and finely tapered, *e* on average slightly shorter than *f*; *h1* very short, and may be interpreted as being minute (Figs 2C; 3I; 5B,E; Table 2).

Legs (Fig. 7) – 5-segmented, with genu absent, probably fused with the femur (Figs 7A,F).

Setal compliment of leg I (trochanter-[femur-genu]-tibia-tarsus): 0– [0–0] –0–3 (*bv*, *l''* and *l'* absent; *ft''*, *ft'* and *u'* present). Setal compliment of leg II (trochanter-[femur-genu]-tibia-tarsus): 0– [0–0] –0–2 (*bv*, *l''*, and *ft'* absent; *ft''* and *u'* present)

Setae-*ft* in both legs long and tapering, *u'* possibly curved or even with a sharp bent, apparent in some specimens (Fig. 8A), appearing about straight in others (Fig. 7C). This may be due to the angle in which the specimens were lying.

Outer surfaces of the coxae below the subshield lateral area ornamented with tubercles and with two ridges on this area of coxae I (Fig. 7A); ventral surface of trochanters I and II with a transverse ridge along the margin with the femorogenua (Figs 7G,H); femorogenua I and II ornamented with a pattern of ridges on the ventral surfaces (Figs 7F–H), usually more pronounced on femorogenu I (Fig. 7G), sometimes causing the illusion of a division of this segment; ventral ridge ornamentation on femorogenu II varying from nearly absent (Fig. 7F) to well developed (Fig. 7H). In slide-mounted specimens the ventral ornamentation on the femorogenua of both legs range from invisible to inconspicuous in most specimens, however discernable in some (Fig. 5B). Shape and structures of tibiae I and II are well discernable in SEM images with two ridges in the length dorsally terminating in well developed spines distally above the positions of *ft*-setae of tarsi I and II (*ft'* absent in tarsus II) (Figs 7A,B,E); shape and structure less discernable in slide-mounted specimens (Figs 2A,B; 7C,D) where the spines and one longitudinal line representing one of the ridges are sometimes visible.

Tarsal solenidion ω, noticeably knobbed with a relatively large knob and slightly curved (Figs 7E; 8B,C). The knob is clearly separated from the shaft, but it is not apparent whether it is separated by a membrane, or whether it is just the fold of the knob creating an illusion of separation. Tarsal empodium *em* deeply and unambiguously divided (Figs 7A,C,E; 8A–C). The rays lie in an angle against the central stem of each branch of the divided empodium, especially at the base of the empodium, and the rays could not be counted accurately on the slide-mounted specimens or most of the SEM images, particularly in dorsal view, and has not been statistically dealt with. The empodia probably 7- or 8-rayed (when 8-rayed, the seventh but especially the eighth ray is inconspicuous and not always easy to discern) (Figs 7A,E; 8B,C).

Coxae, coxigenital region and genitalia (Figs 5B; 6A–F) – Suboral plate mostly smooth or with some granules, with convexly rounded central area (Figs 6A,D); coxisternal plates I and II with rounded to short dash-like granules: almost covering coxisternal plates I entirely, more sparsely on coxisternal plates II in a small area anteriad to *2a* (Figs 6A,D); coxisternal plates I separated by a weak sternal apodeme for most of the inner margin, ending in a diamond-shaped area anteriorly (Fig. 6A).

Setae *1a* and *2a* "normal" (simple and tapering), relatively long and frequently convoluted, with well-developed setal tubercles; *1a* ahead of an imaginary line through tubercles of *2a.* Seta *3a* tapering and probably flexible (Figs 6A,D–F).

Internal genitalia depicted in Fig. 6B; external genital coverflap basally with a slightly raised area, vaguely in the shape of two continuous transverse round areas, covered with granules and dashes that varies in shape and clarity between specimens, distally smooth, with a shallow notch in the rear margin (Figs 6A,D–F).

MALE (Fig. 6G–I).

Morphology, including measurements and counts, similar to female [including ornamentation in coxisternal area, internal apodeme (Figs 6G–I), and rib-pattern ventrally on femorogenua (Fig. 6I)], except for genitalia (Figs 6G,H), albeit some setae are slightly shorter or in the short range of the female setal lengths (Table 2). Opisthosoma – 57 dorsal and 57 ventral annuli. Genitalia – scattered microtubercles just below the eugenital setae, similar to most other eriophyoid species; eugenital setae plainly present in slide-mounted specimens and in SEM images (Figs 6G,H).

Two immature stages could be identified (recorded to date all eriophyoid species studied in this regard with two immature stages):

LARVA (Figs 8D–I; 10A).

Specimens identified to be first immature stages (larvae) by absence of external genitalia, with the smallest size and irregularity of annuli just posterior of rear shield margin (Figs 8D; 10A). The prodorsum mostly smooth with single fold lines (Fig. 8D), single granules lateral on subshield lateral area (Fig. 8D). Scapular tubercles similar to those in adult (Figs 8D; 10A). The irregular annuli dorsally, posteriad of the prodorsum smooth (Fig. 8D), the remainder of the dorsal annuli with small rounded microtubercles near the rear annulus margins (Figs 8D,F), becoming more pointed and sitting more on the rear annulus margins on the rear annuli beyond about the level of *f* (Figs 8D,G). Ventral annuli with triangularly shaped pointed microtubercles further away from the rear annulus margins than the dorsal microtubercles (Figs 8E,I) becoming alongated on ventral annuli beyond *f* (Figs 6E,H), some areas around ventral setae more sparsely microtuberculated (Fig. 6E). Setal compliments the same as in adult, however setae generally much shorter (Table 2); empodium *em* with less rays than in adult.

NYMPH (Figs 9; 10B–D).

Specimens identified to be second immature stages (nymphs) by the absence of external genitalia, their size, regularity of annuli just posterior of rear shield margin and position of scapular setal tubercles. Opisthosoma – 55 dorsal annuli and 45 ventral annuli. No external genitalia present, only slight interruption of annuli where genitalia will be positioned in adult (Fig. 9B). Dorsal annuli with smooth central band flanked by microtubercles laterally (similar to adult), microtubercles sharply pointed, about triangular and situated close to the rear annulus margin (Figs 9A; 10B–D); ventral annuli with microtubercles similar in shape and size to the dorsal microtubercles (Fig. 9B), but possibly slightly further away from rear annuli margins than those on the dorsal annuli (Fig. 10C); microtubercles on ventral annuli becoming more elongated until elongated ridges on about the 7 rear annuli (Figs 9B,E). A central dorsal hump posterior of the dorsal shield which is characteristic of the species, among the new species described here, clearly apparent in specimens studied (Figs 10B,D). Setal compliments the same as in adult, however setae generally shorter than in adult and longer than in larva (Table 2); tarsal empodium *em* possibly 4-rayed (difficult to count).

ETYMOLOGY – The species name is derived from the host genus name, *Faurea*.

HOST PLANT – *Faurea rochetiana* (A. Rich.) Pic. Serm. (= *Faurea speciosa* (Welw.) Welw.), (Proteaceae) (Palgrave, 2002). Common names: Broad-leaved Beechwood (English), *Breëblaarboekenhout* (Afrikaans). It usually grows as a small, leafy tree, 4–7 meters high, in

mixed deciduous woodland, on low open hills or in hilly grassland. The plant has medicinal value as the extract of the roots can be used to treat diarrhea and ear infections (Palgrave, 2002).

TYPE DATA – Hunderd-and-eight type specimens on 17 slides (AcY: 11/223) from type locality and host, *Faurea rochetiana*, Long Tom Pass, Limpopo, South Africa (25.07S, 30.35E), date unknown, S. Neser: holotype female and 4 paratype specimens (unsexable specimen – probably a female, 2 males and 1 nymph) on 1 slide; the holotype (female) can be distinguished by being in a dorso-ventral position; and 103 paratype specimens (about 78 females, 16 males, 5 nymphs and 4 larvae) on 16 slides.

RELATION TO HOST – The mites occurred commonly but sometimes in sparse numbers mostly on the undersurfaces of the leaves amongst natural leaf hairs. No obvious symptoms could be attributed to the mites.

***Diptilomiopus apobrevis* sp. nov.**

DIFFERENTIAL DIAGNOSIS.

Diptilomiopus apobrevis sp. nov. is differentiated from the other new *Diptilomiopus* spp. from South Africa in the key to Diptilomiopidae of South Africa (above). Differences between this new species and *D. gilibertiae* include: prodorsal shield pattern of *D. apobrevis* with cells D1L and D1R present, these are absent in *D. gilibertiae*; dorsal annuli of *D. apobrevis* sp. nov. with microtubercles absent in a central band, flanked by microtubercles on each side, and the empodium with 7–8 rays; while the dorsal annuli are entirely covered with microtubercles in *D. gilibertiae*, and its empodium has 6 rays.

Measurements and counts in Table 3.

