CHAPTER 4

PHYLOGENY AND CLASSIFICATION OF THE ERIOPHYOIDEA

4.1 INTRODUCTION

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

4.1.1 Eriophyoid classifications

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

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

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

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

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

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

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

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

4.1.2 Different eriophyoid life forms in classification and phylogeny

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

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

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

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

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

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

4.1.3 Phylogeny

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.1.3.2 Relationship of the Eriophyoidea with other mite groups

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

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

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

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

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

4.1.3.3 Phenetic and phylogenetic analyses

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.2 MATERIAL AND METHODS

4.2.1 Taxon sampling

4.2.1.1 Ingroup taxa

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

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

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

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

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

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

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

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

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

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

4.2.1.2 Outgroup taxa

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

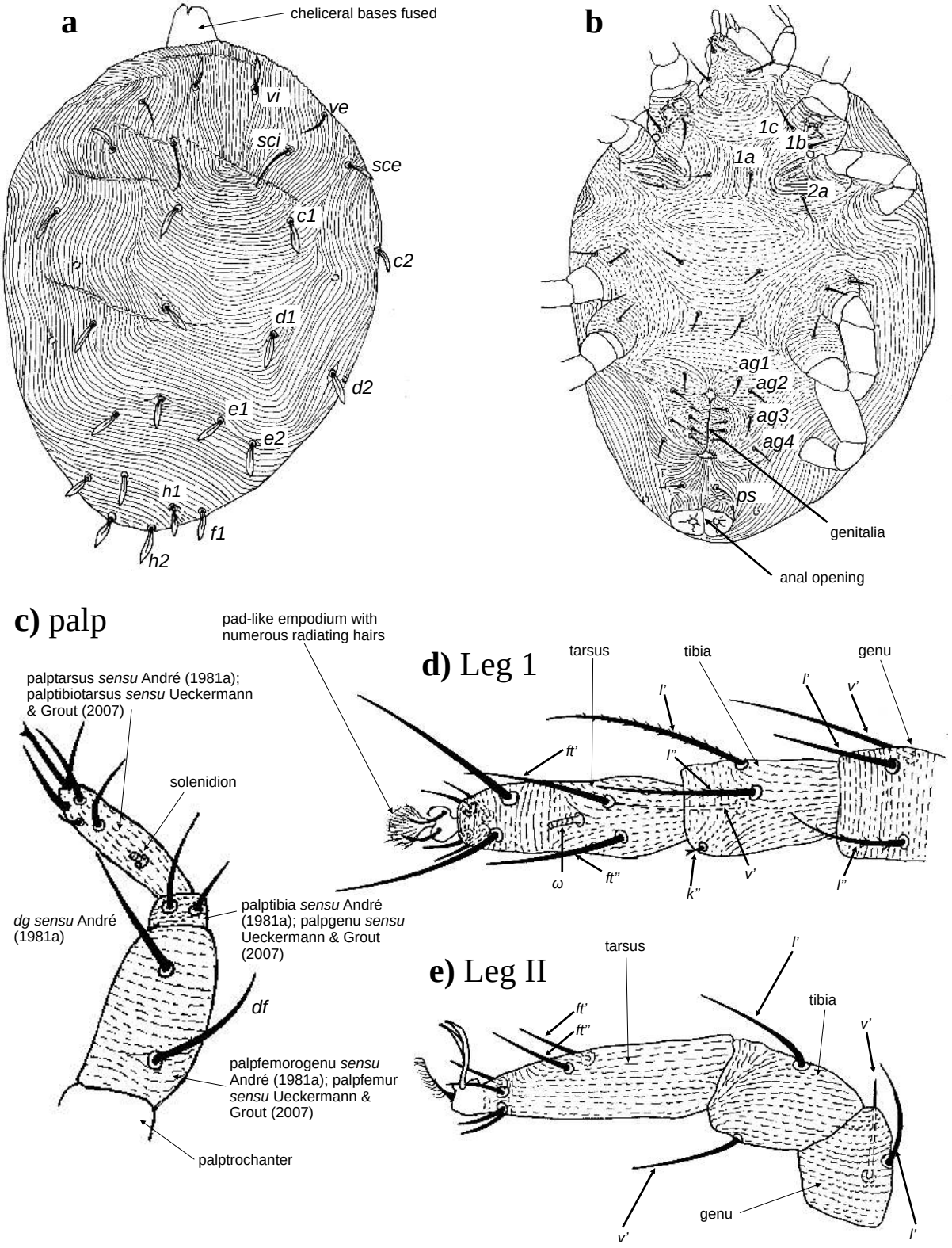

Fig. 4.1. *Orfareptydeus stepheni* Ueckermann & Grout, 2007 (Tydeidae: Tydeinae). Female: **a)** dorsal view; **b)** ventral view; **c)** palp; **d)** leg I; **e)** leg II. Original drawings in Ueckermann & Grout (2007), used with permission.

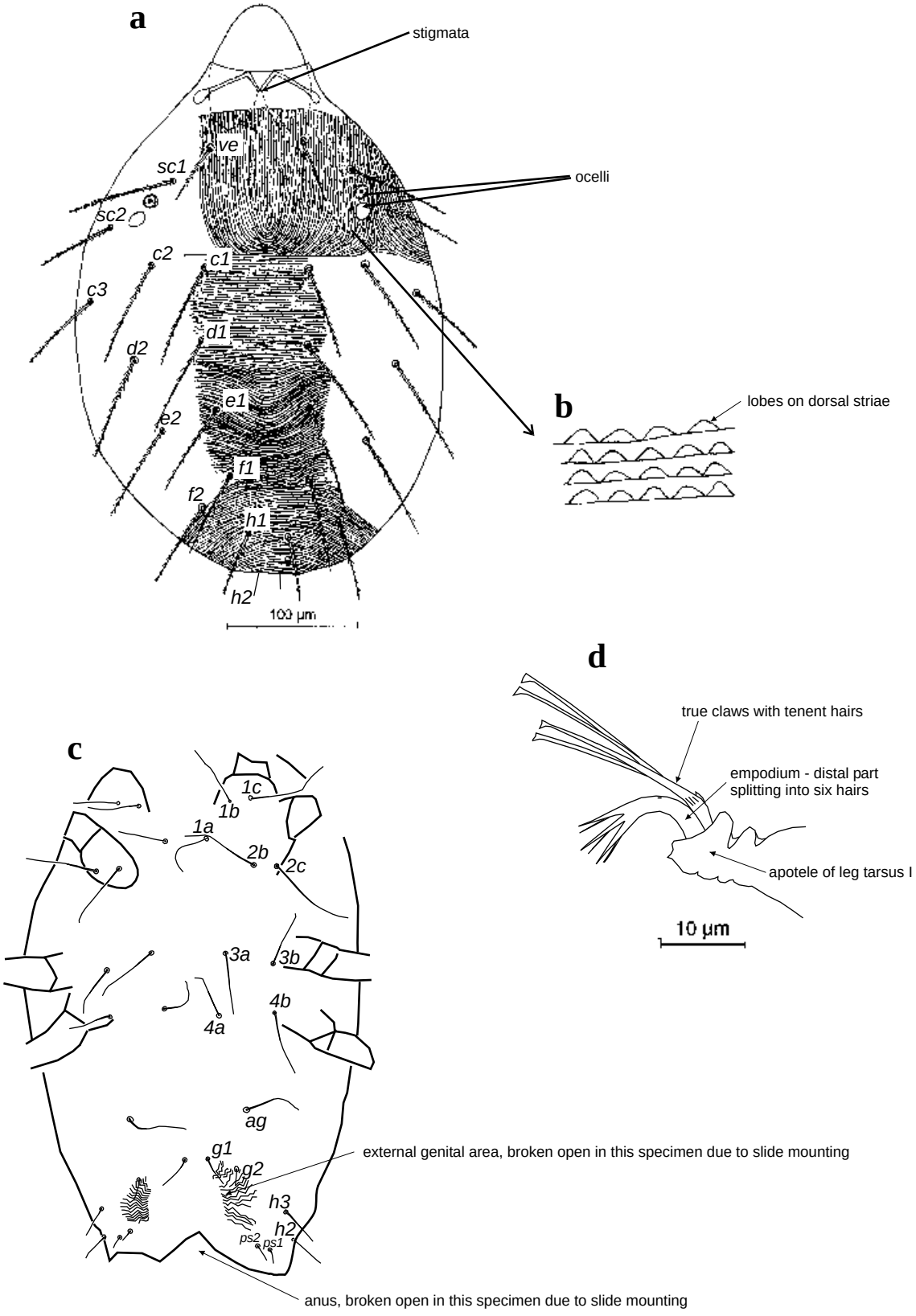

Fig. 4.2. *Mononychellus yemensis* Meyer, 1996 (Tetranychidae). Female: **a)** dorsal view [setae *h2* not included in original drawing by Meyer (1996)]; **b)** enlargement of lobes on dorsal striae; **c)** ventral view; **d)** apotele of tarsus I. Drawings a, b and d modified from Meyer (1996), drawing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

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

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

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4.2.2 Character sampling

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

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

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

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

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

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

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

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

4.2.4 Character scoring and coding

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

4.2.5 Phylogenetic analyses

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

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

4.2.5.1 Different weighting schemes

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

4.2.5.2 Analyses of the 318-taxon data matrix

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

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

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

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

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

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

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

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

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

4.2.5.3 Analyses of the 66-taxon data matrix

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

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

4.2.5.4 Analyses of the 18-taxon data matrices

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

4.2.6 Presentation of trees (cladograms)

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

4.2.7 Group support

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

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

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

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

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

4.3 RESULTS AND DISCUSSION: PREFERRED TREES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

   Trees obtained during this study:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.4 RESULTS AND DISCUSSION: MATERIAL AND METHODS

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

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

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

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

though. The character states they scored for the outgroup were more similar to scoring a hypothetical outgroup than scoring a real Tydeidae exemplar. For example, among many other examples, they coded the body shape of the outgroup to be worm-like, and not rounded or oval as the body of the Tydeidae is in reality.

They reportedly determined character states by examining specimens and original descriptions, but did not specify of what genera and what species within the genera they investigated specimens, and some of the characters were scored erroneously. They stated that all characters were ordered except character 5 (the presence of the frontal lobe). However, this character is binary, and being ordered or unordered is not applicable, and the state transformation is treated in the same way in either scenario. In practice, all the multistate characters in their analysis were thus set as being ordered.

Polymorphic characters were scored and dealt with as unknown (coded as "?") characters in the data matrix constructed by Hong & Zhang (1996a), because the programs then could not analyse these characters. Today, algorithms, for example, those used in Nona and TNT, are able to handle and analyse polymorphic characters.

They analysed the character state matrix with parsimony analysis in PAUP 3.0 (Swofford, 1991), using the "branch-and-bound" procedure. With equal weighting the result was 33 shortest (most parsimonious) trees with length 79, CI 0.506 and RI 0.606. In the current analysis, analysing the exact same data matrix, with equal weighting of characters, the implicit enumeration algorithm (similar to "branch-and-bound" in Paup) in TNT produced three shortest trees with length 77, CI 0.519 (with uninformative characters included, probably the same way Hong & Zhang (1996a) determined the CI), CI 0.46 (calculated with exclusion of the uninformative characters) and RI 0.63 (Table 4.4). The trees from the current re-analyses are more parsimonious with slightly higher CI (when uninformative characters were included) and RI, and thus is a better result.

After analysing the data under equal character weighting, Hong & Zhang (1996a) proceeded by weighting the characters with successive weighting (Farris, 1969, 1988), with a result of three equally parsimonious trees after the first and second reweighting, using the "branch-and-bound" procedure. The strict consensus tree of these was presented as their preferred tree (Fig. 4.3a). They did not report the length or any other tree statistics and support estimations of the three most parsimonious trees, or the resultant consensus tree, and no comparison of these statistics can be made with the re-analysed results in the present study.

The strict consensus of the three equally parsimonious trees found in the present re-analyses under equal character weights is presented in Fig. 4.3b. The unchanged data matrix of Hong & Zhang (1996a)

was further re-analysed with implicit enumeration searches in TNT under implied character weighting with k set to the values 999, 100, 50, 30, 20, 10, 3 and 0.1 (Table 4.4). See the discussion of implied weighting further on for more detail about the implied weighting method.

The preferred tree for the present re-analyses is the tree found under character weighting with k = 999 (Fig. 4.3c). This tree has the same topology as one of the three most parsimonious trees found in the re-analysis under equal weighting, and the one tree found in each analyses with implied weighting of characters with k = 100, 50, 30, 20, 15 and 10 (Table 4.4). The tree found under implied character weighting with k = 3 is also presented (Fig. 4.3d) to present an alternative topology found under heavier weighting against homoplasy for comparison with the tree presented by Hong & Zhang (1996a) and with the preferred tree of the present analyses, to study the type of influence different amounts of weighting against homoplasy (less homoplasy allowed), may have on results.

The topologies of the preferred tree of Hong & Zhang (1996a) (18PublishedHZ96 tree, Fig. 4.3a) and the preferred tree of the present study (18orig-k999 tree, Fig. 4.3c), and the tree obtained under implied character weighting with k = 3 (18orig-k3 tree, Fig. 4.3d) obtained from the same data matrix, differ. The overall retrieval of the families in groups is more or less the same in the trees. Diptilomiopidae was retrieved as a monophyletic group, with the same internal topology in all three trees. The Phytoptidae was never retrieved as one group or clade, but most Phytoptidae taxa are at the base of the trees, with some of them outside a group with the remainder of the Eriophyoidea, but with relationships unresolved between them and the Eriophyoidea group. *Sierraphytoptus* groups with Eriophyidae taxa in the 18PublishedHZ96 tree (Fig. 4.3a) and the 18orig-k999 tree (Fig. 4.3c), but is positioned outside a clade with the Diptilomiopidae and Eriophyidae in the 18orig-k3 tree (Fig. 4.3d). The Eriophyidae was never retrieved as a monophyletic group, and usually was found in one group with the Diptilomiopidae clade, with or without *Sierraphytoptus* included.

Seven clades were found in the 18PublishedHZ96 and 18orig-k3 trees, supported by nine and seven synapomorphies, respectively. Four clades were found in the 18orig-k999 tree supported by four synapomorphies. These include the Diptilomiopidae clade found in all three trees. Additionally, within the Diptilomiopidae clade *Diptacus–Diptilomiopus* was found as a clade, positioned within the Eriophyidae. *Aberoptus–Cecidophyes* was retrieved as a clade in all three trees. Within the Eriophyidae, the positions of *Ashieldophyes* (either found grouping with *Sierraphytoptus*, or with *Nothopoda* constituting a clade), *Phyllocoptes* (either found grouping with *Sierraphytoptus*, or with *Sierraphytoptus–Ashieldophyes*, or as a single species within a clade with all Diptilomiopidae and Eriophyidae, but with its relationship with these taxa unresolved), *Nothopoda* (either found to group with *Eriophyes*, or with *Ashieldophyes* constituting a clade). There are other topology differences within the Eriophyidae which include different relationships between smaller groupings or clades, and

the relationships between the Eriophyidae taxa and the Diptilomiopidae clade, and the inclusion or exclusion of *Sierraphytoptus*.

The largest differences between the three trees are in the basal topology, entailing relationships between the Phytoptidae taxa, and the positions of these taxa. Except for *Sierraphytoptus*, they are all basal in the three trees and outside the group comprising the remainder of the Eriophyoidea in the data set.

The differences include the positions and relationships of the only three genera (*Trisetacus*, *Nalepella* and *Pentasetacus*) of the Nalepellinae in the data set. In the tree presented by Hong & Zhang (1996a) [the 18PublishedHZ96 tree (Fig. 4.3a)], *Pentasetacus*, *Mackiella, Novophytoptus* and *Phytoptus* are outside a clade which includes *Trisetacus* and *Nalepella* and the remainder of the Eriophyoidea, with relationships between the clade and genera outside the clade unresolved. *Pentasetacus* may be sister to a *Novophytoptus-Mackiella* group, and *Nalepella* is sister to a clade constituting the Diptilomiopidae, Eriophyidae and *Sierraphytoptus*, and *Trisetacus* a basal sister to *Nalepella*. In the preferred tree of the re-analyses [18orig-k999 tree (Fig. 4.3c)], *Pentasetacus*, *Trisetacus*, *Novophytoptus* and *Phytoptus*, with relationships between them unresolved, are outside a group with the remainder of the Eriophyoidea, which include a group constituting the Diptilomiopidae, Eriophyidae and *Sierraphytoptus*; and *Nalepella* which is sister to this group and *Mackiella* which is sister to *Nalepella*. The relationships between *Trisetacus*, *Pentasetacus*, *Novophytoptus* and *Phytoptus*, and the group with the remainder of the Eriophyoidea are unresolved. In the 18orig-k3 tree (Fig. 4.3d), *Pentasetacus*, *Trisetacus*, and *Nalepella* are outside a clade which contains the remainder of the Eriophyoidea in the data set. *Trisetacus* and *Nalepella* was found as a weakly supported group, and the relationships between this group, *Pentasetacus*, and the clade with the remainder of the Eriophyoidea are unresolved. The relationships and groupings of the other Phytoptidae also differ, but these are not discussed here.

This exercise was done and included to demonstrate that there can be significant difference in the results of parsimony analyses of the same data set due to the different algorithms used, as well as the execution thereof, and different weighting schemes used. Particularly in the case of analysing the relatively complex character state matrix of the Eriophyoidea, with a weak phylogenetic signal (large amount of homoplasy in the characters), it is very important which algorithm is used, and how the procedure is done, to ascertain that the most parsimonious tree is found, and that all parsimonious trees, with different topologies, are discovered. The problem and necessity of optimal analyses increases with the addition of more data from both taxa and characters to the data set. Different weighting methods and the amount of weighting against homoplasy is also of importance, and should be done in a scientifically defendable manner. The data set of Hong & Zhang (1996a) was further modified, by correcting the scored character states (Appendix H2, and trees in Figs 4.55–4.57), and by modifying the

character definitions and consequent scoring (Appendices H3, G.3, and trees in Figs 4.58–4.62). The largest difference between the topologies of the three series of analyses was caused by the modification of the character definitions. This stresses how immensely important the definition of characters and character states (primary homologies which already defined and scored during alpha taxonomy), and sample thereof, are in the eventual results of phylogenetic analyses. The results of the latter two series of analyses are presented and discussed together with the other analyses in the present study.

4.4.2 Discussion of taxon and character sampling, analyses chosen, and reliability of information from trees, groups and clades found in the present study

4.4.2.1 Taxon sample

The study was designed to be explorative, using published species descriptions, rather than focusing on producing a reliable, robust hypothesis on the phylogeny of the superfamily. The latter is probably impossible at this stage of our knowledge on eriophyoid biodiversity, phylogeny, morphology and molecular data anyway. Despite the small amount of descriptive morphological data available (eventually 66 characters informative for relationships between the eriophyoid ingroup taxa were included), the taxon sample was chosen to represent a major part of morphological variation within the Eriophyoidea at genus level, regardless of the theoretical phylogenetic resolution that one can expect from the number of characters and character states. The largest data matrix analysed in the present study, contained 318 species (including the two outgroup species). The ratio of characters and character states to the number of taxa included is very small. The fewest characters needed for full phylogenetic resolution is one more character than the number of taxa, or in terms of character states, at least two character states per taxon.

When empirically analysing or testing a hypothesis, it is ideal to examine all critical evidence. When testing phylogenetic hypotheses with analyses, e.g., parsimony analyses used in the present study, one will theoretically approach a reliable answer when including all taxa and all possible and particularly more critically important characters, sampled randomly. This is practically impossible though, and one has to take samples of the taxa and characters for inclusion in analyses. The taxon and character sampling is crucial in finding reliable results in a phylogenetic analysis. One way of improving the reliability of an empirical phylogenetic analysis will be to increase characters or taxa. Without extensive additional morphological studies, the number of characters available for studying the phylogeny of the Eriophyoidea is limited, and the sample used in the present study includes a major portion of the published morphological information presently available, and increasing it will not be an explorative exercise. In future the improvement of the quality of morphological studies and the addition of molecular data will hopefully improve the size, value and information of the character sample.

The other option to improve the results and reliability of phylogenetic analyses of the Eriophyoidea would be to increase the number of taxa sampled, and to sample it without bias. Increasing the number of taxa is one of the most important ways to significantly improve the overall accuracy of the phylogenetic analyses (Zwickl & Hillis, 2002). Testing the hypotheses on phylogeny of the Eriophyoidea already starts with an inherent problem regarding the amount of taxa in the data set, because so little of the extant taxa is known and described. The number of taxa included in the analyses, however, could be significantly increased over the 17 taxa included in the previous analysis by Hong & Zhang (1996a). Their taxon choice was also biased in only including one typical taxon of some of the suprageneric taxa, ignoring a significant portion of evidence from the remaining taxa. In a small data set where there are only a few representatives of a given group, the probability of the species appearing together in a phylogenetic analysis *a priori* is much larger, and results are thus less reliable in comparison with a more comprehensive sample where each taxonomic group is represented by significantly more representatives, where each representative have much more alternative placements (Goloboff *et al*., 2009). It was thus decided to sample the taxa from the Eriophyoidea for the present study comprehensively and as unbiased in favour of the current classification as practically possible, by sampling almost maximum amount of genera from each suprageneric grouping.

The complexity of phylogenetic analyses increases exponentially with an increase in taxa (Goloboff *et al*., 2009), though. Combined with the small characters:taxa ratio, and apparent high homoplasy in the large data set for the present study, and also conflict that may be partly caused by errors in descriptive data, analysing the data set only became possible with the availability of the program TNT to the study (see “Material and Methods”). Parsimony algorithms implemented in TNT can successfully process very large and/or complex data sets (Goloboff *et al*., 2009).

The type species of genera were preferably chosen as taxa for the present analyses, conforming to the exemplar method, because individual species were sampled from each suprageneric taxon, and scored as separate terminals (Prendini, 2001). Monophyly of the genera is not implied in this method (Prendini, 2001), and the sample species in the present study were not chosen to completely represent the variation within a genus. The type species were merely chosen to ensure a cross-cutting, representative inclusion of morphological character variety at the genus level within the Eriophyoidea. At least as the name bearing taxa, the sampled type species are supposed to be close to the average characteristics of, and characteristics that delineate the genera. Additional species to test the monophyly of larger genera such as *Aceria* were not included, but by including a large representative sample of species from each suprageneric taxon, the monophyly of the suprageneric taxa were tested while simultaneously testing the relationships between them (Prendini, 2001). This sampling choice was not biased in favour of the present classification, because the genera were sampled randomly and

comprehensively from all suprageneric taxa, and was only biased in favour of groupings of species within the genera.

During preliminary analyses of the data set, it was noticed that most phylogenetic resolution and phylogenetic structure was found within the Diptilomiopidae, and particularly in the Diptilomiopinae (C. Craemer, *unpubl. data*). This subfamily was chosen for a next phylogenetic study where a smaller group from the Eriophyoidea can be studied, and where a largely species specific character–character state data set can be developed. *Diptilomiopus*, with *ca.* 84 species (up to about 2006), is the largest genus in the Diptilomiopinae, and includes new undescribed species from South Africa, and it seems to be largely restricted to the southern hemisphere, which influenced the choice. While scoring the characteristics for the taxon sample for the eriophyoid cladistic analyses, *Diptilomiopus* spp. were scored for the same characters, and was included in the analysis to explore whether the sampled characters would largely give phylogenetic resolution of suprageneric taxa, or may possibly be informative regarding relationships at the species level for the specific species sample. A test analysis of a data set excluding the bulk of *Diptilomiopus* spp. was also run, but it did not have much influence on the phylogenetic resolution of taxa within the remainder of the Eriophyoidea (C. Craemer, *unpublished data*), and they were kept in the data set. Three new *Diptilomiopus* spp. from South Africa were described (Appendix M) and are included in the present study.

Because of the very low characters:taxa ratio sampled when including 318 taxa, it was decided to sample a smaller number of exemplar species from the 316 eriophyoid species, using the preliminary results of the 318-taxon analyses and the eriophyoid classification as guidelines. Sixty-six species were sampled, and 60 characters were included in this data set. The characters/character states:taxa ratio was drastically improved. The size of the data matrix allowed analyses with "traditional searches" (incorporating RAS and TBR branch swapping). Quite comprehensive analyses were done ("Material and Methods"), but there was overflow and for example for the analysis under implied character weighting with k = 999, the best score was only hit 15 times out of 7000, indicating that the shortest, and all the shortest trees for the data matrix were probably not found. It is thus still not certain whether the most optimal tree was found, and it presents the same problem as for the results of the analyses of the 318-taxon data matrix. The results were not necessarily more "accurate" or reliable; although some groupings supported the groupings found in the 318tax trees. Many of the useful hypotheses found in the 318tax trees were lost, due to the exclusion of taxa. The "best" and most informative results for the exploratory aim of the present study, and for presenting new hypotheses, was obtained from analysing the 318 taxa, despite the low characters:taxa ratio.

It was additionally decided to include analyses of the very small sample of 18 taxa (including one outgroup species), representing some of the suprageneric groupings in the Eriophyoidea, analysed by

Hong & Zhang (1996a) to test their study, properly test the results obtainable from such a small set, with "enough" (27 informative) characters, and to compare it with the results obtained from the more comprehensive 318- and 66-taxon analyses as further tests of the robustness of groupings, and presentation of alternative hypotheses, and possible homologies that were not retrieved by the larger analyses. This provided a useful comparison of groupings, and alternative hypotheses, but the groupings found in these small data sets were not regarded as reliable.

4.4.2.2 Character sample

It was decided to largely include characters currently used in eriophyoid taxonomy. It was the best design for a first exploratory study on this scale not to add many new characters which are not yet used in eriophyoid taxon descriptions. This sample also made it possible to code a matrix for a large and comprehensive sample of taxa, and it additionally tested the phylogenetic signal in characters currently used in eriophyoid taxonomy. The available descriptive data were sampled as comprehensively as possible, though, including all characters from the published species descriptions, largely described from slide-mounted specimens, that were appropriate or near appropriate data for phylogenetic analyses. Detailed variation in opisthosomal ridges, furrows and other body shape modifications which are extensively used characters, particularly in the Phyllocoptinae, was however excluded. An attempt was made to score and code the variation, but the determination of homologies was too complex and ambiguous, and a high level of inaccuracies in the description of these characters is suspected due to distortion of slide-mounted specimens (see Chapter 3). Omitting these characters also avoided the inclusion of additional ambiguous data in the data set, but it is important to include this suite of characters in an improved data set, where primary homologies can be defined.

There are too few morphological characters investigated and described, particularly for characters informative for taxa above species level, to allow for any complete phylogenetic resolution of the phylogenetic relationships within the Eriophyoidea. Not many more published characters are available than those used in the present study (see Chapter 3). The number of characters necessary will also depend on the phylogenetic signal inherent in the characters and for what level (higher classification or groupings or relationships between species) this signal is largely informative. The character set used in the present study, turned out to be highly homoplasious, as was suspected from the results of the phylogenetic analysis by Hong & Zhang (1996a), and the biology and simplified morphology of the group. The lack of retrieval of synapomorphies was exacerbated by the low characters:taxa ratio, and consequent lack of congruence.

The data set (taxa and characters and coded character states) is the crucial factor in finding reliable phylogenetic hypotheses using empirical analyses such as parsimony analyses. The analyses themselves are empirical and repeatable, although they should be well executed. It is clear from the

present study that the most important aspect which needs improvement in future studies of the phylogeny of the Eriophyoidea, is the character sample and descriptive data. It is not ideal to use published descriptive data, and usually the person doing the phylogenetic study should study the specimens personally and specifically for the study, with incorporation of new characteristics if necessary. For analyses with higher numbers of taxa, this may not be possible or practically feasible for the Eriophyoidea. It is important that the description of taxa should be standardized, to be able to incorporate the data into standardized data sets for use in data bases; phylogenetic studies and development of electronic integrative keys (see Chapter 2). The improvement of character data, both by the person doing the analyses, and those that are purely describing new taxa, may be partly achieved by improving preparation of the specimens for study, and by improving the quality, detail and accuracy of description (De Lillo *et al.*, 2010). It can also be improved by incorporating better techniques (e.g., SEM) in studying the morphology of specimens (Chapter 3).

Before the development of the algorithms incorporated in TNT, continuous morphometric data had to be gap-coded to change it into discrete data for parsimony analyses. Some of the characters in the present study, e.g., tibial length, were dealt with in this way. In TNT it is now possible to include continuous data in data sets. This will allow the addition of more morphometric data for the Eriophyoidea, but this can not be done from many published descriptions, because the morphometric data are inaccurate and vague. Biological and ecological data can also be carefully included in the character set. Probably most importantly molecular data should be added which will expand the amount of character data available significantly. Like morphological data, molecular data will have problems of its own, though. In a first molecular phylogenetic study on the Eriophyoidea with the aim of studying the phylogeny of the entire superfamily undertaken by M. Lekveishvili and co-workers (West Virginia University, USA), the molecular data in their data set with 27 taxa (including the outgroup taxon) had CI and RI values ranging from about 0.55 to 0.65 (M. Lekveishvili, *unpubl. data*). It seems that homoplasy in molecular data of the Eriophyoidea is as high as found in the morphological data.

4.4.2.3 Analyses

It was decided to analyse the data with parsimony analyses, primarily first of all not to make any prior assumptions about evolution, and to find the most parsimonious and thus most defendable hypotheses or trees for explaining the distribution of character states in the Eriophyoidea. The phylogenetic resolution and groupings found in the preliminary runs of the 318tax data set was largely based on homoplasy with very little retrieval of synapomorphies. Judged on the conventional indications for tree reliability and robustness (different resampling methods, and Bremer's support) almost none of the phylogenetic resolution was reliable, and the trees usually largely collapsed under these criteria. (Some may also regard the collapse of trees under equal character weights e.g., Fig. 4.4, as an indication of weak group supports.) The phylogenetic resolution found under implied weighting is almost complete,

and are probably overresolved (groupings largely supported solely by homoplasy), but the groups are significant and make biological sense. It was decided to rather "test" the robustness of the groups somewhat by congruence between analyses of the data under various parameters, than to solely test it with the conventional methods. Different taxon sample sizes (one of 66 taxa, and another with 18 taxa) was sampled from the original 318-taxon data set (also for the reasons set out above). The analyses were additionally analysed with different algorithms, and under different character weighting schemes (different amounts of weighting (not *a priori*, though) against the influence by homoplasy in the construction of the trees). See "Character weighting" below.

4.4.2.4 Character weighting (implied weighting) used in the present analyses

Characters in real organisms are not equally weighted, and some characters show a lot of homoplasy while others may be completely hierarchical (Goloboff, 1993a). Equally weighted characters are thus based on the wrong assumption that all characters provide equally strong evidence of relationships, and can in fact not be considered unweighted. Characters with more homoplasy are less reliable. Parsimony does not prohibit weighting, but it rather requires weighting (Goloboff, 1993a). Implied weighting is, similar to successive weighting (Farris, 1969), using evidence on homoplasy provided by parsimony analyses, which provides a method for weighting characters (Goloboff, 1993a), and is not an *a priori* weighting method. The implied weighting algorithm is an examination of self-consistency, based on the idea that the trees themselves should give the information about the reliability of characters, and extra steps in highly homoplasious characters should count less (Goloboff, 1993a). Traditionally, trees are compared on the basis of how many steps they require for the data. Implied weighting is based on searching trees with maximum total fit. Those trees which imply the characters to be more reliable, explain the data better (Goloboff, 1993a). Implied weighting "prefers" trees with higher weights. The "weight" of a character is a function of its fit to a tree, and the total fit or weight of a tree is the sum of the fits of the characters (Goloboff, 1993a). Trees found under implied weighting typically produce more resolved, and better supported trees than standard unweighted parsimony (Goloboff, 1993a), and if the data are properly weighted, the results found under weighting should always be preferred, regardless of the results found under equal weights (Goloboff, 1993a). It is important to note, however, that Goloboff *et al*. (2008c) strongly advised that support of trees found under implied weighting should be tested, because in the way implied weighting is computed (with floating point numbers), it may result in overresolved trees.

4.4.2.5 Reliability and robustness of groupings and clades found in the present study

Although the study was not meant to be an exercise in the theory of phylogeny and cladistic analyses, some interesting questions and aspects came to the fore, largely related to the reliability of the results. This dilemma is caused by the phylogenetic resolution and retrieved groupings in the preferred trees

which are largely supported by homoplasy, and additionally, the majority of phylogenetic resolution is not robust (for example, not supported by symmetric resampling), and analyses of the data sets result in huge numbers of equally parsimonious trees. Do the results match or approach good hypotheses about true genealogical relationships between extant eriophyoid species? Or are the results just a coincidence or mimicking the current classification because it is based on the same homoplasious data set, where homology is swamped by homoplasy, and totally unreliable? Will the results largely confuse the systematics of the Eriophyoidea, rather than contribute valid, useful phylogenetic hypotheses to it? To argue the usefulness of the presentation of tree groups found in this study, we need to consider the general phylogenetic concepts and the discovery of natural, monophyletic groupings.

There are only two types of natural taxa that are the products of evolutionary processes: species and monophyletic groups (Brooks & McLennan, 2002). A monophyletic group or clade is a group that consists of a common ancestor and all, and only all, of its descendants (Kitching *et al*., 1998). A natural classification consists of monophyletic groups or taxa (named groups). Artificial taxa represent incomplete or invalid evolutionary units. These are paraphyletic groups (one or more descendants of an ancestor are excluded from the group, making the group an incomplete evolutionary unit) (Brooks & McLennan, 2002), and polyphyletic groups (a group that does not include the most recent common ancestor of all its members) (Kitching *et al*., 1998).

We use characteristics (characters and character states) to describe groups and taxa, and these are also studied or analysed to present hypotheses on the relationships between taxa. Relationship in phylogeny only refers to connections based on genealogy. Characteristics between taxa can differ or be the same. Similar or same characteristics can be the result of a novel feature that developed and is present in the common ancestor (homologous character) – i.e., an apomorphic character in the descendants. Another origin of a similar or same feature shared by organisms, is not due to genealogy, but is a result of convergent or parallel evolution, or reversal, and this type of character is a homoplasious character. Similarity between organisms does not equate with the degree of phylogenetic relatedness (Brooks & McLennan, 2002).

Apomorphic characters (homologies) allow us to specify monophyletic groups when they are shared between taxa (synapomorphies). Only synapomorphies provide evidence of common ancestral relationships (Brooks & McLennan, 2002). Symplesiomorphies (general homologies – a relative status) and homoplasies are useless in this regard (Brooks & McLennan, 2002). Monophyletic groups are discovered by finding synapomorphies, and discovery of homology is at the heart of cladistic analyses (Kitching *et al*., 1998). Monophyletic groups supported by homology are the only groups that can be justified objectively (Kitching *et al*., 1998) and empirically. Homoplasies are *ad hoc* incidences (P. Goloboff, *pers. comm*.), and in finding the most parsimonious explanation of character distribution,

homologies are empirical and the simplest explanation. Homologies are not fixed, though, homologies are hypotheses discovered by analyses, and they can be tested, and also falsified (Kitching *et al*., 1998). Following the equating of homology with synapomorphy, only homologous characters (and not homoplasies) supporting nodes will be called synapomorphies in the present study.

A group only supported by homoplasy is a polyphyletic group (Kitching *et al*., 1998). [In the presented study the definitions by Kitching *et al*. (1998) is followed in this regard, and only groups supported by at least one homology (synapomorphy) will be called clades.] It is thus an artificial group that does not exist in nature, and should not be a taxon in a natural classification. Results (e.g., trees) with groups largely supported by homoplasies thus did not recover evidence of phylogenetic relationships, and can be regarded as "bad" trees. "If the only available tree is a bad one, should you use it? No" (Coddington, 1985 as referred to by Brooks & McLennan, 2002). The biologically logical and robust method of dealing with a weakly supported tree is to collect more data (Brooks & McLennan, 2002).

Homoplasy, however, may contribute to the improvement of the retrieval of well-supported phylogenetic groups (Källersjö *et al*., 1999). They found that the number of well-supported groups and average jackknife resampling frequencies were significantly decreased when the most homoplasious characters which are at the third position were excluded, as is the usual practice, when they analysed a large molecular rbcL matrix. Goloboff *et al*. (2008a) illustrated that proper down-weighting of characters according to their homoplasy also produces more strongly supported groups, and more stable results in morphological data sets. These examples of the influence of homoplasy on the results of parsimony analyses are, however, not exactly applicable to the present study. Although the phylogenetic resolution, support, feasibility and biological sense of groupings in the present study increased highly significantly with down-weighting of homoplasy to the level where maximum total fit was found, and the groups and phylogenetic resolution are obviously provided by homoplasy, the support of the groups were weak when measured on basis of the amount of support by synapomorphies, and in terms of symmetric resampling values.

It is presumed that only one evolutionary history of living organisms exists which resulted in the diversity of extant and extinct organisms we study systematically today, and there is thus only one true phylogeny. In reality homoplasy exists in organisms, and in some groups, e.g., in the Eriophyoidea, homoplasy may be very high in their evolutionary development. It may be so high that it may literally mask the few incidences of "true" homologous characters. The descendants of one ancestor will also inherit an entire suite and certain combination of homoplasies that became part of its lineage. It is plausible that a complex and extensive combination of homoplasies may provide evidence of genealogical relationship if properly retrieved, and if sufficient data were analysed.

Some authors (e.g., Coddington, 1985 and Brooks & McLennan, 2002) may argue that the trees found in the present study are so poor that they should not be used at all. Many of the groups retrieved, however, make biological sense and are feasible in view of the knowledge on the ecology and biology of the species involved, and/or when evaluated on the morphological similarity of the included species. Although similarity does not equate genealogical relationships, if genealogically related, one will expect in many groups that the included species will be morphologically more similar than to species of particularly more distantly related groupings. This might especially be the case if overall, random, and well-defined morphology are compared. These similarities of species within certain groups are additionally in characters, e.g. the genitalia, which are generally found to have good phylogenetic signal.

The analyses in the present study also retrieved groups and positions of single species that brought more insight to the current classification, more than what would have been retrieved by traditional taxonomic practices. Some groups were congruent under the different parameters used in the present study, albeit no additional taxa and characters were added to the largest data set which formed the basis of all analyses. Some groupings (not only the few clades retrieved) were supported by the previous phylogenetic analyses (Hong & Zhang, 1996a, b; 1997) of the Eriophyoidea and its subtaxa. The groups found in the analyses provide good alternative hypothesized groupings, besides those taxa proposed in the classification of the group. Resampling methods largely did not support the groups found, but although these methods test robustness, they do not simulate the addition of new character and taxon data which are not random.

The data were analysed with parsimony analyses, and if the analyses are properly executed, the trees found will be the most parsimonious answer for the available data, which are significantly comprehensively sampled from available data. The results are thus the most defendable given the data, regardless of the robustness, reliability and correctness of the groupings. Under implied weighting, the best fit for the characters was also sought, by down-weighting excessive influence by homoplasy in the analyses. When the homoplasy was heavily down-weighted, up to k = 0.1, when weighting against homoplasy was about 100%, most groupings could not be defended by biological sense, although they may provide alternative hypotheses. Implied weighting may possibly weight the homoplasy down to about the level that really exists in the evolutionary development of the group in nature.

It is impossible to compare any cladogram retrieved with the real phylogeny that exists in nature to determine how close the cladogram (tree) comes to portraying true phylogeny. In theory, groups supported by at least one synapomorphy will always be more defendable (more parsimonious, and with more unambiguous evidence), though, than groups based on *ad hoc* homoplasy, it does not matter how homoplasious a group is in reality. Therefore, although the results and hypotheses of the present study

are presented, it is understood that extreme caution should be followed in the incorporation of the groupings in the current classification, and many groups might be totally artificial. When smaller taxon samples were analysed in the present study, more synapomorphies were retrieved, but this does not mean that the groupings (clades) supported by them are more reliable, because synapomorphies are just hypotheses, and some synapomorphies, alternatively, were retrieved as homoplasies in the analyses with more taxa and more evidence.

The only way to test the robustness of the groups will be to gather more and more data and continuously test the hypothesized groupings. Whether the topologies presented here will change drastically and whether the groupings will be supported, and genealogical relationships in this group are truly retrievable with combinations of homoplasious characters, will only be resolved in future. In the mean time it provides useful information, and parsimony analyses will continue to add useful information to systematic endeavours on the Eriophyoidea, despite “poor” trees.

4.5 RESULTS AND DISCUSSION: GROUPS AND CLADES RECOVERED BY THE DIFFERENT ANALYSES, PROPOSED AS ADDITIONAL HYPOTHETICAL SUPRAGENERIC GROUPINGS FOR THE ERIOPHYOIDEA

In this part of the results and discussion the tree clades and groups recovered from different data sets, under different parameters, are identified, described and named. These groupings will be used and incorporated by names and chronological numbers in the next part of the results and discussion, where the monophyly of suprageneric taxa in the current Eriophyoidea classification will be appraised, without detailed information about them. It should be noted that the groups are proposed on the basis of the data sets (taxon and character samples) in the present study, and the robustness and convergence towards monophyletic groups are particularly uncertain for the present study (see the discussion of reliability and robustness of groups and clades above). The groups did not contain random species, though, and many of the groups found made biological sense. The tree groups and clades are proposed as hypotheses of suprageneric groups additional to existing Eriophyoidea classifications.

The group and clade names (e.g., "*Nalepella* group") usually originate from a taxon name of species within the group or some characteristic of the group, but they are merely handles for referring to a group. These names do not hypothesize anything, or preamble officially incorporating these groups in the eriophyoid classification at this stage. A group is not necessarily a group of species at one node, but may refer to a group of species with about the same topology and making "biological sense" or which seems to be consistent under all parameters. The named groups and clades are chronologically numbered for ease of reference. When a group or clade has already been discussed prior to its use, it, and its chronological number are given in bold and underlined. Any list of taxa given in parentheses does not imply relationships in parenthetic notation, except when so noted.

In the presentation and discussion of results in the text mostly only the genus name is used, but the genus name in these cases is a substitute or alternative name for the species included in the analysis, and does not refer to the entire genus. In the single cases where more than one species of a genus were included in the analyses, the genus and species names are used. Sometimes genus names refer to the entire genus, but this will be clear from the context. The abbreviation "*D.*" before the species name always refers to "*Diptilomiopus*".

Some of the genera are small (see Appendix A), therefore, some extrapolation to the position or relationships of the genus was inferred during the discussion, but these are highly hypothetical, since

the monophyly of genera has not been determined. This is particularly true for the large genera such as *Aceria* (with close to 900 species). Naturally, for monospecific genera, the relationships of the species also extrapolate to the relationships of the genus as it is currently defined.

The complete terminology of characters and character states should be ascertained in the character description and discussion in Appendix B. Sometimes these may be shortened for the sake of brevity. For example, for Character 21 the setal tubercle of *c2* in the two outgroup species are primary absent (State 0), and if absent in the Eriophyidae, they are secondary absent (State 2), but in results and discussion, it is merely noted that the setal tubercles are absent.

The Phytoptidae is traditionally regarded as important in understanding the evolution and phylogeny of the Eriophyoidea, is relatively well discussed and tested in previous hypotheses on the phylogeny and evolution of the Eriophyoidea, and it is a relatively small family in comparison to the Eriophyidae and Diptilomiopidae. The results for this family are, therefore, given and discussed in more detail than for the Eriophyidae and Diptilomiopidae. The detailed topology of a group of species retrieved in the analyses is not necessarily given in the text, or discussed, because the main aim is to find some structure and hypotheses for future phylogenetic studies, and not necessarily to discuss the position found for each species in the data sets.

The groups and clades recovered by the analyses are evaluated more or less according to morphological similarity, host plants, habit, biogeography and any other knowledge about the species involved that may give insight to their relationships. Geographic distribution is used with caution, except where the origins of the host plants are known, because these mites are so closely associated with their host plants, and they are so small and “part” of the plant, that they might have moved with their host plants to different regions of the world where they and their host may not be native. Thus the collection sites may not necessarily be the places where the mites originated and may not be part of their natural distribution.

PHYTOPTIDAE

4.5.1 Groups retrieved comprising largely Phytoptidae [*sensu* Amrine *et al.* (2003)] species

I. Nalepellinae groups (eight groups)

1.) ***Nalepella* groups.**

1a.) ***Nalepella* group 1a:** *Nalepella*, *Phantacrus* (Nalepellinae: Nalepellini).

This is the most supported and robust group of the *Nalepella* groups. It occurs in all the presented 318tax (Figs 4.5, 4.8, 4.28) and 66tax trees (Figs 4.42, 4.43), under all weighting schemes, including the trees obtained under equal weighting. This group is also supported by a relatively high symmetric resampling absolute group frequency (hereon GF) and symmetric resampling group frequency difference (GC in TNT) values in the 318tax-k10 tree: GF value of 64 (Fig. 4.24), and GC value of 61 (Fig. 4.25); and in the 66tax-k999 tree: GF value of 69 (Fig. 4.49), and GC value of 61 (Fig. 4.50) particularly when compared with other groups found in the present study.

The 66tax-k999 (Fig. 4.44) and -k30 (Fig. 4.51) trees: the group (node 122) is supported by three homoplasies: single *vi* and tibial solenidion *φ* present, and tibia length twice tarsal length. The latter character state can be regarded as homologous, although the character itself is homoplasious, because the character is a multistate character, and this state only supports this group in these two trees. The 318taxEq and 66taxEq trees: the group (node 341, Fig. 4.5) is supported by 11 homoplasies, and node 76 (Fig. 4.42) supported by 12 homoplasies, respectively. These homoplasies include the three homoplasies supporting the group in the 66tax-k999 and -k30 trees. Two other homoplasies which support the group in the unweighted trees are: long spermathecal tubes, and very long *sc*.

Nalepella and the monospecific *Phantacrus* are needle vagrants on coniferous trees, a *Pseudotsuga* and *Tsuga* sp., respectively, and are essentially native to the Nearctic Region. The 15 species of the genus *Nalepella* (Amrine *et al.*, 2003) live on conifers (including *Pinus* and *Tsuga* spp.) in largely the Holarctic Region, with possibly single species occurring in the Oriental Region depending on the natural distribution of their hosts. These two species being sister species thus makes biological sense in so far their host plants, niche, geographical distribution and current classification are concerned.

Both species are exposed needle vagrants, with vagrant-like body shapes, however, the dorsal opisthosomal annuli of *Phantacrus* have large projecting lobes (Keifer, 1965c) while *Nalepella tsugifoliae* has an evenly arched body with annuli about subequal (Keifer, 1953). These differences were scored as different states for the two species in the data matrix (see characters 72 and 74 in

Appendices A & C). The relatively strongly supported sister relationship between the species indicate that detailed body shape (the presence of ridges and dorsoventral differentiation of annuli) may not be important in the determining the relationship between *Nalepella* and *Phantacrus*. It may also indicate that detailed body shape, e.g., presence and shape of ridges, may not have a strong phylogenetic signal. *Nalepella triceras* (not included in the present data sets) from Europe, has opisthosomal annuli with strong dorsoventral differentiation (Amrine *et al.*, 2003), which makes it morphologically more similar to *Phantacrus*. *Phantacrus* may eventually be designated a junior synonym of *Nalepella*. These results partly support the view of Boczek *et al*. (1989) that eriophyoid genera are differentiated on species level features, including the shape of opisthosomal ridges and troughs.

1b.) ***Nalepella* group 1b:** *Pentaporca*, *Nalepella, Phantacrus* (Nalepellinae: Nalepellini).

The 318tax-k10 and 318tax-k20 trees: the monospecific *Pentaporca* is sister to and in the same group as *Nalepella-Phantacrus* (***Nalepella* group 1a**). This group (node 558, Fig. 4.8 and node 416, Fig. 4.28, respectively) is supported by the same two homoplasies: single *vi* present, and *1a* slightly ahead of *2a*. The delimitation of the character to which the latter state belongs and its description is frequently ambiguous and the character is not generally used for separating taxa in the Eriophyoidea. The group is not supported by a GF value of 50 or above and weakly by a GC value of 24 (Fig. 4.25) in the 318tax-k10 tree. The group is feasible when evaluating host plants, niche, and current classification. *Pentaporca* is an exposed needle vagrant on *Tsuga chinensis*, a coniferous species indigenous to the Oriental Region. *Pentaporca* was not included in the 66tax and 18tax analyses to test its inclusion in this *Nalepella* group.

2.) ***Trisetacus* group:** *T. pini*, *T. ehmanni* (Nalepellinae: Trisetacini).

The two *Trisetacus* spp. above were included in the 318tax data set. The 318taxEq tree: under equal character weights the group (node 344, Fig. 4.5) is supported by 18 homoplasies, including some that partly differentiates the genus: presence of *c1*, and single *vi*, and long spermathecal tubes. Additionally various character states of *sc*, and character states relating to a more vermiform shaped body are included. These species are in the same genus, and therefore their sister relationship is viable. They were found to group together with *Boczekella* and *Setoptus* under the 318tax-k10 and -k20 character weighting schemes as **Trisetacini-Nalepellini group 3a**, discussed hereafter.

3.) **Trisetacini-Nalepellini groups**

3a.) **Trisetacini-Nalepellini group 3a:** *Trisetacus pini*, *T. ehmanni, Boczekella* (Nalepellinae: Trisetacini); *Setoptus* (Nalepellinae: Nalepellini).

The 318tax-k10 tree: the two *Trisetacus* spp. were found to group with *Setoptus* (node 572, Fig. 4.14) supported by three homoplasies: tibia I with *l'* and *φ*, and prodorsal shield circular. The latter character

state is particularly subjective and ambiguous. Relationships between these species are unresolved. *Boczekella* is sister to this group and included with them (node 491, Fig. 4.14). This group is supported by five homoplasies, and some are more robust and less ambiguous: single *vi* and *c1* present, genital coverflap smooth, and coxisternal plates I and II slightly and faintly ornamented. The 318tax-k20 tree: the four species were recovered in the same group, but with relationships between them unresolved. The group (node 386, Fig. 4.34) is supported by 12 homoplasies including those supporting this group in the 318tax-k10 tree. The group is not supported by a GF value of 50 or above and/or a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree. A GC value of 46 in the same tree for the sister relationship between the two *Trisetacus* spp. [***Trisetacus* group (2)**] within **Trisetacini-Nalepellini group 3a, is higher** (Fig. 4.25).

These species mainly occur on *Pinus* spp. and closely related relatives in the Holarctic Region, with *T. ehmanni* (a refuge-inhabiting mite) and *Setoptus* (vagrant mite) more prevalent in the Nearctic, and *T. pini* (a gall-inhabiting mite) in the Palearctic Region, and *Boczekella* (vagrant mite) occurs on *Larix decidua* (Panacea) native to the mountains of central Europe. The ecological data and their classification in the Nalepellinae, support the group. The division of the species in different tribes based on the presence of *c1* is not supported by the results, and this agrees with the key to genera, and implied classification, proposed by Boczek *et al*. (1989).

3b.) **Trisetacini-Nalepellini group 3b:** *Trisetacus ehmanni* (Nalepellinae: Trisetacini); *Nalepella*, *Phantacrus* (Nalepellinae: Nalepellini).

Only the three species above from the Nallepelinae groups dealt with so far were included in the 66tax data set. The 66tax-k20 tree (Fig. 4.54): *Nalepella-Phantacrus* (***Nalepella* group 1a**) was retrieved in a group with *T. ehmanni* of **Trisetacini-Nalepellini group 3a**, the only other taxon within the Nalepellinae included in the analyses except *Pentasetacus*. This is a less preferred tree due to its longer length than found under other weighting schemes, but which was included because it presents alternative hypotheses. The 66tax-k999 and -k30 trees are the more preferred 66tax trees, and herein *T. ehmanni* is in the **Trisetacini-Phytoptinae group (4)** (discussed below).

3c.) **Trisetacini-Nalepellini group 3c:** *Trisetacus* (Nalepellinae: Trisetacini); *Nalepella* (Nalepellinae: Nalepellini).

When *Phantacrus* was also excluded from the analyses (in the 18tax data set) and only *Nalepella* (Nalepellini) and *Trisetacus* (Trisetacini) were included, *Nalepella* and *Trisetacus* were recovered as sisters when the relationship between them was resolved. The 18correct-k999 tree: this group (node 20, Fig. 3.55b) is supported by one homoplasy: *ve* absent. Sometimes *Nalepella-Trisetacus* groups together with *Pentasetacus* as a **Nalepellinae group or clade (5)** (Figs 4.57, 4.59, 4.60, 4.62) (see below, and under discussion of *Pentasetacus* groups).

