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).

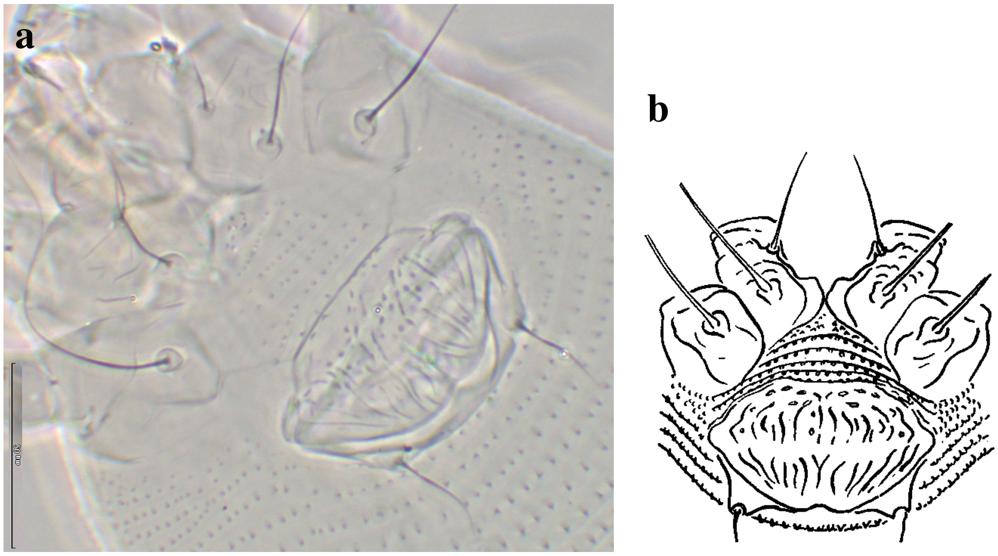


Fig. 3.1. Coxisternal plates and external genitalia of a slide-mounted female specimen of *Cecidophyopsis* sp. *cf. C. hendersoni* (Keifer, 1954): **a)** digital image of slide-mounted specimen viewed with phase contrast light microscopy; **b)** taxonomic drawing of the same area of *C. hendersoni* by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

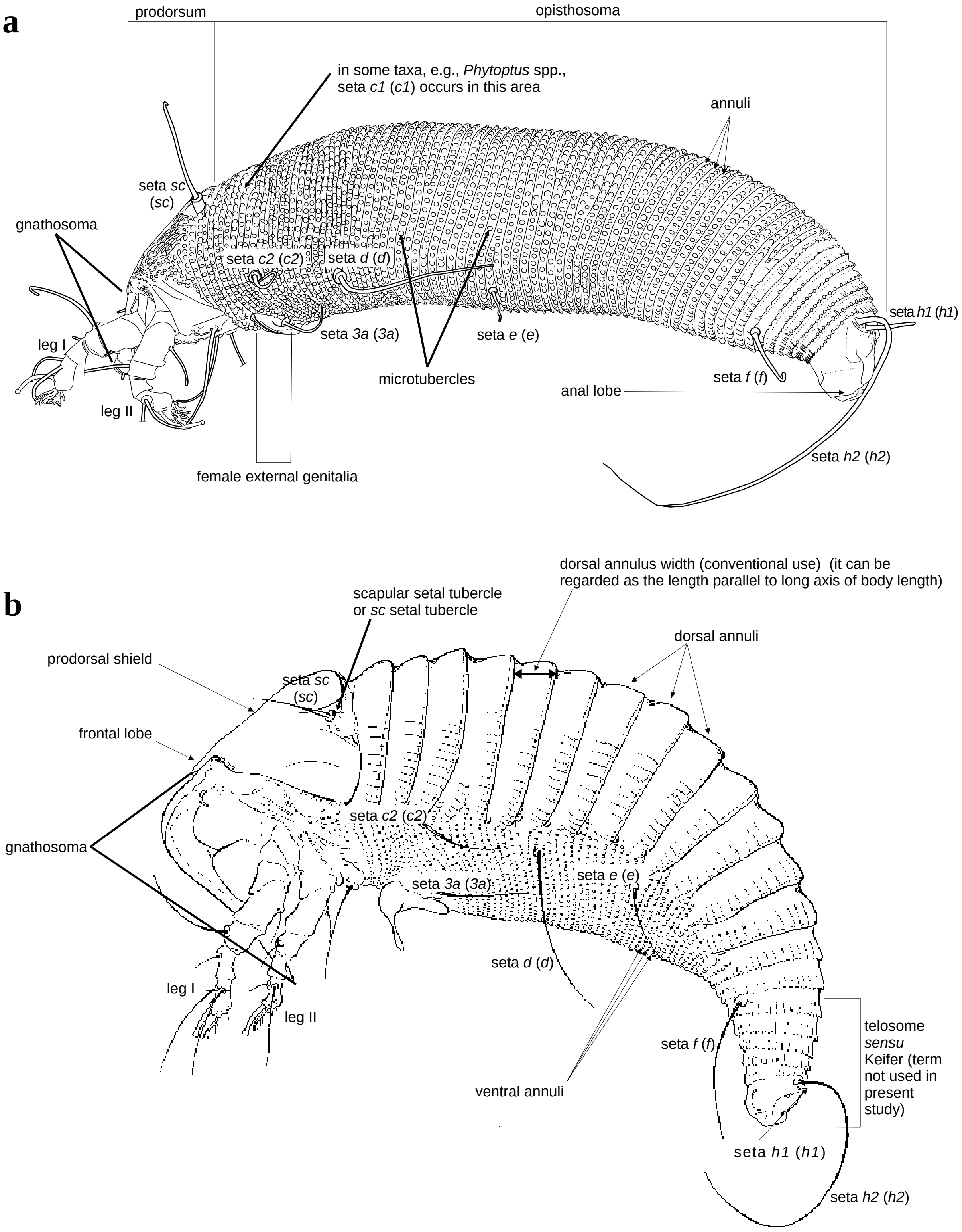


Fig. 3.2. Habitus of the two major forms of eriophyoid mites in lateral view: **a)** vermiform mite, *Aceria* sp. nov. (Eriophyidae), digitally drawn by C. Craemer from a SEM image. Vermiform eriophyoids usually live a relatively sheltered life within micro-spaces e.g., in galls or under bud scales; **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.

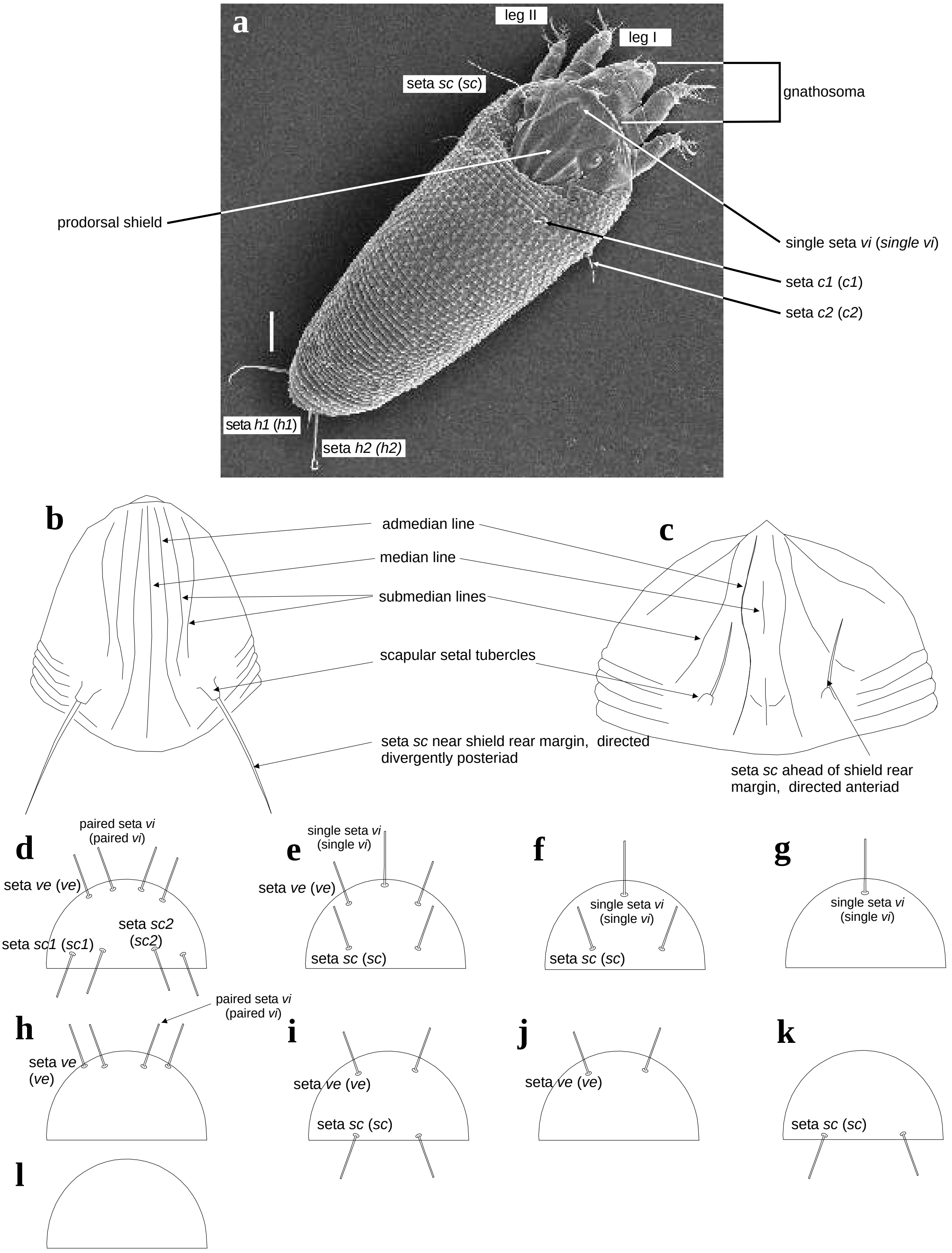


Fig. 3.3. a) Habitus of an eriophyoid mite, represented by the SEM image of *Trisetacus* sp. (Eriophyoidea: Phytoptidae) in dorsal view, scale line = 10 µm; **b, c)** schematic drawings of prodorsal shield in dorsal view with names of general lines of prodorsal shield pattern, and different positions 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).

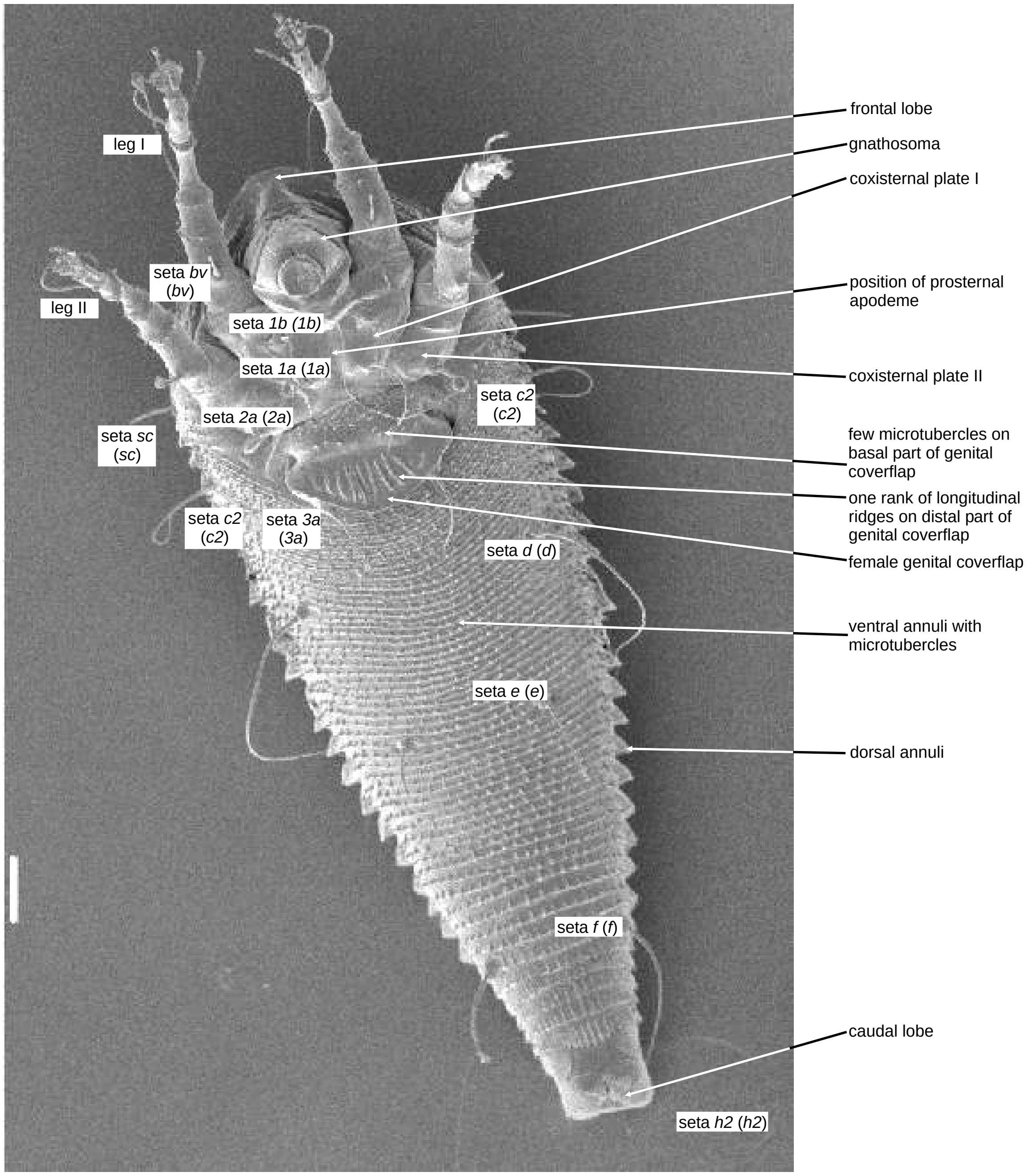


Fig. 3.4. Habitus of an eriophyoid mite, represented by the SEM image of an *Aculus* sp. (Eriophyoidea: Eriophyidae: Phyllocoptinae) in ventral view. Scale line = 10µm.

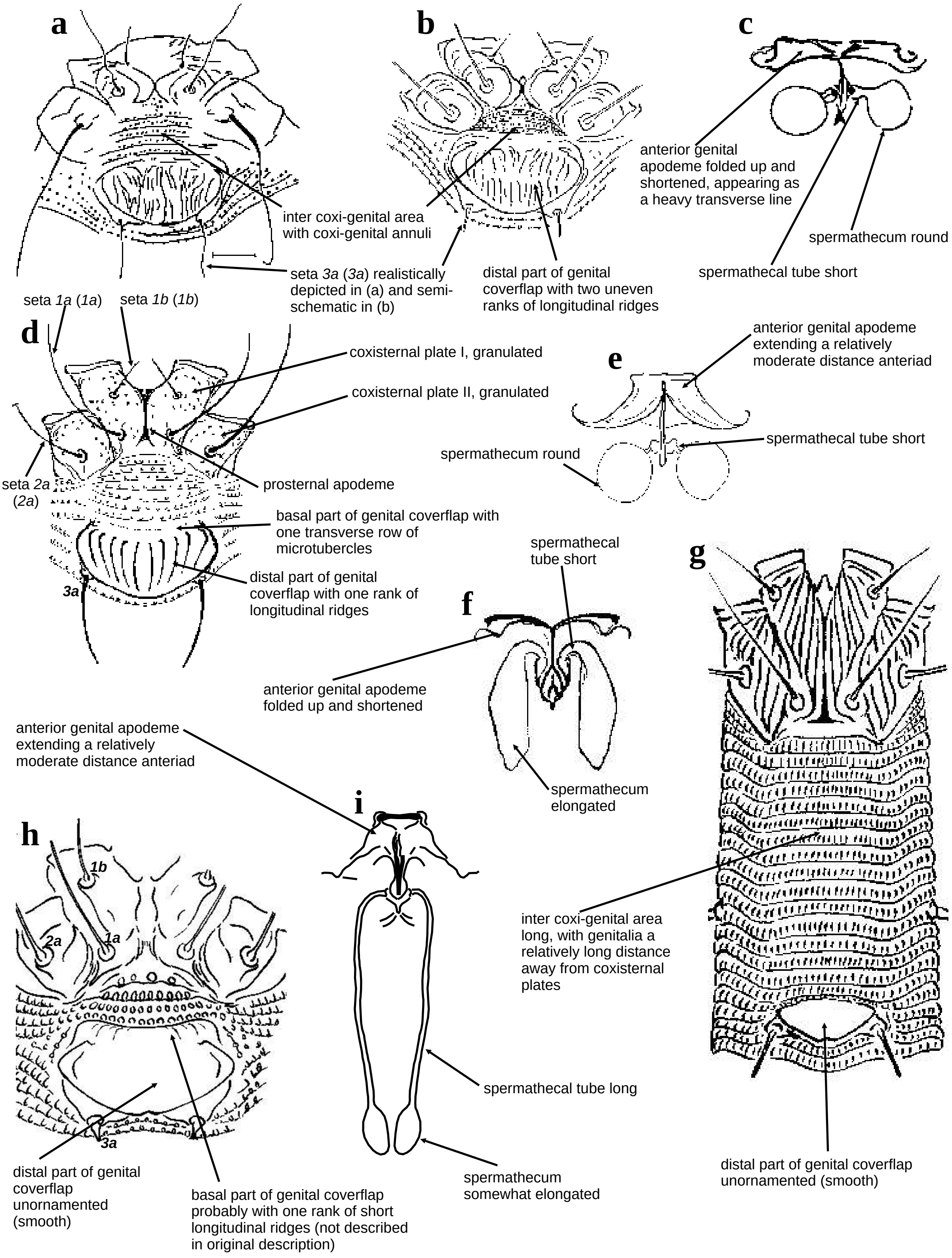
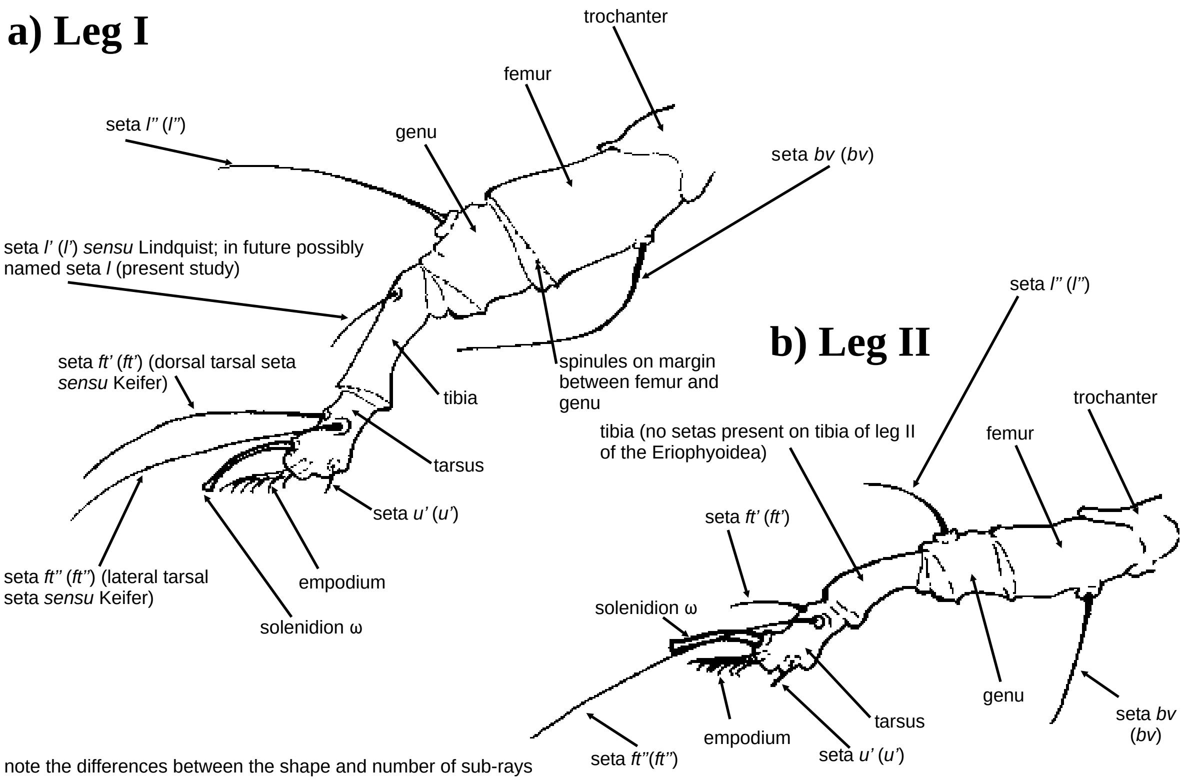
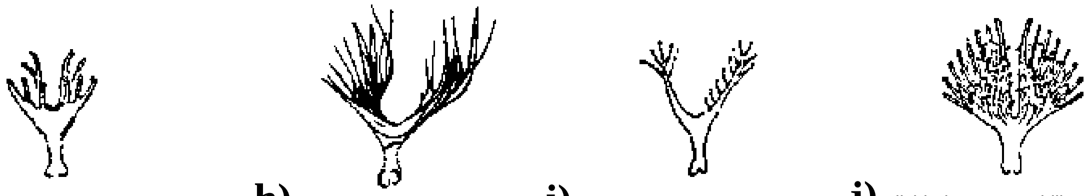


Fig. 3.5. Descriptive drawings of the coxi-genital areas and internal genitalia of slide-mounted adult females of different eriophyoid taxa. *Cecidophyes rouhollahi* Craemer, 1999 (Eriophyidae: Cecidophyinae), reproduced from Craemer *et al*. (1999), specimen depicted in (a) more flattened under coverslip 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.



note the differences between the shape and number of sub-rays between the drawing by C. Craemer (left) and H.H. Keifer (right) of the same species

c) simple, with 5 rays **d)** simple, with 5 rays **e)** simple, distally elongated **f)** simple, rays unsymmetrical



g) partly divided **h)** divided **i)** divided, stems unequal **j)** divided, stems pad-like with numerous rays

k) divided, with central stem **l)** palmate **m)** basal rays finely branched, hair-like **n)** reduced to bristle

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 <u>Low-temperature SEM</u>

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.

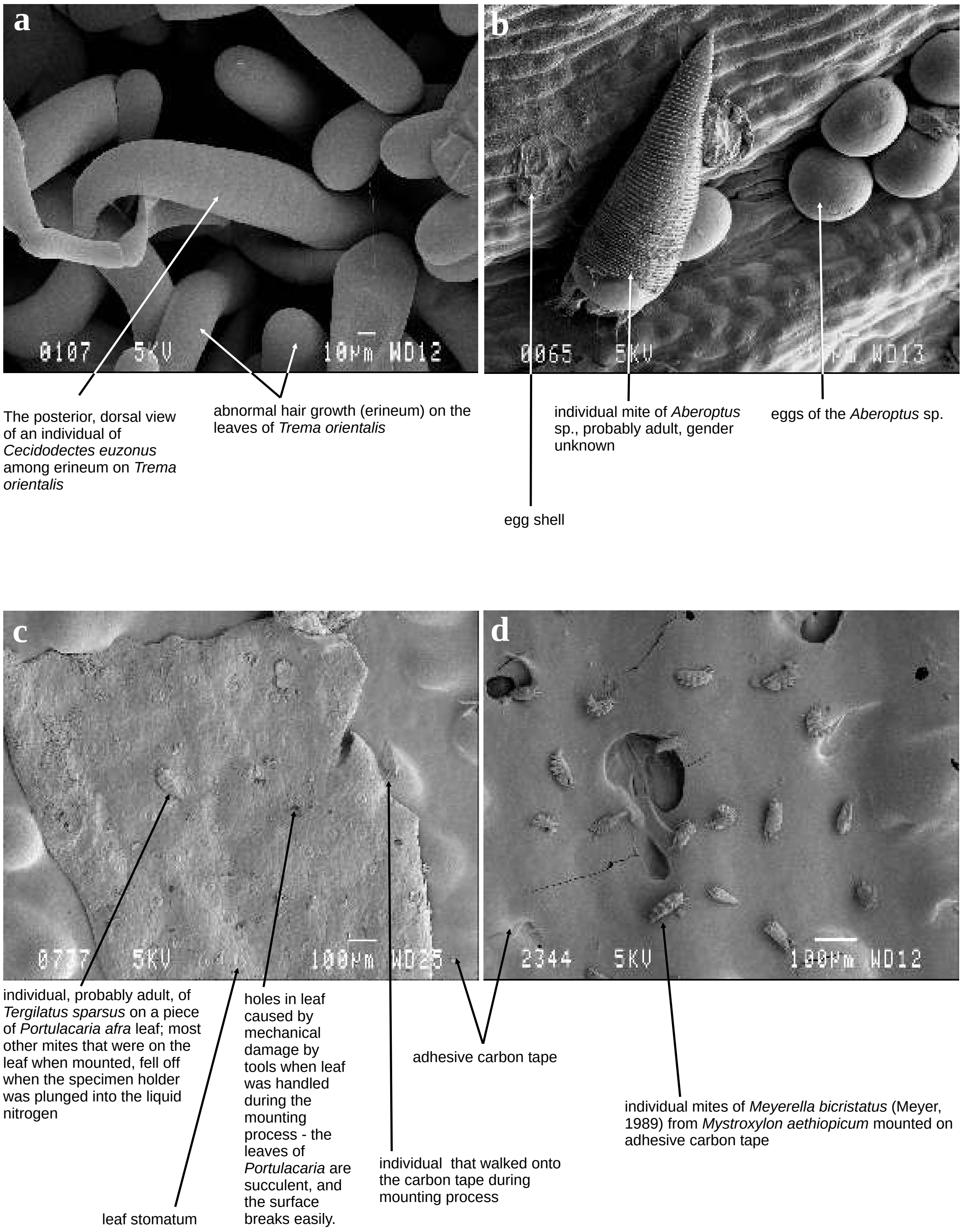


Fig. 3.7. Unmodified SEM images: **a)** Specimens of *Cecidodectes euzonus* Nalepa, 1917 among erineum hairs caused by them on *Trema orientalis*, illustrating the difficulty to sometimes find the mites within complicated plant structures when viewed with SEM. This and the need to view them from different 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

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.

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.

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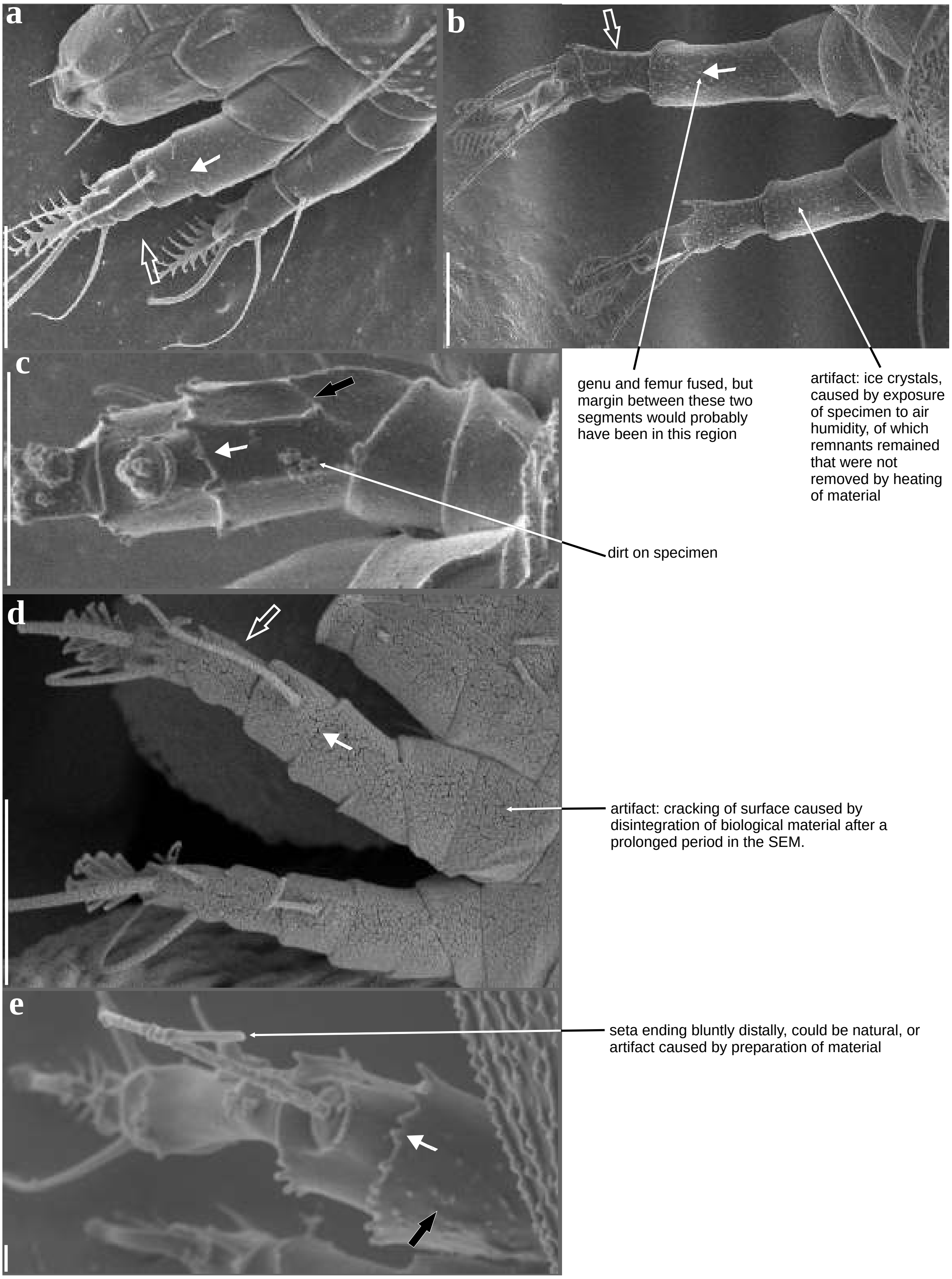
[1] Note that most of the comparisons and critique on observations from slide-mounted material, quality of slide-mounting, and descriptions thereof, entail the work of M.K.P. (Smith) Meyer and/or E.A. Ueckermann from South Africa. This is because the material included in the study was collected in South 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.



genu and femur fused, but margin between these two segments would probably have been in this region

artifact: ice crystals, caused by exposure of specimen to air humidity, of which remnants remained that were not removed by heating of material

dirt on specimen

artifact: cracking of surface caused by disintegration of biological material after a prolonged period in the SEM.

seta ending bluntly distally, could be natural, or artifact caused by preparation of material

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.

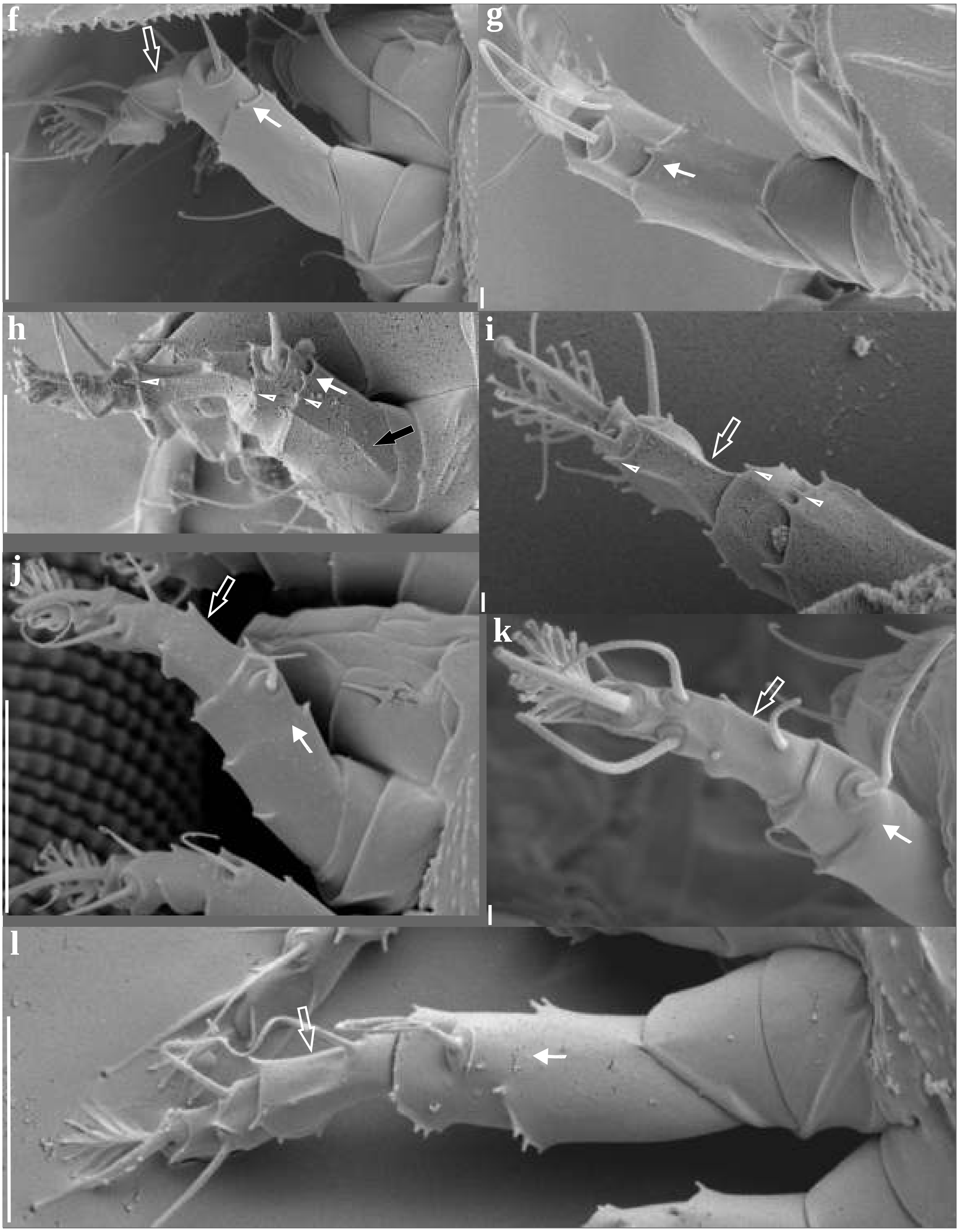


Fig. 3.8. (continued from previous page) **f, g)** *Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini), vagrant on *Lantana trifolia*; **h)** leg I and **i)** leg II of *cf. Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini), leaf vagrant on *Psydrax livida*; **j)** *Acalitus mallyi* (Eriophyidae: 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).

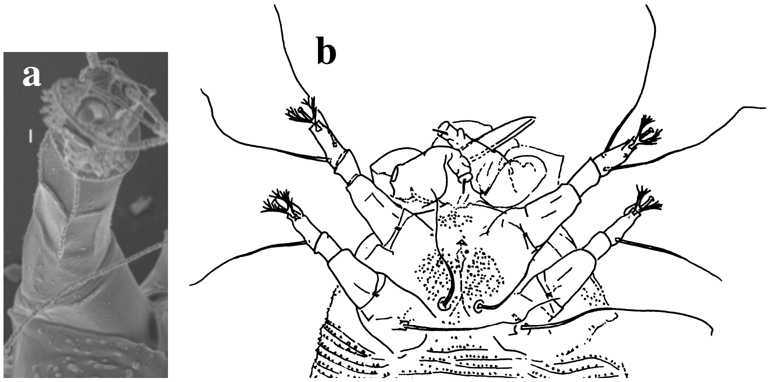


Fig. 3.9. *Diptilomiopus faurius* sp. nov. from *Faurea rochetiana* (Appendix M), ventral view of leg I, with a pattern of ridges, **a)** clearly visible in the SEM images, but, **b)** barely visible in the slide-mounted specimens. This descriptive drawing was drawn from the specimen with the most complete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

- <u>Leg tarsus: empodium</u>

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).

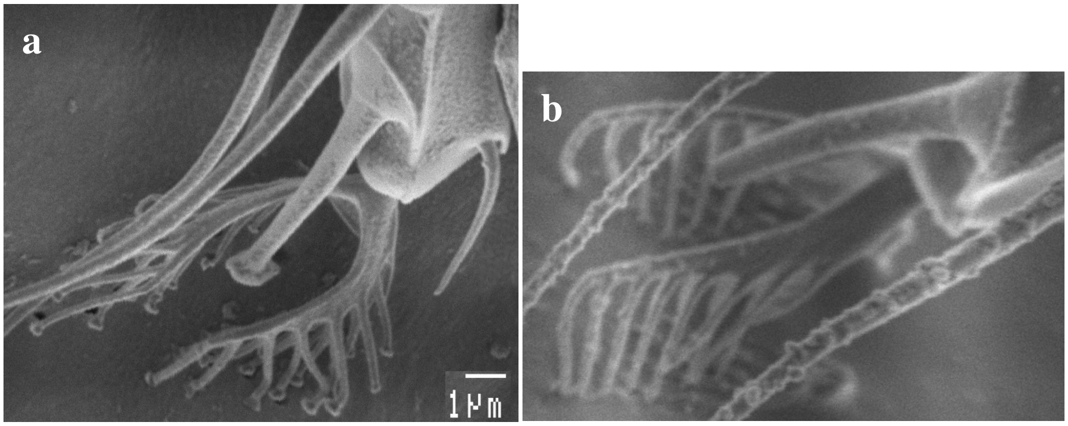


Fig. 3.10. Empodium on tarsus of leg I of *Diptilomiopus faurius* sp. nov. (Appendix M) from *Faurea rochetiana*: **a)** dorsal view depicting shape, **b)** lateral view facilitating count of rays – eight in this species.

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

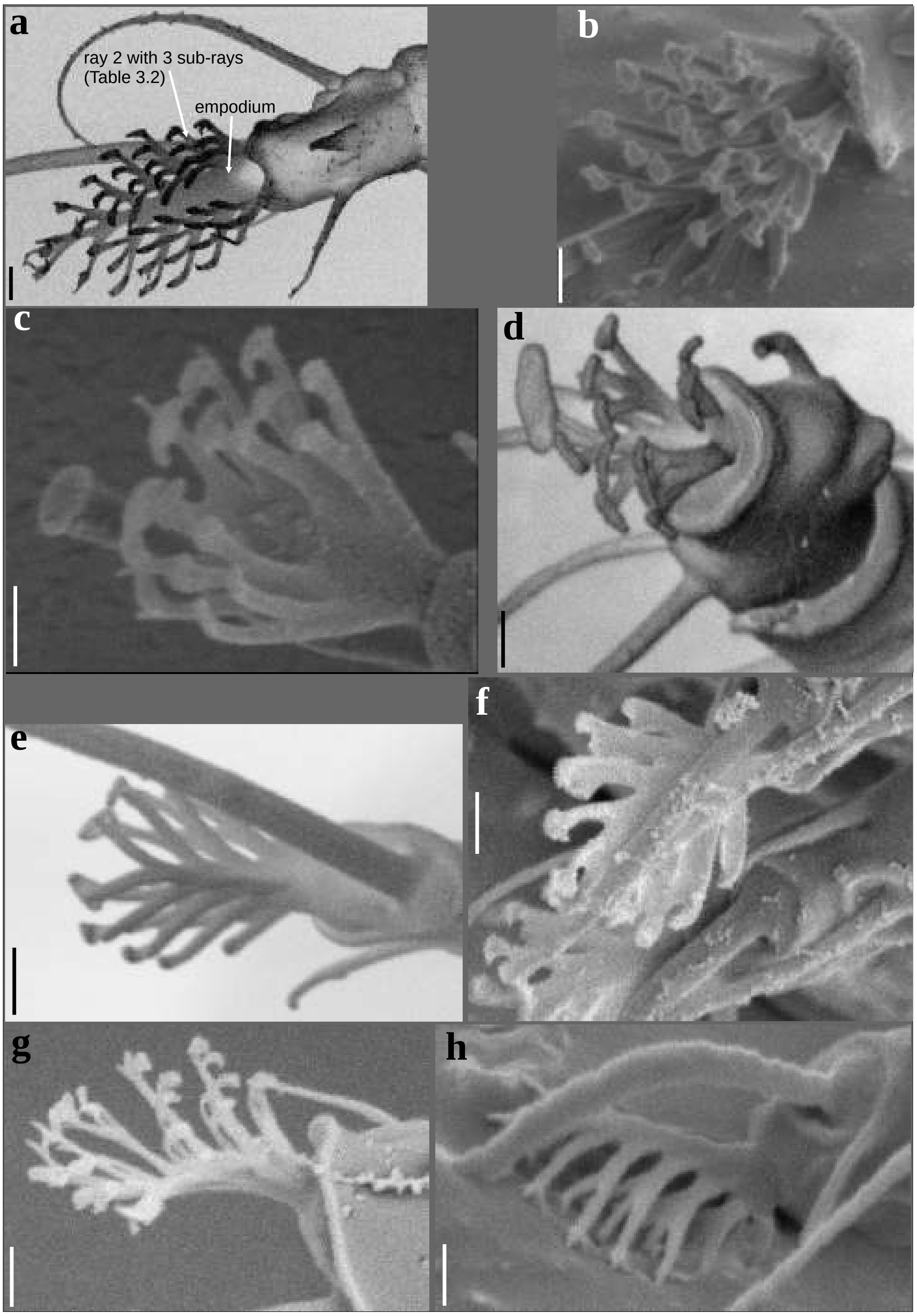


Fig. 3.11. Distal parts of tarsi with focus on the empodia: **a)** *Trisetacus* sp. from *Pinus pinaster*; **b)** *Cecidophyopsis* sp. from *Yucca guatemalensis*; **c)** *Shevtchenkella* sp. from *Psydrax livida*; **d)** unknown species from *Dovyalis*; **e)** unknown species from *Faurea rochetiana*; **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 is evident when published images and drawings are compared with SEM images of the same species. This inaccuracy of conventional eriophyoid descriptions renders the determination of primary homologies between specific areas impossible or ambiguous.

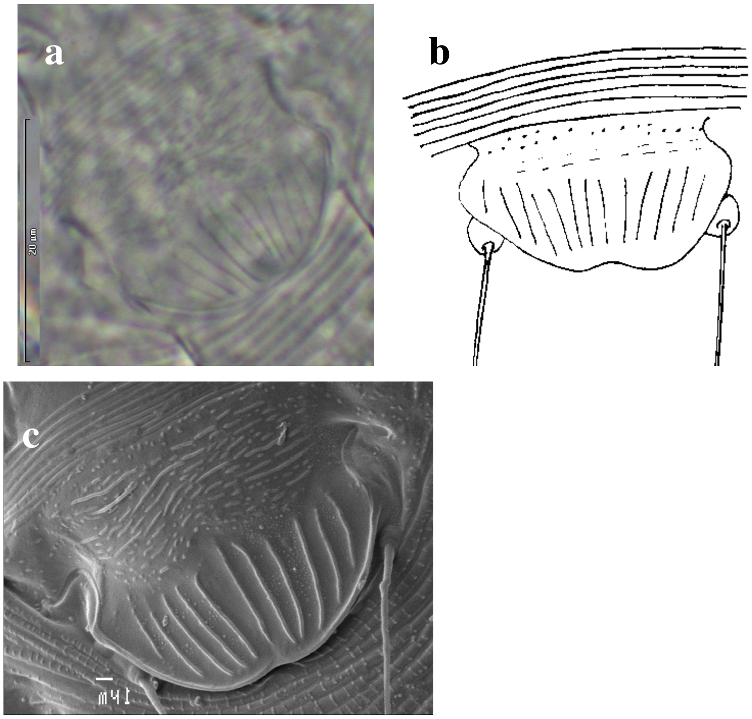


Fig. 3.12. External female genitalia of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Meyer & Ueckermann, 1995): **a)** a slide-mounted specimen (holotype) viewed with phase contrast; **b)** a drawing made from slide-mounted specimen; **c)** SEM image of same area in another specimen. Drawing reproduced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

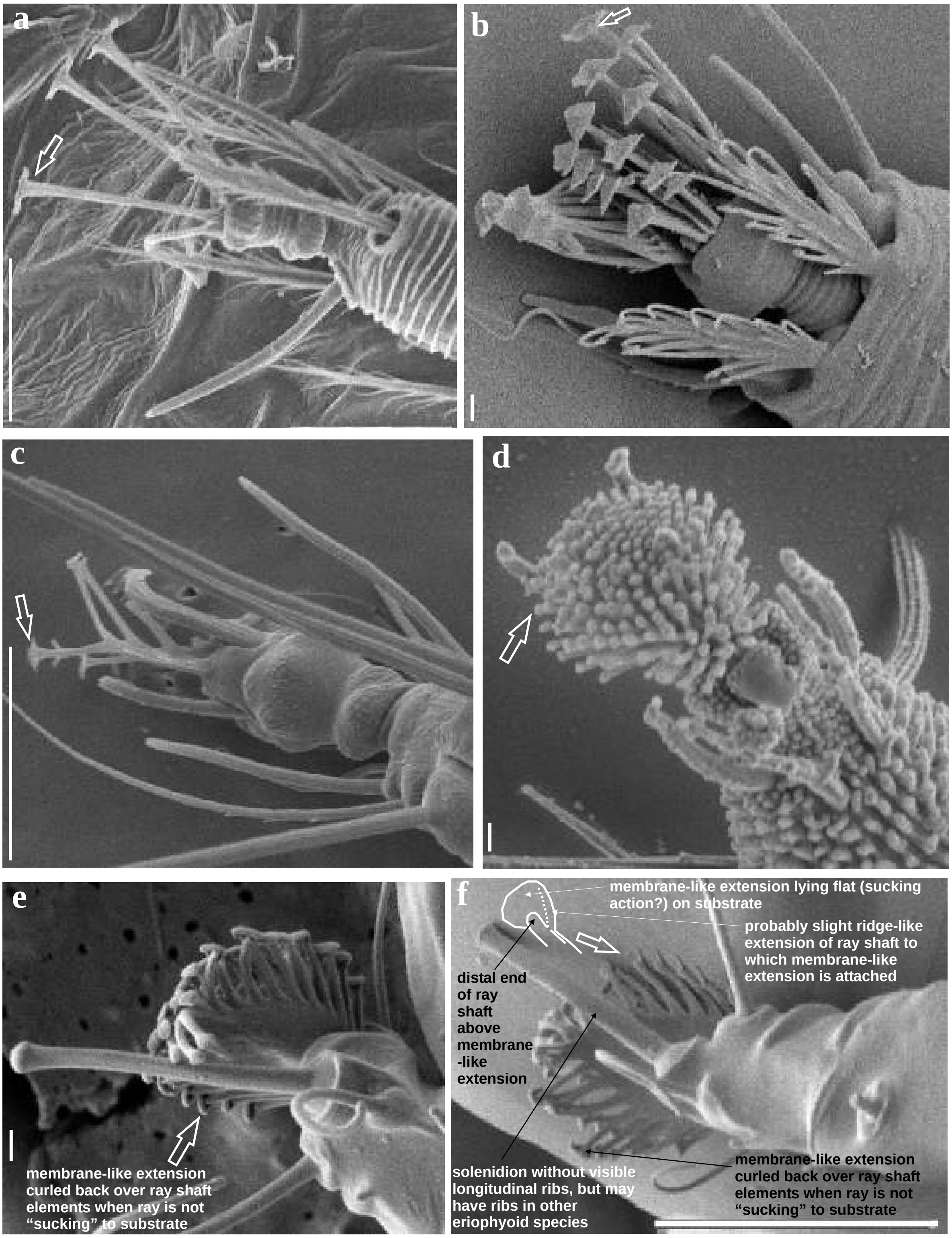


Fig. 3.13. Ambulacra with tenent hairs: **a)** leg II of an *Aponychus* sp. (Tetranychidae) from *Solanum mauritianum*; **b)** leg I of a species of the Tenuipalpidae from a *Senecio* sp.; **c)** leg I of a species of the Stigmaeidae from *Apodytes dimidiata*. Empodia with slightly knobbed hairs or rays (*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).