FEMALE (Figs 11–16; 17A,B)

Idiosoma – Fusiform to somewhat elongated fusiform (Figs 11A,B); a mixture of *Diptilomiopus apobrevis* and *D. apolongus* live together on leaves, and were not distinguishable from each other before being mounted on slides and studied by SEM: in life dark amber (orangey to salmon) (seemingly mostly adults) to light amber (seemingly immatures and younger adults); legs and palpi colourless and translucent; chelicerae (and probably some of the other gnathosomal stylets as well) and tarsal setae *ft* dark-brown (almost black).

Table 3. Measurements and counts on *Diptilomiopus apobrevis* sp. nov. Measured and counted 12 female specimens in dorsal/ventral view, some measurements and counts could not be taken on some specimens. The maximum amount of specimens (n) were included, including the holotype female.

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
BODY SIZE												
body length (pedipalpi included)	221	10	216	222	30	188	265	13.56		197	121	175
idiosomal length (gnathosoma excluded)	190	10	186	187	26	149	223	14.07	212	165	101	140
body width just behind prodorsum	89	10	95	94	5	86	100	5.09		78	60	74
body width at level of setae *f*	44	9	45	46	3	42	52	6.67		38	25	35
body thickness (just below genital flap)									99			
GNATHOSOMA												
length (dorsal) excluding stylets	46	10	46	44	7	33	52	15.95		44	30	43
length (lateral) excluding stylets									54			
seta *ep* (basal seta) length	3	12	3	3	1	3	4	15.08	3	3	3	3
seta *d* (antapical seta)	absent		absent						absent	absent	absent	absent
seta *v* (apico-ventral seta) length	5	11	5	5	1	5	6	9.60	4	4	6	5
chelicerae length	75	12	74	74	3	68	77	3.75	69	58	40	58
PRODORSAL SHIELD												
length	32	11	39	38	3	32	41	9.22	37	29	25	33
width	66	8	74	73	7	65	80	9.27		62	45	60
anterior shield lobe											none	none
shield lobe length		5	3	3	1	2	5	41.59		1		
shield lobe width		4	26	26	1	25	28	4.89		20		
***sc* setal tubercles (dorsal tubercles)**												
distance apart	23	10	28	27	3	23	32	10.84		19	20	29
length	2	5	2	2	< 1	1	2	25.36		1		
base width	2	5	2	2	0	2	2	0		1		
distance ahead of rear shield margin	7	10	10	9	2	6	11	17.09		5	8	10
OPISTHOSOMA												
number of dorsal microtubercles / 20 µm	0	12	0 (smooth)							0	6-10	0
number of ventral microtubercles / 20 µm	18	10	14	15	2	12	18	16.68		11	7/10µm	7
width of smooth band behind prodorsal shield	49	10	50	51	7	41	65	13.07		41	n/a	entirely smooth
position seta *d* (first ventral seta)	32	10	31	31	2	28	34	7.44	32	23	13	17
number of microtubercles between setae *d*	24	10	25	25	3	21	29	11.61		17	9	7
seta *d* length	13	11	12	12	1	10	13	7.10	12	10	9	8
setae *d* distance apart	39	10	44	45	5	39	54	12.37		34	24	30
position setae *e* (second ventral setae)	49	10	49	48	2	45	52	5.07	52	35	17	25

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
number of microtubercles between setae *e*	16	11	16	16	3	13	22	17.27		12	7	6
seta *e* length	11	11	11	10	1	8	12	14.12	11	9	4	7
setae *e* distance apart	24	10	28	27	3	22	31	10.57		19	18	19
position setae *f* (third ventral setae)	69	10	69	69	3	66	73	3.91		50	27	40
position setae *f* from rear	10	12	11	11	1	10	12	6.84		10	8	8
number of microtubercles between setae *f*	22	9	24	24	3	19	28	11.65		20	11	12
seta *f* length	42	11	44	44	2	40	48	5.47		36	14	30
setae *f* distance apart	34	9	36	36	2	34	40	5.44		34	21	24
seta *h2* (caudal seta) length	64	8	59	57	9	45	70	16.83		55	18	> 25
seta *h1* (accessory seta) length	1	11	1	1	0	1	1	0		1	< 1	< 1
number of dorsal annuli lateral to shield	3	8	4	3	1	2	4	22.50		3	4	0
number of dorsal annuli	64	9	64	63	2	60	67	3.75		54	40	51
number of annuli forming central ridge	47	8	39	37	8	21	47	21.17		32	n/a	36
total number of dorsal annuli	67	10	67	66	3	63	70	3.88		57	44	51
total number of ventral annuli	78	10	78	79	3	77	84	3.64		59	32	47
COXAL AREA												
sternal line length	11	4	11	10	1	9	11	9.54		invisible	absent	absent
coxal seta *1a* (2nd coxal seta) length	32	12	37	37	5	28	46	14.87	43	26	12	22
coxal setae *1a* distance apart	11	10	13	13	1	11	14	7.83		10	8	9
coxal seta *2a* (3rd coxal seta) length	49	10	57	55	5	47	61	10.11		31	20	35
coxal setae *2a* distance apart	35	10	37	37	2	33	39	5.82		25	22	26
distance setae *1a* to *2a*	5	10	6	6	2	5	10	26.26		5	4	5
number of complete annuli in coxi-genital region	7	8	6	6	2	3	8	26.42		5	5	11
number of half annuli in coxi-genital region	0 or 3	4	1	1	1	0	2	120.32				none
total number of annuli in coxi-genital region	7	8	6	6	1	5	8	18.77		5	5	11
LEGS I												
length (including coxa) including extremities	73	10	73	75	3	72	80	4.28		56	40	59
length (including coxa) excluding extremities	64	10	68	67	3	64	72	4.17		50	35	53
length (from base of trochanter)	41	12	42	42	2	37	45	5.25	42	30	21	30
trochanter length (dorsal)	8	10	8.5	8.3	1	7	10	13.03	7	6	5	7
femur-genu length	18	11	19	19	1	16	21	7.35		13	9	14
tibia length	8	12	9	9	1	8	9	6.12		8	4	5
tarsus length (excluding extremities)	10	12	11	11	1	10	14	10.40		11	6	10
seta *ft''* (lateral tarsal seta) length	38	12	39	39	1	37	41	3.30		32	17	28
seta *ft'* (dorsal tarsal seta) length	36	11	37	37	2	33	39	5.02		32	17	28
seta *u'* (mesal seta) length	7	12	7	7	1	5	9	15.08		5	4	6
solenidion ω (tarsal solenidion) length	8	12	8	8	1	7	8	6.93		5	4	6
em (tarsal empodium) length	10	12	11	11	1	8	12	11.05		8	5	8

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
LEGS II												
length (including coxa) including extremities	60	10	60	61	2	58	65	3.97		46	34	46
length (including coxa) excluding extremities	52	10	53	53	2	51	57	4.04		41	30	38
length (from base of trochanter)	35	12	37	37	3	34	42	7.01		30	20	25
trochanter length (dorsal)	6	11	7	7	1	6	10	14.18		6	5	5
femur-genu length	15	12	15	16	2	14	19	9.81		15	7	11
seta *bv* (femoral seta)	absent	12	absent						absent	absent	absent	absent
seta *l''* (genual seta)	absent	12	absent						absent	absent	absent	absent
tibia length	7	11	7	7	< 1	7	8	6.56		6	4	5
tarsus length (excluding extremities)	11	12	11	11	< 1	10	11	2.70		9	6	7
seta *ft''* (lateral tarsal seta) length	34	12	34	33	1	32	35	3.04		27	13	24
seta *ft'* (dorsal tarsal seta) length	absent	12	absent						absent	absent	absent	absent
seta *u'* (mesal seta) length	5	12	6	6	1	5	8	15.77		5	4	5
solenidion ω (tarsal solenidion) length	7	12	7	7	< 1	7	8	6.37		5	4	6
em (tarsal empodium) length	10	11	10	11	1	9	12	9.90		9	5	7
EXTERNAL GENITALIA												
genital coverflap width	29	10	30	31	2	27	34	7.07			n/a	n/a
genital coverflap length	20	10	17	17	2	15	20	11.32			n/a	n/a
male genitalia width										22	n/a	n/a
male genital area length										19	n/a	n/a
seta *3a* (genital seta) length	8	11	7	7	1	6	9	11.22		6	3	4
setae *3a* distance apart	20	10	21	22	2	20	24	7.83		14	9	13

Gnathosoma (Figs 12E–H & 13A) – Shape and structures largely determined on SEM images: about basal third to half of palpcoxal base directed anteriad in the same direction as the long axis of the body, where after palpi and gnathosomal stylets bend ventrad perpendicularly to the long body axis, basal part with a slight depression (Figs 12F,G), but not as pronounced as in *D. faurius*.

Infracapitular guides are conspicuous, apparently freely projecting processes originating at the level of the distal margin of the trochanter-femur-genu, interlocked or lying close together and appearing as one elongated triangular structure in the ventral view of the gnathosoma of slide-mounted specimens (Fig. 13A,B).

The cheliceral retainer depicted in Fig. 15B.

Palp with *d* absent; *ep* and *v* present.