4.) **Trisetacini-Phytoptinae group:** *Trisetacus ehmanni* (Nalepellinae: Trisetacini); *Acathrix* (Phytoptinae)**.**

The 66tax-k999 and -k30 trees: *Trisetacus ehmanni* is not closely related to *Nalepella-Phantacrus* (***Nalepella* group 1a**), but was retrieved as the sister of *Acathrix*. This group (66tax-k999 tree, node 103, Fig. 4.44) is supported by three homoplasies: *c1* absent, tibial solenidion *φ* present and coxisternal plates II faintly ornamented. It is not supported by a GF value of 50 or above or by a GC value above 20 (Fig. 4.50) in the 66tax-k999 tree.

Acathrix does not live on a conifer such as *Trisetacus* and other species of the Nalepellinae, but lives in the frond folds of the coconut palm, *Cocos nucifera*, in the Nearctic, Neotropical, and Oriental Regions. The closer relationship between *Trisetacus* and other Nalepellinae species is biologically more meaningful than a close relationship between *Trisetacus* and Phytoptinae species, but the latter is an alternative hypothesis.

5.) **Nalepellinae group and clade:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Nalepella* (Nalepellinae: Nalepellini); *Trisetacus* (Nalepellinae: Trisetacini).

In the 18tax data sets the Nalepellinae is represented by three species (above), one from each of its three tribes, and not species of all seven genera in the Nalepellinae as in the 318tax data set. Where the relationships between the three taxa are resolved in the 18tax trees, they were found as a group.

In the 18taxcorrect trees, the relationships between the Nalepellinae genera are completely resolved in only the 18correct-k3 tree where *Pentasetacus* is sister to a *Trisetacus-Nalepella* group (node 19, Fig. 4.57). This Nalepellinae group is supported by one homoplasy: solenidion *φ* present. The group is not supported by the GF and GC values (Fig. 4.56) in the 18correct-k999 tree.

In the 18modify trees the group is a clade present in all the trees found under implied character weighting. In the 18modify-k999 tree the clade is at node 19 (Fig. 4.59) and in the 18modify-k100 and –k3 trees at node 20 (Figs 4.60, 4.62, respectively). The three clades are each supported by two synapomorphies: single *vi* present and spermathecal tubes long. These characters are used for differential diagnosis of the Nalepellinae. The relationships between the species in the clade are not resolved in the 18modify-k999 tree (Fig. 4.59), but in the 18modify-k100 and –k3 trees, *Pentasetacus* was found as the sister of *Trisetacus* at node 19 in both trees, supported by two homoplasies: *c1* present, and *1a* in line with *2a*. *Nalepella* is sister to the *Pentasetacus-Trisetacus* group. The Nalepellinae clade is not supported by a GF value of 50 or above and relatively weakly by a GC value of 20 (Fig. 4.61) in the 18modified-k100 tree. The unweighted 18modifiedEq tree (Fig. 4.58): the Nalepellinae group is not present, and the Phytoptidae in the analysis, including *Pentasetacus*,

Trisetacus, *Nalepella*, *Novophytoptus* and *Mackiella* (excluding *Phytoptus* and *Sierraphytoptus*), are part of a polytomy together with all other eriophyoid taxa in the analysis.

One could deduce that the modified characters and character states which are similar to the 318tax data set was more "successful and robust" in retrieving the Nalepellinae clade. The loss of this clade when more evidence from more taxa and characters are added with the similar structured characters may thus be real.

II. The Phytoptinae and Sierraphytoptinae groups (10 groups)

6.) *Pentasetacus*-Sierraphytoptini groups.

6a.) ***Pentasetacus*-Sierraphytoptini group 6a:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Austracus* (Sierraphytoptinae: Sierraphytoptini).

The 318taxEq tree: the group is not present. The 318tax-k10 tree: the group (node 490, Fig. 4.11) is weakly supported by one homoplasy: tibial length equal to tarsal length in leg II. It is part of the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (node 409), which is in turn part of the **Phytoptinae-Sierraphytoptinae group (9)** (node 412), both groups are discussed later on. The 318tax-k20 tree (Fig. 4.33, Group 13): *Pentasetacus* and *Austracus* are in the same group (node 356, Fig. 4.33), which includes a group at node 355, consisting of Phytoptinae and Sierraphytoptinae species. Relationships between *Pentasetacus*, *Austracus* and the group at node 355 are unresolved. All these are part of a group at node 358 [the **Phytoptinae-Sierraphytoptinae group (9)**, discussed later on] which includes *Pentasetacus* and all Phytoptidae with single and paired *vi* absent, except the two *Novophytoptus* spp. included in the analysis. *Pentasetacus-Austracus* is not supported by the GF (Fig. 4.24) or GC value (Fig. 4.25) in the 318tax-k10 tree.

6b.) ***Pentasetacus*-Sierraphytoptini group 6b:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini).

In the presented 66-tax trees, including the 66taxEq tree, *Pentasetacus* was recovered as sister of *Sierraphytoptus*. The 66taxEq tree: the group (node 79, Fig. 4.42) is supported by 10 homoplasies: *ve*, *c1* and *h1* present, genital coverflap and coxisternal plates unornamented, prodorsal shield ornamentation obscure, 3-rayed empodium, and *1b* the same distance apart than *1a*. The 66tax-k999 tree: the group (node 125, Fig. 4.46) is supported by three of the 10 homoplasies supporting the group in the 66taxEq tree: prodorsal shield ornamentation obscure, and coxisternal plates I and II unornamented. These supportive homoplasies are characters usually used to differentiate species. *Pentasetacus-Sierraphytoptus* and *Phytoptus* are part of a larger group (node 126, Fig. 4.46) supported by three homoplasies: *ve* and *c1* present, and *1a* slightly ahead of *2a*. The presence of *ve* and *c1* are character states used for differentiating subfamilies and tribes. *Pentasetacus-Sierraphytoptus* is also

present in the 66tax-k30 (Fig. 4.51) and the 66tax-k20 (Fig. 4.54) trees. It is not supported by a GF value of 50 or above and by a GC value of 30 (Fig. 4.50) in the 66tax-k999 tree.

Pentasetacus-Sierraphytoptus in the 66tax trees is more supported than *Pentasetacus-Austracus* in the 318tax trees, but *Austracus* was not included in the 66tax data set. *Pentasetacus* causes galling on an ancient relict coniferous species, *Araucaria araucana* (Gymnospermae: Araucariaceae), in the Chilean Andes in South America (Schliesske, 1985). *Austracus* has also been collected from South America, causing fruit galls on *Nothofagus dombeyi* (Monocotyledones: Nothofagaceae) in Argentina (Keifer, 1944). Their host plants are not closely related, but are more primitive than the Angiospermae on which the bulk of the Eriophyoidea lives. *Sierraphytoptus alnivagrans* is a vagrant on *Alnus tenuifolia* (Betulaceae) which occurs essentially in North America (Keifer, 1939a). Purely based on ecology, one may propose that *Pentasetacus* is rather more closely related to *Austracus*.

7.) **Dorsal-rear-fused clade:** *Prothrix* (Prothricinae); *Neopropilus* (Sierraphytoptinae: Sierraphytoptini); *Propilus*, *Retracrus* (Sierraphytoptinae: Mackiellini).

This clade was recovered by most of the 318tax and 66tax analyses, and is supported by the synapomorphy: dorsal fusion of the rear annuli beyond *f.* The 318tax-k10 tree: the clade (node 562, Fig. 4.11) is additionally supported by two homoplasies: *h1* present, and frontal lobe edge blunt and rounded. The 318tax-k20 tree: the clade (node 418, Fig. 4.33) is additionally supported by three homoplasies: *l'*, *sc* and its setal tubercle absent. Although the supportive homoplasies of the two clades differ, they share the support of the synapomorphy. The clade is confirmed by a clade consisting of a reduced number of species from it, *Prothrix*, *Neopropilus* and *Retracrus*, in all the 66-taxon trees, including in the tree found under equal character weights (66taxEq tree, Fig. 4.41). In these trees, the clade is supported by the same synapomorphy as in the 318tax trees. None of the species were included in the 18-taxon analyses. A subgroup of the clade (*Prothrix-Neopropilus*) is supported by a GF value of 53 (Fig. 4.24) and the entire clade is supported with a GC value of 25 (Fig. 4.25) in the 318tax-k10 tree.

The 318tax analysis under equally weighted characters did not retrieve the clade (318taxEq tree, Figs 4.4, 4.5). This result is regarded to be less reliable, given the morphological similarity of these species (see descriptive drawings in Amrine *et al.*, 2003), and the relatively strong support for the clade in the other trees.

The clade and the phylogenetic resolution found within the clade at first glance seem to be supported by the host plants and distribution of the taxa involved. Within the clade *Prothrix* and *Neopropilus* were always recovered as sisters. Both genera are monospecific and they occur in the Oriental Region, with *Prothrix* collected on an unknown host plant in probably the Philippines (Amrine *et al.*, 2003),

and *Neopropilus* a vagrant from *Jatrophus curcas* (Euphorbiaceae) in Taiwan (Huang, 1992). *Retracrus* was recovered to be sister to, or in the same group as *Prothrix-Neopropilus* with relationships unresolved. In the 318tax-k10 and –k20 trees (Figs 4.11 and 4.33, respectively) *Propilus* is sister to *Retracrus-Prothrix-Neopropilus*. The two known species of *Retracrus* and the four known *Propilus* spp. (Amrine & de Lillo, 2003) were collected on palms (Arecaceae) in mainly the central and southern Americas (Keifer, 1975c; Navia & Flechtmann, 2002).

8.) **Smaller-Phytoptinae-Sierraphytoptinae group (8):** *Phytoptus*, *Anchiphytoptus*, *Oziella*, *Acathrix* (Phytoptinae); *Austracus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini); *Pentasetacus* (Nalepellinae: Pentasetacini) – [these species, apart from *Pentasetacus*, are all the Phytoptinae and Sierraphytoptinae in the data sets, excluding the **Dorsal-rear-fused clade (7)**, *Fragariocoptes*, and *Sierraphytoptus*].

This group is at node 409 in the 318tax-k10 tree (Fig. 4.11) and at node 357 in the 318tax-k20 tree (Fig. 4.33). Apart from relationships mentioned here, the topology of the Smaller-Phytoptinae-Sierraphytoptinae group is not discussed in detail for the present study, because it is not well-supported, and not central to the question about the more important relationships in the Phytoptidae. *Pentasetacus* is sister to *Austracus* in the 318tax-k10 tree (***Pentasetacus*-Sierraphytoptini group 6b**). In an unpublished phylogenetic study of the Phytoptidae by R. Ochoa (R. Ochoa, *pers. comm.*), *Mackiella* and *Austracus* had a close relationship with other Sierraphytoptinae, as found in the present study, but were outside a clade which largely coincides with the **Dorsal-rear-fused clade (7)**. *Anchiphytoptus* and *Phytoptus* were not found to be sisters in the present study, but were found to be relatively closely related, and this partly supports the sister relationship between these taxa found by R. Ochoa (R. Ochoa, *pers. comm.*), and the designation of *Anchiphytoptus* as a junior synonym of *Phytoptus* by Chetverikov *et al*. (2009).

9.) **Phytoptinae-Sierraphytoptinae group: Dorsal-rear-fused clade (7); Smaller-Phytoptinae-Sierraphytoptinae group (8)**; *Fragariocoptes*, *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Pentasetacus* (Nalepellinae: Pentasetacini).

This group comprises the Phytoptinae and Sierraphytoptinae in the data sets. These consist broadly of two groups, namely the **Dorsal-rear-fused clade (7)** and the **Smaller-Phytoptinae-Sierraphytoptinae group (8)**, and two Sierraphytoptinae species, namely *Fragariocoptes* and *Sierraphytoptus*, which were either recovered as closely related taxa and in the same group as the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (318tax-k10 tree, node 411, Fig. 4.11) or the relationships between the two species, and their relationships with the two mentioned groups of the Phytoptinae-Sierraphytoptinae group, are unresolved (318tax-k20 tree, Fig. 4.33). The group includes *Pentasetacus* under some parameters. The two *Novophytoptus* spp. whose relationships with the Phytoptidae and Eriophyidae are uncertain, and *Palmiphytoptus* that does not have a close relationship with the

Phytoptidae and which will be discussed under "species not correctly classified" further on, are not part of the group.

The 318tax-k10 tree: the group (node 412, Fig. 4.11) is supported by the homoplasies: *ve* present and *sc* ahead of rear shield margin. The 318tax–k20 tree: the group (node 358, Fig. 4.33) is supported by a longer branch with the same two homoplasies supporting the group in the 318tax-k10 tree, as well as five others: *c1* present, *1a* slightly ahead of *2a* (an ambiguous state), no opisthosomal ridges or furrows present, coxisternal plates I unornamented and genital coverflap smooth. The presence of *ve* in combination with the other homoplasies, thus support the Phytoptinae-Sierraphytoptinae group, rather than the absence or presence of single *vi*. The topology of the group in the 318tax-k10 and –k20 trees, differs slightly from each other.

R. Ochoa (*pers. comm*.) found *Fragariocoptes* to be closely related to *Boczekella* and *Setoptus* of the Nalepellinae, and these were in the same clade with the outgroup Eriophyidae species (*Eriophyes* and *Ashieldophyes*) in his unpublished study of the phylogeny of the Phytoptidae. These results were not supported by the present study.

10.) Groups retrieved in the 66tax trees of the four species from the **Phytoptinae-Sierraphytoptinae group (9)** included in the 66tax analyses: *Acathrix*, *Phytoptus* (Phytoptinae); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Pentasetacus* (Nalepellinae: Pentasetacini).

Many species in **Phytoptinae-Sierraphytoptinae group (9)** in the 318tax trees are excluded from the 66-tax data set, and only four species, listed above, are included of those species that are not part of the **Dorsal-rear-fused clade (7)**. The **Dorsal-rear-fused clade (7)** was not found to have a close relationship with the remainder of the species of the Phytoptinae-Sierraphytoptinae group (9) by any of the 66-tax analyses and is not taken into consideration for the discussion of this group. With the reduced taxon set, the Phytoptinae-Sierraphytoptinae group (9) as a whole at one node is not present in the 66-taxon trees, and thus these results do not support **Phytoptinae-Sierraphytoptinae group (9)**.

10a.) ***Pentasetacus*-Sierraphytoptini group 6b** (already discussed)

The 66taxEq tree: *Pentasetacus* and *Sierraphytoptus* are in the same group (the ***Pentasetacus*-Sierraphytoptini group 6b**). These are the only species from the **Phytoptinae-Sierraphytoptinae group (9)** exemplar species that were recovered as a group in this tree. The relationships of the group and other eriophyoid taxa and groups in the tree have not been resolved.

10b.) ***Pentasetacus-Sierraphytoptus-Phytoptus*** **group:** *Pentasetacus* (Nalepellinae: Pentasetacini); *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Phytoptus* (Phytoptinae).

In the three 66tax trees under implied character weighting, *Phytoptus* is sister to the ***Pentasetacus-*** **Sierraphytoptini group 6b**, and constitute the *Pentasetacus-Sierraphytoptus-Phytoptus* group. This group (66tax-k999 tree, node 126, Fig. 4.46) is supported by three homoplasies: *ve* and *c1* present, and *1a* slightly ahead of *2a*. The presence of *ve*, rather than the absence of single *vi*, also supports the recovered relatively close relationships between *Pentasetacus* and species without *vi* in this group, similar to the support for other groups with these suprageneric taxa.

10c.) **Trisetacini-Phytoptinae group (4)** (already discussed)

Acathrix is the closest related to *Trisetacus ehmanni* in the 66tax-k999 and –k30 trees.

10d.) ***Pentasetacus-Sierraphytoptus-Phytoptus-Acathrix*** **group (in 66tax-k20 tree):** *Acathrix*, *Phytoptus* (Phytoptinae); *Pentasetacus-Sierraphytoptus* (Nallepellinae – Sierraphytoptinae).

An alternative hypothesis to consider: *Acathrix*, *Phytoptus* and *Pentasetacus-Sierraphytoptus* are in the same group in the less preferred 66tax-k20 tree (Fig. 4.51). The *Acathrix-Phytoptus-Pentasetacus-Sierraphytoptus* group is the only group in the 66tax trees that supports the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** in the 318tax trees, and is sister to the remainder of the Eriophyoidea included in the analysis.

11.) Groups in the 18tax trees recovered from the four species of the **Phytoptinae-Sierraphytoptinae group (9)** – *Phytoptus* (Phytoptinae), *Sierraphytoptus* and *Mackiella* (both of the Sierraphytoptinae, and of the tribes Sierraphytoptini and Mackiellini, respectively) and *Pentasetacus* (Nalepellinae: Pentasetacini).

11a.) **Sierraphytoptinae group 11a:** *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini); and *Phytoptus* (Phytoptinae) positioned separately.

The 18correct-k999 tree (Fig. 4.55b): the three species from the Phytoptinae and Sierraphytoptinae in the 18tax data set (above), were not found as a group at one node, but are single terminal species, with *Mackiella* splitting of first, then *Sierraphytoptus* and then *Phytoptus*. They are part of and basal in a clade containing all the Eriophyoidea in the 18tax data set, except the **Nalepellinae group** (*Pentasetacus*, *Trisetacus*, *Nalepella*). This "Eriophyoidea minus the Nalepellinae" clade (node 25, Fig. 4.55b) is supported by two synapomorphies, single *vi* absent, and spermathecal tubes short; and a homologous character state of a homoplastic character: long *sc*. This clade is not supported by a GF

value of 50 or above (Fig. 4.56a) but is supported by a GC value of 30 (Fig. 4.56b) in the 18correct-k999 tree.

11b.) Sierraphytoptinae group 11b: *Sierraphytoptus* (Sierraphytoptinae: Sierraphytoptini); *Mackiella* (Sierraphytoptinae: Mackiellini).

The 18correct-k3 tree: the Phytoptinae and Sierraphytoptinae species are again part of an "Eriophyoidea minus the Nalepellinae" clade (node 22, Fig. 4.57) supported by one synapomorphy: single *vi* absent. In this clade, *Sierraphytoptus* is the sister of *Mackiella* (node 24, Fig. 4.57) supported by two homoplasies: frontal lobe present, and opisthosoma differentiated dorsoventrally in longer dorsal annuli, and narrower ventral annuli. These are characteristics of vagrant eriophyoid mites, and differentiate the Sierraphytoptinae from the Phytoptinae.

11c.) *Mackiella*-Nalepellinae clade: *Mackiella* (Sierraphytoptinae: Mackiellini); *Pentasetacus* (Nalepellinae: Pentasetacini); *Nalepella* (Nalepellinae: Nalepellini); *Trisetacus* (Nalepellinae: Trisetacini).

Mackiella was recovered with the **Nalepellinae clade** (*Pentasetacus*, *Trisetacus*, *Nalepella*) as a clade in all the 18modify trees under implied weighting. This *Mackiella*-Nalepellinae clade is at nodes 20 (18modify-k999 tree, Fig. 4.59), and 21 (18modify-k100 tree, Fig. 4.60 and 18modify-k3, Fig. 4.62) supported by one synapomorphy: solenidion *φ* present.

III. The *Novophytoptus* groups (three groups)

12.) *Novophytoptus* groups.

12a.) *Novophytoptus* group: *Novophytoptus rostratae*, *N. stipae* (Novophytoptinae).

The 318taxEq tree: the two *Novophytoptus* spp. were recovered as sisters (node 342, Fig. 4.5) supported by 16 homoplasies, including the genital area far removed from the coxae, which is a diagnostic characteristic of *Novophytoptus* spp., but which was found to be homoplastic, because the genital area is also far removed from the coxae in *Stenarhynchus* (Rhyncaphytoptinae) which was not found to be closely related to the *Novophytoptus* spp., but to other Rhyncaphytoptinae in the **Diptilomiopidae groups or clades (27)**. The other supportive homoplasies are: *ve* and *h1* present, *sc* very long and near rear shield margin, *bv* on femur I and II absent, anterior genital apodeme folded up, and spermathecae elongated.

12b.) ***Novophytoptus-Tetra*** **group:** *Novophytoptus rostratae*, *N. stipae* (Phytoptidae: Novophytoptinae), *Tetra*, *Ursynovia* (Eriophyidae: Phyllocoptinae: Anthocoptini).

The 318tax-k10 tree: the group (node 565, Fig. 4.14) is supported by three homoplasies, of which only one is not reversing, but changing towards another state in the included species, namely *sc* very long, which changes to *sc* exceptionally long at node 566 of the group *Ursynovia-N. stipae*. The relationships between *Tetra* and *Ursynovia,* and the *Novophytoptus* spp. are not strongly supported.

The 318taxEq tree: *Ursynovia* and *Tetra* were recovered as a group (node 343, Fig. 4.5). This supports the synonymy of *Ursynovia* with *Tetra* by Amrine *et al.* (2003). The relationships of this group with other taxa are unresolved.

12c.) ***Novophytoptus-Eriophyes*** **group:** *Novophytoptus* (Phytoptidae: Novophytoptinae), *Eriophyes* (Eriophyidae: Eriophyinae: Eriophyini).

Only one *Novophytoptus* sp. is included in each of the 66-tax (Appendix F) and 18-tax (Appendix H) data sets, and a strong relationship between it and any other taxon was not recovered, except in the 18modify-999k (node 23, Fig. 4.59) and -100k (node 24, Fig. 4.60) trees where a sister relationship between it and *Eriophyes* was recovered. This group is weakly supported by one homoplasy: long *sc*. It is not supported by a GF or GC value (Fig. 4.61) in the 18modify-k999 tree.

ERIOPHYIDAE

4.5.2 Groups retrieved comprising largely Eriophyidae [*sensu* Amrine *et al.* (2003)] species

I. The Eriophyidae groups (six groups)

Determination of what constitutes an Eriophyidae group in the presented trees is subjective, but the groups were largely chosen as the smallest group including all Eriophyidae taxa.

13.) Eriophyidae group and clades

13a.) Eriophyidae group 13a (in the 318tax-k10 tree): all Eriophyidae and Phytoptidae [except ***Nalepella* group 1b**] included, and the Diptilomipidae excluded.

The 318tax-k10 tree: the group (node 344, Fig. 4.8) is weakly supported by three homoplasies: *sc* length short in relation to prodorsal shield length, opisthosomal ridges or furrows present, and genital coverflap ornamented and divided into a basal and distal part. The group is not present in the 318taxEq tree, and is not supported by the symmetric resampling values for the 318tax-k10 tree (Figs 4.24, 4.25).

13b.) Eriophyidae clade 13b (in the 318tax-k20 tree): all Eriophyidae, Diptilomiopidae and Phytoptidae included, except ***Nalepella* group 1b**.

In the 318tax-k20 tree (Fig. 4.26), for which weighting against homoplasy was lighter than for the 318tax-k10 tree, the **Diptilomiopidae clade – 318tax trees (27a)** was not recovered outside, but as part of **Eriophyidae group 13a**. Eriophyidae clade 13b (318tax-k20 tree, node 323, Fig. 4.28) is supported by two homoplasies, *sc* short in relation to prodorsal shield length, and long tibia I, and one synapomorphic character state, short spermathecal tubes. The short spermathecal tubes is a state of one of the more reliable characters in the data set: when the internal genitalia are preserved and observable in slide-mounted specimens, the relative length of the spermathecal tubes are easily and unambiguously scorable, and the spermathecal tubes are long in only the Nalepellinae. In other organisms (e.g., spiders) the internal genitalia provide good phylogenetic signal, and the amount of homoplasy in the character seems to be low in comparison with the other characters in the data sets, for example in the present study it has a ci of 0.4. The state is reversed in **Trisetacini-Nalepellini group 3a** (318tax-k20 tree, Fig. 4.34). Most species and groups in **Eriophyidae clade 13b** were retrieved as part of a polytomy with relationships between the taxa and the **Diptilomiopidae clade – 318tax trees (27a)** unresolved, apart from a few phyllocoptine species outside and at the base of the polytomy (Fig. 4.28).

The group at node 320 (Fig. 4.28) may also be regarded as an Eriophyidae group, and exclude four phyllocoptine species, additional to **Nalepella group 1b**. This node is supported by four homoplasies:

sc length average in relation to prodorsal shield length, *1b* slightly further apart than *1a*, tibia I of average length, 4-rayed empodium I. None of these characters are entirely unambiguous, and they are mostly used to differentiate species, and this Eriophyidae group is regarded to be less likely than **Eriophyidae clade 13b.**

13c.) **Eriophyidae clade 13c** (in the 66tax-k999 and –k30 trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but ***Nalepella* group 1a** excluded.

Eriophyidae clade 13c is at node 79 (Fig. 4.44) and the Diptilomiopidae groups are included in this clade and positioned among the Eriophyidae. This clade is supported by two synapomorphic character states: tibia I of average length, and short spermathecal tubes. The short spermathecal tubes are reversed to being relatively long in *Trisetacus ehmanni*. Alternatively, the group at node 76 (Fig. 4.44) may be regarded as an Eriophyidae group. It is supported by two homoplasies: *sc* directed divergently anteriad, *1b* slightly further apart than *1a*. It excludes ***Nalepella* group 1a**, *Novophytoptus stipae*, and two Aceriini species: *Aceria* and *Acunda*. The group at node 75 (Fig. 4.44) may also be regarded as an Eriophyidae group. It is weakly supported by one homoplasy: 6-rayed empodium I. It excludes ***Nalepella* group 1a**, the **Trisetacini-Phytoptinae group (4)** (*Trisetacus-Acathrix*), *Novophytoptus stipae*, and the two Aceriini species.

The same Eriophyidae groups are found in the 66tax-k30 tree. None of the groups are supported by the symmetric resampling values (Figs 4.49, 4.50). The clade at node 79 is the more reliable retrieval, because it is supported by two synapomorphic character states, including the length of the spermathecal tubes which may have a strong phylogenetic signal.

13d.) **Eriophyidae group 13d** (in the 66tax-k20 tree): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but the group comprising the Phytoptinae, Sierraphytoptinae and *Pentasetacus* in the data set, excluded.

This group (Fig. 4.54) is supported by three homoplasies: *ve* and *c1* absent, and the number of empodial rays. This is an important alternative hypothesis.

13e.) **Eriophyidae clade 13e** (in the 18correct trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but the Nalepellinae in the data set, *Pentasetacus*, *Trisetacus* and *Nalepella* comprising the **Nalepellinae group**, excluded.

The 18correct-k999 tree: The clade (node 25, Fig. 4.55b) is supported by two synapomorphic character states of homologous characters, single *vi* absent, and spermathecal tubes short, and one synapomorphic character state, long *sc*, which changes to other states for groups and taxa within the clade. The clade is not supported by a GF value of 50 or above (Fig. 4.56a) but is supported by a GC

value of 30 (Fig. 4.56b). The clade at node 22 in this tree (Fig. 4.55b) can also be regarded as an Eriophyidae clade. This clade includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and *Novophytoptus* of the Phytoptidae. The other Phytoptidae in the tree are not part of this clade and are positioned at the base of the clade, with *Phytoptus* the sister of the clade. The clade is supported by one synapomorphy, *sc* at or near the rear shield margin, and one homoplasy, *c1* absent. It is not supported by the symmetric resampling values (Fig. 4.56a, b). Based on the character supporting the clades, and the symmetric resampling results, the clade at node 25 may be more robust.

Likewise in the 18correct-k3 tree the Eriophyidae clade at node 22 (Fig. 4.57) includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and all Phytoptidae excluding the Nallepelinae, and is supported by one synapomorphy: single *vi* absent. The alternative Eriophyidae group at node 29 in this tree (Fig. 4.57) includes all Eriophyidae and the **Diptilomiopidae clade – 18tax trees (27b)**, but excludes all Phytoptidae in the 18tax data set. This node is weakly supported by two homoplasies: *ve* absent, and *sc* at or near rear shield margin. The exclusion of the Nalepellinae from, and the inclusion of *Novophytoptus* and possibly other Phytoptidae species with single *vi* absent in a predominantly Eriophyidae + Diptilomiopidae group are the strongest hypothesis from the 18correct trees.

13f.) **Eriophyidae clade 13f** (in the 18modify trees): all Eriophyidae, Diptilomiopidae and Phytoptidae included, but *Phytoptus* and *Sierraphytoptus* (sometimes grouped in the **Phytoptinae-Sierraphytoptini group**), excluded.

This clade is present in all the 18modify trees, including the 18modifyEq tree. It is at nodes 19 (18modifyEq tree, Fig. 4.58), 21 (18modify-k999 tree, Fig. 4.59) and 22 (18modify-k100 tree, Fig. 4.60), supported by three synapomorphic character states: *ve* and *c1* absent, and *sc* projected divergently anteriad. At node 26 (18modify-k3 tree, Fig. 4.62), it is supported by only two synapomorphic character states: *c1* absent, and *sc* on or near rear shield margin. The clade is not supported by symmetric resampling values in the 18modify-k100 tree. The Phytoptidae included in this Eriophyidae clade, under some parameters, may constitute the **Nalepellinae clade (5)** and *Mackiella*, or the ***Mackiella-Nalepellinae* clade (11c)**, and *Novophytoptus*.

II. The Nothopodinae groups (six groups)

14.) **Nothopodinae groups and clade.**

14a.) **Nothopodinae group 14a:** *Anothopoda*, *Nothopoda*, *Pangacarus*, *Floracarus*, *Neocosella*, *Cosella* (Nothopodinae: Nothopodini); *Colopodacus*, *Adenocolus* (Nothopodinae: Colopodacini).

The 318tax-k10 tree: all the Nothopodinae species included in the analysis, except *Disella* and *Apontella*, were recovered as a group at node 446 (Fig. 4.16) supported by two homoplasies: tibia entirely fused with tarsus in leg II, and prosternal apodeme absent (coxae I fused medially). Primarily

the reduction or complete fusion of the tibia with the tarsus differentiates the Nothopodinae from the remainder of the Eriophyidae. Tibia I is absent (entirely fused with the tarsus) in all species in this group, except in *Anothopoda*, where tibia I is distinct, but short and without *l'*. Within the group *Colopodacus* and *Adenocolus* (Colopodacini), are in the same group (node 442) supported by two homoplasies: *1b* and the setal tubercle of *1b* present. The presence of *1b* in the latter species is a reversal within Nothopodinae where *1b* is absent.

14b.) ***Disella-Apontella* group:** *Disella* (Nothopodinae: Nothopodini); *Apontella* (Nothopodinae: Colopodacini).

The 318tax-k10 tree: The *Disella-Apontella* group (node 476, Fig. 4.16) is supported by three homoplasies: tibia partly fused with tarsus in legs I and II, genital coverflap entirely ornamented, and ornamentation divided into a clearly defined basal and distal part. The *Disella-Apontella* group is part of a larger group (node 478, Fig. 4.16), weakly supported by one homoplasy: 5-rayed empodium. The latter group also includes species from the Eriophyinae, Cecidophyinae and Phyllocoptinae, and is in the same group with **Nothopodinae group 14a** at node 447, but with the relationship between these two groups unresolved. Within the group at node 478, *Notacaphylla* (Phyllocoptinae: Acaricalini) is sister to *Disella-Apontella* and they group at node 477 (Fig. 4.16) supported by five homoplasies: *sc* ahead of rear shield margin, frontal lobe present, body fusiform flattened with ridges and furrows present, and dorsal annuli smooth (without microtubercles). The close relationship between some Nothopodinae species and *Notacaphylla chinensiae* is feasible, because the tibia of this species also seems quite shortened, and *l'* is absent (Mohanasundaram & Singh, 1988).

14c.) **Nothopodinae group 14c**: all Nothopodinae in the data set are included (including *Disella* and *Apontella*), but *Anothopoda* is excluded.

The 318tax-k20 tree: This group (node 374, Fig. 4.32) is relatively well-supported by 10 homoplasies, but many states change in individual terminal taxa within the group. The supporting homoplasies are: tibia of legs I and II completely fused to tarsus; *l'* absent; *sc* ahead of rear shield margin; *h1* absent, body elongated fusiform, opisthosomal ridges or furrows absent, dorsal annuli with microtubercles, prosternal apodeme absent (coxae I fused), and 5-rayed empodium. *Anothopoda* is part of a large polytomy (Fig. 4.29) including species of which the relationships with most other Eriophyoidea and groups within the Eriophyoidea are not resolved.

The relationships of species within **Nothopodinae groups 14a and 14c** are not conclusive. *Neocosella* and *Cosella* may be more closely related to each other than to other Nothopodinae (nodes 502, Fig. 4.16 and 393, Fig. 4.32), and the *Neocosella-Cosella* group may be closely related to *Floracarus* and *Disella*, supported by the solenidion of leg tarsus I situated on the lateral tarsus aspect, and not dorsally

above the empodium as in most other eriophyoid taxa (node 393, Fig. 4.32). *Colopodacus* may be closely related to either *Adenocolus* (Fig. 4.16) or *Apontella* (Fig. 4.32).

The 318tax-k20 tree (Fig. 4.32): the relationship of the Nothopodinae species with other eriophyoid groups and taxa was not resolved.

Nothopodinae in the 66tax trees.

Nothopoda and *Colopodacus* were sampled from the Nothopodinae for inclusion in the 66tax data set. They were included mainly because they are the type genera of Nothopodini and Colopodacini, respectively, and both are part of **Nothopodinae groups 14a and 14c** in the 318tax-k10 and -k20 trees, respectively.

14d.) Nothopodinae in the 66tax-k999 tree.

A close relationship between *Nothopoda* and *Colopodacus* is not supported in this tree. *Nothopoda* was recovered as the sister of *Cenaca* (Eriophyinae: Aceriini) (node 112, Fig. 4.46), supported by three homoplasies: *1b* and setal tubercle of *1b* absent, and 4-rayed empodium. *Cenaca-Nothopoda* is sister to a group (node 84, Fig. 4.46) including largely Cecidophyinae, and single Eriophyinae and Aberoptinae. These two groups were recovered as a group (node 85, Fig. 4.46) supported by homoplasies: *l'* and *h1* absent, and *sc* directed divergently posteriad. *Colopodacus* is in a group (node 101, Fig. 4.48) which includes *Epicecidophyes* (Cecidophyinae) and a weakly supported group (node 100, Fig. 4.48) with Phyllocoptinae species and the Phytoptidae group *Retracrus-Neopropilus-Prothrix*, but the relationship of *Colopodacus* with these taxa was not resolved.

14e.) Nothopodinae clade: *Colopodacus* (Nothopodinae: Colopodacini); *Nothopoda* (Nothopodinae: Nothopodini).

The 66tax-k30 tree: The relationship between *Colopodacus* and *Nothopoda* supports the hypothesis gained from the 318tax analyses that at least part of the species in the Nothopodinae may be a monophyletic group. Only one tree was obtained under this weighting scheme, and in this tree *Colopodacus* and *Nothopoda* are retrieved as a clade (node 116, Fig. 4.52) relatively well-supported by two synapomorphies: reduction of tibia and its complete fusion with tarsus in legs I and II. The *Colopodacus-Nothopoda* clade is included in a group (node 86, Fig. 4.52) that comprises the same species than the group (node 85, Fig. 4.46) to which *Nothopoda* belongs in the 66tax-k999 tree, except for the addition of *Colopodacus*. Node 86 (Fig. 4.52) is supported by four homoplasies: *l'* absent (with reversals in *Cecidophyes* and *Colomerus*) and *h1* absent (all species in the group with *h1* absent); *sc* directed divergently posteriad (several character state changes within the group); and *1b* slightly closer together than *1a* (state changes within group, but none of the included species with *1b* further apart than *1a*).

The 66tax-k30 and -20 trees: the "Nothopodinae" group (with *Nothopoda* and *Colopodacus*) is in the same group with two other groups: a group with several Cecidophyinae species (including *Cecidophyes-Dechela*) and *Aberoptus* (Aberoptinae), and another group with the Aceriini (Eriophyinae) *Cenaca* and *Acalitus*. *Ashieldophyes* was not included in the 66tax analyses. The relationship of the Nothopodinae or part of the Nothopodinae with other eriophyoid taxa is not clear, but there is a weak hypothesis that they may have a somewhat close relationship with the Aberoptinae, some Cecidophyinae and some Eriophyinae (Aceriini).

15.) *Nothopoda* in the 18tax trees.

Only *Nothopoda* of the Nothopodinae was included in the 18tax data set. In the 18correct-k999 (Fig. 4.55b) and –k3 (Fig. 4.57) trees *Nothopoda* is sister to a clade with *Aberoptus-Ashieldophyes-Cecidophyes*, and *Phyllocoptes* is sister to *Nothopoda*. In the 18modify trees *Nothopoda* is included in the *Aberoptus-Ashieldophyes-Cecidophyes* group, with the closest relationship to *Aberoptus* in a weakly supported group. In the 318tax-k10 tree the nothopodine species were not in a close relationship with *Aberoptus* (Aberoptinae), *Ashieldophyes* (Ashieldophyinae) or with *Cecidophyes* (Cecidophyinae), but the nothopodine species were in the same larger, weakly supported group (node 447, Fig. 4.16) than *Dechela* (Cecidophyinae).

III. The Aberoptinae groups (two groups)

16.) Aberoptinae groups.

16a.) *Cisaberoptus* deutogyne group: *Cisaberoptus pretoriensis*, *C. kenyae* [originally Cecidophyinae: Aberoptinae reassigned to Eriophyinae: Aceriini by Amrine *et al.* (2003)].

The inclusion of the *Cisaberoptus* spp. is essentially flawed, because the characteristics of the presumed deutogyne females of *Cisaberoptus* were scored in the data set, while all other species in the data set were scored for the same characters from protogyne females. Nevertheless, in the 318tax-k10 tree (the same groups are in the 318tax-k20 tree), the two *Cisaberoptus* spp. were recovered as sisters (node 499, Fig. 4.18) supported by the homoplasies: palp apical ends spatulate or with triangular projections, and body shape flattened fusiform. *Palmiphytoptus* (currently probably erroneously classified in the Phytoptidae) is sister to this group, and *Acunda* (Eriophyinae: Aceriini) sister to the *Palmiphytoptus-Cisaberoptus* group. These four species were recovered as a group at node 440 (Fig. 4.18) supported by four homoplasies: *1a* slightly ahead of *2a*, opisthosomal ridges or furrows absent, coxisternal plates II unornamented, and 8-rayed empodium I. These are used as largely species differentiating characters (except the presence of opisthosomal ridges or furrows).

16b.) ***Aberoptus* groups:** *Aberoptus samoae* (Eriophyidae: Aberoptinae).

Aberoptus samoae is the only species from the Aberoptinae *sensu* Amrine *et al*. (2003) in the present data sets. The 318tax-k10 tree: *Aberoptus* and *Cymoptus* (Eriophyinae: Aceriini) were recovered as sisters (node 348, Fig. 4.18) supported by four homoplasies: *l'* absent, frontal lobe absent, and coxisternal plates I and II unornamented. *Aberoptus-Cymoptus* is part of a group also including *Tergilatus* and *Phyllocoptruta arga* (Phyllocoptinae: Phyllocoptinae) at node 350 (Fig. 4.18). The Aberoptinae were not found to be closely related to the Nothopodinae or the Cecidophyinae in the 318tax trees.

Aberoptus is in the 66tax data set, but *Cymoptus* and *Tergilatus*, both in the same group (node 349, Fig. 4.18) and relatively closely related to *Aberoptus* in the 318tax trees, were not included. *Phyllocoptruta arga*, the other species that was relatively closely related to *Aberoptus* in the 318tax trees, was not found to have a close relationship with *Aberoptus* in the 66tax trees. *Aberoptus* was found rather to have a close relationship with four of the six Cecidophyinae included in the 66tax data set, within the **Cecidophyinae group 17c** (66tax-k999 tree, node 83, Fig. 4.46, and the same group in Fig. 4.51) to be discussed further on.

The 18correct-k999 (Fig. 4.55b) and -k3 (Fig. 4.57) trees: *Aberoptus* is sister to an *Ashieldophyes-Cecidophyes* group, and these three taxa are in a clade supported by one synapomorphy: female genitalia appressed to coxae II. *Nothopoda* (Nothopodinae) is sister to this three taxon group. *Aberoptus* under these parameters is thus more closely related to *Ashieldophyes* and *Cecidophyes* than to *Nothopoda*. *Phyllocoptes* is sister to *Nothopoda*, and these five species were recovered as an "Eriophyidae group" which is included in the same weakly supported group as the group that contains all the Diptilomiopidae in the analysis. The only taxon of the Eriophyidae that is not part of this grouping is *Eriophyes*, which is sister to the Eriophyidae-Diptilomiopidae group. Broadly, the same relationships are found in the 18modify trees.

IV. The Cecidophyinae groups (five groups)

17.) **Cecidophyinae groups.**

17a.) **Cecidophyinae group 17a** (in 318tax trees)**:** *Achaetocoptes*, *Johnella*, *Glyptacus*, *Chrecidus*, *Coptophylla*, *Cecidophyes*, *Bariella* (Cecidophyinae: Cecidophyini); *Epicecidophyes*, *Neocecidophyes*, *Ectomerus*, *Colomerus*, *Indosetacus*, *Circaces* (Cecidophyinae: Colomerini).

The 318tax-k10 tree: Thirteen of the nineteen Cecidophyinae species included in the 318tax data set were recovered as a group (node 424, Fig. 4.13) supported by three homoplasies: dorsoventral differentiation variably different, opisthosoma without ridges or furrows, and genital apodeme folded up, appearing as a thick transverse line. The latter character state is the primary characteristic

diagnosing the Cecidophyinae. The retrieval of the Cecidophyinae as a group on the basis of similarity in female genitalia makes biological sense. The genitalia are a more complex character, less exposed to the outside environment, and this type of character may have strong phylogenetic signal. Unfortunately, it is difficult to study the internal genitalia of the Eriophyoidea accurately, and requires excellent slide-mounting of specimens, and there may be errors in the description of this character in some species. The species of this group are morphologically not particularly uniform, and if the grouping is monophyletic, it serves as a reminder that similar morphology should not be the major or sole reason for evaluating groupings retrieved by phylogenetic analyses.

Not many subgroups were recovered within the group, but rather sister relationships, with taxa splitting off one after the other. The species of the Cecidophyini are generally closer related to each other than to the Colomerini, and *vice versa*. Most of the Cecidophyini species are in the group at node 437 (Fig. 4.13) supported by six homoplasies: *sc* short in relation to prodorsal shield length (which is interesting, because *sc* is absent in the Cecidophyini, and was coded as inapplicable, a state which is computed the same way as unknown characters, substituted with all states possible during the analysis), *l'* vertically on half of tibia, tibia as long as tarsus, frontal lobe edge blunt and rounded, opisthosoma with ridges and/or furrows, and dorsal annuli without microtubercles. *Neocecidophyes* and *Epicecidophyes* of the Colomerini are part of this group. They are the only two Colomerini species of those species included in the 318tax data set with smooth, and much longer dorsal than ventral annuli, and may possibly belong in the Cecidophyini.

Johnella and *Achaetocoptes* were recovered as sisters at node 430 (Fig. 4.13), supported by two homoplasies: shield ornamentation faint and obscure, and dorsal annuli extremely longer than ventral annuli. *Achaetocoptes* and *Johnella* were also found to be sister taxa in the phylogenetic analysis of the Cecidophyini by Hong & Zhang (1996b), supported by two synapomorphies: fewer, broad dorsal annuli which extend laterally, and dorsal annuli of variable width. The sister-taxon relationship between *Johnella* and *Achaetocoptes* is possible. They are morphologically similar, and both are vagrants on *Quercus* spp. in the northern hemisphere. *Johnella* and *Achaetocoptes* each have two species (Amrine *et al*., 2003) and may eventually be placed in one genus, pending results of a phylogenetic analysis of all species in these two and related genera.

The group consisting of only Cecidophyini (node 435, Fig. 4.13), with relationships between the species presented in parenthetical notation are: (*Bariella* (*Cecidophyes* (*Coptophylla* (*Chrecidus* (*Glyptacus* (*Achaetocoptes*, *Johnella*)))))). This group of species is about the same group ("Clade A") found by the analysis of Hong & Zhang (1996b) which includes all the Cecidophyini in their analysis, except *Dechela* and *Neserella* which were part of "Clade B" in their tree. The present results thus supports the retrieval of "Clade A" in the Hong & Zhang (1996b) analysis. In the present study, this

Cecidophyini group seems to be somewhat robust, but apart from *Achaetocoptes-Johnella*, the relationships found between the other species in the group, are weakly supported.

The Colomerini (*Circaces*, *Indosetacus*, *Colomerus* and *Ectomerus*) which are not part of the group at node 437 (Fig. 4.13) are from the southern hemisphere.

The 318tax-k20 tree: Cecidophyinae group 17a is also present (node 368, Fig. 4.34). The topology of the group is slightly different found for the same group in the 318tax-k10 tree, though. The group consisting primarily of Cecidophyini species, together with the Colomerini *Neocecidophyes* and *Epicecidophyes* is still present (at node 367), but particularly the phylogenetic resolution of relationships between the Colomerini species in Cecidophyinae group 17a are unresolved. *Cenalox* (Phyllocoptinae: Phyllocoptini) is sister to Cecidophyinae group 17a, and it seems feasible, primarily because the genitalia of *Cenalox* also seems to be pressed up against the coxae, although the anterior genital apodeme is not folded up in the characteristic single line (Keifer, 1961b).

17b.) *Dechela-Neserella* groups

Dechela and *Neserella* are not in **Cecidophyinae group 17a** in the present study, and was not recovered as part of the broadly corresponding "Clade A" (which includes all other Cecidophyini species) in the tree presented by Hong & Zhang (1996b). In the present study, they were found to be closely related to and in the same group as the **Extended southern-Aceriini group (19)** which is discussed later on. The 318tax-k20 tree: They were found as sisters at node 395 (Fig. 4.30). The 318tax-k10 tree: they are in a group at node 427 (Fig. 4.16) which includes **Nothopodinae group 14a**, as well as a group with diverse species and genera of the Eriophyinae [including the **Extended southern-Aceriini group (19)**], and Calacarini. The group consisting of species from diverse subfamilies (excluding **Nothopodinae group 14a**) is at the base of the group at node 427 and largely originates from the southern hemisphere, and particularly the Oriental, Australian and Afrotropical Regions. The group may be a natural group, or species may be part of natural groupings different from their present classification *sensu* Amrine *et al.* (2003).

17c.) **Cecidophyinae group 17c** (in the 66tax weighted trees): *Colomerus*, *Epicecidophyes* (Cecidophyinae: Colomerini); *Cecidophyes* (Cecidophyinae: Cecidophyini).

Three species (above) of **Cecidophyinae group 17a** were included in the 66tax data set. If the 66tax trees support the close relationships between Cecidophyinae species found by the 318taxon analyses, these species should be positioned in close proximity to each other, and to *Cosetacus* (Fig. 4.40). This is partly the case. The 66tax-k999 tree (Fig. 4.46): They were found in the same group, which includes *Aberoptus* (Aberoptinae) and *Cosetacus* and *Dechela* of the Cecidophyinae which were not part of

Cecidophyinae group 17a in the 318tax trees. The group is at node 83, supported by two homoplasies: genitalia appressed against coxae, and anterior genital apodeme folded up to appear as a thick transverse line. The 66tax-k30 and –k20 trees: the same group is present.

If the Cecidophyinae is monophyletic, the data set as it is at the moment is not sufficient to facilitate discovery of the shape of the genitalia diagnostic of the Cecidophyinae as a synapomorphy for the group. The group with largely Cecidophyinae is converging on being a natural grouping.

17d.) ***Cecidophyes* groups in 18tax trees**: *Cecidophyes* (Cecidophyinae: Cecidophyini); *Ashieldophyes* (Ashieldophyinae); *Aberoptus* (Aberoptinae); sometimes including *Nothopoda* (Nothopodinae: Nothopodini).

Only *Cecidophyes* of the Cecidophyinae was included in the 18tax data sets. The 18correct trees under implied weighting: *Cecidophyes*, *Aberoptus* and *Ashieldophyes* was found as a clade at node 26 (18correct-k999 tree, Fig. 4.55b) and at node 25 (18correct-k3 tree, Fig. 4.57) supported by one synapomorphy: genitalia appressed to coxae. The 18modify-k3 tree: The same clade is present at node 29 (Fig. 4.62) supported by the same synapomorphy, and *Cecidophyes-Ashieldophyes* is at node 31 (Fig. 4.62) supported by one synapomorphy: setal tubercles of *sc* absent. *Cecidophyes* is sister to *Ashieldophyes* in all three clades. All 18modify trees under implied weighting: *Nothopoda* was found in a group with *Cecidophyes*, *Ashieldophyes* and *Aberoptus*. In the 318tax analyses *Ashieldophyes* was thus not found to have close relationships with the Cecidophyinae, but rather with the Phyllocoptinae (Figs 4.10, 4.32).

18.) **Broadly-folded-apodeme group:** *Keiferophyes*, *Acunda* (Eriophyinae: Aceriini); *Brachendus* (Eriophyinae: Eriophyini); *Paracolomerus* (Cecidophyinae: Colomerini); *Palmiphytoptus* (Sierraphytoptinae *sensu* Amrine *et al*., 2003); *Cisaberoptus pretoriensis*, *C. kenyae* (Aberoptinae).

The 318tax-k10 and -k20 trees: This group is at node 441 (Fig. 4.18) and node 373 (Fig. 4.33), respectively, supported by one homoplasy: female genital apodeme broadly folded up, but not forming a characteristic, thin line as found in most Cecidophyinae. The 66tax trees: Only *Acunda* and *Paracolomerus* from this group were included in in the 66tax data set. If the group was supported in the 66-taxon trees, *Acunda* and *Paracolomerus* should have been recovered as sister taxa (Fig. 4.40), or being relatively closely related, but they were not. *Acunda* was recovered to have a closer relationship with *Aceria* at the base of the Eriophyoidea groups (with *Novophytoptus stipae* basal to them and sister to *Aceria*) (66tax-k999 tree, Fig. 4.44). *Paracolomerus* was not recovered in a close relationship with *Acunda* or the other Cecidophyinae in the analyses. It was found to be sister to *Eriophyes pyri* at node 119 (66tax-k999 tree, Fig. 4.46) supported by one homoplasy: *sc* long in relation to prodorsal shield length. No taxa from the **Broadly-folded-apodeme group** was included in the 18tax data sets

The **Broadly-folded-apodeme group** is viable. The description of the anterior genital apodeme, however, may be inaccurate, or not in enough detail, and the grouping may be entirely artificial. Attempts should be made to study the female genitalia in finer detail to find primary homologies. Additionally careful study of non-genitalia morphology study may find other common characteristics that may be of use in differentiating this group, such as the shape of the female genital coverflap.

V. The Eriophyinae group (one group)

19.) Extended southern-Aceriini group: *Acerimina*, *Cenaca*, *Ramaculus* and *Scoletoptus* (Eriophyinae: Aceriini); the group may also include the following species – *Dechela*, *Neserella* (Cecidophyinae: Cecidophyini); *Nacerimina* (Eriophyinae: Eriophyini); *Jutarus* (Phyllocoptinae: Calacarini).

The 318tax-k10 tree: *Ramaculus* and *Cenaca* were recovered as sister species (node 497, Fig. 4.16), supported by one homoplasy: *sc* long in relation to prodorsal shield length. *Scoletoptus*, *Neserella-Jutarus* and *Acerimina*, are outside and at the base of *Ramaculus-Cenaca*, in this order from closest to furthest related to the latter group. These six species were recovered in the same group as *Nacerimina* and species from the Cecidophyinae, Phyllocoptinae, and Nothopodinae (node 427, Fig. 4.16). The latter group is supported by the homoplasies: frontal lobe absent, body vermiform, annuli subequal and not differentiated dorsoventrally and the genital coverflap entirely ornamented but not divided into a basal and distal part. The 318tax-k20 tree: the four Aceriini species are in a relatively large polytomy (Fig. 4.29), and the relationships retrieved between these species in the 318tax-k10 tree are thus not supported.

Only *Cenaca* of the four Aceriini species was included in the 66tax data set. If the relationships of *Cenaca* with other eriophyoid species in the 318tax-k10 tree were supported by the 66tax trees, it should be roughly in the same group as *Dechela*, *Nothopoda*, and *Colopodacus*, and slightly less closely related to *Aequsomatus*. The 66tax-k999 tree: the fairly close relationship of *Aequsomatus* and *Colopodacus* to *Dechela*, *Nothopoda* and *Cenaca* in the 318tax trees is not supported. *Cenaca* and *Nothopoda* were recovered as sister species (node 112, Fig. 4.46), supported by the homoplasies: *1b* and its tubercle absent, and 4-rayed empodium. *Dechela* was found to be less related, but in the same general group (node 85, Fig. 4.46) as *Cenaca*, supported by the homoplasies: *sc* directed divergently posteriad, *h1* and *l'* absent. The 66tax-k30 tree: there is still a fairly close relationship between *Cenaca*, *Nothopoda*, *Colopodacus*, and *Dechela* (they are in the same group at node 86, Fig. 4.52), supported by the homoplasies: *sc* directed divergently posteriad, *h1* and *l'* absent, and *1b* slightly closer together than *1a*. The relationships between the species were retrieved as different from those in the 66tax-k999 tree, though.