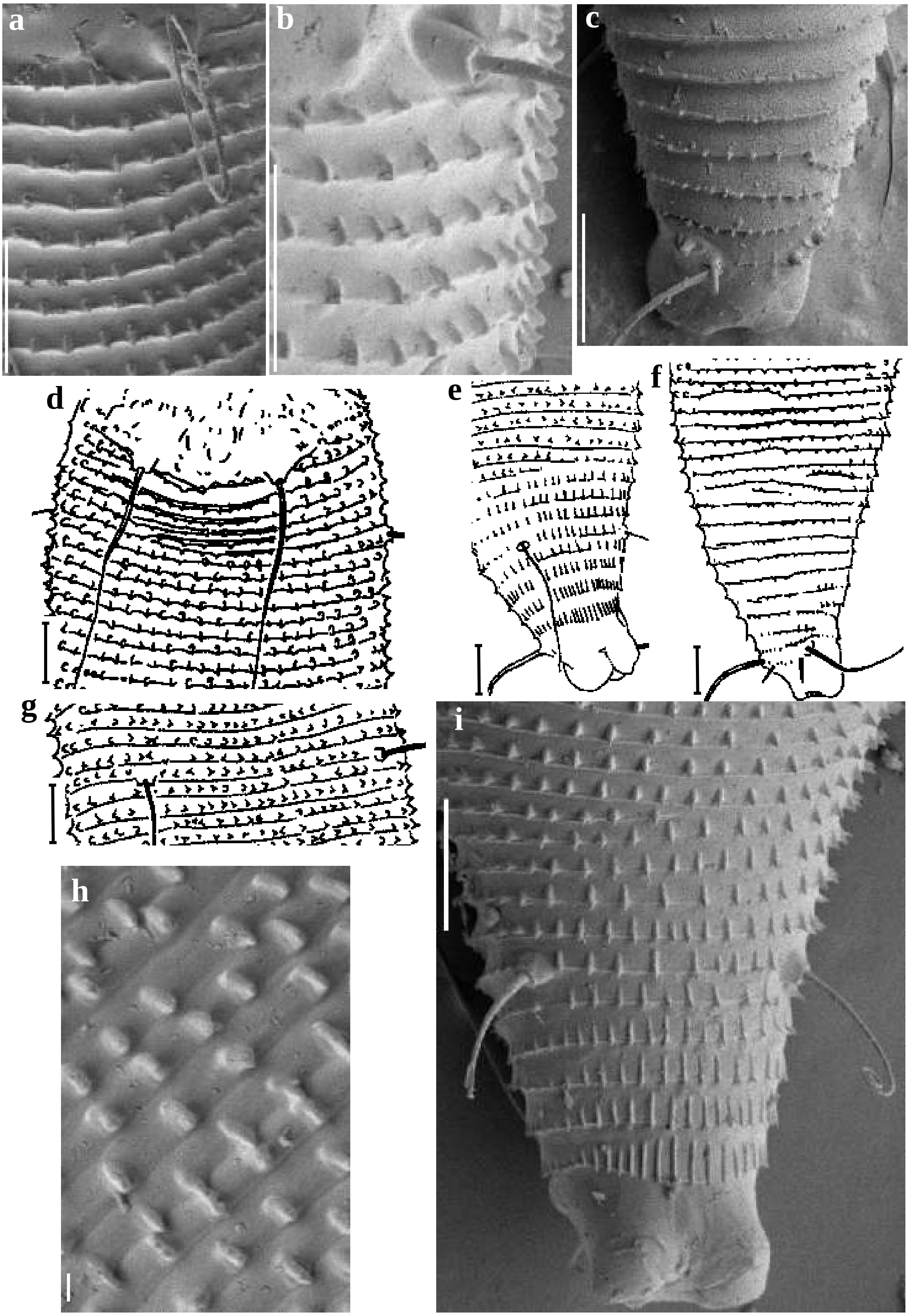


Fig. 3.14. Microtubercles of *Aceria* sp. nov. from *Ipomoea batatas*: dorsally on first annuli behind the prodorsal shield rear margin - **a, b)** SEM images, **d)** line drawing; dorsally on rear caudal annuli - **c)** SEM image, **f)** line drawing; on ventral annuli between setae *e* - **g)** line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

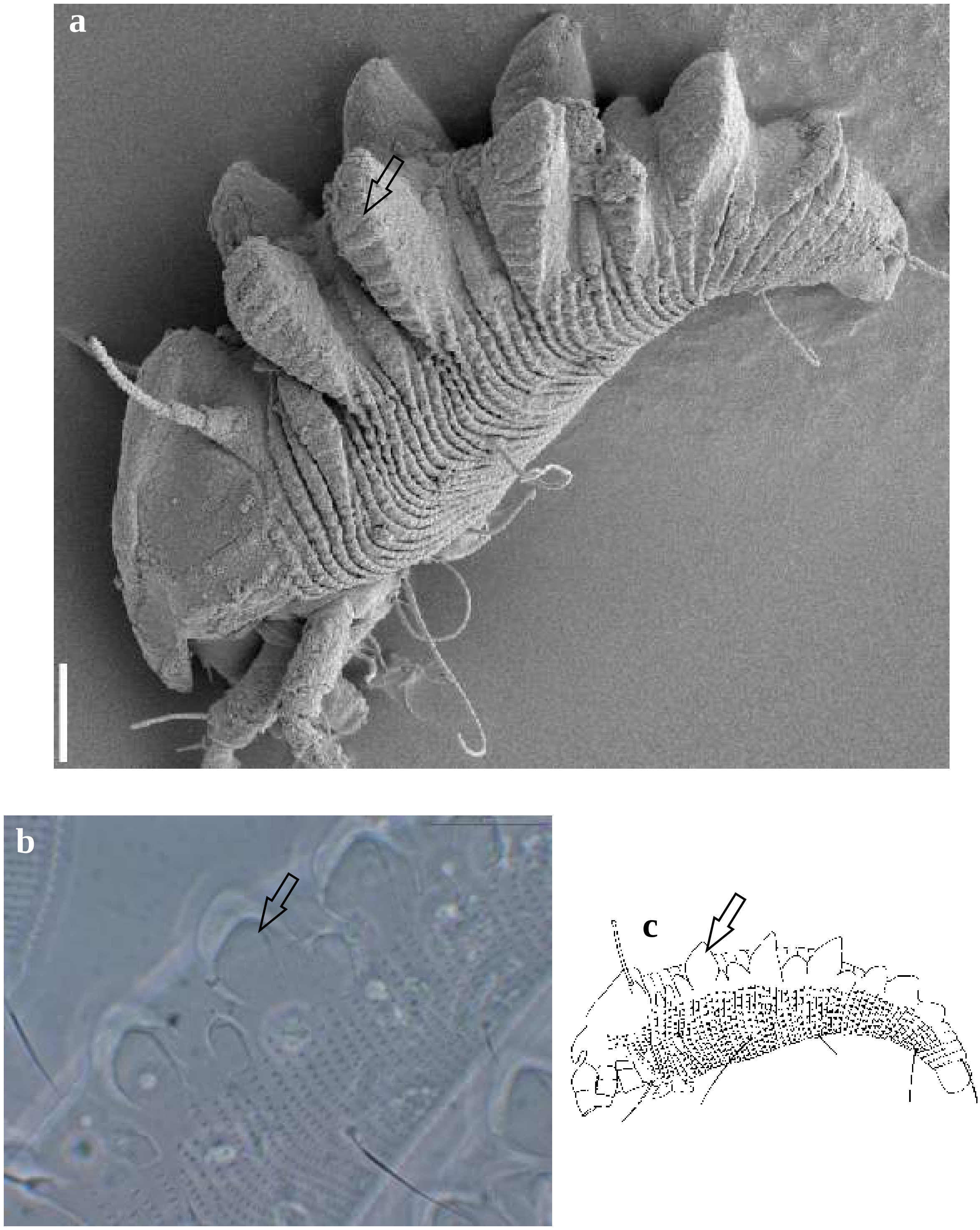


Fig. 3.15. *Meyerella bicristatus* (Meyer, 1989), leaf vagrant on *Mystroxylon aethiopicum* subsp. *aethiopicum*: **a)** SEM image of dorso-lateral aspect (scale line = 10 µm); **b)** part of lateral aspect of slide-mounted specimen (female) viewed with phase contrast light microscopy; **c)** line drawing [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.

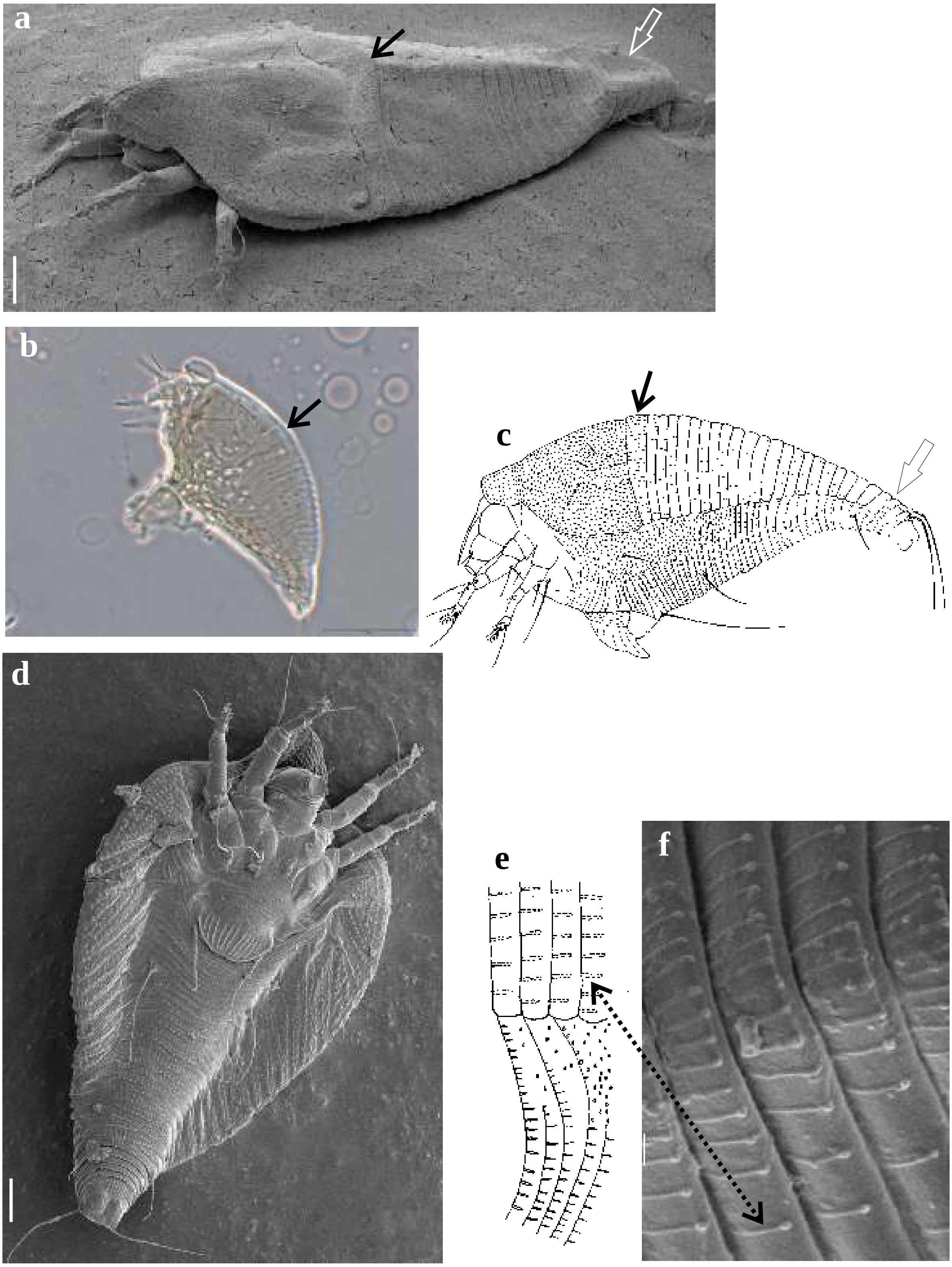


Fig. 3.16. (continued on next page). *Tergilatus sparsus* Meyer & Ueckermann, 1995, leaf vagrant on *Portulacaria afra*: SEM images (a, d, f, h, j), line drawings (c, d, g) [from Meyer & Ueckermann (1995)], and slide mounted specimens viewed with phase contrast (b, i, j, k): **a)** dorsal view; **b, 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.

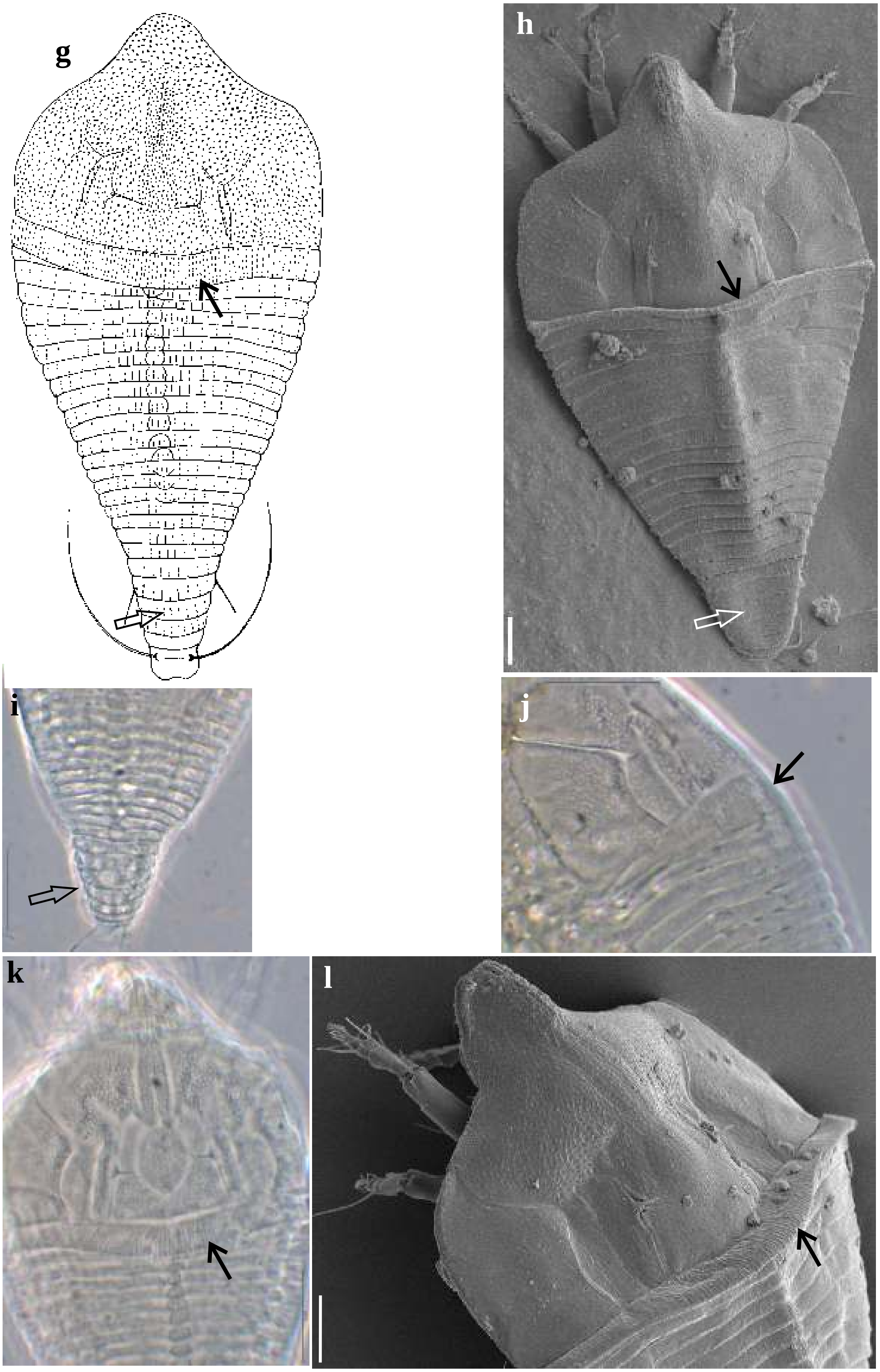


Fig. 3.16. (continued from previous page).

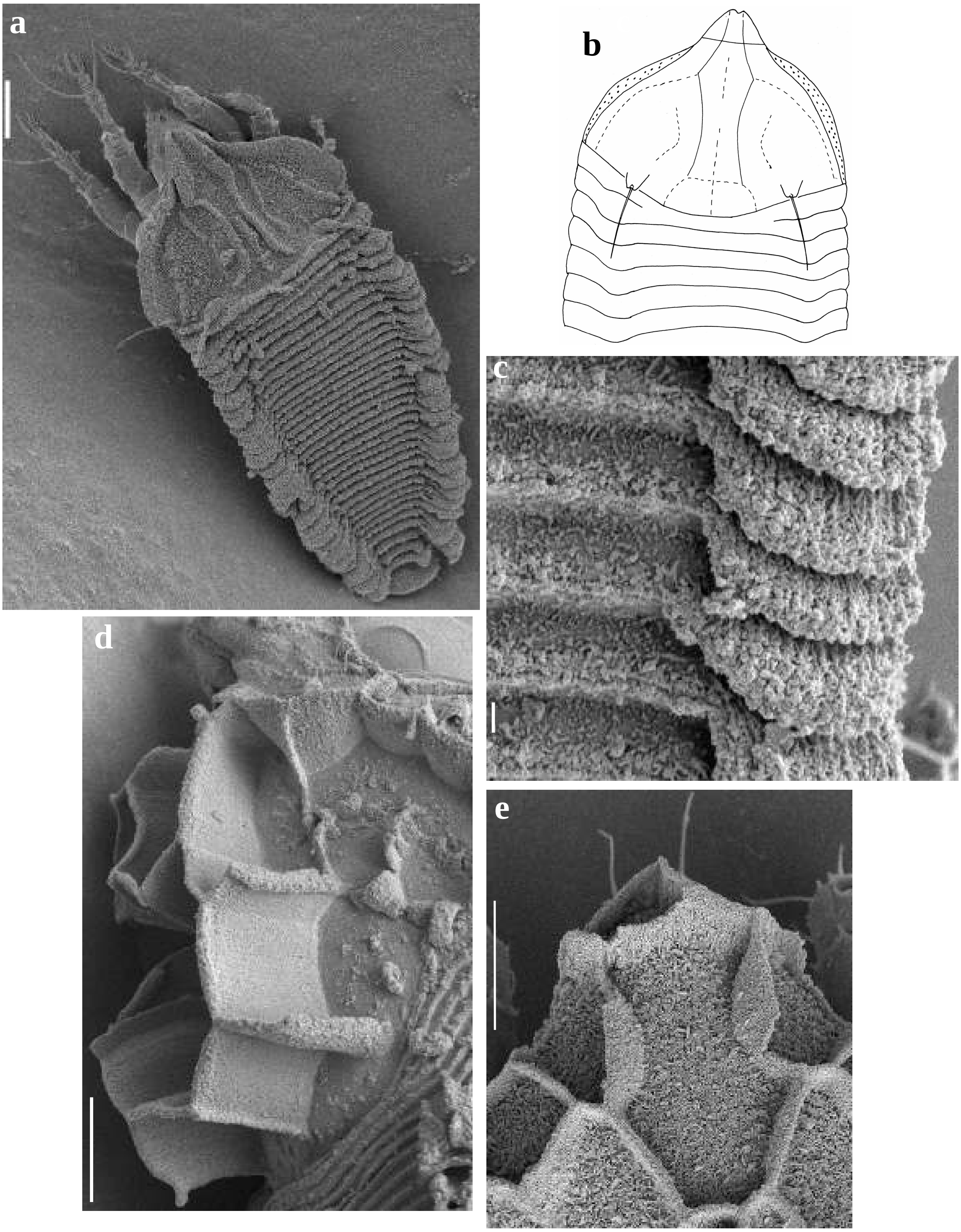


Fig. 3.17. *Tetra retusa* Meyer, 1992 from *Bauhinia galpinii* (Meyer, 1992b): **a, c, e)** wax secretions and enlargements thereof on about the entire body, but particularly on the ridges of the opisthosoma and prodorsal shield, all specimens in dorsal view; **b)** descriptive drawing (Meyer, 1992b) 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.

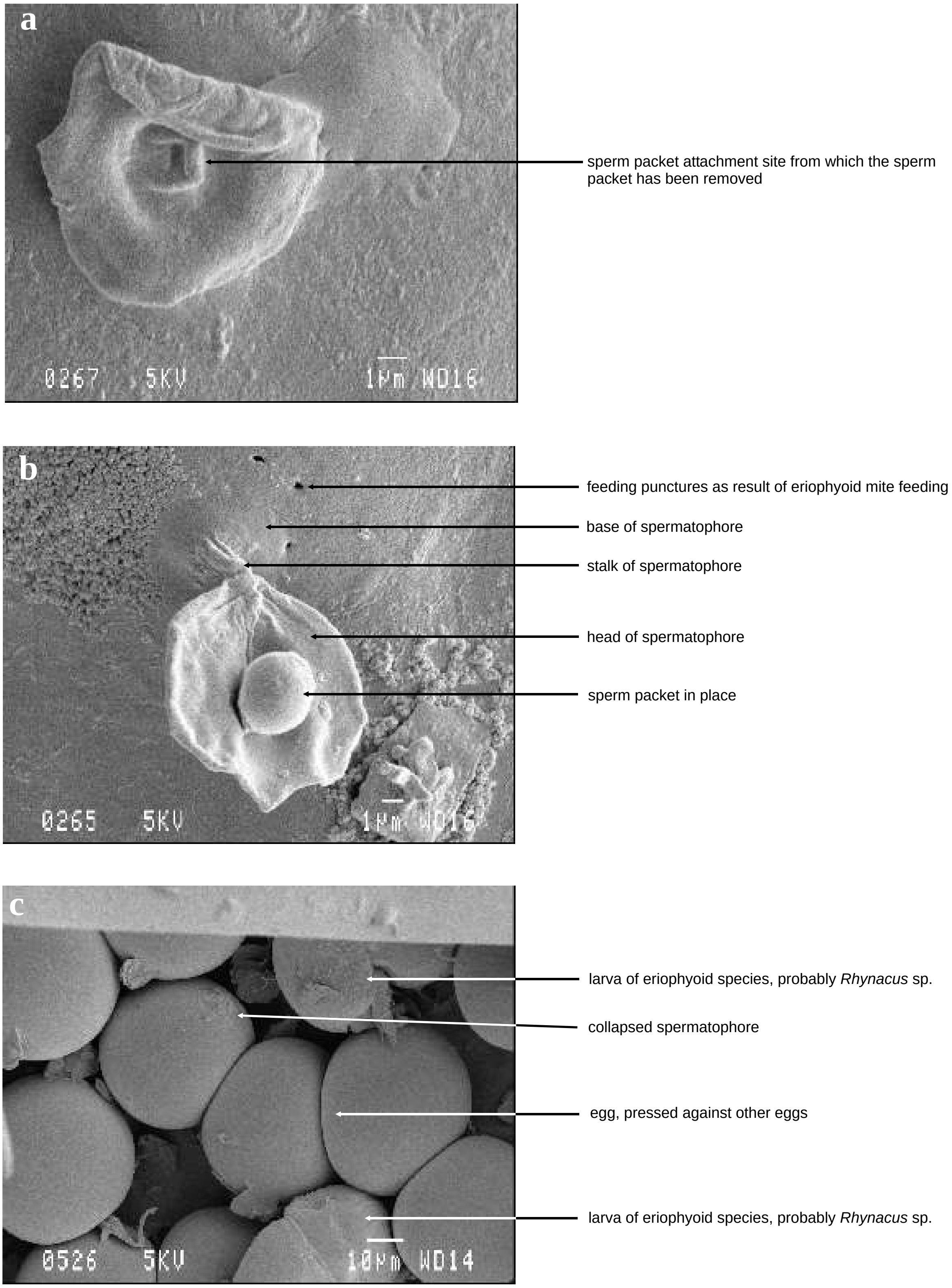


Fig. 3.18. Spermatophores of *Aculus* sp. from *Lantana trifolia*: **a)** with sperm packet in tact; **b)** without sperm packet. Possibly *Rhynacus* sp. from *Mystroxylon aethiopicum* subsp. *aethiopicum*: **c)** eggs and immatures; scale line length representations given below scale lines. SEM images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

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[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.

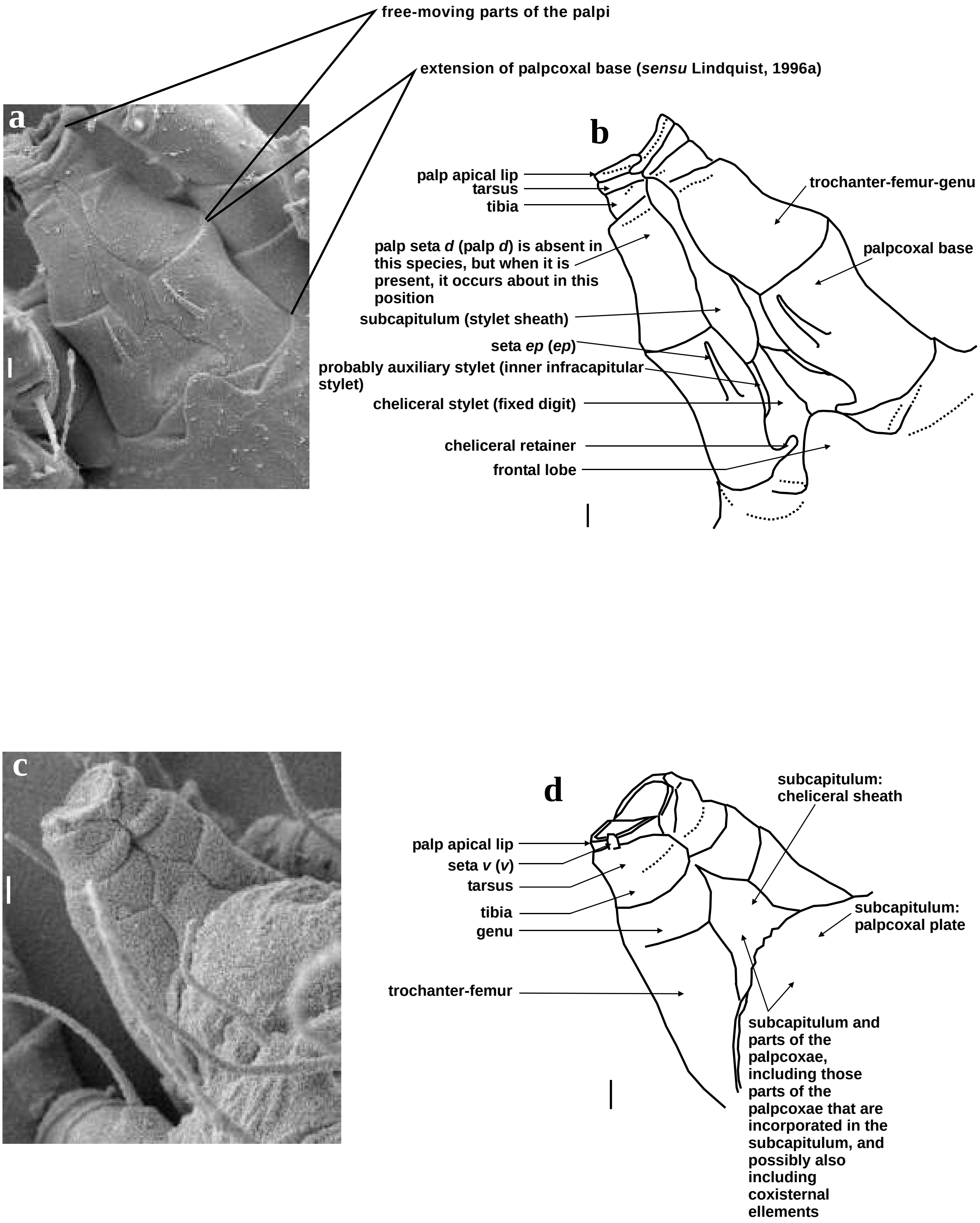
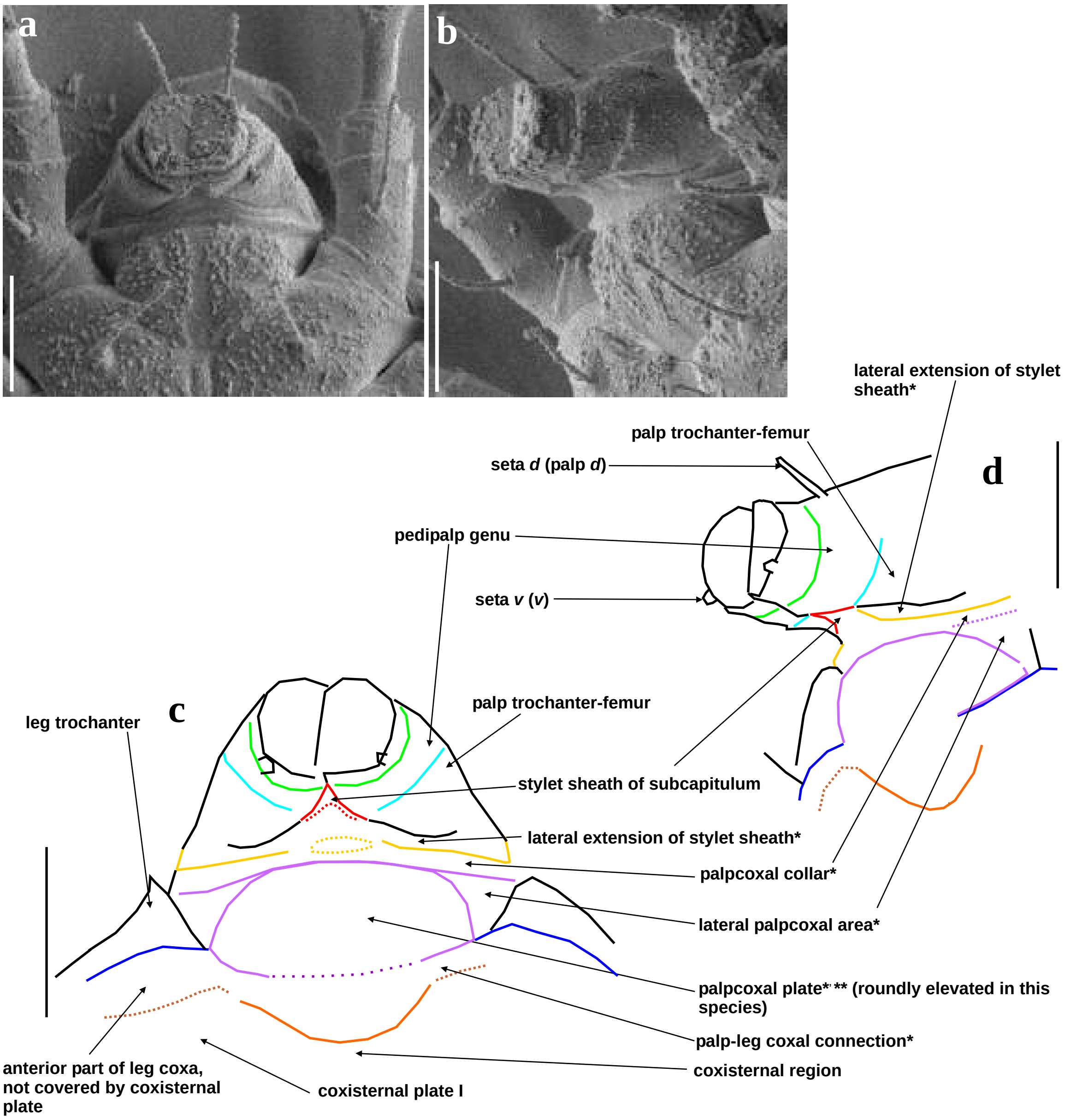


Fig. 3.19. Eriophyoid gnathosoma: **a)** dorsal view; **b)** line drawing of gnathosoma in image 3.19a; **c)** ventral view; **d)** line drawing of the gnathosoma in image 3.19c. Scale lines = 1 µm.



<u>Key to colours in Figs 3.20 and 3.21</u>

- 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.

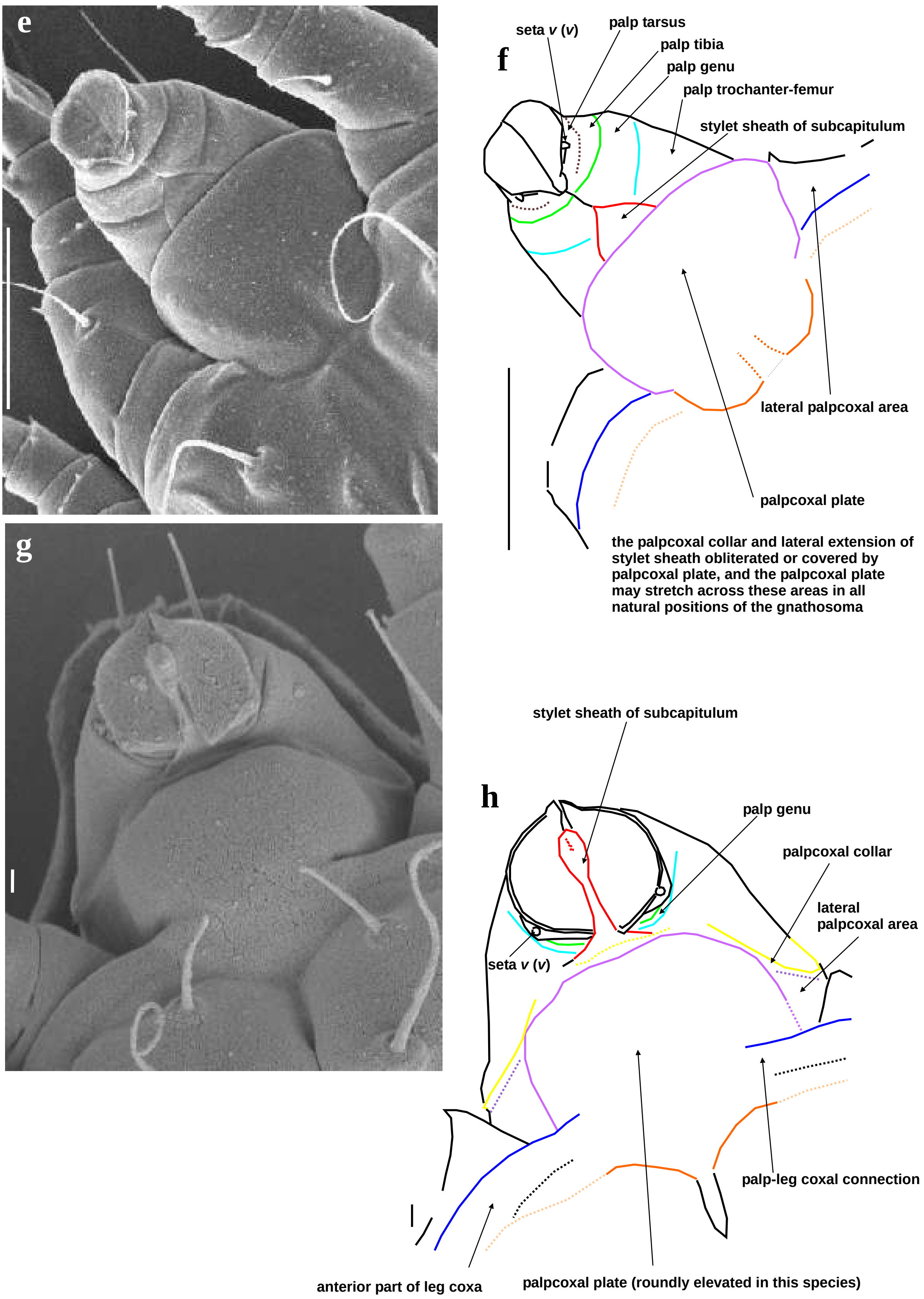
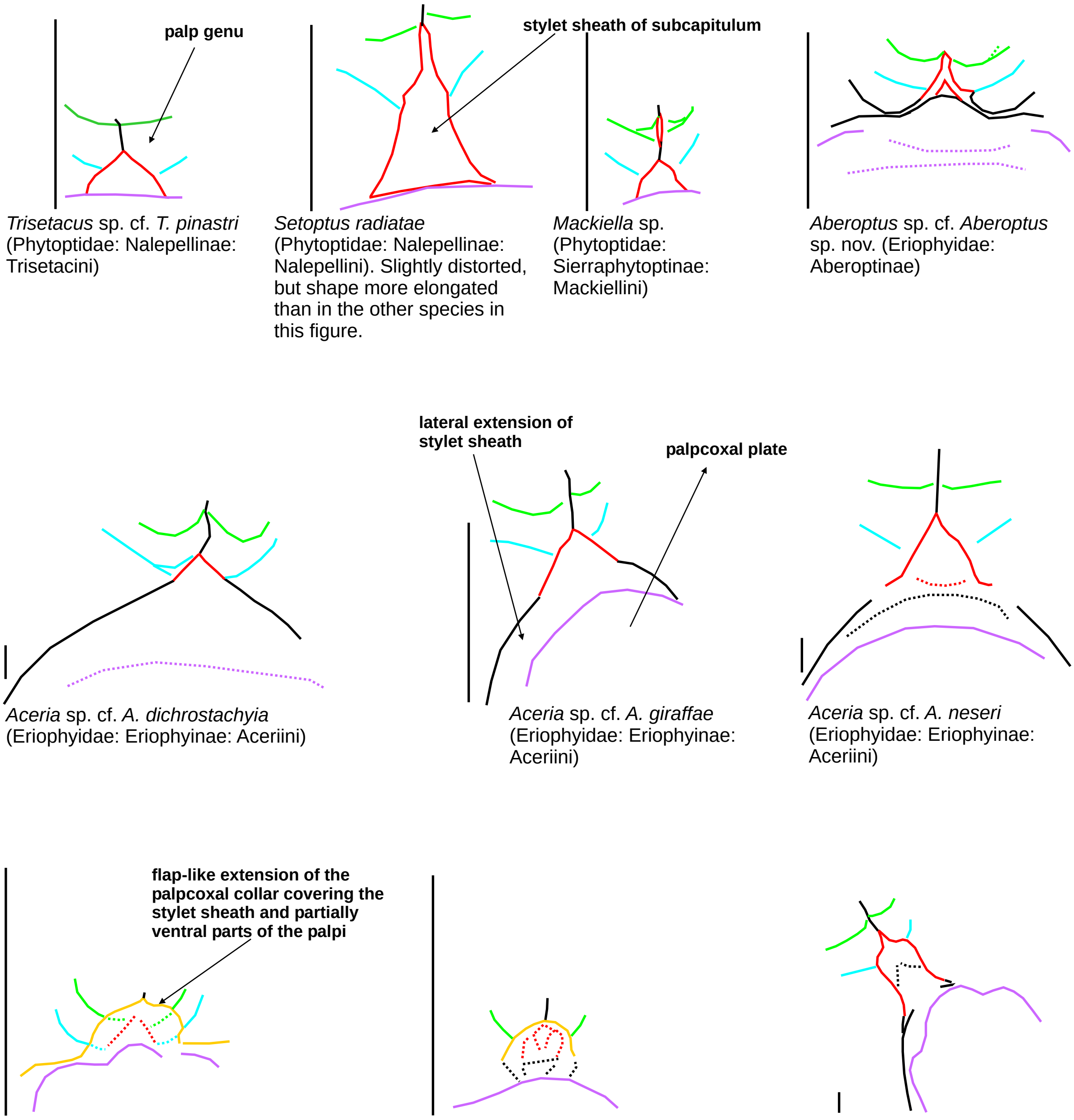


Fig. 3.20. (continued from previous page). Eriophyoid gnathosomas in ventral view. *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from *Pinus* sp.: **e)** SEM image; **f)** line drawing of Fig. 3.20e. *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: 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.

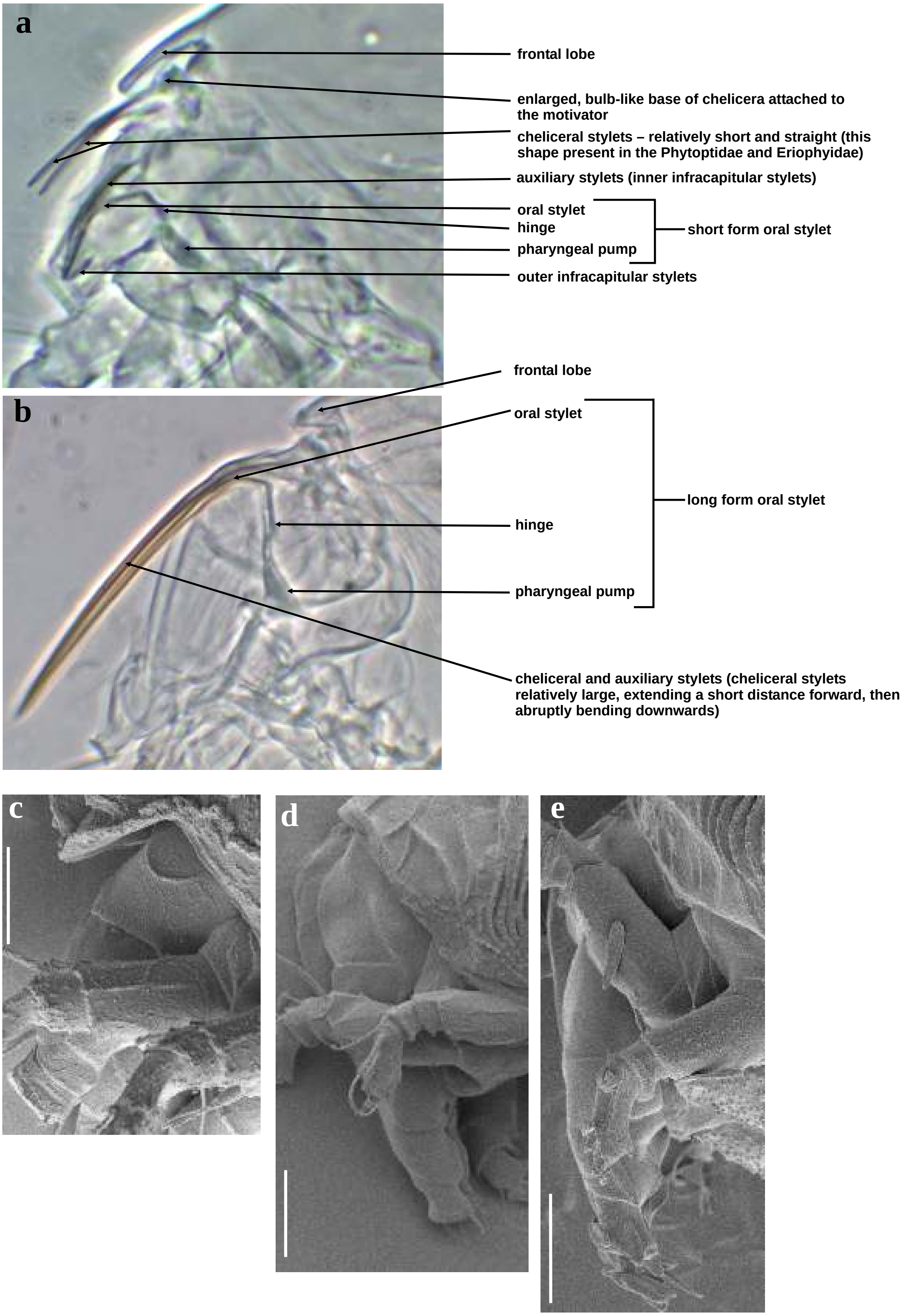


Fig. 3.22. Eriophyoid gnathosoma. The gnathosoma of all the Eriophyoidea except the Diptilomiopidae has relatively short and straight chelicerae, and the short form oral stylet: **a)** digital image of slide-mounted specimen viewed with light microscope; **c)** SEM image of lateral view. "Diptilomiopid"-like 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.

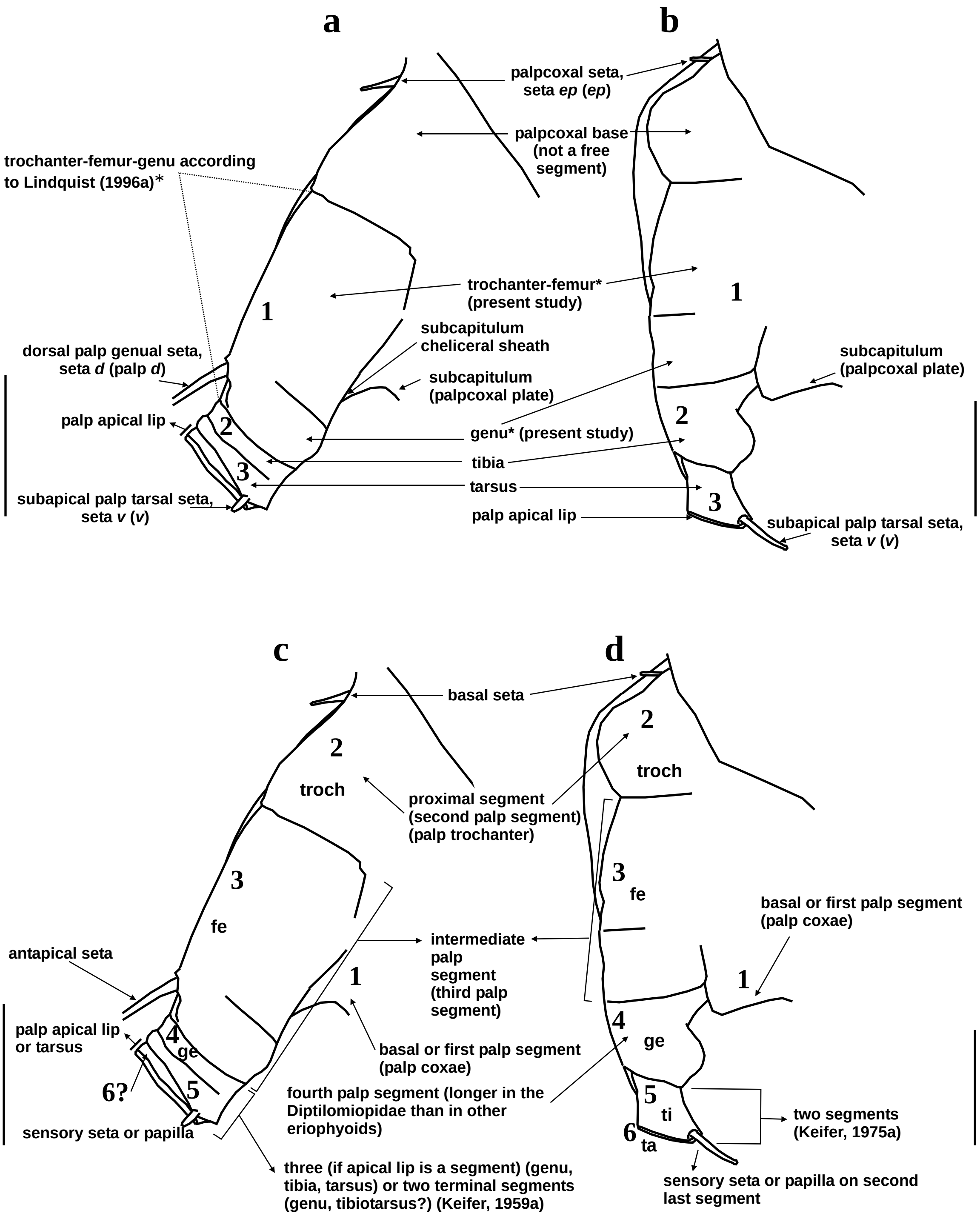


Fig. 3.23. Different hypotheses regarding the homology of the pedipalpal segments of the Eriophyoidea with other Acariform pedipalpi: **a, b)** segments according to Lindquist (1996a) (according to him palpi with three free segments), and present study, *according to Lindquist (1996a) the first free 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 <u>Gnathosomal characters currently used in phylogenetic treatises</u>

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

		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)**
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	9 (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	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	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)**
3.71	*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	(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?	(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	(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	(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?	(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	(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	(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	(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

		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)**
3.46	*Aceria* sp. *cf. Aceria* sp. nov. from *Xymalos monospora*	?	separated	5.5 (lateral)	erect	converging	(lateral)	(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	?	(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?	(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	(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	(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	(lateral)	?	no ridges?	unornamented?
3.55	*Cecidodectes euzonus* from *Trema orientalis*	absent	separated	7 (lateral)	erect	parallel?	(lateral)	2.0	no ridges	unornamented
3.56	*cf. Phyllocoptes* sp. from *Anthocleista grandiflora*	present	separated	?	erect	converging	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?	(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?	(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	(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

		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)**
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	3 (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	5 (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).