Prodorsal shield (Fig. 12A–D) – broadly oval and short, with the characteristic convex shape with declivitous rear area, of other *Diptilomiopus* species (Fig. 12A). Shield pattern is formed by ridges in a cell-like pattern (Figs 12A,B) consisting broadly of three rows of cells numbered here as follows: 12 cells (A1L–A6L and A1R–A6R) in anterior row, five cells (B1L and B1R fused to form one cell, B2L–B3L and B2R–B3R) in second row and two cells (C1L and C1R) in basal row. The ridge (part of median line) dividing B1L and B1R from each other in some *Diptilomiopus* species (e.g. *D. faurea*) is invisible or absent in slide-mounted specimens (Fig. 12B), however vaguely present in SEM images (Fig. 12A). Two open cell-like areas, D1L and D1R are formed at the base of the shield pattern on the declivitous basal part of the shield (Fig. 12D). Due to the compression of this area on the slides, D1L and D1R are not always clearly visible in the slide-mounted specimens (Fig. 12B). Subshield lateral area with granules somewhat arranged in lines (Figs 12G).

Frontal lobe present, broad transversely but narrow longitudinally and probably thin and flexible, varying from clearly to vaguely visible in slide-mounted specimens (Fig. 12B), and could be identified especially after becoming aware thereof in SEM images (Figs 12A,F).

Scapular setal tubercles are present, relatively small, rounded and ahead of rear shield margin (Figs 12A,B). In some slide-mounted specimens it seems as if there is a slight bump or slightly darker spot in the center of the tubercles. This could not be conclusively determined to be a bump on the tubercle, or distortion of the tubercle by the slide mounting process, or possibly a remnant of *sc*. Although indications of this “bump” are present in some SEM images (Fig. 12C), the exact nature of this feature cannot be conclusively determined here either, because resolution is too poor, images of this aspect captured at too low magnification, and presence or possible presence of ice crystals obscures and confuses the detailed morphology. With evidence at hand and for practical reasons I regard *sc* absent.

Opisthosoma – Evenly rounded with a shallow, central ridge, flanked by shallow troughs and a barely discernable subdorsal ridge on either side, all fading towards the rear, absent on average from annulus 37 onwards. In most of the slide-mounted specimens the outer ridges and troughs are barely visible (Fig. 11B), while in SEM imaged specimens they are more conspicuous (Fig. 11A).

Ventral annuli on average 13 annuli more than dorsal annuli (Table 3). Microtubercles on dorsal annuli: absent in a central band, flanked by microtubercles on each side (Figs 11F,G). Dorsolateral opisthosomal microtubercles, smaller, obviously more sparsely spaced than on ventral annuli (Figs 11B; 13E), and situated on the rear annulus margins (Figs 11B; 13E). In slide-mounted specimens they are fine and small and some appears slightly elongated with the proximal part beneath the dorsal surface, lightly coloured, with the slightly darker apical point exposed on the rear annulus margin (Fig. 11E). About six rear dorsal annuli entirely covered with triangular, pointed microtubercles (Figs 11D). Opisthosomal microtubercles on ventral annuli pointed, about triangularly shaped in slide-mounted specimens, close to the rear edges of the annuli, becoming progressively elongated ridges from about the level of *f* (on the rear about 10 ventral annuli) (Figs 13,E,F). Ventral laterally, from about the mid-distance between *d* and *e*, up to *f*, bordering the boarder between the dorsal and ventral annuli, a band of the ventral opisthosomal microtubercles appears, particularly on the slide-mounted specimens, to be more elongated than the remainder of the ventral microtubercles (Fig. 15E).

Setae *c2* absent; *d*, *e*, *f*, *h1* and *h2* present. Setae *f* and *h2* relatively long and finely tapered, *d* and *e* unmistakably quite shorter than *f*; *h1* very short, and may be interpreted as being minute (Figs 13B; 11C & Table 3).

Legs (Figs 16A–F) – 5-segmented, with genu absent, probably fused with the femur (Figs 16A,B).

Setal compliment of legs I (trochanter– [femur-genu] –tibia–tarsus): 0– [0–0] –0–3 (*bv*, *l''* and *l'* absent; three tarsal setae present: *ft*'', *ft*' and *u*').

Setal compliment of legs II (trochanter– [femur-genu] –tibia–tarsus): 0– [0–0] –0–2 (*bv*, *l*'' and *ft'* absent; two tarsal setae present: *ft*'' and *u*').

Setae *ft* in both legs of all slide-mounted specimens are bluntly truncated in comparison with the tapering *ft* usually found in eriophyoid species described to date, and it seems unlikely that all these setae broke off. The shape of *ft* could not be confirmed in the SEM images where these setae sunk into the glue of the double sided sticky carbon tape used to mount the mites on the stub.

Particularly femorogenua I (Fig. 16B,C; 17A) ornamented with a pattern of ridges on the ventral surfaces. In slide-mounted specimens the ventral ornamentation on the femorogenua of legs I ranges from invisible to inconspicuous in most specimens, however discernable in some (Figs 16C).

Tarsal solenidion ω, noticeably knobbed and virtually straight (Figs 16H–E). The knob is clearly separated from the shaft, but it is not apparent whether it is separated by a membrane, or whether it is just the fold of the knob base creating an illusion of separation. Tarsal empodium *em* deeply and unambiguously divided (Figs 16H,G,K,J). The rays lie in an angle against the central stem of each branch of the divided empodium, especially at the base of the empodium, and the rays could not be counted accurately on the slide-mounted specimens or on most of the SEM images, particularly in dorsal view, and has not been statistically dealt with. The empodia mostly unambiguously 7- , but some 8-rayed (sometimes the seventh but especially the eighth ray is not easily seen).

Coxae, coxi-genital region and genitalia (Figs 14A,C–F) – Suboral plate mostly smooth (Fig. 14A,D); coxisternal plates I and II with rounded to very short dash-like (oval) granules: almost covering coxisternal plates I entirely (Figs 14A,C,D), coxisternal plates II with a few fine tubercles in a small area anteriad to *2a* (Figs 14A,C); coxisternal plates I seems separated on slide-mounted specimens and SEM images for most of the inner margin, however the inner sternal apodeme(s) (sternal line) is either absent or too vague to be discerned clearly in slide-mounted specimens (Fig. 14A) and appear as a depression or narrow furrow on the dorsal surface terminating in a triangular area anteriorly in the SEM images (Fig. 14D).

Seta *1b* absent; *1a* and *2a* present and "normal" (simple and tapering), relatively long and frequently convoluted, with well-developed setal tubercles; *1a* ahead of an imaginary line through tubercles of *2a* (Fig. 14C).

Internal genitalia depicted in Figs 14B; external genital coverflap basally with a slightly raised area, vaguely in the shape of two continuous transverse rounded areas, covered with granules and dashes that varies in shape and clarity between specimens, distally smooth (Figs 14C,E,F).

Seta *3a* present, tapering and probably flexible (Fig. 14C).

MALE (Figs 14G; 17C–F).

Morphology, including measurements and counts, similar to female, except for genitalia (Figs 14G; 17C–F), albeit some setae are slightly shorter or in the short range of the female setal lengths (Table 3). Genitalia – scattered microtubercles or granules just below the eugenital setae similar to many other eriophyoid species described to date; eugenital setae not clearly visible, and their presence could not be ascertained without doubt. Two half-circular ridges are present, one on each side, where eugenital setae are usually situated, and these are probably associated with the eugential setae, obscuring them. Centrally in these ridges in slide-mounted specimens is an

indication of seta-like structures (Fig. 17F) and in the SEM image, particularly on the ridge in the right hand side of the image, a possible seta-like structure can be seen (Figs 17D,E).

Two immature stages could be identified (recorded to date all eriophyoid species studied in this regard with two immature stages):

LARVA (Fig. 18).

Specimens identified to be first immature stages (larvae) by absence of external genitalia, the smallest size and smooth area and some half, rounded irregular annuli just posterior of rear shield margin (Figs 18B,K). The prodorsal shield with a central cell that is probably the combined B1L and B1R, about radial lines from the central cells, the basal three forming probably C1L and C1R (Figs 18B,K); subshield lateral area smooth (Fig. 18H). Scapular setal tubercles present and smaller but similar to those in adults (Fig. 18A,B). Some of the irregular annuli dorsally posteriad of the prodorsum smooth (Fig. 18K), the remainder of the dorsal annuli with small rounded, vague microtubercles near the rear annulus margins (Fig. 18E) almost invisible in SEM image (Fig. 18K), becoming more pointed and sitting more on the rear annulus margins on the rear annuli beyond about the level of *f* and particularly on the rear four annuli (Fig. 18F). Ventral annuli smooth laterally with microtubercles in a central band in the area margined by *3a*, *d*, *e*, and *f*, from *f* to the rear the ventral annuli are entirely microtuberculate; the ventral opisthosomal microtubercles are triangularly shaped and pointed, situated further away from the rear annulus margins than the dorsal microtubercles (Figs 18C,F,J) becoming alongated on ventral annuli beyond *f* (Fig. 18I), but particularly on the rear three annuli (Fig. 18G). All setal compliments the same as in adult, however setae generally much shorter (Table 3); empodial (*em*) possibly 4-rayed (difficult to count), however, definitely less rays than those in adult.