Acerimina, *Cenaca*, *Ramaculus* and *Scoletoptus* key out together as a group with *1b* absent within the Aceriini (Amrine *et al.*, 2003). All the species (also those not included in the present analyses) of the four Aceriini genera (*Acerimina*, *Cenaca*, *Ramaculus* and *Scoletoptus*) occur in the southern hemisphere (Gondwana), and although the relationships are surely not well-supported, it is worth exploring the relationships between Aceriini species with *1b* and/or *l'* absent. Regarding the sister relationship found between *Ramaculus* and *Cenaca* in the 318tax-k10 tree: the genus *Ramaculus* has two species, and the species included in the present data sets causes galls on a Violaceae in New Zealand, and *Cenaca* has three species, and the species included in the present data sets causes witches' broom on a Myrtaceae in Singapore. The included species are morphologically similar, except for the differential absence of some setae. *Dechela* and *Neserella* also part of this **Extended southern-Aceriini group** did not form part of a group with most of the Cecidophyinae in the data set, **Cecidophyinae group 17a**, and also formed a separate clade from the other Cecidophyini in an analysis by Hong & Zhang (1996b). In their study, *Neserella* and *Dechela* were recovered as sisters which were found to be part of a larger clade supported by *1b* and *l'* absent.

In conclusion, *Acerimina*, *Neserella*, *Jutarus*, *Scoletoptus*, *Ramaculus*, *Cenaca*, *Nacerimina* and *Dechela* were not retrieved as one group or clade for example in the 318tax-k10 tree (Fig. 4.16), but they are positioned close to each other, they are all from the southern hemisphere, and *1b* and *l'* may be absent. It is hypothesized that these species or some of them, possibly with the inclusion of other closely related species, may be a natural grouping, which may have a close relationship with **Nothopodinae group 14a**.

VI. The Eriophyini (Eriophyinae) (five species positions)

20.) Eriophyini species positions.

20a.) Position *Proartacris*.

The 318tax-k10 tree: *Proartacris* is sister to a group (node 412, Fig. 4.11) including mostly the Phytoptidae species without *vi*, and *Pentasetacus* (**Phytoptinae-Sierraphytoptinae group (9)**). The group (node 413, Fig. 4.11) consisting of *Proartacris* and the **Phytoptinae-Sierraphytoptinae group (9)**, is weakly supported by one homoplasy: opisthosomal ridges or furrows absent. The 318tax-k20 tree: the sister relationship between the **Phytoptinae-Sierraphytoptinae group (9)** and *Proartacris* has not been found, and *Proartacris* is included in a large polytomy (Fig. 4.29). *Proartacris* was not included in the 66-tax and 18tax data sets. The relationship of *Proartacris* stays highly uncertain, but a close relationship with either the other Eriophyinae or Phyllocoptinae included in the 318tax analyses, was not found. A tentative weakly supported relationship was found with some Phytoptidae. This may be feasible, since the three known *Proartacris* spp. live on hosts in the Pinaceae and Arecaceae in the Oriental and Neotropical Regions. Amrine (in a personal communication to Navia & Flechtmann, 2002) pointed out that *Proartacris* spp. should rather be in the Phyllocoptinae based on the presence of

a frontal lobe, the differentiation in the appearance of their annuli dorsoventrally, and the more fusiform shape of the type species, *P. pinivagrans*.

20b.) Position *Trimeracarus*

The monospecific *Trimeracarus* was collected in Hungary from leaf galls on an Araliaceae tree. The 318tax-k10 tree: *Trimeracarus* was found to be closely related to some phyllocoptine species (Fig. 4.12). It was found to be the sister of *Thamnacus* (node 573, Fig. 4.12) weakly supported by one homoplasy: *l'* on vertical proximal quarter of tibia. The sister to this group is *Monotrymacus*, at node 555, weakly supported by two homoplasies: *1a* slightly ahead of *2a*, and frontal lobe edge bluntly rounded. The sister to the *Trimeracarus-Thamnacus-Monotrymacus* group is *Tegoprionus* at node 556, supported by two homoplasies: *sc* ahead, but less than half of shield ahead, of rear shield margin, and *h1* absent. The 318tax-k20 tree: *Trimeracarus* is part of the Eriophyidae polytomy (Fig. 4.29). *Trimeracarus* was not included in the 66-tax and 18-tax data sets. In conclusion, the relationship of *Trimeracarus* with other Eriophyidae species is uncertain. It may have a closer relationship with some phyllocoptine species.

20c.) Position *Eriophyes pyri*

Two *Eriophyes* spp., *E. pyri* and *E. quadrifidus*, were included in the 318tax data sets. Seta *sc* of *E. pyri* is situated very close to the rear shield margin, similar to their position in the Aceriini, and are slightly more ahead of the rear shield margin in *E. quadrifidus*, depending on the interpretation of the exact position and extent of the rear shield margin. Seta *sc* is directed anteriad in both species. *Eriophyes* is a fairly large genus with more than 299 species worldwide (Amrine *et al.*, 2003).

The 318tax-k10 tree: *E. pyri* is included in the same group (node 416, Fig. 4.14) than another group (node 415, Fig. 4.14) with Aceriini, Anthocoptini and the *Novophytoptus* spp. The group at node 416 is weakly supported by one homoplasy: 5-rayed empodium I. This group is one of two groups in a probably more robust larger group (node 418) supported by five homoplasies: *1b* slightly further apart than *1a*, *l'* situated on vertical half of tibia, coxisternal plates II ornamented, genitalia not appressed but close to coxae, and female genital apodeme moderately extended forward and not folded up. *Eriophyes pyri* is the only Eriophyini member in the latter group, and it does not seem to have a close relationship to other Eriophyini species, including *E. quadrifidus*. The 318tax-k20 tree: The latter, largest group is also present in this tree (node 361, Fig. 4.34) and is supported by homoplasies of which some are usually used in the differentiation of supraspecific taxa: long *sc*, body vermiform with annuli dorsoventrally subequal and similar, furrows or ridges absent, dorsal annuli with microtubercles, leg tibia shorter than tarsus, but longer than half tarsus length, and 5- or 6-rayed empodium I.

Eriophyes pyri was included in the 66tax and 18tax data sets. If the 66tax tree fully supported the relationships in the 318tax trees, *E. pyri* would be closely related to *Aceria*, *Novophytoptus*, and slightly further related to *Trisetacus* and *Cosetacus*. These relationships are not supported in the 66tax-k999 tree where *E. pyri* and *Paracolomerus* of the Cecidophyinae were recovered as sisters (node 119, Fig. 4.46). In the 18correct-k999 (Fig. 4.55b) and -k3 trees (Fig. 4.57), the Phytoptidae are at the base of the tree, and *Eriophyes pyri* is sister (at nodes 30 and 29, respectively) to a group consisting of the Diptilomiopidae and Eriophyidae. The *Eriophyes pyri*-Diptilomiopidae-Eriophyidae group (node 30, Fig. 4.55b) is supported by one homoplasy: *ve* absent. The same group is present in the 18correct-k3 tree. In the 18modify trees, *Eriophyes* and *Novophytoptus* were recovered as sisters (nodes 23, Fig. 4.59 and 24, Fig. 4.60). The *Eriophyes-Novophytoptus* group supports this close relationship in the 318tax-k10 tree, but the relationship of the group with other species is not the same.

20d.) Position *Nacerimina*

The 318tax-k10 tree (Fig. 4.16): The genus *Nacerimina* has two species. The species included in the analyses, *N. gutierrezi*, is a vagrant on a palm (Arecaceae) from Samoa and the other, *N. maesae*, was collected in the deformed inflorescence of a host in the Myrsinaceae in South Africa. *Nacerimina* was recovered to be the sister of the Philippine *Dechela* (Cecidophyinae) (node 515) supported by one homoplasy: *l''* on genu II absent. The two species also have other characteristics in common, e.g., the dorsal shield pattern is broadly similar, *1b* is absent, and the internal female genitalia may be similar. The recovered relationships of *Nacerimina* are very weakly supported, though, and in the 318tax-k20 tree *Nacerimina* is included in the Eriophyidae polytomy (Fig. 4.29), and so are most of the other eriophyine and phyllocoptine species in the group at node 427 (Fig. 4.16). *Nacerimina* was not included in the 66tax and 18tax data sets.

20e.) Positions *Eriophyes quadrifidus* and *Asetilobus*

See general information about the genus *Eriophyes* above under the discussion of the relationships of *E. pyri.* The 318tax-k10 tree (Fig. 4.18): the two eriophyine species were recovered in a group with *Phyllocoptes calisorbi* (Phyllocoptinae) (node 484), supported by one homoplasy: annuli subequal and similar dorsoventrally. *Neocolopodacus* (Phyllocoptinae) (a genus with two species from India) is sister to this group at node 485, supported by two homoplasies: body fusiform and fat, and opisthosomal ridges of furrows absent. *Eriophyes quadrifidus* causes the pinule edges of a Dennstaedtiaceae plant to thicken and curl, and was collected in South Africa. *Asetilobus* is monospecific and causes galls on a Verbenaceae in New Zealand. It is feasible that *Asetilobus* may be closely related to open living species currently of the Phyllocoptinae, because it has an obvious frontal lobe, but the lobe is flexible, and the species is without dorsoventral differentiation in the annuli, currently placing it in the Eriophyinae. None of these relationships are supported in the 318tax-k20 tree, and all four species are included in the Eriophyidae polytomy (Fig. 4.29).

VII. The Aceriini (Eriophyinae) (six species positions)

21.) Aceriini species positions.

21a.) Position *Acalitus* (and possibly *Cenaca*).

The genus *Acalitus*, with 87 species (Amrine *et al.*, 2003), occurs widely in all ecozones of the world, and include bud, erineum, and gall mites (Meyer, 1990a). The genus is distinguished by particularly: *bv* and *l'* on leg I absent, *h1* and palp *d* minute or absent, coxisternal apodeme usually weak or absent, with coxae fused medially, and coxisternal plates and female genital coverflap frequently granulated (Keifer, 1965b; Manson, 1984b; Meyer, 1990a; Amrine *et al.*, 2003). The 318tax-k10 tree: *Acalitus* was recovered in a group with two Anthocoptini mites, *Nothacus* and *Quintalitus* (node 361, Fig. 4.16), supported by four homoplasies: palp *d* and *l'* absent, tibia shorter than tarsus, but longer than half tarsus length, and *1b* clearly closer together than *1a*. This group is absent in the 318tax-k20 tree, though, and these three species are part of the Eriophyidae polytomy (Fig. 4.29). *Acalitus* was included in the 66tax data set. If the 66tax trees support the groups found in the 318tax analyses, *Acalitus* should be closely related to *Paracalacarus*, while the other Aceriini species in the 66tax data set, *Cenaca* and *Acunda*, are not closely related to *Acalitus*, but they are in the same larger group with mainly Eriophyinae and Phyllocoptinae species (Fig. 4.40). Particularly close relationships between these three Aceriini species were not found by the 318tax analyses. The 66tax-k999 tree: *Acalitus* and *Nothopoda* (Nothopodinae) were recovered as sisters (Fig. 4.46). *Acalitus* and *Cenaca* are more closely related than both are to other eriophyine species (Fig. 4.43). The 66tax-k30 tree: *Acalitus* and *Cenaca* were recovered as sisters (node 88, Fig. 4.52) supported by two homoplasies: palp *d* and *bv* on leg I absent. *Acalitus-Cenaca* is closely related to **Nothopodinae clade (14e)** and **Cecidophyinae group 17c** (Fig. 4.52). *Acalitus* may thus have a close relationship with *Cenaca*, and they may have a close relationship with, or eventually be in the same monophyletic group with some Nothopodinae. This is feasible, because *l'* and *1b* are absent, the tibia fused or short, ornamentation on the genital coverflaps are similar in these species, and they have 4- or 5-rayed empodia. The close relationship between *Acalitus*, *Nothacus* and *Quintalitus* found by the 318tax analyses is equally well-supported, though, and is a strong alternative hypothesis. Similar to other large eriophyoid genera, however, one exemplar for *Acalitus* is not nearly enough to represent the variation within the genus, and only after including more species will one be able to get a more accurate result regarding the relationships of *Acalitus* spp. with each other, and with other eriophyoid species.

21b.) Position: *Baileyna*.

The genus *Baileyna* has five species (Amrine *et al.*, 2003). The 318tax-k10 tree: *Baileyna* is at the base of a large group (node 426, Fig. 4.13) supported by four homoplasies: *1b* slightly closer together than *1a*, tibia shorter than tarsus, but half or more of tarsus length, body with slightly longer dorsal than ventral annuli, and lateral lobes absent. It is the closest related to *Cenalox* (Phyllocoptini), but the two

species were not recovered as a group at one node. The remainder of the group (excluding *Baileyna*) (node 425) is supported by the genitalia being appressed to the coxae (which is not the case in *Baileyna*). Most of the Cecidophyinae in the 318tax data set (**Cecidophyinae group 17a**) are present in the group at node 426, together with another group at node 418 (Fig. 4.14), which is supported by, among other homoplasies: genital area at "usual" distance from coxae (not appressed to coxae), and genital apodeme moderately extended forward. This differentiates the group from the cecidophyine-like genitalia of the Cecidophyinae in the group at node 426. Two Aceriini, *Paraphytoptella* and *Aceria*, are included in the group at node 418, but in the 318tax trees, *Baileyna* is not particularly closely related to them, but more closely related to *Cenalox* (Phyllocoptini) and some of the Colomerini (*Circaces*, *Indosetacus*, and *Colomerus*) in the group at node 426. These relationships are probably not robust, because *Baileyna* is part of the Eriophyidae polytomy in the 318tax-k20 tree (Fig. 4.29). *Baileyna* was not included in the 66tax and 18tax data sets.

21c.) Position *Cymoptus*.

The genus *Cymoptus* has five species, occurring in both the southern and northern hemispheres. The 318tax-k10 tree: *Cymoptus* and *Aberoptus* were recovered as sisters at node 348 (Fig. 4.18), supported by three homoplasies: *l'* and frontal lobe absent, and coxisternal plates I and II ornamented. *Tergilatus* is sister to the *Cymoptus-Aberoptus* group (node 349, Fig. 4.18) supported by one homoplasy: 2-rayed empodium I. *Phyllocoptruta arga* is sister to *Tergilatus* (node 350). This four-species group is also present in the 318tax-k20 tree, but it is weakly supported by one homoplasy in both trees: 3-rayed empodium I. These relationships are weakly supported. *Cymoptus* was not included in the 66tax and 18tax data sets.

21d.) Position *Notaceria*.

Notaceria is monospecific, and its species is a vagrant collected on *Cordia tetrandra* (Boraginaceae) in Guyana, described by Mohanasundaram and Muniappan (1990). The 318tax-k10 tree: *Notaceria* is the closest related to species of the Phyllocoptinae (Phyllocoptini and Anthocoptini). A sister relationship between it and *Sinacus* (Anthocoptini) was recovered (node 563, Fig. 4.18), supported by three homoplasies: *l'* and lateral opisthosomal lobes absent, and tibia and tarsus of leg I the same length. *Notaceria* itself has many character changes. *Notaceria-Sinacus* was recovered in a group (node 374) which contains other Phyllocoptinae species, weakly supported by two homoplasies: dorsal annuli smooth with slight lateral lobes. The relationships between the species in this group are not well-supported, and all are part of the Eriophyidae polytomy in the 318tax-k20 tree (Fig. 4.29). It is quite plausible, though, that *Notaceria* may be closely related to the vagrant-like species of the Phyllocoptinae. The descriptive drawings of *Notaceria tetrandiae* (Mohanasundaram & Muniappan, 1990) are very schematic. The presence of a frontal lobe is not recorded, and it is not clearly present in the drawings, but the prodorsal shield is quite robust and more rounded anteriorly than e.g., in most

Aceria spp., and it may be partly covering the cheliceral bases. Additionally *Notaceria* is a vagrant species, and both *Notaceria* and *Sinacus* are from the Oriental Region.

21e.) Position *Aceria* and *Paraphytoptella*

Aceria is the type genus of the Aceriini. It probably has close to a 1000 species, and a worldwide distribution. It is the largest genus in the Eriophyoidea (Amrine *et al.*, 2003), with many more unknown species likely to be described in the near future. The type species, *Aceria tulipae*, has been included in some of the analyses, but it is understood that only one species does not represent the potential variation found in such a large genus, even if the characters included in the analyses are focused on character states used for generic and higher taxon differentiation. The genus *Paraphytoptella* is a small genus with two species, but is morphologically (particularly in body shape) very similar to *Paraphytoptus* with 33 species, apart from the absence of opisthosomal *e* in *Paraphytoptella* (Amrine *et al.*, 2003). The 318tax-k10 tree: Although a sister relationship between *Aceria* and *Paraphytoptella* was not found, they are closely related (they are more closely related to each other, than to any other Aceriini species in the analysis), and are included in a group (node 415, Fig. 4.14) weakly supported by one homoplasy: *l'* inserted on proximal third of tibia. This group includes *Heterotergum* (Anthocoptini) as well as a more strongly supported group (node 565) which includes *Tetra*, *Ursynovia*, *Novophytoptus rostratae* and *N. stipae* (***Tetra-Novophytoptus* group**). *Eriophyes* is sister (node 416) to the group at node 415, supported by one homoplasy: 5-rayed empodium I. *Aceria* is sister to ***Tetra-Novophytoptus* group** (node 414), but this relationship is only weakly supported by one homoplasy: *sc* very long in relation to prodorsal shield length. The species and groups discussed so far, is part of a larger group (node 418, Fig. 4.14) supported by five homoplasies: genitalia "usual" distance from coxae, internal genital apodeme not folded up, *1b* slightly further apart than *1a*, coxisternal plates II ornamented, and *l'* inserted vertically on half of tibia. The 318tax-k20 tree: the latter group in the 318tax-k10 tree is also present in this tree (node 361, Fig. 4.34) and is fairly strongly supported by seven homoplasies: long *sc*, body vermiform with annuli dorsoventrally subequal and similar, furrows or ridges absent, dorsal annuli microtuberculated, leg tibia shorter than tarsus, but longer than half tarsus length, and 5- or 6-rayed empodium I. These character states broadly define a "normal, usual or average" vermiform Eriophyoidea species, similar to the morphology of *Aceria* spp., with no particular outstanding "modifying" characteristics. The relationships of the species in the group are roughly the same in the two trees, although some relationships present in the 318tax-k10 tree have not been found by the 318tax-k20 analysis.

Five species, *Cosetacus*, *Trisetacus* (exemplar of the **Phytoptidae group**), *Eriophyes*, *Aceria* and *Novophytoptus* [exemplar of the ***Novophytoptus* group (12a)**] of the largest group just discussed, were included in the 66-tax data set. If the 66tax analyses would broadly retrieve the relationships in the 318tax trees, these five species would be recovered in the same group, placed within a group with all

Eriophyidae in the analysis, and some Phytoptidae, except *Nalepella-Phantacrus* which was retrieved as sister to this group (Fig. 4.40). *Aceria* may be closely related to *Novophytoptus* and *Eriophyes* (Fig. 4.40). The 66tax-k999 and –k30 trees: the five species were not recovered in an exclusive group at one node, but some relationships between the species are supported. *Novophytoptus*, *Aceria* and *Trisetacus* were retrieved in, and at the base of a large group (node 79, Fig. 4.44) and Fig. 4.51, including all the Eriophyoidea in the analysis except *Nalepella-Phantacrus*. The latter is sister to this "Eriophyoidea" group. *Novophytoptus* is sister basally to *Aceria*. They were not recovered as sisters at the same node, but a relatively close relationship between them is supported. *Acunda* is also closely related to *Aceria* in these trees (Figs. 4.44, 4.51) although a close relationship between them was not found by the 318tax analyses. *Trisetacus* and *Acathrix* were recovered as sisters (node 103, Fig. 4.44), and is fairly closely related to *Aceria* and *Novophytoptus*. *Cosetacus* and *Eriophyes* are positioned separately from each other (Fig. 4.46), and from the other three of the five species. The relatively close relationships between them found by the 318tax analyses are thus not supported. *Cosetacus* was, however, found to be more closely related to *Eriophyes* than to the other three species (Fig. 4.46).

In summary, it roughly makes morphological sense that *Eriophyes* spp. (those morphologically similar to *Eriophyes pyri*), *Aceria*, *Paraphytoptella* and *Heterotergum* are closely related, based on a similar body shape, and particularly prodorsum and frontal lobe shapes. *Paraphytoptus* of the Aceriini (not included in the data sets) may also be included in this grouping. In essence, the longer dorsal annuli in *Heterotergum* can be regarded as an anterior extension of the longer dorsal annuli restricted to the posterior part of the opisthosoma in *Paraphytoptus* and *Paraphytoptella*. The relatively close relationships of species *Aculodes*, *Cosetacus*, *Catachela*, *Tetra*, *Ursynovia*, and the group with the two *Novophytoptus* spp., and the group with some of the Phytoptidae species with single *vi* present (namely *Trisetacus*, *Setoptus* and *Boczekella*), within the larger group discussed above based on relationships recovered by the 318tax analyses, are proposed for further study. These relationships could be supported by similar body characteristics, with the possible exception of *Catachela*. As mentioned earlier, it does not seem that the markedly longer distance of the genitalia of *Novophytoptus* from the coxae phylogenetically deeply separates it from the "average" Eriophyidae, however, in order to be positioned closely with these species, the *Novophytoptus* spp. had to undergo numerous character changes, based on the character sample in the present analyses. These are preliminary hypotheses, and should be tested rigorously.

Sixteen *Aceria* species were included in a data set with 26 eriophyoid species in an ongoing, molecular phylogenetic study on the Eriophyoidea (M. Lekveishvili, *unpubl. data*) (see Introduction of this chapter). The analysis of this preliminary data set showed that the genus *Aceria* is not monophyletic, and some species are clustered in small groups, with the other Eriophyidae species scattered among the *Aceria* spp. and retrieved in groups together with *Aceria*

spp. A *Tetra* sp. was found to group with two *Aceria* spp., an *Aculops* sp. was found to group with *Aceria* spp., and an *Acalitus* sp. seemed to be most basal in a (Eriophyidae + Diptilomiopidae) clade. Three *Eriophyes* spp., as well as two Diptilomiopidae species, were retrieved in clusters within the (Eriophyidae + Diptilomiopidae) clade.

21f.) Position *Acunda* and *Keiferophyes*.

Acunda is monospecific, and its type species, *A. plectilis* was collected on grass (Poaceae) in California, USA. *Keiferophyes* has two species, and the type species, included in the data sets, *K. avicenniae*, was collected in the inflorescences of a Verbenaceae in South India. The 318tax-k10 tree: *Acunda* and *Keiferophyes* are in the same group together with other species (node 441, Fig. 4.18) supported by one homoplasy: female genital anterior apodeme broadly folded up. This character is probably phylogenetically highly informative, the interpretation and description of it is unfortunately, surely flawed for most species. This group (node 441) consists of *Keiferophyes* and two groups (nodes 494 and 440), with the relationships between them unresolved. *Paracolomerus* (Colomerini) and *Brachendus* (Eriophyini) were recovered as sisters at node 494 (Fig. 4.18), supported by one homoplasy: *sc* longer in relation to prodorsal shield length. The group at node 440 (Fig. 4.18) is supported by four homoplasies: *1a* slightly ahead of *1b*, opisthosomal ridges or furrows absent, coxisternal plates II unornamented, and 8-rayed empodium I. *Acunda* is part of the latter group, and is sister to a group consisting of *Palmiphytoptus*, and two *Cisaberoptus* spp. (node 500, Fig. 4.18) supported by two homoplasies: *h1* minute, and frontal lobe present. The 318tax-k20 tree: The entire group (318tax-k10 tree, node 441, Fig. 4.18) is also present (node 373, Fig. 4.33) in this tree, supported by the same character state, and it has the same internal topology.

Acunda, but not *Keiferophyes*, was included in the 66tax data set and both were not included in the 18tax data sets. If the group was supported in the 66tax trees, *Acunda* and *Paracolomerus* should be recovered in the same group (Fig. 4.40). The 66tax-k999 and -k30 trees: this relationship is not confirmed. *Acunda* was found to have a greater affinity with *Aceria* at the base of the Eriophyoidea groups, and *Novophytoptus*, *Nalepella* and *Phantacrus* are closely related to them.

VIII. The Phyllocoptinae groups (six groups)

22.) *Schizacea-Knorella* group: *Schizacea*, *Knorella* (Phyllocoptinae: Acaricalini).

This group is present in all the presented 318tax trees. It is well-supported by a GF value of 84 (Fig. 4.24), and a GC value of 83 (Fig. 4.25) in the 318tax-k10 tree. Only *Knorella* was included in the 66tax analyses, and the robustness of the relationship was thus not additionally tested.

The 318taxEq tree (Fig. 4.5): the group (node 339) is supported by 14 homoplasies. A suite of setae are absent: *sc* and its tubercle, *d*, *e*, *bv* on femur I and II, and *l''* on genu II; *l'* vertically on half of tibia; and *1b* clearly further apart than *1a* (this is also reflected by the shape of the coxisternal plates). Two homoplasies are usually regarded as species level characters: coxisternal plates II ornamented, and genital coverflap basally ornamented. Three homoplasies reflect the placement of the species in the Acaricalini of the Phyllocoptinae: dorsal annuli longer than ventral annuli, frontal lobe present and divided empodium.The 318tax-k10 tree: the group (node 551, Fig. 4.17) is supported by five homoplasies: divided empodium, dorsal annuli longer than ventral annuli, and *sc* and its setal tubercle, and *l''* on genu II, absent. The 318tax-k20 tree: the group (node 413, Fig. 4.32) is supported by four homoplasies: three which supported the group in the 318tax-k10 tree – empodium divided, and *sc* and its setal tubercle absent, and additionally genital coverflap is ornamented basally.

This sister relationship is likely. The species are dorsoventrally flattened vagrants on Poaceae in the southern hemisphere. *Knorella* is from a bamboo species in Thailand (Keifer, 1975c) and *Schizacea* is from a large grass species in Colombia, South America (Keifer, 1977a). They are also morphologically very similar, and might have belonged to the same genus, if they did not have differently shaped dorsal ridges and troughs. It will only be possible to test the monophyly of the genera (*Knorella* with eight species, and *Schizacea* with two species Amrine *et al*., 2003) when all the species are included in analyses.

23.) Flat-monocot group: *Tumescoptes*, *Schizacea*, *Knorella* (Phyllocoptinae: Acaricalini); *Acamina*, *Euterpia*, *Neocupacarus* (Phyllocoptinae: Phyllocoptini).

This group is present in the 318tax-k10 and –k20 trees, but not in the 318taxEq tree. It is also not, as a group at one node, supported by a GF value of 50 or above (Fig. 4.24) or by a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree. The well-supported ***Schizacea-Knorella* group (22)** is part of this group.

The 318tax-k10 tree: the group (node 364, Fig. 4.17) is supported by five homoplasies: *bv* absent on femur I and II; *l'* vertically on half of tibia; dorsal annuli slightly longer than ventral annuli (becoming even longer in the ***Schizacea-Knorella* group (22)**, and in *Tumescoptes-Euterpia*); and genital coverflap ornamented, divided into a basal and distal part. The absence of *bv* on both legs is the most unambiguous character. The 318tax-k20 tree: the group (node 335, Fig. 4.32) is supported by three homoplasies: *d* and *e* absent, and tibia longer, but less than half tarsus length longer.

Acamina and *Knorella* from the group were included in the 66tax data set. Their relatively close relationship was not supported by the 66tax analyses, and therefore the monophyly of the group was not supported either. In particular, *Acamina* was recovered in a group with some Diptilomiopinae

species and it may have a diptilomiopid-like gnathosoma, and may be wrongly placed within the Phyllocoptinae (see ***Apodiptacus* group 32b** further on). This is not likely, though, because Keifer, who described *Acamina* (Keifer, 1939) was a careful and accurate taxonomist, and the long form oral stylet of the Diptilomiopidae is distinctively different from the short form oral stylet in the other families.

The group is defensible, although it was not supported in the 66tax trees. The species of the group included in the 318tax data set are all vagrants on Monocotyledones (particularly on grasses and palms), and probably all originated from the southern hemisphere, and particularly from South America and the Oriental Region. Although they are different in specific body modifications, they are all flattened dorsoventrally.

24.) One-Phyllocoptini group: *Neometaculus*, *Indonotolox*, *Metaplatyphytoptus*, *Aequsomatus* (Phyllocoptinae: Phyllocoptini).

The 318taxEq tree: *Neometaculus* and *Metaplatyphytoptus* were recovered as sister species at node 340 (Fig. 4.5), supported by 10 homoplasies, including: *sc* short in comparison with prodorsal shield length, *1b* and its setal tubercle absent, and coxae I medially fused. Three homoplasies are characteristics placing it in the Phyllocoptinae: frontal lobe present, body fusiform flattened, and dorsal annuli longer than ventral annuli. Three homoplasies are regarded as species level characteristics: coxisternal plates I unornamented, tibia longer than tarsus, but less than half tarsus length longer, genital coverflap ornamented, divided into a basal and distal part. The 318tax-k10 tree: the group (node 451, Fig. 4.16) is supported by two homoplasies: *sc* ahead of rear shield margin, and dorsal annuli without microtubercles. The 318tax-k20 tree: the group (node 376, Fig. 4.31) is supported by four homoplasies: *sc* ahead of rear shield margin, *1b* and its setal tubercle absent, and coxisternal plates unornamented. Only *Aequsomatus* of the group was included in the 66tax data set, and the robustness of the group was thus not tested in the 66tax analyses.

The rational for the close relationship between the species in this group is not obvious, apart from all are from the southern hemisphere. They are broadly morphologically similar, but for instance *Indonotolox* has a distinct narrow prodorsal shield projection to the rear. This kind of detail and variation in body modification was not included in the data sets. Nevertheless, the projection would have been autapomorphic for this species among the species in the data sets and could not have had an influence on the retrieval of relationships. The species of the group seem to belong to Phyllocoptini species in which *1b* are absent. Other species in this group (without *1b*), e.g., *Gilarovella*, *Visinus* and *Garcinyes*, have not been included in the data sets in the present study. *Neometaculus* and *Metaplatyphytoptus* are more similar than the other species in the group. Although their bodies do not seem to be equally thick (Mohanasundaram, 1983a; Hong & Kuang, 1989, respectively), it is probably

caused by different mounting procedures. They are differentiated in the same couplet in the genus key of Amrine *et al.* (2003).

25.) ***Tetra-Ursynovia*** **group:** *Tetra*, *Ursynovia* (Phyllocoptinae: Anthocoptini).

The 318taxEq tree: the group (node 343, Fig. 4.5) is supported by six homoplasies: *sc* very long, and in comparison with prodorsal shield length very long, *sc* on or near rear shield margin, *h1* present, body fusiform flattened, and dorsal annuli longer than ventral annuli. The latter two characteristics place the species in the Phyllocoptinae, and *sc* on or near the rear shield margin, place them in the Anthocoptini. The 318tax-k10 and –k20 trees: the species are still in the same groups, but these groups include the two *Novophytoptus* species in the data set. The relationships between them are weak. See the discussion of the ***Novophytoptus-Tetra group*** **(12b)**.

These results do not conclusively confirm, but are supportive of the designation of *Ursynovia* as a junior synonym of *Tetra* by Amrine *et al*. (2003). *Tetra* has 87 species (Amrine *et al*., 2003). These species have a distinctive body shape, with a broad middorsal furrow, and with prominantly long *sc*. The particularly long *sc* contributes towards the retrieval of these relationships.

26.) ***Abacarus*** **groups.**

26a.) ***Abacarus*** **group 26a:** *Abacarus acalyptus, A. hystrix, Porcupinotus* (Phyllocoptinae: Anthocoptini).

The 318taxEq tree: the group (node 320, Fig. 4.5) is supported by 11 homoplasies: *sc* on or near rear shield margin, *h1* present, frontal lobe present, front edge of frontal lobe blunt and rounded, but narrow, body elongated fusiform, wax secretion present in adults, and secreted from ridges, tibia longer than tarsus, but less than half the tarsus length longer, coxisternal plates II ornamented, genital coverflap entirely ornamented, and 6-rayed empodium. The latter four characteristics are usually used at the species level. The 318tax-k10 tree: the group (node 320, Fig. 4.17) is supported by one homoplasy: 6-rayed empodium.

26b.) ***Abacarus*** **group 26b:** *Abacarus hystrix*, *Porcupinotus* (Phyllocoptinae: Anthocoptini).

The 318tax-k20 tree: the group (node 325, Fig. 4.30) is supported by five homoplasies: body elongated fusiform, 8-rayed empodium, genital coverflap ornamented entirely, and wax secretion present in adults, secreted from ridges. Fifty *Abacarus* spp. are known (Amrine *et al*., 2003), most species occur on grasses (Amrine, 1996; Skoracka, 2009), and the genus may be monophyletic. *Porcupinotus* has two species, and the species included in the present study is a vagrant on the leaves of a *Cassia* sp. (Fabaceae) (Amrine *et al*., 2003). The possible reasons for the close relationships between *Abacarus* and *Porcupinotus* is not obvious, but they are morphologically similar, both have ridges on the body,

and wax secretion is present in the adults. The two *Abacarus* spp. being in one genus, and the classification of the three species in one higher taxon, are supported by the recovered relationships.

DIPTILOMIOPIDAE

4.5.3 Groups retrieved comprising largely Diptilomiopidae [*sensu* Amrine *et al.* (2003)] species

I. Diptilomiopidae groups (three groups)

27.) Diptilomiopidae groups and clades.

27a.) Diptilomiopidae clade – 318tax trees: all Diptilomiopidae species in the data set. The Diptilomiopidae were recovered as a clade in the 318tax-k10 and –k20 trees (Figs 4.6, 4.19, 4.26, 4.35). The 318tax-k10 tree: the clade (node 395, Fig. 4.20) is supported by two synapomorphies: gnathosoma with long form oral stylet, and chelicerae relatively long, large, and abruptly bent down at base (Figs 3.22b, d, e; 3.23). These are two characteristics of a complex of structures of the gnathosoma that differentiate the Diptilomiopidae from the Eriophyidae and Phytoptidae. The clade is also supported by one homoplasy: *l'* vertically on proximal third of tibia I. The 318tax-k20 tree: the clade (node 349, Fig. 4.36) is supported by the same two synapomorphies as in the 318tax-k10 tree, and additionally by three homoplasies: *sc* directed parallel or converging anteriad, 5- or 6-rayed empodium I, and genital coverflap smooth. The homoplasies are character states usually used at either the genus or the species level. The clade was not found by the 318tax analysis under equal weighting (Fig. 4.5), which recovered only a few smaller clades and groups of a subgroup of Diptilomiopidae species each. The clade was additionally not supported by a GF value of 50 or above (Fig. 4.24), or by a GC value of 20 or above (Fig. 4.25) in the 318tax-k10 tree.

27b.) Diptilomiopidae clade – 18tax trees: all Diptilomiopidae species in the data sets. Only four species, two of the Rhyncaphytoptinae (*Rhyncaphytoptus* and *Rhinophytoptus*) and two of the Diptilomiopinae (*Diptacus* and *Diptilomiopus*) were included in the 18tax data sets. The four species were retrieved as a clade in all the 18correct, and 18modify analyses under all character weighting schemes, as well as in the trees found with equally weighted characters. The clade seems to be robust and even occurred in all the trees found by the analyses of the flawed data set of Hong & Zhang (1996a) (Fig. 4.3). The clade is always supported by one synapomorphy: the chelicerae abruptly curved downwards. This clade is not supported by symmetric resampling values; only the group with the two Diptilomiopinae species which is part of the clade, is supported by a GF value of 76 (Fig. 4.56a) and GC value of 72 (Fig. 4.56b) in the 18correct-k999 data tree.

27c.) **Diptilomiopidae groups – 66tax trees:** all Diptilomiopidae species in the data set, except *Catarhinus* and *Cheiracus*; or all Diptilomiopidae species, excluding *Rhyncaphytoptus* (Rhyncaphytoptinae) and including *Acamina* (Eriophyidae: Phyllocoptinae: Phyllocoptini).

The 66tax analyses did not recover the Diptilomiopidae as a clade under any of the weighting schemes. The 66tax-k999 and –k30 trees: most Diptilomiopidae species are in the same group (Fig. 4.43, and node 92, Fig. 4.45, respectively), except *Catarhinus-Cheiracus* which is a group positioned among largely Phyllocoptinae. The Diptilomiopidae group (node 92, Fig. 4.45) is supported by two homoplasies which were retrieved as synapomorphies in the 318tax analyses: long form oral stylet, and chelicerae relatively long, large, and abruptly bent down at the base (Figs 3.22b, d, e; 3.23). The 66tax-k20 tree: this tree is not a preferred tree, but as alternative hypothesis, in this tree (Fig. 4.54) the group includes all Diptilomiopidae species in the data set, except *Rhyncaphytoptus*, and it includes *Acamina*. It is supported by the two homoplasies which support the *Diptilomiopus* group in the other 66tax trees. Similar to the 318tax analysis under equal character weights, only some smaller groups with a few Diptilomiopidae species each were found by the 66taxEq analysis.

II. Two major parts within the Diptilomiopidae

Based on the interpretation of results from all the trees, and according to the framework of the classification of the Diptilomiopidae, one can tentatively divide the **Diptilomiopidae groups and clades (27)** of the 318tax and 66tax trees into two loosely defined parts:

28.) **"Rhyncaphytoptinae" part**: Part 2A in the 318tax-k10 tree (Figs 4.19, 4.20); 318tax-k20 tree (Figs 4.35, 4.36, 4.37); 66tax-k999 (Figs 4.43, 4.45); 66tax-k30 (Fig. 4.51); 66tax-k20 (Fig. 4.54).

The 318tax-k10 tree: all Rhyncaphytoptinae included in the 318tax data set (Table 4.1), except *Sakthirhynchus*, are in the **"Rhyncaphytoptinae" part**. It also contains 14 of the 40 non-*Diptilomiopus* Diptilomiopinae species included in the 318tax data set (Table 4.1), and no *Diptilomiopus* spp. This part is basal to the **"Diptilomiopinae" group (29)**, and was not found as a group at one node, but is part of **Diptilomiopidae clade – 318tax trees (27a)** at node 395 (Fig. 4.20). The 318tax-k20 tree: the part consists of the same species, and has more or less the same topology than in the 318tak-k10 tree. **Diptilomiopidae clade – 318tax trees (27a)** is at node 349 (Fig. 4.36) and the **"Rhyncaphytoptinae" part** is part of this clade, and part of it is basal (at node 348, Fig. 4.36) to the **"Diptilomiopinae" group (29)**, but some smaller groupings are at node 349 with unresolved relationships between themselves and the group at node 348. All the 66tax trees: the species of the **"Rhyncaphytoptinae" part** were not retrieved as a group with close relationships between the species, but all are outside the

"Diptilomiopinae" group (29), which was retrieved as a clade when the reduced number of species were analysed (see discussion of the **"Diptilomiopinae" group (29)** hereafter).

29.) "Diptilomiopinae" group: Parts 2B-2D in the 318tax-k10 tree (Figs 4.19, 4.21, 4.22, 4.23); 318tax-k20 tree (Figs 4.35, 4.37, 4.38, 4.39); 66taxEq tree (Figs 4.41, 4.42); 66tax-k999 tree (Figs 4.43, 4.45); 66tax-k30 (Fig. 4.51); 66tax-k20 (Fig. 4.54).

The 318tax-k10 tree: the group constitutes all the *Diptilomiopus* spp. included in the 318tax data set (Table 4.1), and the 26 non-*Diptilomiopus* Diptilomiopinae species not included in the **"Rhyncaphytoptinae" part (28)**. Only one species of the Rhyncaphytoptinae, *Sakthirhynchus*, is in this group. Apart from one species, *Diptilostatus* [see the discussion of the **One-Diptilomiopinae group (34)** further on] the **"Diptilomiopinae" group** is at node 20 (Fig. 4.21) supported by one homoplasy: the absence of *c2*. *Diptilostatus* may not be part of the **"Diptilomiopinae" group**. One species with *c2* absent, *Steopa*, is not within this group.

The 318tax-k20 tree: the **"Diptilomiopinae" group** (excluding *Diptilostatus*) is at node 342 (Fig. 4.37) supported by one synapomorphy, *c2* absent, and three homoplasies: *l''* on genu I absent, and coxisternal plates I and II unornamented. This group includes all the species found in the **"Diptilomiopinae" group** in the 318tax-k10 tree, but also *Steopa* which was in the **"Rhyncaphytoptinae" part (28)** in the latter tree. The position of *Steopa* is thus uncertain.

All the 66tax trees (including the 66taxEq tree): five exemplar species from the **"Diptilomiopinae" group** in the 318tax trees were included in the 66tax data set. They were recovered as an apparently robust clade [see the discussion of the **66-Diptilomiopinae clade (40)** later on] supported in all the 66tax trees by two synapomorphies: *c2* and its setal tubercle absent. The clade is also additionally supported by some homoplasies. The relationships between the species within this clade are resolved and seem to be robust.

Hong & Zhang (1997) found a clade in their phylogenetic study of the Diptilomiopinae, constituting all the genera which are part of the **"Diptilomiopinae" group** in the present study. The Diptilomiopinae genera which were largely (except for *Diptiloplatus*) found to be outside this clade in their study are part of the **"Rhyncaphytoptinae" part (28)** in the present study. This division of the Diptilomiopinae in roughly two groupings supports the "division" of the Diptilomiopinae species into the **"Rhyncaphytoptinae" part (28)** and **"Diptilomiopinae" group (29)** in the present study.

III. Groups and clades within the "Rhyncaphytoptinae" part (28) (Part 2a in the 318tax-k10 tree; Figs 4.19, 4.20)

30.) *Cheiracus* groups.

A ***Cheiracus* group** is present in all the 318tax trees. Only *Cheiracus*, of the species present in the ***Cheiracus* groups**, is included in the 66tax data set, and the robustness of the groups was thus not tested in the 66tax analyses.

30a.) ***Cheiracus* group 30a:** *Cheiracus*, *Brevulacus* (Rhyncaphytoptinae); *Acarhynchus* (Diptilomiopinae).

The 318taxEq tree: the group (node 325, Fig. 4.5) is supported by seven homoplasies, of which two were retrieved as synapomorphies supporting **Diptilomiopidae clade – 318tax trees (27a)**: long form oral stylet, and chelicerae bending down abruptly at the base. Two homoplasies concern body shape brought about by a more vagrant life-style: frontal lobe present, and dorsal annuli longer than ventral annuli. The remaining homoplasies are: *sc* directed converging or parallel anteriad, tibia longer than tarsus, but less than half tarsus length longer, and empodium I with numerous rays. The latter homoplasy is the most obvious morphological indication why these species were recovered as a group (discussed further on).

30b.) ***Cheiracus* group 30b:** *Cheiracus*, *Brevulacus*, *Stenarhynchus* (Rhyncaphytoptinae); *Acarhynchus* (Diptilomiopinae).

The 318tax-k20 tree: the group (node 352, Fig. 4.36) is supported by one homoplasy: 10-rayed empodium. It consists of ***Cheiracus* group 30a**, with the additional retrieval of *Stenarhynchus* (Rhyncaphytoptinae) as sister to the latter group (node 351) supported by one homoplasy: empodium I with numerous rays.

30c.) ***Cheiracus* group 30c:** *Cheiracus*, *Brevulacus*, *Stenarhynchus* (Rhyncaphytoptinae); *Steopa, Acarhynchus* (Diptilomiopinae).

The 318tax-k10 tree: *Steopa* is part of the ***Cheiracus* group** at node 400 (Fig. 4.20) supported by the same homoplasy supporting ***Cheiracus* group 30b**: empodium I with numerous rays. The group is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

The ***Cheiracus* groups (30)** are plausible. The central stems of the empodia from which the rays originate, are thickened and pad-like, in the species of the ***Cheiracus* groups (30)**, or when the empodia have not been specifically drawn and described as such, they probably have shape. These central empodial stems are usually relatively slender in other Eriophyoidea. The empodium of *Cheiracus* seems to be rounded and pad-like in its descriptive drawing, and was described as being pad-like, with no definite central stem, with about 16 rays around the margin, and much internal branching, and it is

not divided (Keifer, 1977a). The empodium of *Brevulacus* (Fig. 3.6m) consists mainly of bundles of rays basally, with normal apical rays which are faintly visible, depicted and described by Manson (1984a). He described the empodium as being divided, but Amrine (1996) regarded the empodium to be entire, based on the descriptive drawing by Manson (1984a) (Fig. 3.6m), and placed it in the Rhyncaphytoptinae. Although the depicted empodia of *Cheiracus* and *Brevulacus* differ, they may be more similar in reality, but drawn in different styles and probably on different focus levels. The empodium of *Acarhynchus* is depicted as a divided empodium with two pad-like stems (Fig. 3.6j) (Keifer, 1959b), and was described by him as a divided empodium which have the medium rays parallel for most of their length, rather than diverging. These three species, always present in the ***Cheiracus* groups (30)** under different weighting schemes, are morphologically relatively similar, in comparison different from the morphology of particularly Diptilomiopinae that belongs to the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. The morphology of *Stenarhynchus* is different in some structures from the three species just discussed, and the empodium is not described or depicted as particularly different in shape than the usual shape, and is only described as having 10 rays (Mohanasundaram, 1983c). The empodium is only drawn laterally, and its real shape can not be seen. Its inclusion in ***Cheiracus* group (30a)**, albeit weakly supported, causes doubt about the accuracy of the description. In contrast with the other ***Cheiracus* groups (30)** species, the morphology of *Steopa* is very similar to that of *Diptilomiopus* spp., and other species in the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. It also is the only species in the **"Rhyncaphytoptinae" part (28)** with *c2* absent (similar to all the species which are part of the **"Diptilomiopinae" group (29)**), with all the other species in the **"Rhyncaphytoptinae" part (28)** with *c2* present. The drawing of the empodium of *Steopa* is very schematic and without detail, and to do an exact comparison with the other empodia in question, is impossible. It is described as having broad branches and many rays on each branch (Chandrapatya & Boczek, 2001b). There are *Diptilomiopus* spp. with similar pad-like or broadened empodia (C. Craemer, *unpubl. data*), e.g., the empodium of *Diptilomiopus championi* (Huang, 1992). Although the author included a SEM image of the empodia, it is not clear, but the stems definitely seem broadened. The author did not mention about this in the text description. The same species (a junior synonym of *D. championi*) (Craemer *et al.*, 2005; Huang, 2005), is described again as *D. septimus* by Huang (2001c), and in this description and drawing nothing is visible and nothing is described in the text of the broadened stems of the empodium.

This account of the empodia of this group illustrates the importance of describing morphology of eriophyoid structures in detail and accurately and in such a way that they are comparable with similar structures that may be primary homologous in other taxa. To alleviate different interpretations and drawings of similar structures, ideally the original mite specimens themselves must be studied again to determine the exact morphology of structures in different species when compared by one person. The latter is unfortunately not always feasible or practically possible in the Eriophyoidea, because of the

sometimes rapid degradation and eventual loss of slide-mounted material (De Lillo *et al.*, 2010). Studying the morphology with techniques such as SEM (Chapter 3) will also aid in preventing different interpretations which frequently happens with descriptions from slide-mounted material. Some structures may also be distorted by slide-mounting (Chapter 3).

In their phylogenetic study of the Diptilomiopinae, Hong & Zhang (1997) included *Brevulacus* as part of the ingroup Diptilomiopinae probably on the basis of the placement of this genus in this subfamily by Manson (1984a). *Brevulacus* was found to be sister to the remainder of the Diptilomiopinae in their analysis supported by the presence of *bv* on leg I, and the absence thereof in the remainder of the Diptilomiopinae. These and the present results strongly support the placement of *Brevulacus* in the Rhyncaphytoptinae, and its exclusion from the **"Diptilomiopinae" group (29)** found in the present study.

This account about the ***Cheiracus* groups (30)** is a hypothesis, but it may illustrate the problems encountered with coding characters from descriptions for the present study, and the necessity for the improvement of accuracy and standardization of eriophyoid descriptions.

31.) Long-tibia groups.

31a.) Long-tibia group 31a: *Dialox, Neodialox* (Diptilomiopinae).

The 318tax-k10 tree: the group (node 516, Fig. 4.20) is supported by three homoplasies: wax secretion in adults, prosternal apodeme present, and tibia length (22 µm) in the category "very, very long" (Character 101), and it is even longer, category "exceptionally long" (30 µm or more), in *Dialox*. The 318tax-k20 and -Eq trees: the group (node 333, Fig. 4.5) is supported by 10 homoplasies, including the same character transformation of Character 101 found in this group in the 318tax-k10 tree, and additionally by the homoplasy, the tibia exceptionally longer than the tarsus, which is also based on the presence of a particularly long tibia. The other supportive homoplasies are: long form oral stylet, and chelicerae relatively long and abruptly bent at the base, empodium divided, 8-rayed empodium, *bv* on femur I absent, *l'* displaced to inner side of tibia, *1b* clearly further apart than *1a*, and adults with wax.

This group is feasible when evaluated on the similar morphology of these monospecific species, their distribution, habit and host plants, and the homoplasies supporting the group. *Neodialox* and *Dialox* both have distinctively long tibia, and they are vagrants on palms in the Oriental Region. They may even belong to the same genus, but are separated at couplet one of the key to Diptilomiopinae genera (Amrine *et al.*, 2003), because *sc* and its setal tubercles are absent in *Neodialox* (Mohanasundaram, 1983a), but present in *Dialox* (Keifer, 1962b). It is surprising that the group is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

31b.) Long-tibia group 31b: *Dialox, Neodialox*, *Diptacus pandanus* (Diptilomiopinae). In the 318tax-k10 and –k20 trees *Diptacus pandanus* is sister to **Long-tibia group 31a**. The 318tax-k10 tree: the group (node 517, Fig. 4.20) is supported by four homoplasies: 8-rayed empodium, tibia length (Character 101) "average long" (14–15 µm), but becoming longer in *Neodialox* and *Dialox* as discussed above, *h1*, and *l''* on genu II, present. The 318tax-k20 tree: the group (node 397, Fig. 4.37) is supported by six homoplasies: the four homoplasies supporting the group in the 318tax-k10 tree, and additionally *bv* on femur II present, and genital coverflap smooth with a change of the state in *Dialox*.

Diptacus has 43 species (Amrine *et al.*, 2003, Appendix A). Two *Diptacus* spp. were included in the 318tax data set, *D. pandanus*, and the type species, *D. sacramentae*. *Diptacus pandanus* was included because it previously belonged to *Diptilomiopus* and was re-assigned to *Diptacus* by Hong & Zhang (1997), but does not seem to belong in *Diptacus*, because it has *bv* present on femur II among other characteristics. Keifer (1962d) implied a close relationship between *Diptacus* and *Dialox*, because he differentiated *Dialox* from *Diptacus*. Although *Diptacus pandanus* was recovered in a group with *Dialox* and *Neodialox*, the type species *D. sacramentae* was not. The latter species is part of a group in the 318tax-k20 tree (node 379, Fig. 4.37) which is relatively closely related to the groups (node 345 and 344, Fig. 4.37) to which **Long-tibia group 31b** belongs. The three species of the **Long-tibia groups (31)** were not included in the 66tax and 18tax analyses for additional testing of the robustness of the groups.

32.) *Apodiptacus* groups.

32a.) *Apodiptacus* group 32a: *Apodiptacus*, *Asetadiptacus*, *Diptacus sacramentae*, *Duabangus*, *Pararhynacus*, *Trimeroptes* (Diptilomiopinae); *Asetacus*, *Konola* (Rhyncaphytoptinae).

The 318tax-k20 tree: the group (node 379, Fig. 4.37) is supported by four homoplasies: *sc* length average in relation to prodorsal shield length, wax secretion present in adults (with reversals in *Pararhynacus* and *Asetadiptacus*), tibia medium long (12-13 µm) (Character 101), but change to average (4–11 µm) in *Konola* and *Duabangus*, empodium I divided, but change to simple in the Rhyncaphytoptinae species, *Asetacus* and *Konola*. Within the group, *Pararhynacus* was recovered as a sister of *Asetadiptacus* (node 382) and *Diptacus sacramentae* as a sister of *Asetacus* (node 381).

The 318tax-k10 tree: ***Apodiptacus* group 32a** species is positioned at the base of **Diptilomiopidae clade – 318tax trees (27a)**, with close relationships between the species, but they were not recovered as a group at one node. *Pararhynacus* was again recovered as the sister of *Asetadiptacus* (node 483) supported by three homoplasies: *sc* absent, wax secretion in adults absent, and tibia more than half tarsus length longer than tarsus. *Trimeroptes* was found as the sister of *Apodiptacus* (node 474) supported by two homoplasies: *1a* ahead of *2a*, and body flattened fusiform. The relationship between

these two species was not resolved by the 318tax-k20 analysis. *Trimeroptes-Apodiptacus* is the sister group of *Pararhynacus-Asetadiptacus* (node 475), supported by one homoplasy: 5-rayed empodium.