- <u>Palpcoxal base ("basal palp segment")</u>

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.

  - <u>Shape of the palpcoxal base segment (dorsally)</u>

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. **<u>Character 2</u>** (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>

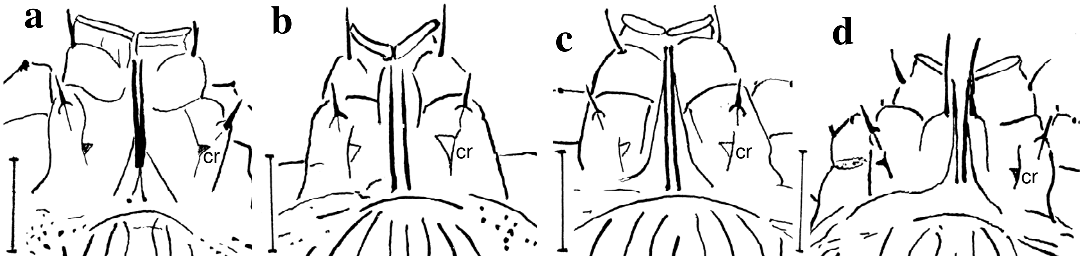
Two structures on the dorsal surface of the palpcoxal base are sometimes included in eriophyoid taxonomy:

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. Character 4 (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.

- <u>Ornamentation of the palpcoxal base segment</u>

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. **<u>Character 8</u>** (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. **<u>Character 9</u>** (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).

- <u>First or proximal articulating palp segment (dorsally)</u>

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. **<u>Character 17</u>** (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. **<u>Character 18</u>** (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).

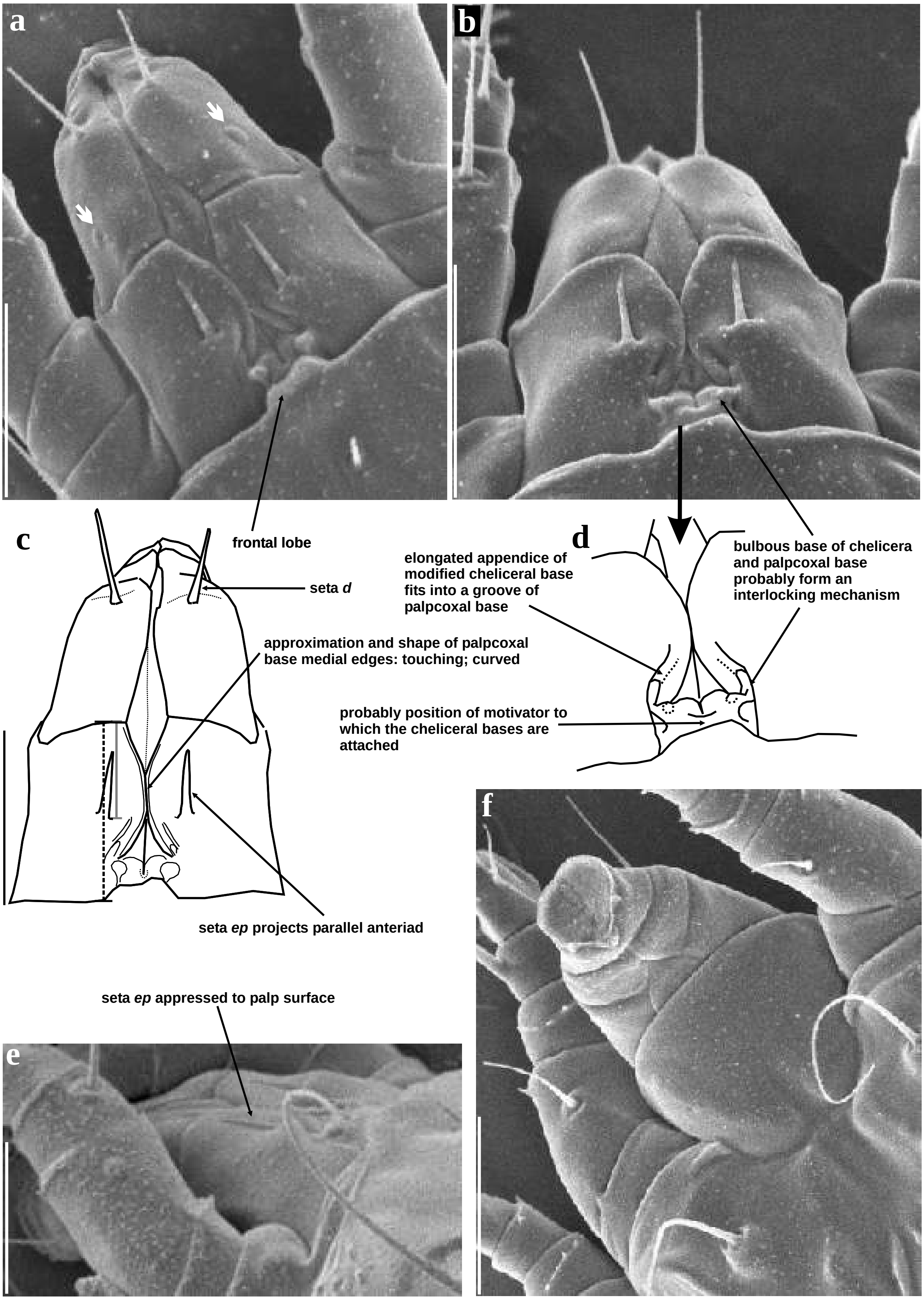
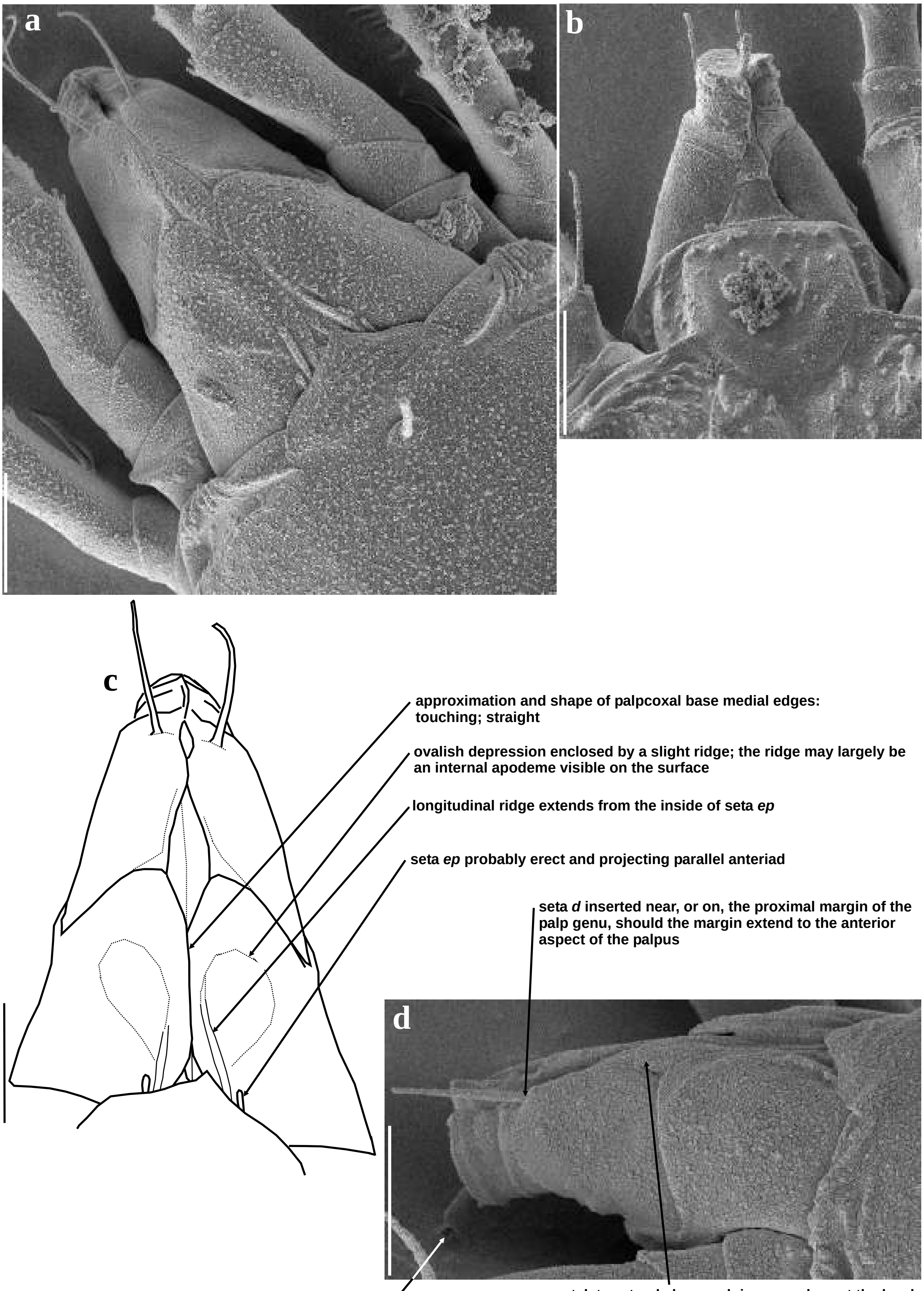


Fig. 3.25. Gnathosoma of *Trisetacus* sp. *cf. T. pinastri* Nuzzaci, 1975 (Phytoptidae: Nalepellinae: Trisetacini) from *Pinus pinaster*: **a, b)** dorsal views (probably adults, genders unknown), white arrows indicate droplet-like structures that are probably not part of the mite, but artefacts; **c)** 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.



approximation and shape of palpcoxal base medial edges: touching; straight

ovalish depression enclosed by a slight ridge; the ridge may largely be an internal apodeme visible on the surface

longitudinal ridge extends from the inside of seta *ep*

seta *ep* probably erect and projecting parallel anteriad

seta *d* inserted near, or on, the proximal margin of the palp genu, should the margin extend to the anterior aspect of the palpus

feeding puncture

stylets extend above palpi more or less at the level of the margin between the palpcoxal base and fused trochanter-femur-genu, similar to the gnathosomas of the Diptilomiopidae in this study, but to a lesser extent

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.

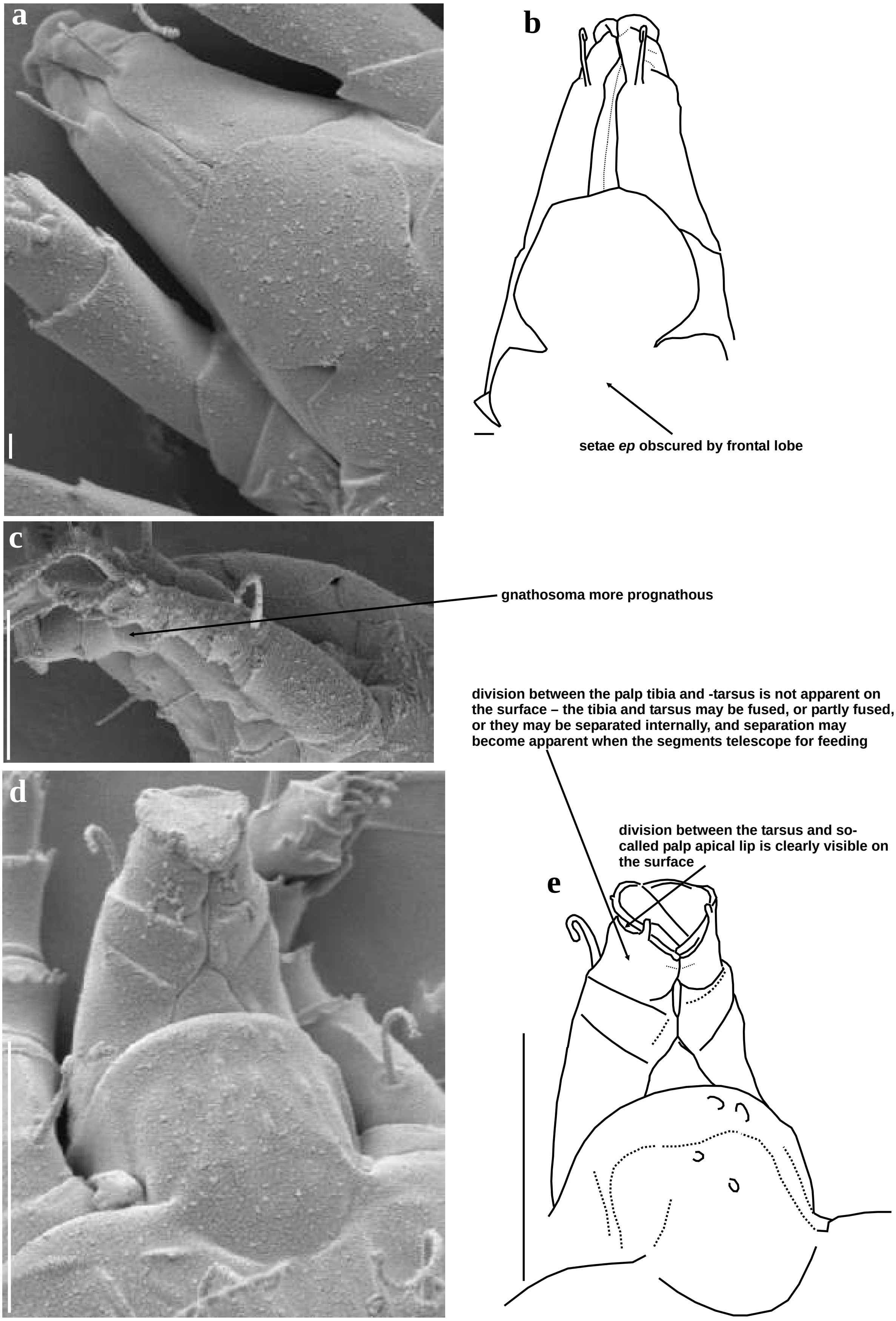


Fig. 3.27. Gnathosoma of *Mackiella* sp. (Phytoptidae: Sierraphytoptinae: Mackiellini) from *Phoenix reclinata*: **a**) dorsal view (probably adult, gender unknown); **b**) line drawing of Fig. 3.27a; **c**) lateral view (male); **d**) ventral view (male); **e**) line drawing of Fig. 3.27d; **a, b)**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

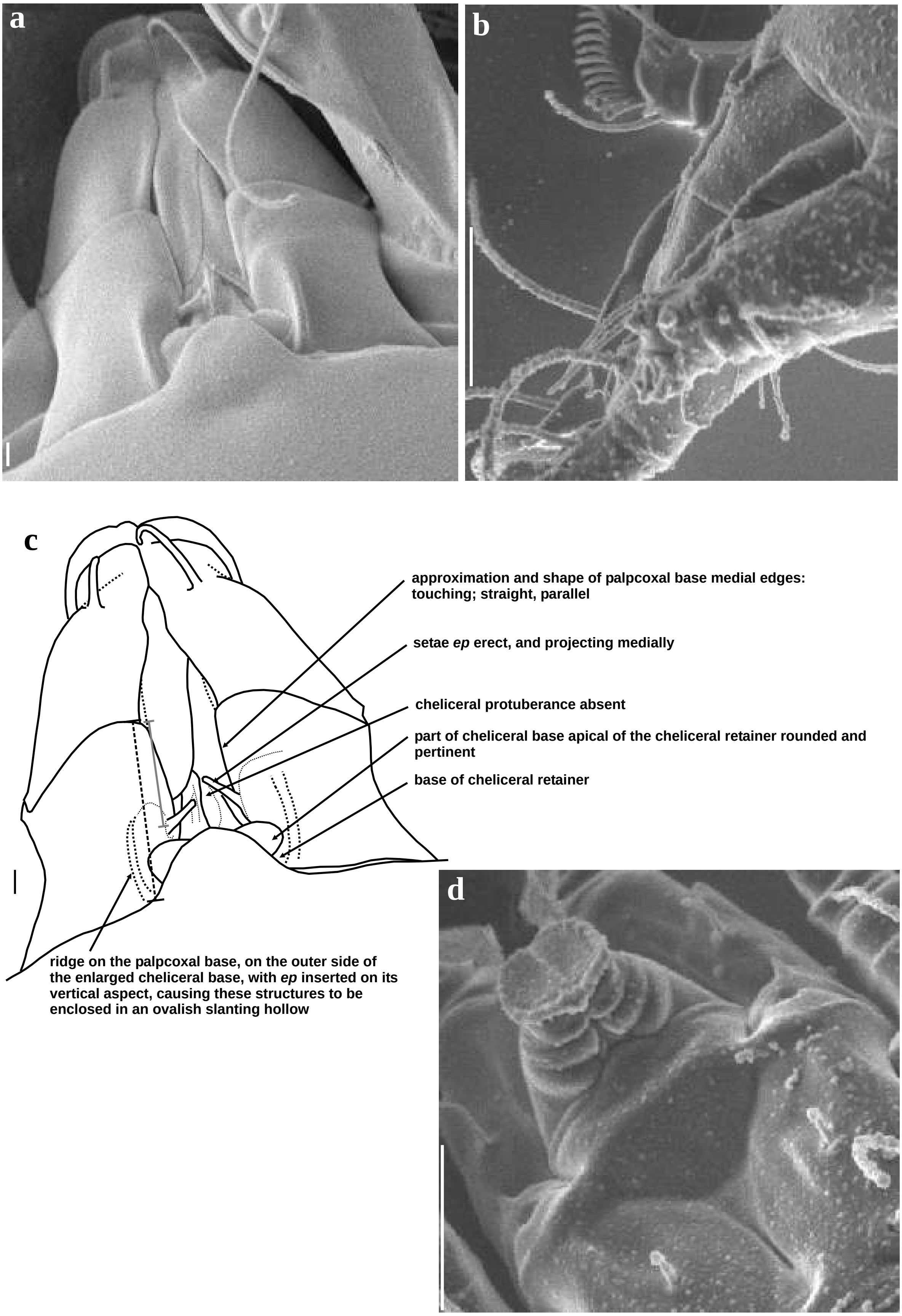


Fig. 3.28. Gnathosoma of *Aberoptus* sp. *cf. Aberoptus* sp. nov. (Eriophyidae: Aberoptinae) from *Schotia brachypetala*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female); **c)** line drawing of Fig. 3.28a, dashed black line indicates length of palpcoxal base, grey line 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.

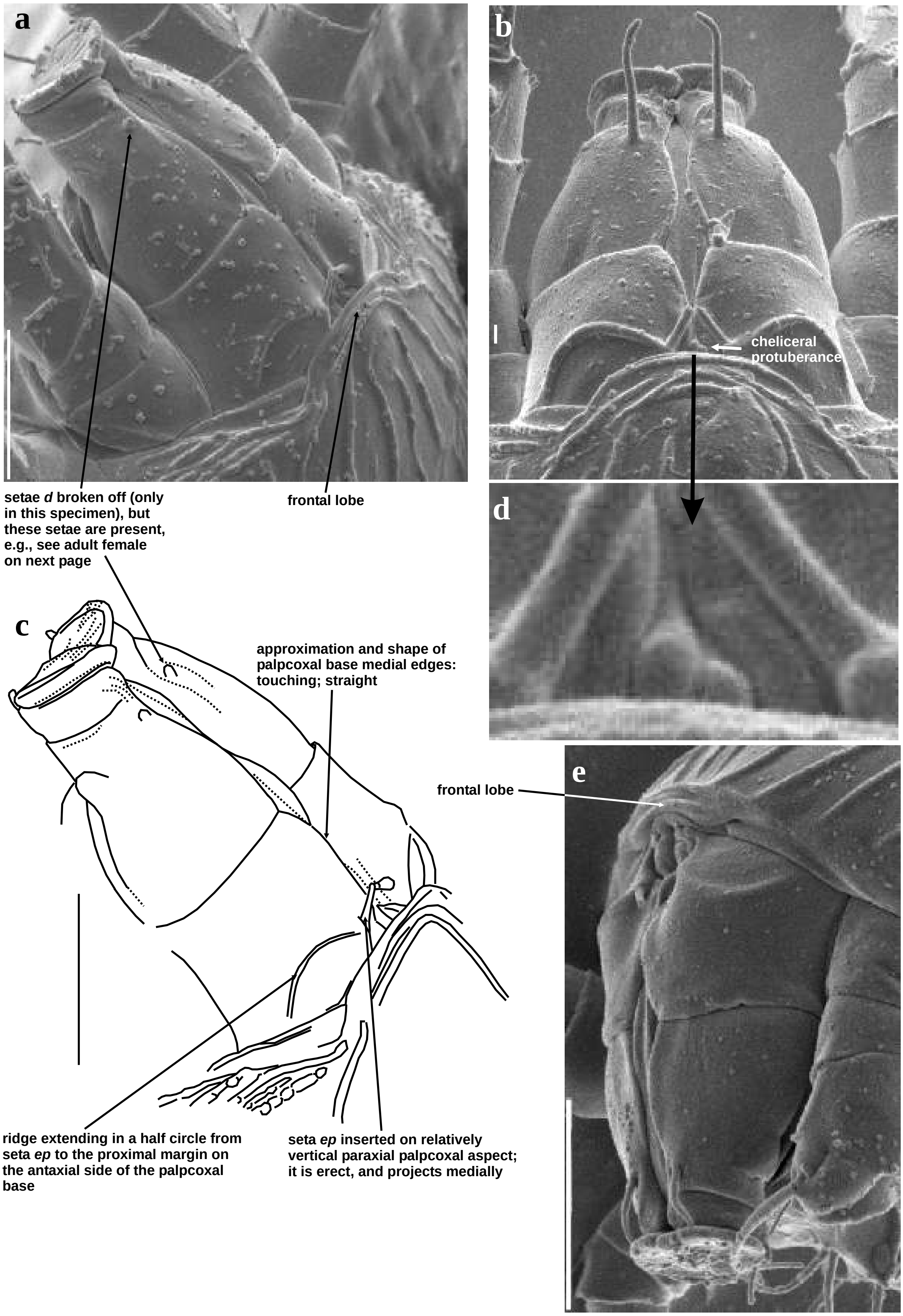


Fig. 3.29. (continued on next page). Gnathosoma of *Cecidophyopsis* sp. *cf. C. hendersoni* (Keifer, 1954) (Eriophyidae: Cecidophyinae: Cecidophyini) from *Yucca guatemalensis*: **a)** dorso-lateral view (female); **b)** dorsal view (possibly immature based on gnathosoma morphology); **c)** line drawing 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.

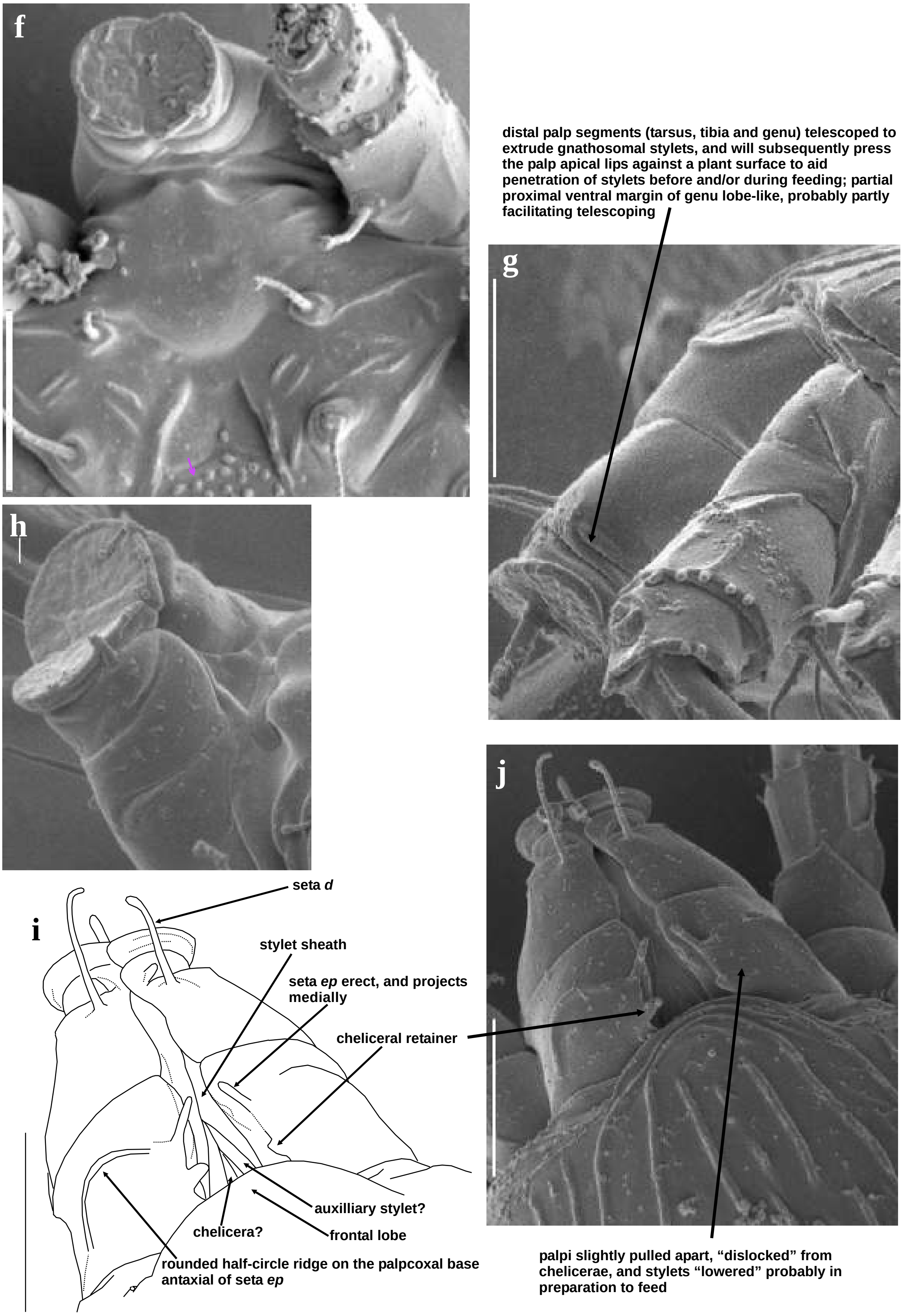


Fig. 3.29. (continued from previous page). Gnathosoma of *Cecidophyopsis* sp. *cf. C. hendersoni*: **f)** ventral view (female); **g)** lateral view, gnathosoma with apical palp segments telescoping for feeding (female); **h)** lateral view (female); i) line drawing of Fig. 3.29j; **j)** ventro-lateral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

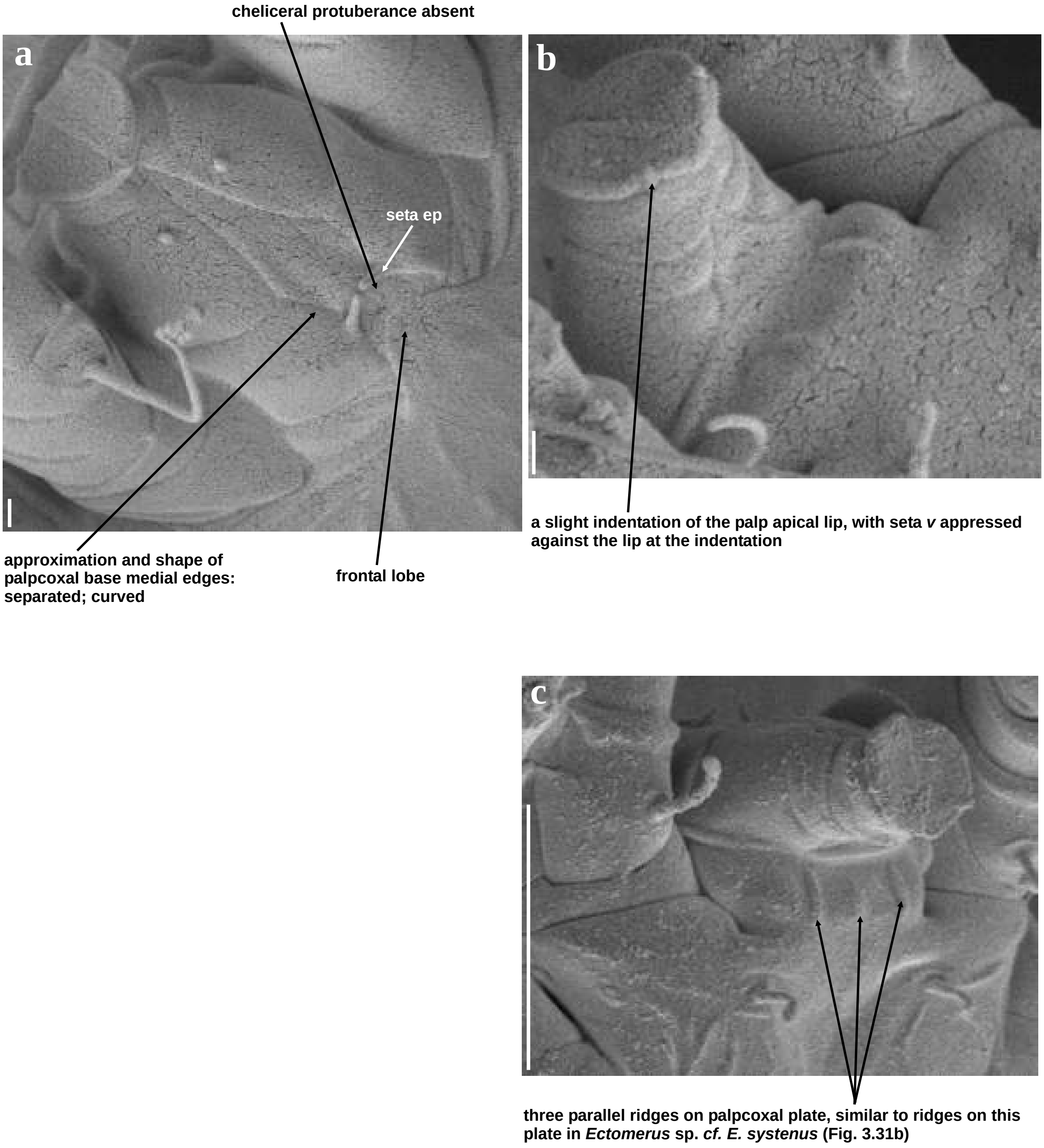
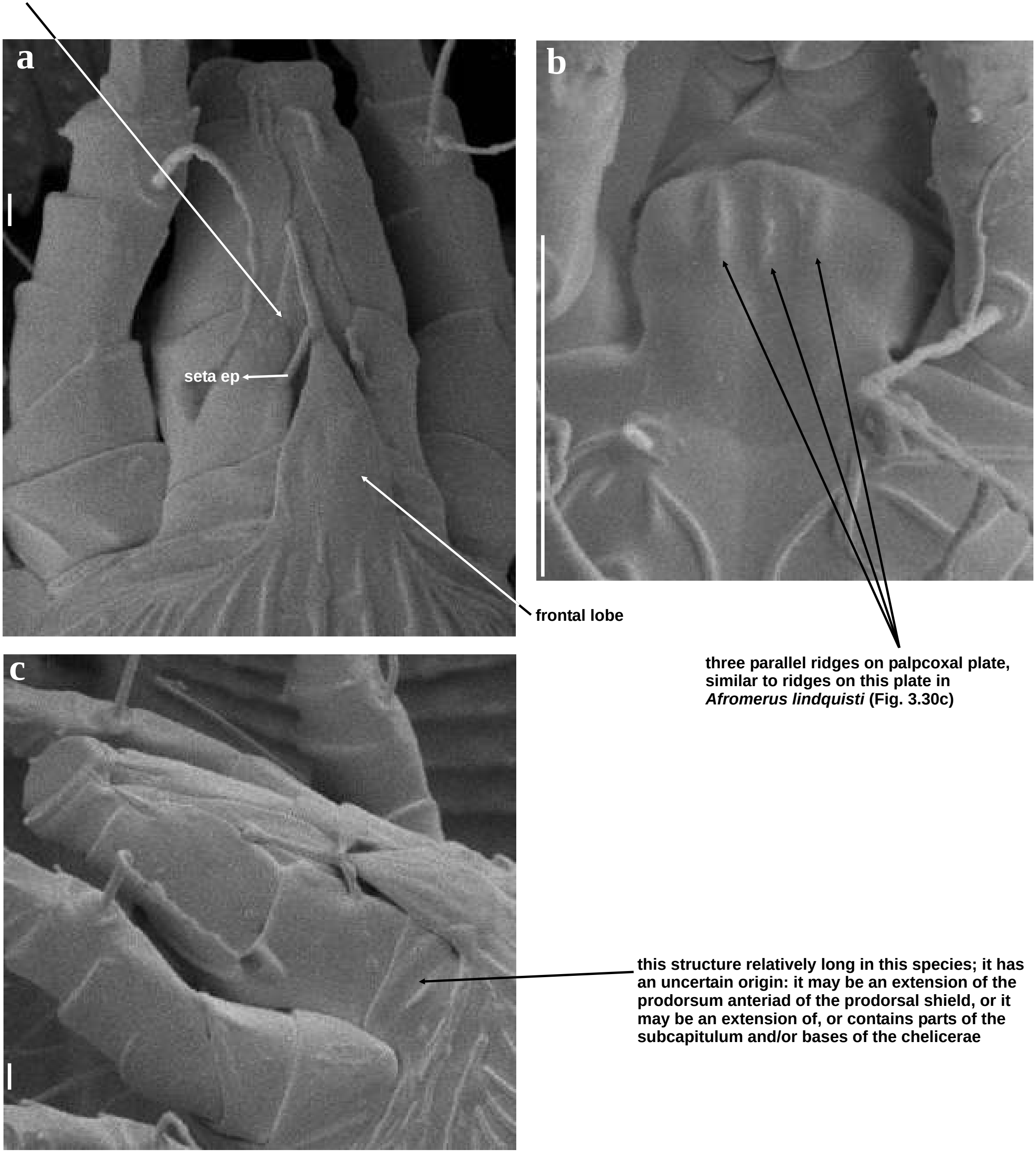


Fig. 3.30. Gnathosoma of *Afromerus lindquisti* Meyer, 1990 (Eriophyidae: Cecidophyinae: Colomerini) from *Psydrax livida*: **a)** dorsal view (female); **b, c)** ventro-lateral views (males); **a, b)** scale lines = 1 µm; **c)** scale line = 10 µm.



approximation and shape of palpcoxal base medial edges: separated; slightly curved

frontal lobe

three parallel ridges on palpcoxal plate, similar to ridges on this plate in *Afromerus lindquisti* (Fig. 3.30c)

this structure relatively long in this species; it has an uncertain origin: it may be an extension of the prodorsum anteriad of the prodorsal shield, or it may be an extension of, or contains parts of the subcapitulum and/or bases of the chelicerae

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.

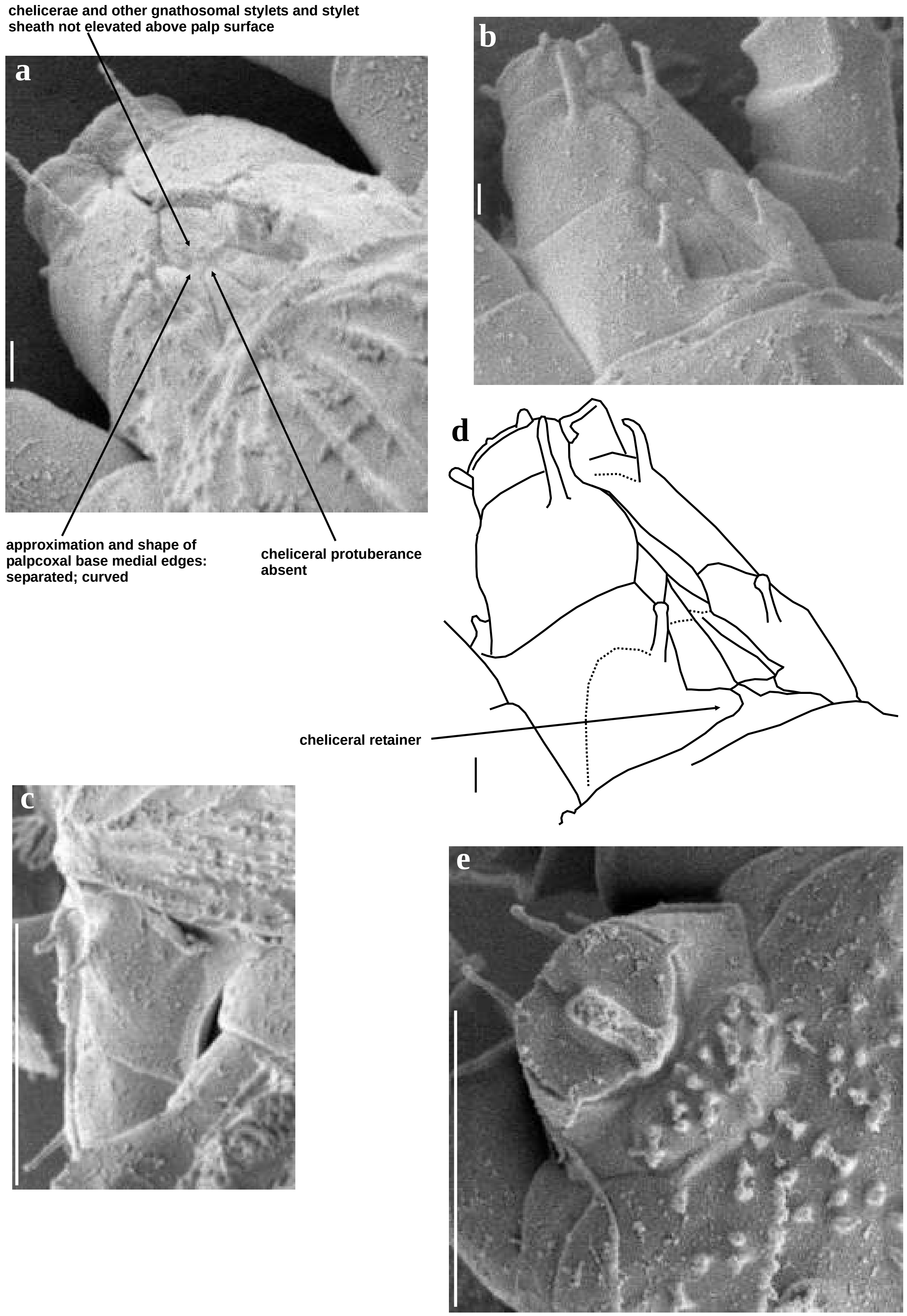


Fig. 3.32. Gnathosoma of *Neserella* sp. *cf. N. tremae* Meyer & Ueckermann, 1989 (Eriophyidae: Cecidophyinae: Colomerini) from *Trema orientalis*: **a)** dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (immature); **c)** lateral view (probably adult, gender unknown); **d)** line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

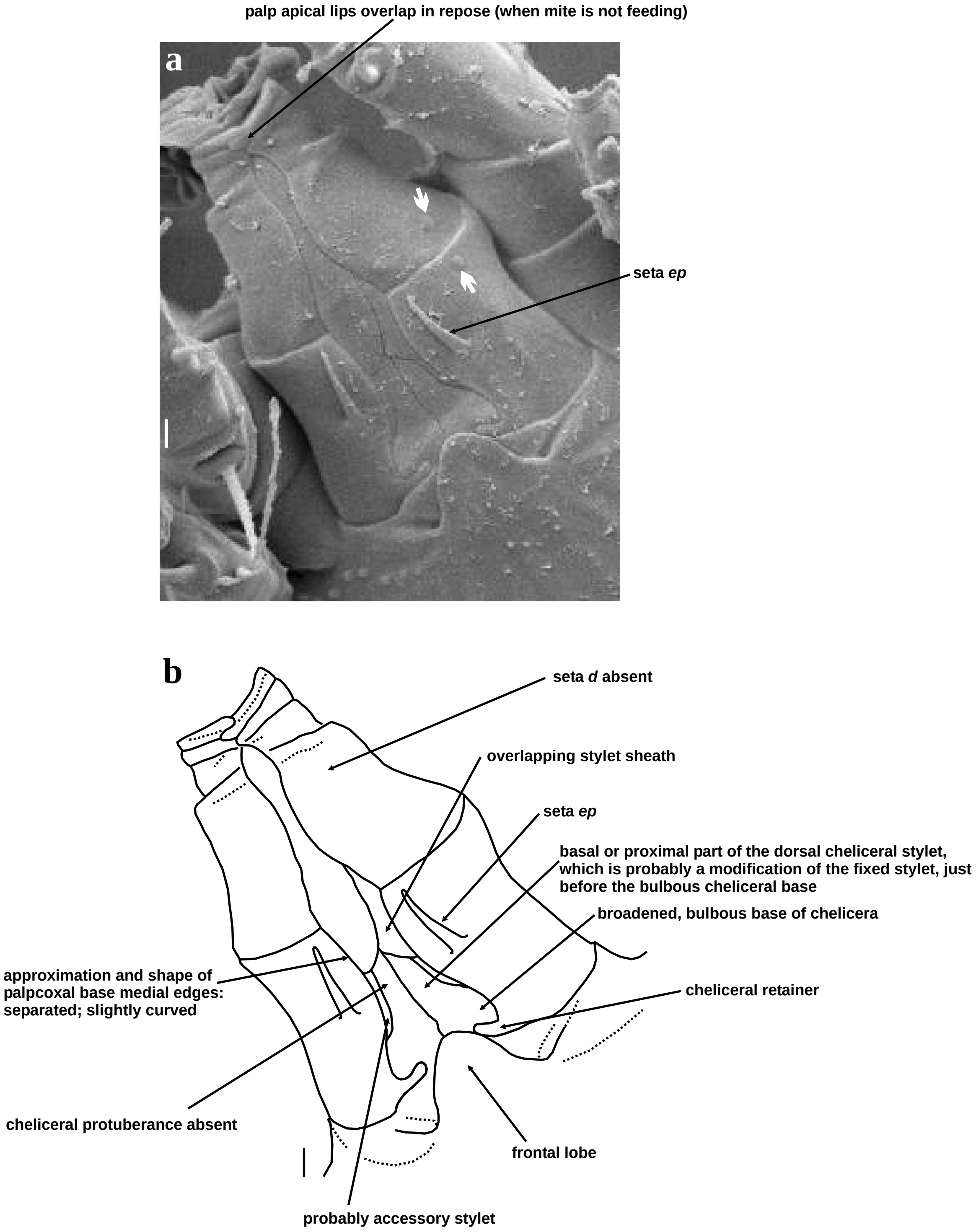


Fig. 3.33. (continued on next page). Gnathosoma of *Acalitus mallyi* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Vangueria infausta* subsp. *infausta* leaf galls: **a)** dorsal view (probably adult, gender unknown), white arrows indicate droplet-like structures that are probably not part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

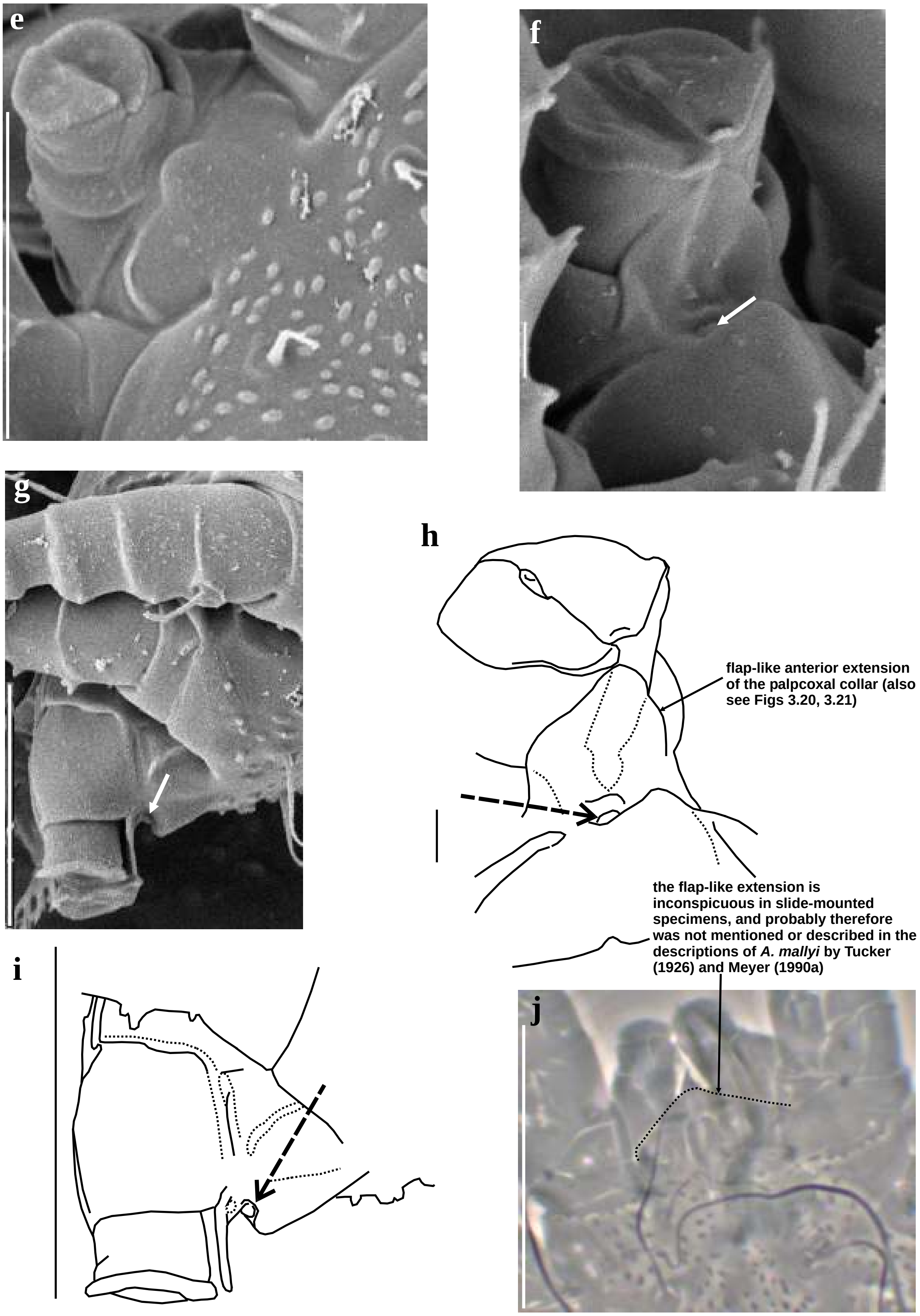


Fig. 3.33. (continued from previous page). Gnathosoma of *Acalitus mallyi*: **e)** ventral view (female); **f)** ventro-lateral view (female); **g)** lateral view (female); **h)** line drawing of Fig. 3.33f; **i)** line drawing of Fig. 3.33g; **j)** digital image captured of slide-mounted female specimen, 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.