NYMPH (Figs 19; 20).

Specimens identified to be second immature stages (nymphs) by the absence of external genitalia, their size, regularity of annuli just posterior of rear shield margin and body shape. Opisthosoma – ... dorsal annuli and ... ventral annuli. No external genitalia present, only a discontinuance in annuli where genitalia will be in adult. A shallow middorsal ridge is visible in some specimens (Fig. 19A). First few dorsal annuli posteriad of prodorsum entirely smooth, thereafter a lateral band of microtubercles on each side becoming broader towards the middorsum, until annuli are entirely microtuberculate from about 14th annulus from the rear (Figs 19A; 20A,C), microtubercles sharply pointed, about triangular and situated on or close to the rear annulus margin (Fig. 19C) becoming more densely spaced and slightly more elongated (in the slide-mounted specimens) towards the rear (Figs 19A,D); ventral annuli with microtuberculate with smooth areas in parts particularly around future genitalia, and ahead of *d* and *e* (Fig. 19B), microtubercles triangular and pointed,

slightly larger and more densely spaced than dorsal microtubercles (Fig. 19E) becoming more elongated until elongated ridges on about the 8 rear annuli (Figs 19B,F). All setal compliments the same as in adult, however setae generally shorter than in adult and longer than in larva (Table 3); tarsal empodium *em* probably 5-rayed (Fig. 20B) (difficult to count), however, definitely less rays than those in adult. Tarsal solenidion similar in shape as in adult, with a clear central longitudinal line in some (Fig. 20C).

ETYMOLOGY – The species name is a combination of the first syllable of the host genus name, *Apodytes*, and the Latin word *brevis,* which means short, referring to the short body setae in comparison with the other *Diptilomiopus* sp. found on this host.

HOST PLANT – *Apodytes dimidiata* E.Mey. ex Arn. (Icacinaceae) (Palgrave, 2002). Common names: White-pear (English), *Witpeer* (Afrikaans). It frequently is a small bushy tree 4–5 m tall, but can become 20 m tall in forests. It occurs in coastal evergreen bush, at the margins of medium-altitude evergreen forests, in riverine fringes and open woodland, and on grassy mountain slopes, aften among rocks. It has medicinal value, and the wood is suitable for agricultural implements and furniture. It is an attractive tree used as garden ornamentals. (Palgrave, 2002).

TYPE DATA – Eighty-six type specimens on 20 slides (AcY: 11/222) from type locality and host, *A. dimidiata*, Botanical Garden, Nelspruit, Mpumalanga, South Africa (25.28S, 30.59E), date unknown, A. Witt with directions from S. Neser (X03/130): holotype female and 3 paratype females on 1 slide, together with 1 female paratype of *Diptilomipus apolongus* sp. nov.; the holotype can be distinguished by ; and 82 paratype specimens (31 females, 13 males, 29 nymphs and 9 larvae) on 19 slides. Twenty-two paratype specimens of *D. apolongus* sp. nov. (8 females, 8 males, 3 nymphs and 3 larvae) are present on 11 of the 19 slides. Three paratype specimens on 2 of 10 slides (AcY: 11/224) from *Apodytes dimidiata* (planted for ornamental purposes), Baberton Road, Nelspruit, Mpumalanga, South Africa (25.28S, 30.59E), 30 June 1988, S. Neser (NF1415, X88/148): 1 female, male and larva; with 45 *D. apolongus* type specimens, 5 specimens of a *cf. Tetra* sp. with 4-rayed empodia, and 9 specimens of another Phyllocoptinae species with 6-rayed empodia.

RELATION TO HOST – The mites occurred sparsely (many leaves devoid of them, and further about one to three specimens per leaf) on the underside of the leaves, in many cases close to or even on inner walls of turret galls probably caused by an insect. Mites also occurred on healthy looking leaves without any galls or other symptoms. No symptoms could be attributed to the mites.

DESCRIPTION

***Diptilomiopus apolongus* sp. nov.**

DIFFERENTIAL DIAGNOSIS.

Diptilomiopus apolongus sp. nov. is differentiated from the other new *Diptilomiopus* spp. from South Africa in the key to Diptilomiopidae of South Africa (above). Differences between this new species and *D. gilibertiae* include: dorsal annuli of *D. apobrevis* sp. nov. with microtubercles absent in a central band, flanked by microtubercles on each side, and the empodium with 7–8 rays; while the dorsal annuli are entirely covered with microtubercles in *D. gilibertiae*, and its empodium has 6 rays.

Measurements and counts in Table 4. No SEM studies were done on this species, and it is described entirely from slide-mounted specimens, except colour.

FEMALE (Figs 21; 22B-F)

Idiosoma – Fusiform to somewhat elongated fusiform (Fig. 21A,F); a mixture of *Diptilomiopus apobrevis* and *D. apolongus* living together on leaves, the two species were not distinguishable from each other before being mounted on slides and studied by SEM: colour in life dark amber (orangey to salmon) (seemingly mostly adults) to light amber (seemingly immatures and younger adults); legs and palpi colourless and translucent; chelicerae (and probably some of the other gnathosomal stylets as well) and fastigial tarsal setae dark-brown (almost black).

Gnathosoma (Figs 21A,F; 22F) – about basal third to half of palpcoxal base directed anteriad in the same direction as the long axis of the body, where after palpi and gnathosomal stylets bend ventrad perpendicularly to the long body axis (Fig. 22F). Doesn't seem to have the pronounced depression on basal part as in *D. faurea*, because no obvious signs of such a depression similar to that seen on the outer edge of the basal part of the palpcoxal base present.

Infracapitular guides are conspicuous, apparently freely projecting processes originating at the level of the distal margin of the trochanter-femur-genu, interlocked or lying close together and appearing as one elongated triangular structure in the ventral view of the gnathosoma (Fig. 21F).

Palpi with palp *d* absent; *ep* and *v* present (Fig. 22F).

Table 4. Measurements and counts on *Diptilomiopus apolongus* sp. nov. Too few specimens in dorsal/ventral view to count and measure 12 specimens, thus included all usable mounted adult female specimens available, of which 8 specimens were more or less in a dorsal/ventral view, and 8 specimens in a lateral view. Some measurements may differ in lateral and dorsal view, and in the cases where the CV* became larger with inclusion of lateral view specimens (e.g. body length), the data of only 8 specimens (dorsal view specimens) were included. ? = measurement/count unknown.

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
BODY SIZE												
body length (pedipalpi included)	287	8	284	280	25	232	311	9.14		231	177	174
idiosomal length (gnathosoma excluded)	225	8	222	226	26	195	261	11.51		202	146	148
body width just behind prodorsum	94	7	91	92	4	87	98	4.05		76	68	78
body width at level of setae *f*	48	5	48	47	2	44	49	5.28		35	29	35
body thickness (just below genital flap)									95			
GNATHOSOMA												
length (dorsal) excluding stylets	50	6	57	56	7	45	65	13.31		32	31	44
length (lateral) excluding stylets									71			
seta *ep* (basal seta) length	3	16	4	4	1	3	4	14.08		4	2	3
seta *d* (antapical seta)	absent	16	absent						absent	absent	absent	absent
seta *v* (apico-ventral seta) length	6	8	6	6	< 1	5	6	6.14		?	5	5
chelicerae length	85	16	85	85	4	81	98	4.88		76	50	66
PRODORSAL SHIELD												
length	35	8	39	38	2	35	42	5.68		34	31	33
width	63	8	71	72	7	63	80	10.50		58	58	60
anterior shield lobe											absent	absent
shield lobe length	2	11	2	2	1	2	3	21.72		2		
shield lobe width	15	6	27	25	7	15	34	29.18		23		
***sc* setal tubercles (dorsal tubercles)**												
distance apart	26	8	28	28	2	25	30	6.82		24	24	30
length	1	8	2	2	1	1	2	32.51		1	1	1
base width	2	12	2	2	0	2	2	0		2	2	2
distance ahead of rear shield margin	6	13	7	8	2	6	13	28.39		6	10	14
OPISTHOSOMA												
number of dorsal microtubercles / 20 µm	0	8	0 (smooth)							0	6	0
number of ventral microtubercles / 20 µm	8	7	8	10	2	8	13	22.92		11	6	8
width of smooth band behind prodorsal shield	40	8	42	42	3	39	47	7.04		37	n/a	38
position seta *d* (first ventral seta)	29	15	31	31	2	28	35	7.25		23	12	20
number of microtubercles between setae *d*	23	6	23	23	4	18	29	16.35		?	8	11
seta *d* length	60	8	59	58	4	53	63	6.42		45	25	36
setae *d* distance apart	56	6	55	53	4	49	57	6.70		?	35	40