The relatively close, but loose, relationships between the species of ***Apodiptacus* group 32a** are possible, although the group was found to be polymorphic. They are morphologically more similar to each other, than the species are to most other taxa in their respective subfamilies. The group, or part of the group, may be monophyletic, but the species belonging to such a clade will probably change with new information. Within ***Apodiptacus* group 32a**, *Trimeroptes*, *Apodiptacus*, *Asetacus* and *Konola* are morphologically roughly similar, based on their general shape, prodorsal shield shapes and ornamentations, and presence and shape of the frontal lobe. Although the characteristic was not included in the data set *per se*, all these species have some kind of indentation or notch (emarginated *sensu* Amrine *et al.*, 2003) medially in the frontal lobe. *Pararhynacus*, *Asetadiptacus*, *Duabangus* and *Diptacus* are morphologically more similar. The group's position within the **"Rhyncaphytoptinae" part (28)** of the 318tax-k10 tree is also more feasible, morphologically, than a position within the **"Diptilomiopinae" group (29)** which largely contains species that are more similar to *Diptilomiopus* spp., and are without *c2*.

The sister relationship found between the monospecific *Pararhynacus* described by Kuang (1986a) and *Asetadiptacus* described by Carmona (1970) (which has two species), and their retrieval outside the **"Diptilomiopinae" group (29)**, and thus the lack of a close relationship with *Diptilomiopus* and morphologically similar species, are feasible. They are morphologically similar in several characteristics, including: *sc* absent, but its tubercle present, and broadly similar, cell-like, dorsal shield patterns, which are not similar to the general dorsal shield cell-pattern of *Diptilomiopus* spp. Amrine (1996) synonymized *Pararhynacus* with *Asetadiptacus*, but Amrine *et al.* (2003) reversed the synonymy, and regarded *Pararhynacus* as a distinct, valid genus, because it is described as having a short median ridge behind the prodorsal shield, followed by a broad furrow (Kuang, 1986a), while the body of *Asetadiptacus* is evenly rounded (Carmona, 1970). They are differentiated from each other, on the basis of these different dorsal body shapes, in the same key couplet in Amrine *et al.* (2003). It is possible that the rounded body shape of *Asetadiptacus*, and/or the dorsal shape of *Pararhynacus* may be artefacts caused by slide-mounting.

The sister relationship found between *Trimeroptes* and *Apodiptacus* is plausible. They are morphologically similar, except for slight differences in the shape of their opisthosomal ridges. They are differentiated from each other in the same genus couplet in Amrine *et al.* (2003). The two species included in the analyses are both from North America (Amrine *et al.*, 2003).

32b.) ***Apodiptacus* group 32b:** *Apodiptacus*, *Diptacus sacramentae* (Diptilomiopinae); *Asetacus* (Rhyncaphytoptinae); *Acamina* (Eriophyidae, Phyllocoptinae, Phyllocoptini).

Three of the species in ***Apodiptacus* group 32a** were included in the 66tax data set, and they were recovered as a group, together with *Acamina*, under all character weighting schemes except equal weighting.

The 66tax-k999 tree: the group (node 89, Fig. 4.45) is supported by five homoplasies: adults secrete wax, tibia 12–13 µm or 14–15 µm long (these two homoplasies are also present in the homoplasies supporting ***Apodiptacus* group 32a**), *sc* directed parallel or converging anteriad, *h1* absent, and frontal lobe present. This group supports ***Apodiptacus* group 32a** retrieved by the 318tax analyses, and likewise was not recovered in the same group than species included from the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. This group, together with its sister species, *Hoderus*, is sister to **One-*Diptilomiopus* group** which will be discussed later.

The retrieval of *Acamina* (Phyllocoptinae) within this group may be wrong. It has been recovered as the sister of *Apodiptacus* (node 87, Fig. 4.45) supported by two homoplasies: opisthosomal ridges or furrows present, and 5-rayed empodium. If Diptilomiopidae are a monophyletic group supported by the synapomorphies that are characteristic of the gnathosoma of the Diptilomiopidae (Fig. 3.22b, d, e), the position of *Acamina* among the Diptilomiopidae is incorrectly retrieved by the 66tax analyses, except if the characteristics of the gnathosoma in the present data set were reversed in *Acamina*, which is unlikely. This characteristic is complex, and several homoplasious states can be identified from it. There is a possibility that *Acamina nolinae* may have the "typical" Diptilomiopidae gnathosoma. Its gnathosoma is quite robust (Keifer, 1939a), but so is the gnathosoma of some other Phyllocoptinae and Phytoptidae, but additionally on evaluation of the drawing of its gnathosoma (Keifer, 1939a) it may have a diptilomiopid-like gnathosoma. J. W. Amrine Jr. (*pers. comm.*) noted that this may be possible, and if *Acamina* belongs in the Diptilomiopidae, he will place it near *Asetacus madronae*. Another extrapolation from this position of *Acamina* could be that it indicates a close relationship between the Diptilomiopidae and the Phyllocoptinae. *Asetacus* is sister to *Apodiptacus-Acamina* in ***Apodiptacus* group 32b**. The group is also present in the 66tax-k30 (Fig. 4.51) and -k20 (Fig. 4.54) trees, but with a different topology in the –k20 tree.

The ***Apodiptacus* groups (32)** are not present in the 318taxEq and 66taxEq trees, and are not supported by any of the GF values of 50 or above (Figs 4.24, 4.49), or by a GC value of 20 or above (Figs 4.25, 4.50) in the 318tax-k10 and 66tax-k999 trees, respectively.

33.) *Rhyncaphytoptus* groups.

33a.) *Rhyncaphytoptus* group 33a: *Rhyncaphytoptus*, *Rhinophytoptus*, *Peralox* (Rhyncaphytoptinae).

The 318tax-k10 tree: the group (node 569, Fig. 4.20) is supported by three homoplasies: opisthosomal ridges or furrows absent (with a change in *Peralox* to the state "deep cleft behind shield"), and coxisternal plates I and II unornamented. The latter character is presently used for species differentiation. The relationships found between the species in this group are weak, with *Rhyncaphytoptus* sister to *Rhinophytoptus-Peralox*.

33b.) *Rhyncaphytoptus* group 33b: *Rhyncaphytoptus*, *Rhinophytoptus*, *Peralox*, *Rhinotergum*, *Hyborhinus* (Rhyncaphytoptinae).

The 318tax-k20 tree: the group (node 410, Fig. 4.36) is supported by five homoplasies: opisthosomal ridges or furrows absent, coxisternal plates I unornamented (these are two of the three homoplasies supporting ***Rhyncaphytoptus* group 33a**), body elongated fusiform, *1b* in line with *1a*, and *sc* directed divergently anteriad. In the 318tax-k10 tree *Hyborhinus* is sister to and basal to a group at node 393 (Fig. 4.20) consisting of the remainder of the Diptilomiopidae in the data set, except *Rhinotergum*, which is sister to and basal to *Hyborhinus*, and they are not in ***Rhyncaphytoptus* group 33a**.

Only *Rhyncaphytoptus* of the species in the **Rhyncaphytoptus groups (33)** was included in the 66-tax data set. *Rhyncaphytoptus* was not recovered in a group with any particular species in any of the 66tax analyses. The 66tax-k999 tree: it is included in a group (node 92, Fig. 4.45) with most of the Diptilomiopidae in the 66tax data set, and is sister to the remainder of the species in this group, and it is not part of the clade (node 118, Fig. 4.45) with the species sampled from the **"Diptilomiopinae" group (29)** in the 318tax-k10 tree. The 66tax-k30 tree has the same topology for these species. The 66tax-k20 tree: *Rhyncaphytoptus* is not part of a group with most of the Diptilomiopidae, but sister to all the Eriophyoidea in the tree apart from the **Phytoptinae and Sierraphytoptinae and *Pentasetacus*** group outside the larger Eriophyoidea group. The latter is not obviously feasible as a strong hypothesis, but it additionally indicates that the relationships of *Rhyncaphytoptus* with particularly other Diptilomiopidae species are uncertain. It is, however, probably part of a Diptilomiopidae clade in reality, similar to **Diptilomiopidae clade – 318tax trees (27a)** in the preferred 318tax-k10 tree, due to the characteristic and relatively complex gnathosomal morphology.

The ***Rhyncaphytoptus* groups** are not present in the 318taxEq tree (Fig. 4.5), and were not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree. Only *Rhyncaphytoptus* of the ***Rhyncaphytoptus* groups**' species were included in the 66tax data set (Table 4.1), and the robustness of the groups was thus not tested in the 66tax analyses. *Rhyncaphytoptus* and *Rhinophytoptus* were the only and all Rhyncaphytoptinae included in the 18tax

data sets. In the 18tax trees (Figs 4.55, 4.57, 4.58, 4.59, 4.60, 4.62) the relationship between *Rhyncaphytoptus* and *Rhinophytoptus* was not conclusive, but they are always part of a **Diptilomiopidae clade or group (27)** which includes the two Rhyncaphytoptinae species, and two Diptilomiopinae species.

With all evidence at hand it seems that the ***Rhyncaphytoptus* groups** are not well-supported and robust. *Rhyncaphytoptus*, which is part of these groups, is the type genus of the Rhyncaphytoptinae Roivainen, 1953 (Newkirk & Keifer, 1971), though, and I propose that it may eventually be part of a monophyletic group of species of which most are currently in the Rhyncaphytoptinae and some of the species in the Diptilomiopinae, such as *Bucculacus*. This group will probably exclude Rhyncaphytoptinae species that may eventually turn out to belong to other monophyletic groups, of which some possibly may correspond with e.g., the ***Cheiracus* groups (30)**, **Long-tibia groups (31)** and the ***Apodiptacus* groups (32).**

IV. Groups and clades within the "Diptilomiopinae" group (29) (Part 2a; Figs 4.19, 4.21, 4.22, 4.23)

34.) One-Diptilomiopinae group: *Diptilostatus*, *Thailandus*, *Prodiptilomiopus*, *Neorhynacus*, *Neoacarhis*, *Davisella*, *Acarhis lepisanthes*, *A. diospyrosis* (Diptilomiopinae); and the three species of ***Lithocarus* group (35)** which will be discussed later – *Mediugum*, *Lithocarus*, *A. siamensis* (Diptilomiopinae).

This group occurs in the 318tax-k10 (Figs 4.21, 4.22) and -k20 (Fig. 4.37) trees, but with different topologies. The 318tax-k10 tree: *Diptilostatus*, the remainder of the **One-Diptilomiopinae group**, and other **"Diptilomiopinae"group** species, are in one group (node 383, Fig. 4.21) supported by three homoplasies: prodorsal shield broadly oval, opisthosoma with dorsal annuli slightly longer than ventral annuli, and 5-rayed empodium I. The latter characteristic, particularly, is regarded as a species level character for the Eriophyoidea. **One-Diptilomiopinae group** (node 382, Fig. 4.21) is supported by one homoplasy: *c2* absent. Seta *c2* is absent in all species of this group, except *Diptilostatus*. Four species, including *Diptilostatus*, are at the base of the **One-Diptilomiopinae group** as well as the **"Diptilomiopinae" group (29)**. These are sister and basal to each other in the order: *Diptilostatus*, *Neorhynacus*, *Davisella*, and *Neoacarhis aglaiae* (Fig. 4.21). The remaining seven species of **One-Diptilomiopinae group** were recovered as a group (node 378, Fig. 4.22) supported by one homoplasy: *l''* on genu I absent. The latter group consists of two groups, namely ***Lithocarus* group (35)** (to be discussed further on); and *Thailandus* and *A. diospyrosae*, retrieved as sisters (node 375, Fig. 4.22) supported by two homoplasies: *sc* directed divergingly posteriad, and 6-rayed empodium I.

The 318tax-k20 tree: the group, and its subgroups, are also present in this tree (Fig. 4.37), but with a different topology. The topologies differ as follows: *Diptilostatus*, the remainder of the **One-Diptilomiopinae group** and the other **"Diptilomiopinae"group** species, were recovered as a group (node 343, Fig. 4.37), supported by three homoplasies: *l'* absent, prodorsal shield broadly oval, and frontal lobe absent. **One-Diptilomiopinae group** (except *Diptilostatus*) (node 342, Fig. 4.37) is supported by four homoplasies: *c2*, and *l''* on genu I, absent, and coxisternal plates I and II unornamented. The absence of *c2* may be one of the more important characteristics supporting this group, similar to the support of node 382 (Fig. 4.21) in the 318tax-k10 tree. Relationships between the species in the **One-Diptilomiopinae group** (except *Diptilostatus*) are unresolved, as well as the relationship between this group of species and the larger group at node 378, to which they are sister. *Diptilomiopus ervatamiae* was recovered together with the One-Diptilomiopidae species in this unresolved group, but in the present study the recovery of this species as part of the ***Africus* clade (38a)** (discussed further on) in the preferred 318tax-k10 tree, is favored.

The species of the **One-Diptilomiopinae group**, except *Davisella* and *Diptilostatus*, are from the Oriental Region (Taiwan, Thailand and India), and are morphologically similar, including similar body shapes, and broadly similar dorsal shield patterns. *Diptilostatus* and *Davisella*, more basal in the **One-Diptilomiopinae group**, are morphologically less similar, and a close relationship between them and the other species of the group is not particularly supported by their recovered positions within the group. Particularly *Diptilostatus*, with *c2* present, might eventually rather belong to the **"Rhyncaphytoptinae" part (28)**.

The sister relationship recovered between *Thailandus* and *A. diospyrosae* is feasible. *Acarhis diospyrosae* is wrongly placed in *Acarhis*, and may belong to *Thailandus*. Both species were collected in Thailand and are vagrants on the leaf under-surfaces of *Diospyros gracilis* (Chandrapatya & Boczek, 1997b) and *D. rhodacalyx* (Chandrapatya & Boczek, 1991c), respectively. They are morphologically similar, but must be re-examined due to unclear species descriptions with various mistakes, before their classification can be determined.

35.) ***Lithocarus* group:** *Lithocarus*, *Mediugum*, *Acarhis siamensis* (Diptilomiopinae).

This group is present in the 318taxEq (Fig. 4.5) and -k10 (Fig. 4.22) trees, but not in the 318tax-k20 tree. In the latter tree the species are part of the polytomy of **One-Diptilomiopinae group (34)** species (Fig. 4.37). The three species were not included in the 66tax and 18tax data sets.

The 318tax-k10 tree: the group (node 396, Fig. 4.22) is supported by four homoplasies: genu fused with femur in legs I and II, dorsal annuli with microtubercles only on ridges, and tibia shorter than half tarsus length. Although the latter can be quite subjective, these are relatively reliable characteristics.

The 318taxEq tree: the group (node 324, Fig. 4.5, Group E16) is supported by 19 homoplasies. The homoplasies include the four homoplasies supporting the group in the 318tax-k10 tree. The additional homoplasies include characters that are of importance at family and subfamily level: long form oral stylet, chelicerae abruptly bent down at the base (Fig. 3.22b, d, e), and divided empodium (Fig. 3.6h); at genus level: *c2* and its tubercle absent, and *bv* and *l''* absent on legs I and II; and normally differentiating species: *sc* short and short in relation to prodorsal shield length, coxisternal plates I and II unornamented, anterior coxae separated, 7-rayed empodium, and the prodorsal shield broadly oval. The relationships of this group with other eriophyoid taxa are not resolved in this tree.

This group is feasible. Its three species are morphologically similar, in particular, the genu is fused with the femur in legs I and II, and dorsally they have three longitudinal ridges, with microtubercles only present on the ridges. These detailed characteristics of the shape of the opisthosomal ridges were not included in the data set. *Acarhis siamensis* should not be in *Acarhis*, because its genu is fused with the femur in both legs I and II, while the genu is present in legs I and II in *Acarhis*. *Acarhis siamensis* keys out near *Acarhis* and/or *Suthamus* in the key of Amrine *et al*. (2003). Close relationships were not found between *A. siamensis* and the other two *Acarhis* spp. in the data set, although all three *Acarhis* spp. are part of the **One-Diptilomiopinae group (34)**. The absence of *l'* in *Mediugum* and *Lithocarus*, and its presence in *A. siamensis*, and the absence of *e* in *Mediugum*, are the most important morphological difference between them. The three species are leaf vagrants, and occur in the Oriental Region (Boczek & Chandrapatya, 2000; Chandrapatya & Boczek, 2000c; Huang, 2001d).

36.) *Dacundiopus* clade: *Dacundiopus*, *Lambella*, *Levonga papaitongensis* (Diptilomiopinae). This clade was recovered in the 318taxEq (Fig. 4.5) and 318tax-k10 (Fig. 4.21) trees, but not in the 318tax-k20 tree where they are part of a polytomy consisting mostly of *Diptilomiopus* spp. (Fig. 4.38). The three species were not included in the 66tax and 18tax data sets.

The 318taxEq tree: the clade (node 332, Fig. 4.5) is supported by one synapomorphy – the tarsus with two segments, and 15 homoplasies. Three of the homoplasies are characteristics placing them in the Diptilomiopidae and Diptilomiopinae. One homoplasy concerns their more vagrant bodies: dorsal annuli longer than the ventral annuli. The remainder of the homoplasies are coxae I being fused, and setal characters: *sc* present, directed anteriad, either parallel or convergent, *c2* and *1b*, as well as their tubercles absent, and *bv* on legs I and II, *l'* on leg I and *l''* on leg II absent. The relationships of this clade with other eriophyoid species and groups in this tree are unresolved. The 318tax-k10 tree: the clade (node 509, Fig. 4.21) is supported by the same synapomorphy as in the 318taxEq tree: tarsus with two segments. It is additionally supported by two homoplasies: *sc* present, and prodorsal shield sub-rectangular. The shield shape is an ambiguous character, scored on subjective interpretation. The clade

is not supported by a GF value of 50 or above (Fig. 4.49), or by a GC value of 20 or above (Fig. 4.50) in the 318tax-k10 tree.

The three species in the ***Dacundiopus* clade** were described from New Zealand by Manson (1984a). *Dacundiopus* and *Lambella* are monospecific, and *Levonga* has six species (Amrine *et al.*, 2003). The tarsus of five *Levonga* spp. (apart from the type species *Levonga papaitongensis*), is not divided into two segments, and some previously belonged to the genus *Pseudodiptacus* Chakrabarti *et al*., 1992. *Pseudodiptacus* has been assigned as a junior synonym of *Levonga* (Amrine *et al*., 2003). Three *Levonga* spp. have been included in the present study (Table 4.1) and only *Levonga papaitongensis*, with the tarsus divided into two segments, is part of the ***Dacundiopus* clade**. The tarsi may not be divided in reality, because sometimes in eriophyoid species it seems that the tarsus is divided because it has a deep indentation below *ft*. In the three ***Dacundiopus* clade** species, however, the tarsi may indeed be divided, because enlargements of the divided tarsi were included. Nevertheless, specimens of these taxa should be re-examined to confirm the characteristic. Specimens could not be obtained for the present study.

These results from the present study supports the close relationship between *Dacundiopus*, *Levonga* and *Lambella* (and *Pseudodiptacus*) found in the phylogenetic study of the Diptilomiopinae by Hong & Zhang (1997). Although their ingroup taxa were genera, and not exemplar species, they probably scored the characteristics of *Levonga* only from the type species, *L. papaitongensis*.

37.) Separate-coxae group: *Levonga litseae*, *Diptilomiopus guajavae*, *D. thangaveli* (Diptilomiopinae).

This group is present in the 318tax-k10 (node 537, Fig. 4.21) and -k20 (node 404, Fig. 4.39) trees. It is not present in the 318taxEq tree, and none of the species were included in the 66tax and 18tax data sets.

The 318tax-k10 tree: the group (node 537, Fig. 4.21) is supported by two homoplasies: *ft'* on tarsus II absent, and dorsal annuli with microtubercles. *Norma* is sister to the group. The 318tax-k20 tree: the group (node 404, Fig. 4.39) is supported by six homoplasies: genu present, and not fused with femur in legs I and II, *l''* on genu I present (change to genu fused with femur in legs I and II, and *l''* absent in *Diptilomiopus*), opisthosoma evenly rounded without ridges or furrows, dorsal annuli with microtubercles, and coxae I separated.

The recovered close relationships between these three species are not strongly supported, but they are morphologically similar, and the close relationship with each other and not with other *Diptilomiopus* spp. and/or *Levonga* spp., is feasible. *Diptilomiopus thangaveli* and *D. guajavae* do not belong in *Diptilomiopus* as the genus is currently diagnosed. The genu of legs I and II, and *l''* on genu I are

present in *D. thangaveli* (Mohanasundaram, 1983c). This species keys out to be *Vimola* in the key by Amrine *et al.* (2003). The description of *D. guajavae* is flawed. Mohanasundaram (1985) described the species as having a tibiotarsus in legs I and II (tibia fused with tarsus), but this is not likely, and in the drawing it seems that rather the genu is absent. If the latter is the case, *l'* is present in this species according to the descriptive drawing (*l'* is not present in *Diptilomiopus*). Apart from these ambiguities, there are also other inconsistencies in the description that need to be clarified. *Levonga litseae* previously belonged to *Pseudodiptacus*, but *Pseudodiptacus* was made a junior synonym of *Levonga* by Amrine & Stasny (1996) without an explanation. *Levonga litseae* keys out to be *Levonga* in the key by Amrine *et al.* (2003), but differs from the type species of *Levonga*, *L. papaitongensis*, among other characteristics, by having an entire and not a divided tarsus. It is proposed that close relationships between the species in the separated-coxae group, as well as between them and *Vimola* may exist.

38.) *Africus* group and clade.

38a.) *Africus* clade: *Africus*, *D. ervatamiae*, *Neodiptilomiopus* (Diptilomiopinae).

The 318tax-k10 tree: the clade (node 453, Fig. 4.23) is supported by one synapomorphy: *1a* absent. *Africus* and *Neodiptilomiopus* were recovered as sisters (node 452, Fig. 4.23), supported by two homoplasies: setal tubercle of *1a* absent (which is present in *D. ervatamiae*), and 5-rayed empodium I.

Africus is a monospecific genus described from South Africa (Meyer & Ueckermann, 1995) and *Neodiptilomiopus* is a monospecific genus described from India (Mohanasundaram, 1982b). They are morphologically broadly (particularly in shape, dorsal shield pattern, coxisternal plates and genital coverflap) similar, but have many differences, which are of importance at genus level, particularly in the legs and leg segments. *Diptilomiopus ervatamiae*, described from Thailand (Chandrapatya & Boczek, 1991a) does not belong in *Diptilomiopus*, particularly due to the presence of *1b* and absence of *1a*, but with the setal tubercles of *1a* present. With the traditionally accepted genus differentiations in the Eriophyoidea (Amrine *et al*., 2003) *D. ervatamiae* would probably be placed in a new genus. *Diptilomipus ervatamiae* is not morphologically particularly similar to either *Africus* or *Neodiptilomiopus*. The recovery of these three species in a clade is a relatively strong hypothesis in the present study, though, because it is supported by a synapomorphy in the preferred 318tax-k10 tree. Although the clade is feasible, it should be investigated further.

38b.) *Africus* group: *Africus*, *D. knorri* (Diptilomiopinae).

***Africus* clade (38a)** was not retrieved by the 318taxEq and –k20 analyses, where *Africus* was recovered as a sister to *D. knorri*. The 318taxEq tree: the group (node 326, Fig. 4.5) is supported by 20 homoplasies, which is a relatively high number of supportive homoplasies for one group in the present study. The most relevant (also excluding those characteristics supporting their placement in the Diptilomiopidae and Diptilomiopinae), are the absence of a suite of setae: palp *d*, *c2*, *1b*, *bv* and *l''* in

legs I and II, *l'*, and *ft'* on tarsus II, of which most traditionally position them in relatively close relationship with other *Diptilomiopus* spp. and with other species in the **"Diptilomiopinae" group (29)** of the 318tax-k10 tree. Additionally the homoplasies include: prodorsal shield broadly oval, coxisternal plates II ornamented, coxae I separated, and genital coverflap ornamented basally. The most important homoplasy is probably: genu partially, and not completely, fused with femur in legs I and II. The 318tax-k20 tree: the group (node 377, Fig. 4.39) is supported by six homoplasies, of which five is also supporting it in the 318taxEq tree: palp *d* absent, coxae I separated, genital coverflap ornamented basally, partial fusion of genu and femur of legs I and II, and additionally (not supporting the group in 318taxEq tree), 5-rayed empodium. *Diptilomiopus knorri* was described from Thailand.

The ***Africus* clade (38a)** and **group (38b)** found in the present study which includes *Africus*, were not found by Hong & Zhang (1997), possibly because they included the genus *Diptilomiopus* in their taxon sample and did not include individual *Diptilomiopus* spp. as was done in the present study. In their study *Africus* and *Diptilomiopus* were found to be positioned relatively close to each other in the same group which also included taxa which are in the ***Dacundiopus* clade (36)** of the present study. This result is not supported in the present study. In their study, however, *Neodiptilomiopus* was found to be sister to the group which includes *Africus* and *Diptilomiopus* and the close relationships between *Africus*, *Diptilomiopus* and *Neodiptilomiopus* found in the present study, support this relationship.

39.) SA *Diptilomiopus* group: *D. apobrevis* sp. nov., *D. apolongus* sp. nov., *D. faurius* sp. nov. (Diptilomiopinae, *Diptilomiopus*).

The three *Diptilomiopus* spp. from South Africa (SA) (Appendix M) were recovered as a group in all the 318tax trees, including the tree obtained under equal character weights. The group was also relatively strongly supported, in comparison with other eriophyoid groups found in the present study, by many homoplasies, and is supported by a GF value of 56 (Fig. 4.24), and a GC value of 52 (Fig. 4.25) in the 318tax-k10 tree. They were not included in the 66tax and 18tax analyses for additional testing of the robustness of the group.

The 318taxEq tree (Fig. 4.5): the group is part of the large Eriophyoidea clade (Fig. 4.4) at node 337 (Fig. 4.5), and is supported by 26 homoplasies. Some of these homoplasies are those characteristics supporting the suprageneric and generic placement of the three species: Diptilomiopidae (gnathosoma with long form oral stylet, with chelicerae relatively long and bent down at the base), Diptilomiopinae (empodium divided) and *Diptilomiopus* (*sc*, *c2*, *1b* and its setal tubercle, *bv*, *l''* on legs I and II, and *l'* absent, genu fused to femur in legs I and II). The other homoplasies are additional character states from the suite of characteristics differentiating *Diptilomiopus* spp., and some of these states are ambiguously described for *Diptilomiopus* spp. in general (see discussion below). The relationships of **SA *Diptilomiopus* group** with other eriophyoid species, groups and clades are unresolved in this tree.

The 318tax-k10 tree: the group (node 543, Fig. 4.23) is supported by four homoplasies: palp *d* absent, frontal lobe present, microtubercles on dorsal annuli absent in a central band, and 7-rayed empodium. The group is included in a group (node 454, Fig. 4.23) which largely consists of *Diptilomiopus* and some other Diptilomiopinae species. The relationships of the **SA *Diptilomiopus* group** with the other species and groups in this larger group are unresolved.

The 318tax-k20 tree (Fig. 4.35): the group (node 406, Fig. 4.39) is in a similar position than in the 318tax-k10 tree, supported by seven homoplasies including the four homoplasies supporting the group in the 318tax-k10 tree, and additionally: *h1* minute, frontal lobe anterior edge square with rounded corners, and genital coverflap ornamented basally. Apart from the genital coverflap ornamentation, the homoplasies which are supporting the 318tax-k10 and –k20 trees are also part of the series of homoplasies supporting the group in the 318taxEq tree, and particularly those that are species specific and which are probably ambiguous, as mentioned.

The closer relationship between the South African *Diptilomiopus* spp., which are the first *Diptilomiopus* spp. described from southern Africa, than their relationship with other *Diptilomiopus* spp. in the analyses, was not expected *a priori*. They were not morphologically clearly different from the remainder of most *Diptilomiopus* spp. when compared manually. The group might have been recovered and is relatively strongly supported, because some characters were described accurately for these three species in contrast to many other *Diptilomiopus* spp. in which these particular characters are frequently not described, thus scored "unknown" (e.g., the presence or absence of *ft'* and palp *d* which is not usually noted or described), or structures may be scored as absent, when they are actually present, or they may be described erroneously (e.g., the presence and shape of the frontal lobe, and a minute *h1*, which is hard to detect in slide-mounted specimens) (C. Craemer, *unpubl. data*). Seta *ft'* on tarsus II and palp *d* are absent, and *h1* is minute in the SA spp. The frontal lobe, which might have been wrongly recorded as absent in many *Diptilomiopus* spp., because it is so difficult to detect in slide-mounted specimens, is present in the SA species, and is thin and flexible, and the anterior edge is square with rounded corners. The description of the shape of the prodorsal shield was scored as broadly oval in the SA spp., but other shapes were also, subjectively, recorded for *Diptilomiopus* spp. These differences may be due to distortion of slide-mounted specimens, inaccurate drawings, and different subjective interpretations, and are ambiguous. The SA spp. have a 7-rayed empodium, but the number of empodial rays recorded for *Diptilomiopus* spp. is ambiguous, because it is difficult to count the empodial rays in slide-mounted specimens, since the rays are skew, and are partly overlapping (Chapter 4). Additionally, the number of empodial rays was not recorded for many *Diptilomiopus* spp. The remaining two species' characteristics supporting **SA *Diptilomiopus* group** are: microtubercles on dorsal annuli absent in a central band, and coxisternal plates II ornamented. Adding more species

specific characters to the data set, e.g., the prodorsal shield ornamentation, which has been done in a parallel study to the present study (C. Craemer, *unpubl. data*), improves the phylogenetic phylogenetic resolution and the reliability of clades and groups found in *Diptilomiopus*.

40.) **66-Diptilomiopinae clade:** *Rhynacus*, *Neorhynacus*, *Diptilomiopus averrhoae*, *D. assamica*, *D. jevremovici* (Diptilomiopidae: Diptilomiopinae).

These species, sampled as exemplar species from the **"Diptilomiopinae" group (29)** of the 318tax trees and included in the 66tax data set, were recovered as a clade (**66-Diptilomiopinae clade**). This clade is present in all the presented 66tax trees, and it supports the **"Diptilomipinae" group**.

The 66taxEq tree: the clade (node 75, Fig. 4.42) is supported by two synapomorphies, *c2* and its setal tubercle absent, and by three homoplasies: *l''* on genu II absent, tibia shorter than tarsus, but half or more of tarsus length, and empodium divided. The 66tax-k999 and –k30 trees: the clade (node 118, Figs 4.45 and 4.51, respectively) is supported by the same synapomorphies and homoplasies as in the 66taxEq tree, but the homoplasy, tibia shorter than the tarsus, is here replaced by the homoplasy *h1* minute. The 66tax-k20 tree: the clade is supported by the two synapomorphies supporting the clade in the other trees, and by homoplasies.

The phylogenetic phylogenetic resolution and topology within the clade is the same in all the 66tax trees, and the recovered groups are supported by the same synapomorphies and homoplasies. The relationships, with the 66tax-k999 tree as example, follow. *Diptilomiopus assamica* and *D. jevremovici* were recovered as a group (node 115, Fig. 4.45) supported by the synapomorphy, *ft'* absent on tarsus II, and by two homoplasies: coxisternal plates II ornamented, and prodorsal shield subtriangular. The homoplasies are characters used at the species level. Particularly the shape of the prodorsal shield is ambiguous in many descriptions, and prone to distortion by slide-mounting. *Diptilomiopus averrhoae* is sister to the *D. assamica-D. jevremovici* group, and this three-taxon clade is at node 116 (Fig. 4.45) supported by two synapomorphies, the genu fused to the femur in legs I and II, and by three homoplasies: *l''* on genu I, and *l'* absent, and dorsal annuli without microtubercles. *Neorhynacus* is sister to this clade at node 117 (Fig. 4.45) supported by two homoplasies: *sc* ahead of rear shield margin, and coxisternal plates I ornamented. *Rhynacus* is sister basally to *Neorhynacus*. *Neorhynacus* and *Rhynacus* were not recovered as a group or clade at one node and *Neorhynacus* is more closely related to the *Diptilomiopus* spp. than *Rhynacus*. Morphologically *Neorhynacus* is more similar to most *Diptilomiopus* spp. than *Rhynacus*, particularly the dorsal shield ornamentation.

4.6 RESULTS AND DISCUSSION: TWO MONOSPECIFIC GENERA WRONGLY CLASSIFIED

The analyses in the present study retrieved many relationships and placements of species that either confirmed doubts about their placement, wrong interpretation of structures, or "pointed out" species wrongly placed by error in the current classification. Two of the most certain and important are:

41.) *Prothrix aboula*

Amrine (1996) placed *P. aboula* in a new monospecific subfamily, Prothricinae (Phytoptidae), based on the presence of paired *vi* in addition to *ve* in *P. aboula*. When *vi* is present in other eriophyoid species, single *vi* is present in a mid-dorsal position. Due to the inclusion of *Prothrix* (Prothricinae) in the **Dorsal-rear-fused clade (7)**) together with sierraphytoptine species with single and paired *vi* absent, but a pair of *ve* present, *Prothrix* should be in the Sierraphytoptinae. The presumed pair of *vi* in *Prothrix* seems to be rather *sc* that moved far forward, as originally proposed by Keifer (1965a) when he described this species. Sierraphytoptinae contain species with and without *sc*. Prothricinae is thus a junior synonym of the Sierraphytoptinae (**new synonymy**). In future data sets for cladistic analyses, the absence of paired *vi* and presence of *sc* in a far forward position should be coded for this species and this may strengthen the support for the **Dorsal-rear-fused clade (7)**, and possibly even a closer and more robust relationship between this clade and the other sierraphytoptine species.

42.) *Palmiphytoptus oculatus*

Palmiphytoptus oculatus was tentatively placed in the Mackiellini of the Sierraphytoptinae by Navia & Flechtmann (2002), based on the presence of *ve* anteriorly on the prodorsum. They hypothesized that the genus belongs in the Phytoptidae, but regarded it as being similar to the Phytoptinae, as well as the Sierraphytoptinae. This species was included only in the 318tax data set. It was not found to have a close relationship with Phytoptidae taxa. It was in a group deeply imbedded in a large group of Eriophyidae taxa from various subfamilies and tribes. The 318tax-k10 tree: it was found to be sister to a *Cisaberoptus* group (node 500, Fig. 4.18), weakly supported by two homoplasies: minute *h1*, and frontal lobe present. This group is also in the 318tax-k20 tree, but it is not supported by the symmetric resampling values (Figs 4.24, 4.25). The relationship of *Palmiphytoptus* with other eriophyoid taxa is highly uncertain, and not resolved by the present analyses, but it does not seem to belong in the Phytoptidae. This supports the suggestion by Amrine *et al.* (2003) that *Palmiphytoptus* may belong to the Eriophyidae, and may possibly be an *Eriophyes* sp., and that the setae proposed to be *ve* by Navia & Flechtmann (2002) may be *sc* displaced far forward. *Palmiphytoptus* is re-assigned to the Eriophyinae.

318taxEq
Fig. 4.4

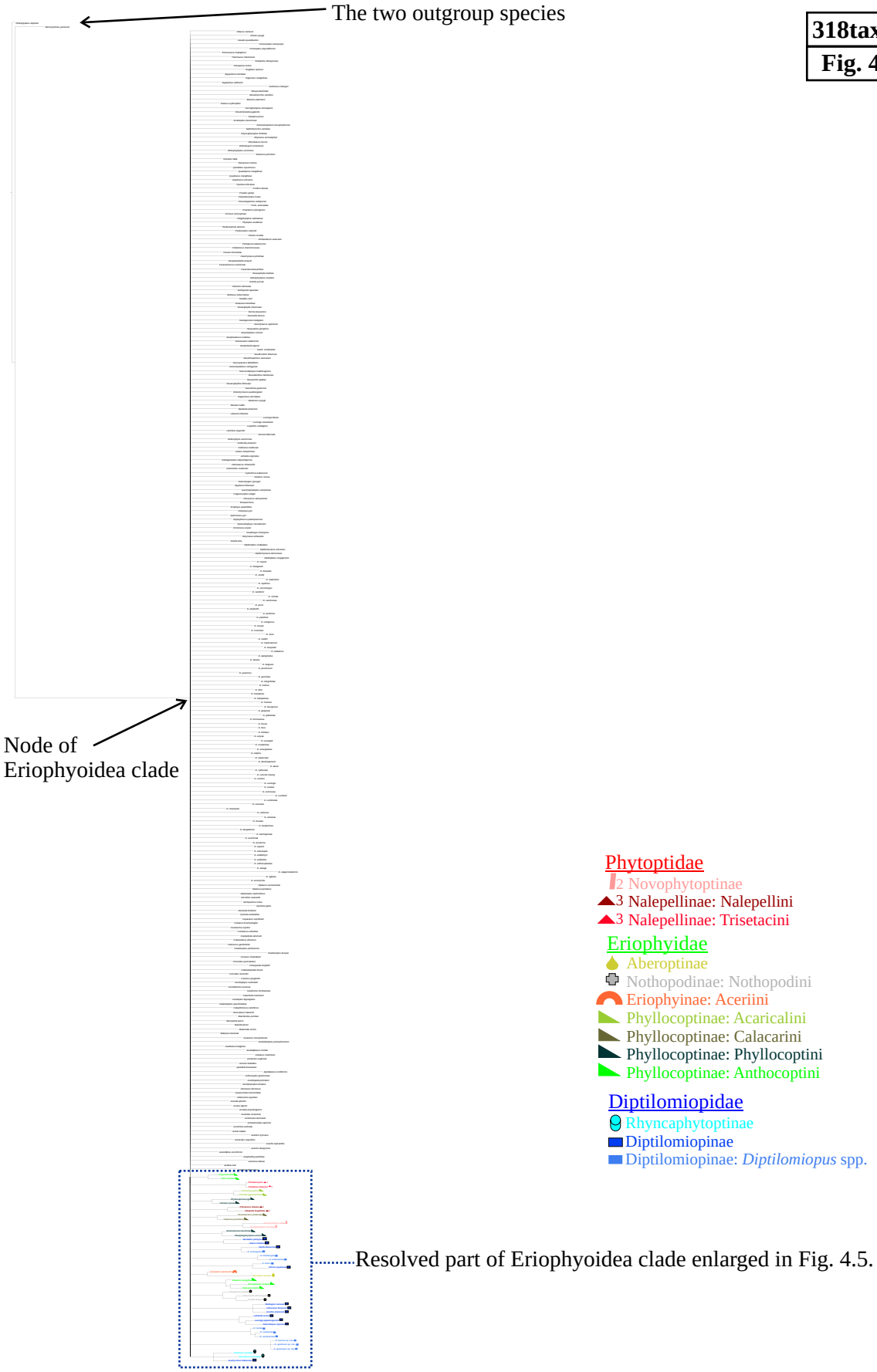


Fig. 4.4. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under equal weighting of characters in TNT: entire tree presented to show topology, and it is a metric tree. Total fit = 57.71; Adjusted homoplasy = 72.29; Total length = 5396; CI = 0.056; RI = 0.086.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

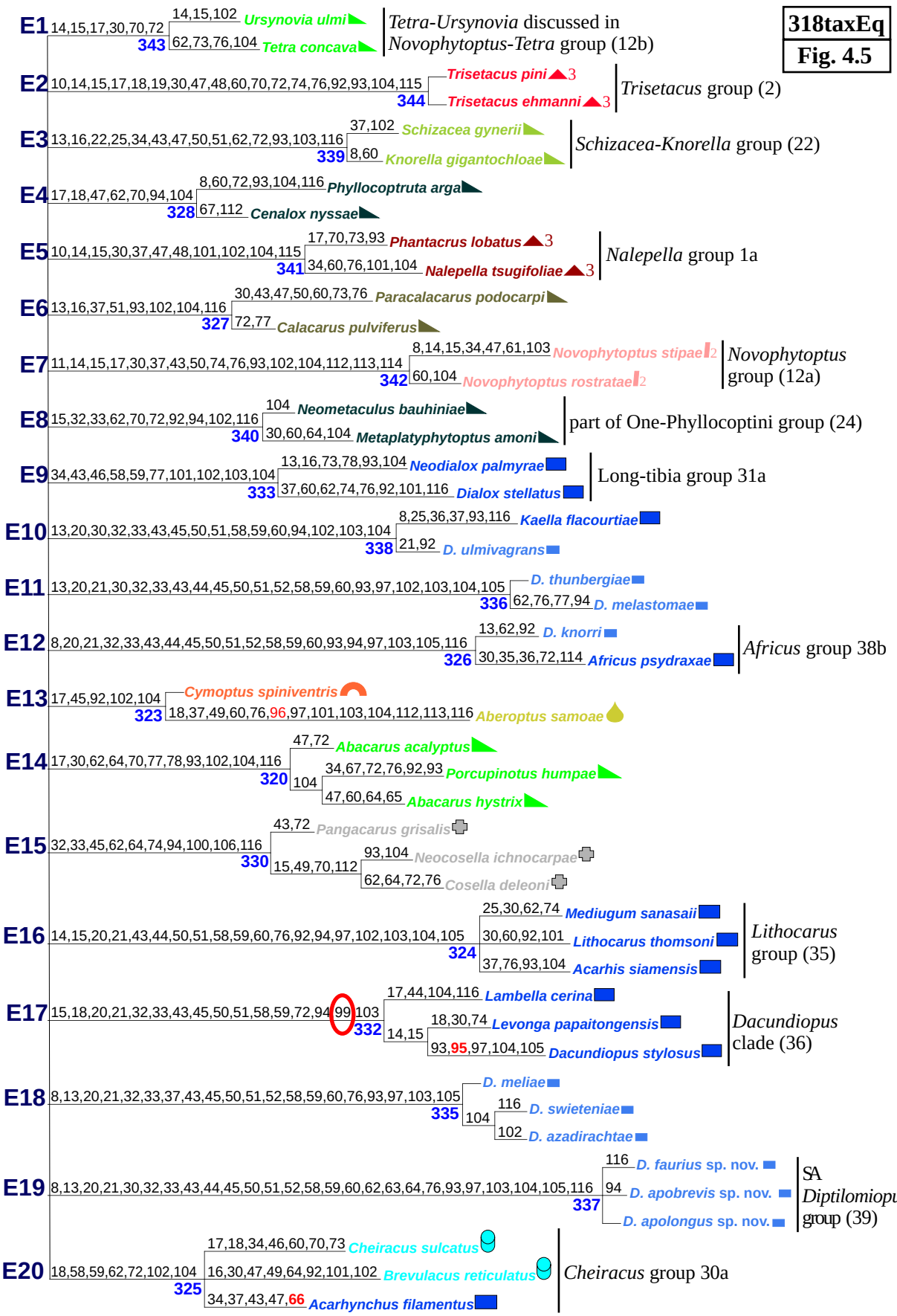


Fig. 4.5. Estimated consensus tree found with the analysis of the 318-taxon data matrix under equal weighting of characters in TNT (318taxEq tree, Fig. 4.4): enlarged resolved part of the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies (encircled in red)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

Table 4.7. Character consistency indices (ci) and character retention indices (ri) of characters of the estimated consensus tree, found in TNT, of the 318 taxon data matrix under equal character weighting (Fig. 4.3, 4.4.). The indices in light grey are of characters which are uninformative regarding the relationships between ingroup taxa because they are autapomorphic for the Eriophyoidea, or the same for all taxa in the analysis (Characters 7 and 41), the indices within a block with a grey background are those of characters autapomorphic for a terminal ingroup taxon, and the indices in bold and in a block with thickened edges, are of homologous characters.

Character consistency indices (ci)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.108	1.000
10	0.250	0.063	1.000	0.009	0.096	0.048	0.063	0.019	0.051	0.077
20	0.010	0.020	0.063	--	1.000	0.050	--	1.000	1.000	1.000
30	0.013	1.000	0.009	0.018	0.034	0.333	0.600	0.045	0.500	1.000
40	1.000	--	--	0.007	0.011	0.008	0.222	0.063	0.154	0.417
50	0.008	0.008	0.018	1.000	1.000	--	1.000	0.500	0.008	0.015
60	0.093	0.500	0.019	0.080	0.094	0.571	--	0.070	1.000	1.000
70	0.065	1.000	0.043	0.099	0.052	0.400	0.091	0.083	0.313	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.020	0.026	0.063	1.000	--	0.037	--	**1.000**
100	0.222	0.109	0.039	0.079	0.035	0.024	0.200	1.000	1.000	1.000
110	--	--	0.111	0.118	0.167	0.286	0.027			

Character retention indices (ri)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.132	1.000
10	0.250	0.118	1.000	0.066	0.190	0.123	0.063	0.063	0.043	0.143
20	0.099	0.100	0.063	--	1.000	0.050	--	1.000	1.000	1.000
30	0.068	1.000	0.097	0.104	0.026	0.000	0.333	0.056	0.000	1.000
40	1.000	--	--	0.092	0.064	0.084	0.125	0.043	0.154	0.125
50	0.096	0.098	0.098	1.000	1.000	--	1.000	0.000	0.097	0.097
60	0.062	0.000	0.060	0.080	0.040	0.000	--	0.019	1.000	1.000
70	0.048	1.000	0.048	0.000	0.044	0.250	0.048	0.120	0.083	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.034	0.075	0.129	1.000	--	0.092	--	**1.000**
100	0.222	0.197	0.082	0.092	0.114	0.090	0.200	1.000	1.000	1.000
110	--	--	0.111	0.063	0.091	0.286	0.045			

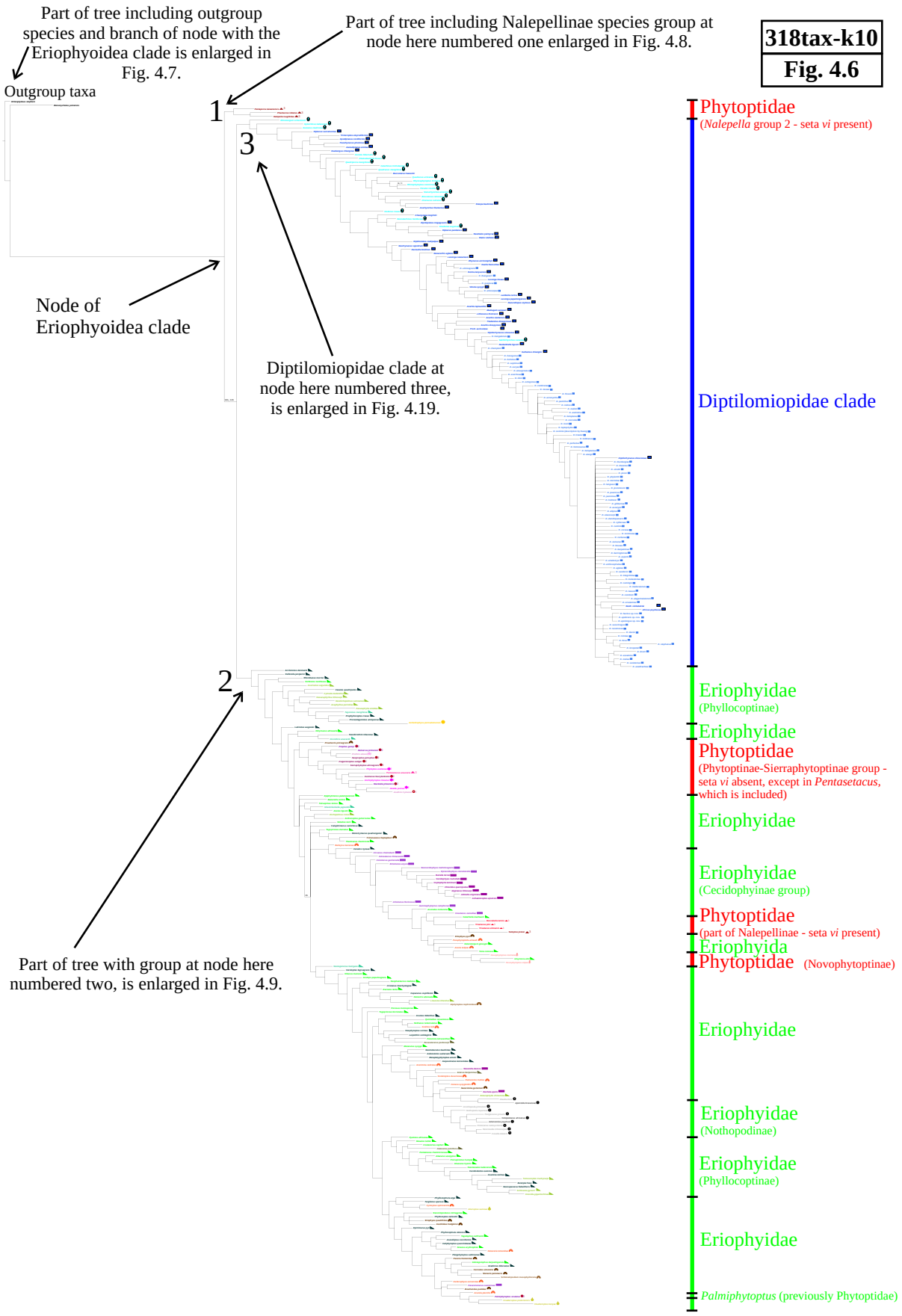


Fig. 4.6. Caption on next page.

318tax-k10
Fig. 4.7

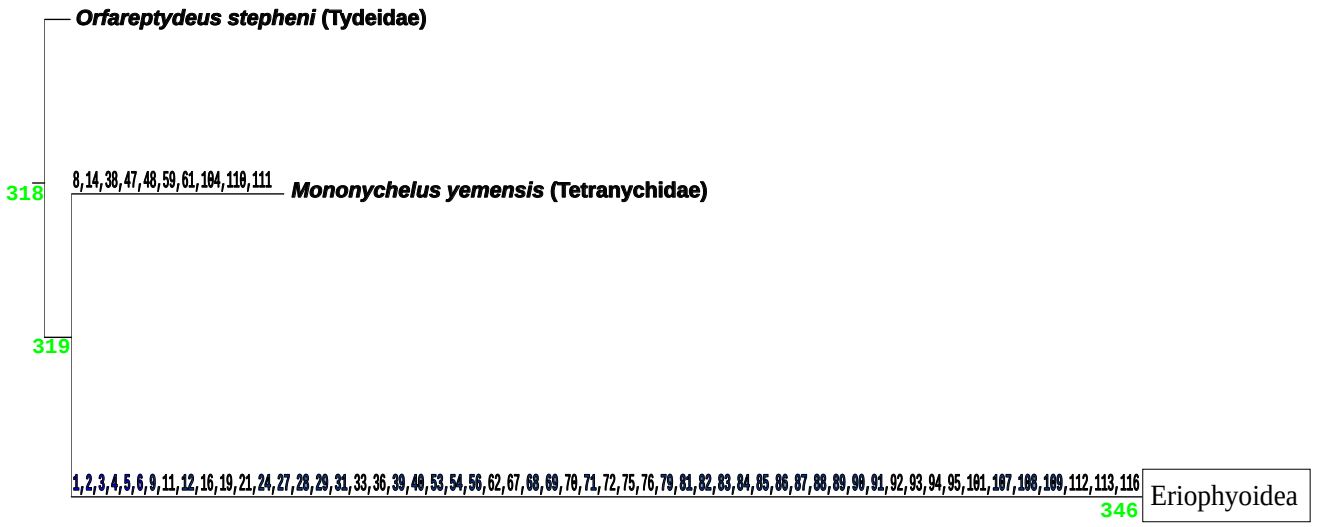
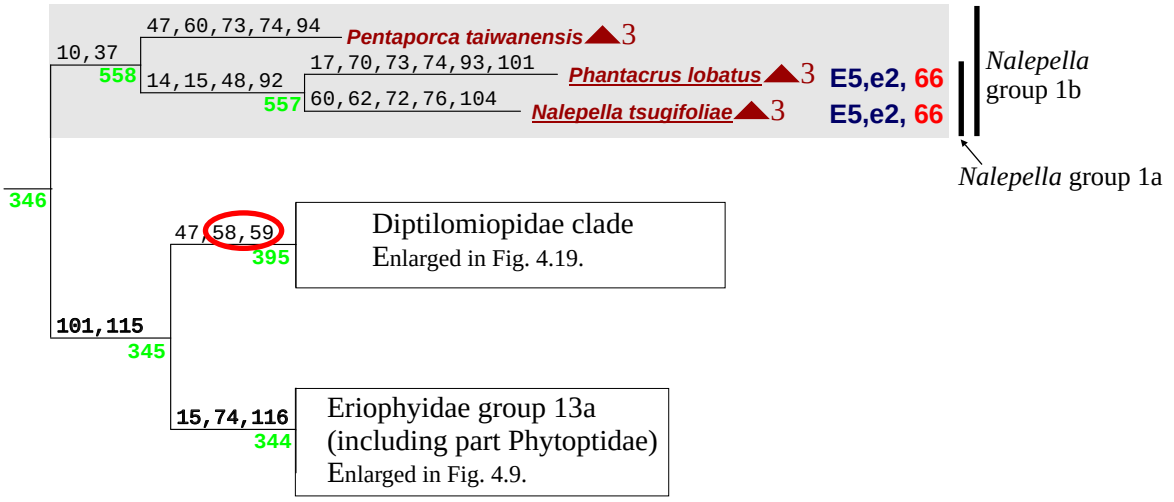


Fig. 4.6. (previous page). Strict consensus (Total fit = 72.29; Adjusted homoplasy = 57.71; Total length = 2402; CI = 0.125; RI = 0.623; Nodes = 255) of 32 most parsimonious trees (each - Total fit = 72.36; Adjusted homoplasy = 57.64; Total length = 2347; CI = 0.128; RI = 0.633; Nodes = 316) found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, with the best score hit 10 times, under implied weighting of characters with k=10. Uninformative characters were included. Unsupported branches were not collapsed. The entire tree is presented to show topology, and it is a metric tree. Tree presented from TNT. The tree name is 318tax-k10 tree. The bar on the right hand side indicate families and some notes on broad groups and clades. The red bar and text = Phytoptidae, the green bar and text = Eriophyidae and the blue bar and text = Diptilomiopidae. Although the bar indicates subdivisions within families, and largely relationships between them, it doesn't always indicate relationships between the groups correctly, and also not necessarily indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node. The tree is divided into four parts, which are enlarged in Figs 4.7, 4.8, 4.9 and 4.19.