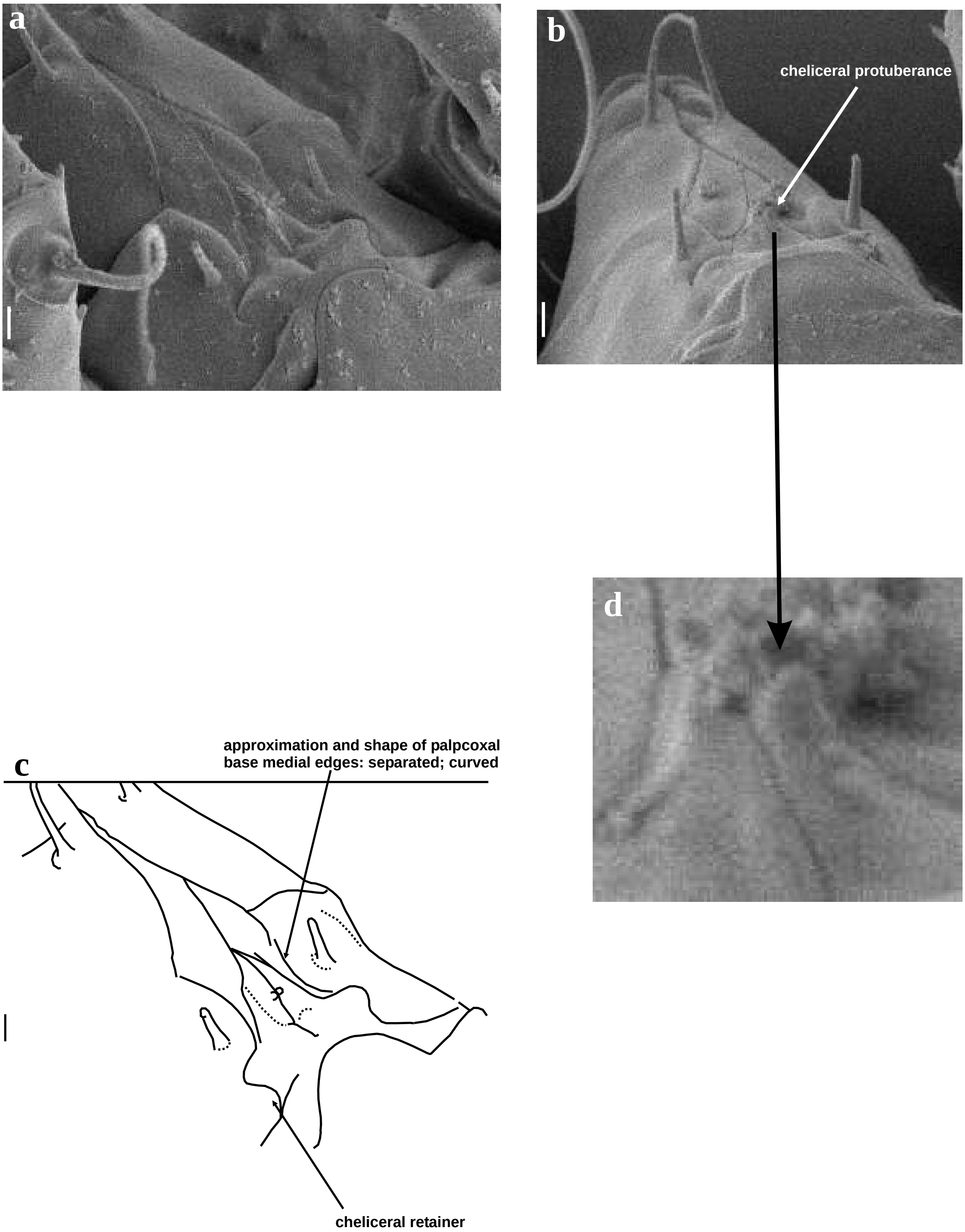


Fig. 3.34 (continued on next page). Gnathosoma of *Aceria lantanae* (Cook, 1909) (Eriophyidae: Eriophyinae: Aceriini) from *Lantana* x *camara* (hybrid complex) flower galls: **a, b)** dorsal views (probably adults, gender unknown); **c)** line drawing of Fig. 3.34a; **d)** enlargement of cheliceral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

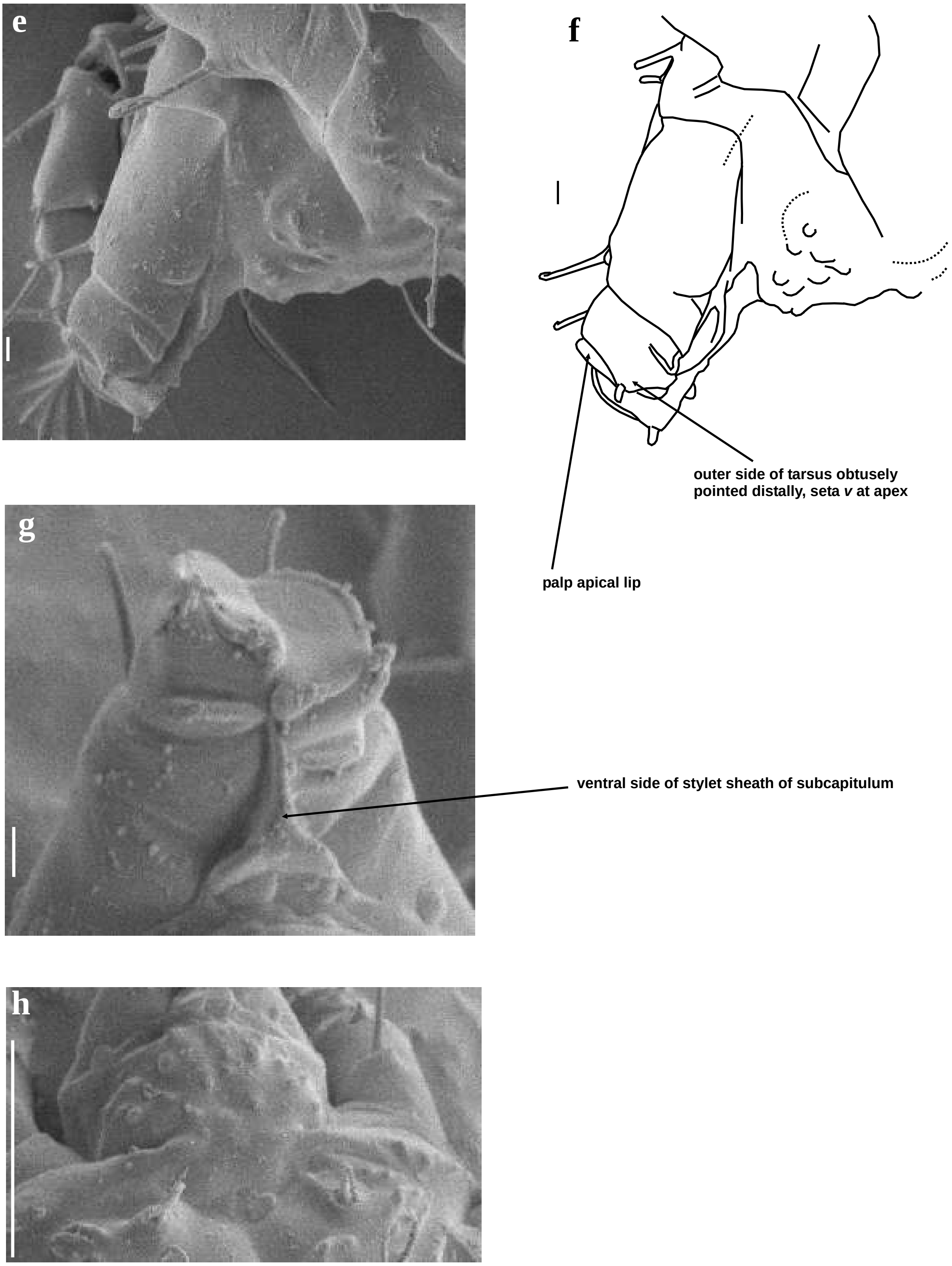
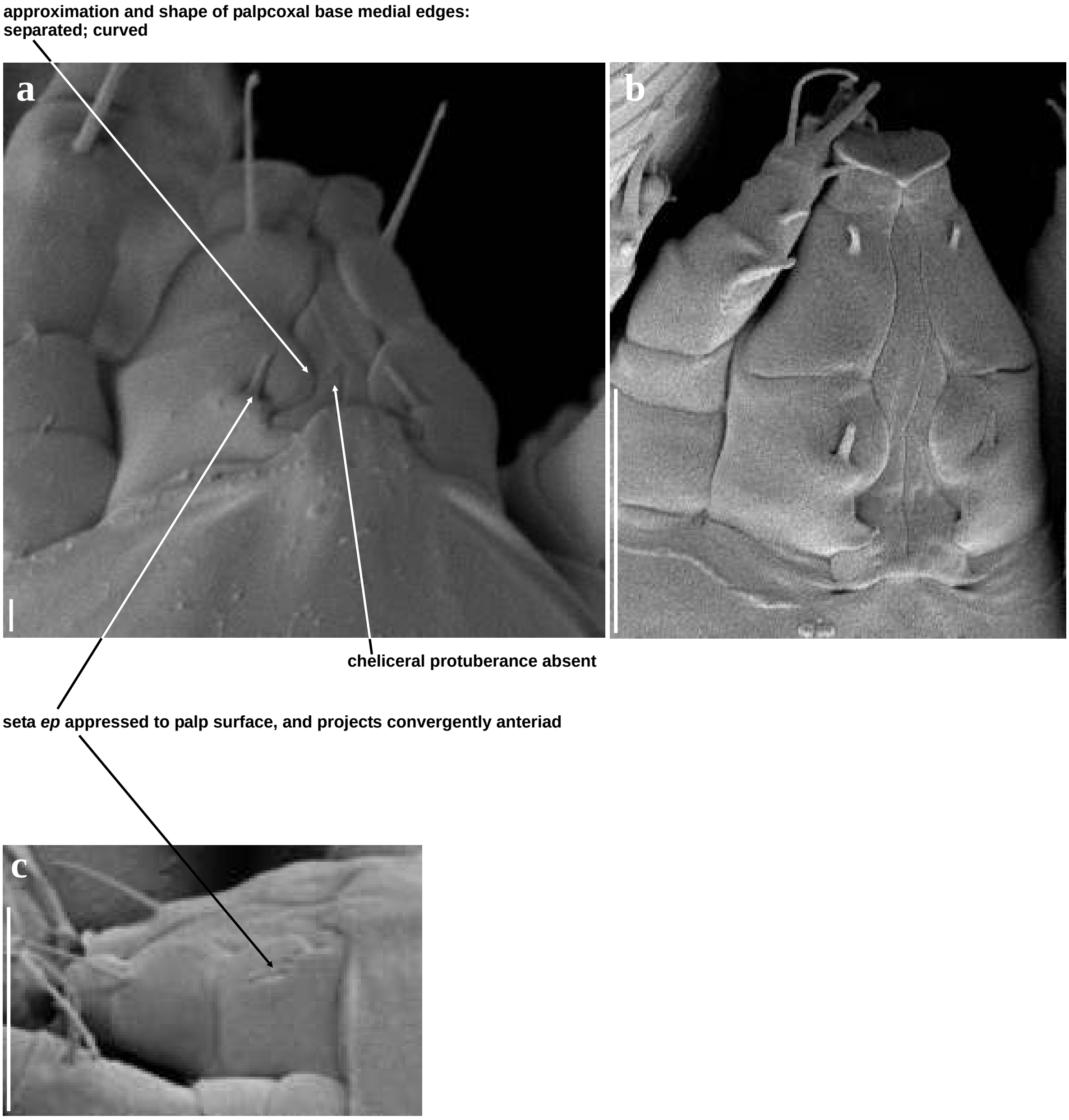


Fig. 3.34. (continued from previous page). Gnathosoma of *Aceria lantanae*: **e)** lateral view (female); **f)** line drawing of Fig. 3.34e; **g, h)** ventral views of the same specimen (female); **e, f, g)** scale lines = 1 µm; **h)** scale line = 10 µm.



approximation and shape of palpcoxal base medial edges: separated; curved

cheliceral protuberance absent

seta *ep* appressed to palp surface, and projects convergently anteriad

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.

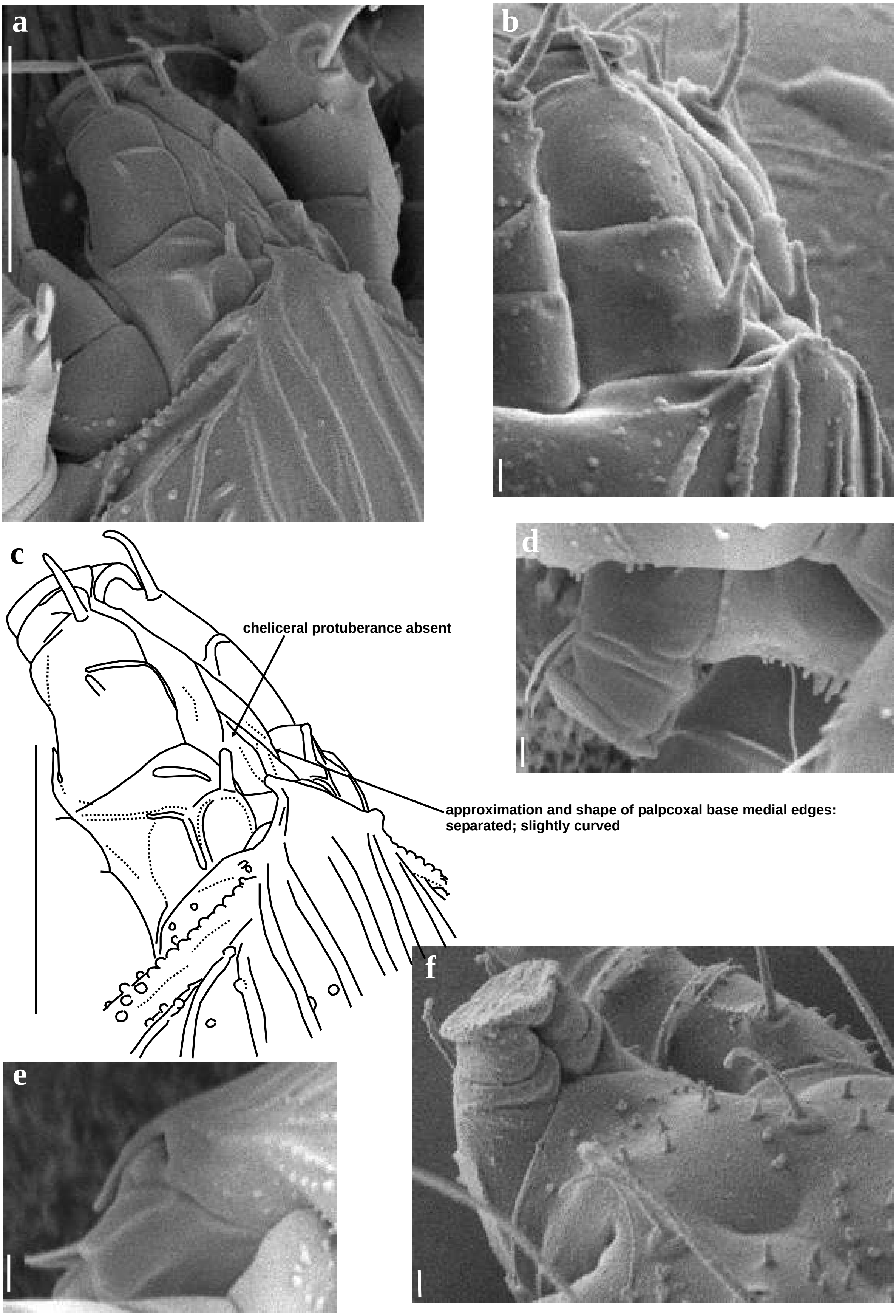


Fig. 3.36. Gnathosoma of *Aceria* sp. *cf. A. dichrostachyia* (Tucker, 1926) (Eriophyidae: Eriophyinae: Aceriini) from *Dichrostachys cinerea* subsp. and var. unknown: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorso-lateral view (larva); **c)** line drawing of Fig. 3.36a; **d, 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.

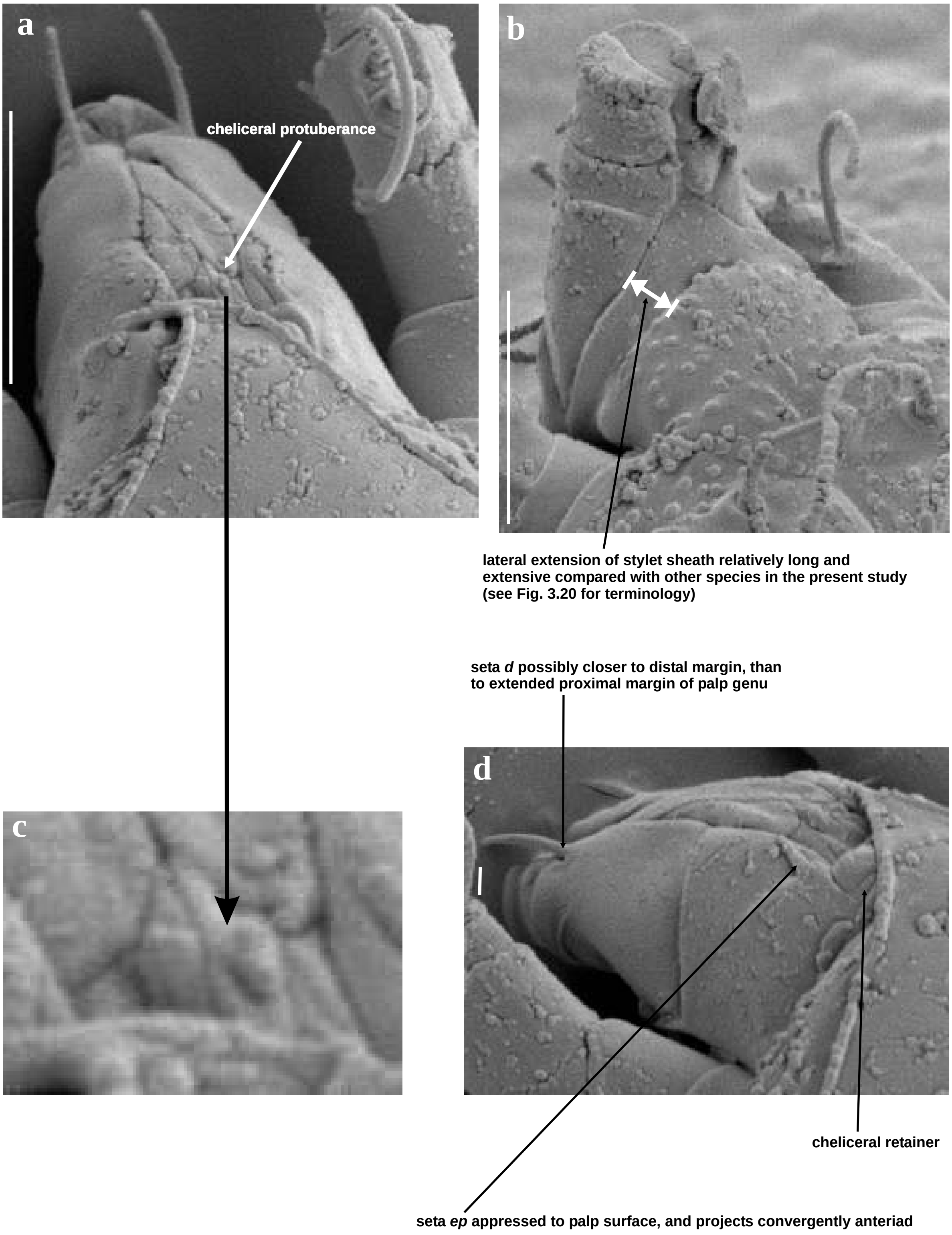


Fig. 3.37. Gnathosoma of *Aceria* sp. *cf. A. giraffae* Meyer, 1990 (Eriophyidae: Eriophyinae: Aceriini) from *Acacia erioloba*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** enlargement of cheliceral protuberances in Fig. 3.37a; **d)** dorso-lateral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

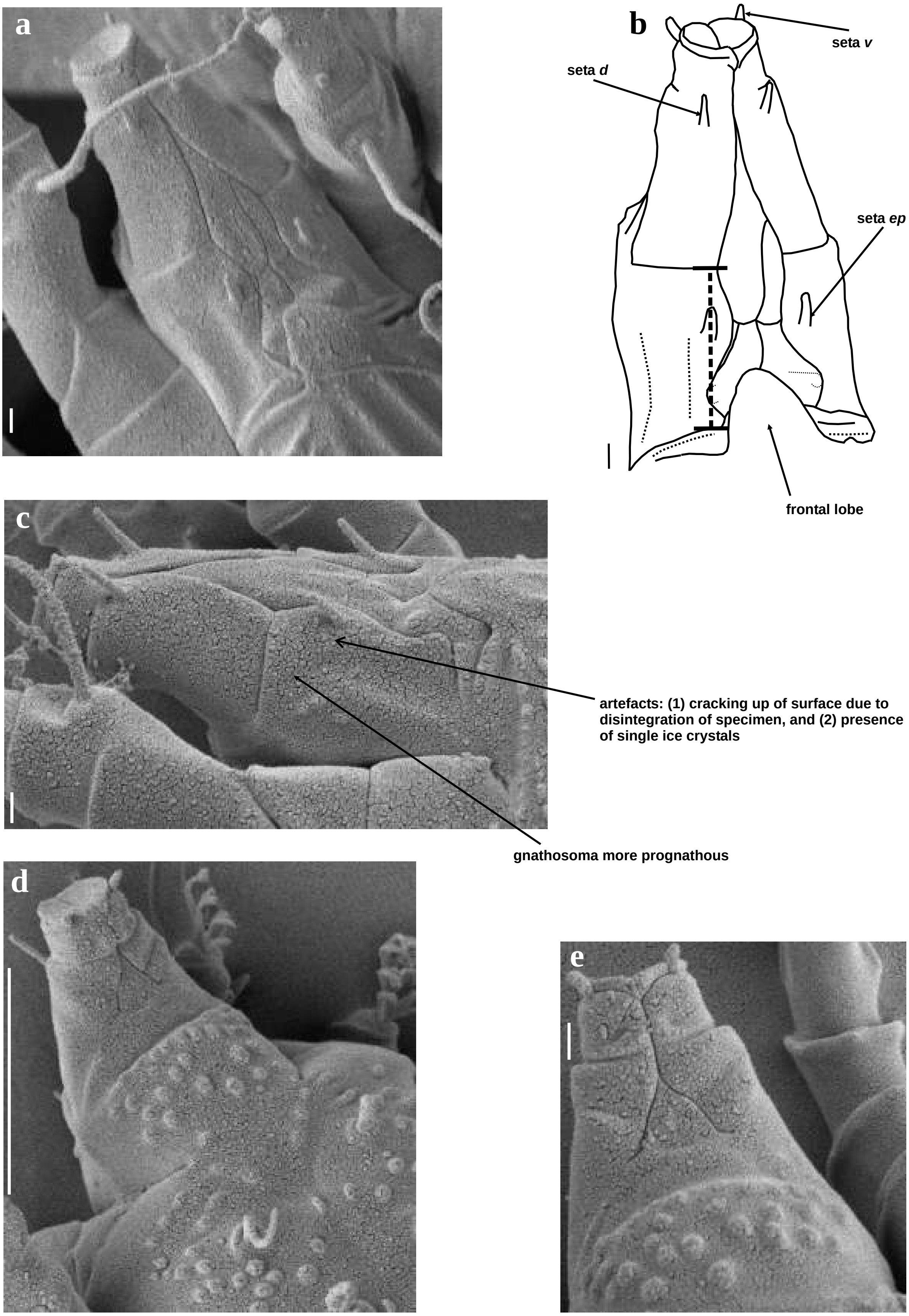
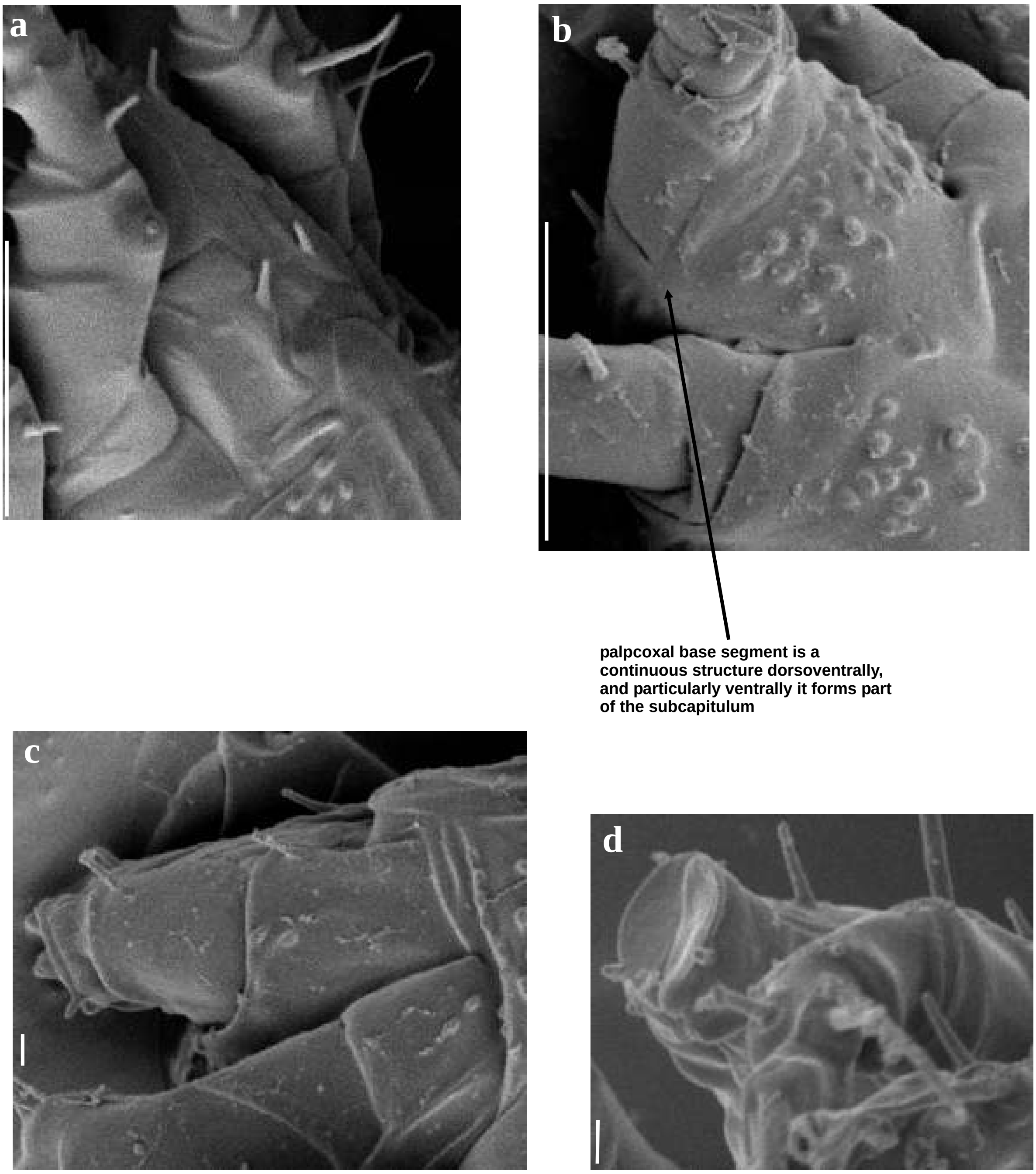


Fig. 3.38. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Chrysanthemoides incana*: **a)** dorsal view (probably adult, gender unknown); **b)** line drawing of Fig. 3.38a, dashed black line indicates length of palpcoxal base; **c)** lateral view (female);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



palpcoxal base segment is a continuous structure dorsoventrally, and particularly ventrally it forms part of the subcapitulum

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.

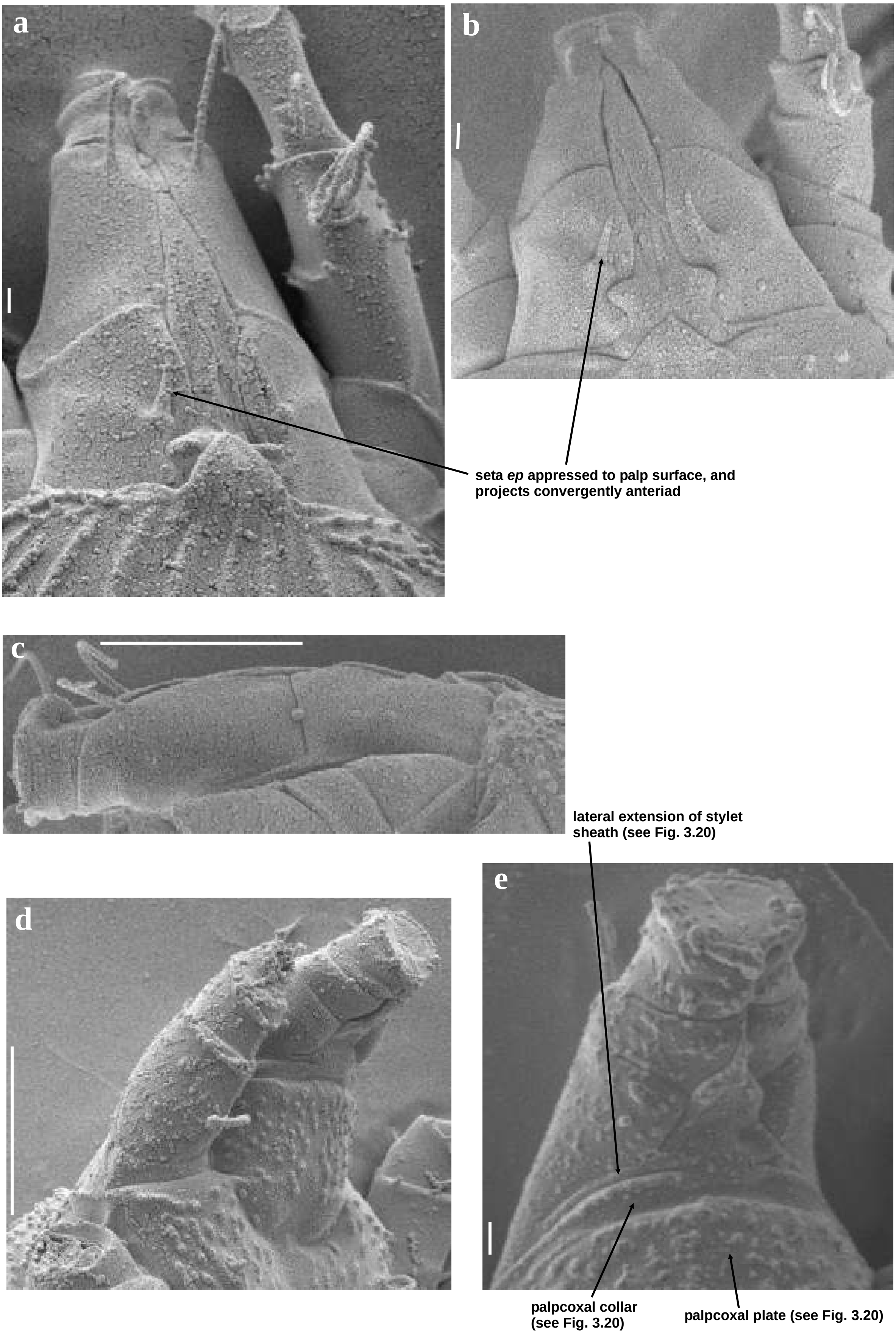


Fig. 3.40. Gnathosoma of *Aceria* sp. *cf. A. proteae* Meyer, 1981 (Eriophyidae: Eriophyinae: Aceriini) from *Protea caffra* subsp. *caffra*: **a)** dorsal view (probably adult, gender unknown); **b)** dorsal view (larva); **c)** lateral view (female); **d, e)** ventro-lateral views (females); **a, b,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

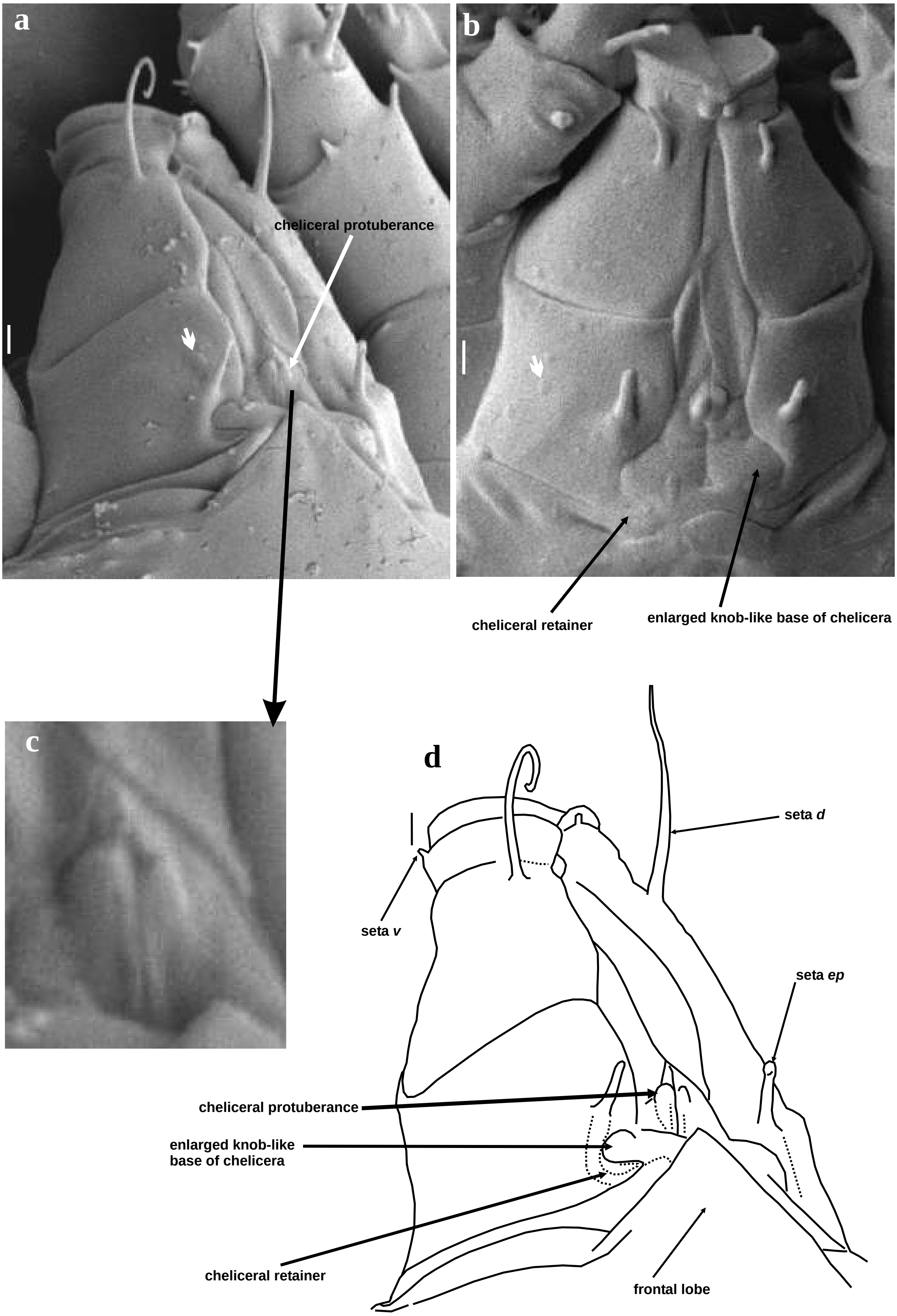


Fig. 3.41. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Ipomoea batatas* var. *batatas*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably larva); **c)** enlargement of cheliceral protuberances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

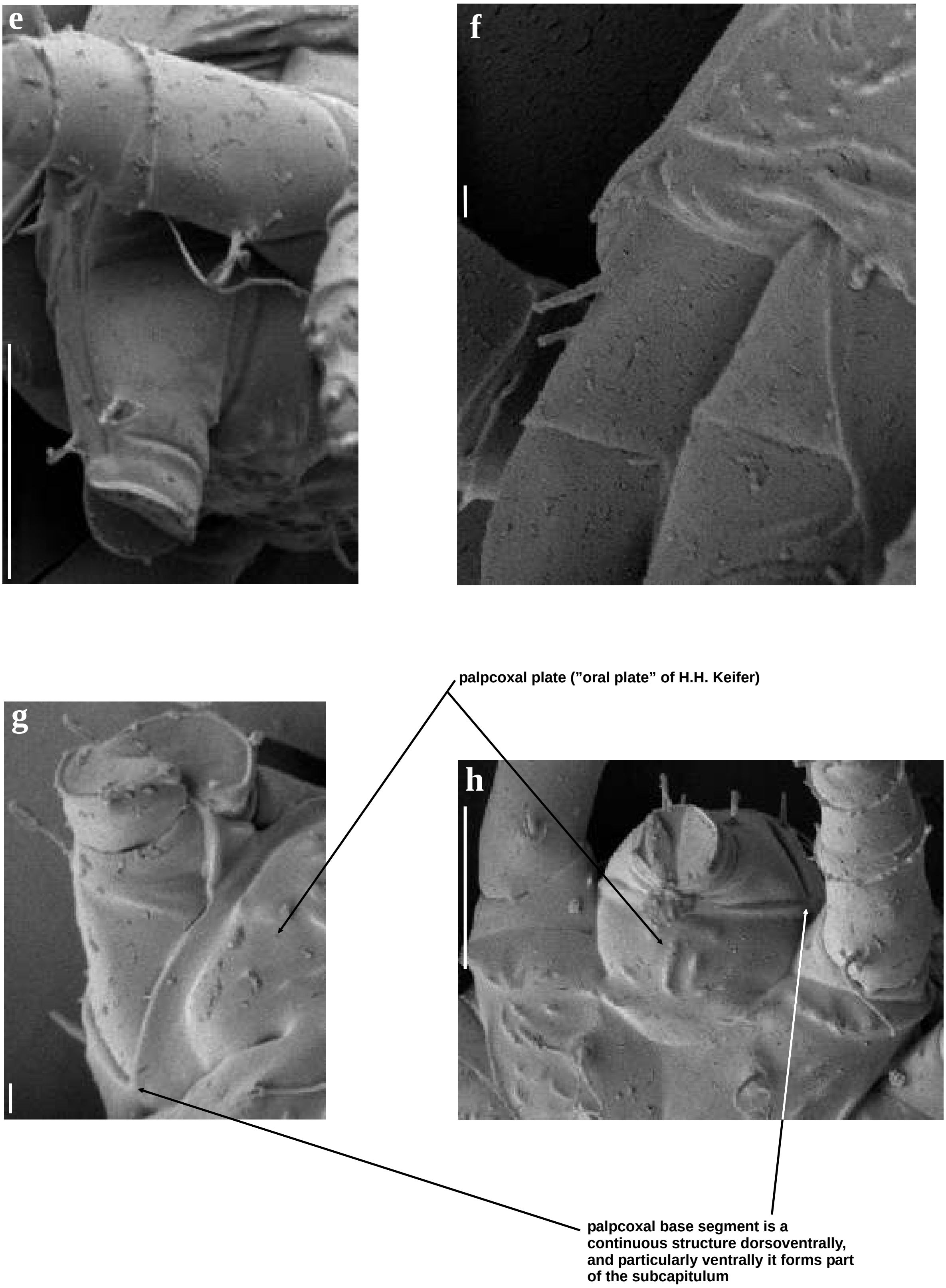


Fig. 3.41. (continued from previous page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **e)** dorso-lateral view (male); **f)** lateral view of basal part of gnathosoma (female); **g)** ventro-lateral view (female); **h)** ventral view (female); **e, h)** scale lines = 10 µm; **f, g)** scale lines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

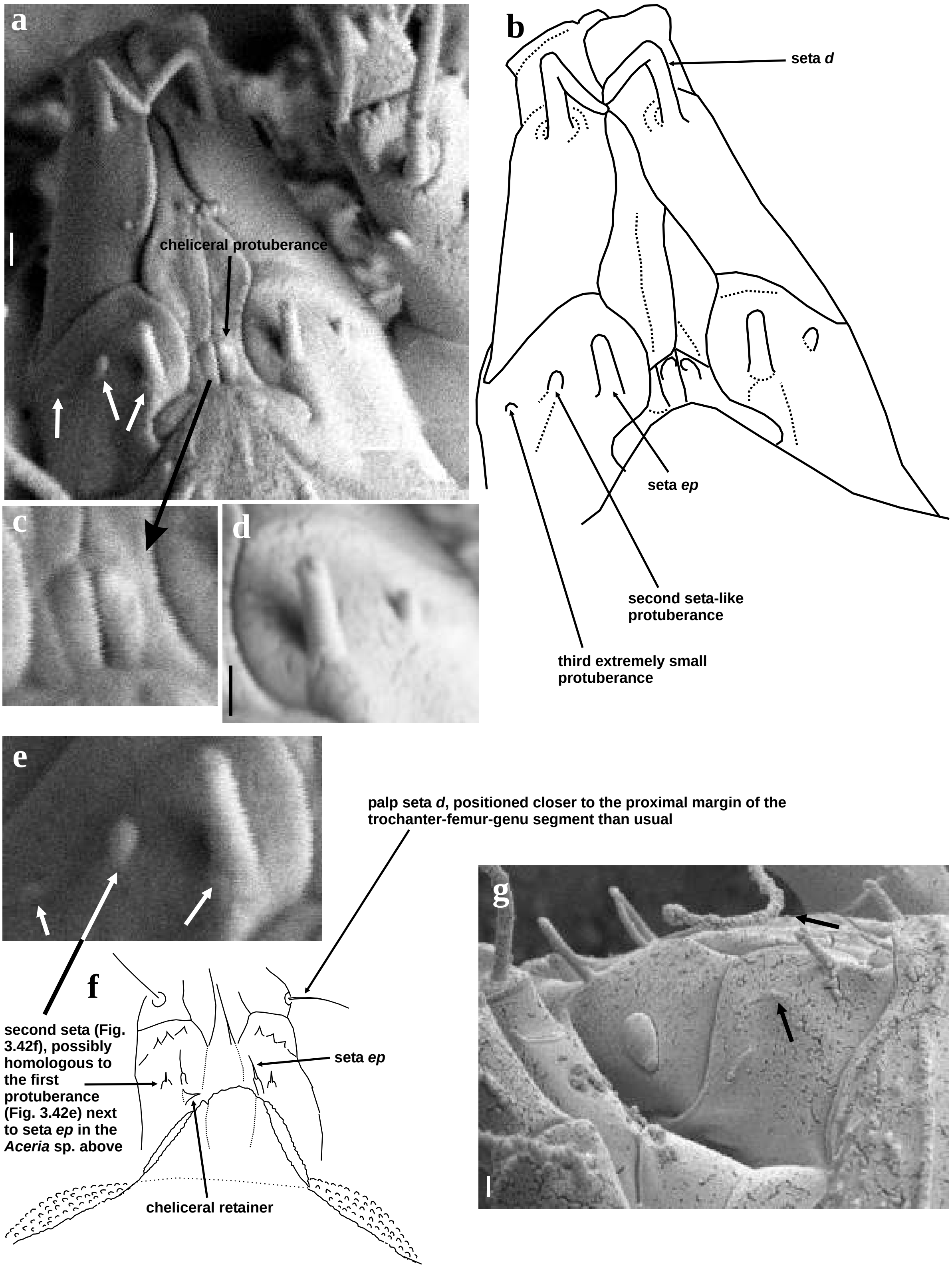


Fig. 3.42. (continued on next page). Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Oxalis corniculata*: **a)** dorsal view (probably adult, gender unknown), white arrows indicate seta *ep* (closest to dorsal exposed parts of the chelicerae), and two protuberances 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.

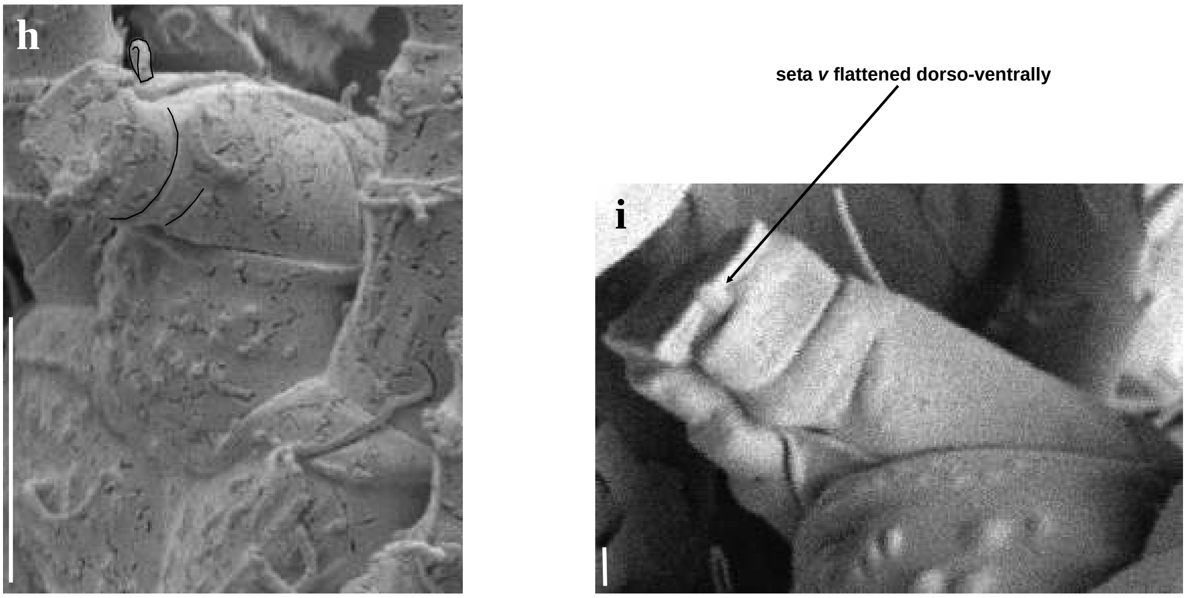


Fig. 3.42. (continued from previous page).Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov.: **h)** ventro-lateral view (male), some detail enhanced with black drawing line to make it more visible; **i)** ventro-lateral view (male); **h)** scale line = 10 µm; **i)** scale line = 1 µm.