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
position setae *e* (second ventral setae)	48	14	50	49	3	44	54	6.32		37	16	29
number of microtubercles between setae *e*	14	6	15	15	1	13	16	8.43		11	6	9
seta *e* length	55	16	54	53	4	47	59	7.22		42	21	27
setae *e* distance apart	36	6	35	34	3	30	36	7.83		28	21	28
position setae *f* (third ventral setae)	66	15	68	68	4	59	73	6.49		53	25	41
position setae *f* from rear	12	16	12	12	1	10	13	5.66		13	6	9
number of microtubercles between setae *f*	17	5	21	22	5	17	27	21.31		?	8	16
seta *f* length	43	8	45	46	2	43	48	4.13		35	17	31
setae *f* distance apart	37	5	37	37	2	33	39	6.33		?	22	30
seta *h2* (caudal seta) length	100	12	86	84	11	59	100	13.69		?	34	53
seta *h1* (accessory seta) length	1	16	1	1	< 1	1	2	30.99		< 1	< 1	1
number of dorsal annuli lateral to shield	4	8	4	4	1	3	5	16.88		3	3	3
number of dorsal annuli	61	14	59	58	3	54	62	4.32		55	39	46
number of annuli forming central ridge	34	5	33	30	7	18	34	23.34		?	none	about 14
total number of dorsal annuli	65	14	62	62	3	57	66	4.49		58	42	49
total number of ventral annuli	78	15	79	79	5	68	84	5.98		65	30	49
COXAL AREA												
sternal line length	12	5	12	11	1	9	12	11.88		5	absent	absent
coxal seta *1a* (2nd coxal seta) length	36	8	46	45	6	36	55	14.35		41	15	21
coxal setae *1a* distance apart	12	8	12	11	2	9	14	16.63		10	7	8
coxal seta *2a* (3rd coxal seta) length	56	8	61	61	5	53	68	8.15		45	24	47
coxal setae *2a* distance apart	28	8	31	32	6	26	43	17.67		28	21	29
Distance setae *1a* to *2a*	8	8	8	8	2	6	11	23.62		6	5	7
number of complete annuli in coxi-genital region	4	6	5	5	1	4	7	19.77		5	about 7	about 10
number of half annuli in coxi-genital region	2	6	2	2	< 1	2	3	18.23		0?	none	none
total number of annuli in coxi-genital region	6	5	8	8	1	8	9	15.31		5	about 7	about 10
LEGS I												
length (including coxa) including extremities	76	8	85	84	8	74	92	9.79		73	48	67
length (including coxa) excluding extremities	67	8	76	75	9	65	86	12.03		65	44	58
length (from base of trochanter)	45	16	49	49	3	45	57	6.71		44	27	35
trochanter length (dorsal)	8	14	9	10	2	8	15	20.54		8	4	6
femur-genu length	20	16	21	21	1	18	24	6.29		19	12	15
tibia length	10	8	10	10	1	9	11	5.46		10	6	8
tarsus length (excluding extremities)	14	16	15	15	1	14	17	6.59		13	7	11
seta *ft''* (lateral tarsal seta) length	45	8	47	47	2	43	49	4.17		40	27	32
seta *ft'* (dorsal tarsal seta) length	40	16	41	41	1	39	44	3.03		35	25	28
seta *u'* (mesal seta) length	6	13	7	7	1	6	8	11.94		7	4	5
solenidion ω (tarsal solenidion) length	9	16	9	9	1	8	10	5.75		8	5	7
em (tarsal empodium) length	12	15	12	12	1	9	13	8.67		10	6	8

character	holotype ♀	measurements and counts of ♀ structures (dorsal/ventral view) (rounded)							♀ lateral view (n=1)	♂ (n=1)	larva (n=1)	nymph (n=1)
		n	median	mean	SD	min	max	CV*				
LEGS II												
length (including coxa) including extremities	66	7	68	68	5	62	74	7.45		57	39	51
length (including coxa) excluding extremities	56	7	58	59	5	54	65	7.94		50	35	45
length (from base of trochanter)	42	14	43	43	2	39	47	5.19		37	25	33
trochanter length (dorsal)	10	14	9	9	1	7	11	13.58		7	5	5
femur-genu length	19	15	19	19	1	17	20	5.79		16	10	12
tibia length	8	8	8	9	1	8	10	12.08		8	4	6
tarsus length (excluding extremities)	12	8	14	14	1	12	14	5.25		11	6	9
seta *ft''* (lateral tarsal seta) length	42	16	41	41	2	39	45	4.07		36	20	26
seta *ft'* (dorsal tarsal seta) length	absent	16	absent						absent	absent	absent	absent
seta *u'* (mesal seta) length	5	8	7	7	1	5	7	11.87		5	3	4
solenidion ω (tarsal solenidion) length	8	15	8	8	1	8	9	6.16		7	5	6
em (tarsal empodium) length	11	8	11	11	< 1	10	11	4.40		9	6	9
EXTERNAL GENITALIA												
genital coverflap width	33	8	36	36	4	30	43	11.82		n/a	n/a	n/a
genital coverflap length	20	6	22	22	3	19	28	15.48		n/a	n/a	n/a
male genitalia width	n/a									25	n/a	n/a
male genital area length	n/a									20	n/a	n/a
seta *3a* (genital seta) length	10	16	12	12	1	10	13	9.05		9	5	7
setae *3a* distance apart	26	8	26	27	3	22	33	12.59		18	11	16

Measurements or counts that may have been influenced by position of the specimen were: lengths – body, idiosomal, prodorsal shield, gnathosomal seta *v*, *sc* setal tubercle, tibia, and seta *ft''* of leg 1, tibia, tarsus, seta *u'* and empodium of leg 2, coxal setae *1a* and *2a*, opisthosomal setae *d* and *f*, and number of dorsal annuli lateral to shield.

Prodorsal shield (Fig. 21A) – broadly oval and short, with the characteristic convex shape (Fig. 22F), presumably with declivitous rear area similar to some other *Diptilomiopus* spp. Shield pattern is formed by ridges in a cell-like pattern (Figs 21A,G). After studying several specimens it could be determined that the pattern consists broadly of three rows of cells numbered here as follows: 12 cells (A1L–A6L and A1R–A6R) in anterior row, with cells A6L and A6R incompletely formed, five cells (B1L and B1R fused to form one cell, B2L–B3L and B2R–B3R) in second row and two cells (C1L and C1R) in basal row. Subshield lateral area with granules and dashes arranged somewhat in lines (Fig. 22F).

Frontal lobe present, broad transversely but narrow longitudinally and probably thin and flexible, varying from clearly to vaguely visible (Figs 21A; 22F).

Scapular setal tubercles relatively small, rounded and ahead of rear shield margin (Figs 21A; 22F).