Fig. 4.7. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree including outgroup species and branch of node with the Eriophyoidea clade. Black numbers above branches are the character numbers of the synapomorphies or homoplasious characters supporting the nodes, and those on the branch supporting node 346 (Eriophyoidea clade) in bold and dark blue are autapomorphies for the Eriophyoidea. The node numbers from TNT are the green numbers underneath the branches and close to the nodes.

318tax-k10
Fig. 4.8



▲3 Phytoptidae: Nalepellinae: Nalepellini

Node 558 :
setae vi (10): absent (2) --> one seta mid-anterior (1)
setae *1a* vs setae *2a* (37): ahead (0) –> slightly ahead (1)

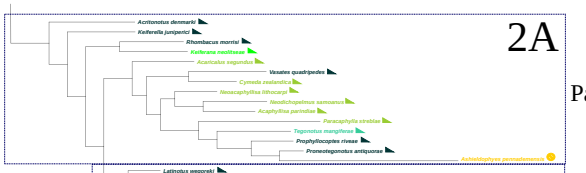
Node 345 :
leg 1 tibia length (101): very long (6) --> long (5)
spermathecal tubes (115): long (2) --> short (1)

Node 395 :
leg tibia 1 setae *l'* vertical position (47): distal third --> basal third
oral stylet (58): short form –> long form
chelicerae (59): short straight --> long bent

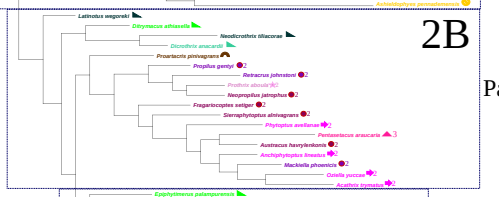
Node 344 :
sc length : prodorsal shield length (15): average length (3) --> short (4)
opisthosomal ridges or furrows (74): absent (0) --> present (1)
genital coverflap (116): smooth (1) --> ornamented basal distal area (5)

Fig. 4.8. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree including Nalepellinae species group at node numbered one in Fig. 4.6. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

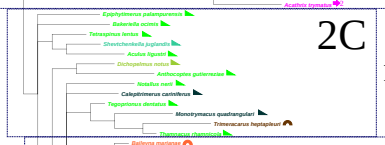
318tax-k10
Fig. 4.9



Part 2A is enlarged in Fig. 4.10.

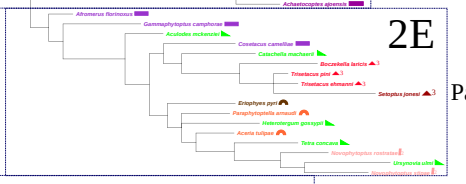


Part 2B is enlarged in Fig. 4.11.

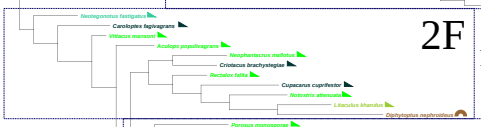


Part 2C is enlarged in Fig. 4.12.

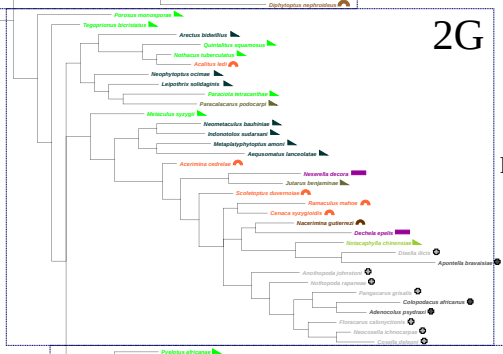
Part 2D is enlarged in Fig. 4.13.



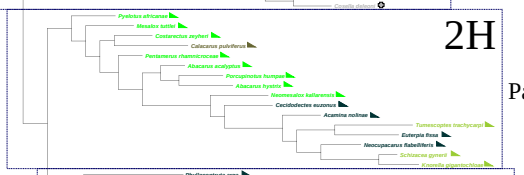
Part 2E is enlarged in Fig. 4.14.



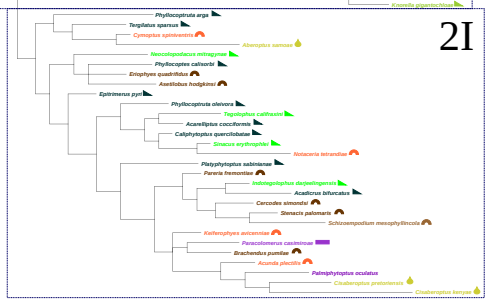
Part 2F is enlarged in Fig. 4.15.



Part 2G is enlarged in Fig. 4.16.



Part 2H is enlarged in Fig. 4.17.



Part 2I is enlarged in Fig. 4.18.

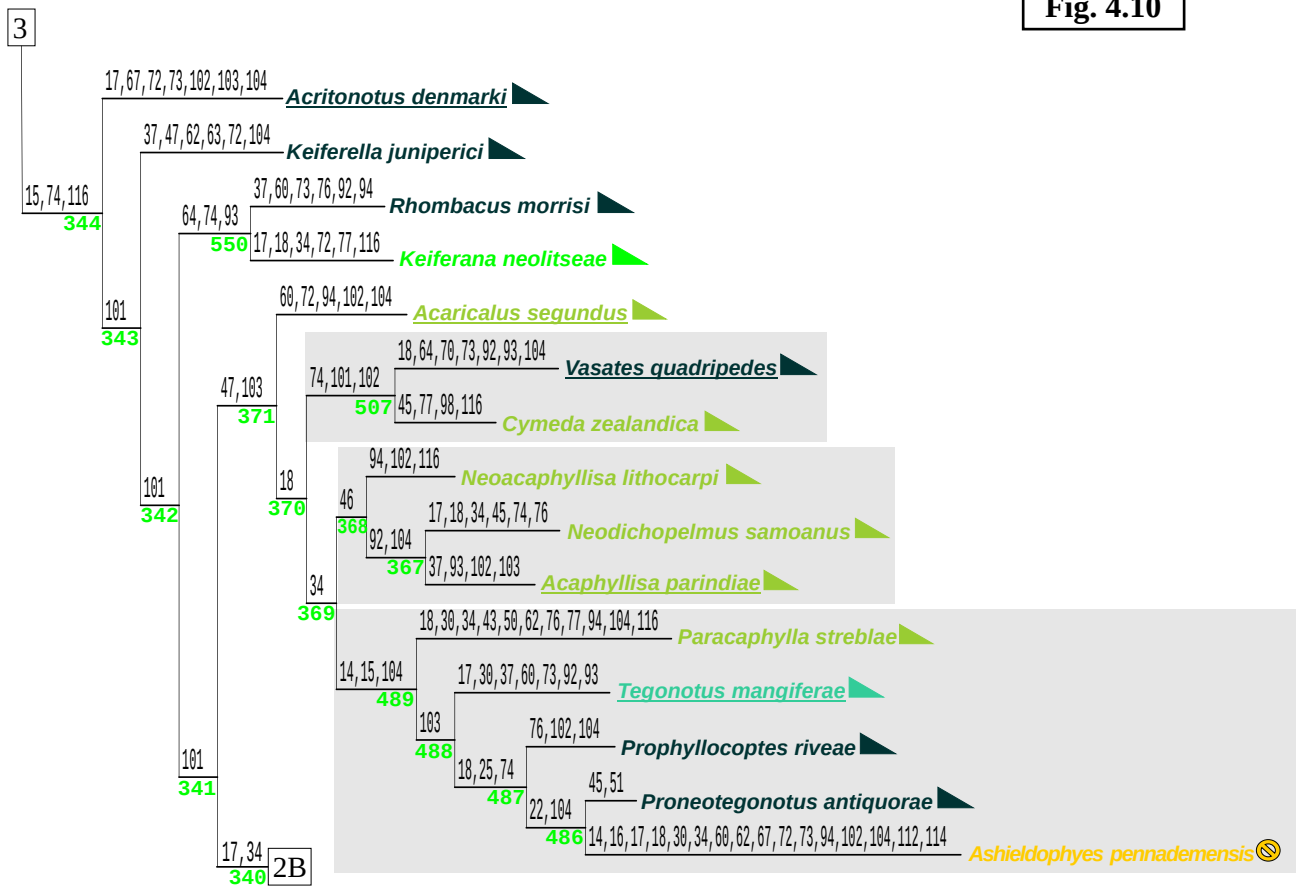
Eriophyidae
- Aberoptinae
- Nothopodinae: Colopodacini
- Nothopodinae: Nothopodini
- Ashieldophyinae
- Cecidophyinae: Cecidophyini
- Cecidophyinae: Colomerini
- Eriophyinae: Diphytoptini
- Eriophyinae: Eriophyini
- Eriophyinae: Aceriini
- Phyllocoptinae: Acaricalini
- Phyllocoptinae: Calacarini
- Phyllocoptinae: Tegonotini
- Phyllocoptinae: Phyllocoptini
- Phyllocoptinae: Anthocoptini

Phytoptidae
- ★2 Phytoptidae: Prothricinae
- 2 Phytoptidae: Novophytoptinae
- 3 Phytoptidae: Nalepellinae: Pentasetacini
- 3 Phytoptidae: Nalepellinae: Nalepellini
- 3 Phytoptidae: Nalepellinae: Trisetacini
- 2 Phytoptidae: Phytoptinae
- 2 Phytoptidae: Sierraphytoptinae: Sierraphytoptini
- 2 Phytoptidae: Sierraphytoptinae: Mackiellini

Fig. 4.9. Caption on next page.

Part 2A

318tax-k10
Fig. 4.10



Eriophyidae: Ashieldophyinae
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.9. (previous page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree at node numbered two in Fig. 4.6, which includes the Eriophyidae and part of the Phytoptidae, to largely show topology. The tree is divided into parts 2A-2I which are enlarged in Figs 4.10-4.18.

Fig. 4.10. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318 taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66 taxon data matrix.

Part 2B

318tax-k10
Fig. 4.11

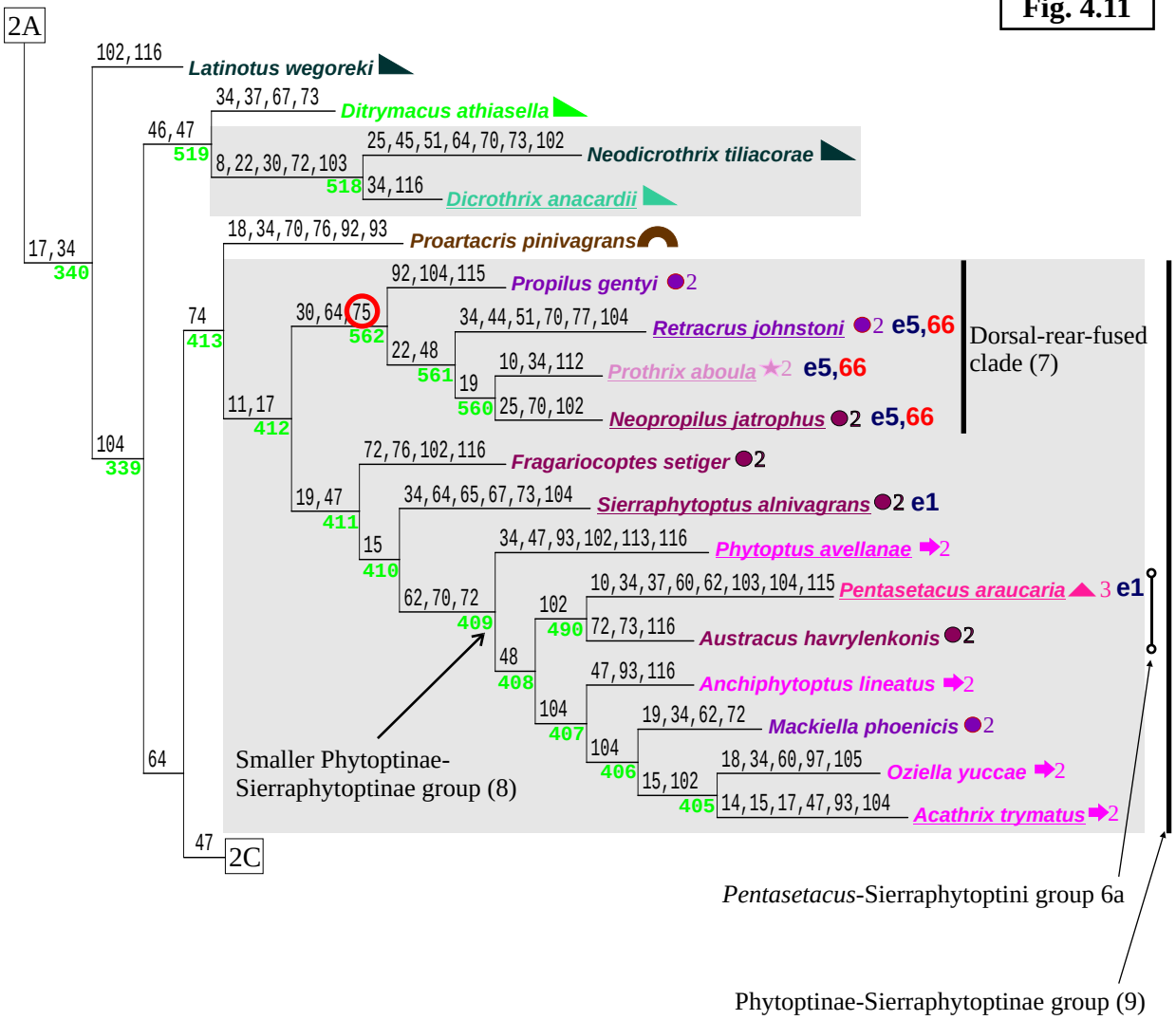
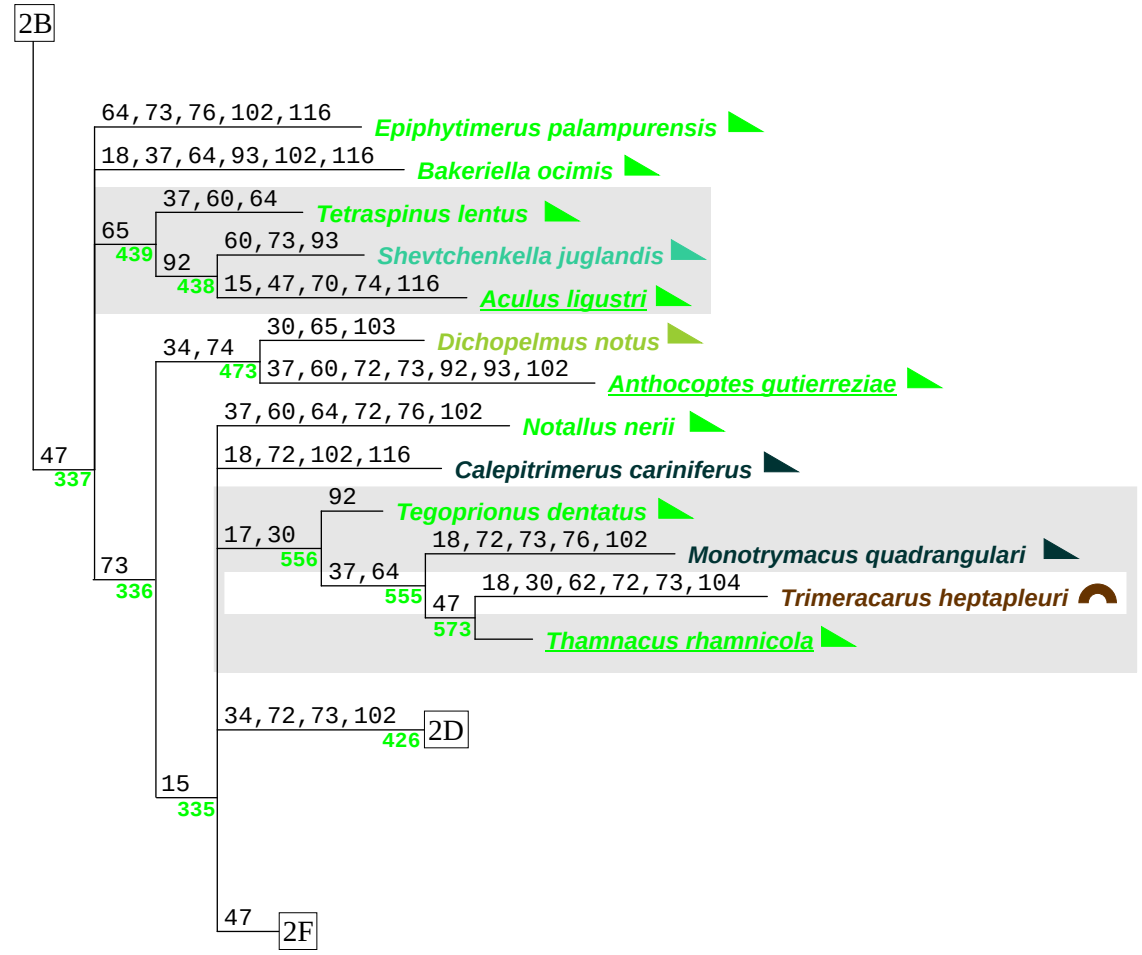


Fig. 4.11. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right, and indicated with arrows. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42), red 66 indicates those taxa found in the same groups, or part of same groups, in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2C

318tax-k10
Fig. 4.12



Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.12. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2C. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). Underlined terminal taxa are included in the 66-taxon data matrix.

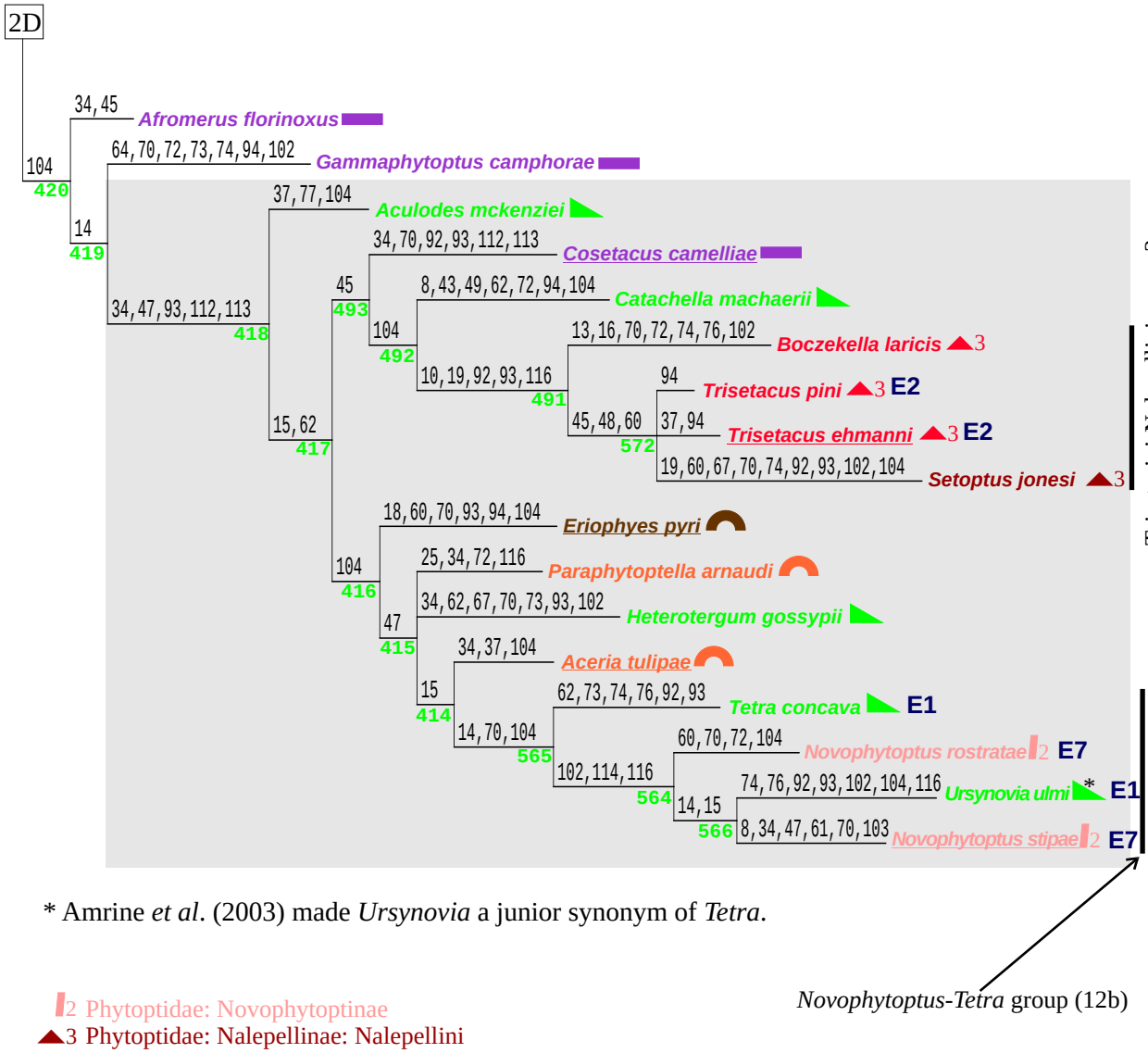
Part 2D

318tax-k10
Fig. 4.13

Fig. 4.13. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2D. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2E

318tax-k10
Fig. 4.14



* Amrine *et al*. (2003) made *Ursynovia* a junior synonym of *Tetra*.

2 Phytoptidae: Novophytoptinae
3 Phytoptidae: Nalepellinae: Nalepellini
3 Phytoptidae: Nalepellinae: Trisetacini
Eriophyidae: Cecidophyinae: Colomerini
Eriophyidae: Eriophyinae: Eriophyini
Eriophyidae: Eriophyinae: Aceriini
Eriophyidae: Phyllocoptinae: Anthocoptini

Fig. 4.14. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2E. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of the groups discussed in the text are on the right. Part of tree blocked in grey also occurs, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2F

318tax-k10
Fig. 4.15

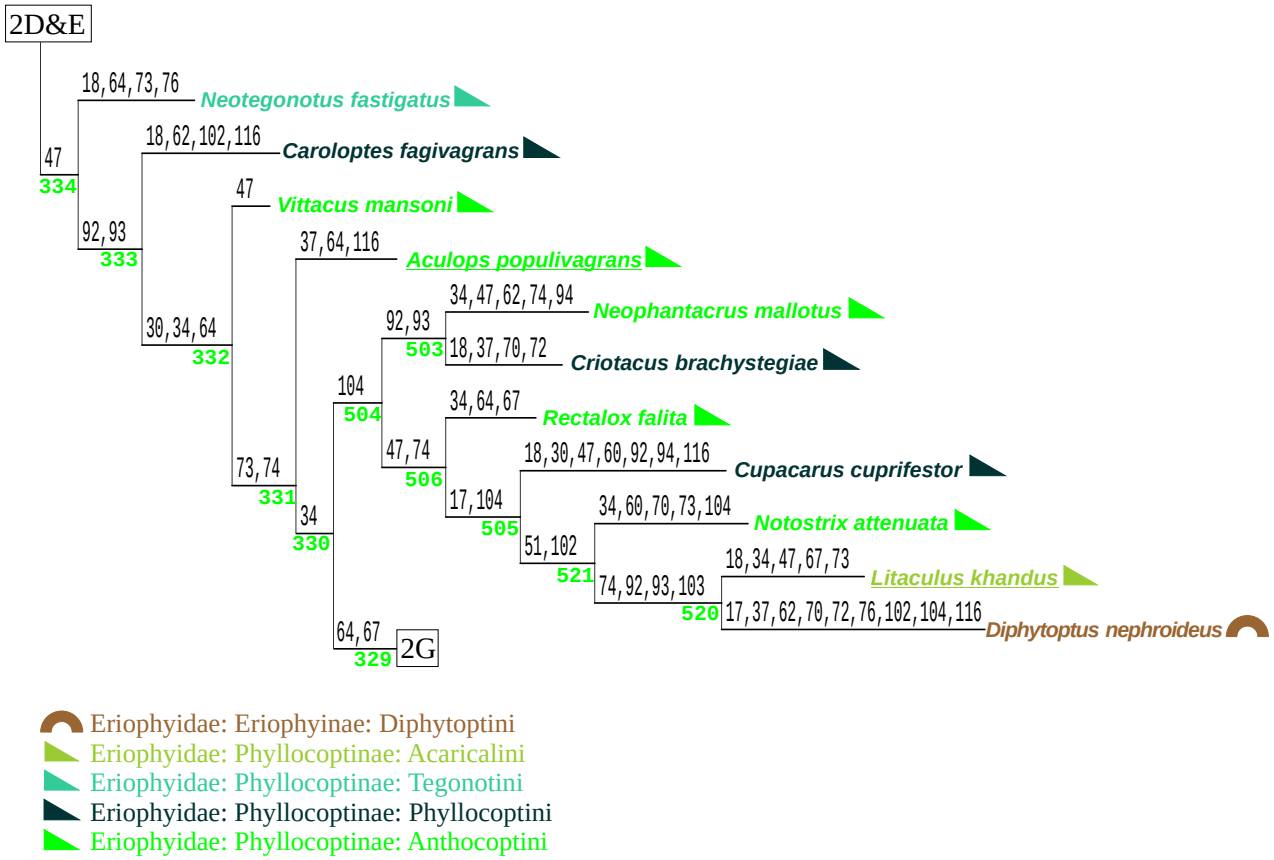


Fig. 4.15. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2F. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.16. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2G. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2G

318tax-k10
Fig. 4.16

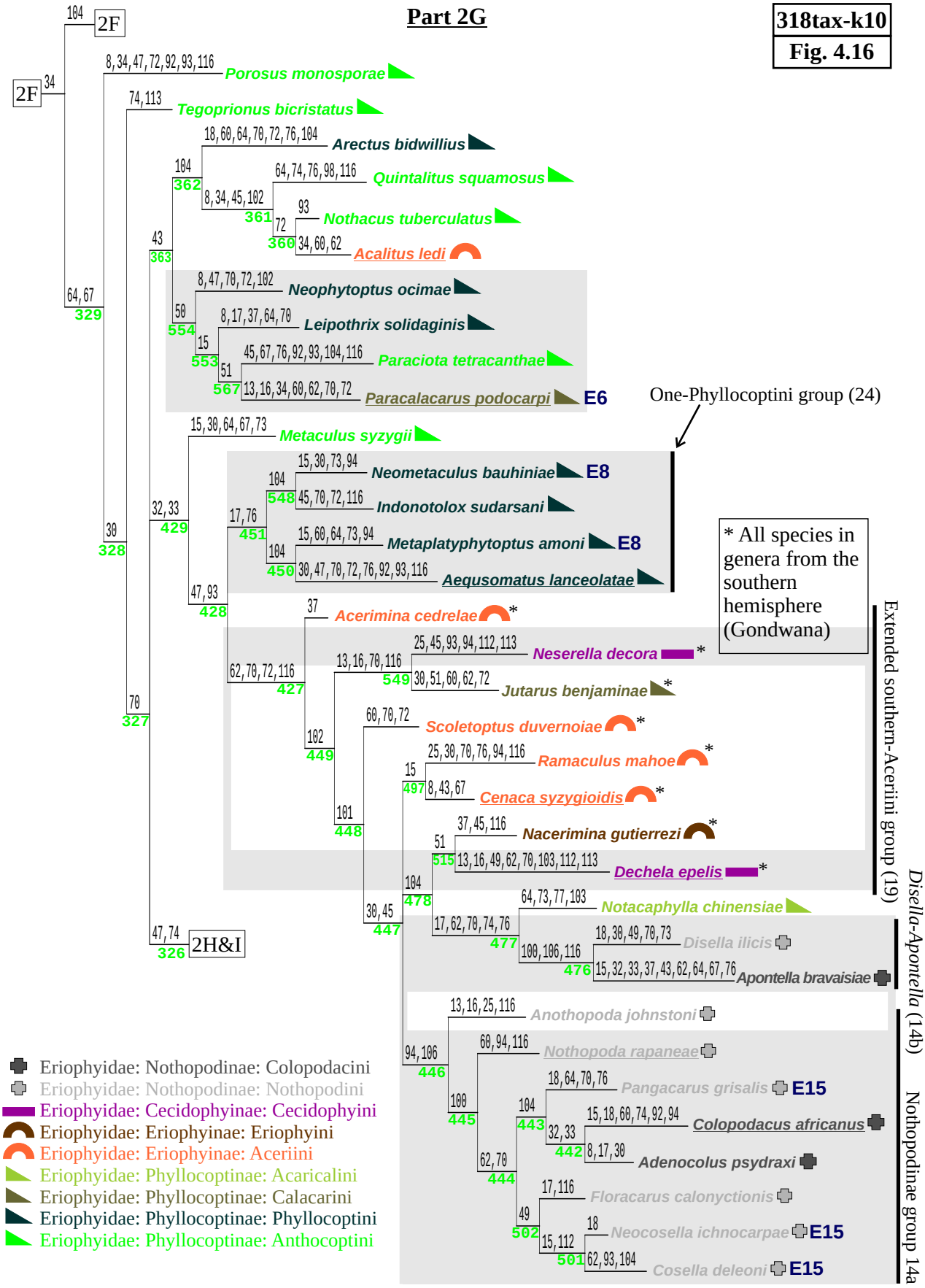


Fig. 4.16. Caption on previous page.

Part 2H

318tax-k10
Fig. 4.17

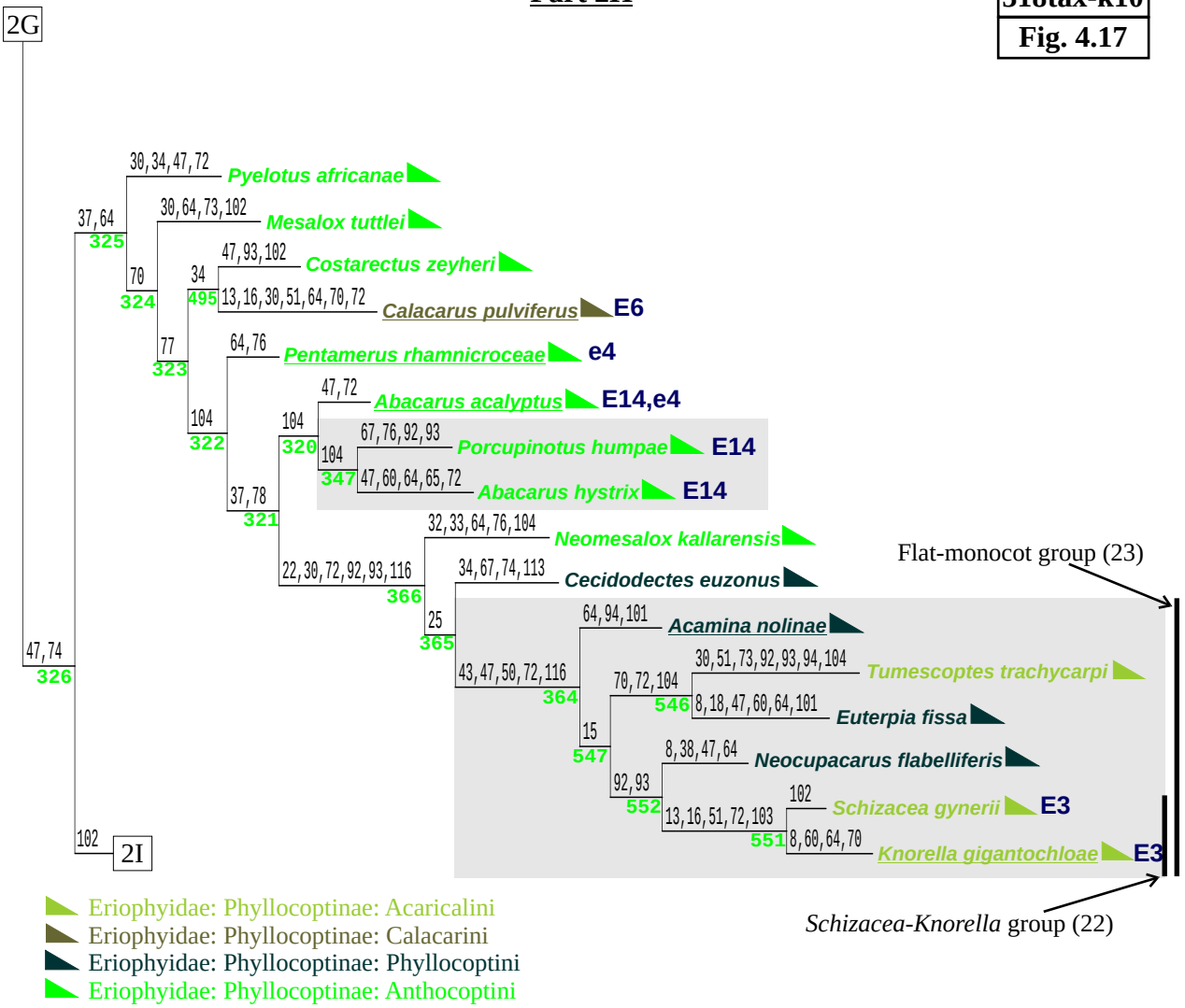


Fig. 4.17. (this page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2H. Black numbers above branches are the character numbers of the homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.18. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged part of the group with the Eriophyidae and part of the Phytoptidae (Fig. 4.9): enlarged part 2I. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal name of the group discussed in the text is indicated with an arrow. Parts of tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 2I

318tax-k10
Fig. 4.18

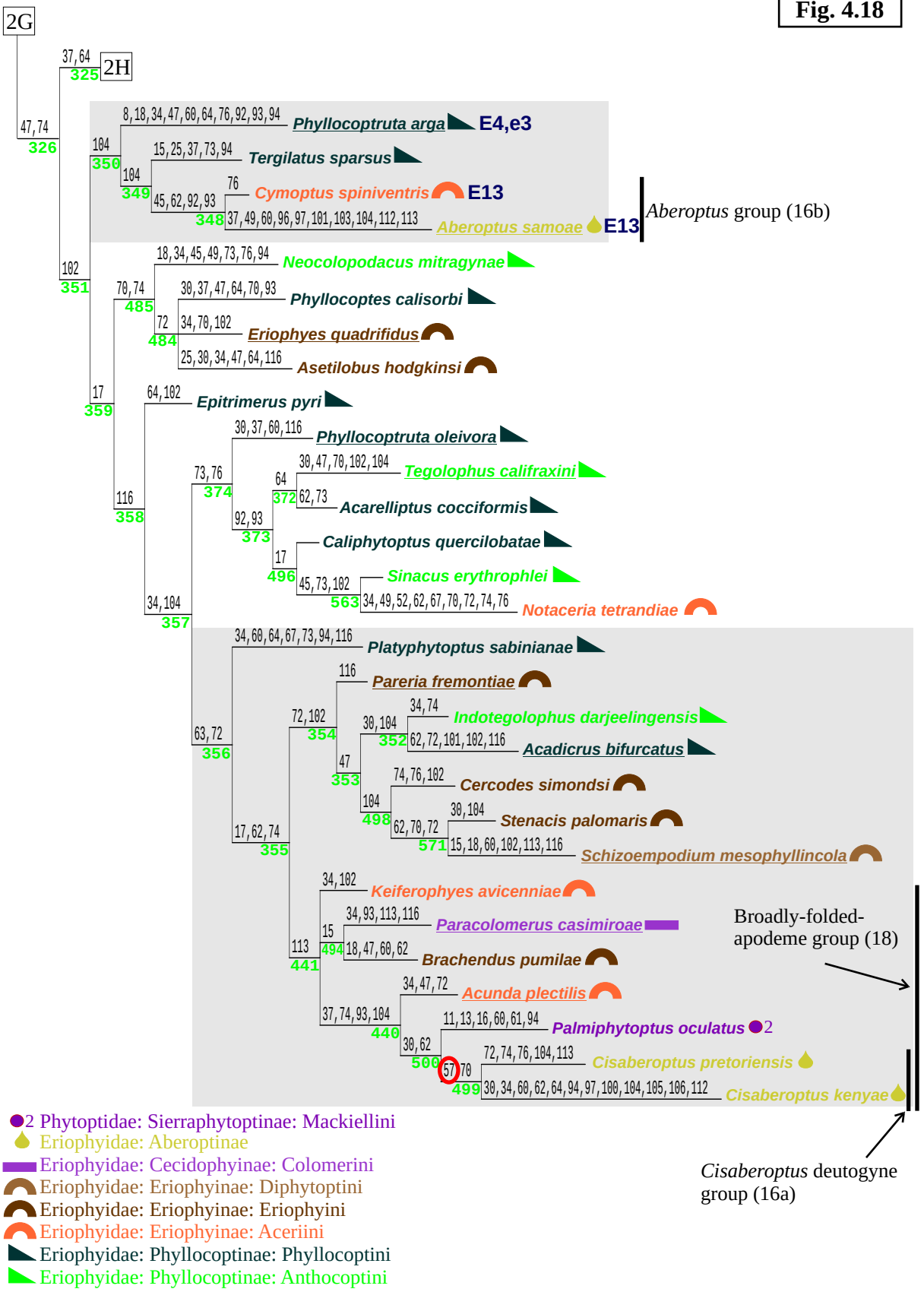


Fig. 4.18. Caption on previous page.

318tax-k10
Fig. 4.19

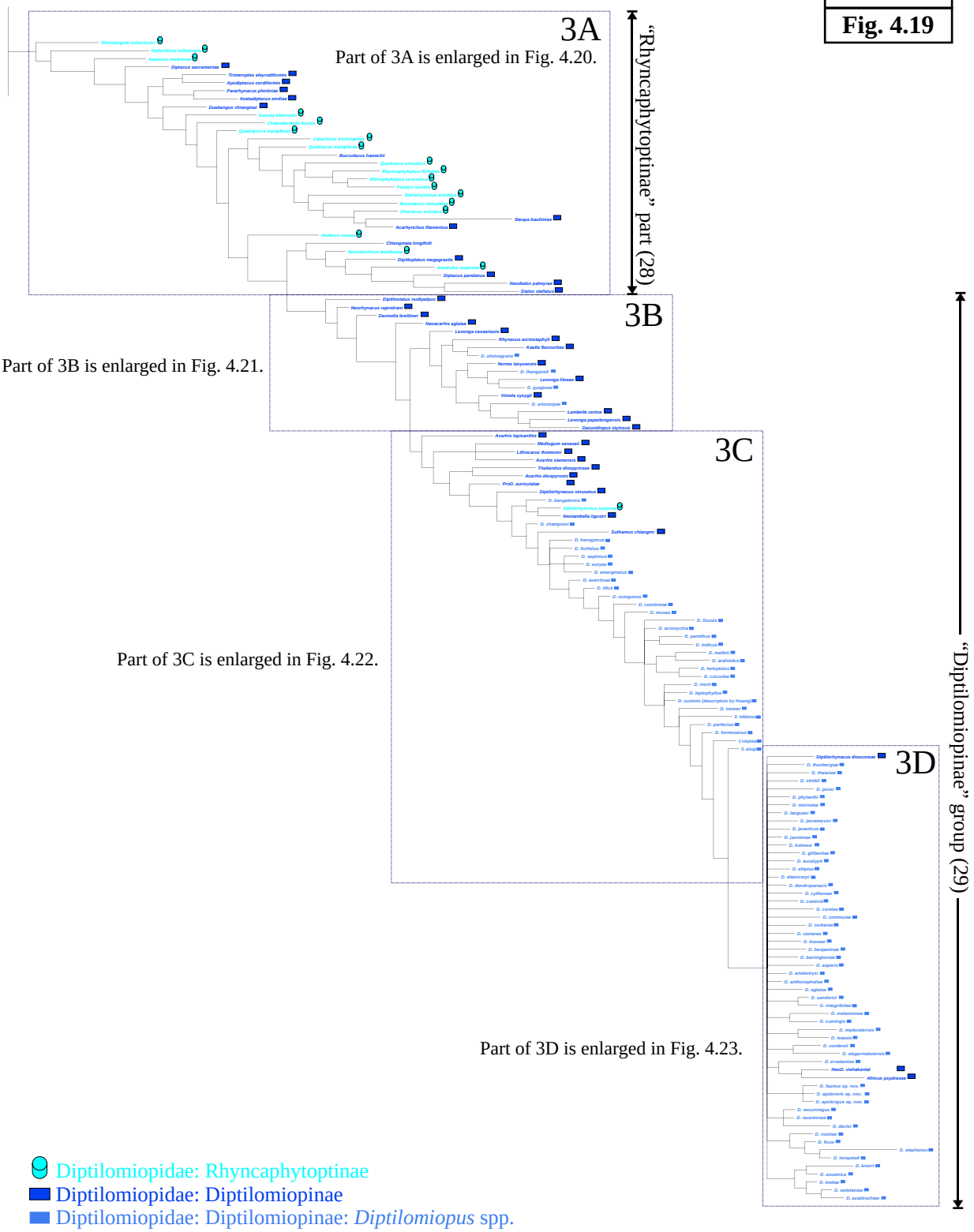


Fig. 4.19. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6): enlarged part of tree at node numbered three in Fig. 4.6, which consists of the Diptilomiopidae clade, to largely show topology. The tree is divided into four parts 3A-3D which are enlarged in Figs 420-4.23.

Part 3A [”Rhyncaphytoptinae” part (28)]

318tax-k10
Fig. 4.20

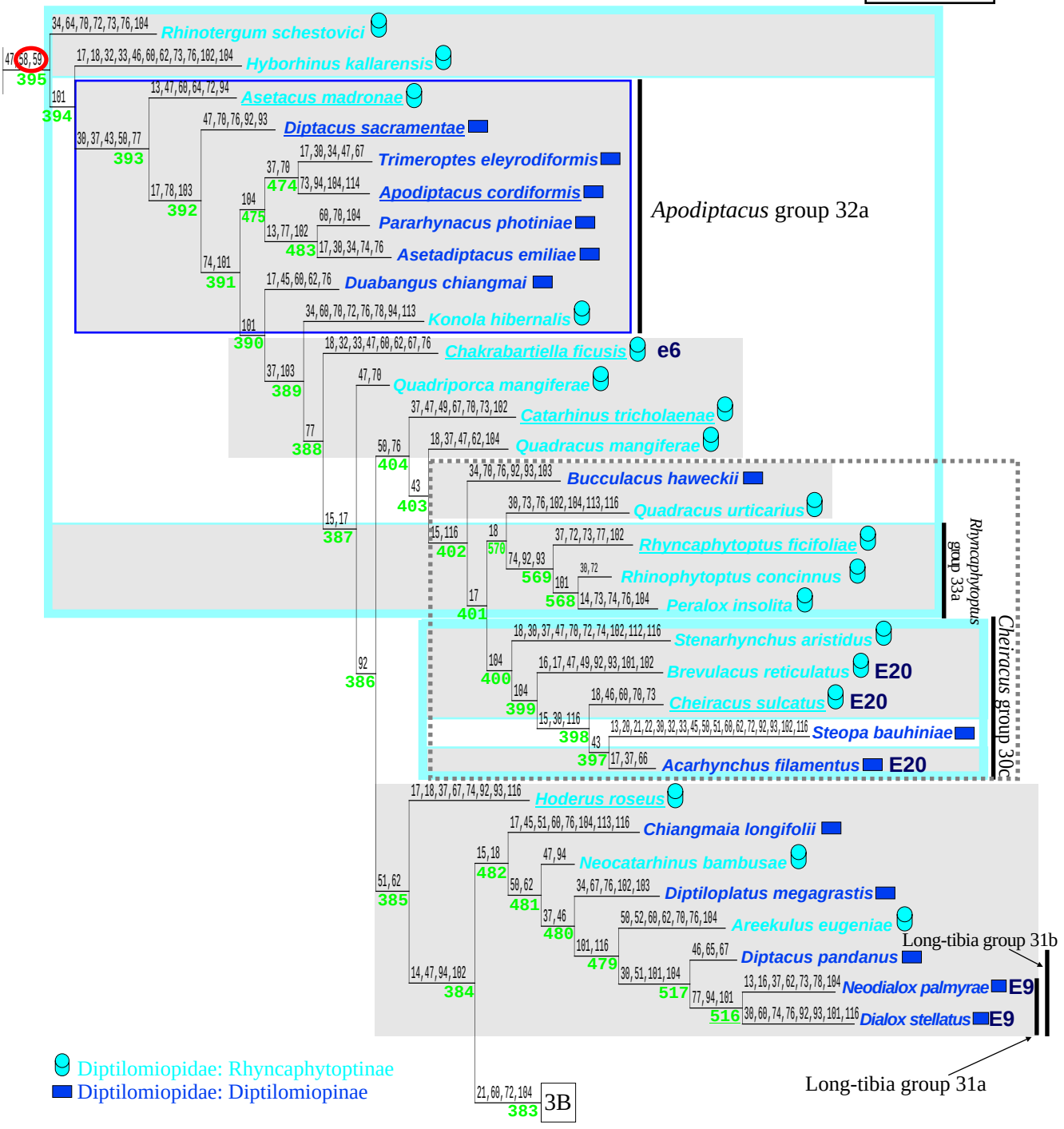


Fig. 4.20. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using “new technologies” in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3A. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). The grey blocks with a thick light blue margin connecting them, are one larger group in Fig. 4.26 split up in two smaller groups in the tree above. The taxa included in the area margined by the grey stipple line, are positioned close together in the 318-taxon data matrix analysed under implied character weighting with k=20 (Fig. 4.36), excluding *Steopa* and including *Rhinotergum* and *Hyborhinus*. On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 3B

318tax-k10
Fig. 4.21

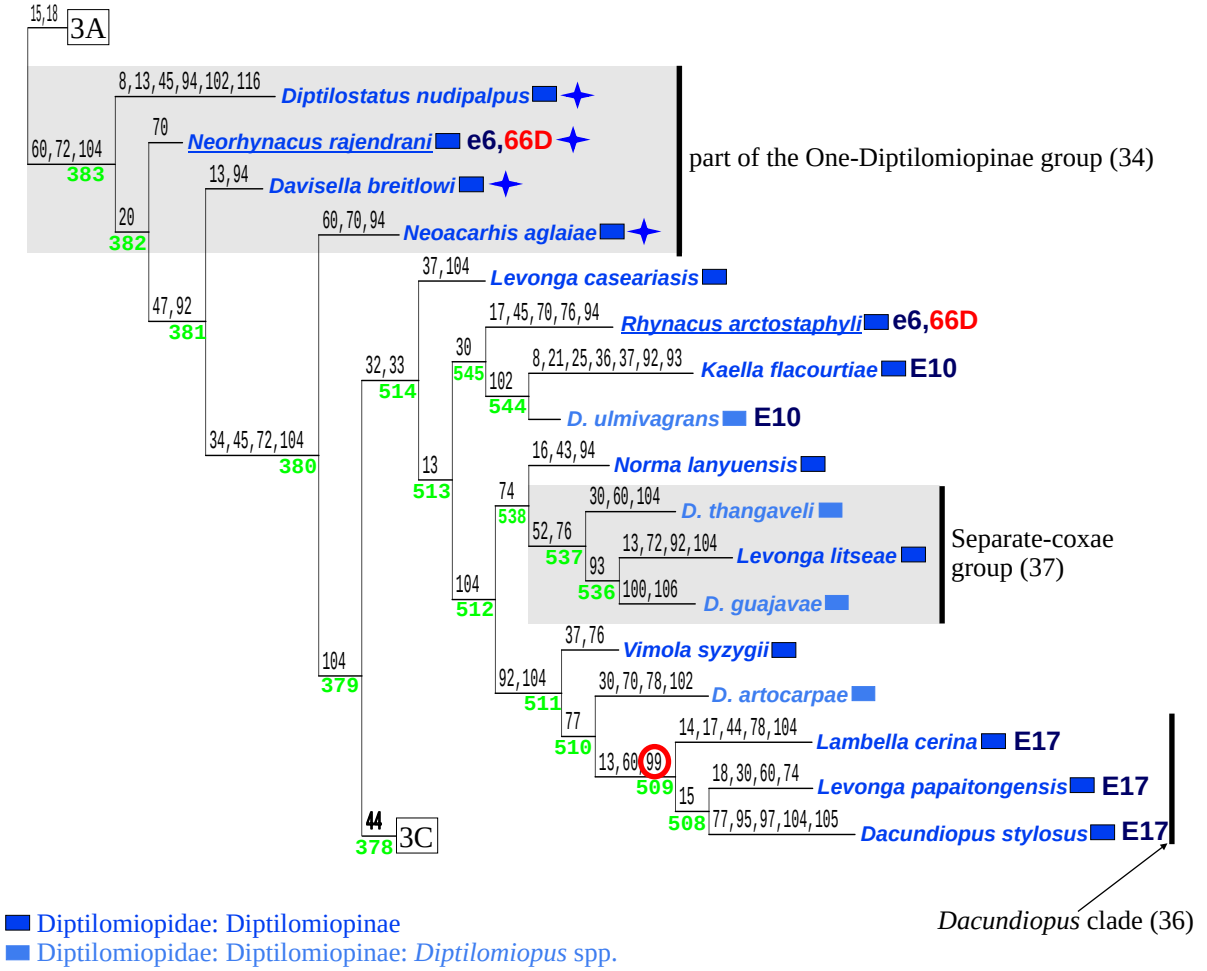


Fig. 4.21. The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3B. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66-taxon data matrix.

Captions for figures (Figs 4.22, 4.23 which are on next two pages).

Fig. 4.22. (next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3C. Black numbers above branches are the character numbers of homoplasies supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43), the taxa marked with the blue cross are part of the One-Diptilomiopinae group (polytomy) in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.37). Underlined terminal taxa are included in the 66-taxon data matrix.

Fig. 4.23. (page after next page). The strict consensus of 32 trees found with heuristic parsimony analysis of the 318 taxon x 117 character data matrix, using "new technologies" in TNT, under implied weighting of characters with k=10 (318tax-k10 tree, Fig. 4.6) - enlarged Diptilomiopidae clade (Fig. 4.19): enlarged part 3D. Black numbers above branches are the character numbers of the synapomorphies (encircled in red) or homoplasious characters supporting the nodes. Green numbers underneath the branches close to the nodes are the node numbers from TNT. Informal names of groups discussed in the text are on the right. The parts of the tree blocked in grey also occur, with the same topology, in the estimated consensus tree found from analyzing the 318-taxon data matrix under implied character weighting with k=20 (Fig. 4.26). On the right of terminal taxon names - blue E-numbers are reference numbers for groups found in the estimated consensus tree of the 318-taxon data matrix found under equal character weighting (Fig. 4.5), blue e-numbers are reference numbers for groups found in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under equal character weighting (Fig. 4.42), the red 66D indicates those taxa which are part of a clade at node 118 (Fig. 4.45) supported by two synapomorphies in the strict consensus of most parsimonious trees found for the 66-taxon data matrix under implied character weighting with k=999 (Fig. 4.43). Underlined terminal taxa are included in the 66-taxon data matrix.