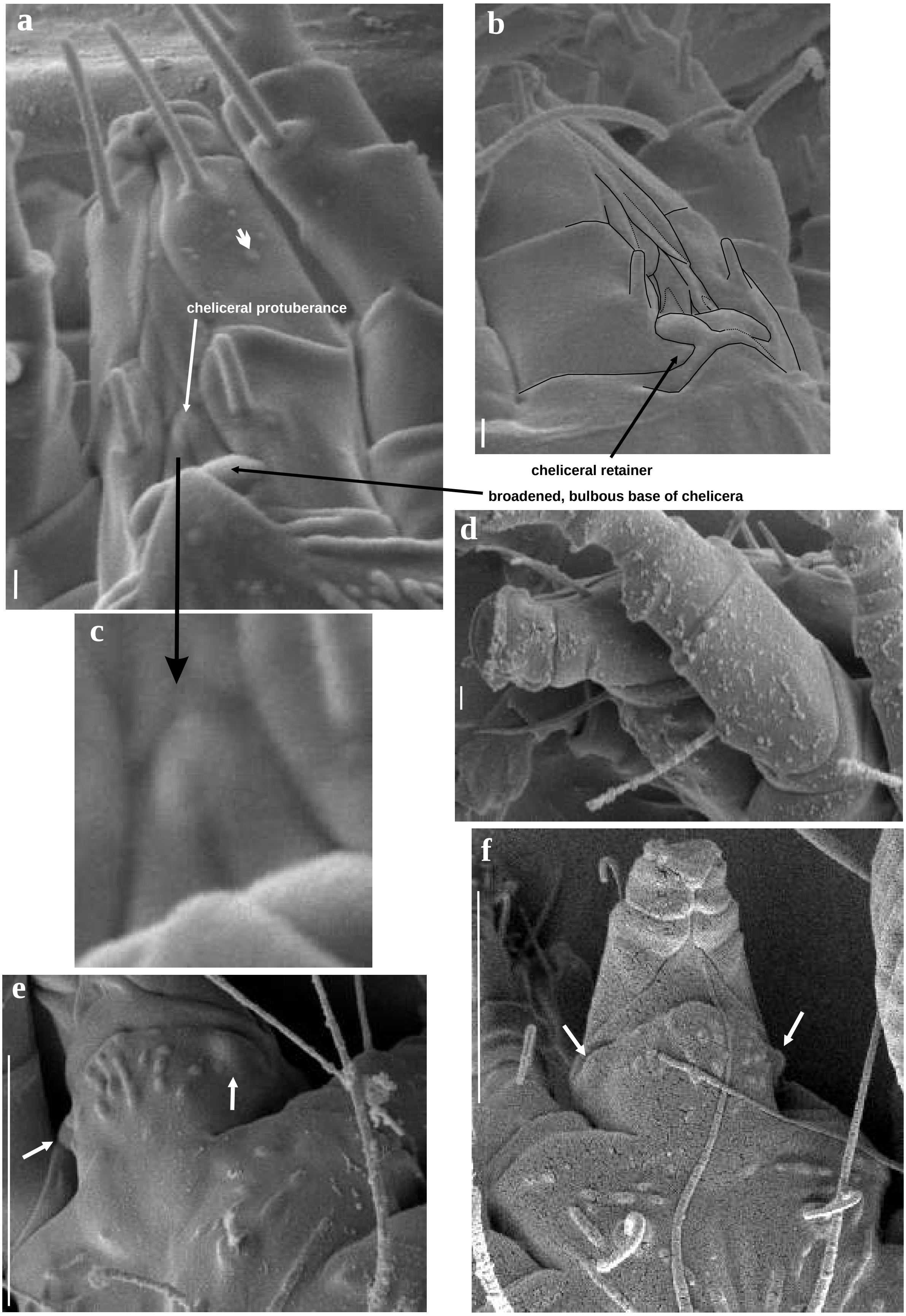


Fig. 3.43. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Acacia rehmanniana*: **a)** dorso-lateral view (probably adult, gender unknown), short white arrow indicates one of the droplet-like structures which are probably not part of the mite, but artefacts; **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.

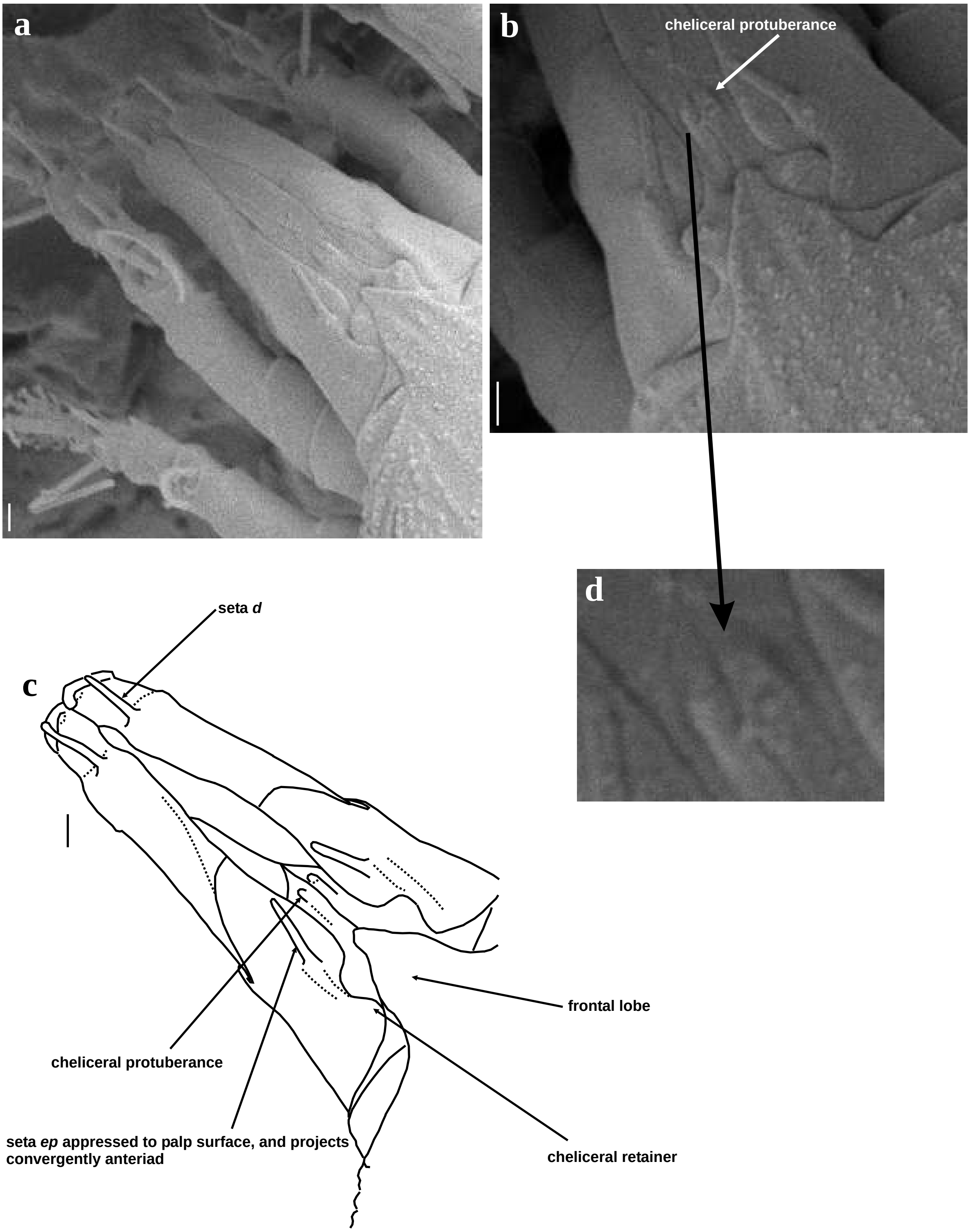


Fig. 3.44. (continued on next page). Gnathosoma of unknown genus, nr. *Aceria* (Eriophyidae: Eriophyinae: Aceriini) from *Apodytes dimidiata* subsp. *dimidiata* flower buds: **a, b)** dorsal views of the same specimen (probably adult, gender unknown); **c)** line drawing of Fig. 3.44a; **d)** enlargement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

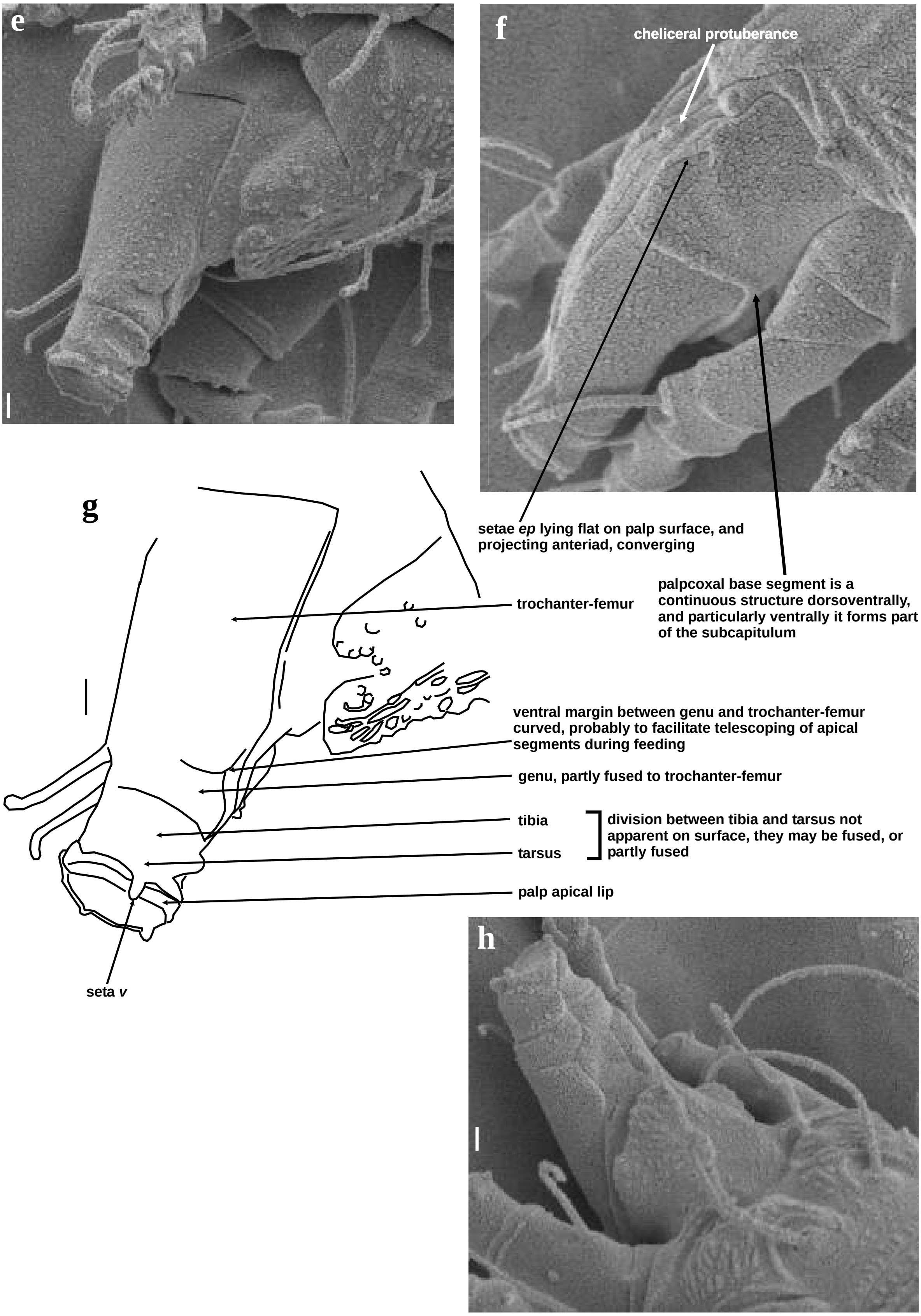


Fig. 3.44. (continued from previous page). Gnathosoma of unknown genus, nr. *Aceria*: **e)** ventro-lateral view (male); **f)** dorso-lateral view (probably adult, gender unknown); **g)** line drawing of Fig. 3.44e; **h)** ventro-lateral view (female); **e, g, h)** scale lines = 1 µm; **b)** scale line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

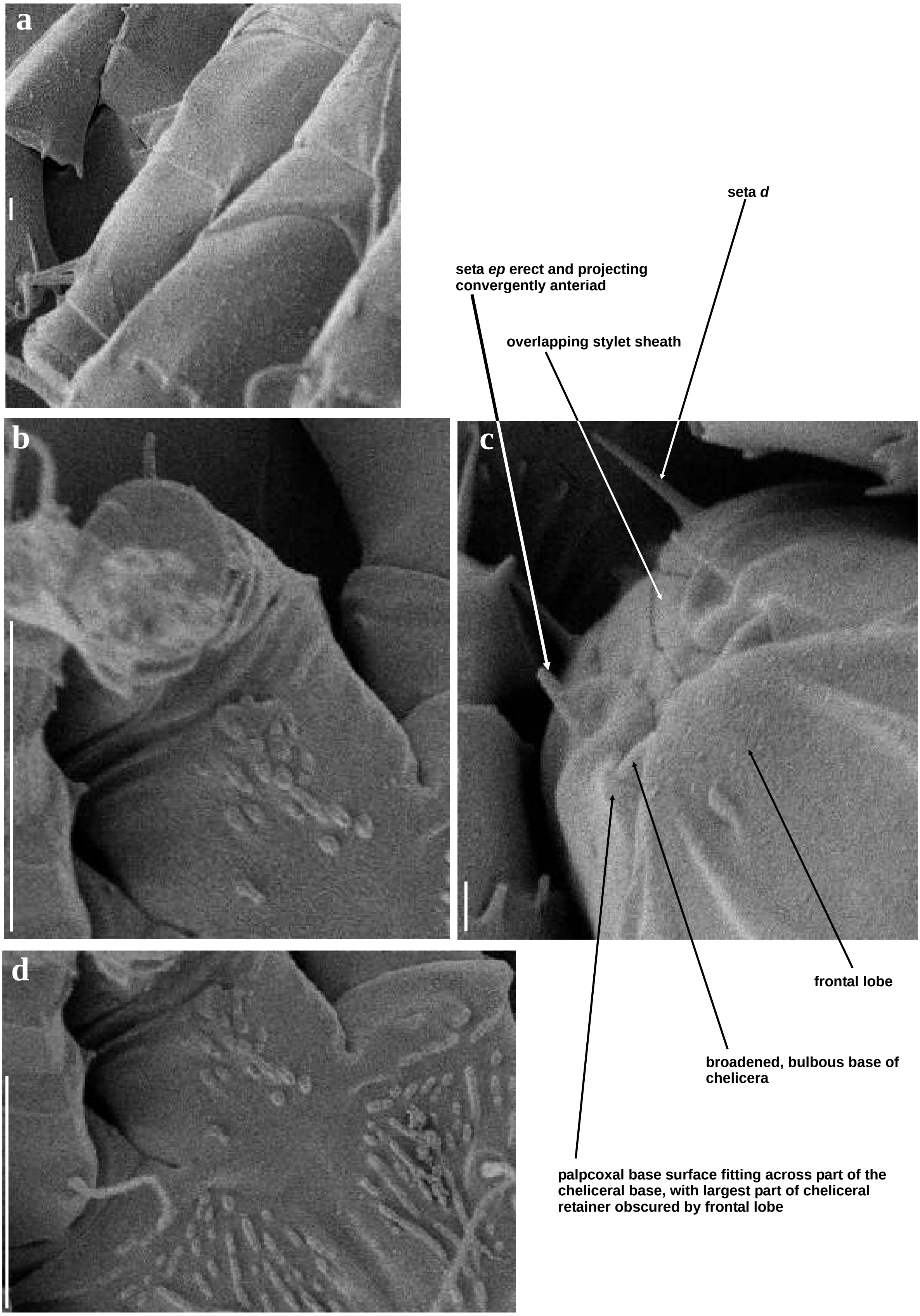


Fig. 3.45. Gnathosoma of *cf. Aceria* sp. (Eriophyidae: Eriophyinae: Aceriini) from *Cineraria* sp. blisters: **a)** lateral view (female); **b, d)** ventral views of the same specimen (female); **c)** dorsal view (probably adult, gender unknown); **a, c)** scale lines = 1 µm; **b, d)** scale lines =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

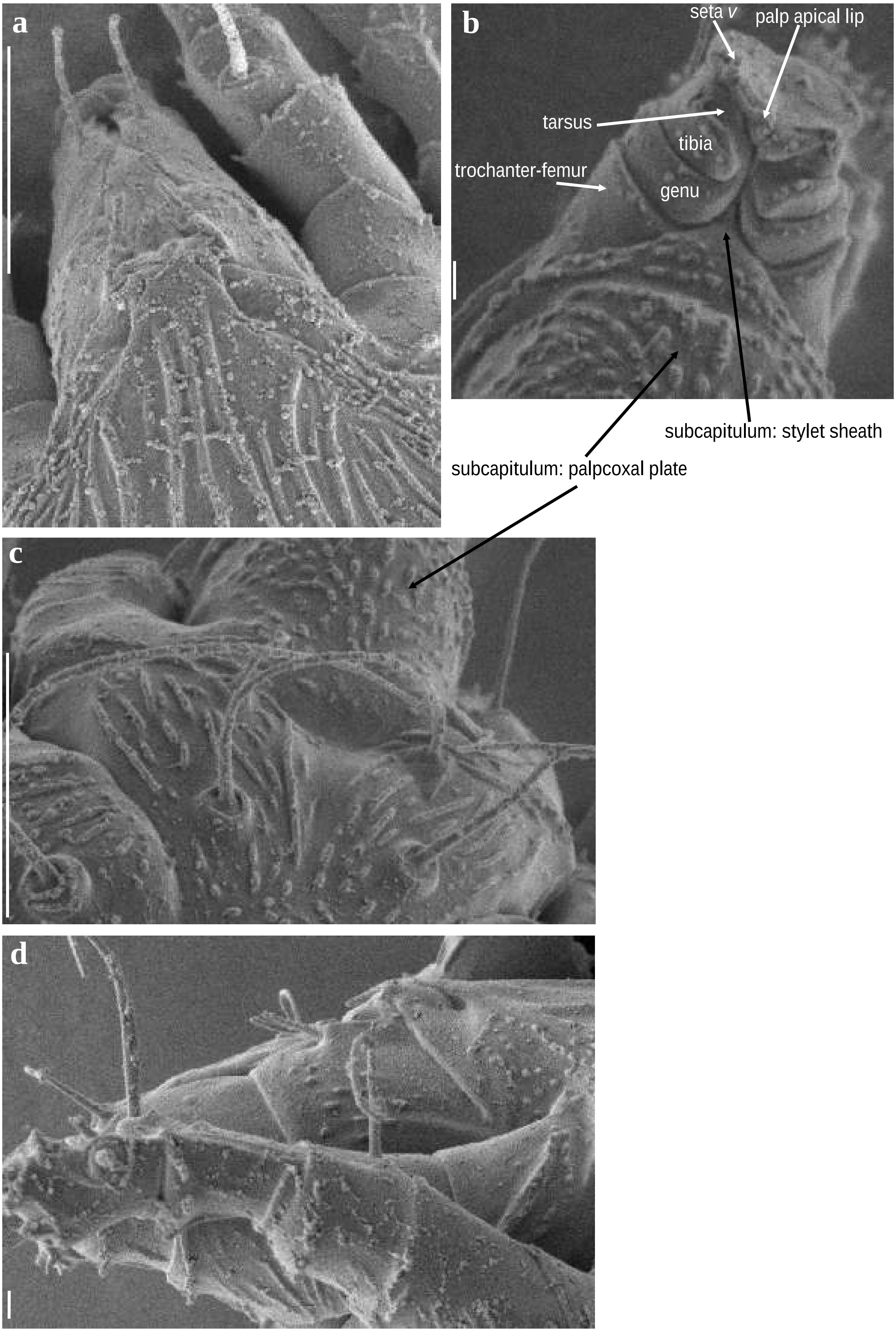


Fig. 3.46. Gnathosoma of *Aceria* sp. *cf. Aceria* sp. nov. (Eriophyidae: Eriophyinae: Aceriini) from *Xymalos monospora*: **a)** dorsal view (probably adult, gender unknown); **b, c)** ventral views of the same specimen (female); lateral view (female); **a, c)** scale lines = 10 µm; **b, d)** scale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

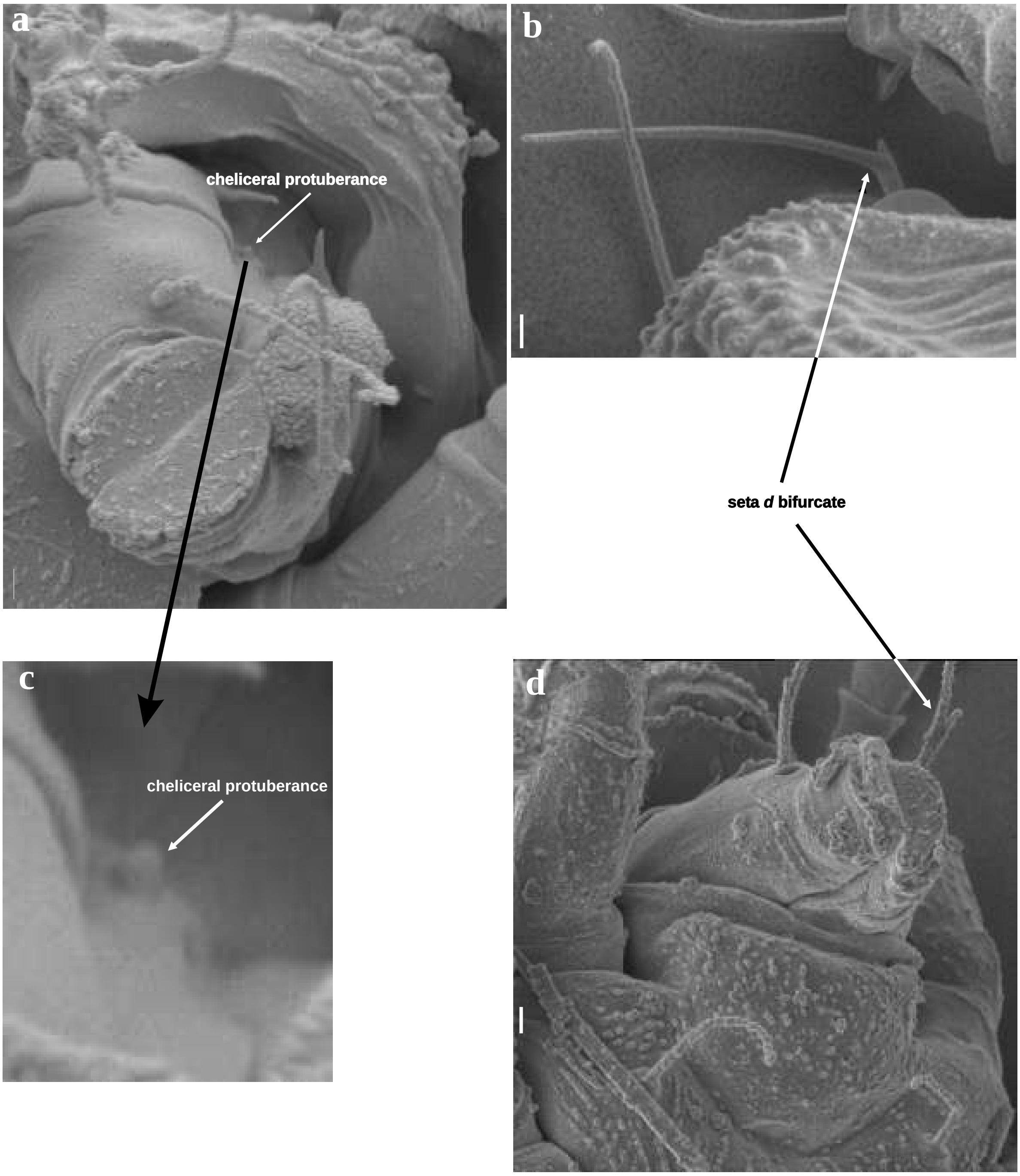
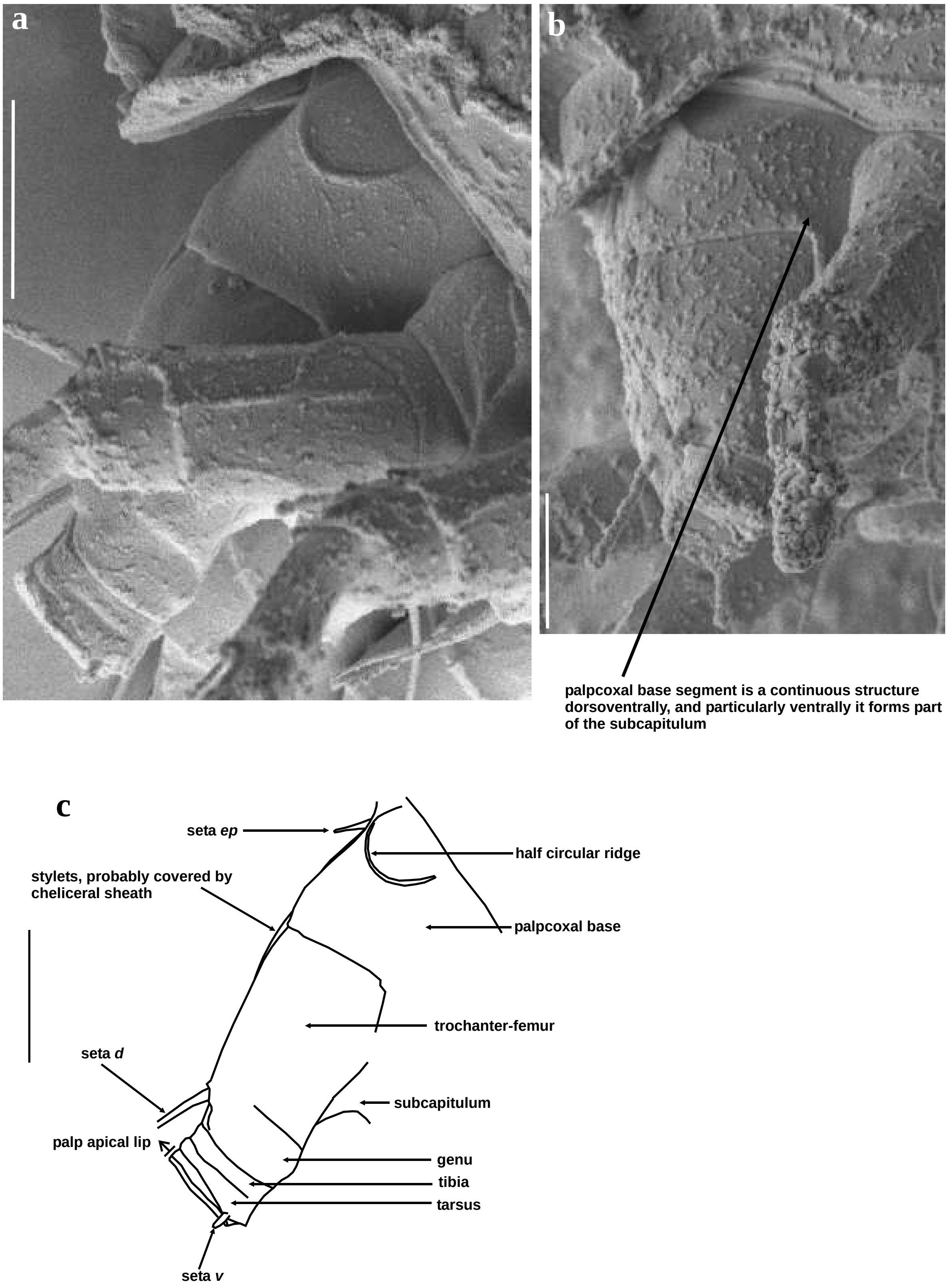


Fig. 3.47. Gnathosoma of *Tumescoptes* sp. *cf. T. dicrus* (Eriophyidae: Phyllocoptinae: Acaricalini) from *Phoenix reclinata*: **a)** ventro-dorsal view (female); **b)** bifurcate setae *d* enlarged to show tiny side branch (probably adult, gender unknown); **c)** enlargement of cheliceral protuberance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



palpcoxal base segment is a continuous structure dorsoventrally, and particularly ventrally it forms part of the subcapitulum

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.

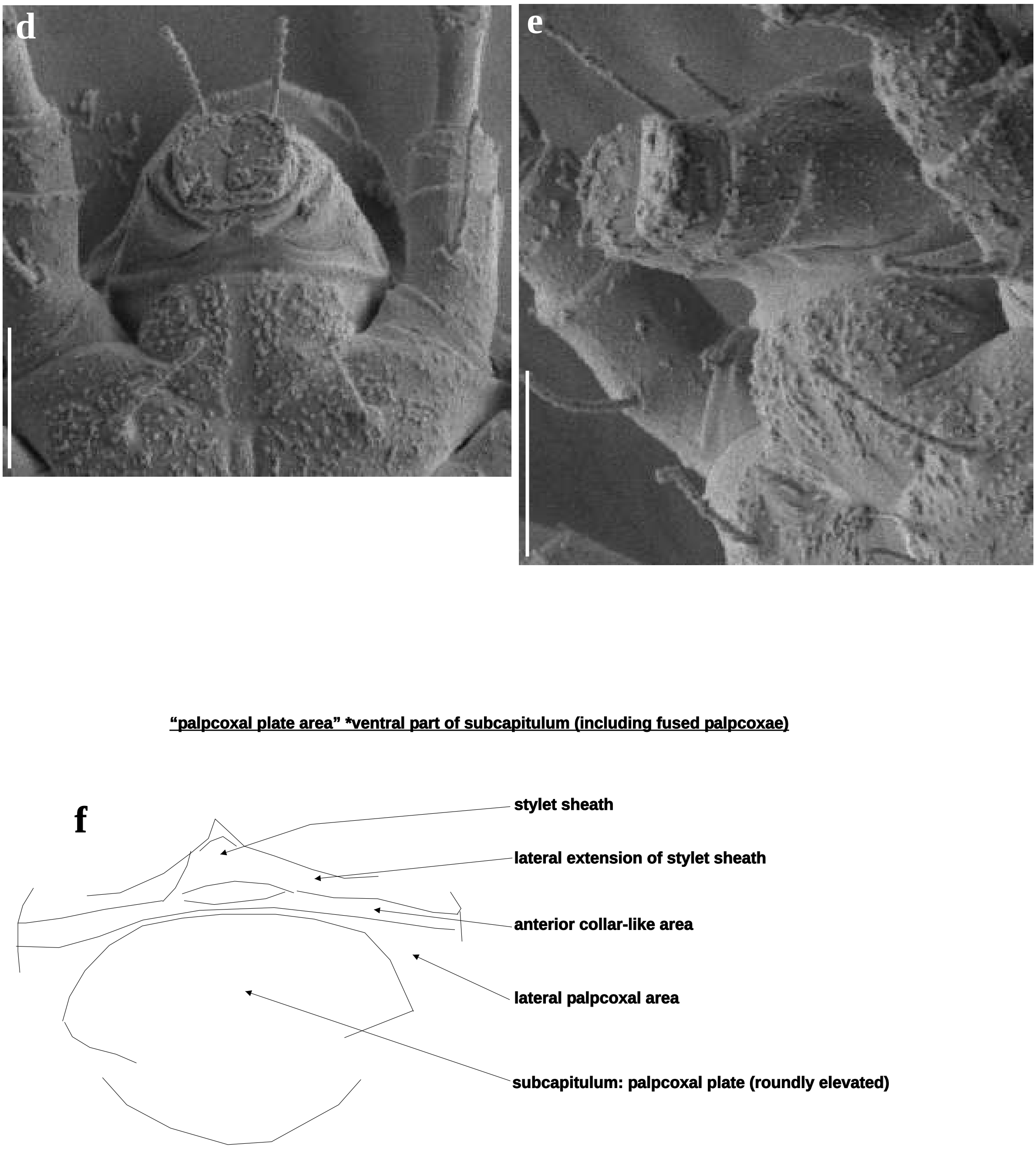


Fig. 3.48. (continued from previous page). Gnathosoma of *Calacarus* sp.: **d)** ventral view (female); **e)** ventro-lateral view (female); **f)** line drawing of "palpcoxal plate area" of Fig. 3.48d, *names for different areas are preliminary (also see Fig. 3.20). Scale lines = 10 µm.

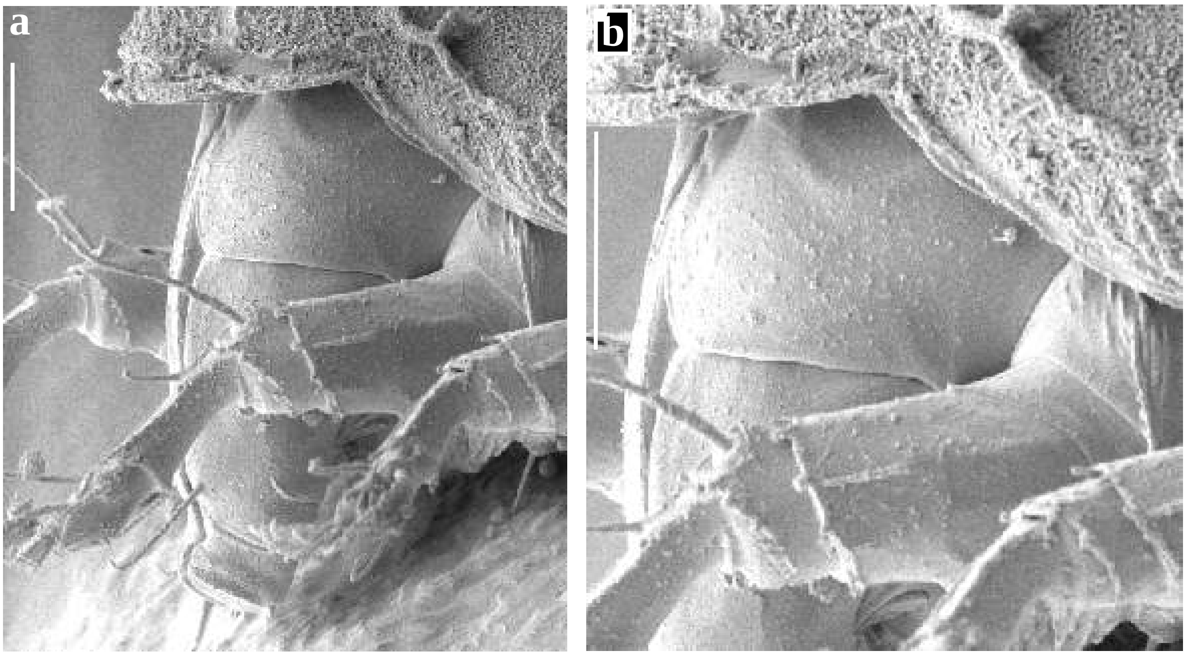


Fig. 3.49. Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Faurea rochetiana*: **a, b)** lateral view of the same specimen (probably adult, gender unknown). Scale lines = 10 µm.

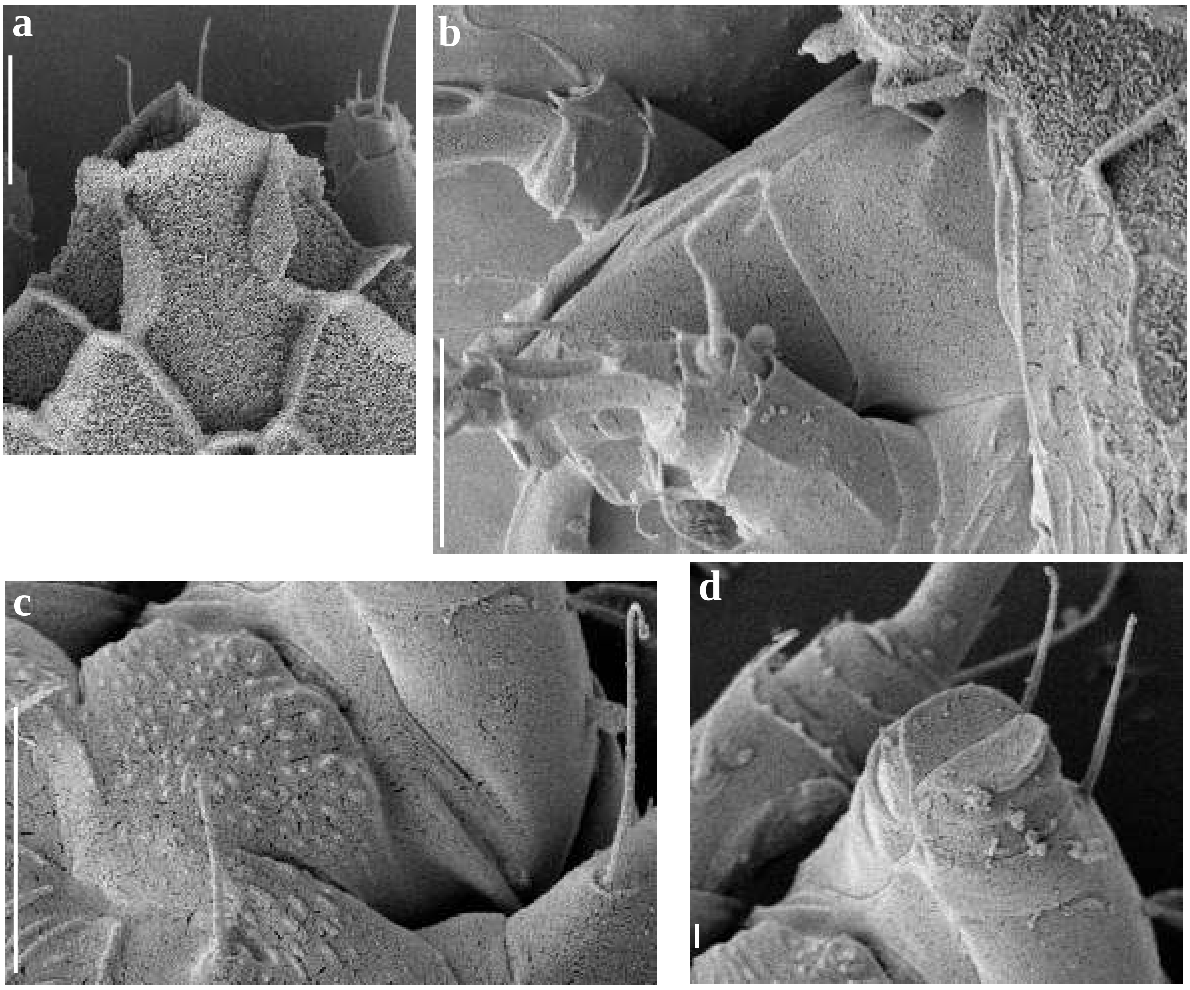


Fig. 3.50. Gnathosoma of *Calacarus* sp. (Eriophyidae: Phyllocoptinae: Calacarini) from *Psydrax livida*: **a)** dorsal view (probably adult, gender unknown), in vagrants, like this *Calacarus* sp., the frontal lobe obscures the gnathosoma which is also usually more hypognathous in these species, in 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.

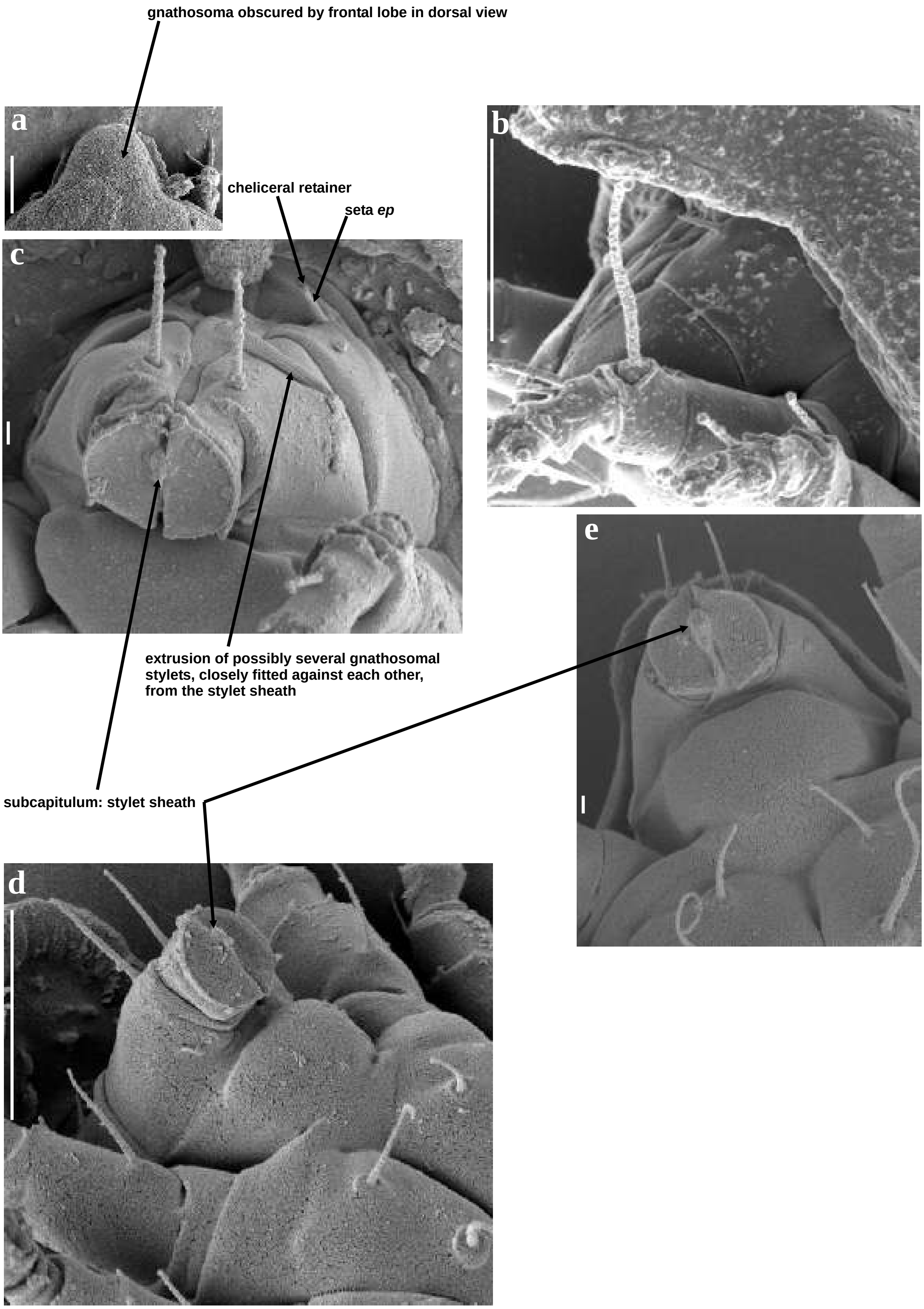
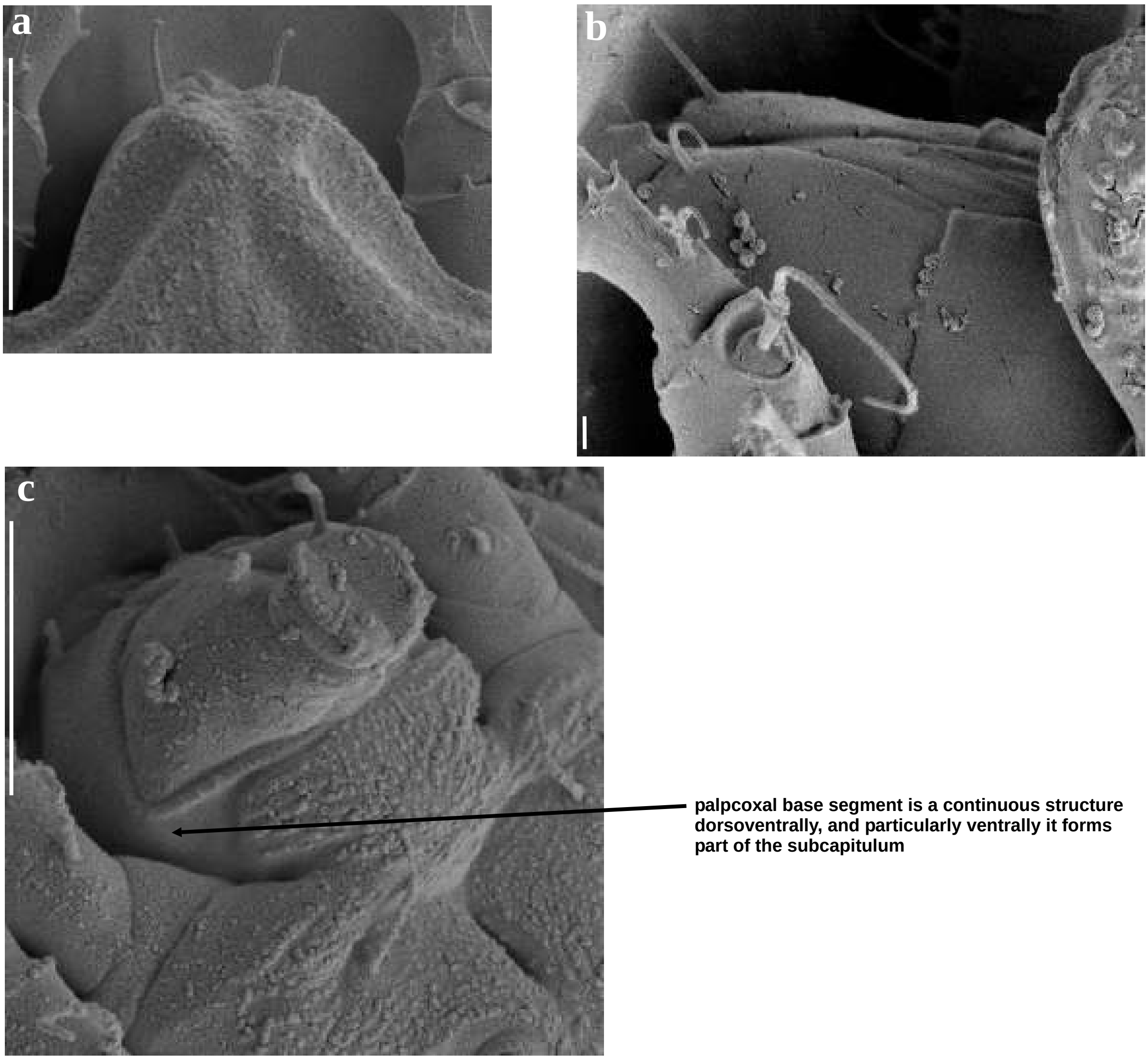
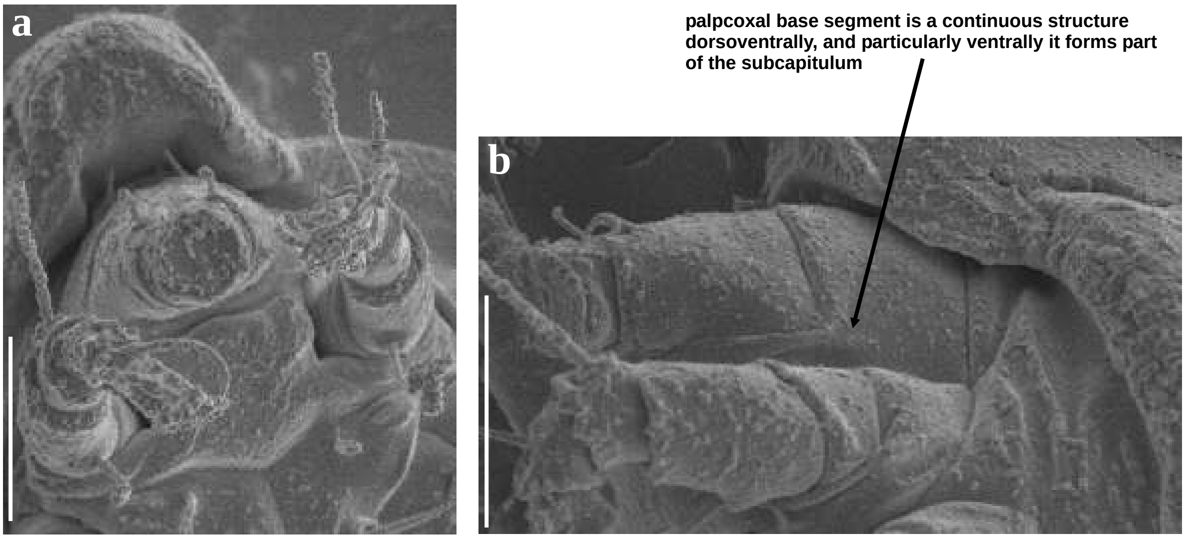


Fig. 3.51. Gnathosoma of a *Shevtchenkella* sp. *cf. S. lividae* (Meyer, 1990) (Eriophyidae: Phyllocoptinae: Tegonotini) from *Psydrax livida*: **a)** gnathosoma obscured by frontal lobe in dorsal view (probably adult, gender unknown); **b)** dorso-lateral view (male); **c)** ventral-dorsal view (female), 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.



palpcoxal base segment is a continuous structure dorsoventrally, and particularly ventrally it forms part of the subcapitulum

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.



palpcoxal base segment is a continuous structure dorsoventrally, and particularly ventrally it forms part of the subcapitulum

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.