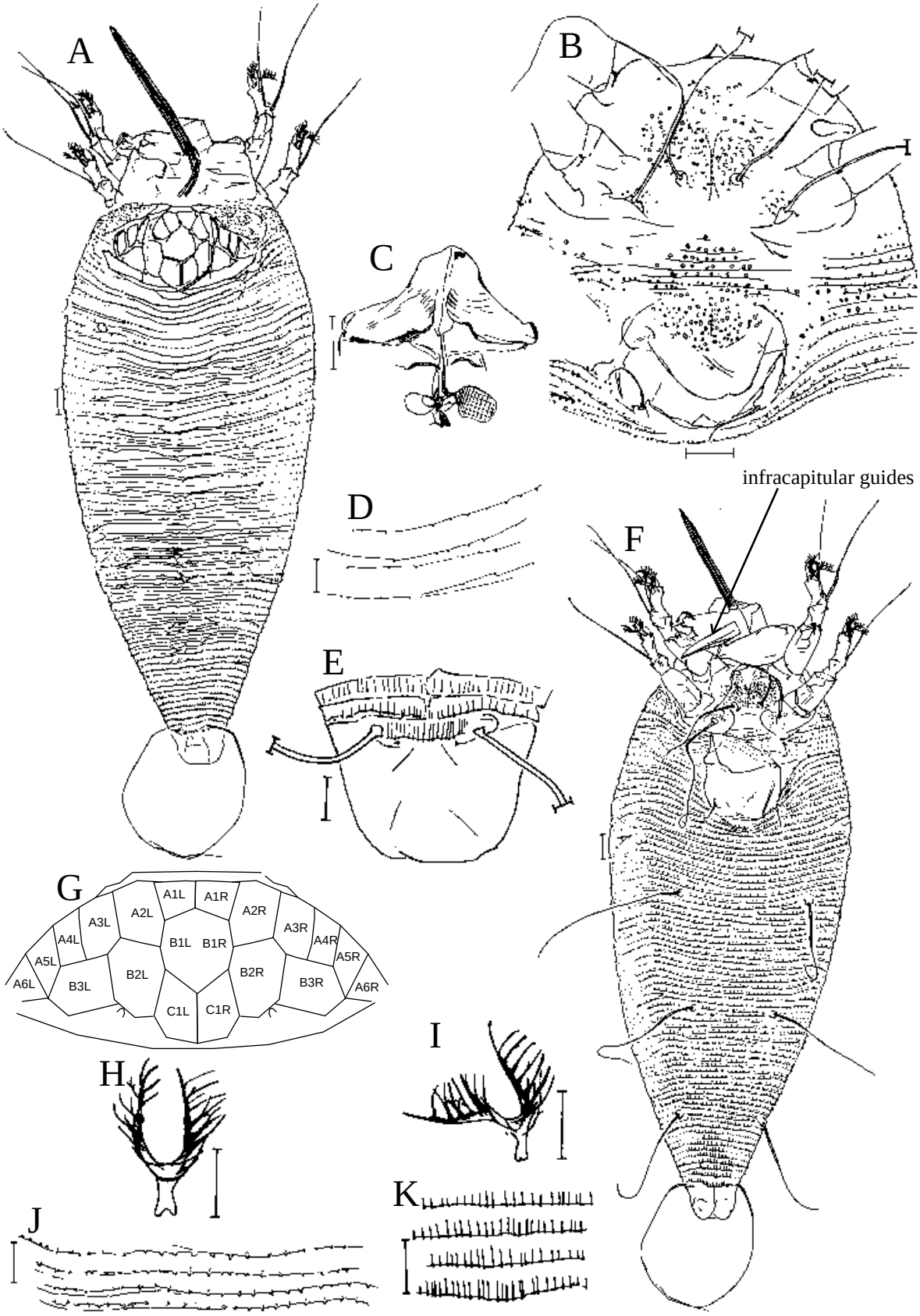

Figure 21. ***Diptilomiopus apolongus*** **sp. nov., female**. **A**. dorsal view; **B**. coxisternal region and genitalia; **C**. internal genitalia; **D**. opisthosomal microtubercles laterad of middorsal area just anteriad of the level of seta *d*. **E.** dorsal view of rear caudal area; **F**. ventral view; **G**. labelled schemical drawing of cell netword of ridges on prodorsal shield; **H**. empodium of leg I; **I**. empodium of leg II; **J**. opisthosomal microtubercles midventrally just posterior of seta *d*; **K**. opisthosomal microtubercles ventrally on rear four annuli.

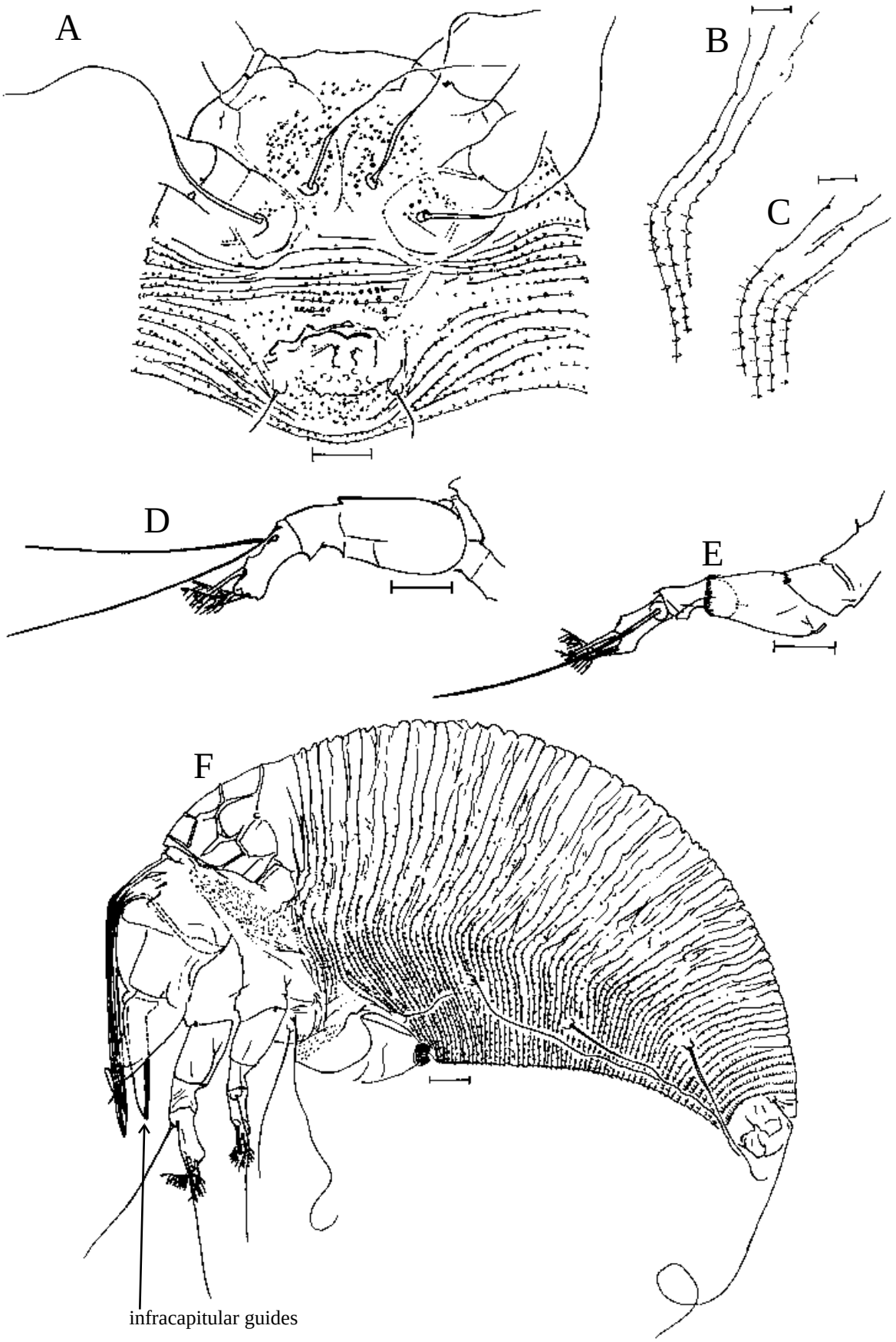

Figure 22. ***Diptilomiopus apolongus*** **sp. nov. Male. A**. coxisternal area and genitalia. **Female. B**. opisthosomal microtubercles on lateral area just posterior of seta *d*; **C**. opisthosomal microtubercles on lateral area just posterior of seta *e*; **D**. leg I; **E**. leg II; **F**. lateral view.