Part 3C

318tax-k10
Fig. 4.22

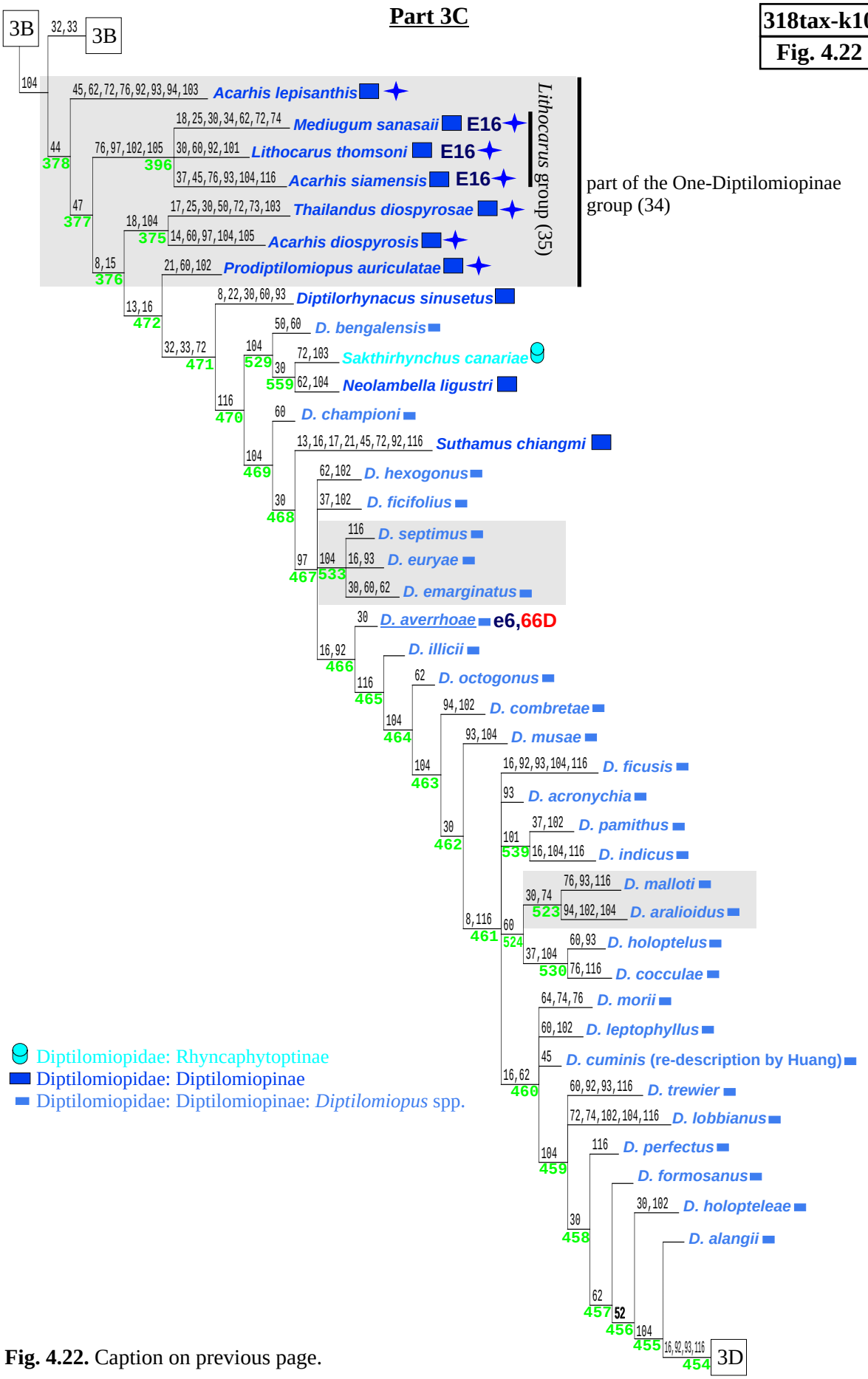


Fig. 4.22. Caption on previous page.

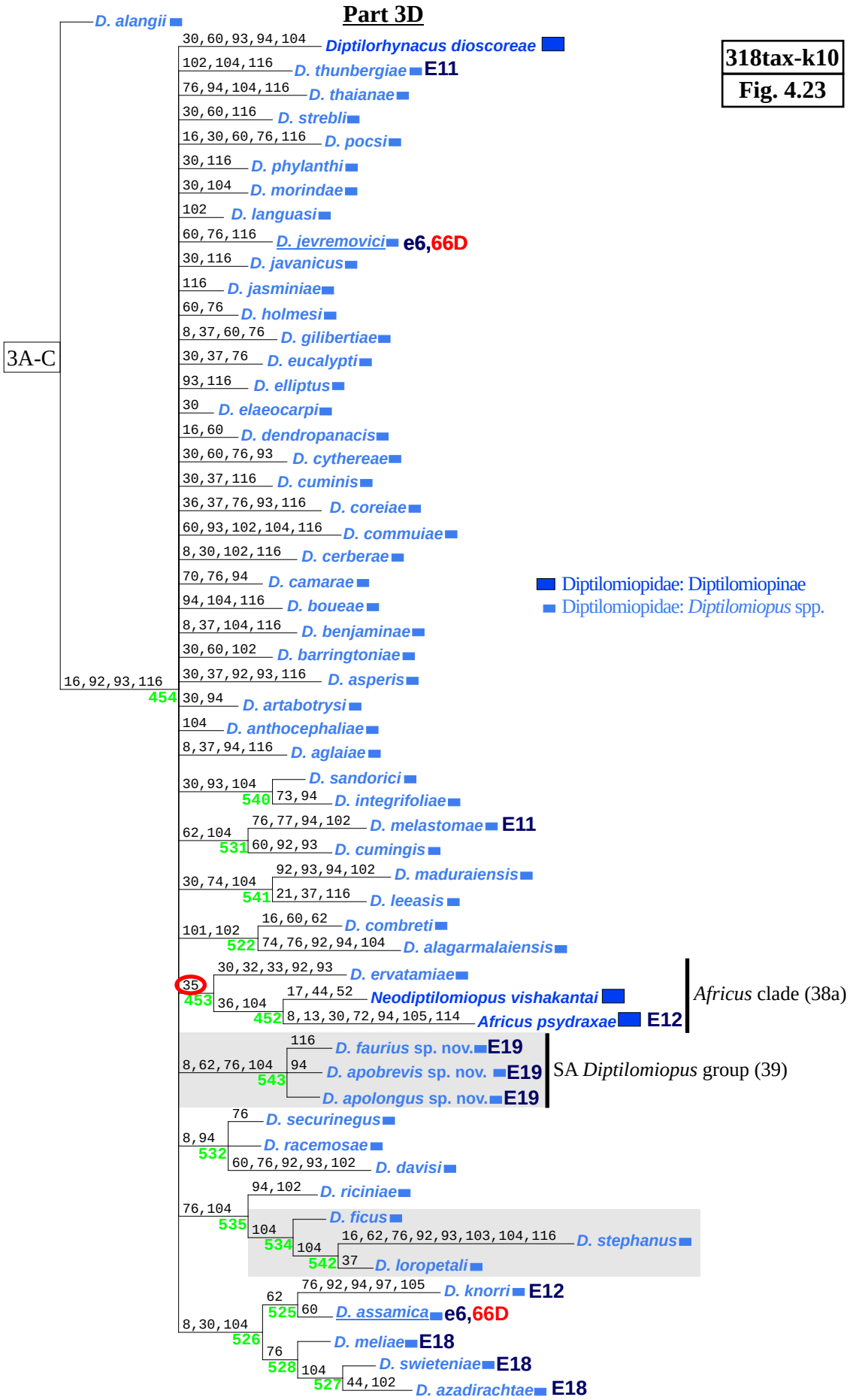


Fig. 4.22. Caption on page before previous page.

318tax-k10
Fig. 4.24

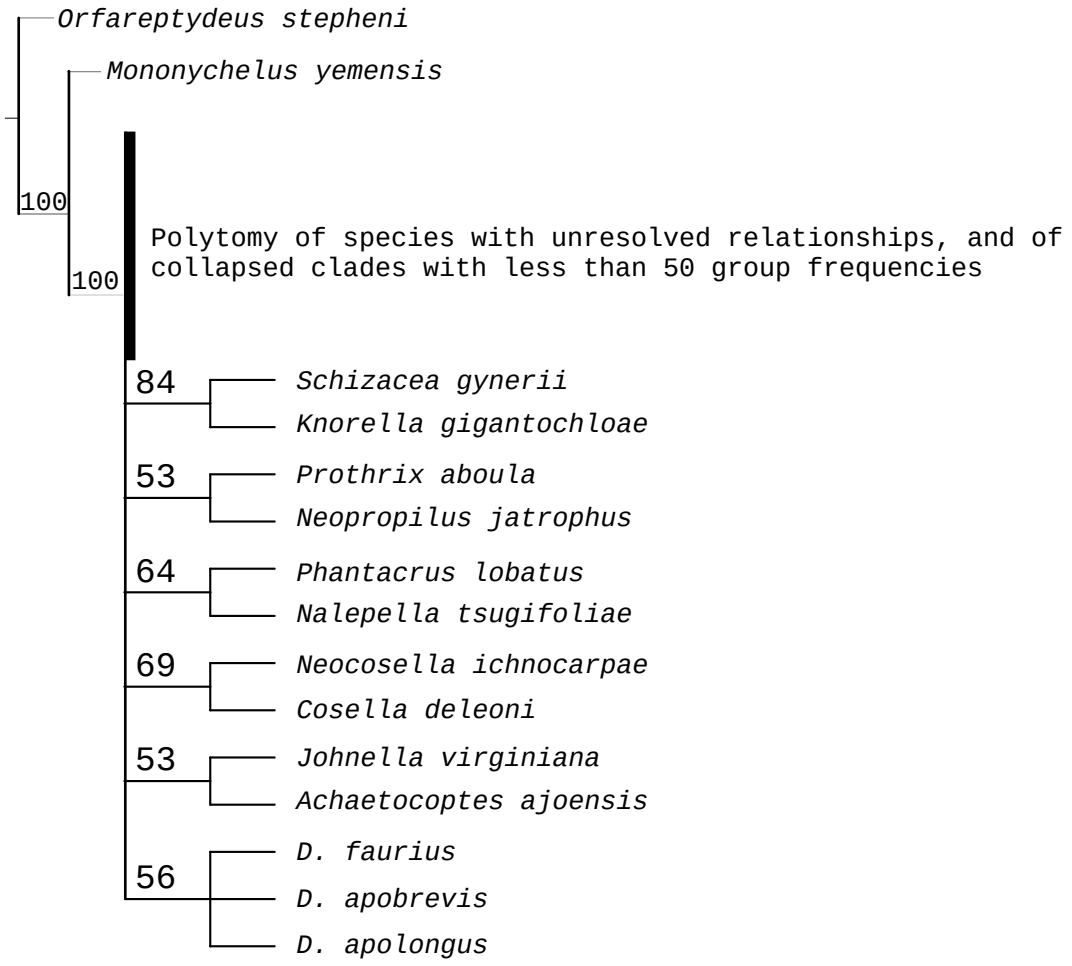


Fig. 4.24. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 318 taxon x 117 character data matrix, done in TNT with heuristic ("traditional" in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 50. Values are given above branches. Only those groupings which were not collapsed are presented, the taxa with unresolved relationships and the collapsed groups are substituted by the thick vertical bar.

318tax-k10
Fig. 4.25

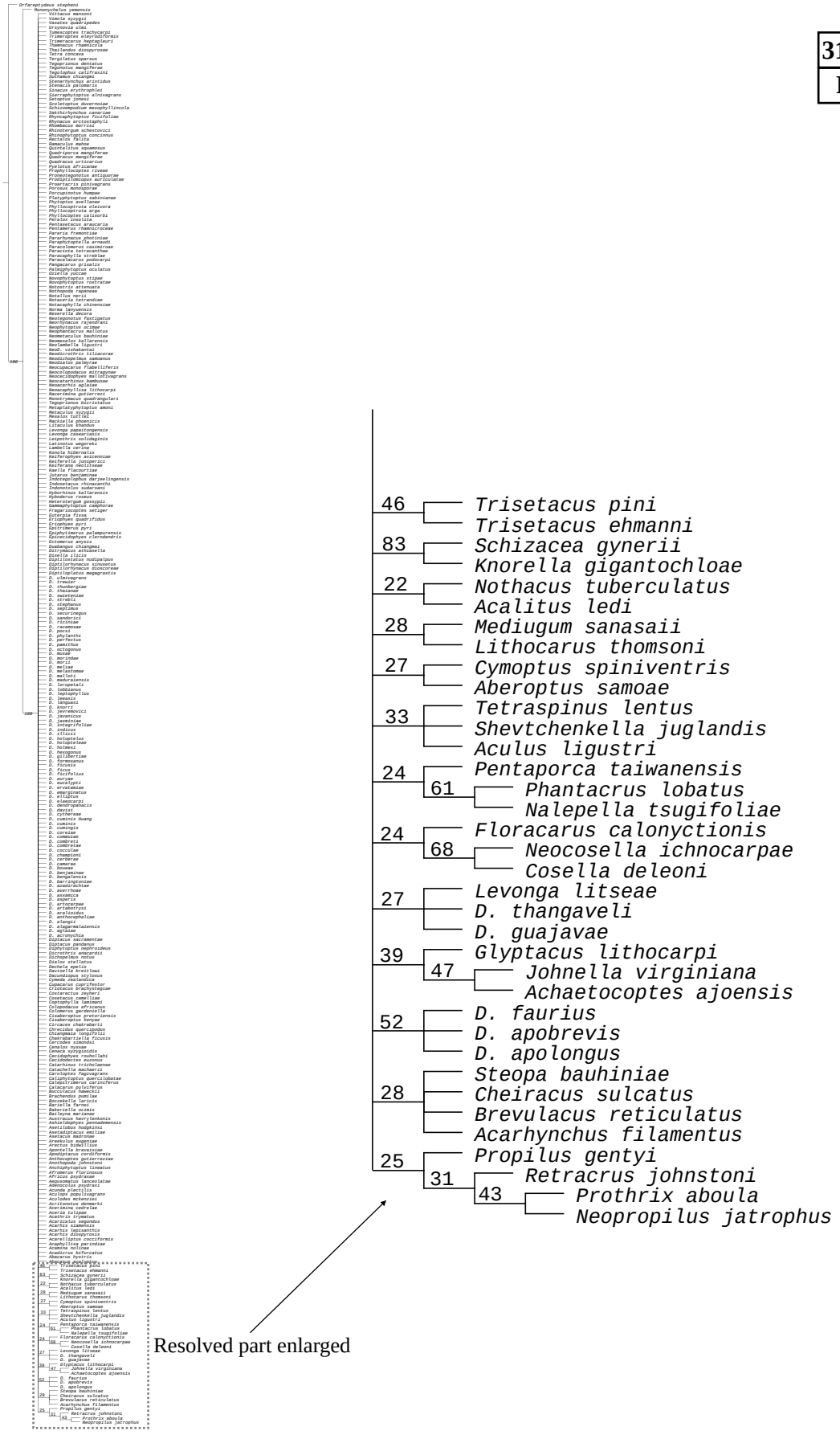


Fig. 4.25. Symmetric resample group frequency differences (GC) values of symmetric resampling (P=33) of the 318-taxon data matrix done in TNT with heuristic (”traditional” in TNT) search under implied weighting of characters with k=10, with 1000 replicates, cut at 20. Values are given above branches.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

Table 4.8. Character consistency indices (ci) and retention indices (ri) of characters in the strict consensus of 32 most parsimonious trees found with new technology searches in TNT under implied character weighting with k=10. A total of 117 characters are included in the data matrix, of which 52 are uninformative regarding the relationships between the ingroup (eriophyoid) taxa (the information for characters autapomorphic for the Eriophyoidea, and one character the same for all taxa in the analysis, are in grey, and the cell backgrounds of information for the characters autapomorphic for terminal taxa of the ingroup, are grey). Sixteen of the 65 informative characters are binary characters, and 49 are multistate characters. The number of character states for each character is listed in the column with the heading "state", 2 is a binary character and M is a multistate character followed by the number of character states. The characters with information in bold,are homologous for this tree.

Character	ci	ri	State
0	1.000	1.000	
1	1.000	1.000	
2	1.000	1.000	
3	1.000	1.000	
4	1.000	1.000	
5	1.000	1.000	
6	1.000	1.000	
7	-	-	
8	0.133	0.316	M5
9	1.000	1.000	
10	0.400	0.625	M3
11	0.200	0.765	2
12	1.000	1.000	
13	0.043	0.820	2
14	0.278	0.776	M7
15	0.156	0.763	M7
16	0.107	0.479	M4
17	0.043	0.604	M5
18	0.078	0.393	M8
19	0.167	0.643	2
20	0.500	0.991	2
21	0.286	0.955	M3
22	0.167	0.688	2
23	1.000	1.000	
24	1.000	1.000	
25	0.077	0.400	2
26	1.000	1.000	
27	1.000	1.000	
28	1.000	1.000	
29	1.000	1.000	
30	0.020	0.385	M3
31	1.000	1.000	
32	0.100	0.927	2
33	0.182	0.928	M3
34	0.046	0.278	M8
35	**1.000**	**1.000**	**2**
36	0.750	0.667	M4
37	0.055	0.233	M7
38	0.500	0.000	
39	1.000	1.000	
40	1.000	1.000	
41	-	-	
42	1.000	1.000	
43	0.071	0.914	2
44	0.200	0.957	2
45	0.033	0.797	2
46	0.333	0.500	M4
47	0.082	0.287	M8
48	0.400	0.769	M3
49	0.455	0.250	M6
50	0.083	0.919	2
51	0.063	0.887	2
52	0.200	0.934	2
53	1.000	1.000	
54	1.000	1.000	
55	1.000	1.000	
56	1.000	1.000	
57	**1.000**	**1.000**	**2**
58	**1.000**	**1.000**	**2**
59	**1.000**	**1.000**	**M3**
60	0.157	0.483	M16
61	0.500	0.000	M3
62	0.046	0.629	M4
63	0.667	0.960	M4
64	0.111	0.200	M13
65	0.800	0.667	M6
66	1.000	1.000	
67	0.103	0.352	M5
68	1.000	1.000	
69	1.000	1.000	
70	0.113	0.485	M12
71	1.000	1.000	
72	0.082	0.524	M9
73	0.108	0.094	M8
74	0.097	0.509	M7
75	**1.000**	**1.000**	**M3**
76	0.128	0.354	M16
77	0.118	0.400	M3
78	0.455	0.500	M8
79	1.000	1.000	
80	-	-	
81	1.000	1.000	
82	1.000	1.000	
83	1.000	1.000	
84	1.000	1.000	
85	1.000	1.000	
86	1.000	1.000	
87	1.000	1.000	
88	1.000	1.000	
89	1.000	1.000	
90	1.000	1.000	
91	1.000	1.000	
92	0.034	0.436	M4
93	0.043	0.438	M5
94	0.069	0.212	M6
95	1.000	1.000	
96	1.000	1.000	
97	0.300	0.920	M4
98	1.000	1.000	
99	**1.000**	**1.000**	**2**
100	0.500	0.778	M3
101	0.250	0.704	M9
102	0.057	0.371	M8
103	0.344	0.852	M13
104	0.070	0.573	M14
105	0.250	0.933	M3
106	0.500	0.800	M3
107	1.000	1.000	
108	1.000	1.000	
109	1.000	1.000	
110	1.000	1.000	
111	1.000	1.000	
112	0.214	0.593	M4
113	0.190	0.469	M5
114	0.286	0.545	M3
115	0.400	0.571	M3
116	0.040	0.359	M7

318tax-k20
Fig. 4.26

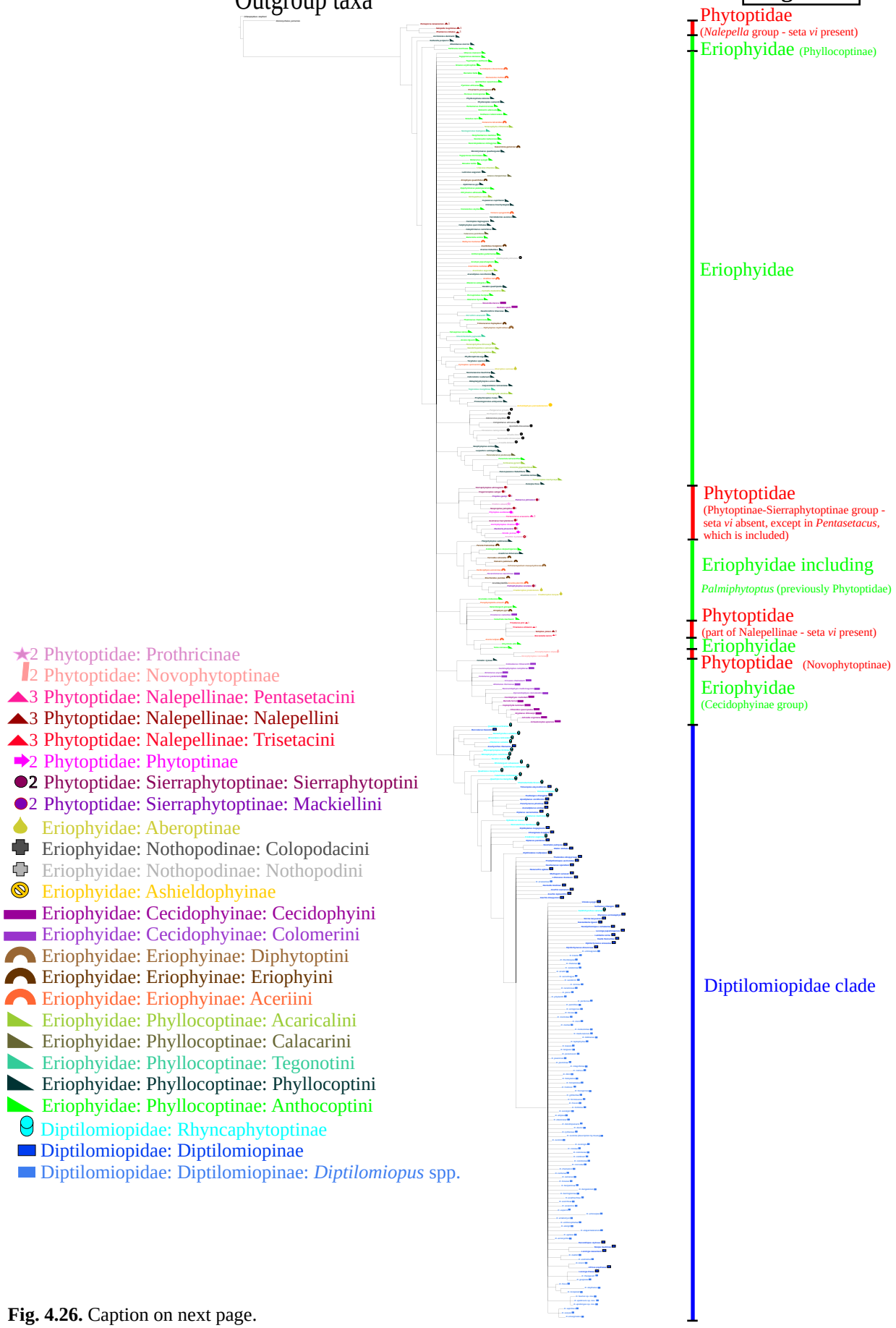


Fig. 4.26. Caption on next page.

318tax-k20
Fig. 4.27

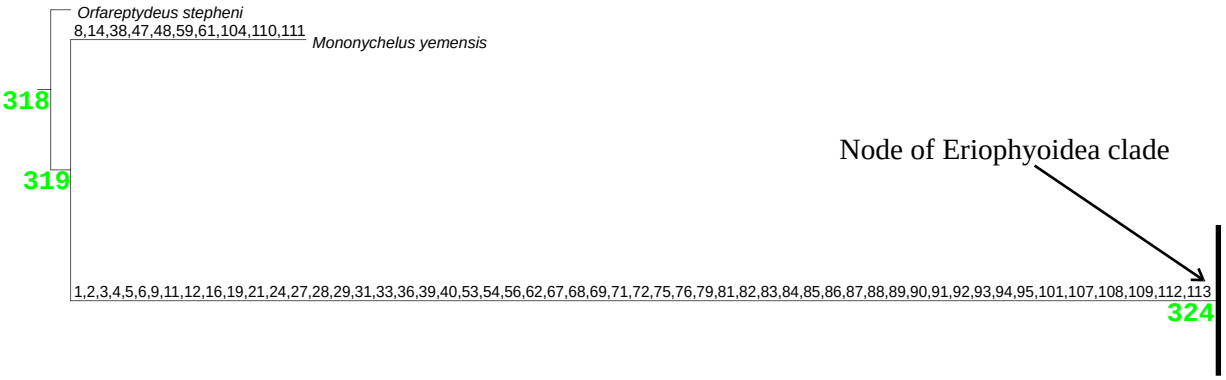


Fig. 4.26. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 in TNT. Total fit = 94.47; Adjusted homoplasy = 35.53; Total length = 2970; CI = 0.101; RI = 0.521; Nodes = 103. Uninformative characters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

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

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

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

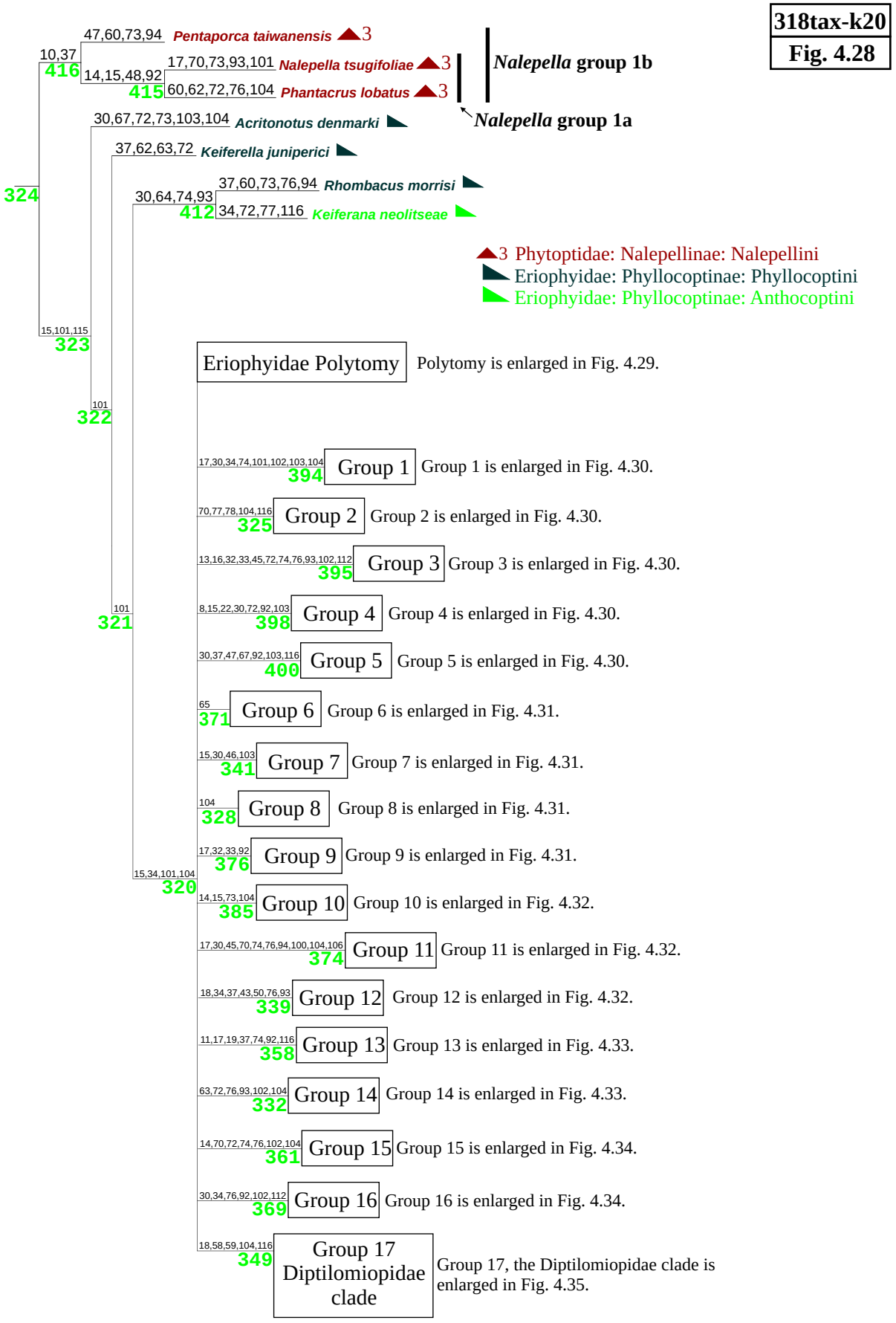


Fig. 4.28. Caption on previous page.

Eriophyidae Polytomy

318tax-k20
Fig. 4.29

Fig. 4.29. Caption on page before previous page.

318tax-k20
Fig. 4.30

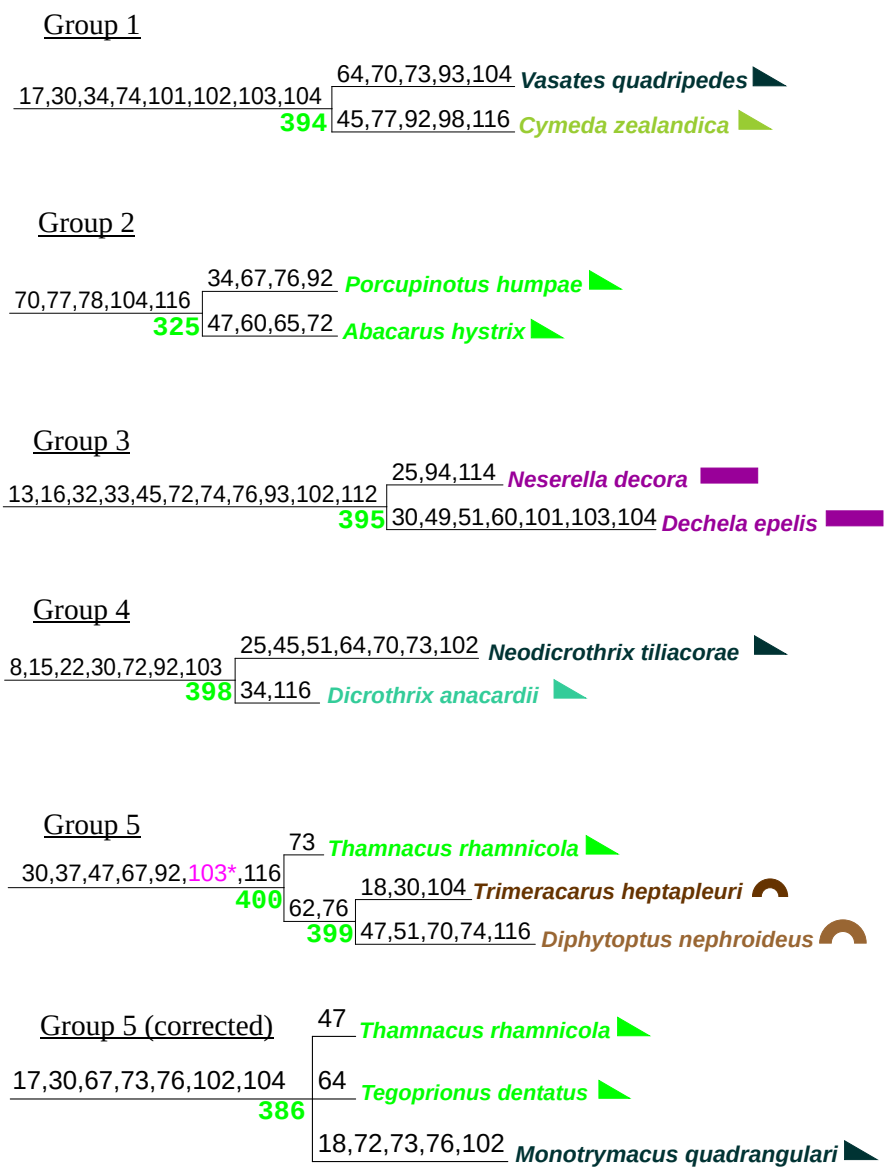
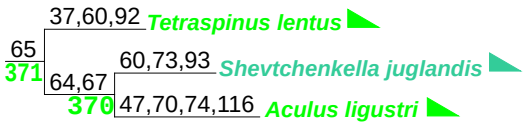


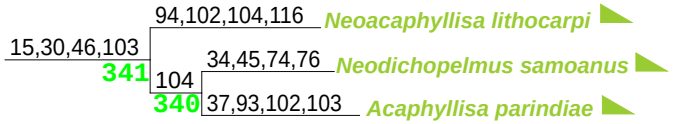
Fig. 4.30. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 1-5 of Fig. 4.28, and corrected Group 5. Black numbers above branches are the character numbers of the homoplasious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

318tax-k20
Fig. 4.31

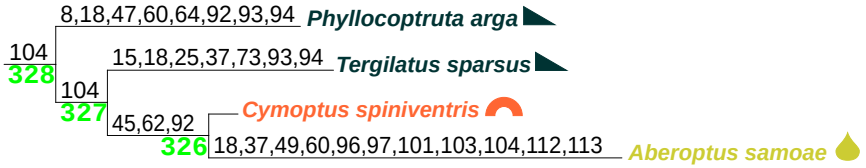
Group 6



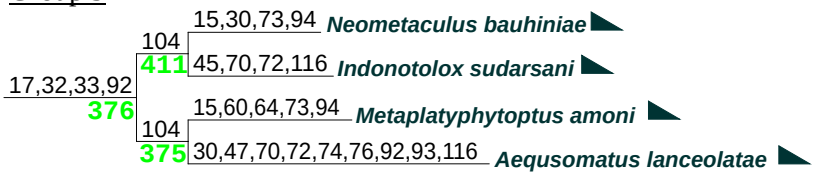
Group 7



Group 8



Group 9

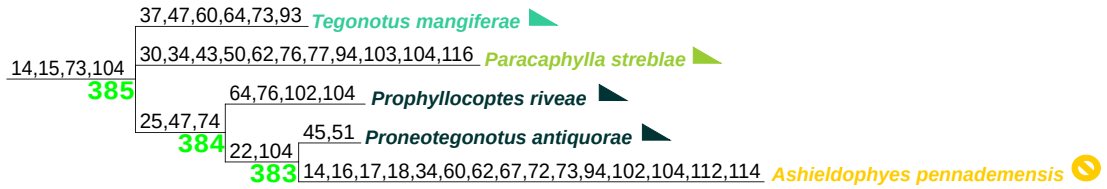


Eriophyidae: Aberoptinae
Eriophyidae: Eriophyinae: Aceriini
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini
Eriophyidae: Phyllocoptinae: Anthocoptini

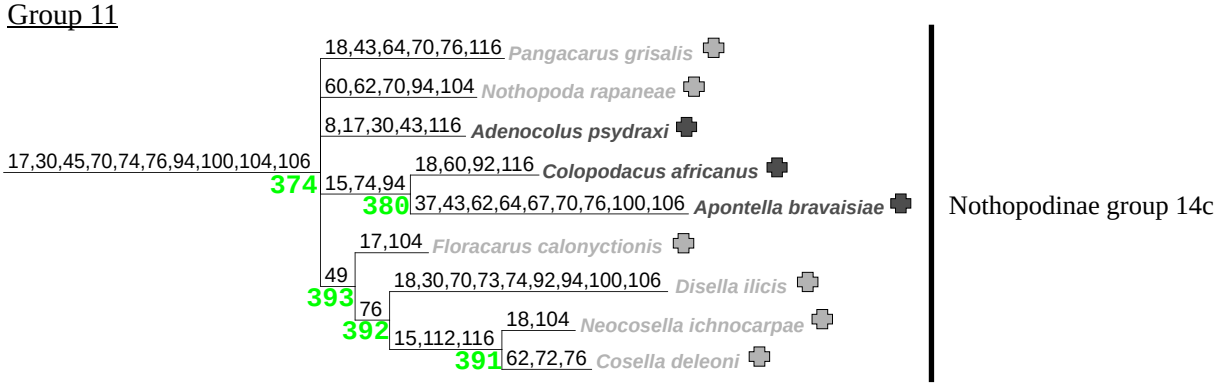
Fig. 4.31. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 6-9 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters supporting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

318tax-k20
Fig. 4.32

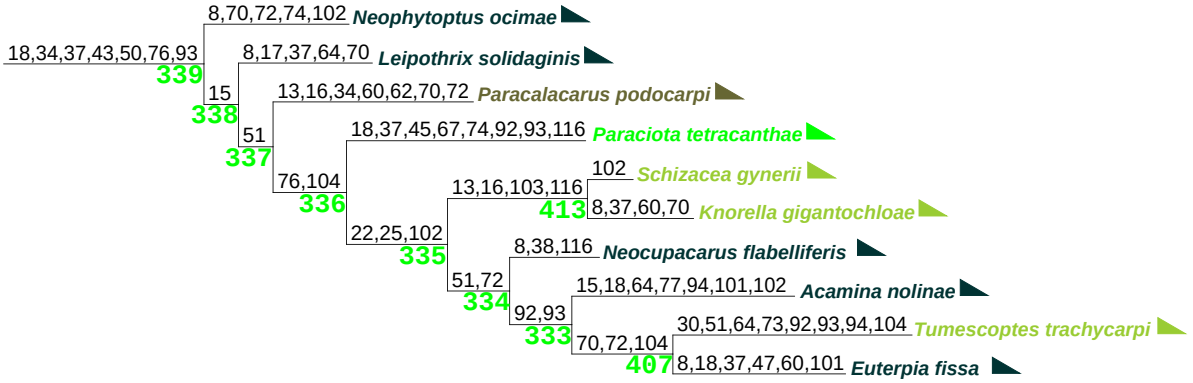
Group 10



Group 11



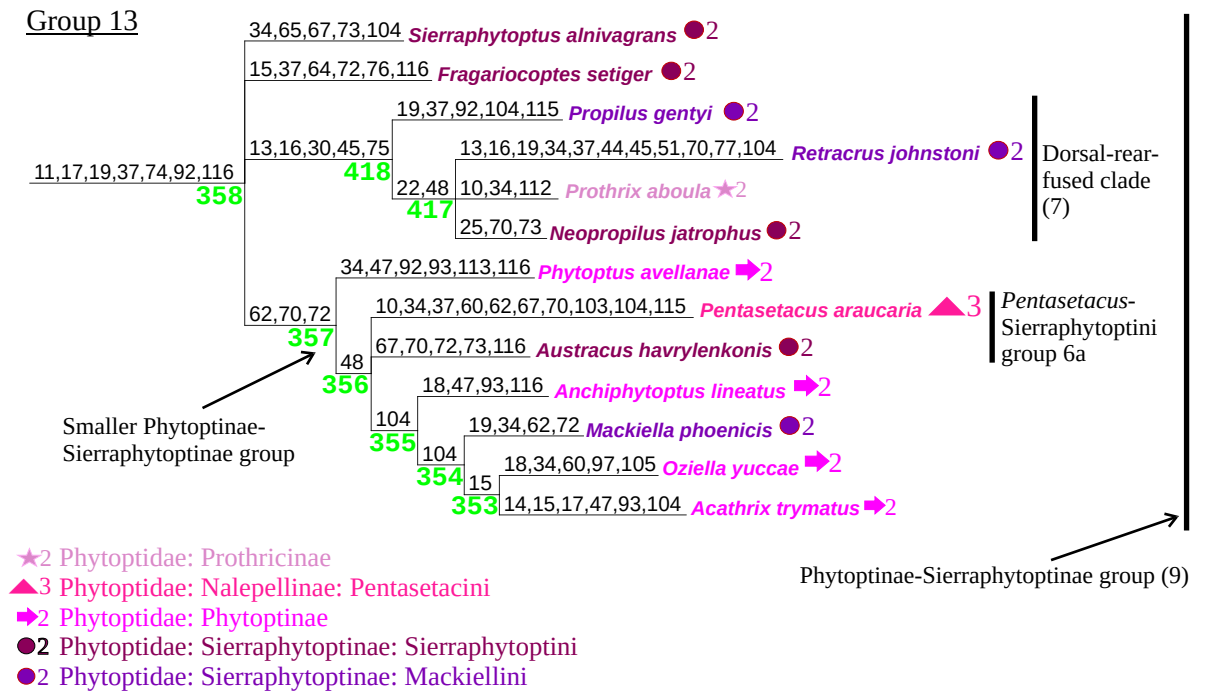
Group 12



Eriophyidae: Nothopodinae: Colopodacini
Eriophyidae: Nothopodinae: Nothopodini
Eriophyidae: Ashieldophyinae
Eriophyidae: Phyllocoptinae: Acaricalini
Eriophyidae: Phyllocoptinae: Calacarini
Eriophyidae: Phyllocoptinae: Tegonotini
Eriophyidae: Phyllocoptinae: Phyllocoptini

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

318tax-k20
Fig. 4.33



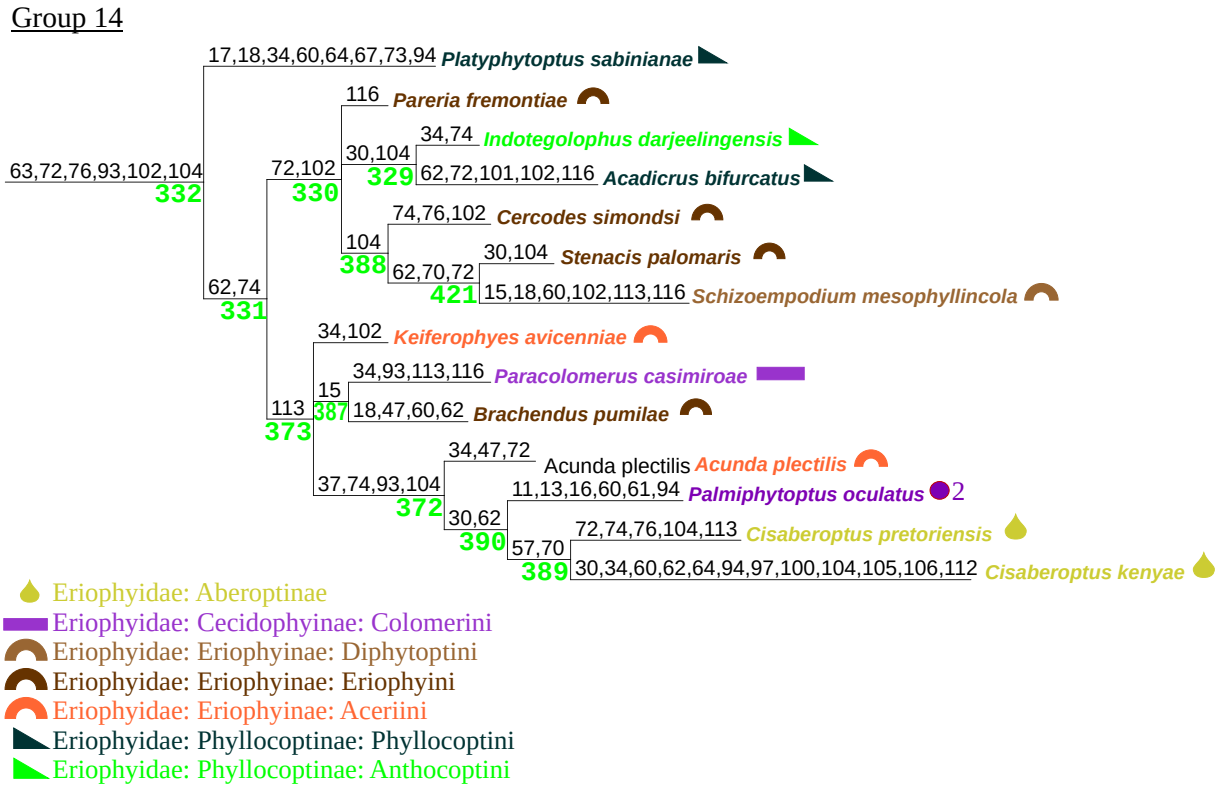


Fig. 4.33. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 13-14 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters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

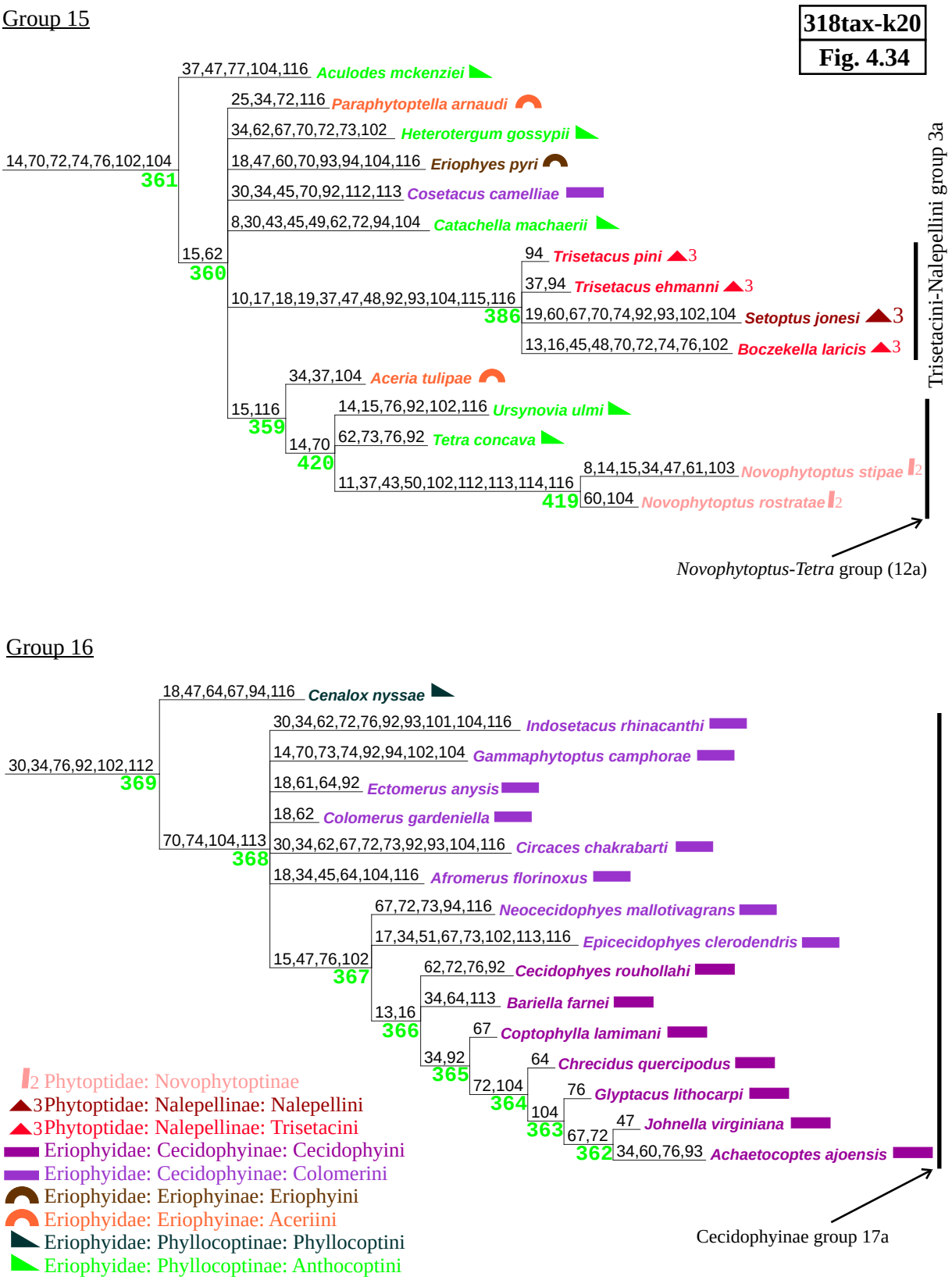


Fig. 4.34. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Groups 15-16 of Fig. 4.28. Black numbers above branches are the character numbers of the homoplasious characters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

318tax-k20
Fig. 4.35

Group 17
Diptilomiopidae clade

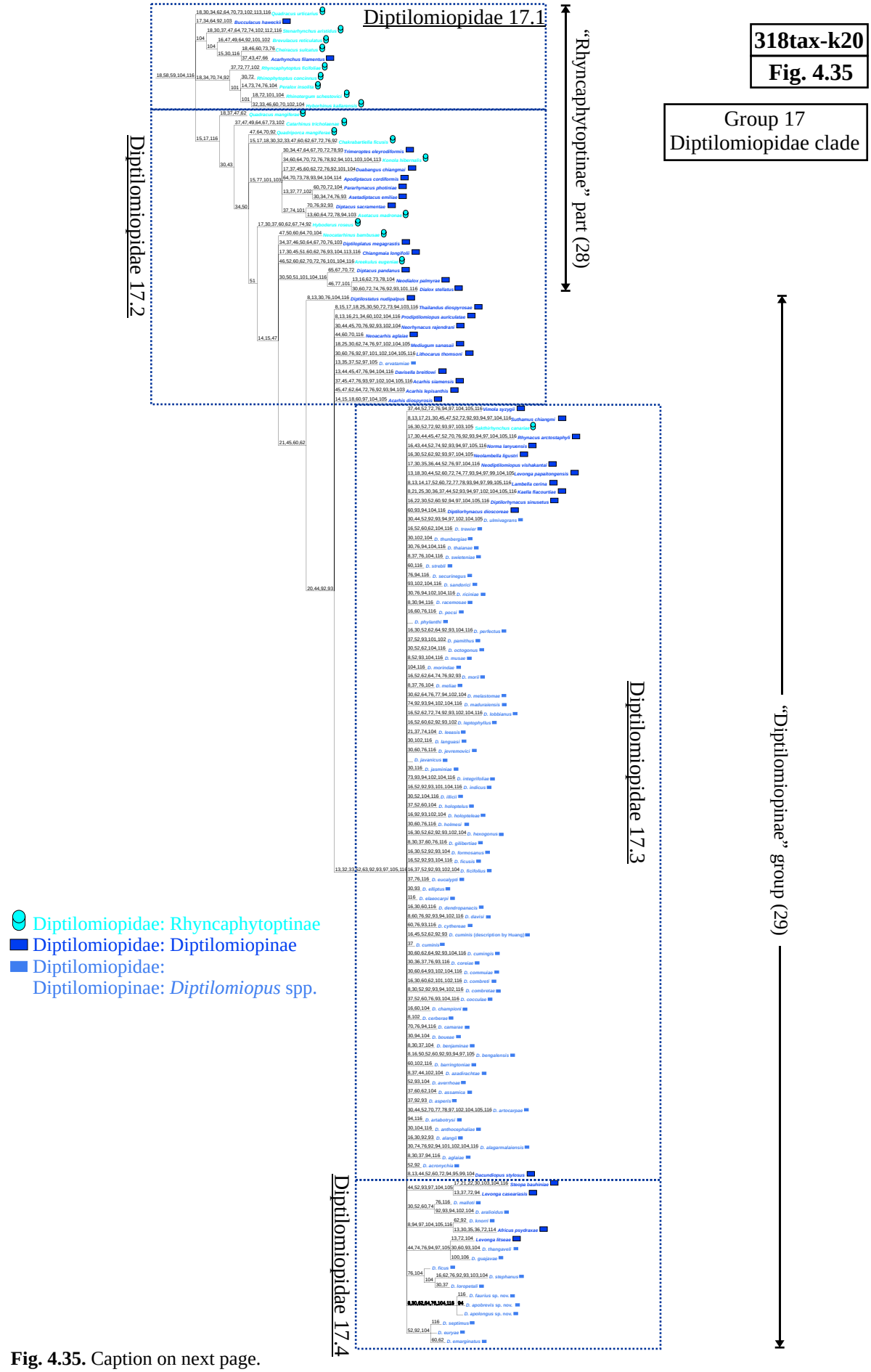


Fig. 4.35. Caption on next page.