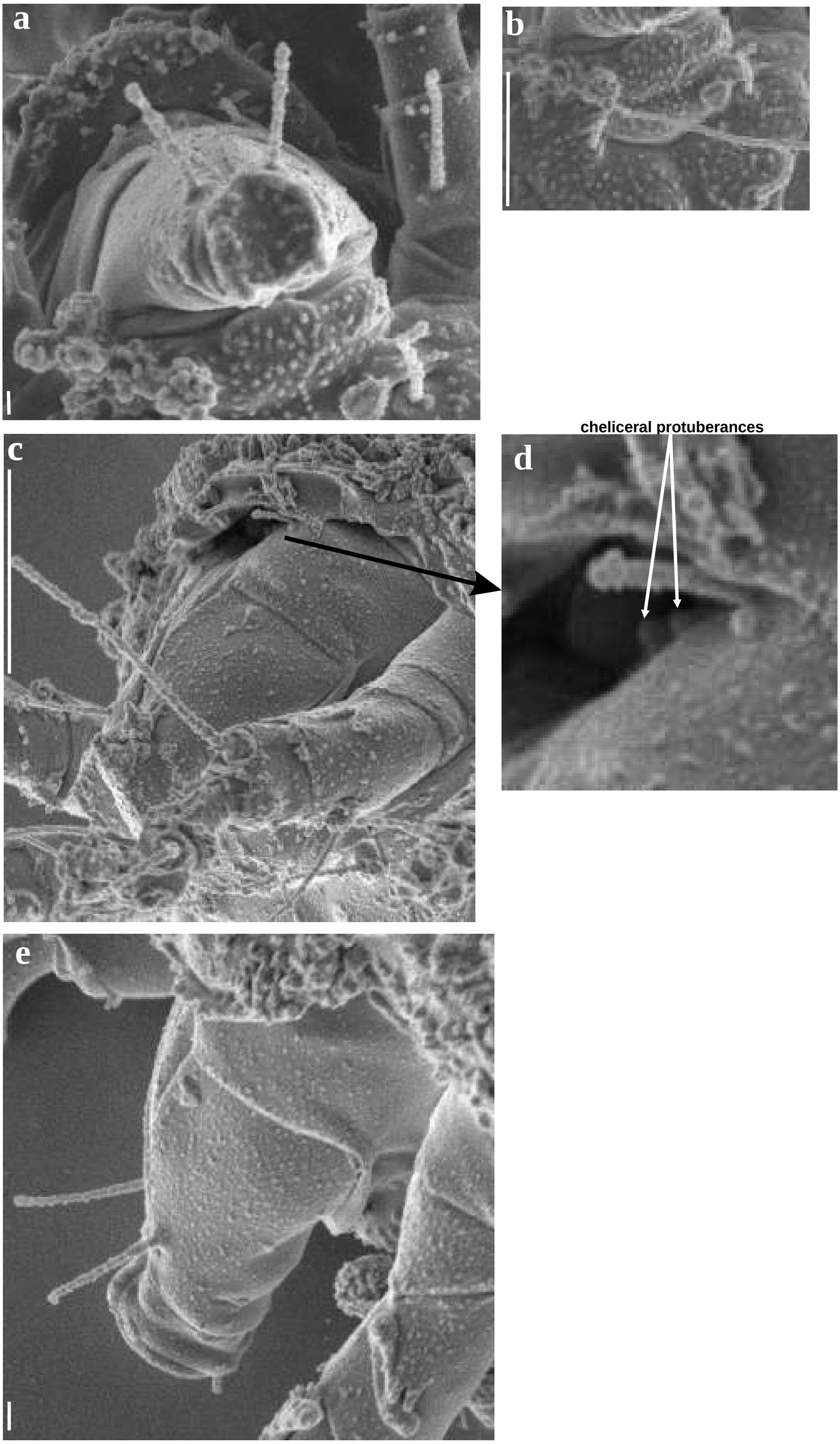


Fig. 3.54. Gnathosoma of *cf. Calepitrimerus* sp. (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Celtis africana*: **a, b)** ventral views of the same specimen (female); **c)** dorso-lateral view (female); **d)** enlargement of cheliceral protuberances in Fig. 3.54c; **e)** dorso-lateral view (probably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

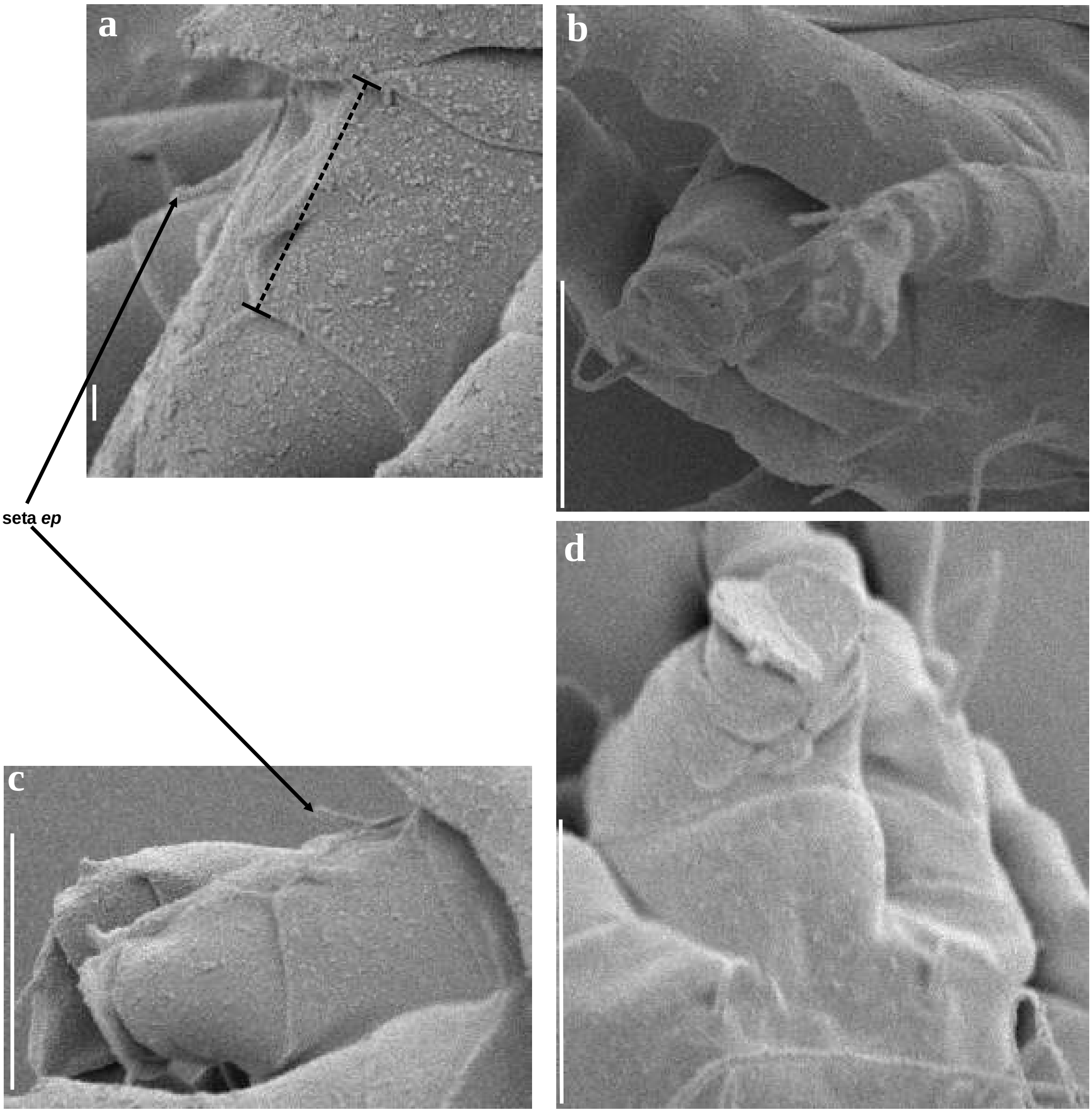
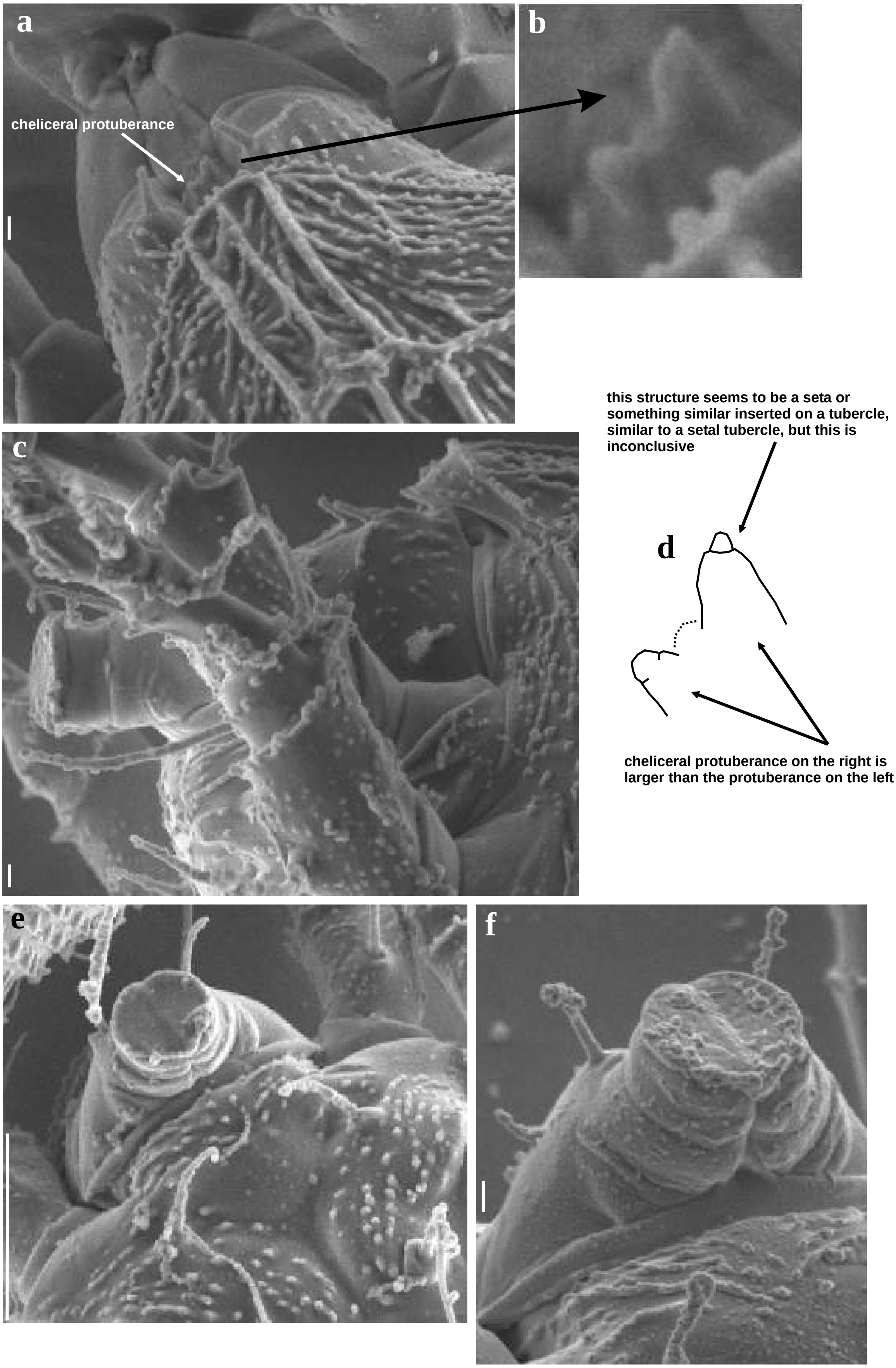


Fig. 3.55. Gnathosoma of *Cecidodectes euzonus* Nalepa, 1917 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Trema orientalis*: **a)** dorso-lateral view (probably adult, gender unknown), dashed black line indicates length of palpcoxal base; **b)** ventro-lateral view (female); **c)** lateral view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



this structure seems to be a seta or something similar inserted on a tubercle, similar to a setal tubercle, but this is inconclusive

cheliceral protuberance on the right is larger than the protuberance on the left

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.

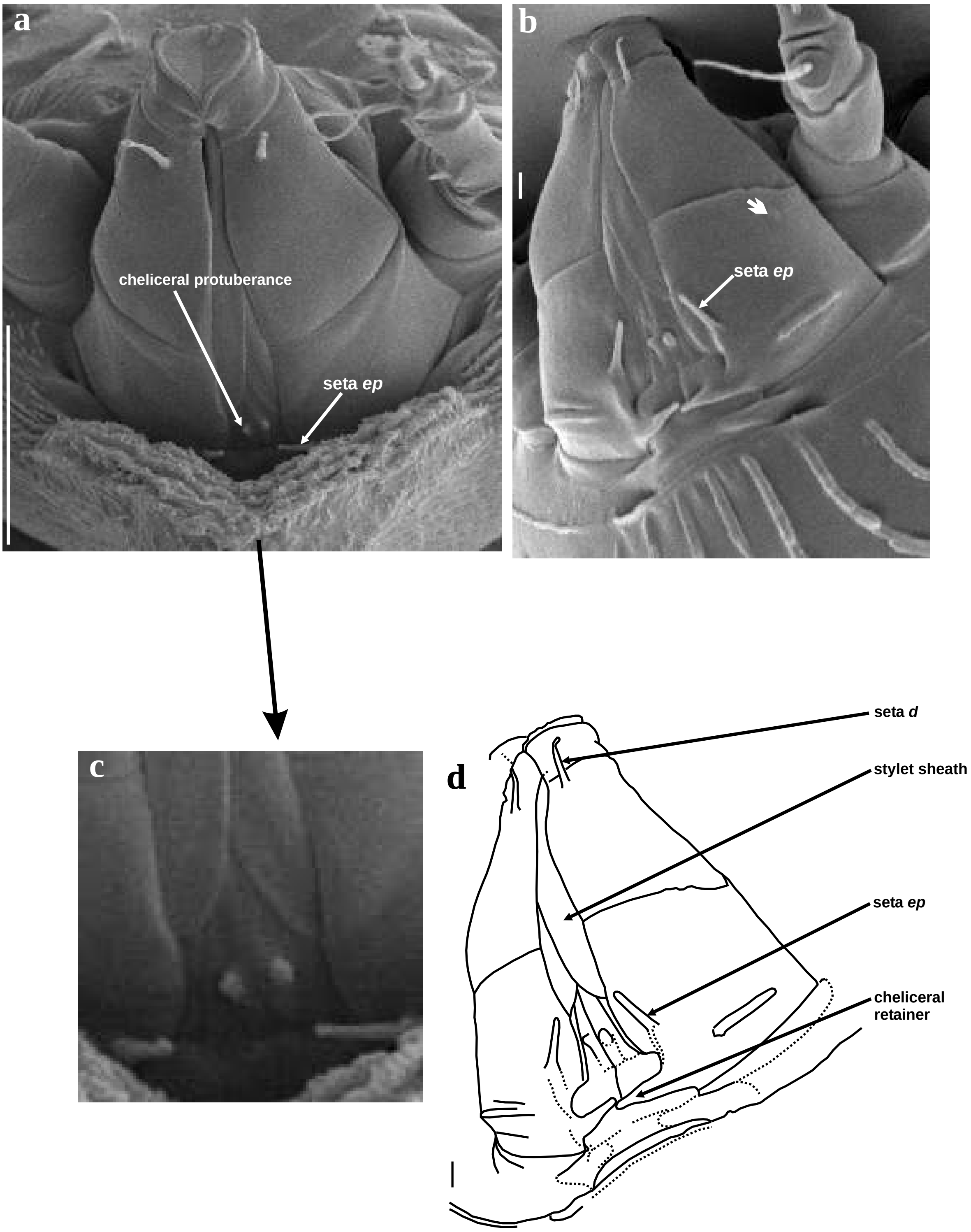


Fig. 3.57. (continued on next page). Gnathosoma of *Tergilatus sparsus* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Phyllocoptini) from *Portulacaria afra*: **a)** dorsal view (female); **b)** dorso-lateral view (larva), short white arrow indicates droplet-like structure that is probably not 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.

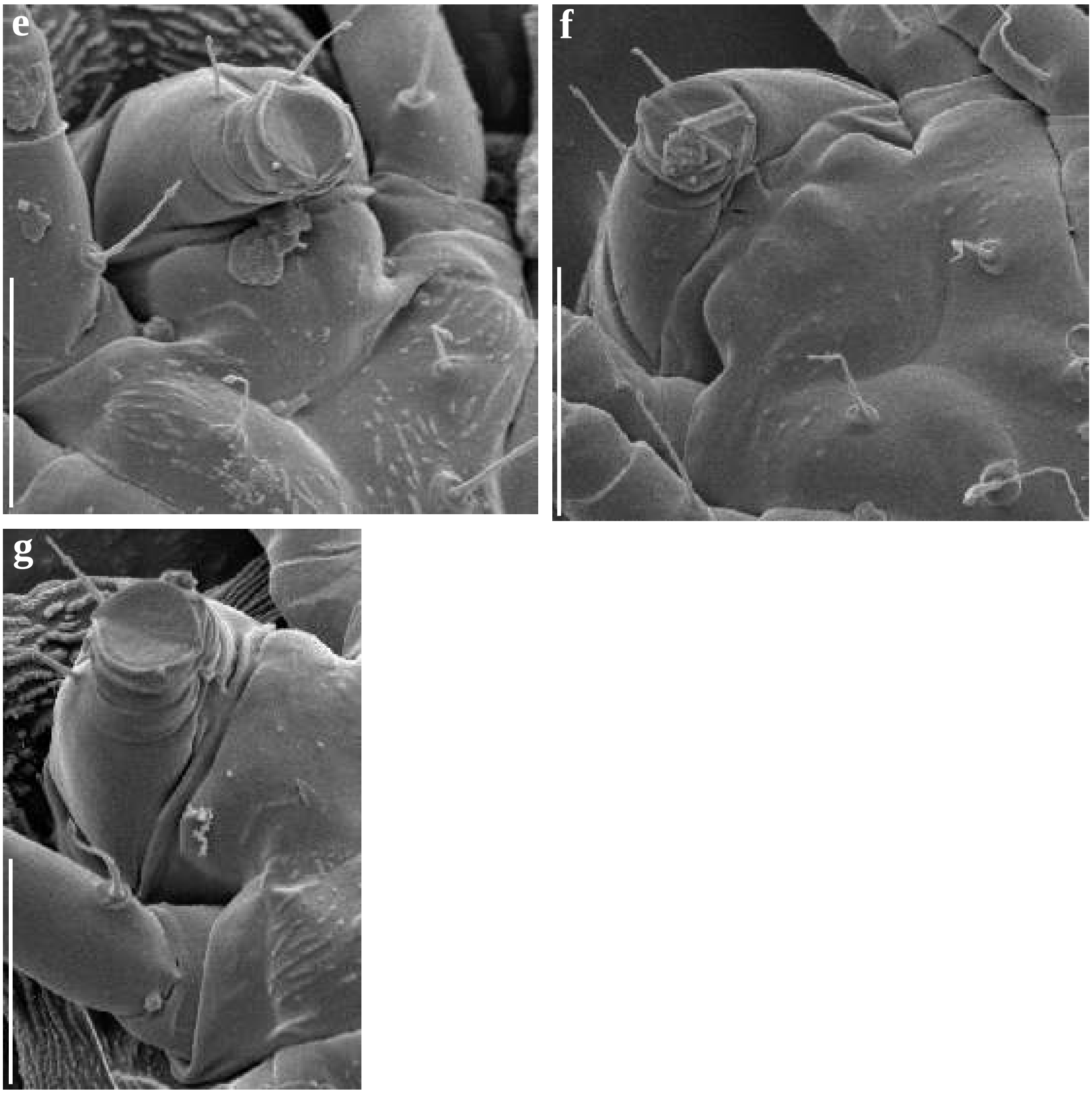


Fig. 3.57. (continued from previous page). Gnathosoma of *Tergilatus sparsus*: **e)** ventro-lateral view (male); **f)** ventral view (immature, stage unknown); **g)** ventro-lateral view (female). Scale lines = 10 µm.

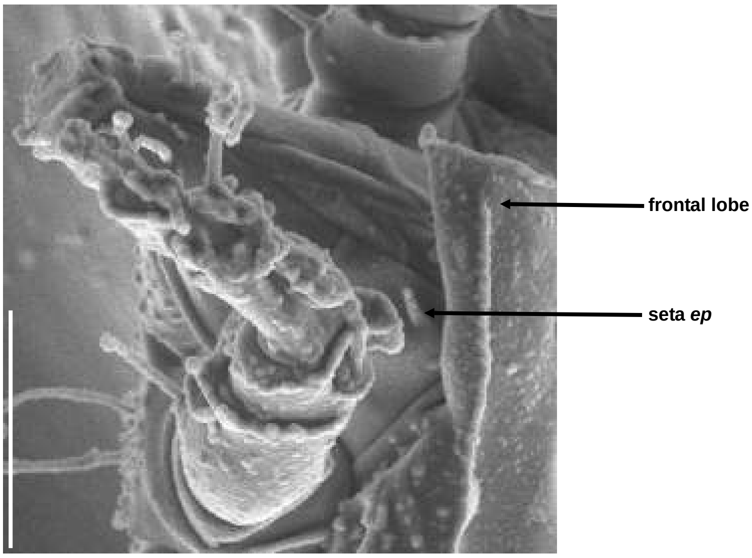


Fig. 3.58. Gnathosoma of possibly *Aculops* or *Metaculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Anthocleista grandiflora*: dorso-lateral view (probably adult, gender unknown). Scale line = 10 µm.

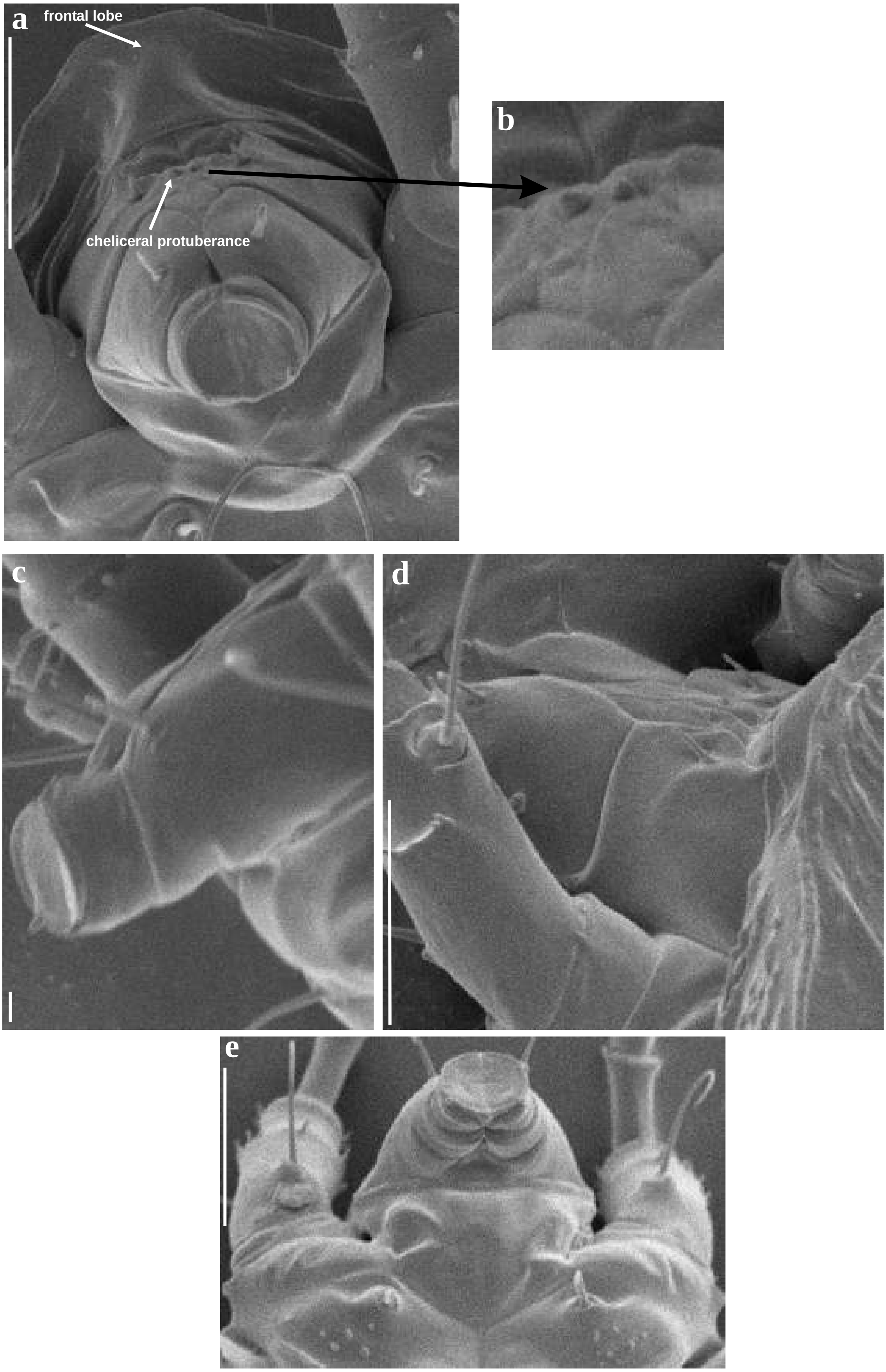


Fig. 3.59. Gnathosoma of *Aculus* sp. *cf. Aculops lycopersici* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Physalis peruviana*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in Fig. 3.59a; **c)** lateral view (female); **d)** dorso-lateral view (female); ventral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

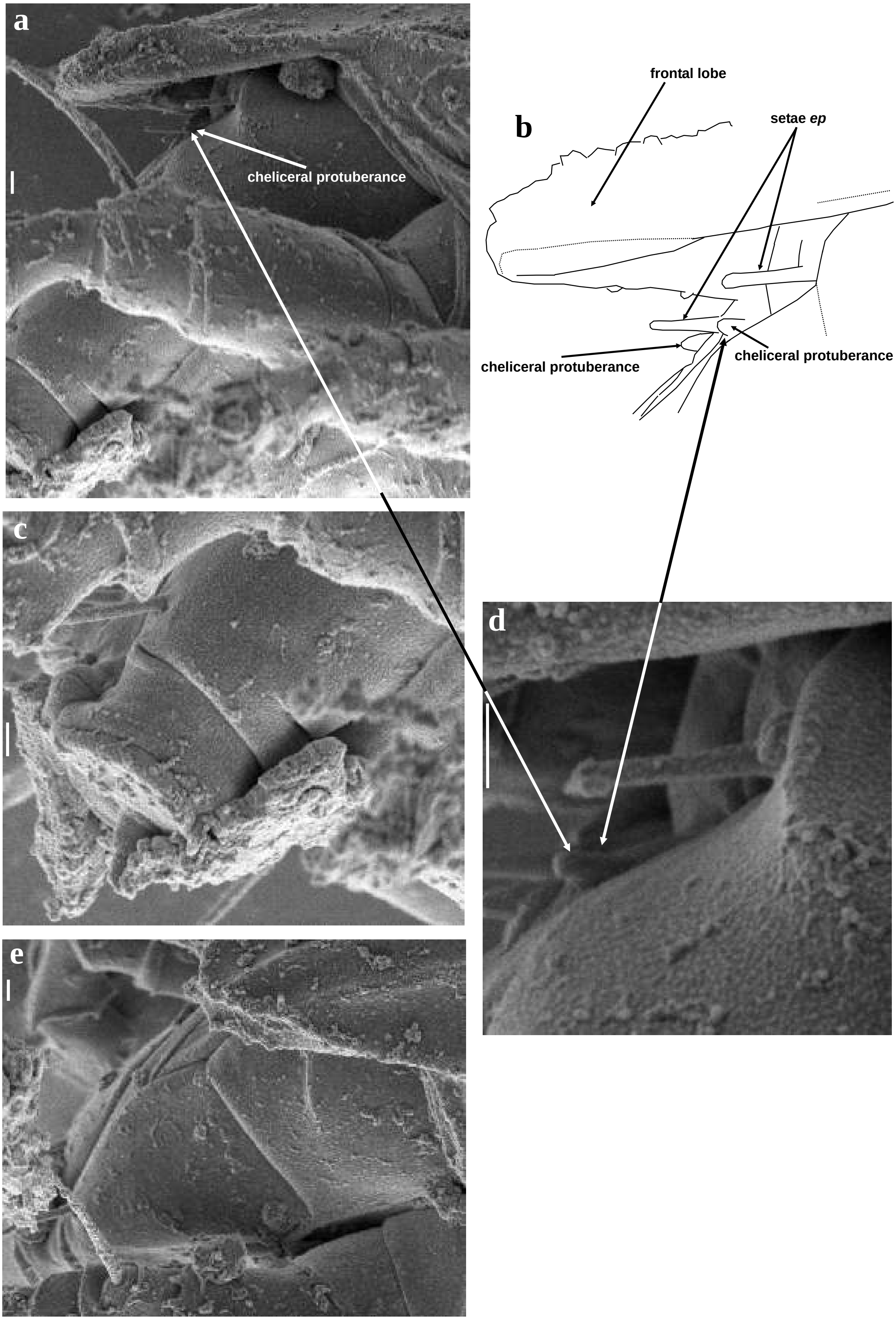


Fig. 3.60. Gnathosoma of *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Acacia burkei*: **a, c, d)** lateral views of different areas and enlargements of the same female specimen; **b)** line drawing of the cheliceral protuberances in Fig. 3.60a (enlarged in Fig. 3.60d); **e)** dorso-lateral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

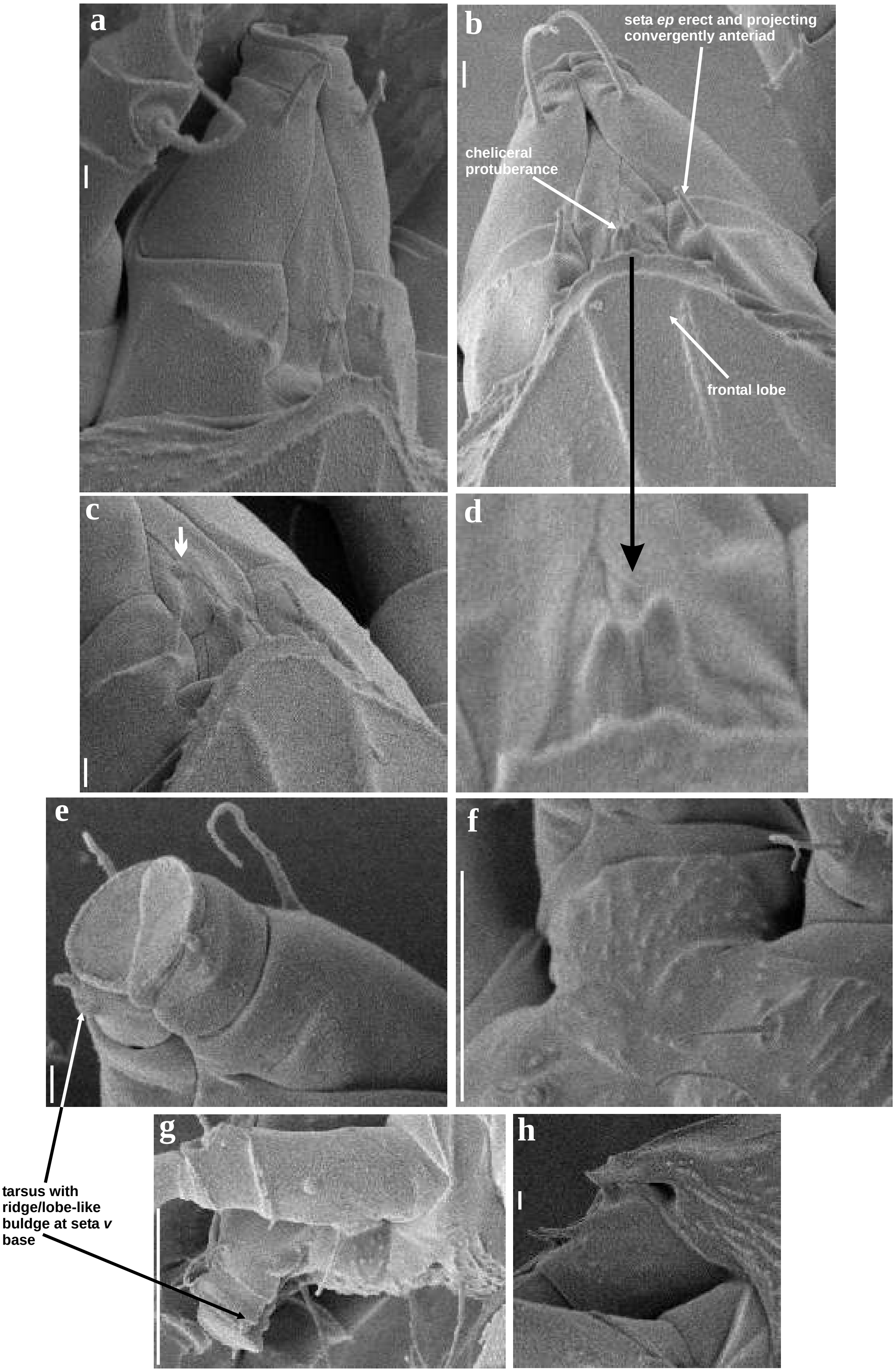


Fig. 3.61. Gnathosoma of *cf. Aculus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Lantana trifolia*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (probably adult, gender unknown); **c)** basal part, dorso-lateral view (probably adult, gender unknown), short 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.

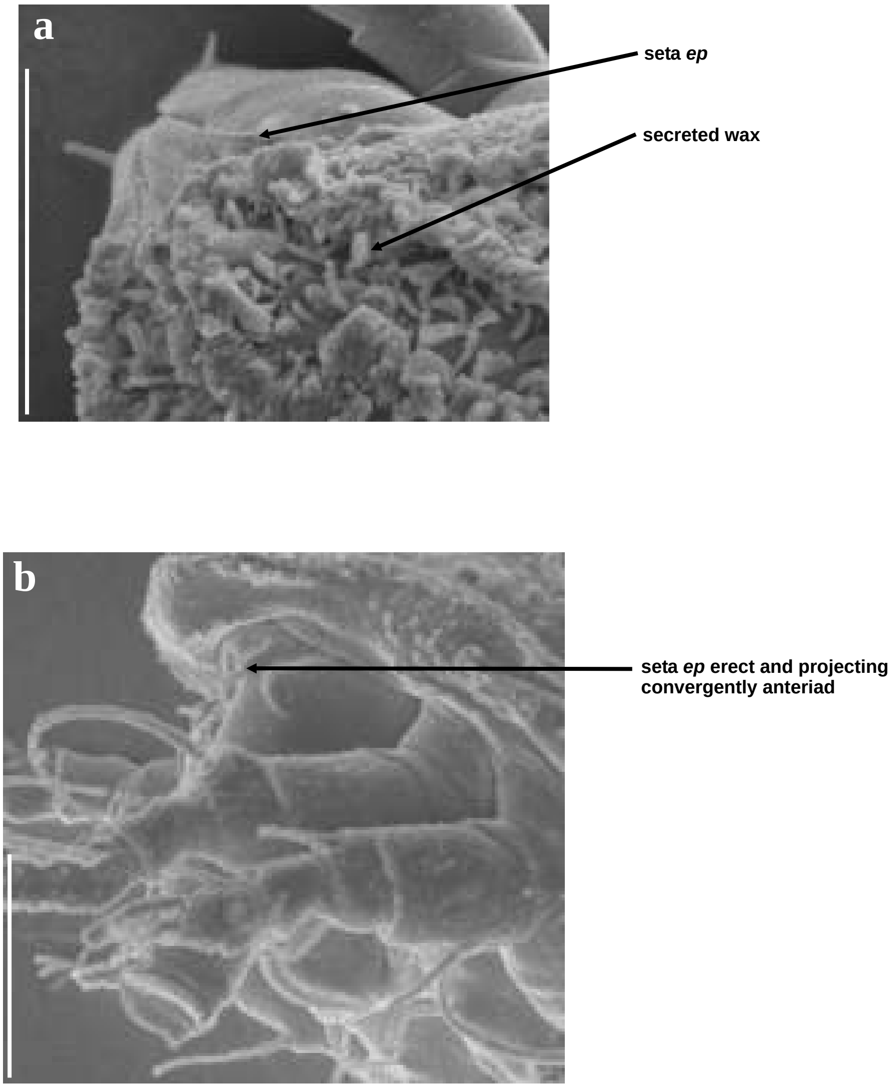


Fig. 3.62. Gnathosoma of *cf. Aculus* sp. or possibly an immature of *Quantalitus* (Eriophyidae) from *Rothmannia capensis*: a) dorsal view, frontal lobe obscures most of gnathosoma (possibly immature); b) lateral view (immature). Scale lines = 10 µm.

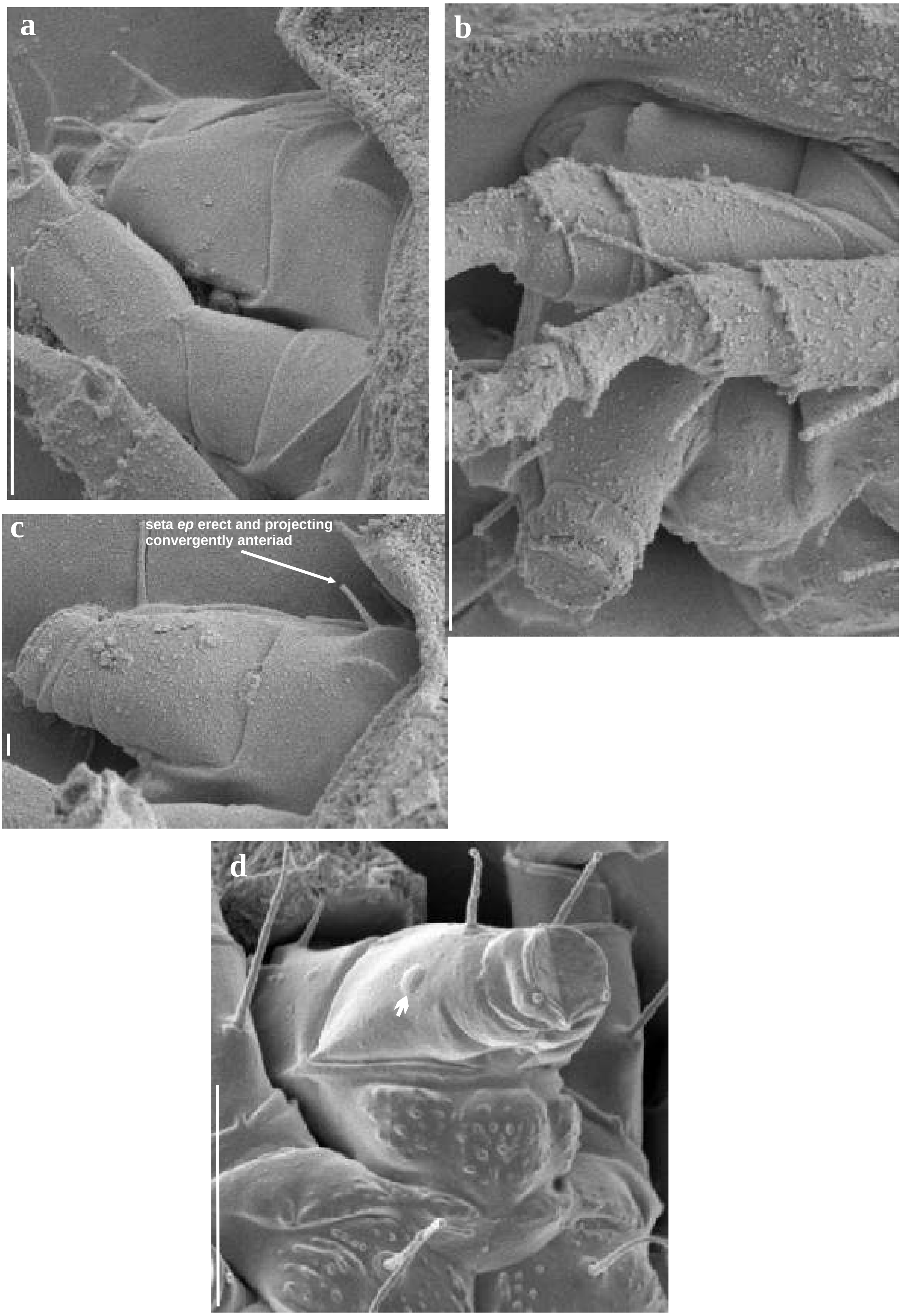


Fig. 3.63. Gnathosoma of *Costarectus zeyheri* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Dovyalis zeyheri*: **a)** dorso-lateral view (adult, probably female); **b)** dorso-lateral view (male); **c)** lateral view (female); **d)** ventro-lateral view (female), short white 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.

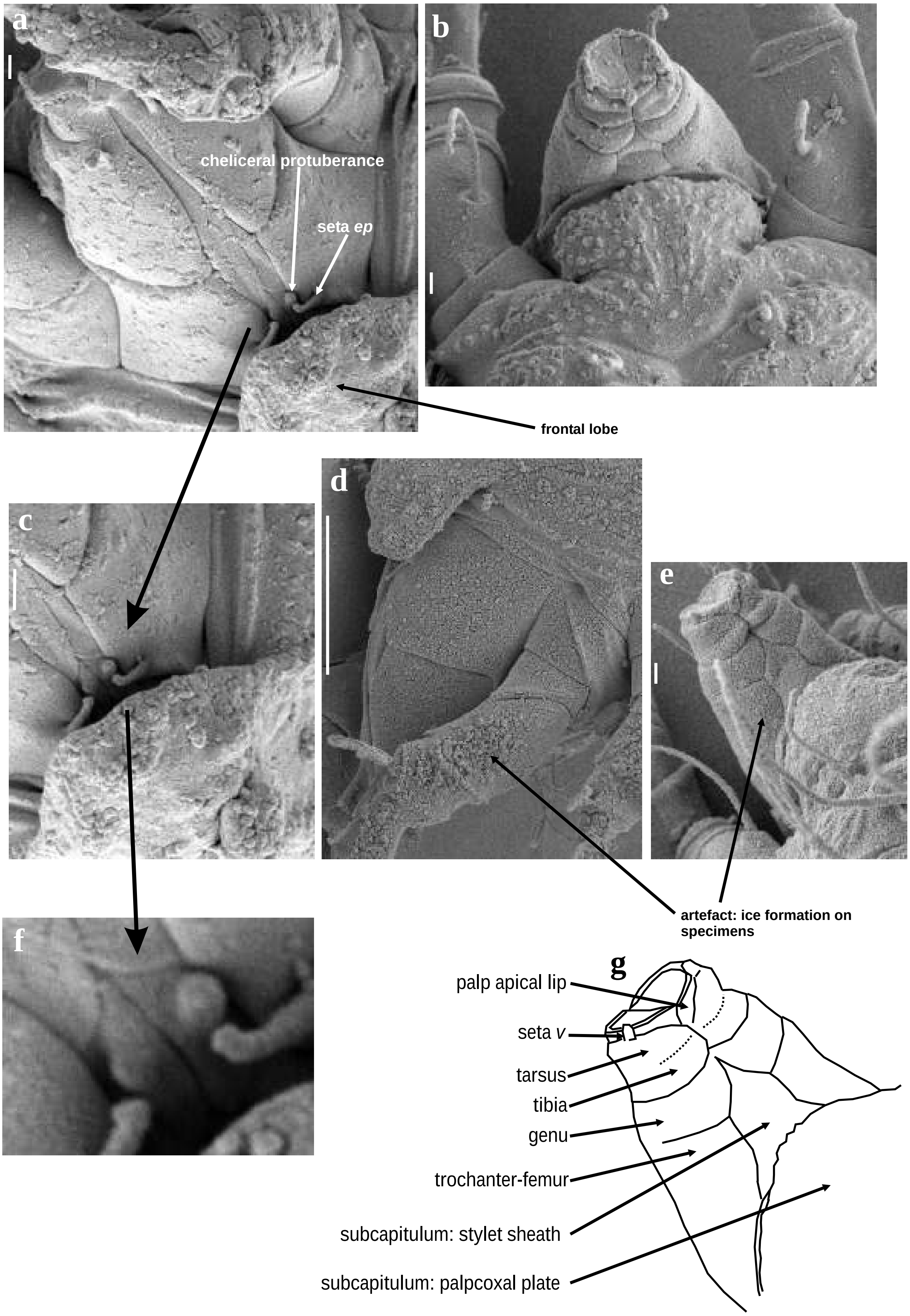
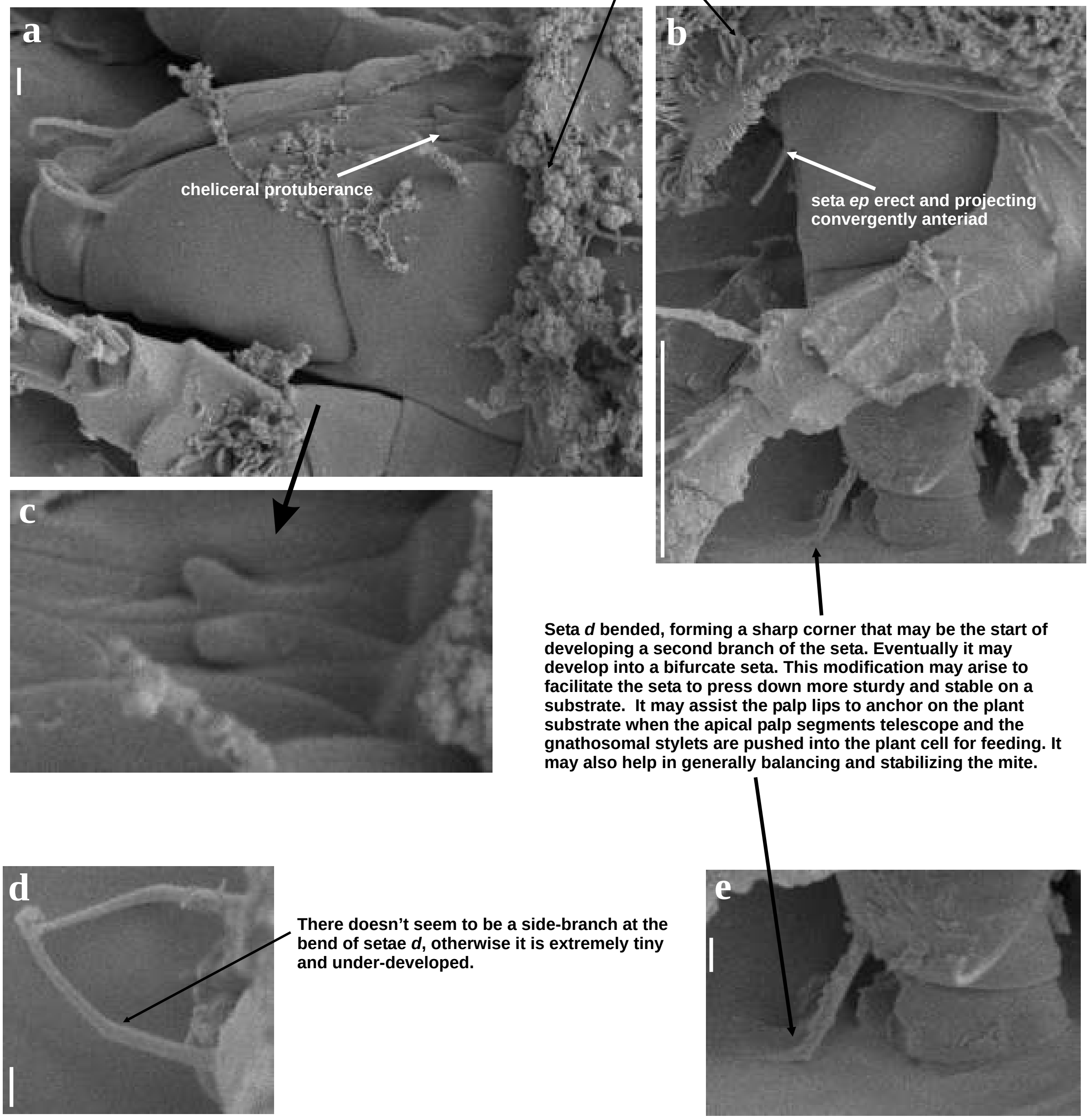


Fig. 3.64. Gnathosoma of *Meyerella bicristatus* (Meyer, 1989) females (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Mystroxylon aethiopicum*: **a, c, f)** ventro-dorsal views of the same specimen, with cheliceral protuberances in Fig. 3.64a enlarged in c and further enlarged in f; **b)** ventral 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.

wax secreted by the mite, possibly mixed with dirt



cheliceral protuberance

seta *ep* erect and projecting convergently anteriad

Seta *d* bended, forming a sharp corner that may be the start of developing a second branch of the seta. Eventually it may develop into a bifurcate seta. This modification may arise to facilitate the seta to press down more sturdy and stable on a substrate. It may assist the palp lips to anchor on the plant substrate when the apical palp segments telescope and the gnathosomal stylets are pushed into the plant cell for feeding. It may also help in generally balancing and stabilizing the mite.