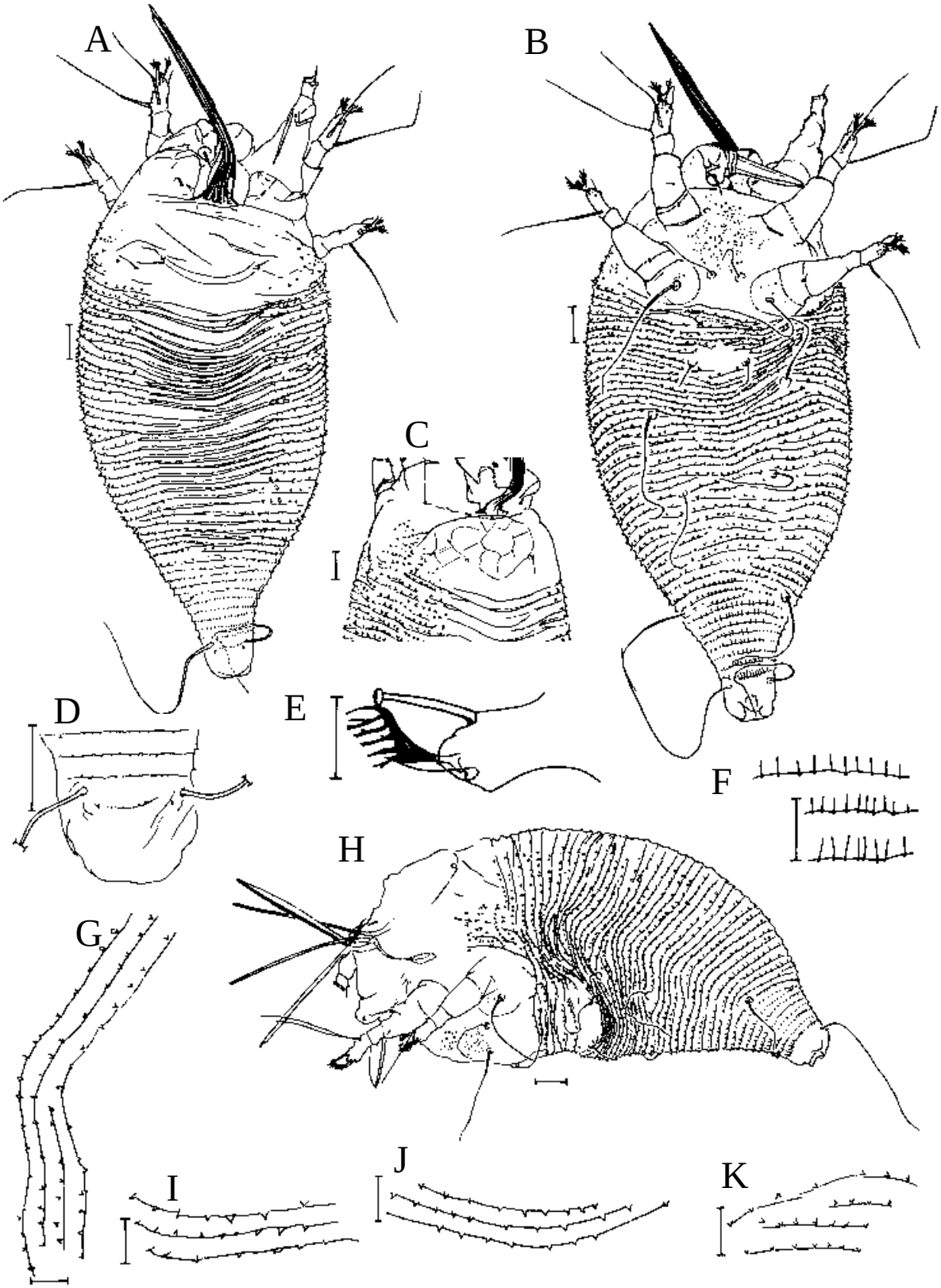

Figure 23. ***Diptilomiopus apolongus*** **sp. nov., nymph**. **A**. dorsal view; **B**. ventral view; **C**. dorso-lateral view of anterior part of idiosoma; **D**. dorsal view of rear, caudal area; E. lateral view of anterior part of tarsus of leg I, including empodium, solenidion and *u'*; **F**. opisthosomal microtubercles ventrally on rear three caudal annuli; **G**. opisthosomal microtubercles laterally, arrow denotes border between dorsal annuli above arrow and ventral annuli below arrow; **H**. lateral view; opisthosomal microtubercles: **I**. lateral area of dorsum, at about level of seta *d*; **J**. midventrally just posterior of seta *d*; **K**. midventrally just anteriad of seta *f*.

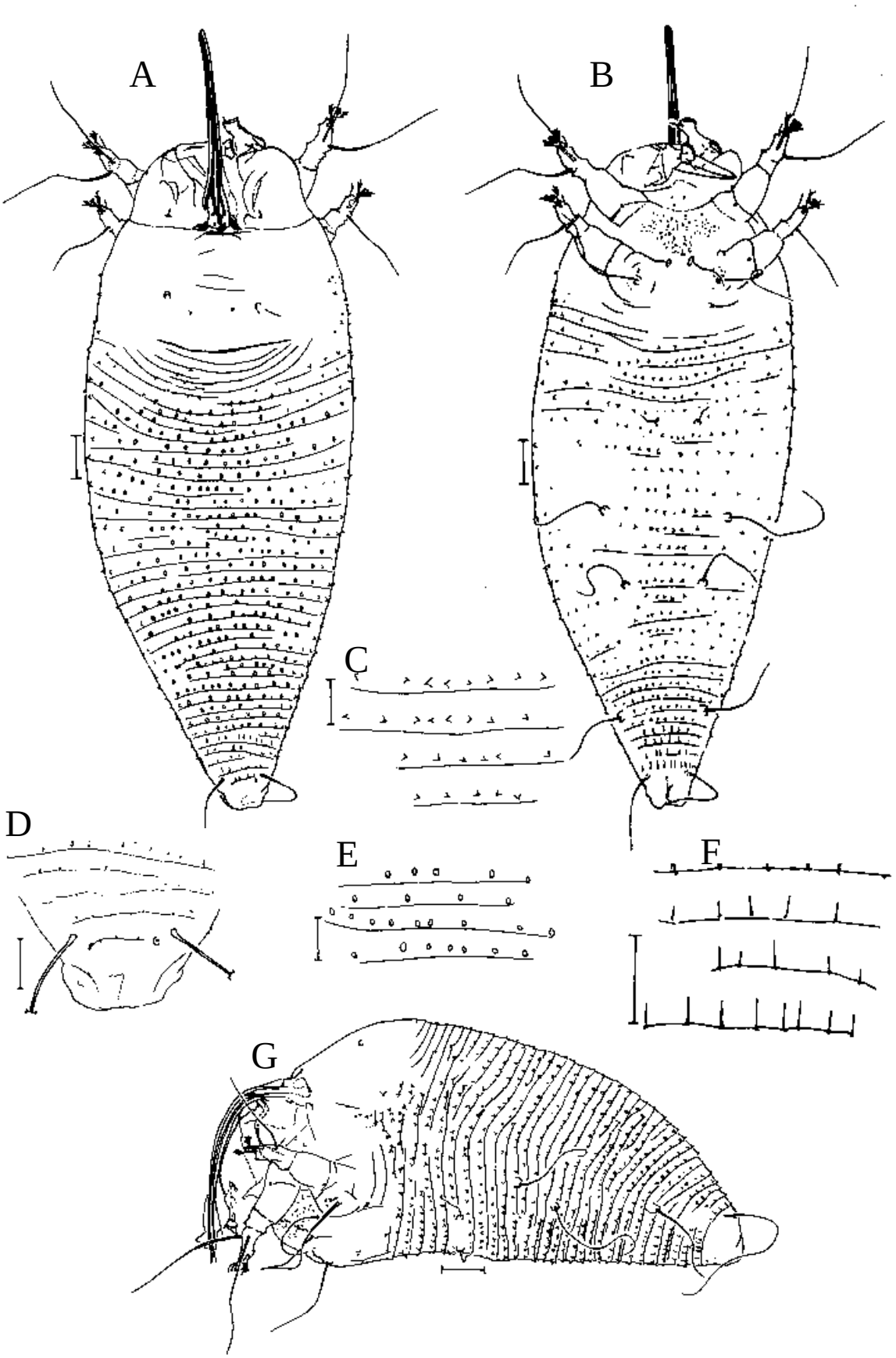

Figure 24. ***Diptilomiopus apolongus*** **sp. nov., larva**. **A**. dorsal view; **B**. ventral view; **C**. opisthosomal microtubercles midventrally at about the level of seta *d*; **D**. dorsal view of caudum; **E**. opisthosomal microtubercles middorsally in area at level of seta *d* towards *e*, microtubercles become smaller towards the rear; **F**. opisthosomal microtubercles ventrally on rear four caudal annuli; **G**. lateral view.

Opisthosoma – Evenly rounded with a shallow, middorsal longitudinal ridge (Fig. 21A) fading towards the rear. In some specimens the outer ridges and troughs are detectable, but in others they are for all practical purposes invisible.

Microtubercles on dorsal annuli: absent in a central band, flanked by microtubercles on each side, however, about 14 rear dorsal annuli entirely microtuberculate (Fig. 21A). Dorsolateral opisthosomal microtubercles obviously more sparsely spaced than on ventral annuli (Figs 21D,J), situated on the rear annulus margins, and are triangular, pointed, fine and small. From the first annulus that are entirely microtuberculate towards the rear, the microtubercles become gradually elongated with the proximal part beneath the dorsal surface, lightly coloured, with the slightly darker apical point exposed and on the rear annulus margin (Fig. 21E). Opisthosomal microtubercles on ventral annuli pointed, about triangularly shaped, close to the rear edges of the annuli, sometimes seemingly on the rear annulus margins, projecting over the rear annulus margin (Figs 21J; 22B,C), becoming progressively elongated ridges from about the level of *f* (on the rear about 12 ventral annuli) (Fig. 21K). Ventral laterally, from about *d* up to *f*, bordering the boarder between the dorsal and ventral annuli, a band of the ventral opisthosomal microtubercles appears to be more elongated than the remainder of the ventral microtubercles (Fig. 22C).

All opisthosomal setae relatively long and finely tapered (Figs 21F; 22F & Table 4), except *h1* that are very short, and may be interpreted as being minute (Fig. 21E & Table 4).

Legs (Figs 22D,E) – 5-segmented, with genu absent, probably fused with the femur.

Setal compliment of legs I (trochanter– [femur-genu] –tibia–tarsus): 0– [0–0] –0–3 (*bv*, *l''* and *l'* absent; three tarsal setae present: *ft*'', *ft*' and *u*').

Setal compliment of legs II (trochanter– [femur–genu] –tibia–tarsus): 0– [0–0] –0–2 (*bv*, *l*'' and *ft'* absent; two tarsal setae present: *ft*'' and *u*').

Setae *ft* in both legs strong, long and tapering.

Femorogenua I and II ornamented with a pattern of ridges on the ventral surfaces (Figs 22D,E), however the ornamentation on femorogenua is less developed and in some specimens seems almost to be absent.

Tarsal solenidion ω, noticeably knobbed and virtually straight (Figs 22D,E). Tarsal empodium *em* deeply and unambiguously divided. The rays lie in an angle against the central stem, especially at the base, of each branch of the divided empodium, and could not be counted accurately, particularly in dorsal view, and has not been statistically dealt with. The empodia 7- or 8-rayed (sometimes the seventh but especially the eighth ray is not easily seen) (Figs 21H,I).