318tax-k20
Fig. 4.36

Diptilomiopidae 17.1

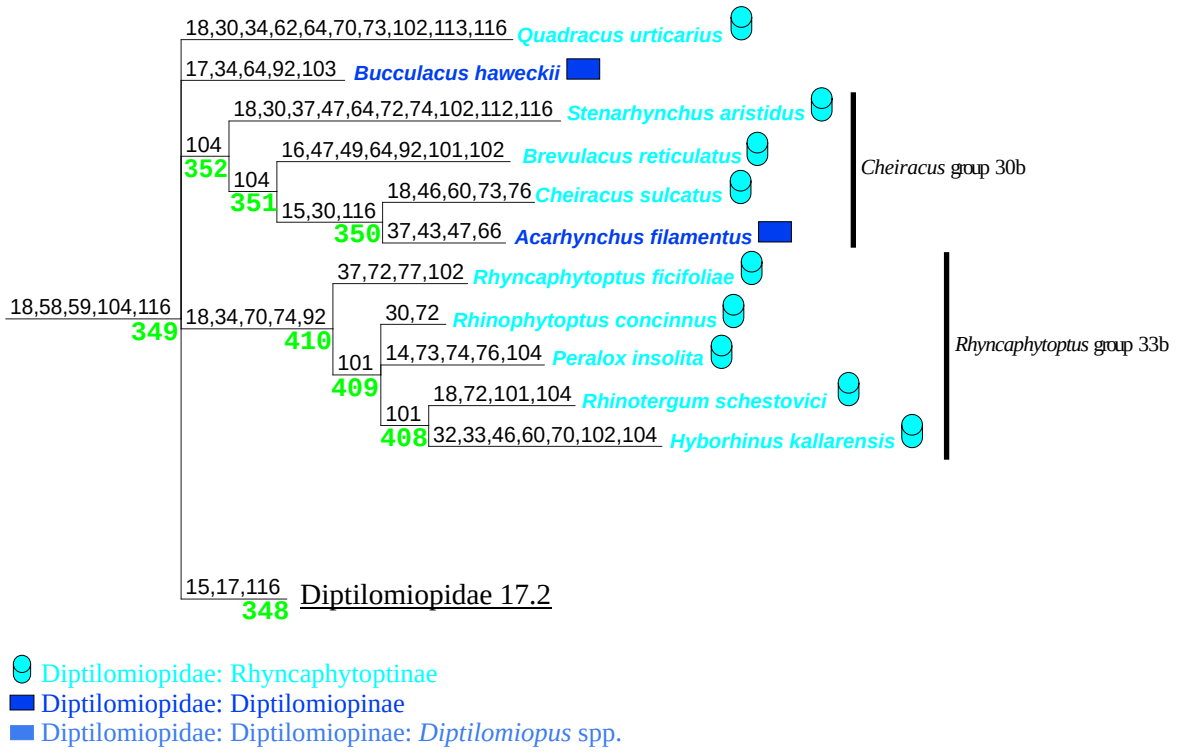


Fig. 4.35. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26): enlarged Group 17 (Diptilomiopidae clade) of Fig. 4.28. The clade in this figure and at this enlargement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

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

Diptilomiopidae 17.2

318tax-k20
Fig. 4.37

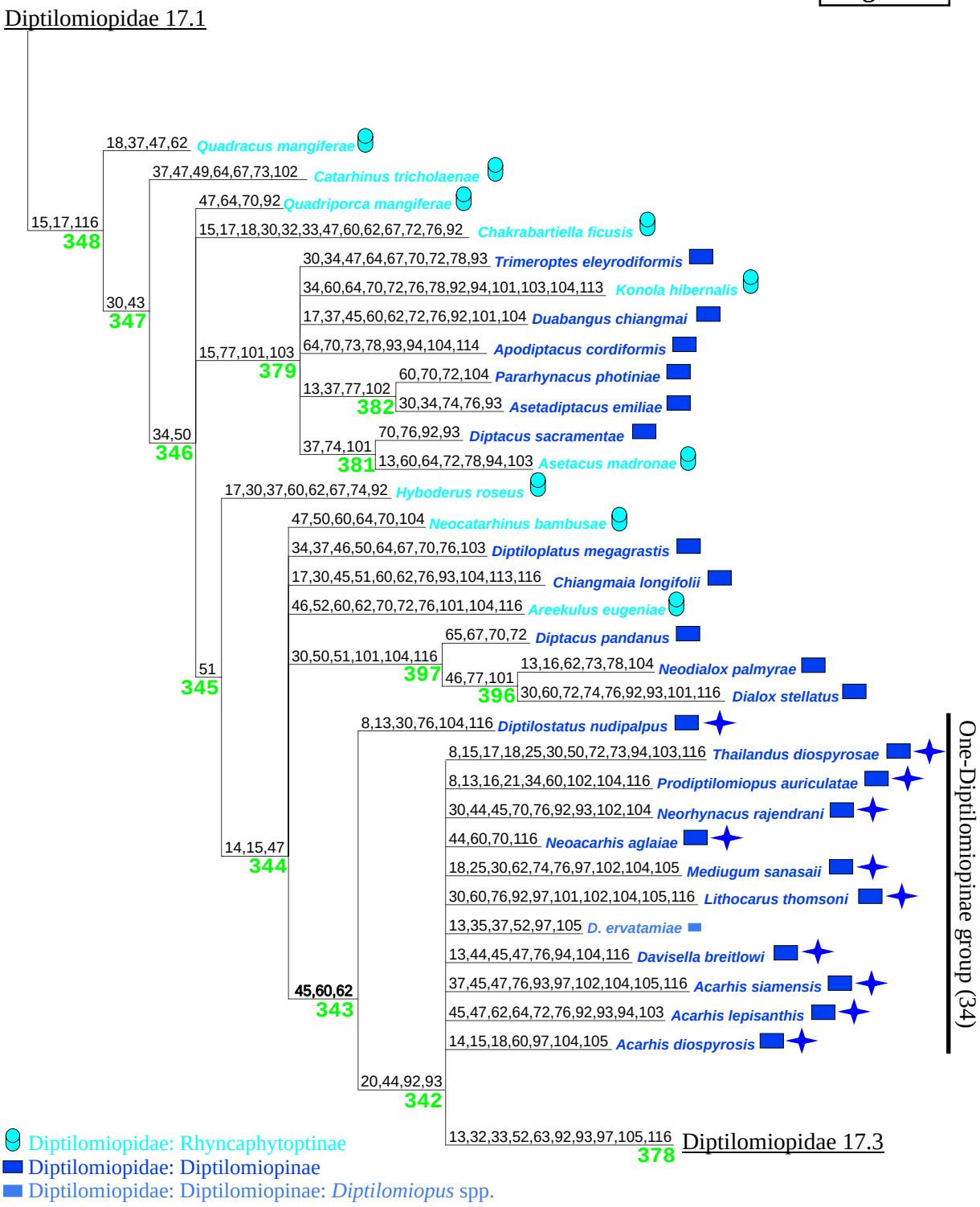


Fig. 4.37. Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.2. Black numbers above branches are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

Diptilomiopidae 17.3

318tax-k20
Fig. 4.38

Diptilomiopidae 17.2
13,32,33,52,63,92,93,97,105,116
378

Diptilomiopidae: Rhyncaphytoptinae
Diptilomiopidae: Diptilomiopinae
Diptilomiopidae:
Diptilomiopinae: *Diptilomiopus* spp.

Diptilomiopidae 17.4

Fig. 4.38. Caption on next page.

Diptilomiopidae 17.4

318tax-k20
Fig. 4.39

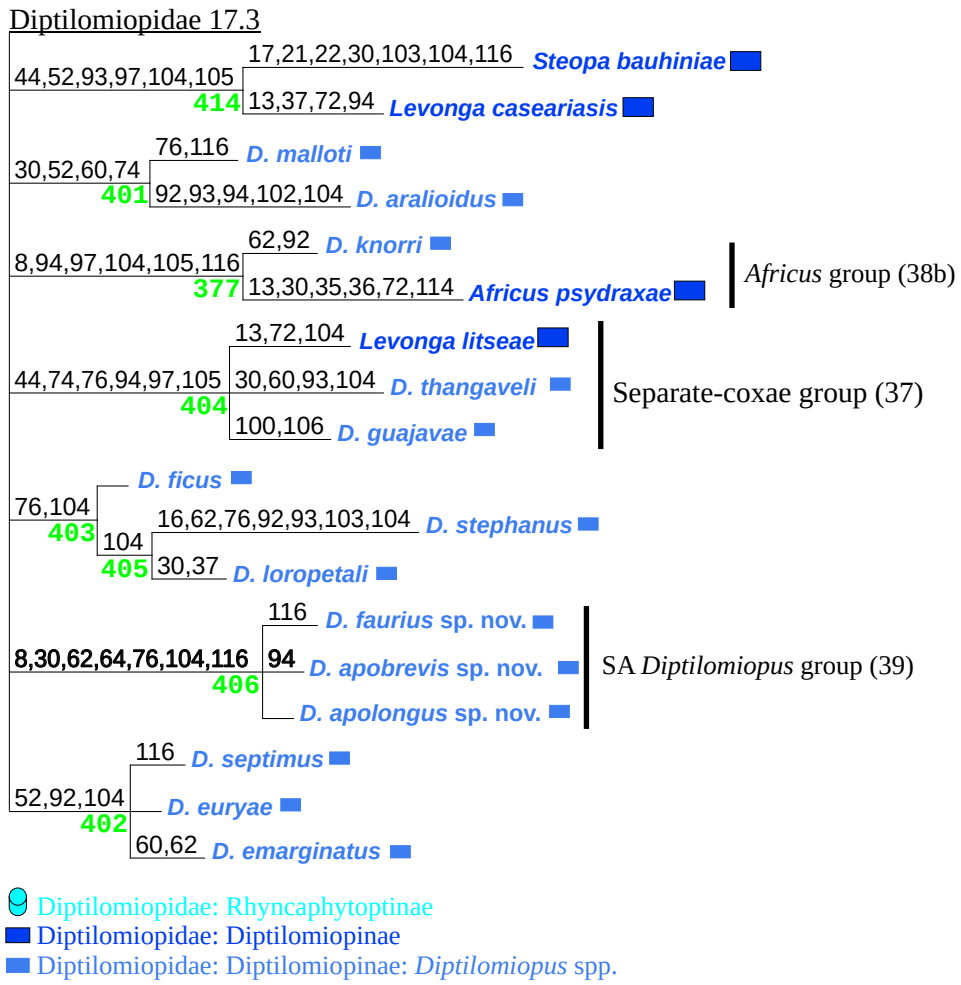


Fig. 4.38. (previous page). Estimated consensus tree found with the analysis of the 318 taxon x 117 character data matrix under implied character weighting with k=20 (318tax-k20 tree, Fig. 4.26), enlarged Group 17 (Diptilomiopidae clade) (Fig. 4.35): enlarged group Diptilomiopidae 17.3, which is a polytomy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

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

Table 4.9. Character consistency indices (ci) and character retention indices (ri) of characters of the estimated consensus tree found with the analysis of the 318 taxon data matrix under implied weighting of characters with k=20 in TNT (Fig. 4.26). A total of 117 characters are included in the data matrix, of which 52 are uninformative regarding the relationships between the ingroup (eriophyoid) taxa (ci indices of characters autapomorphic for the Eriophyoidea, and one character the same for all taxa in the analysis are in grey, and the cell backgrounds of the ci indices of characters autapomorphic for terminal taxa of the ingroup, are grey). The characters with ci indices in bold are homologous for this tree.

Character consistency indices (ci)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.105	1.000
10	0.400	0.250	1.000	0.038	0.250	0.094	0.073	0.031	0.069	0.143
20	**1.000**	0.286	0.125	--	1.000	0.071	--	1.000	1.000	1.000
30	0.016	1.000	0.056	0.105	0.042	0.333	0.600	0.051	0.500	1.000
40	1.000	--	--	0.067	0.059	0.027	0.250	0.074	0.333	0.500
50	0.111	0.056	0.024	1.000	1.000	--	1.000	**1.000**	**1.000**	**1.000**
60	0.154	0.500	0.040	0.667	0.099	0.800	--	0.077	1.000	1.000
70	0.094	1.000	0.072	0.101	0.072	**1.000**	0.113	0.095	0.313	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.025	0.031	0.060	1.000	--	0.115	--	0.333
100	0.400	0.175	0.047	0.306	0.051	0.087	0.333	1.000	1.000	1.000
110	--	--	0.273	0.211	0.250	0.400	0.035			

Character retention indices (ri)

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0	--	1.000	1.000	1.000	1.000	1.000	1.000	--	0.105	1.000
10	0.625	0.824	1.000	0.795	0.741	0.579	0.208	0.432	0.308	0.571
20	**1.000**	0.955	0.563	--	1.000	0.350	--	1.000	1.000	1.000
30	0.242	1.000	0.863	0.864	0.200	0.000	0.333	0.178	0.000	1.000
40	1.000	--	--	0.908	0.830	0.748	0.250	0.202	0.692	0.375
50	0.941	0.872	0.328	1.000	1.000	--	1.000	1.000	**1.000**	**1.000**
60	0.469	0.000	0.569	0.960	0.090	0.667	--	0.111	1.000	1.000
70	0.365	1.000	0.449	0.031	0.325	**1.000**	0.252	0.240	0.083	1.000
80	--	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
90	1.000	1.000	0.201	0.212	0.071	1.000	--	0.736	--	0.000
100	0.667	0.535	0.233	0.824	0.395	0.764	0.600	1.000	1.000	1.000
110	--	--	0.704	0.531	0.455	0.571	0.251			

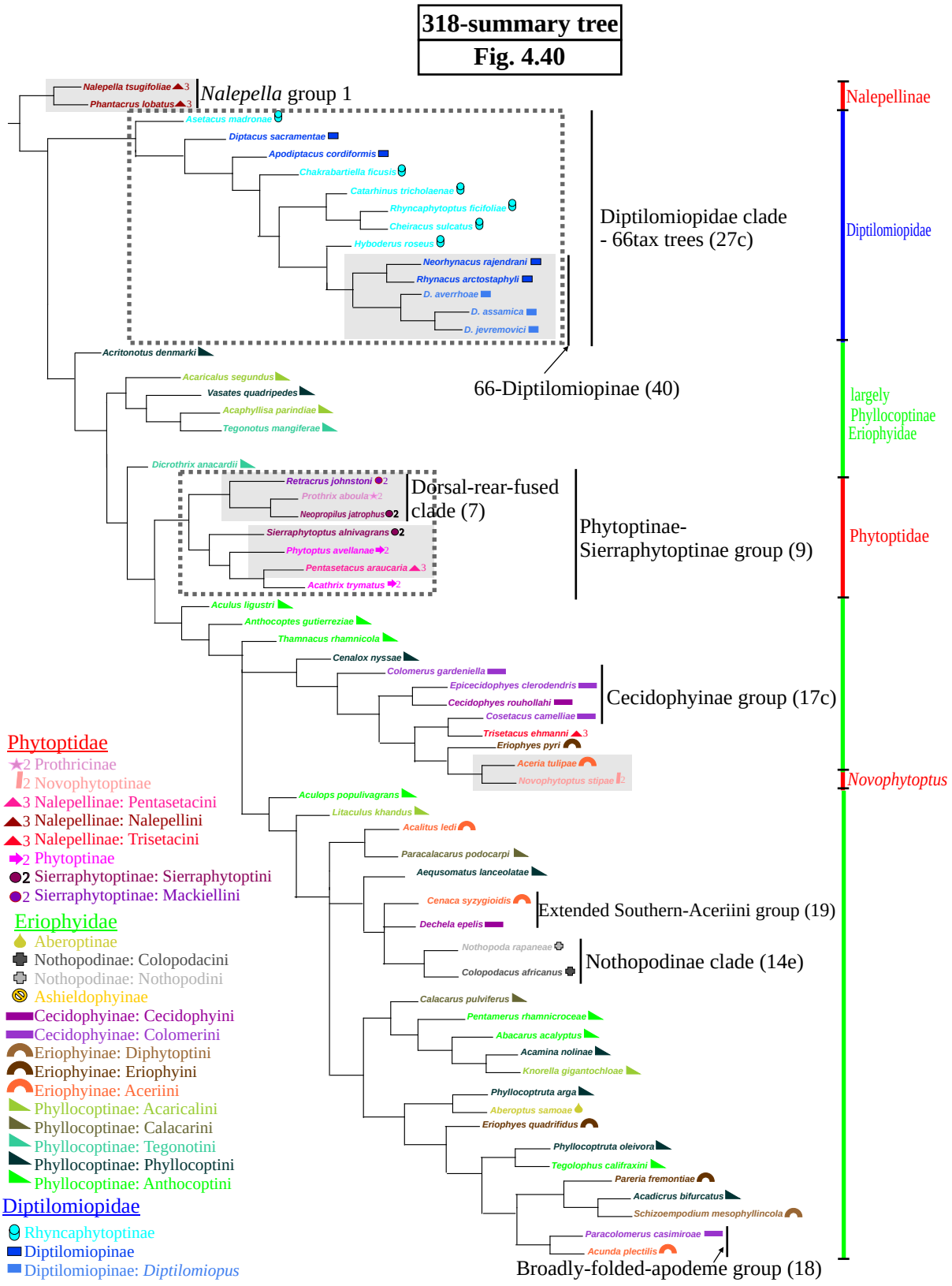


Figure 4.40. Summary (318-summary tree) of the 318tax-k10 tree (Fig. 4.6), constructed manually to schematically reflect the broad relationships between taxa from the 318-taxon data set which were included in the 66-taxon data set. It is a non-metric tree. It was literally done by eliminating those taxa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

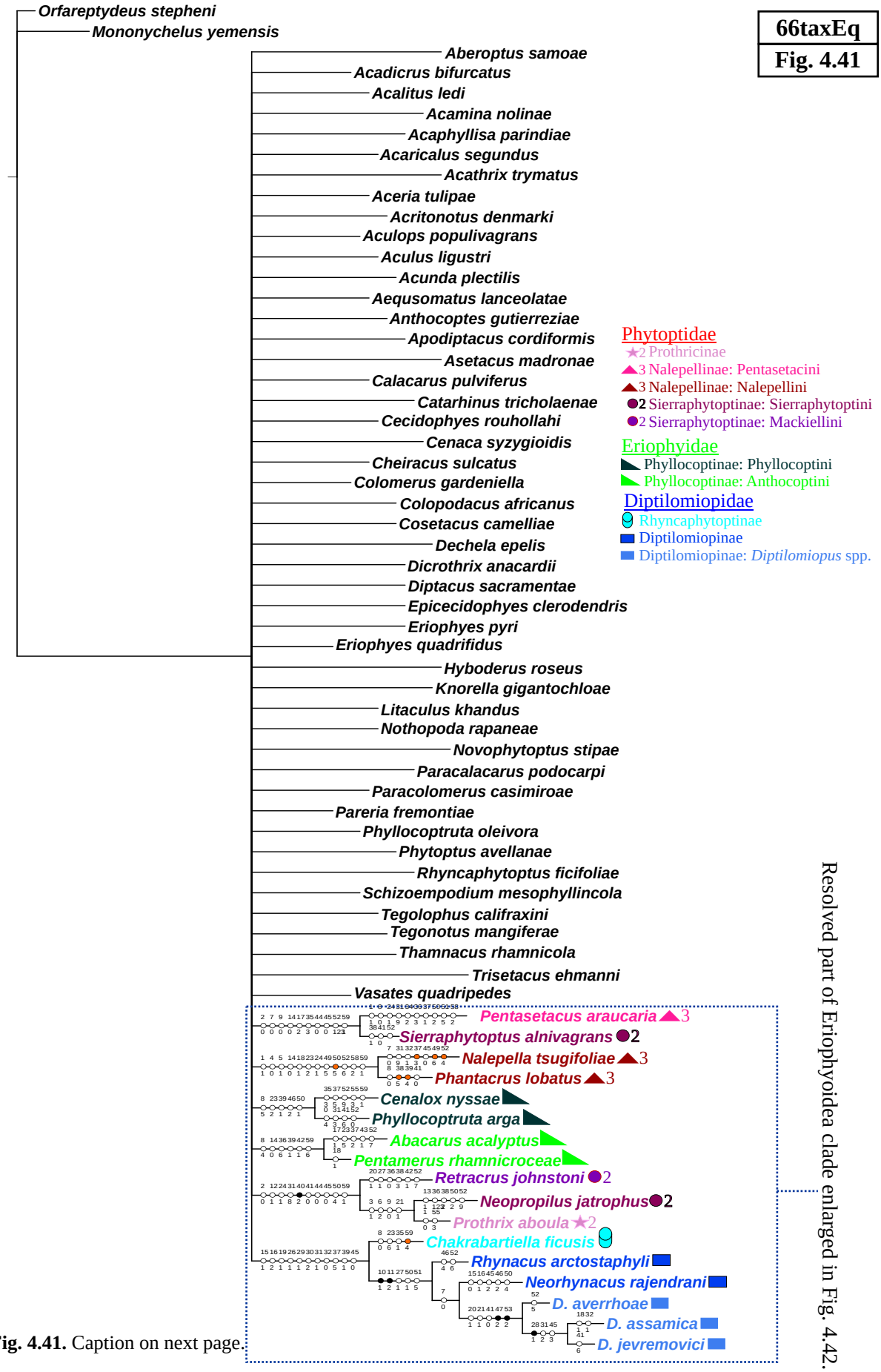


Fig. 4.41. Caption on next page.

66taxEq
Fig. 4.42

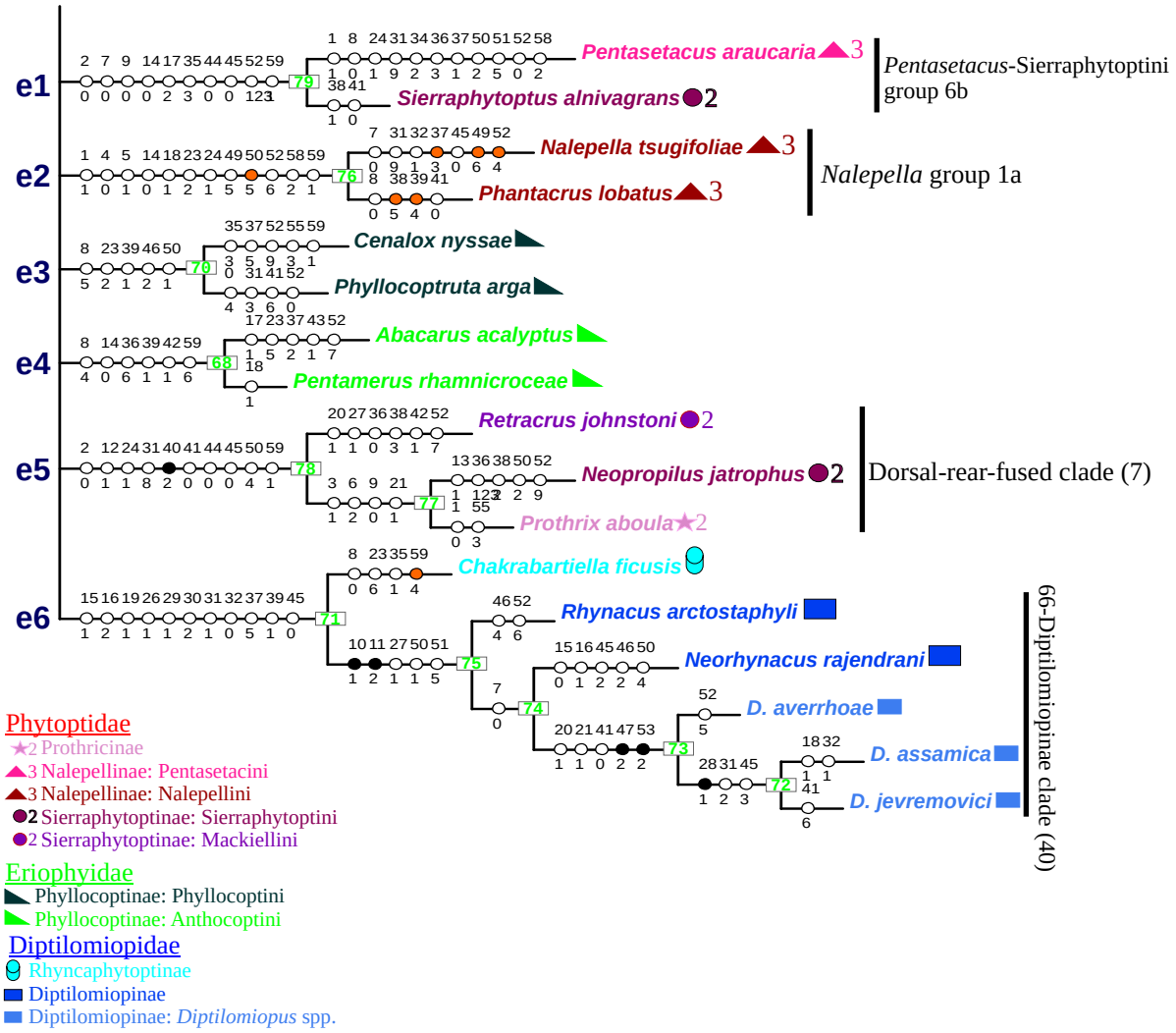


Fig. 4.41. (previous page). Strict consensus (Total fit = 38.91; Adjusted homoplasy = 47.09; Total length = 942; CI = 0.201; RI = 0.181) of 768 most parsimonious trees (each - Total fit = 44.20; Adjusted homoplasy = 41.80; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis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

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

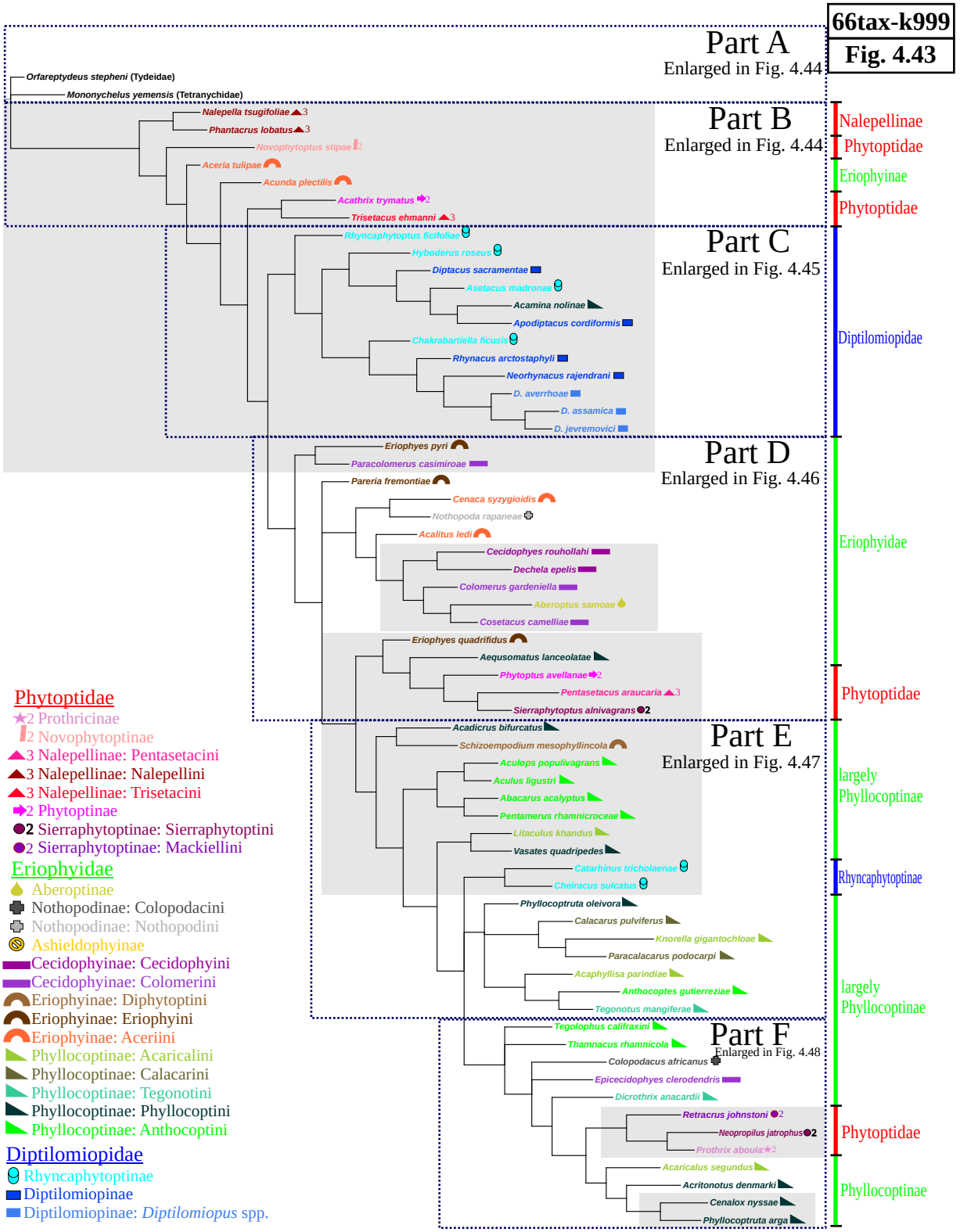


Fig. 4.43. Strict consensus (Total fit = 85.54; Adjusted homoplasy = 0.45; Total length = 649; CI = 0.291; RI = 0.501) of 3 most parsimonious trees (each - Total fit = 85.55; Adjusted homoplasy = 0.45; Total length = 648; CI = 0.292; RI = 0.501) found with heuristic parsimony analysis of the 66 taxon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

66tax-k999
Fig. 4.44

Part A

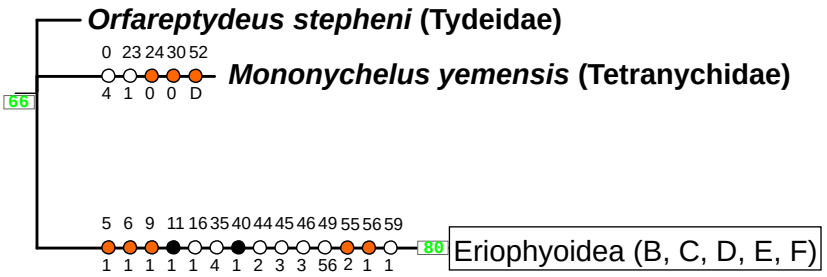


Fig. 4.44 Part A. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged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

Part B

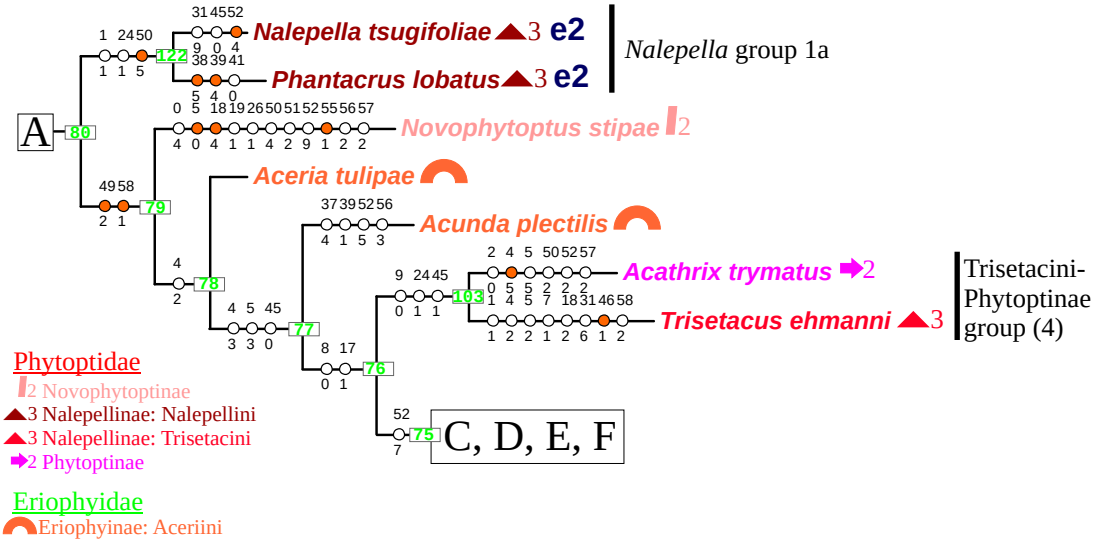


Fig. 4.44 Part B. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged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

Part C

66tax-k999
Fig. 4.45

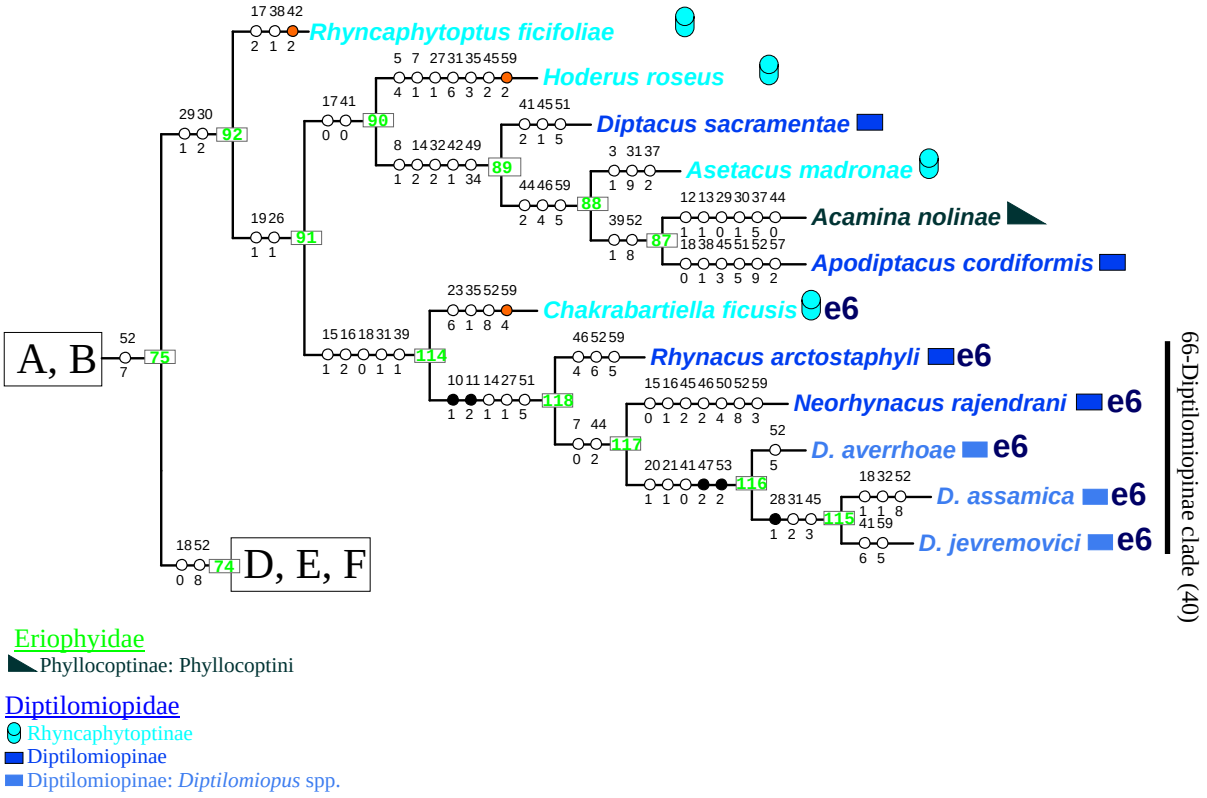
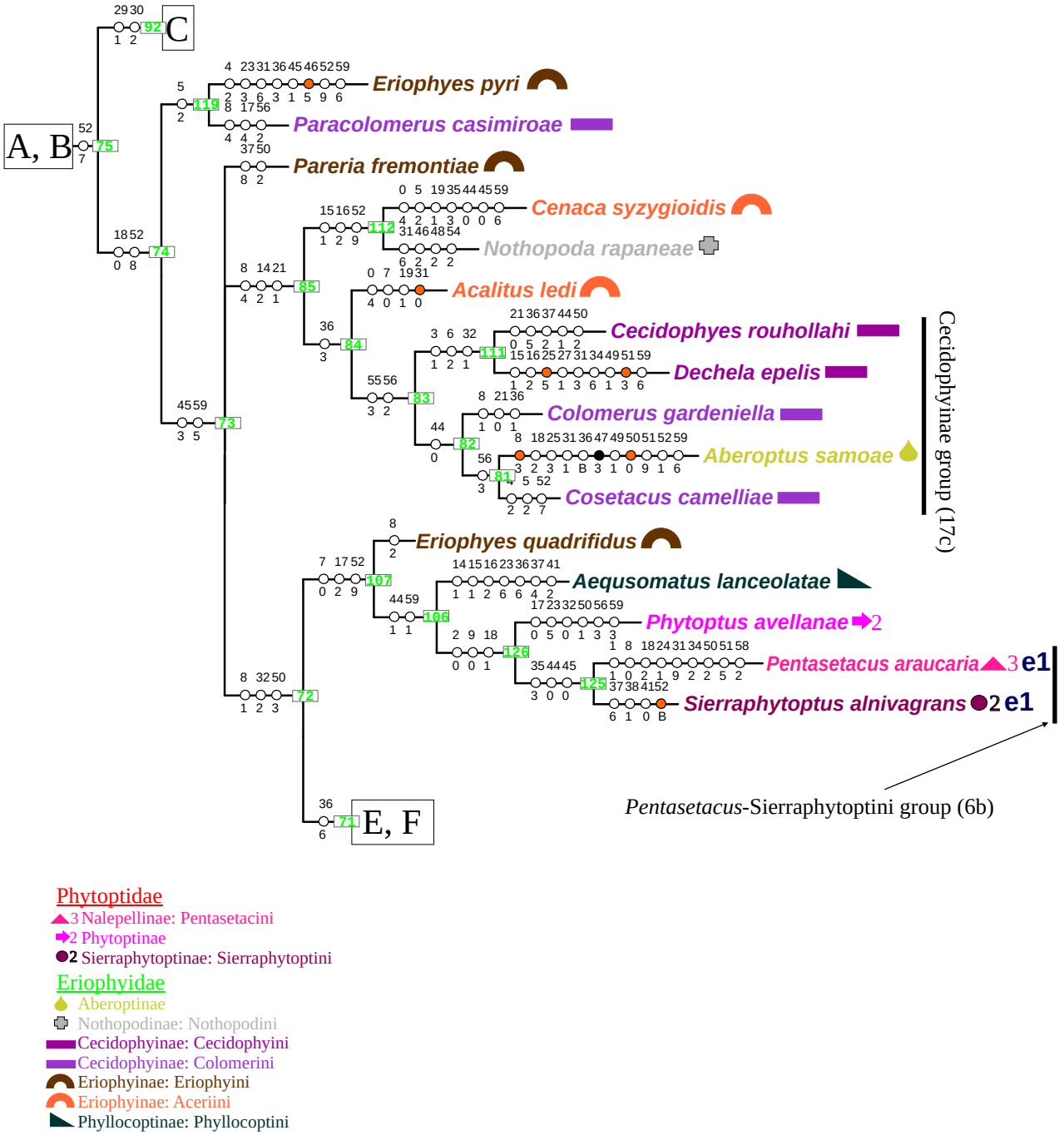


Fig. 4.45. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part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

Part D

66tax-k999
Fig. 4.46



Phytoptidae
▲3 Nalepellinae: Pentasetacini
➡2 Phytoptinae
●2 Sierraphytoptinae: Sierraphytoptini
Eriophyidae
Aberoptinae
Nothopodinae: Nothopodini
Cecidophyinae: Cecidophyini
Cecidophyinae: Colomerini
Eriophyinae: Eriophyini
Eriophyinae: Aceriini
Phyllocoptinae: Phyllocoptini

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

Part E

66tax-k999
Fig. 4.47

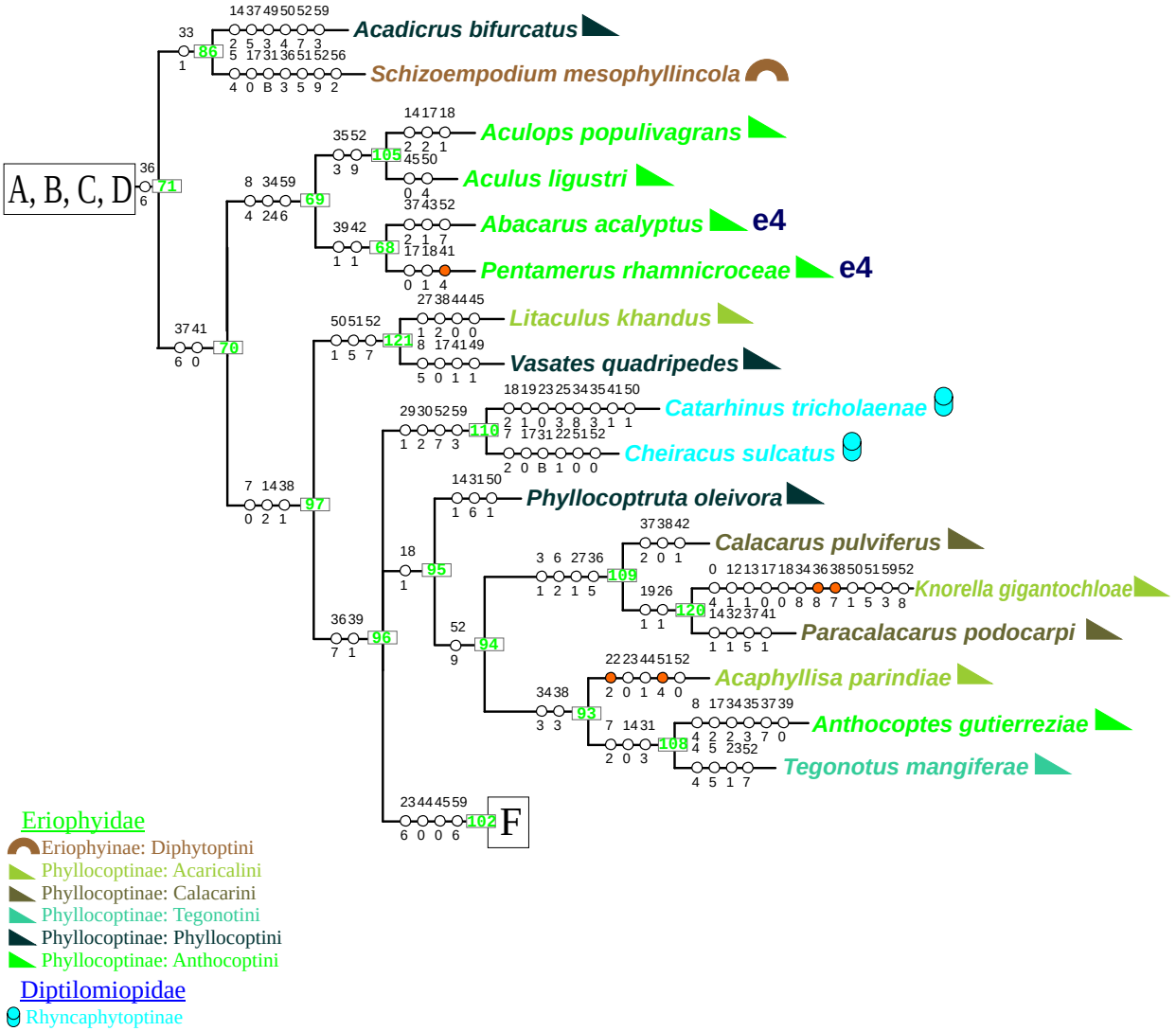
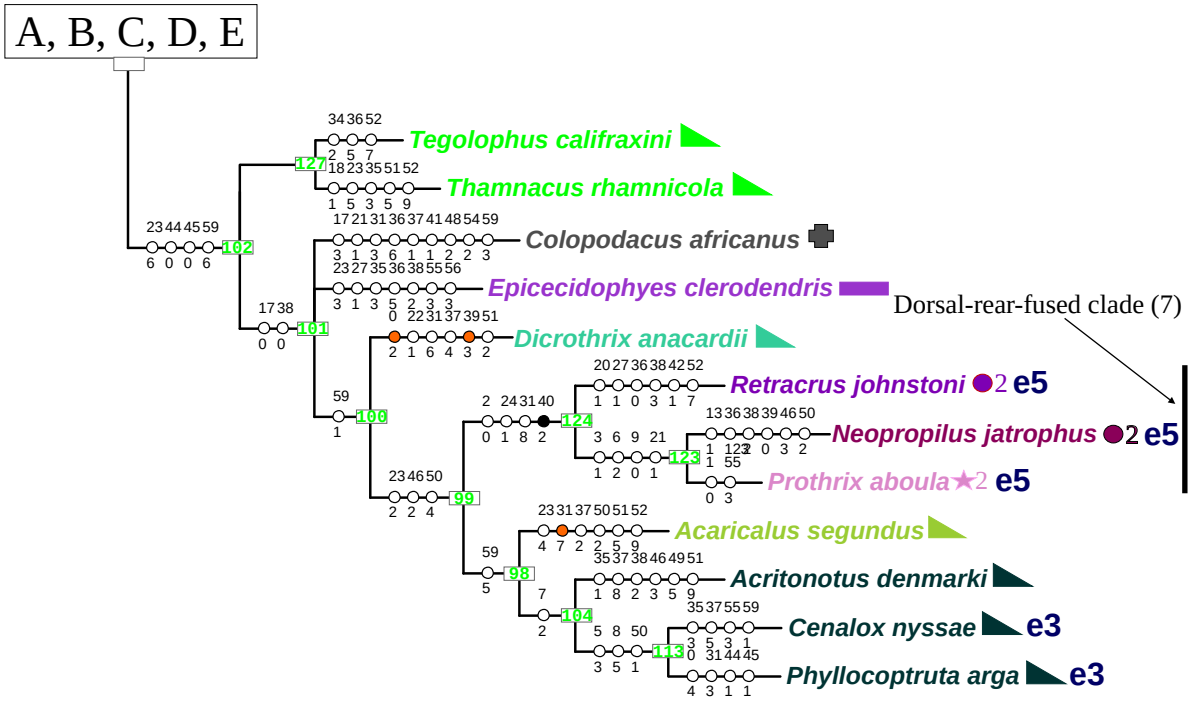


Fig. 4.47. Strict consensus of 3 most parsimonious trees found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied weighting of character with k=999, k=500, k=100, k=80, k=50 and k=40 (66tax-k999 tree, Fig. 4.43): enlarged Part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

Part F

66tax-k999
Fig. 4.48



Phytoptidae
★2 Prothricinae
●2 Sierraphytoptinae: Sierraphytoptini
●2 Sierraphytoptinae: Mackiellini

Eriophyidae
Nothopodinae: Colopodacini
Cecidophyinae: Colomerini
Phyllocoptinae: Acaricalini
Phyllocoptinae: Tegonotini
Phyllocoptinae: Phyllocoptini
Phyllocoptinae: Anthocoptini

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

66tax-k999
Fig. 4.49

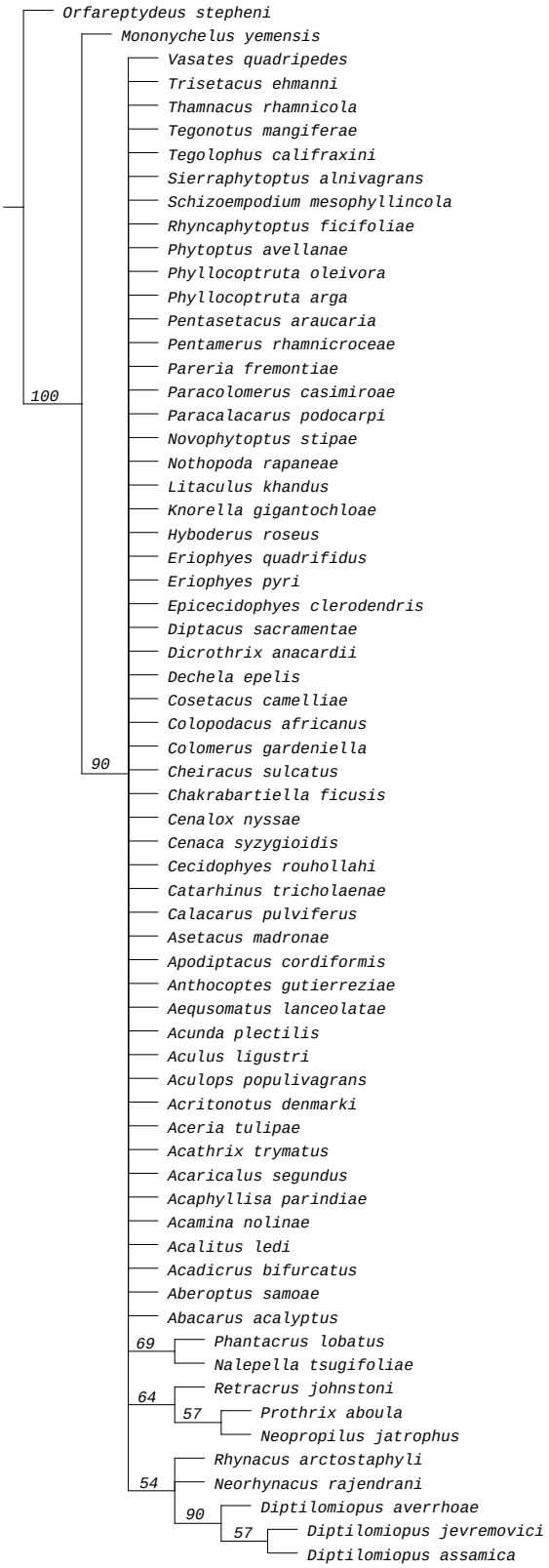


Figure 4.49. Symmetric resample absolute group frequency (GF) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic (”traditional” in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 50. Values are given above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

66tax-k999
Fig. 4.50

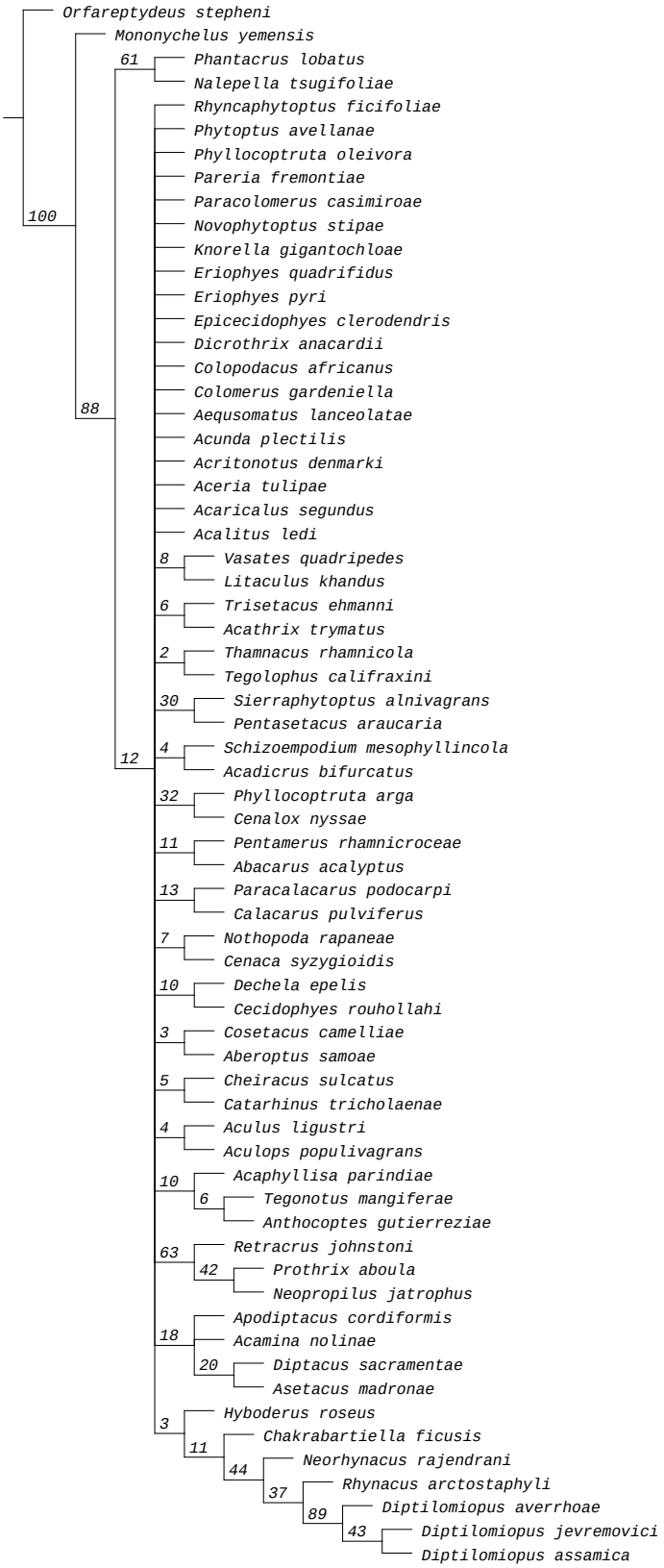


Figure 4.50. Symmetric resample group frequency difference (GC) values of symmetric resampling (P=33) of the 66 taxon x 60 character data matrix done in TNT with heuristic (”traditional” in TNT) searches under implied character weighting with k=999, with 1000 replicates, cut at 1. Only values of 20 or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

66tax-k30
Fig. 4.51

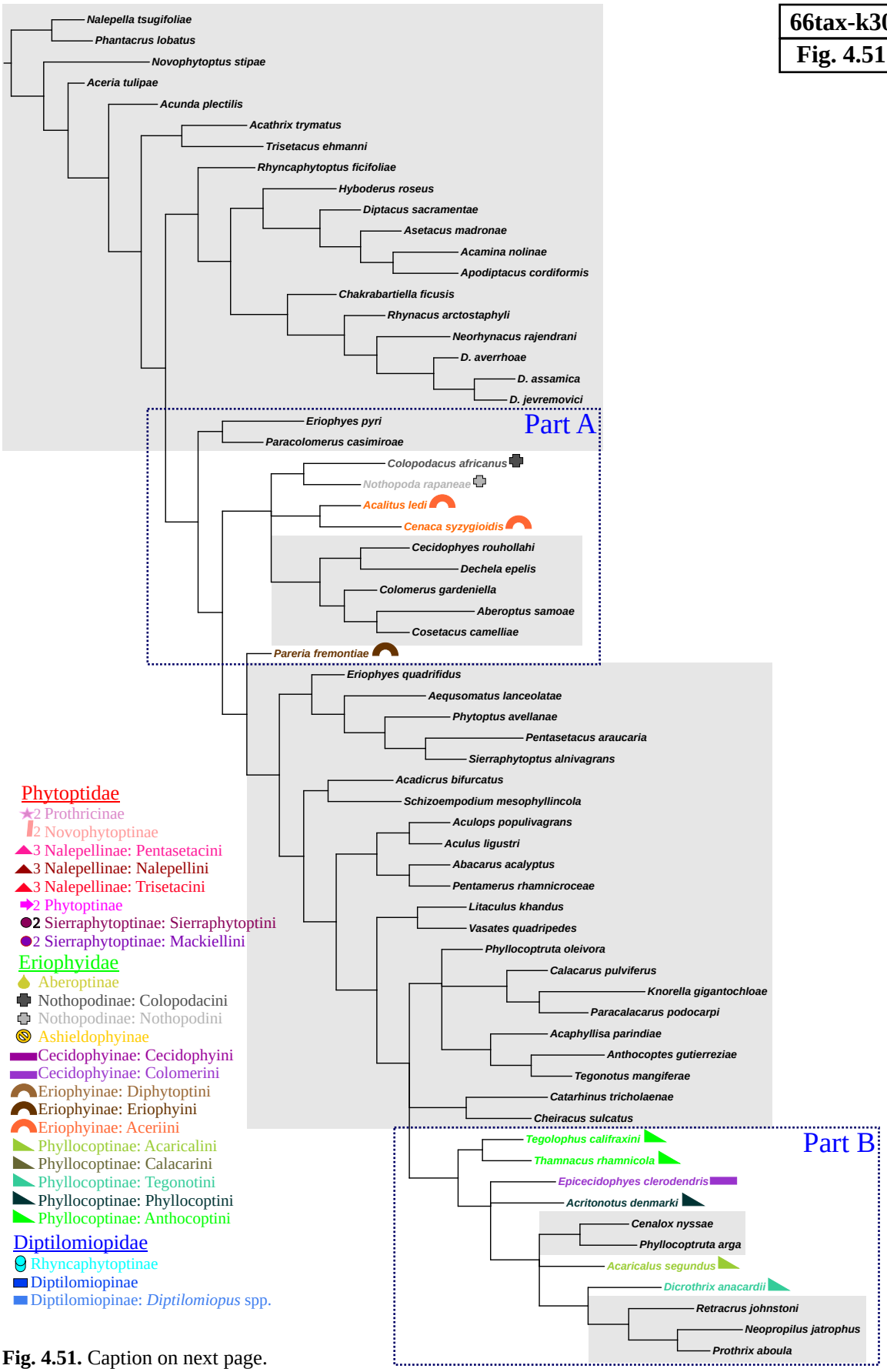


Fig. 4.51. Caption on next page.