There doesn't seem to be a side-branch at the bend of setae *d*, otherwise it is extremely tiny and under-developed.

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.

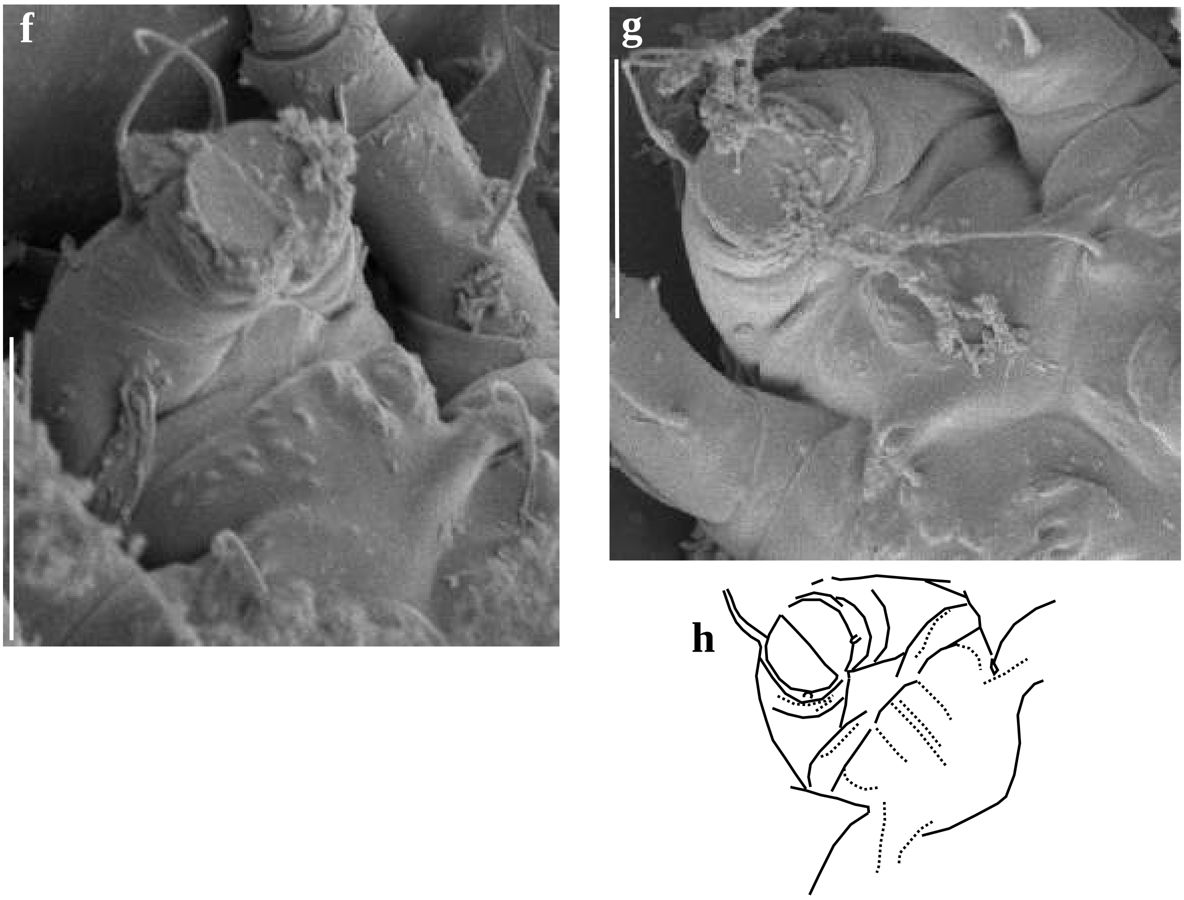


Fig. 3.65. (continued from previous page). Gnathosoma of possibly a new genus nr. *Costarectus*: **f)** ventro-lateral view (male); **g)** ventral view (male); **h)** line drawing of Fig. 3.65g. Scale lines = 10 µm.

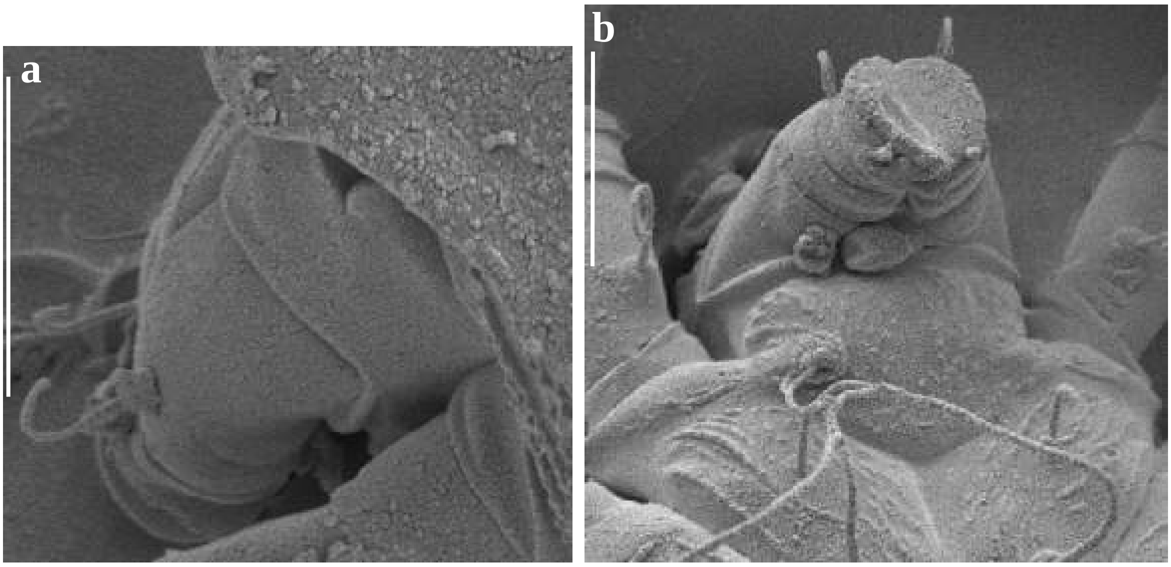


Fig. 3.66. Gnathosoma of possibly a new genus nr. *Tetra* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Protea caffra* subsp. *caffra*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female). Scale lines = 10 µm.

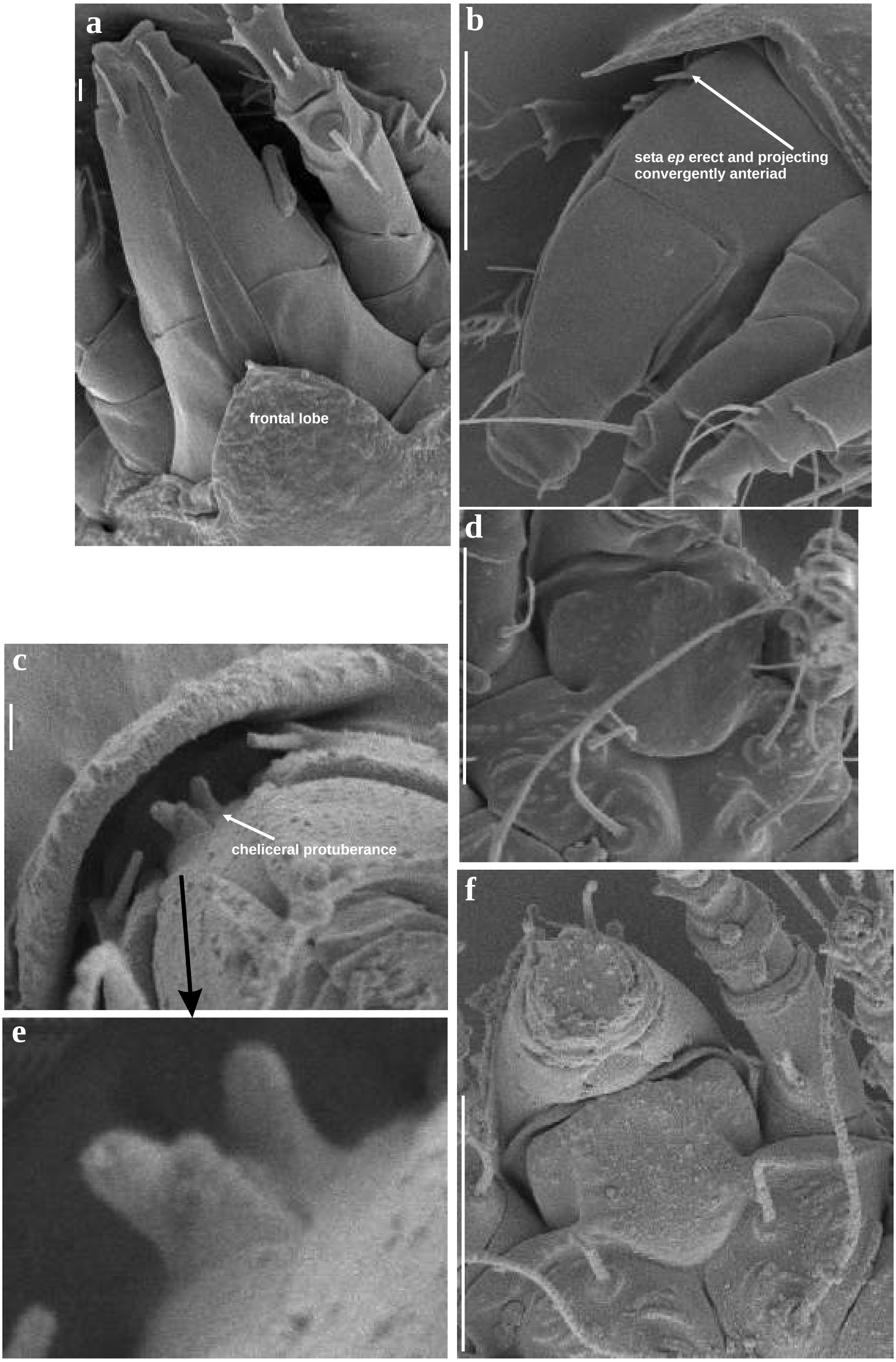


Fig. 3.67. Gnathosoma of possibly a new genus nr. *Mesalox* (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Apodytes dimidiata*: **a)** dorsal view (probably adult, gender uknown); **b)** lateral view (female); **c)** ventro-dorsal view (female); **d)** ventro-lateral view (female); **e)** enlargement 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.

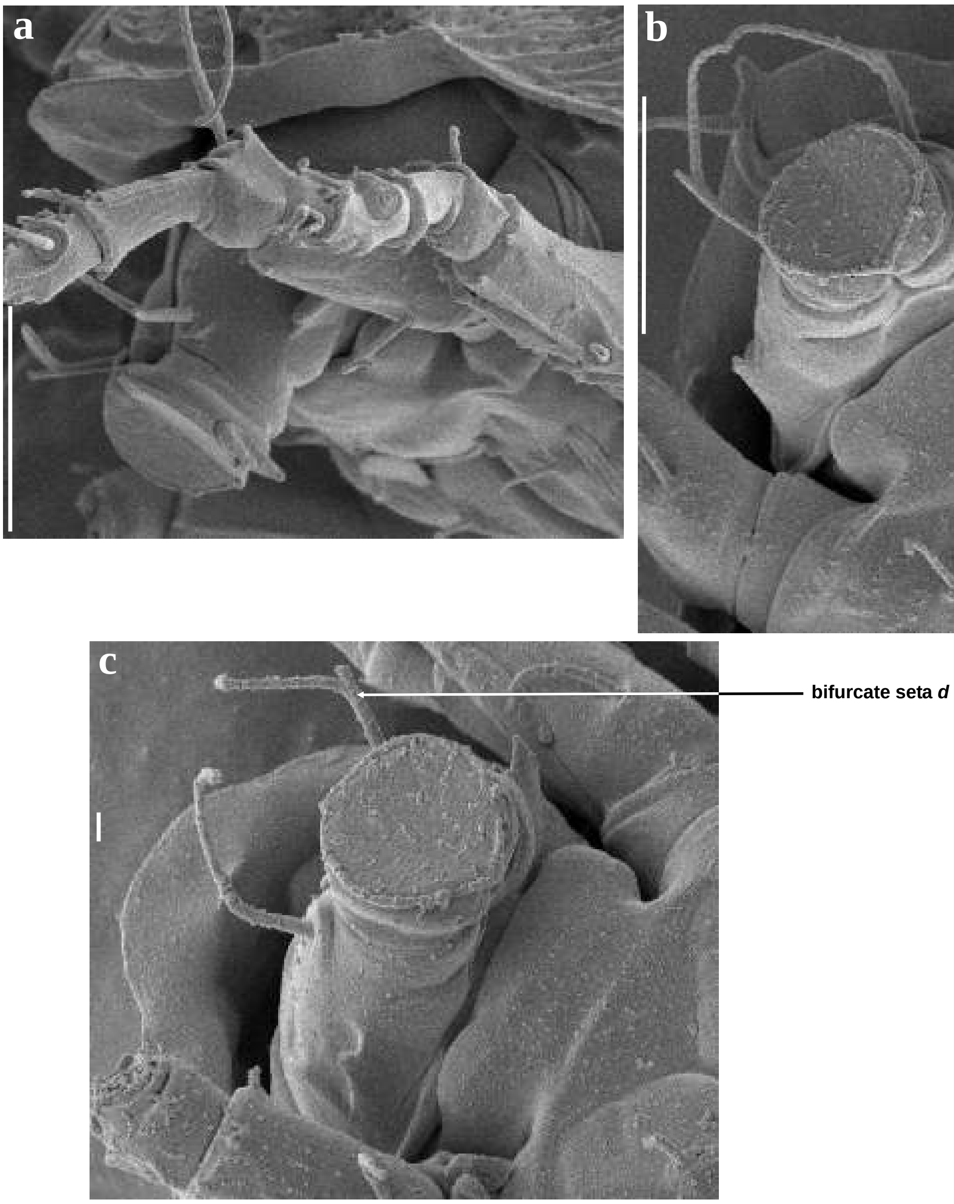


Fig. 3.68. Gnathosoma of *Porosus monosporae* Meyer & Ueckermann, 1995 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Xymalos monospora*: **a)** ventro-lateral view (female); **b)** ventral view (female); **c)** ventro-lateral view (male); **a, b)** scale lines = 10 µm; **c)** scale line = 1 µm.

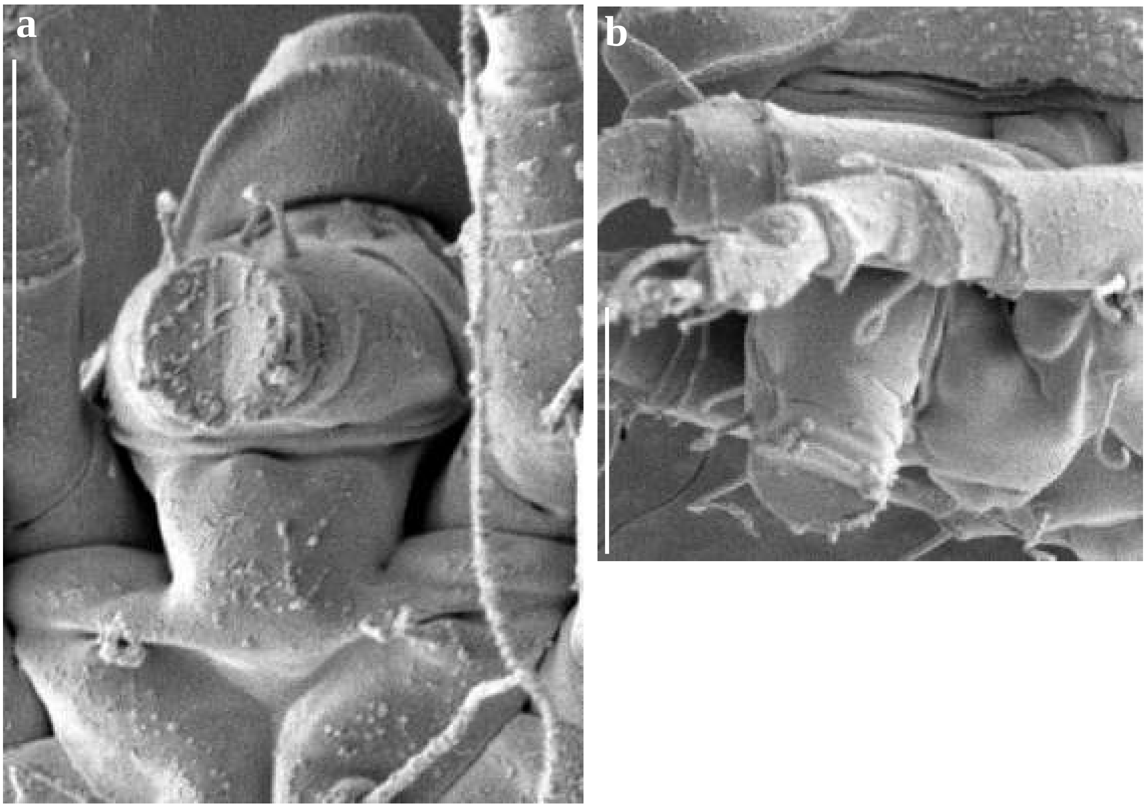


Fig. 3.69. Gnathosoma of *Tegolophus* sp. *cf. T. orientalis* Meyer, 1990 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Trema orientalis*: **a)** ventro-lateral view (female); **b)** lateral view (female). Scale lines = 10 µm.

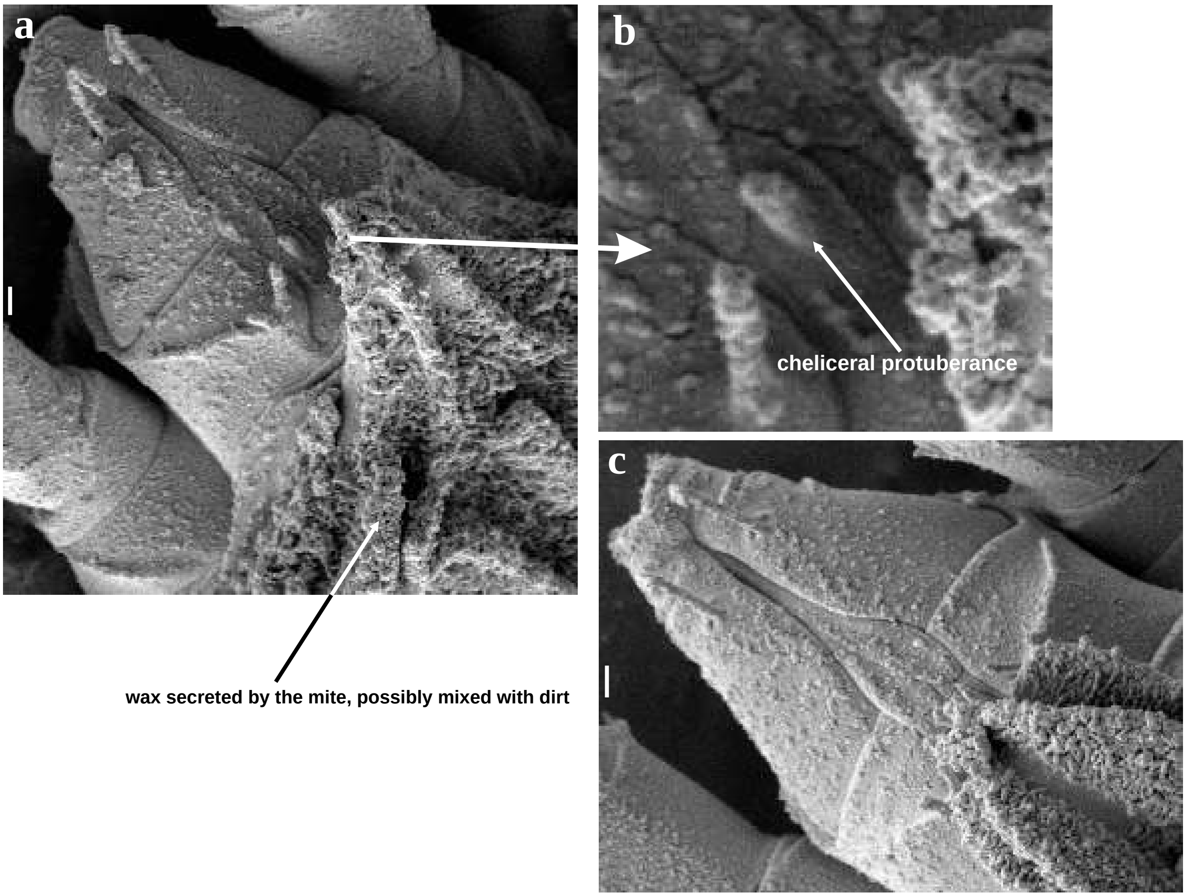


Fig. 3.70. (continued on next page). Gnathosoma of *Tetra retusa* Meyer, 1992 (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Bauhinia galpinii*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** enlargement of cheliceral protuberances in Fig. 3.70a; **c)** dorsal view (probably adult,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

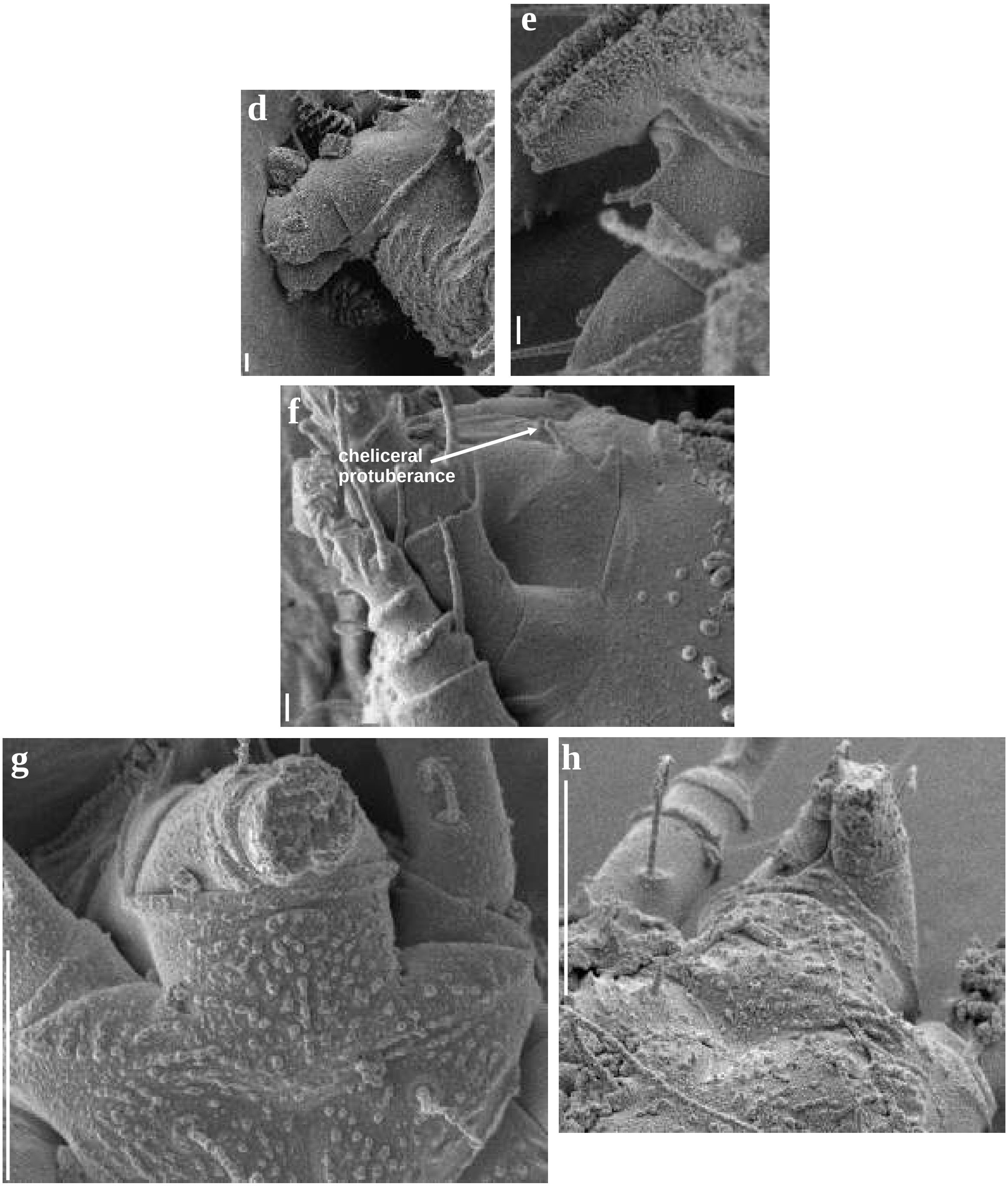


Fig. 3.70. (continued from previous page). Gnathosoma of *Tetra retusa*: **d)** ventro-lateral view (female); **e)** lateral view (female); **f)** dorso-lateral view (larva); **g)** ventral view (female); **h)** ventral view (male); **d, e, f)** scale lines = 1 µm; **g, h)** scale lines = 10 µm.

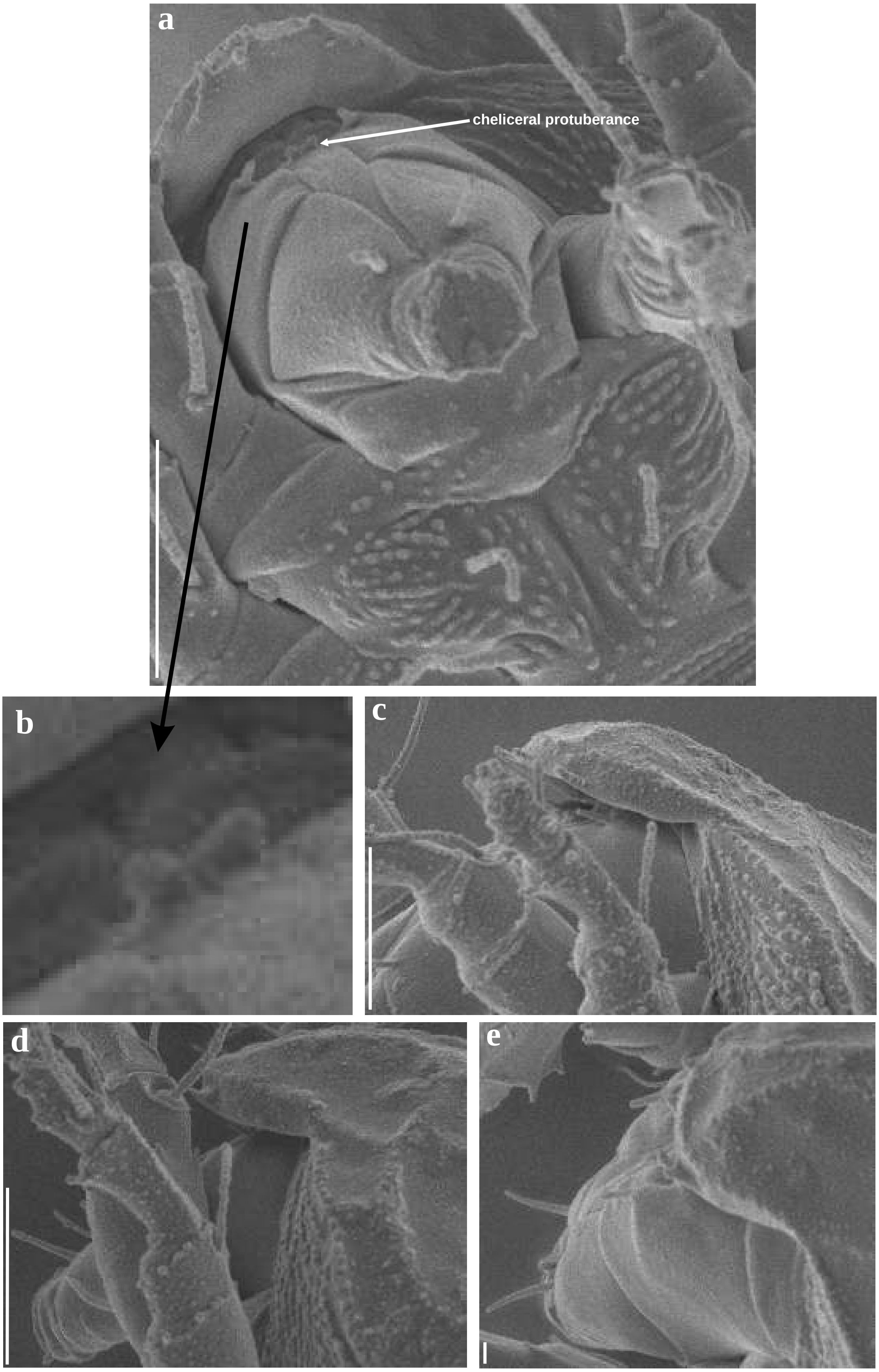


Fig. 3.71. Gnathosoma of *Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Chrysanthemoides monilifera* subsp. *monilifera*: **a)** dorso-ventral view (female); **b)** enlargement of cheliceral protuberances in Fig. 3.71a; **c, d)** lateral views (females); **e)** dorso-lateral view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

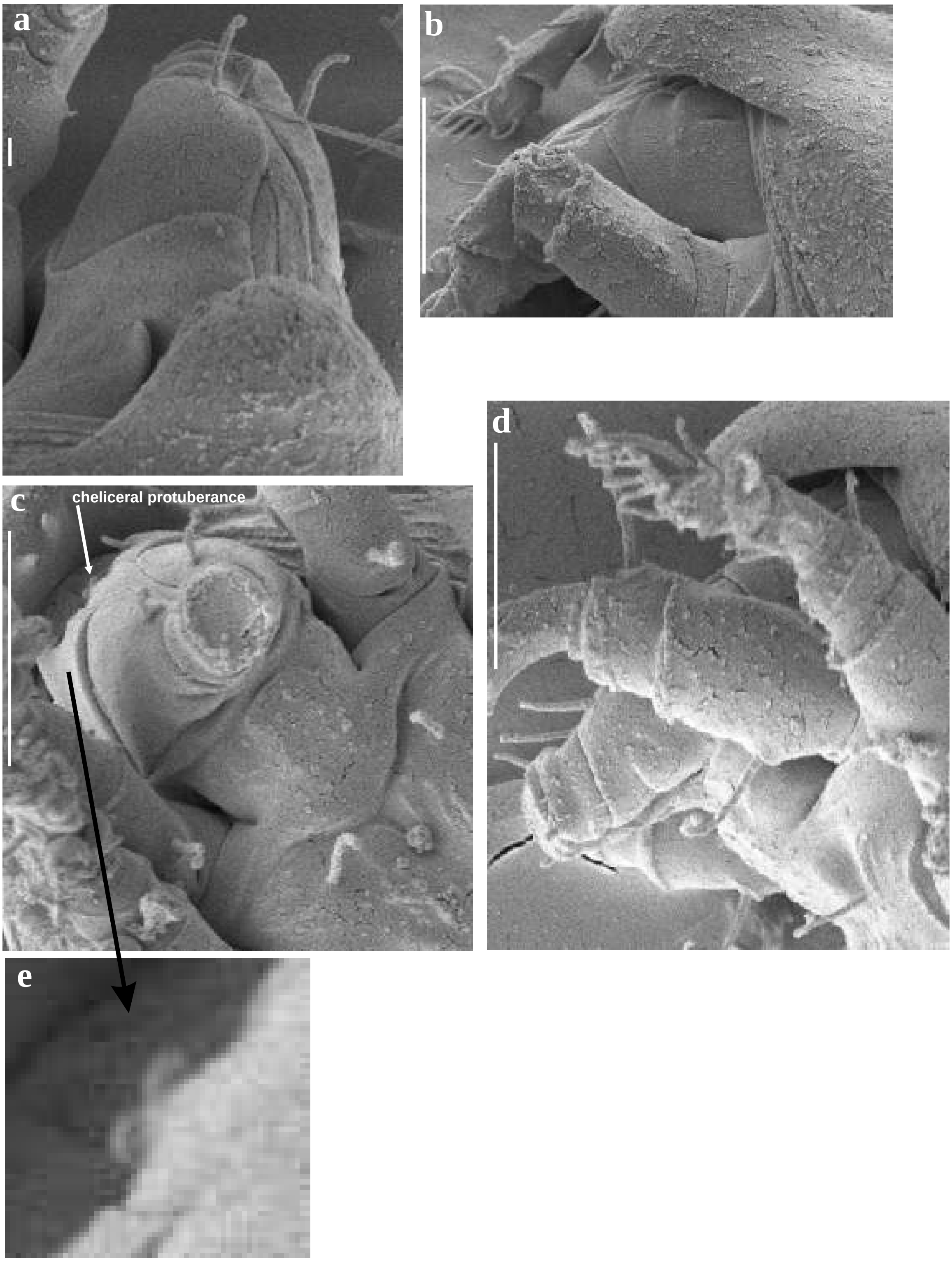
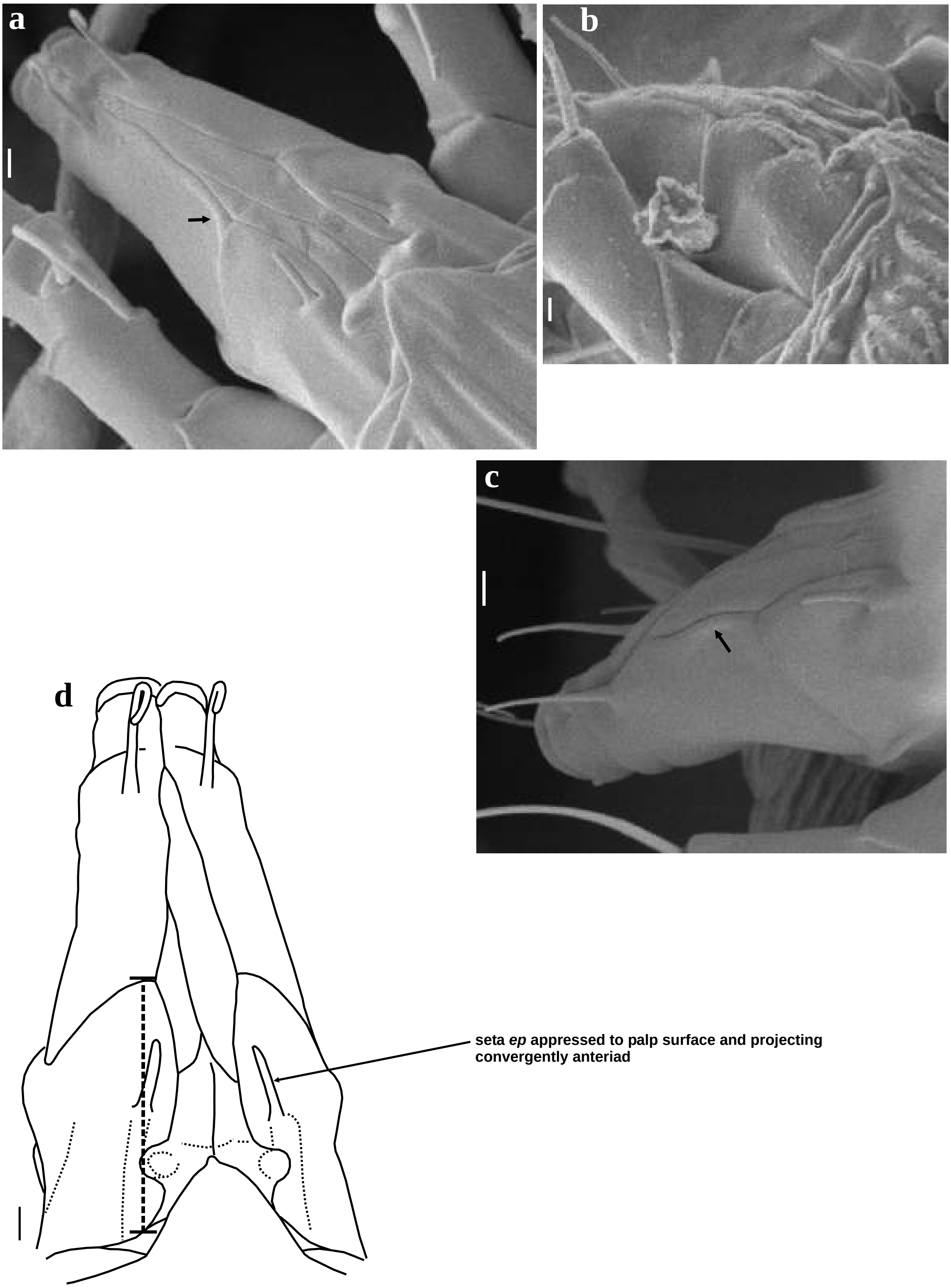


Fig. 3.72. Gnathosoma of *cf. Tetraspinus* sp. (Eriophyidae: Phyllocoptinae: Anthocoptini) from *Faurea rochetiana*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** lateral view (female); **c)** dorso-ventral view (female); **d)** lateral view (female); **e)** enlargement of cheliceral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



seta *ep* appressed to palp surface and projecting convergently anteriad

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.

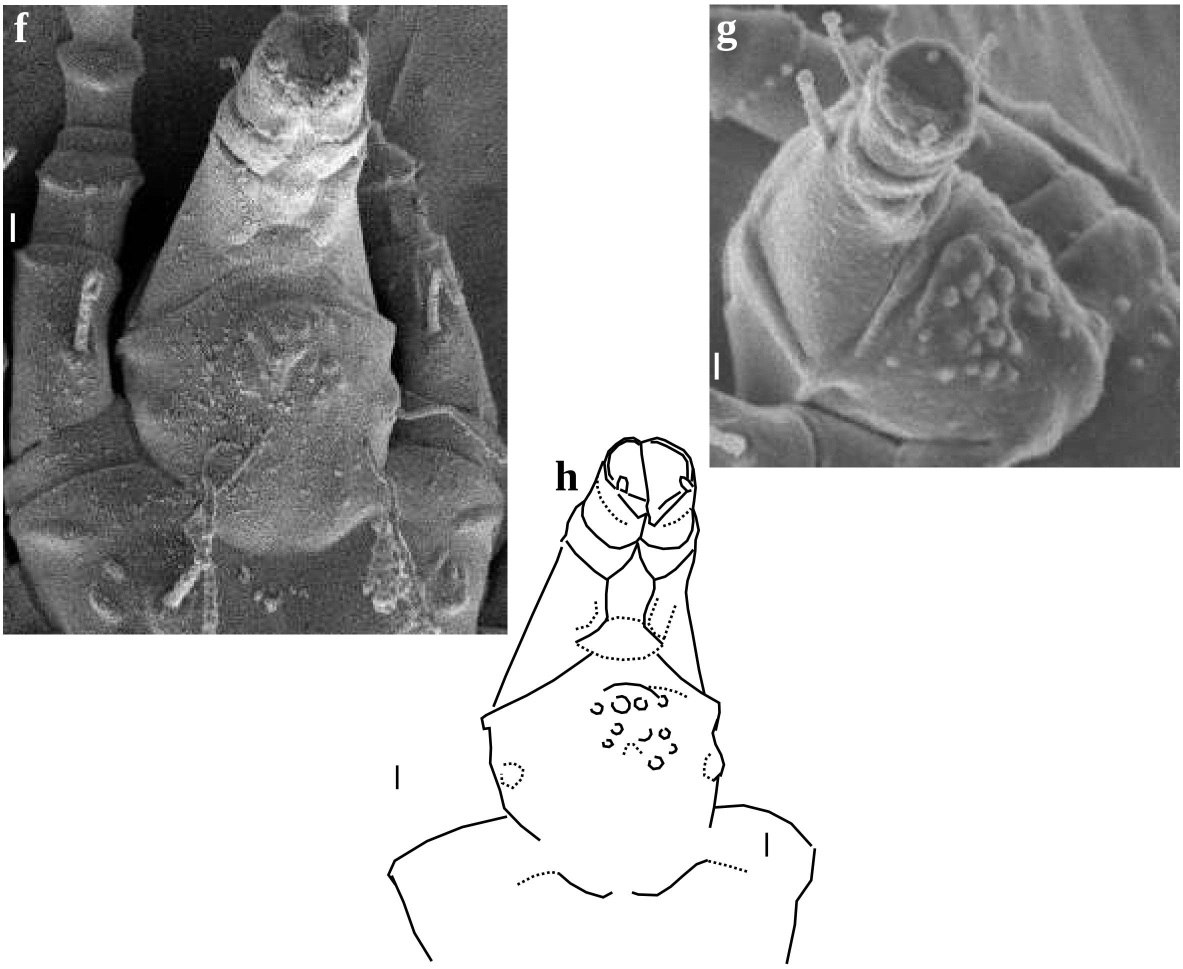


Fig. 3.73. (continued from previous page). Gnathosoma of a possibly new worm-like genus (Eriophyidae: Eriophyinae?: Aceriini?): f) ventral view (female); g) ventro-lateral view (male); h) line drawing of Fig. 3.73f. Scale lines = 1 µm.

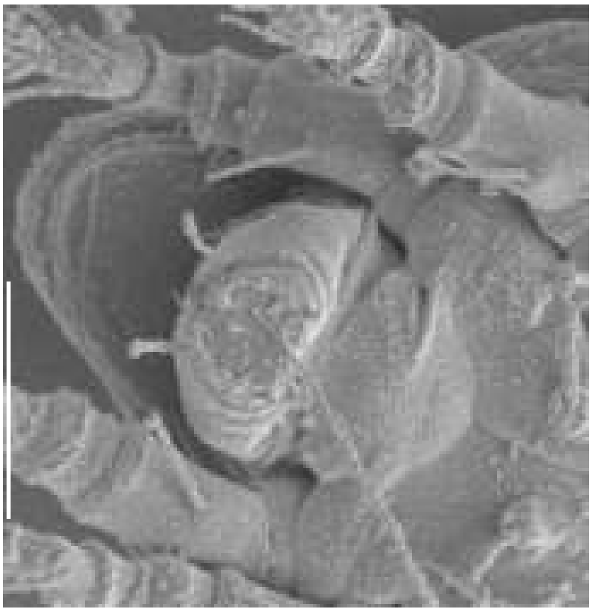


Fig. 3.74. Gnathosoma of an unknown genus (could not be identified) (Eriophyidae: Phyllocoptinae?) from *Ekebergia capensis*: ventral view (male). Scale line = 10 µm.