Coxae, coxigenital region and genitalia (Fig. 21B) – Suboral plate with granules similar to those on the coxisternal plates (Fig. 21B); coxisternal plates I and II with rounded to slightly pointed granules and dashes more to the outside of the plates: almost covering coxisternal plates I entirely, coxisternal plates II with a small patch of granules anteriad to *2a* (Fig. 21B); the inner margins (apodemes) of coxisternal plates I light but clearly present, forming two shallow half circles, with central part broadly touching or uniting, forming a so called sternal line that can be categorized as simple and forked anteriorly and posteriorly (Fig. 21B).

Setae *1a* and *2a* present and "normal" (simple and tapering), relatively long, strong and frequently convoluted, with well-developed setal tubercles; *1a* ahead of an imaginary line through tubercles of *2a* (Fig. 21B).

Internal genitalia, particularly the anterior part, quite strongly present, with clear striae on the anterior apodeme and associated tissue (Fig. 21C); external genital coverflap basally covered with granules similar to those on coxisternal plates, distally smooth (Fig. 21B).
Seta *3a* tapering (Fig. 21F).

MALE.
Morphology, including measurements and counts, similar to female, except for genitalia (Fig. 22A), albeit some setae are slightly shorter or in the short range of the female setal lengths (Table 4). Genitalia – scattered microtubercles or granules just below the eugenital setae similar to many other eriophyoid species described to date; granules close to eugenital setae large and rounded becoming smaller and more pointed lower down. Eugenital setae clearly present, with well defined setal tubercles (Fig. 22A)

Two immature stages could be identified (recorded to date all eriophyoid species studied in this regard with two immature stages):

LARVA (Fig. 24).
Specimens identified to be first immature stages (larvae) by absence of external genitalia, the smallest size and rounded incomplete annuli just posterior of rear shield margin (Figs 24A,G). The prodorsal shield mostly smooth with a few lines that could be fold lines and two pointed, triangular granules of microtubercles one each on the inside of the dorsal tubercles (Figs 24A,G); subshield lateral area with a few pointed triangular granules or microtubercles in one small area (Figs 24A,G). Scapular setal tubercles present and smaller but similar to those in adults (Fig. 24A). The incomplete annuli dorsally posteriad of the prodorsum smooth (Fig. 24A), the remainder of the dorsal annuli with small rounded microtubercles near the rear annulus margins, sometimes looking as if they may have a small protrusion (darker and possibly pointed on one side) (Fig. 24E), becoming smaller and pointed, and sitting more on the rear annulus margins on the rear

annuli beyond about the level of *f* and particularly on the rear four annuli (Fig. 24D). Ventral annuli entirely microtuberculate, but with smooth areas about on the outside and anteriorly of *d* and *e*; ventral opisthosomal microtubercles triangularly shaped and pointed, near the rear annulus margins (Figs 24B) becoming alongated on the rear four annuli (Figs 24B,F). All setal compliments the same as in adult, however setae generally much shorter (Table 4); empodial (*em*) with less rays than in adult.

NYMPH (Fig. 23).

Specimens identified to be second immature stages (nymphs) by the absence of external genitalia, their size, and complete and regular annuli just posterior of rear shield margin. Prodorsal shield varying from almost smooth, without ridges in cell pattern (Fig. 23A) to ridges in a more complete cell-like pattern towards the pattern seen in adults (Fig. 23C). Opisthosoma – No external genitalia present, only a discontinuance in annuli where genitalia will be in adult. A middorsal ridge present (Fig. 23A). Dorsal annuli with a middorsal smooth band, with a lateral band of microtubercles, annuli entirely microtuberculate from about 12th annulus from the rear (Fig. 23A), microtubercles sharply pointed, about triangular and situated on or close to the rear annulus margin (Figs 23G,I) becoming smaller towards the rear (Fig. 23D); ventral annuli entirely microtuberculate with microtubercles triangular and pointed similar to dorsolateral microtubercles (Figs 23J,K) becoming more elongated on about the 9 rear annuli (Fig. 23F). All setal compliments the same as in adult, however setae generally shorter than in adult and longer than in larva (Table 4); tarsal empodium *em* probably 6-rayed (Fig. 23E) (difficult to count in most specimens). Tarsal solenidion similar in shape as in adult (Fig. 23E).

ETYMOLOGY – The species name is a combination of the first syllable of the host genus name, *Apodytes*, and the Latin word *longus,* which means long, referring to the long body setae in comparison with the other *Diptilomiopus* sp. found on this host.

HOST PLANT – *Apodytes dimidiata* E.Mey. ex Arn. (Icacinaceae) (Palgrave, 2002). Common names: White-pear (English), *Witpeer* (Afrikaans). It frequently is a small bushy tree 4–5 m tall, but can become 20 m tall in forest. It occurs in coastal evergreen bush, at the margins of medium-altitude evergreen forest, in riverine fringes and open woodland, and on grassy mountain slopes, aften among rocks. It has medicinal value, and the wood is suitable for agricultural implements and furniture. It is an attractive tree used as garden ornamentals. (Palgrave, 2002).

TYPE DATA – Fourty-five type specimens on 10 slides (AcY: 11/224) from type locality and host, *A. dimidiata* (planted for ornamental purposes), Baberton Road, Nelspruit, Mpumalanga,

South Africa (25.28S, 30.59E), 30 June 1988, S. Neser (NF1415, X88/148): holotype female and 4 paratype specimens (2 females and 2 nymphs) on 1 slide, together with a Phyllocoptinae specimen (6-rayed); the holotype can be distinguished by being the only *D. apolongus* sp. nov. female in a dorso-ventral position on this slide; and 40 paratype specimens (19 females, 7 males, 9 nymphs and 1 larva) on 9 slides. Three paratype specimens of *D. apobrevis* sp. nov. (1 female, male, and larva) are present on 2 of the 9 slides, and 5 specimens of a *cf. Tetra* sp. with 4-rayed empodia, and 8 specimens of another Phyllocoptinae species with 6-rayed empodia are dispersed on the 9 slides. Twenty-two paratype specimens on 12 of 20 slides (AcY: 11/222) from *A. dimidiata*, Botanical Garden, Nelspruit, Mpumalanga, South Africa (25.28S, 30.59E), date unknown, A. Witt with directions from S. Neser (X03/130), together with 86 type specimens of *D. apobrevis* dispersed on the 20 slides.

RELATION TO HOST – The mites occurred sparsely (many leaves devoid of them, and further about one to three specimens per leaf) on the underside of the leaves, in many cases close to or even on inner walls of turret galls probably caused by an insect. Mites also occurred on healthy looking leaves without any galls or other symptoms.

GENERAL DISCUSSION AND CONCLUSIONS

It is important to use the best techniques for slide-mounting of specimens to improve the morphological study of eriophyoid mites (De Lillo *et al.*, 2010). Apart from this, it is clear from the present study that many artefacts are present in slide-mounted specimens, and there are limitations inherent in light microscopy of these specimens that cannot be enhanced and rectified by improving slide-mounting techniques, and these inadequacies are already built into eriophyoid descriptions and classifications. Scanning electron microscope images reveal shape and structures which may be of systematic use, particularly for phylogenetic analyses, and which are not visible, discernable or are distorted in slide-mounted specimens. For example, the shape of the gnathosoma of the slide-mounted specimens is distorted, and furthermore, description of the morphology and even presence and length of gnathosomal setae are largely omitted in the published descriptions of other *Diptilomiopus* spp.

Information from SEM studies not only improved on and rectified information from light microscopic studies and resultant descriptions, but additionally provided a surprisingly large number of new structures that have not been previously reported, and can be of use in systematics. This increase in characters is essential for phylogenetic studies of the Eriophyoidea. Information from SEM studies additionally improves the information and clarity of morphological characters to such a degree that it will aid in the improvement of the identification and delimitation of characters and character states which are urgently required in eriophyoid systematics. For all these

reasons, the inclusion of SEM studies should not just be a mere enhancement of primary light microscopic studies for taxon descriptions. Morphology studied with SEM should be seriously and routinely incorporated into descriptions of taxa, and making it a requirement in some instances should be advocated. The inclusion of SEM studies is compulsory for the description of many nematode groups, largely implemented by peer review practices, and a description will hardly be accepted for publication if these are not included without acceptable reasons (M. Marais, *pers. comm.*). Numerous phylogenetic studies in spiders are also extensively incorporating information from SEM studies.

Thorough and precise descriptions of eriophyoids are extremely important when it is taken into account that slide-mounted specimens are not permanent, and that most type material is lost over time (Amrine & Manson, 1996; De Lillo *et al*., 2010).

In reality, however, SEM facilities are not readily and widely available worldwide. Consequently, morphological information from SEM studies cannot be solely incorporated in the practical description, classification, differentiation and identification of eriophyoid mites, without concurrent and corroborating usable character states from slide-mounted specimens. This is similar to the situation with information from molecular studies.

The improvement of descriptions by including SEM studies is demonstrated and the SEM studies contributed additional novel characteristics which may be of use in systematics.

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