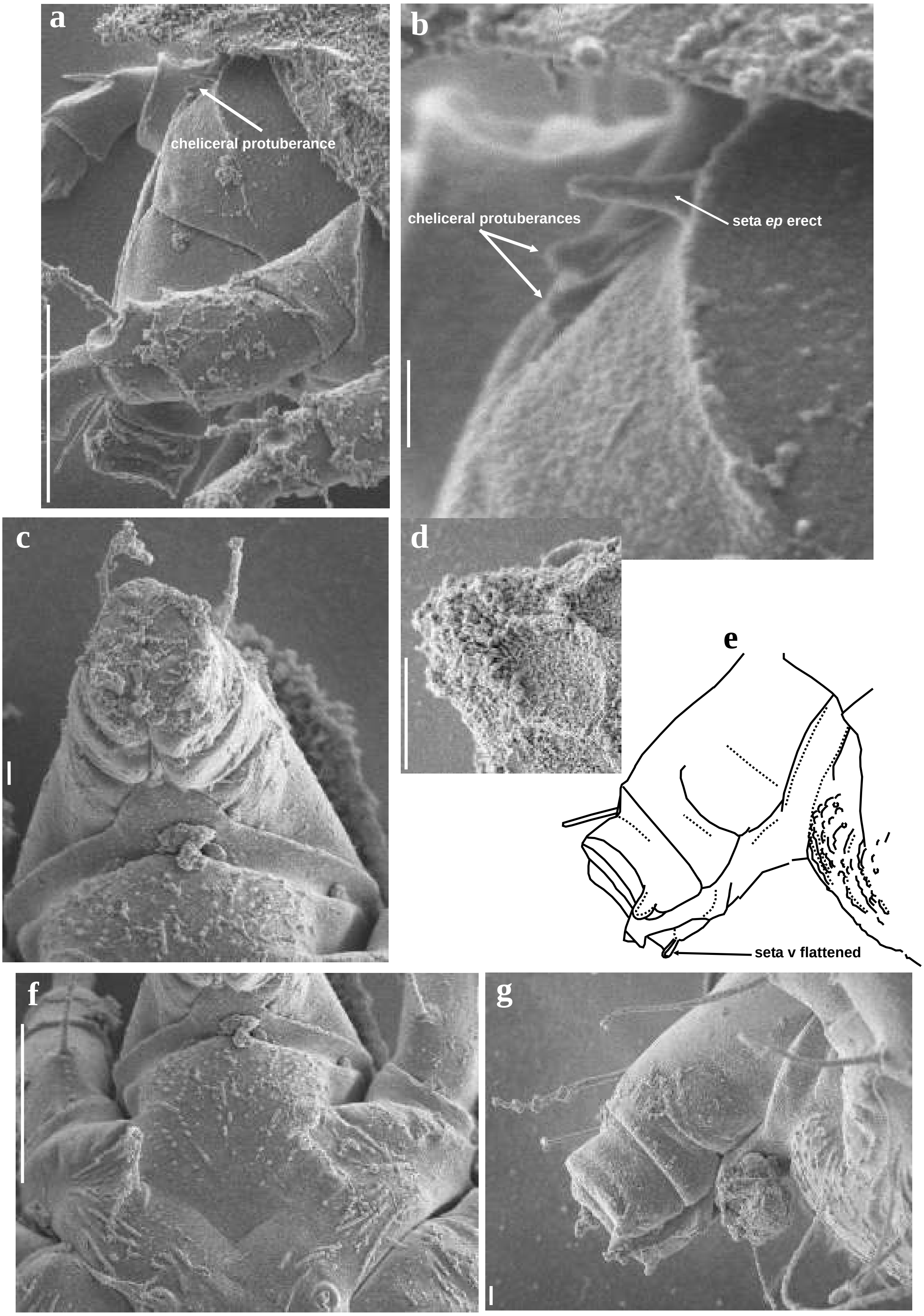


Fig. 3.75. Gnathosoma of a possibly new genus in the Phyllocoptinae or Cecidophyinae (Eriophyidae) from *Acacia burkei*: **a)** lateral view (possibly nymph); **b)** same specimen as in Fig. 3.75a, enlargement of cheliceral protuberances; **c, f)** ventral views of the same specimen (female); **d)** 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.

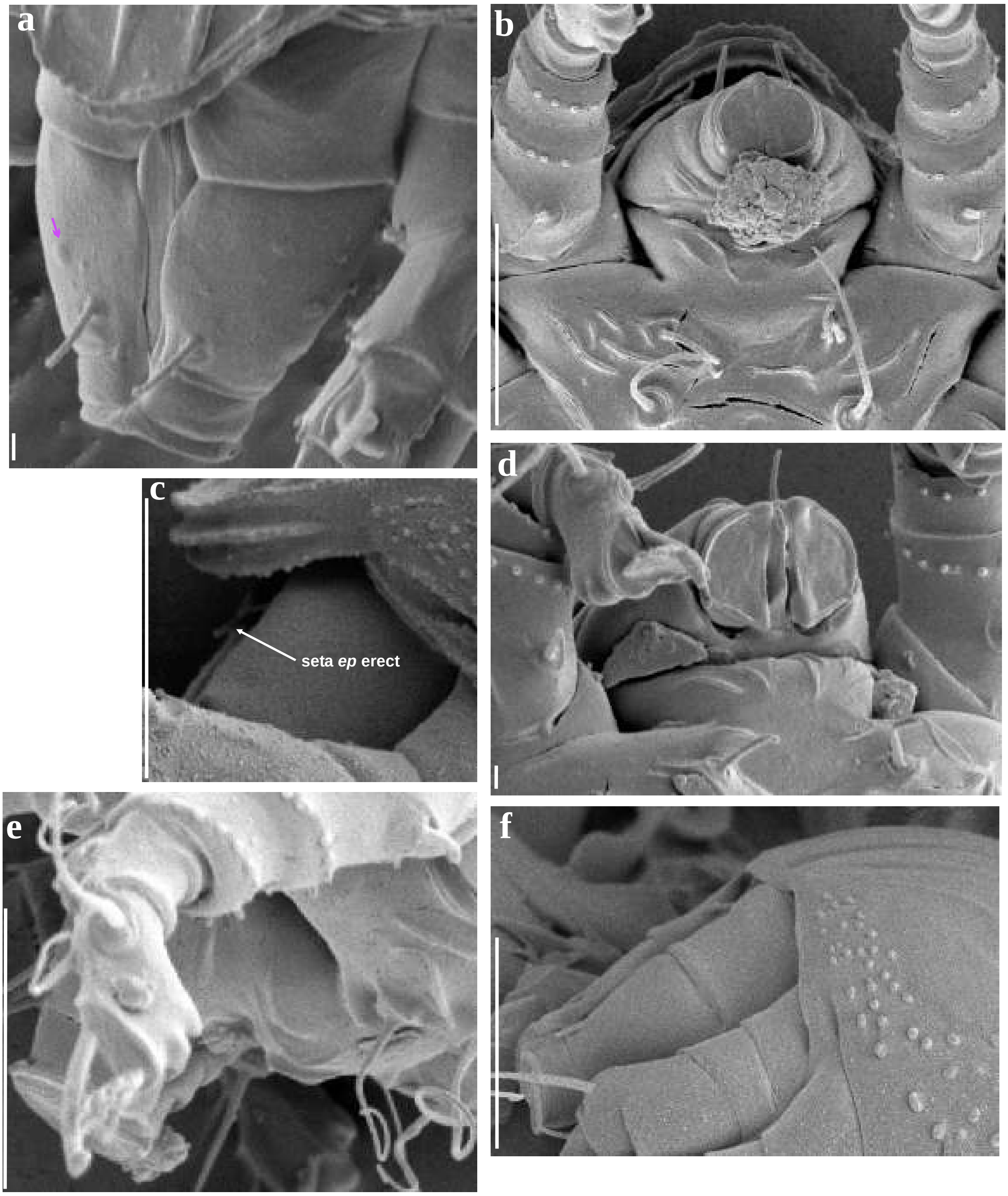


Fig. 3.76. Gnathosoma of *Phyllocoptes* sp. (Phyllocoptinae) or new genus (Cecidophyinae) from *Dovyalis zeyheri*: **a)** dorsal view, basal part of gnathosoma obscured by frontal lobe (probably adult, gender unknown); **b)** ventral view (male); **c)** lateral view of basal part of gnathosoma (female); **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.

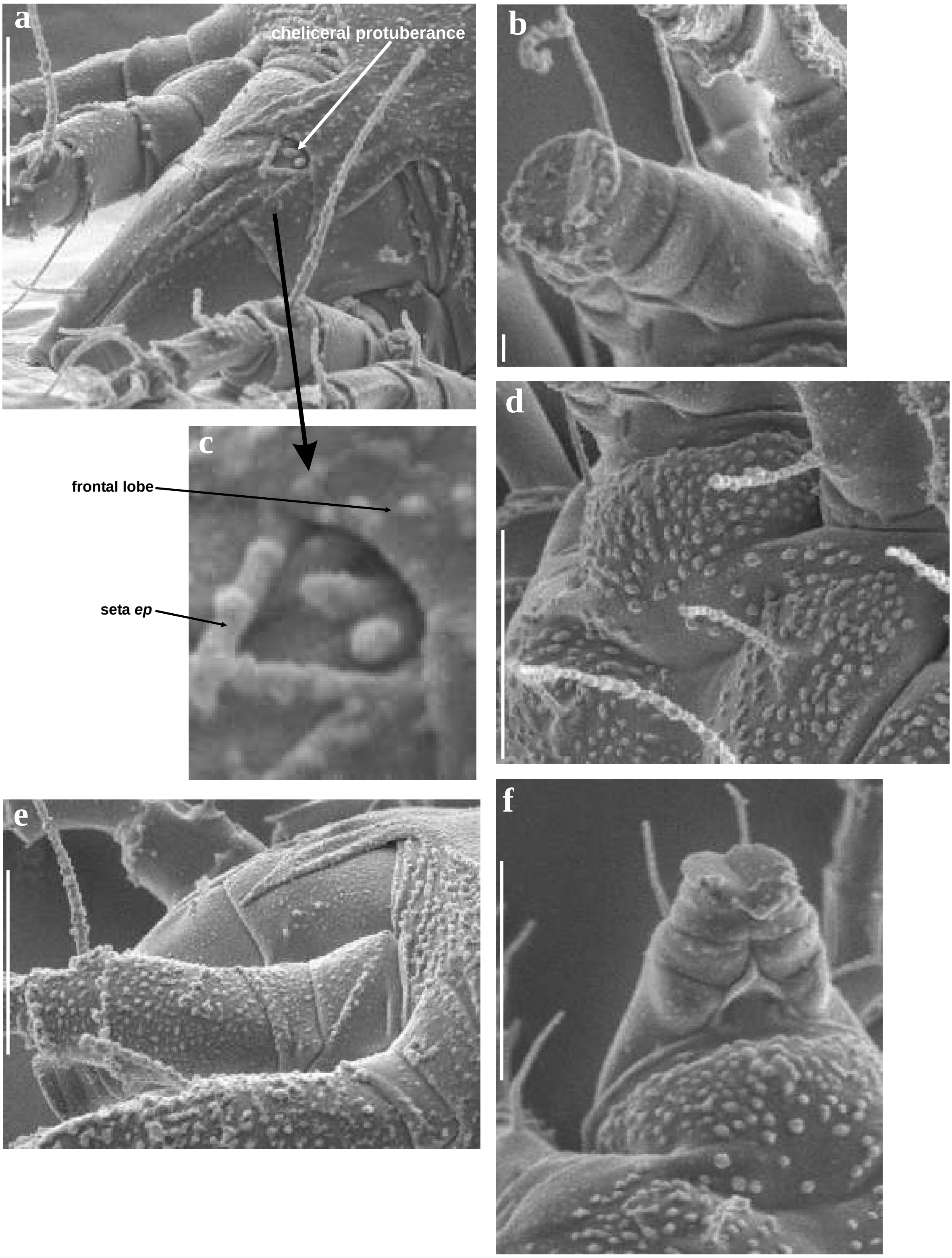


Fig. 3.77. Gnathosoma of a probably new genus (Eriophyidae, subfamily uncertain) from *Cussonia* sp. flowers: **a)** dorso-lateral view (probably adult, gender unknown); **b, d)** ventro-lateral views of the same specimen (female); **c)** enlargement of cheliceral protuberances in Fig. 3.77a; **e)**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

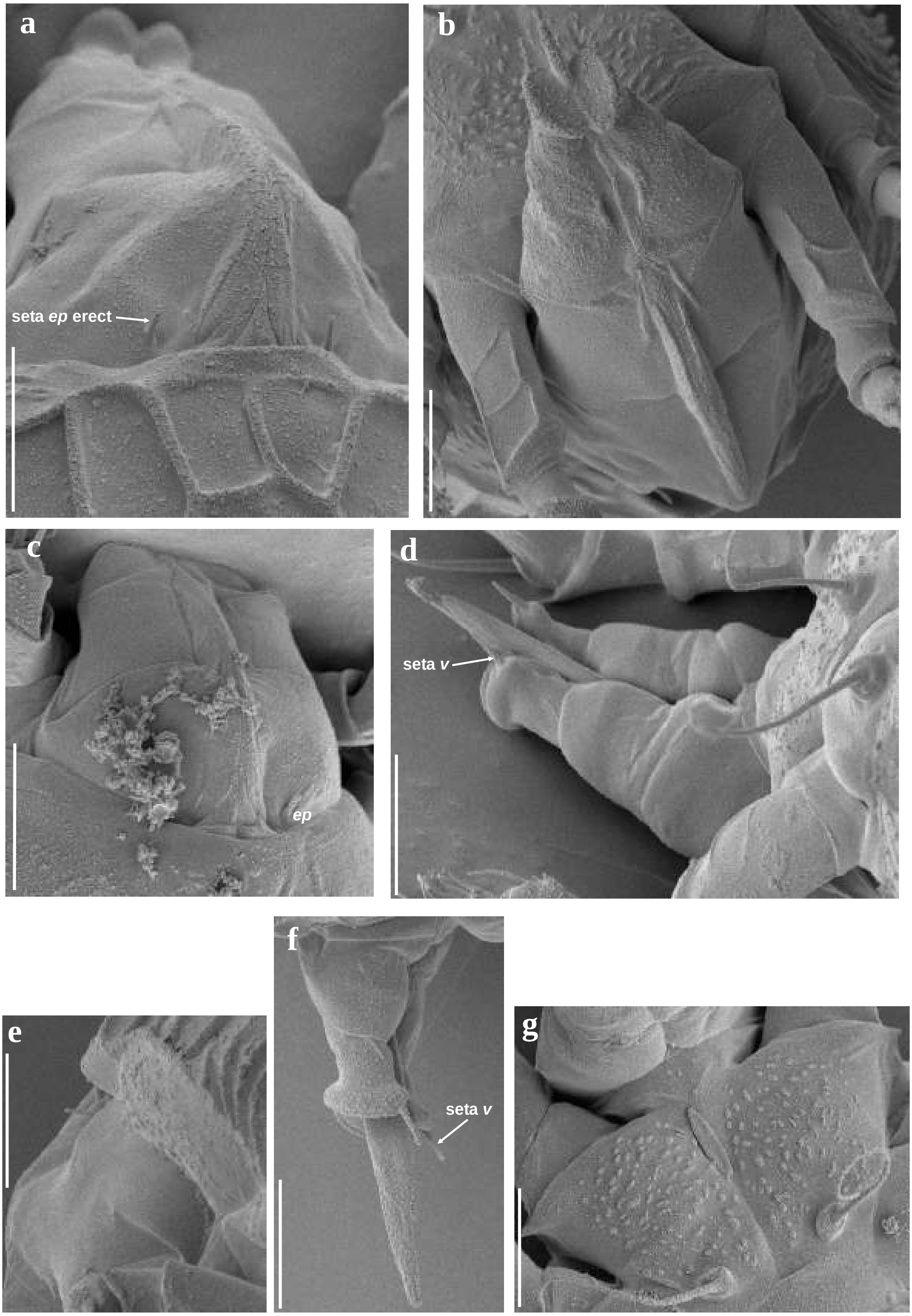


Fig. 3.78. Gnathosoma of *Diptilomiopus apobrevis* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Apodytes dimidiata*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorso-lateral view (larva); **d)** ventro-lateral view (female); **e)** lateral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

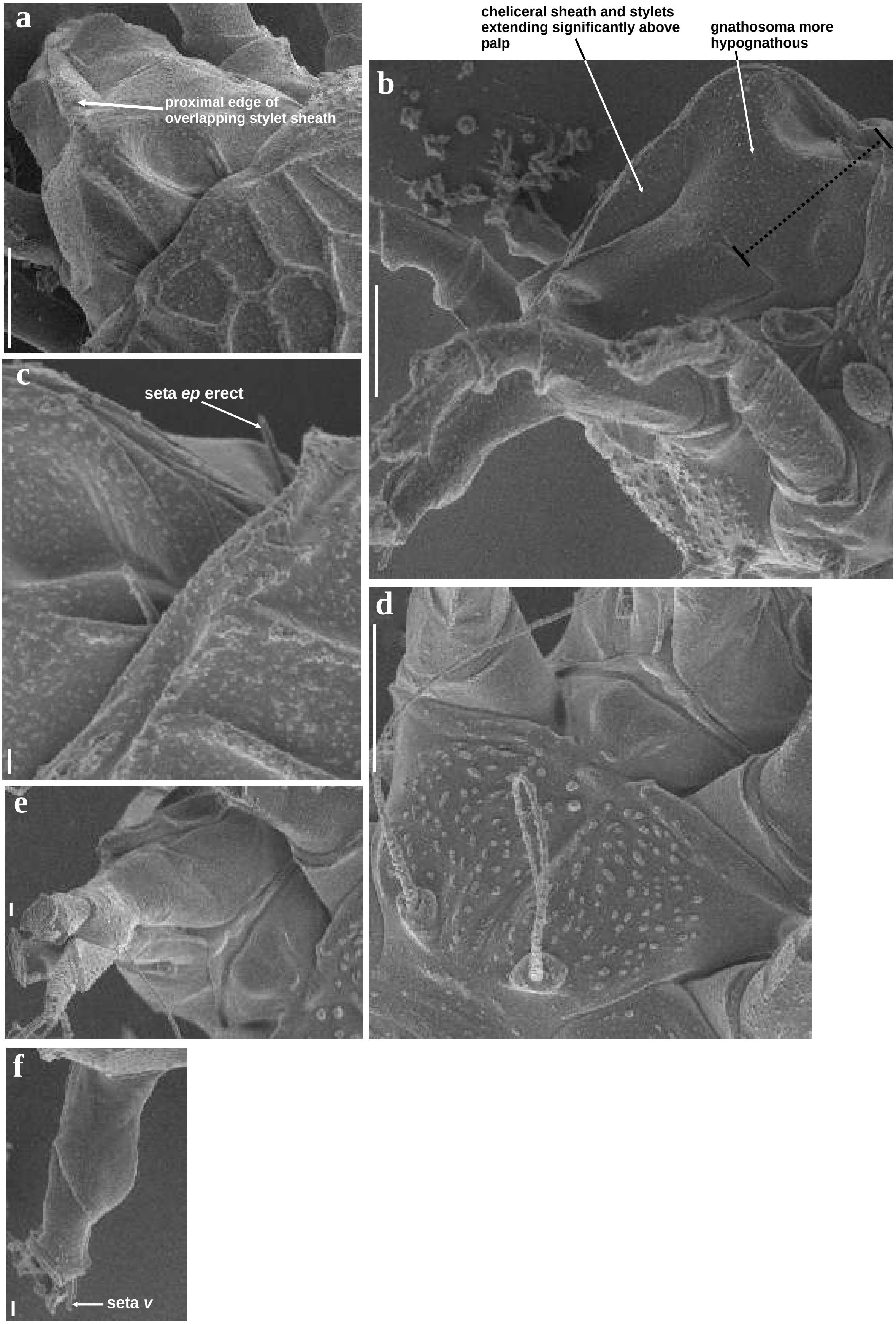


Fig. 3.79. Gnathosoma of *Diptilomiopus faurius* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Faurea rochetiana*: **a)** dorsal view (probably adult, gender unknown); **b)** lateral view (female), dashed black line indicates length of palpcoxal base; **c)** dorso-lateral view, basal part (female); **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.

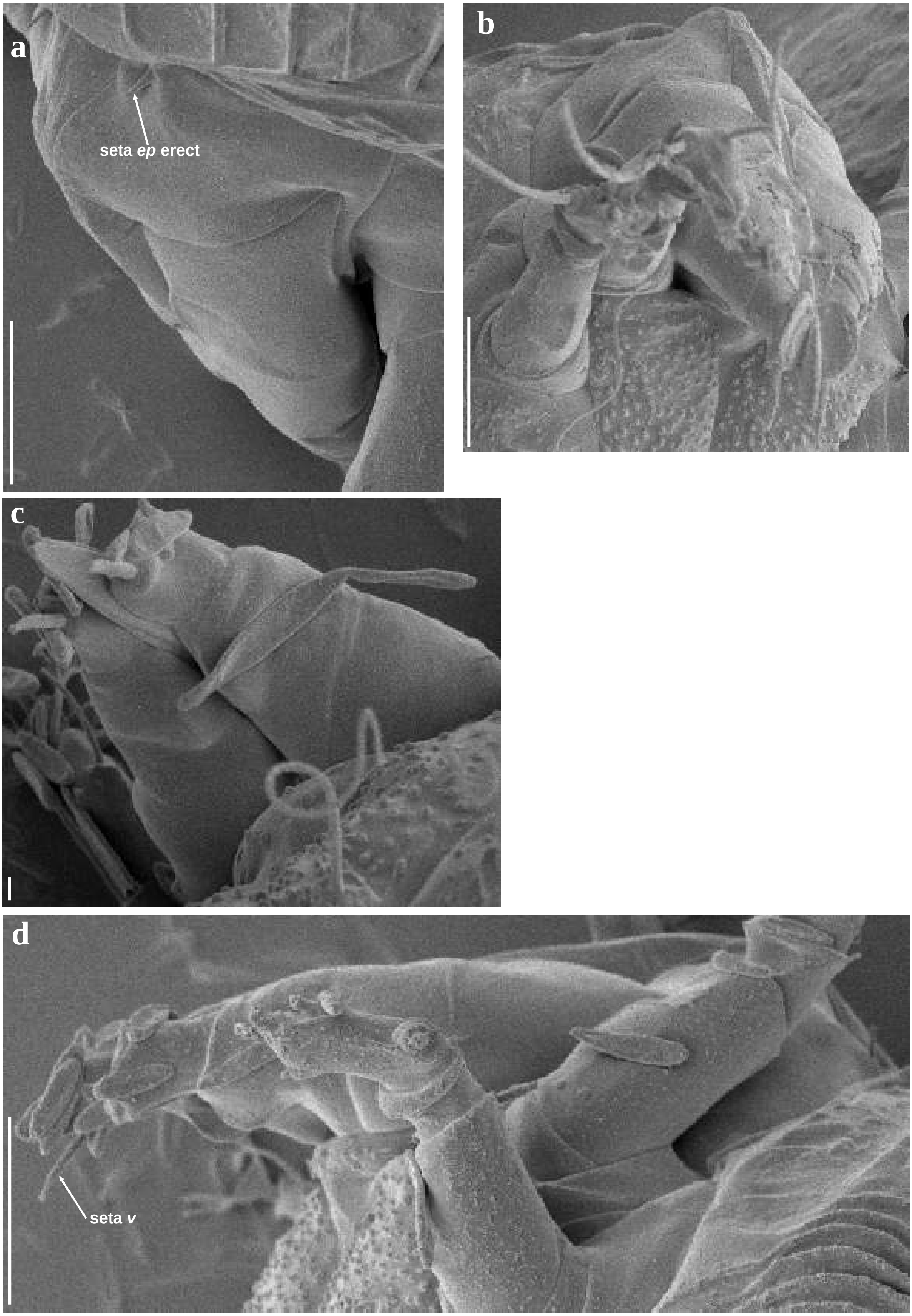


Fig. 3.80. Gnathosoma of unidentified species (genus and species could not be identified) (Diptilomiopidae: Diptilomiopinae) from *Xymalos monospora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** ventro-lateral view (female); **c)** ventral view (male); **d)** lateral view (female);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

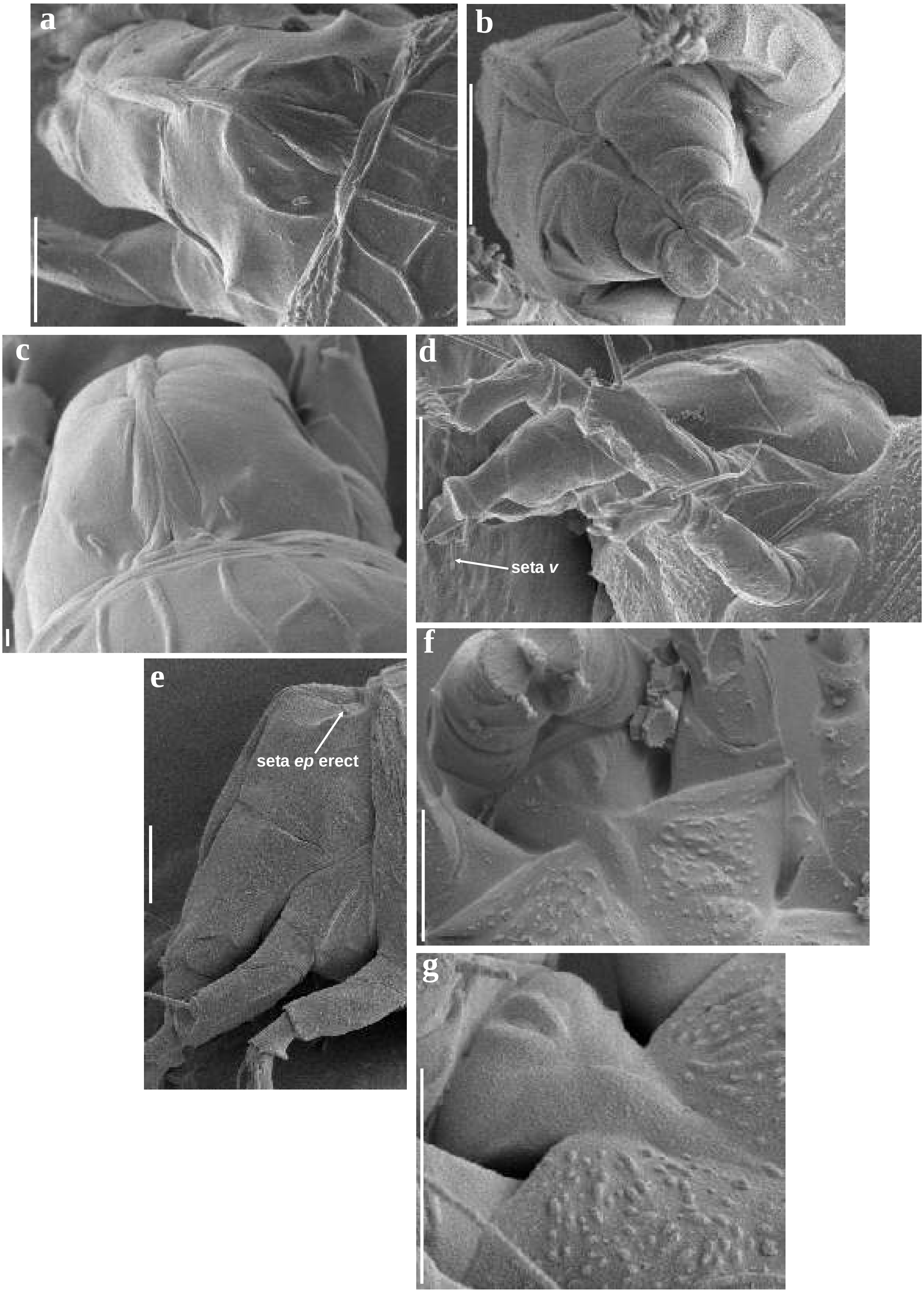


Fig. 3.81. Gnathosoma of probably a new genus nr. *Dacundiopus* (Diptilomiopidae: Diptilomiopinae), from *Mystroxylon aethiopicum*: **a)** dorsal view (probably adult, gender unknown); **b)** ventro-dorsal view (female); **c)** dorsal view (immature); **d, e)** lateral views (females); **f)** ventral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

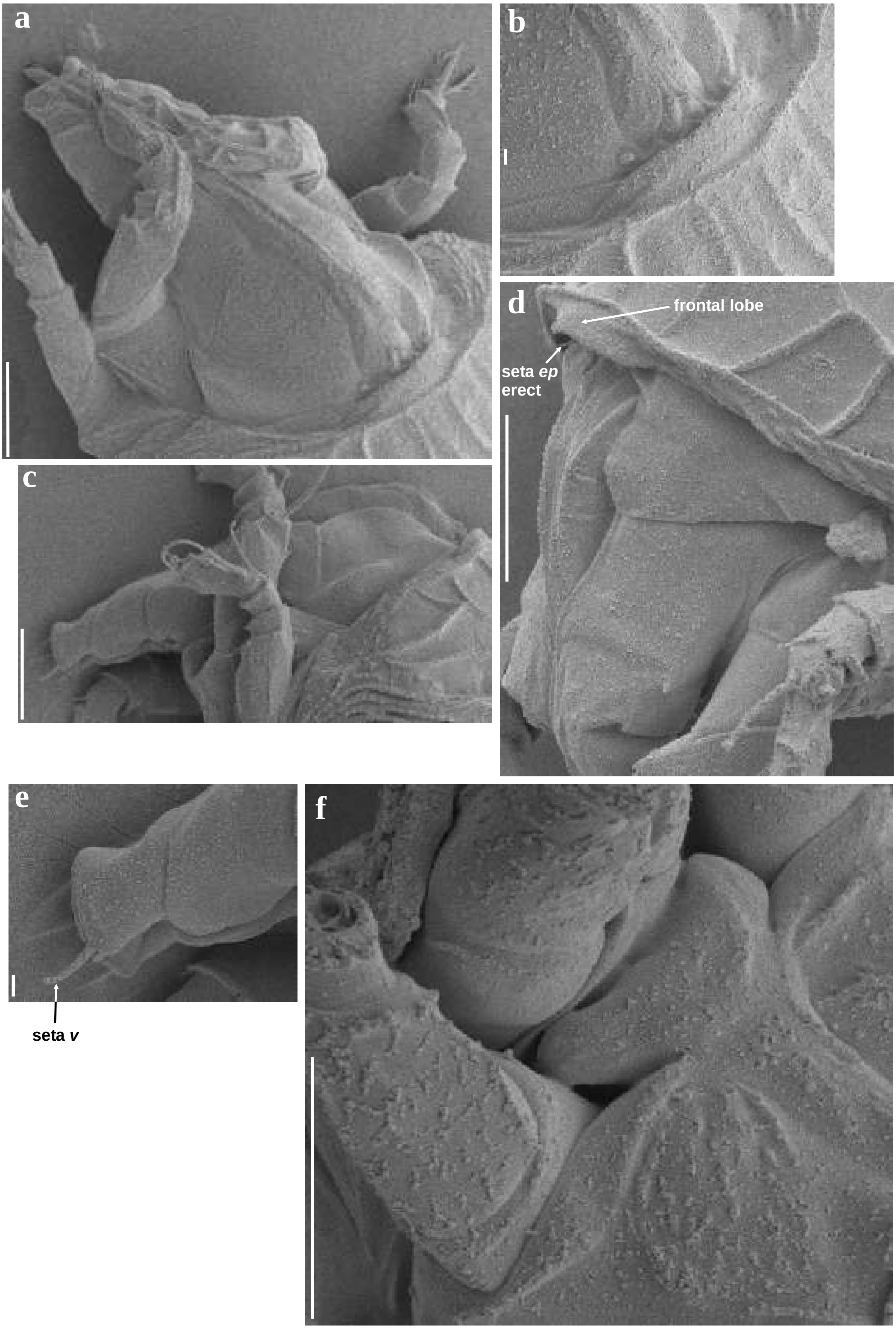


Fig. 3.82. Gnathosoma of *Rhynacus* sp. *cf. Rhynacus* sp. nov. (Diptilomiopidae: Diptilomiopinae) from *Dovyalis zeyheri*: **a, b)** dorso-lateral view and enlargement of the basal area respectively of the same specimen (probably adult, gender unknown); **c, e)** lateral view and enlargement of the 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.

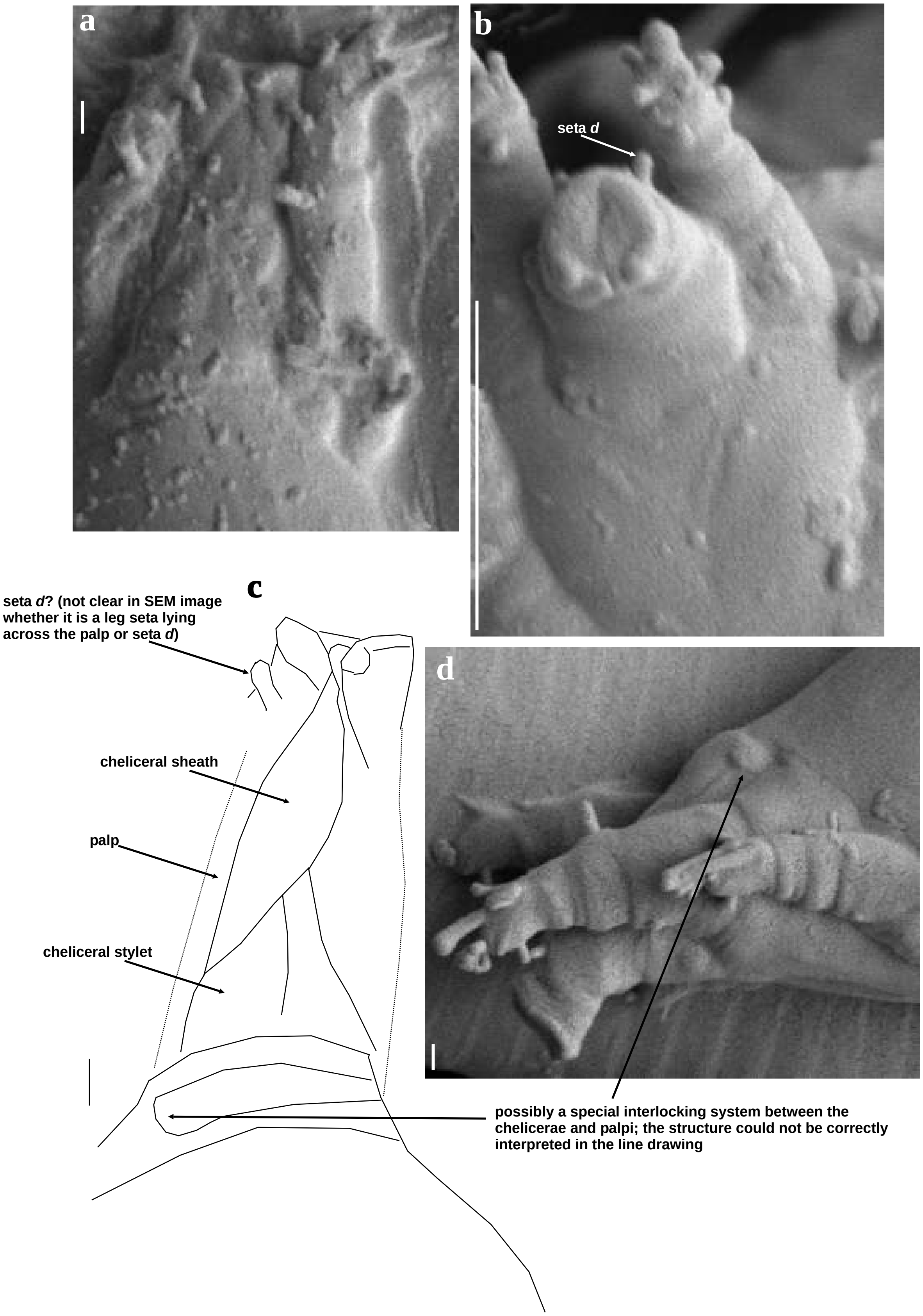


Fig. 3.83. Gnathosoma of probably a new genus (Eriophyidae) from *Searsia lancea* (previously *Rhus lancea*) leaf blisters: **a)** dorsal view (probably adult, gender unknown); **b)** ventral view (immature); **c)** preliminary attempt at a line drawing (which is probably still wrong and incomplete, 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.

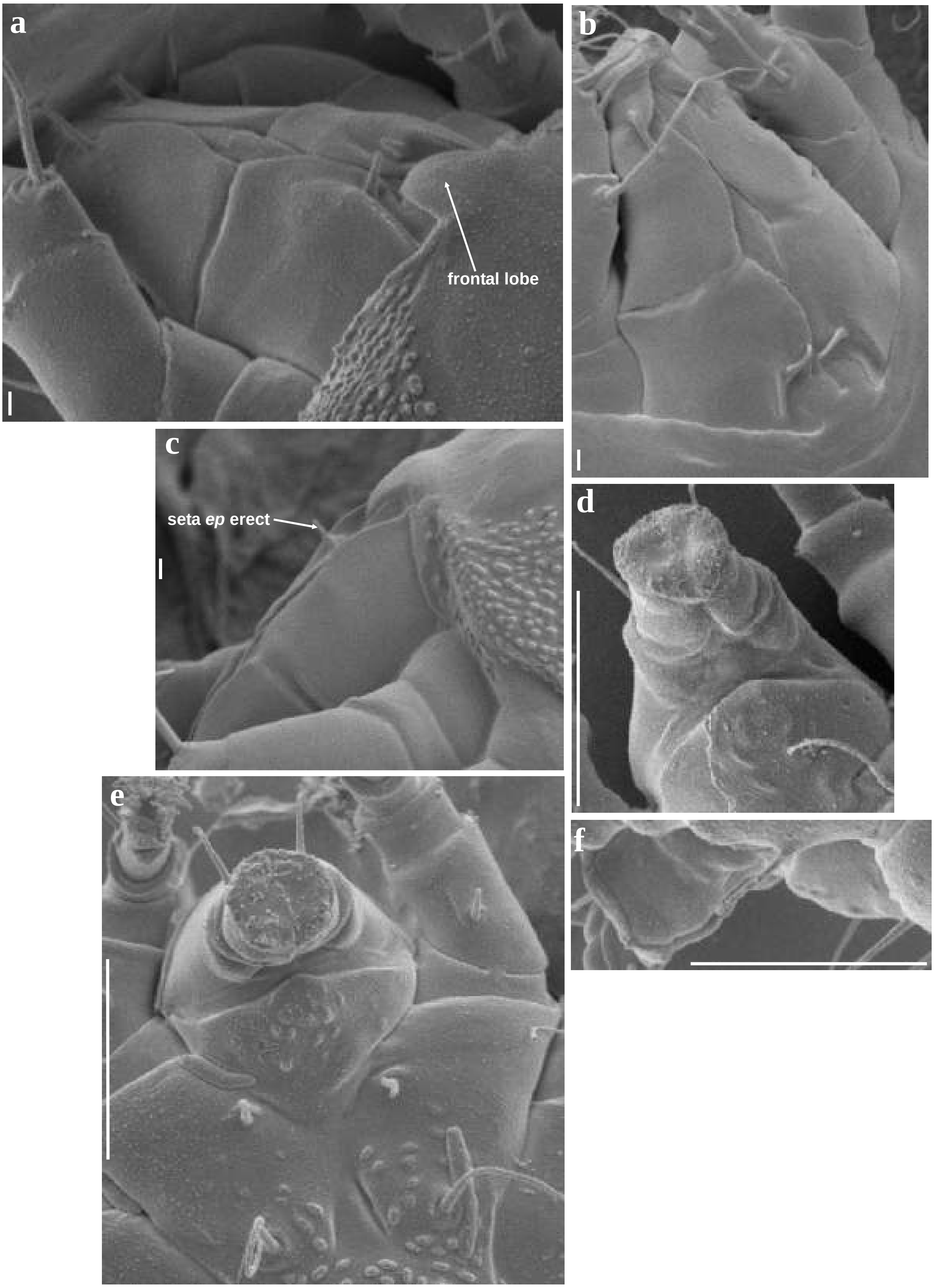


Fig. 3.84. Gnathosoma of unidentified morphospecies 2 (Eriophyoidae: Eriophyidae or Phytoptidae, but it is probably Eriophyidae) from green fruit of *Anthocleista grandiflora*: **a)** dorso-lateral view (probably adult, gender unknown); **b)** dorsal view (larva); **c, f)** lateral views of the same 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.

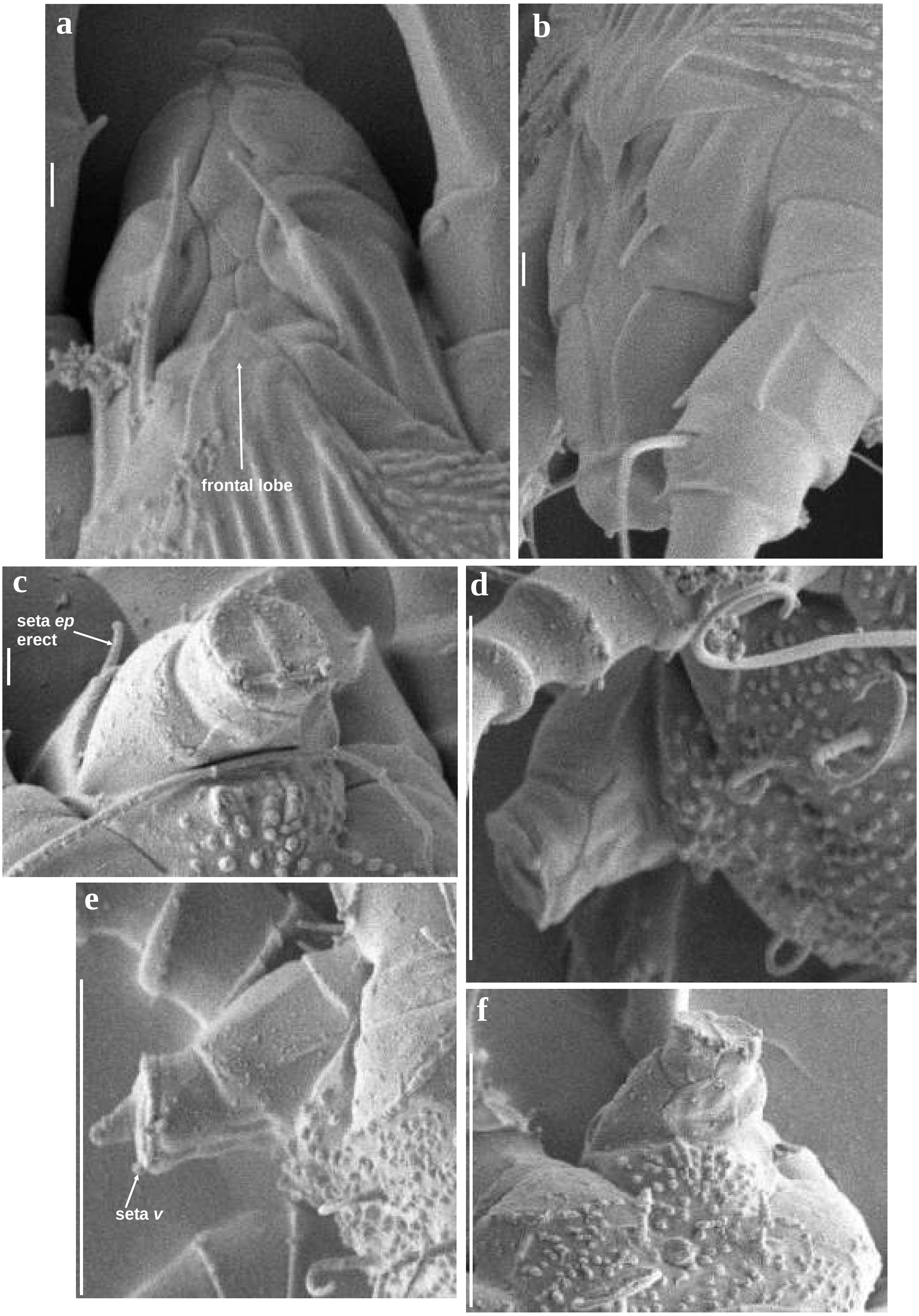


Fig. 3.85. Gnathosoma of unidentified species (genus and species could not be identified) (Eriophyoidea) from *Sideroxylon inerme* subsp. *inerme*: a) dorso-lateral view (probably adult, gender unknown); b) dorso-lateral view (female); c) ventro-lateral view (female); d) ventro-lateral view (female);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

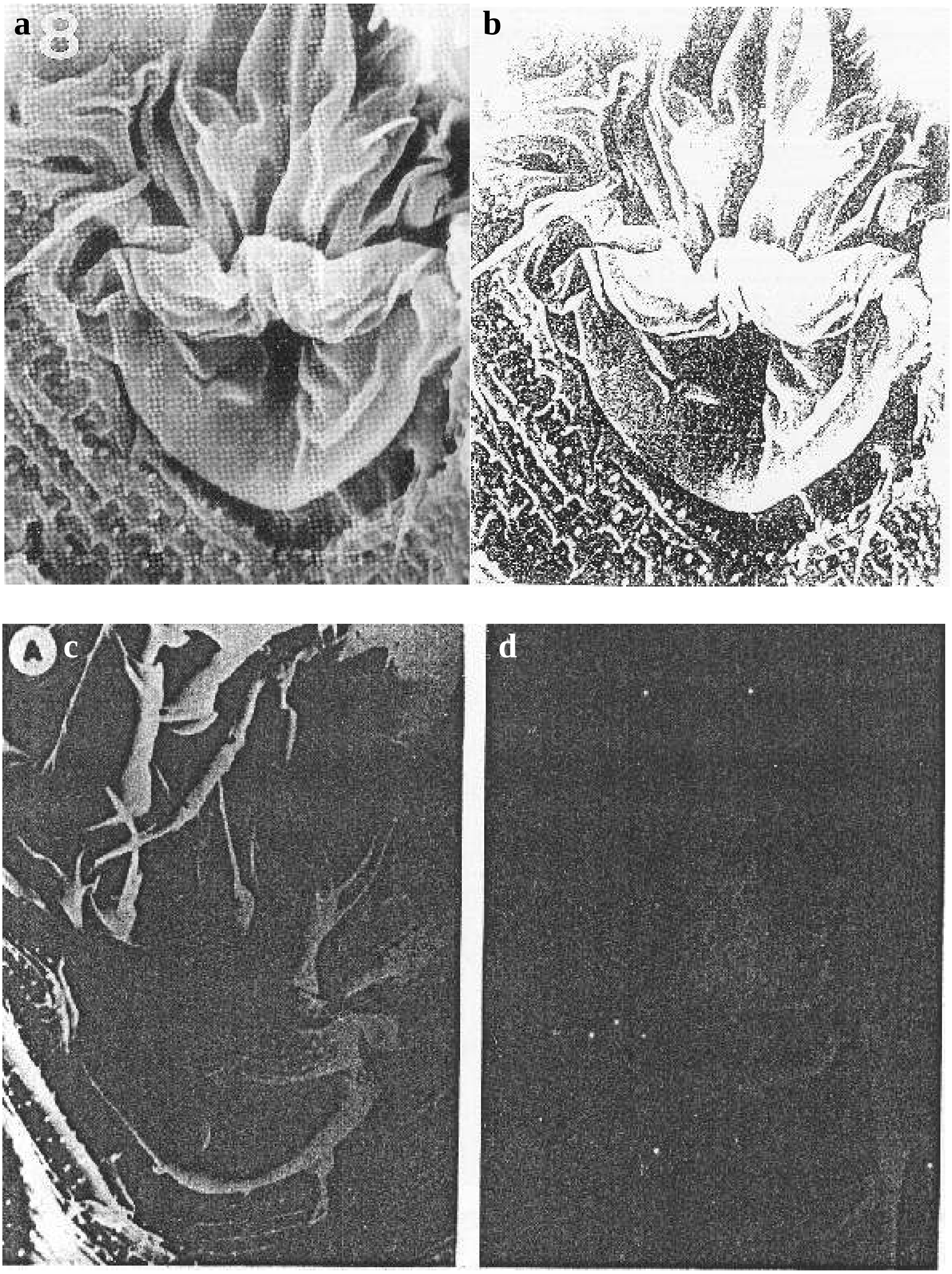


Fig. 3.86. Examples of loss of quality of SEM images of species in the current study, in the publishing and photocopying processes, all printed images scanned with the same scanner in Grayscale at a resolution of 200 dpi, and saved as *.tiff: **a)** original printed image Fig. 6, p. 232 in Huang (1992); **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.