Part A

66tax-k30
Fig. 4.52

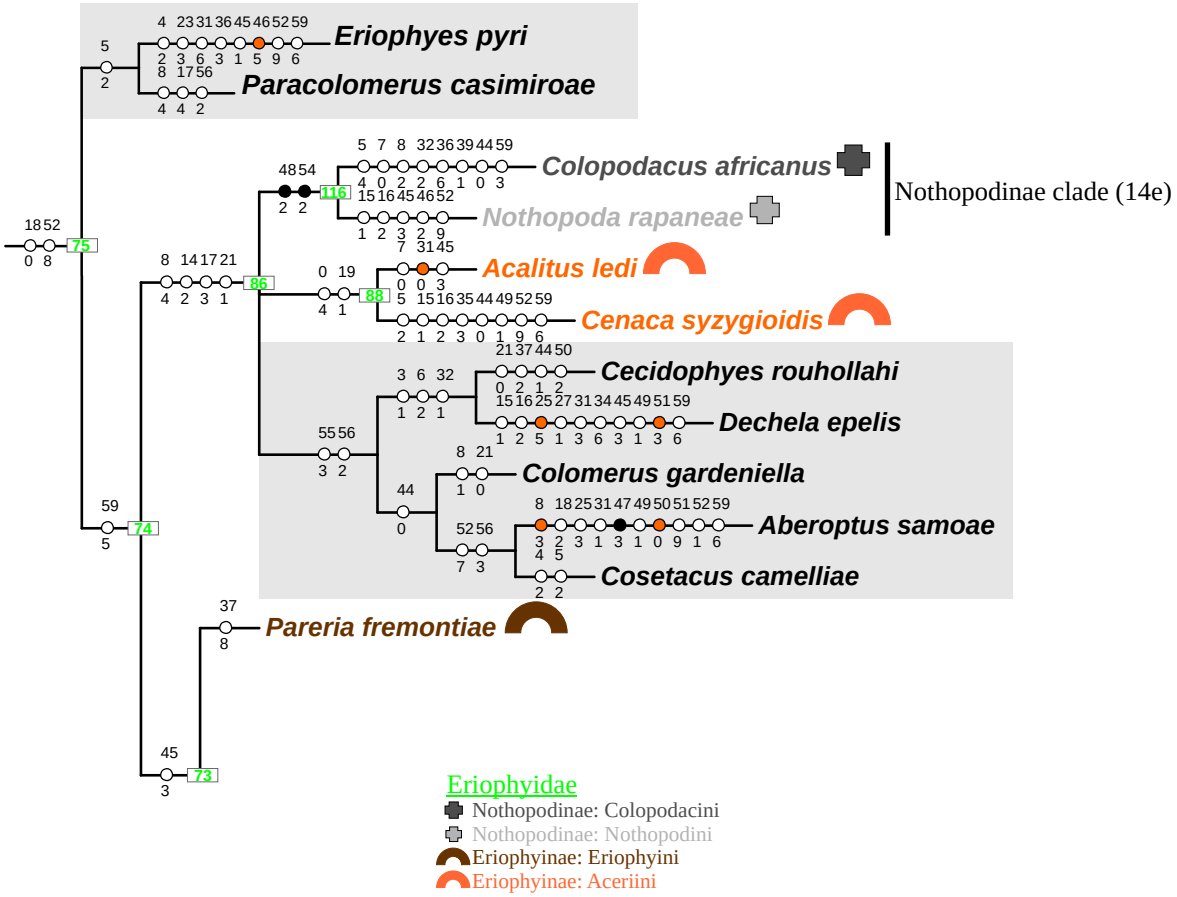


Fig. 4.51. (previous page) One most parsimonious tree (Total fit = 74.68; Adjusted homoplasy = 11.32; Total length = 651; CI = 0.290; RI = 0.497) found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT, with the best score hit 2 times out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

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

Part B

66tax-k30
Fig. 4.53

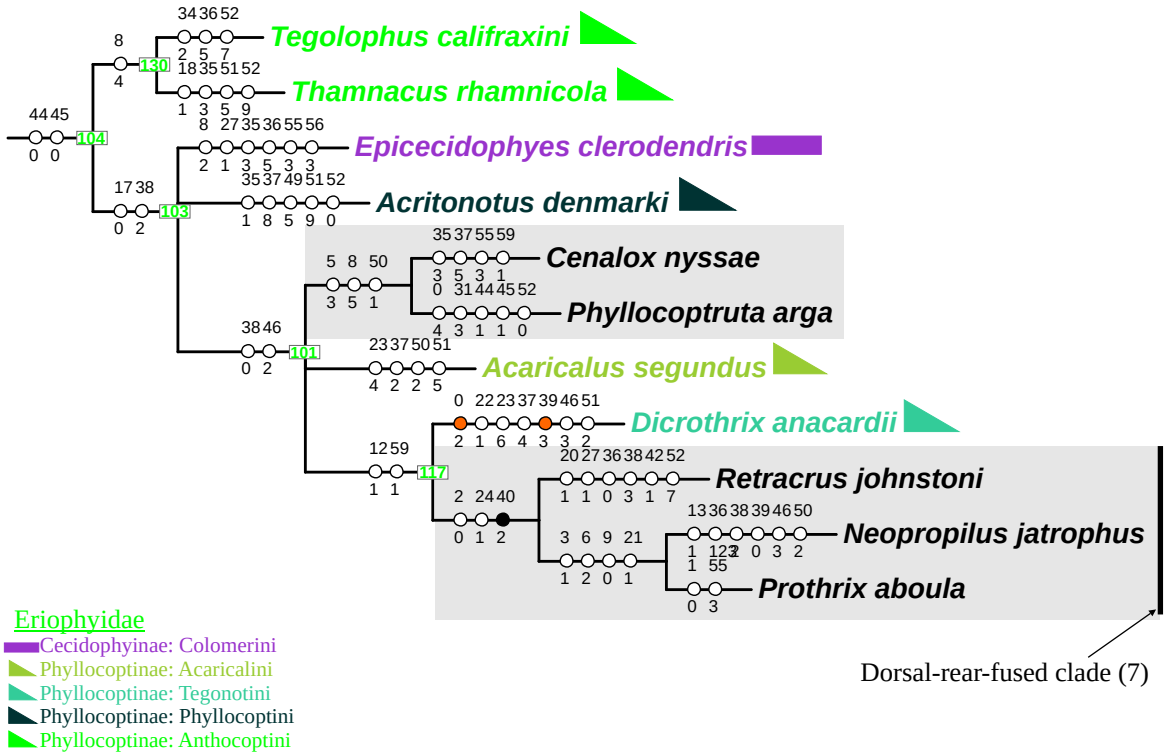


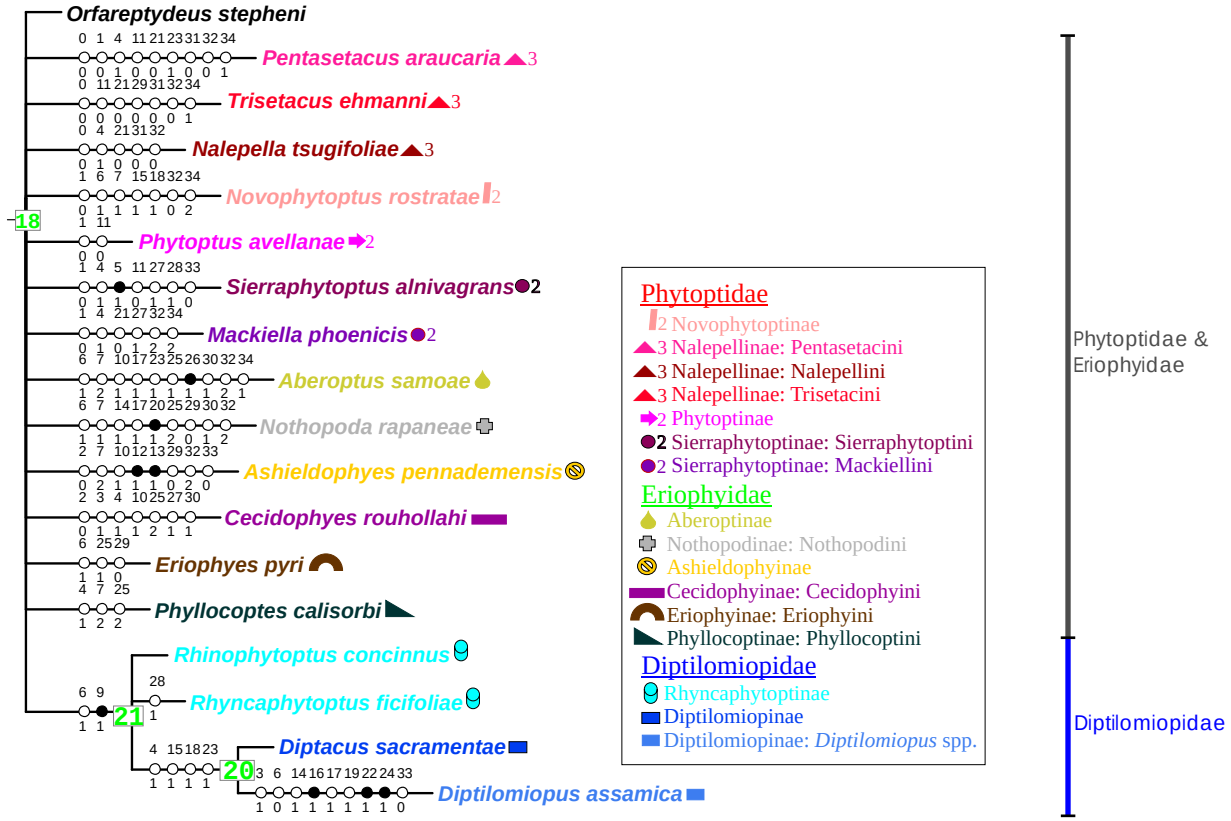
Fig. 4.53. (this page). One most parsimonious tree found with heuristic parsimony analysis of the 66 taxon x 60 character data matrix, using "traditional searches" in TNT under implied character weighting with k=30 (66tax-k30 tree, Fig. 4.51): enlarged Part B. Unsupported nodes were collapsed. The parts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

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

66tax-k20
Fig. 4.54

Fig. 4.54. Caption on previous page.

18correctEq
Fig. 4.55a



18correct-k999
Fig. 4.55b

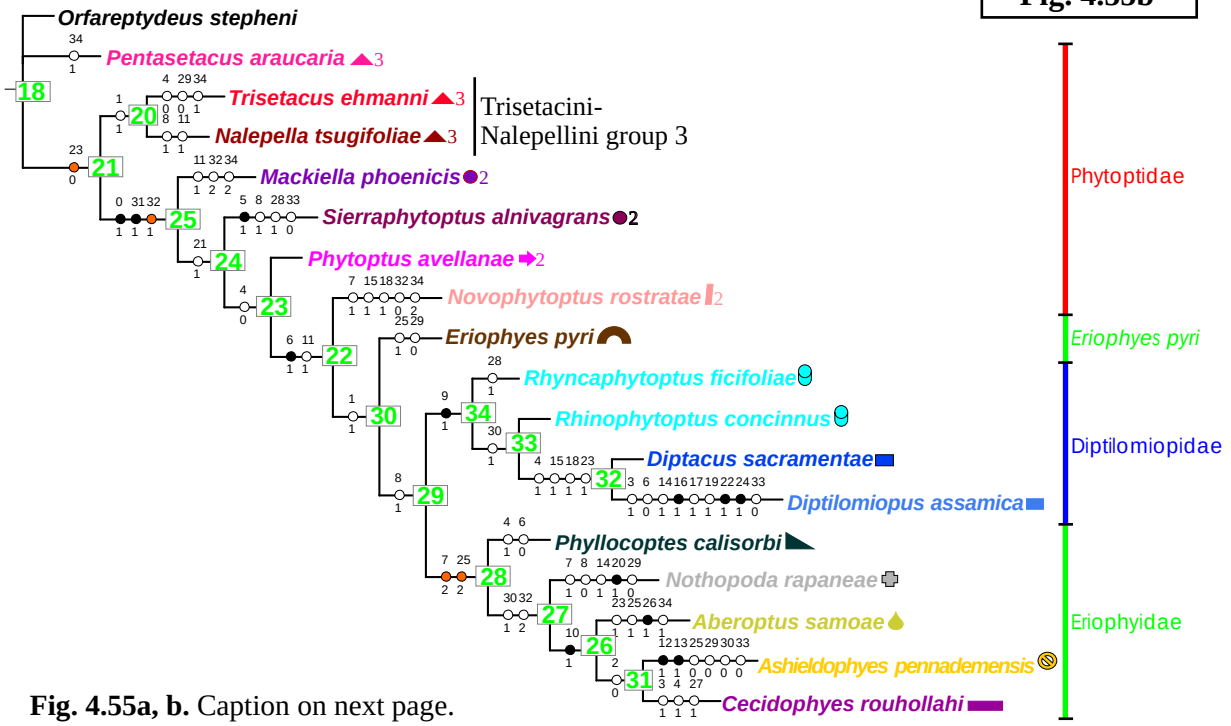
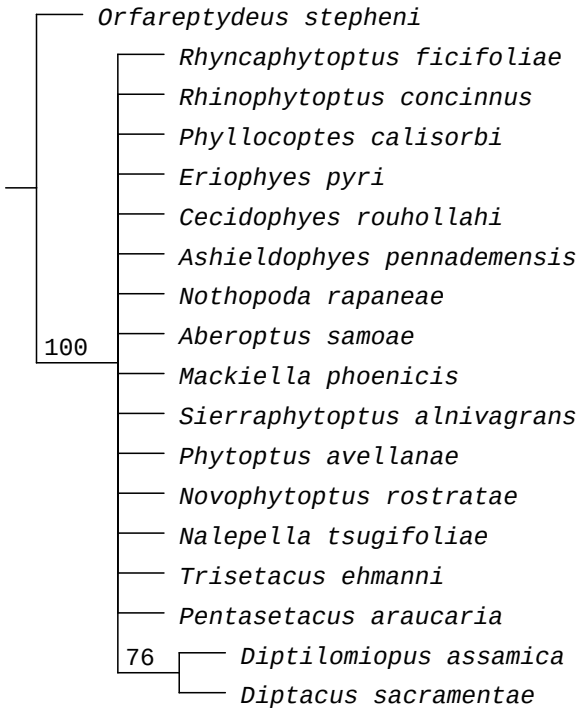


Fig. 4.55a, b. Caption on next page.

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

a



b

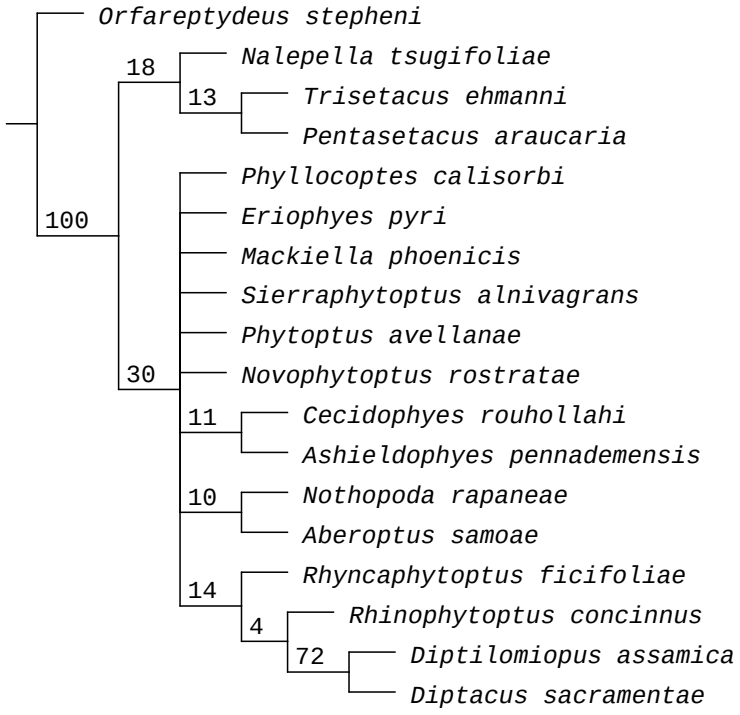


Fig.4.56. Symmetric resampling (P=33) with heuristic (”traditional” in TNT) searches of corrected Hong & Zhang (1996a) data set, 5000 replicates, done under implied weighting of characters with k=999 in TNT: **a)** group frequencies given above branches, branches with group frequency values of less than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

18correct-k3
Fig. 4.57

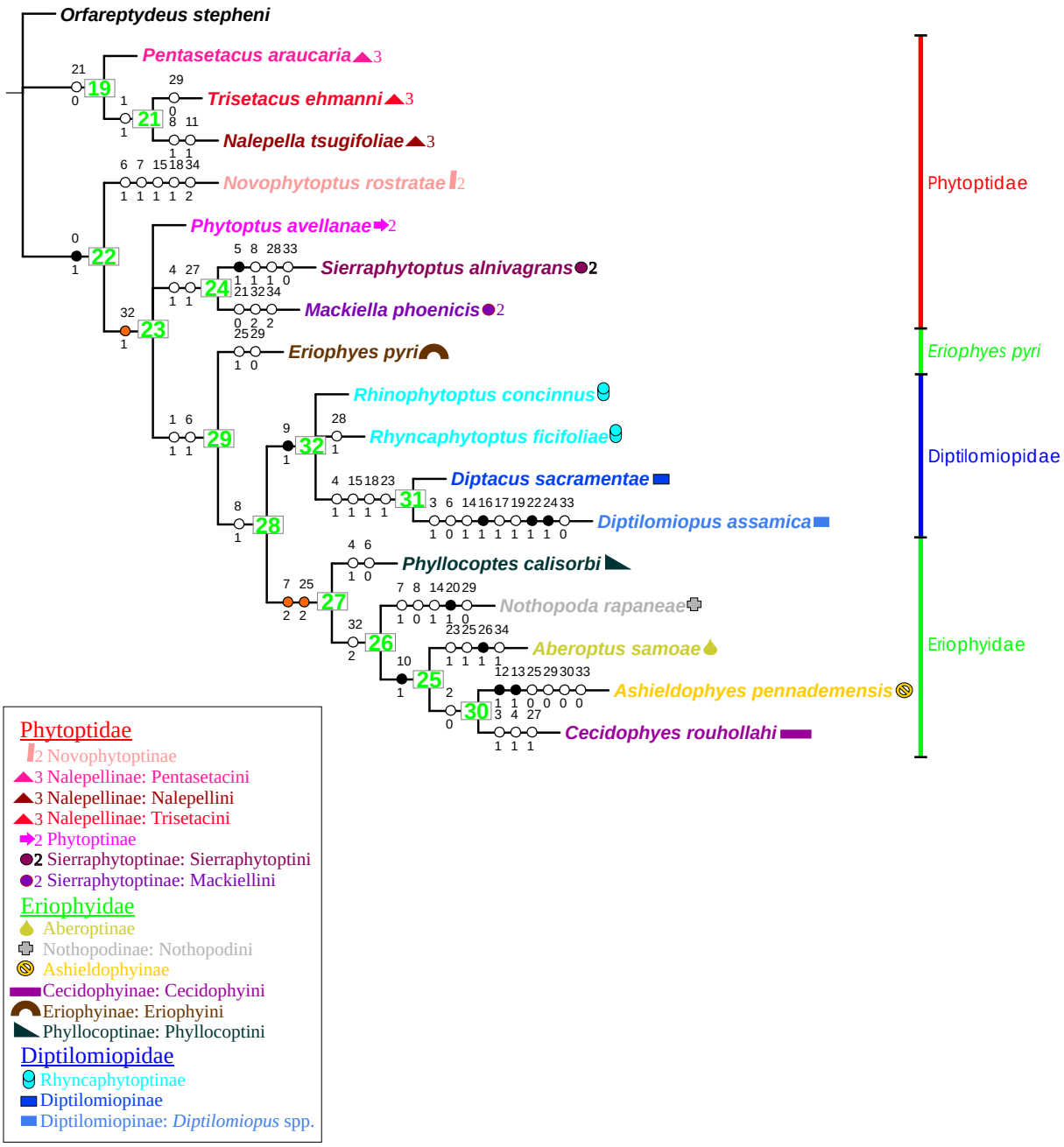


Fig. 4.57. Corrected data of Hong & Zhang (1996a) using characters and character states as defined by Hong & Zhang (1996a). Strict consensus (L=87, ci=0.448, ri=0.461) of 2 trees (each L=86, ci=0.453, ri=0.472), analysed with implicit enumeration in TNT under implied weighting of characters with k=3.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

18modifyEq
Fig. 4.58

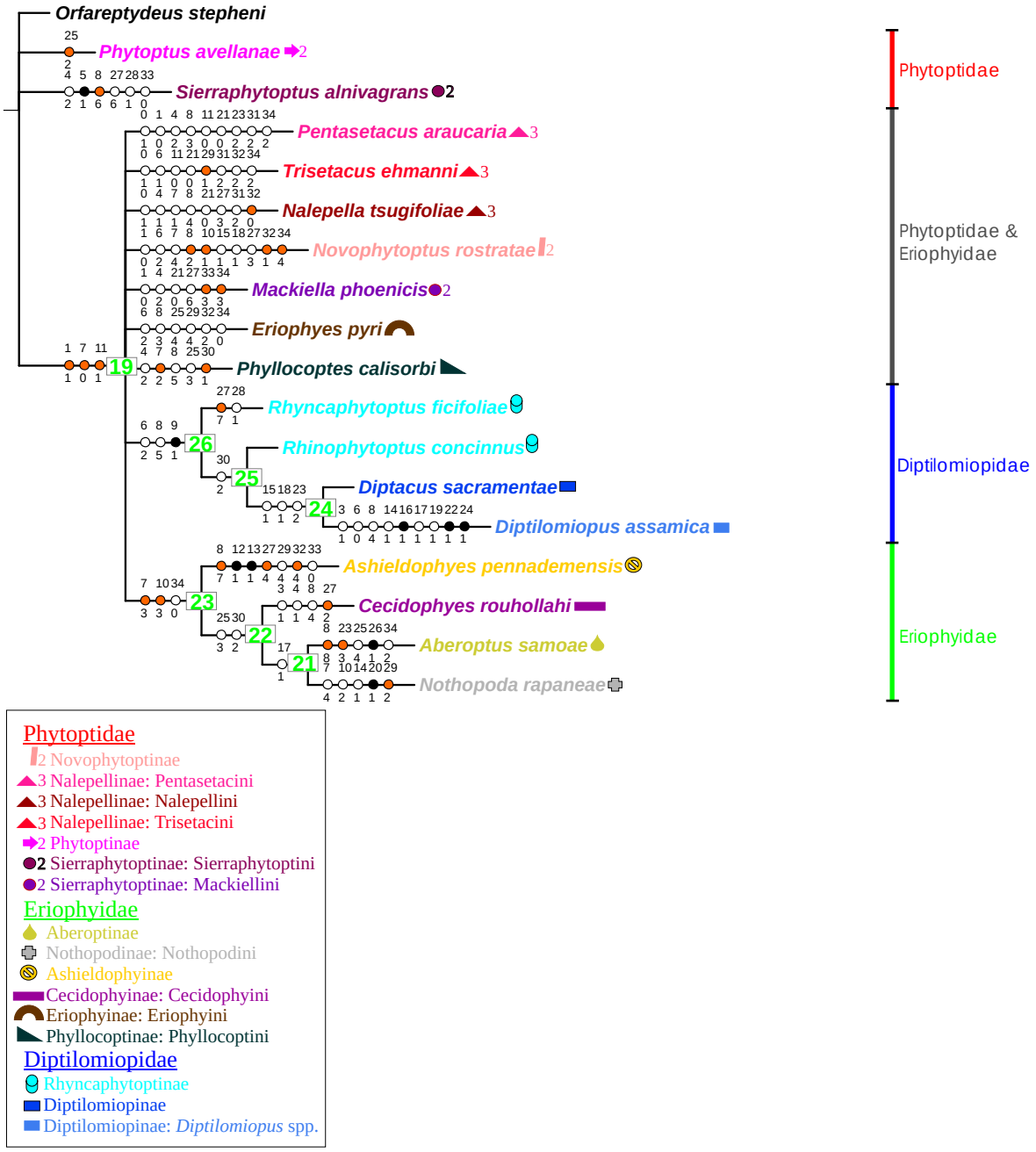


Fig. 4.58. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. I.) Strict consensus (L=132, ci=0.576, ri=0.309) of 10 trees (each L=117, ci=0.650, ri=0.494), analysed under equal weighting; II.) strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494) (a subcollection of 10 trees obtained under equal weighting). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, the blue bars and text = Diptilomiopidae, and the gray bar and text = a mixture of species of the Phytoptidae and Eriophyidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

18modify-k999
Fig. 4.59

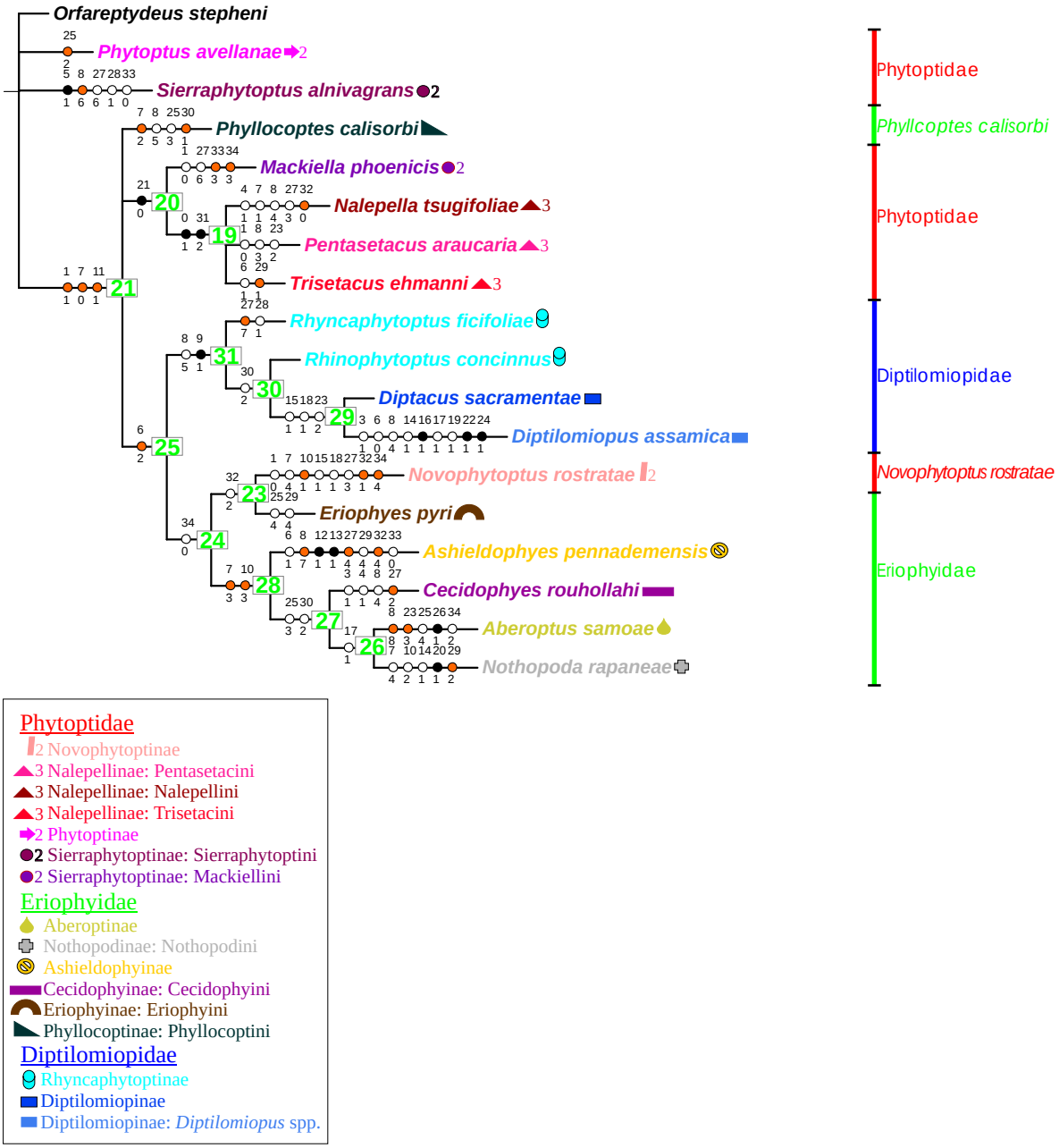


Fig. 4.59. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. Strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494), under implied weighting, k=100). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

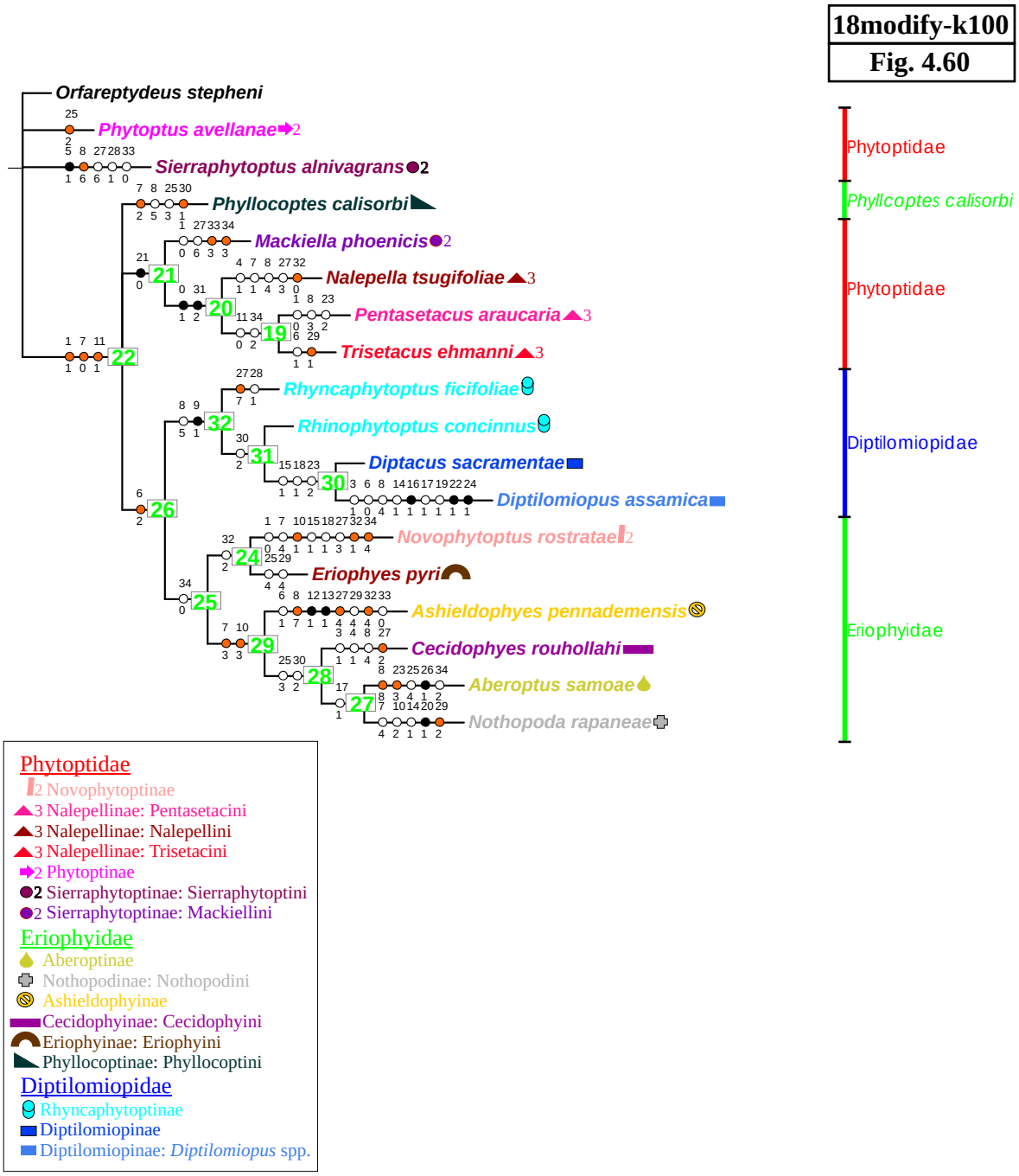


Fig. 4.60. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. Strict consensus (L=118, ci=0.644, ri=0.481) of 3 trees (each L=117, ci=0.650, ri=0.494), under implied weighting, k=100). Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have “polarity” or “order” and can rotate around the node.

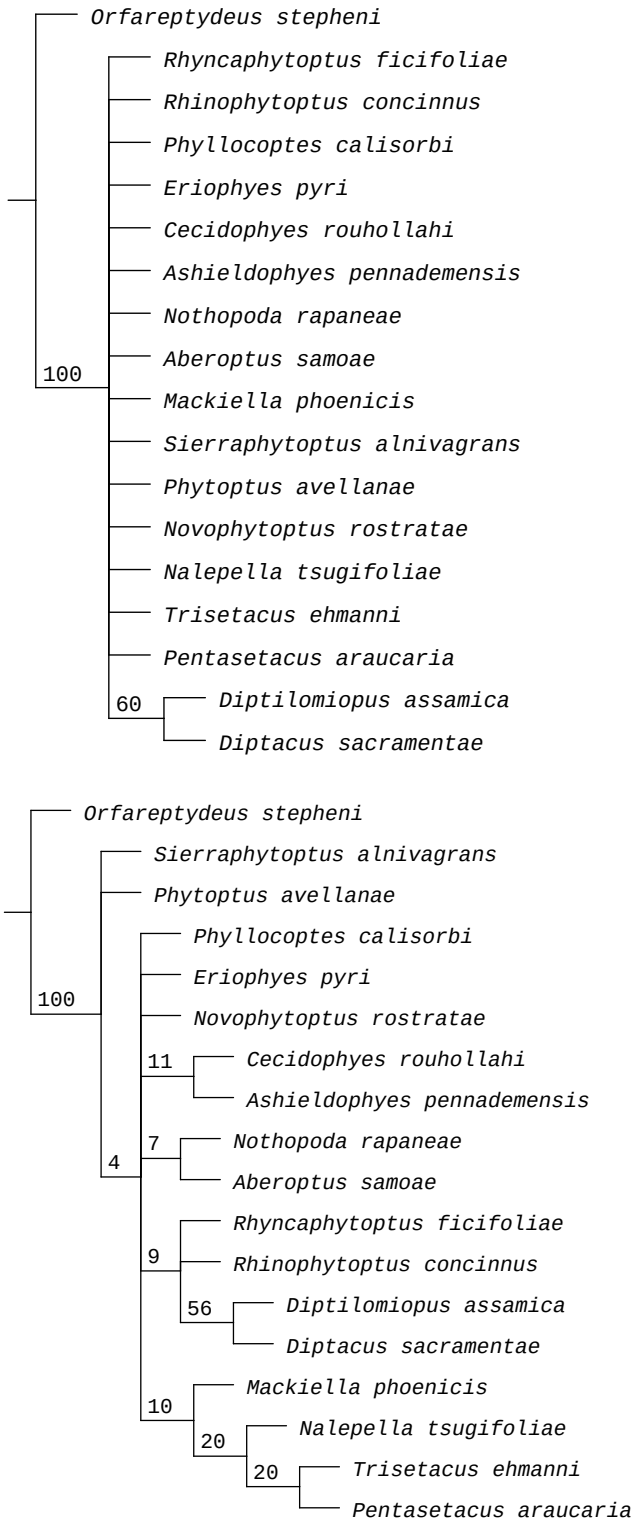


Fig.4.61. Symmetric resampling (P=33) with heuristic (”traditional” in TNT) searches of corrected Hong & Zhang (1996a) data set, with modified character states (this study), 5000 replicates, done under implied weighting of characters with k=100 in TNT: **a)** group frequencies given above branches, branches with group frequency values of less than 50 are collapsed, average group support of 10; **b)** frequency differences (GC values) given above branches, branches with group frequency values of less than 1 are collapsed, average group support of 15.

18modify-k3
Fig. 4.62

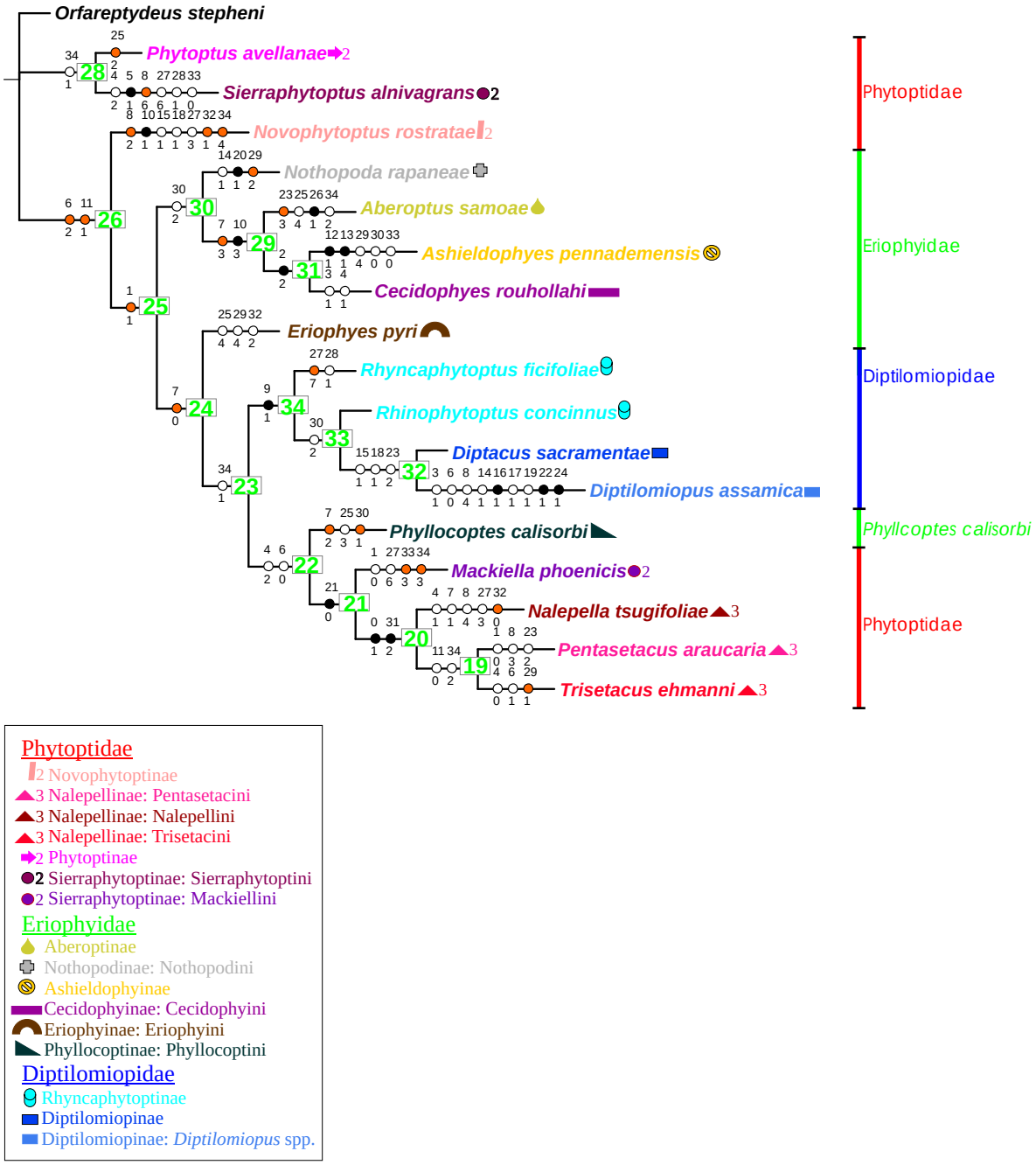


Fig. 4.62. Corrected data of Hong & Zhang (1996a) using characters and character states similar to the present analyses. One tree (L=118, ci=0.644, ri=0.481) resulted from implicit enumeration search in TNT under implied weighting, k=3. Data analysed with implicit enumeration in TNT under equal character weights. Uninformative characters included, white circles homoplasy, black circles characters without any homoplasy, orange circles character state not interrupted (state not homoplasious). Unsupported nodes collapsed. Character numbers above, and character states below branches. Tree search in TNT, tree plotted with Winclada. The bars on the right hand side of the tree indicate families and other taxa. The red bars and text = Phytoptidae, the green bars and text = Eriophyidae, and the blue bars and text = Diptilomiopidae. Although the bars indicates subdivisions of families, and largely relationships between them, it doesn't always indicate the order in which the groups occur in the tree, because groups or taxa at one node, or groups in a polytomy do not have "polarity" or "order" and can rotate around the node.

4.7 RESULTS AND DISCUSSION: APPRAISAL OF THE MONOPHYLY OF ERIOPHYOIDEA SUPRAGENERIC TAXA OF THE CLASSIFICATION *sensu* Amrine *et al.* (2003)

This section largely concerns the assessment of the monophyly of the suprageneric taxa in the Eriophyoidea, and the first formal alternative classification partly based on empirical phylogenetic studies is proposed for the superfamily.

The trees obtained in the present study are the most parsimonious or approaching the most parsimonious and defendable hypotheses for the relationships and groups within the Eriophyoidea given the data sets analyzed. The best fit for the characters was also found by using implied weighting of characters. Most groupings are solely supported by homoplasies, though, and can not be regarded as monophyletic, although many groups make biological sense, and there is a chance that they may approach natural groupings. The groups are mostly not supported by resampling statistics, and the topology of the present results may change drastically in future, particularly when the character data are improved. Despite these shortcomings, useful hypotheses were obtained, even if just for consideration in decisions made according to traditional taxonomy within the Eriophyoidea. These should be done cautiously and keeping the lack of support for the results in consideration. The results indicate that the characters currently used for eriophyoid taxonomy are highly homoplasious anyway, and incorporating probably better hypotheses from the present phylogenetic study without disrupting the classification, will be an improvement. Groups and clades found by the different analyses and presented and discussed above are incorporated in this section by their names which are in bold and underlined, followed by their chronological number in brackets if the number is not inferred by the group name.

4.7.1 PHYTOPTIDAE

The Phytoptidae is one of three Eriophyoidea families (Table 1.1), and is regarded by some (e.g., Farkas, 1968b; Shevchenko, 1971; Sukhareva, 1994) as a key group in understanding the evolution of the Eriophyoidea. It is considered the earliest derived Eriophyoidea family, because they have characteristics which are regarded to be more primitive within the superfamily, and they additionally largely live on plants which are more primitive, including early derived Gymnospermae (Shevchenko, 1962; Das & Chakrabarti, 1989; Sukhareva, 1994; Lindquist & Amrine, 1996). The Phytoptidae *sensu* Keifer (1944, 1964a), Lindquist & Amrine (1996) and Amrine *et al*. (2003) are diagnosed by setae present anteriorly on the prodorsal shield: single or paired *vi* and/or *ve*. Shevchenko (1971, 1974a) did not regard the Phytoptidae *sensu* Amrine *et al*. (2003) as a monophyletic group. He divided this group of species into two of three superfamilies within the Tetrapodili which is the same taxon group

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as the Eriophyidae *sensu* Nalepa (1929), and Eriophyoidea *sensu* Keifer (1964a), but at the suborder level. These superfamilies were: Trisetoidea (single *vi* present) which are the same grouping as Nalepellinae *sensu* Newkirk & Keifer (1971), and Phytoptoidea (single *vi* absent, *ve* present) which are the same grouping as Phytoptinae + Novophytoptinae + Sierraphytoptinae, taxa *sensu* Amrine & Stasny (1994). Shevchenko (1976) changed the two superfamilies, Trisetoidea and Phytoptoidea, to family level (Nalepellidae and Phytoptidae *sensu* Shevchenko, 1976), the same as in the classification presented by Boczek *et al.* (1989), but stressed that he still regards them as two separate, natural lineages. Shevchenko (in Boczek *et al.*, 1989) proposed a family rank taxon, Pentasetacidae (same group as Pentasetacini *sensu* Amrine & Stasny, 1994) for *Pentasetacus* Schliesske, 1985 (single *vi*, *ve* and *sc* present).

Species of all 21 Phytoptidae genera (Amrine *et al.*, 2003) were included in the present study. The Phytoptidae was never recovered as a clade, or as an exclusive group at one node, by any of the cladistic analyses under various parameters, and is proposed to be polyphyletic and partly paraphyletic [see for example the 318tax-k10 (Fig. 4.6) and –k20 (Fig. 4.26) trees]. These results do not support the classification presented in Amrine *et al*. (2003), but is more in accordance with the classification proposed by Boczek *et al.* (1989), although not entirely. The results also support the proposal that the Phytoptidae is not monophyletic by, among others, Lindquist (1996b) and Lindquist & Amrine (1996). They came to this conclusion because they regarded the diagnostic characters of the Phytoptidae as plesiomorphic character states within the Eriophyoidea, *a priori* phylogenetic analyses. This argumentation leads to the conclusion that the family is paraphyletic, which is also partly supported by the present study, since some Phytoptidae groups were recovered imbedded among the Eriophyidae.

Although the Phytoptidae was not retrieved as a monophyletic group in its entirety, it seems that classifying Phytoptidae subgroups as taxa largely exclusively with Phytoptidae species, is well-supported by the present results. Phytoptidae species were recovered in several relatively robust groups and clades under all parameters, and these groups, mostly, did not include Eriophyidae and never Diptilomiopidae species.

The Phytoptidae have five subfamilies (Amrine *et al*., 2003; Table 1.1), and the appraisal of their monophyly is as follows.

Prothricinae

This Phytoptidae *sensu* Amrine *et al*. (2003) subfamily is proposed to be a junior synonym of the Propilinae (new subfamily, Table 4.10), which is proposed to be a subfamily of the Phytoptidae *sensu* the present study (Table 4.10). See earlier discussion of the position of *Prothrix*. In his unpublished study (R. Ochoa, *pers. comm.*) *Prothrix* was also recovered in an exclusive group consisting of Sierraphytoptinae taxa, supporting the present proposal to include *Prothrix* in a subfamily of the Phytoptidae *sensu* the present study (Table 4.10).

Novophytoptinae

This subfamily comprises *Novophytoptus* spp., which have genitalia positioned much further away from the coxisternal area than usually found in the Eriophyoidea (Fig. 3.5g) (Roivainen, 1953: 85–86). Two of the six *Novophytoptus* spp. (Amrine *et al.*, 2003; Chetverikov & Sukhareva, 2007) were included in the 318tax data set, and were found to be sisters [***Novophytoptus* group (12a)**] under equal character weights, and the Novophytoptinae (or indeed the genus *Novophytoptus*) may be monophyletic. This supports the proposal by Lindquist & Amrine (1996) that the Novophytoptinae may be a clade, supported by one synapomorphy, the position of the genitalia. The position of the genitalia (Character 112, Appendices B & C), including the state "about 9-15 annuli removed from coxae, located posterior to c2" was always found to be homoplastic in the present study, though. When more phylogenetic phylogenetic resolution was found with implied weighting, the *Novophytoptus* spp. were found to be paraphyletic, and were recovered as sisters of some Phyllocoptinae species [***Novophytoptus-Tetra* group (12b)**], and when only one *Novophytoptus* sp. was included in a data set, it was sometimes recovered as sister of *Eriophyes* (Eriophyinae) [***Novophytoptus-Eriophyes* group (12c)**], but these relationships are weakly supported. The relationships of *Novophytoptus* spp. with each other and other Eriophyoidea taxa have not been resolved conclusively by the present study and are uncertain. It seems, though, that *Novophytoptus* probably have a closer relationship with some Eriophyidae than with Phytoptidae taxa. The subfamily is therefore assigned to the Eriophyidae (**comb. nov.**).

In Boczek *et al.* (1989) the Novophytoptinae is a subfamily of their more restricted Phytoptidae (which excludes species with single *vi* present), and not a subfamily on the same level with other subfamilies of the Phytoptidae *sensu* Keifer (1964a) which include subfamilies with single *vi* present. Boczek *et al.* (1989) thus implied the loss of single *vi* in *Novophytoptus* is earlier derived than the position of the genitalia. Neither of these classifications was supported by the present results, because the *Novophytoptus* spp. were not recovered in close relationships with other Phytoptidae species.

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Table 4.10. A proposed new classification of suprageneric and genera of the Eriophyoidea, partly based on the phylogeny recovered in the present study. A priority was the preservation of the stability of the classification *sensu* Amrine *et al.* (2003), but with changes based on groups found with phylogenetic analyses in the present study, and which are proposed to render the classification more natural. Drastic changes, particularly to nomenclature and practicality (for classifying and identification), were regarded premature. The proposed classification is thus not entirely phylogenetic, purely based on the phylogeny found in the present study. The relationships and taxonomic positions of the genera are extrapolated from the relationships of the species (usually type species) found in the present study. This essentially assumes the monophyly of genera which is not necessarily true or implied. Where more than one species of a genus were included in the present study, they are included as separate species in the proposed classification. Many *Diptilomiopus* spp. were included in the analyses, but all remain in the Diptilomiopinae, and only the genus name is used.). The genera within a suprageneric taxon are listed alphabetically, and the order in which they are listed does not imply relationships. "*Comb. nov*." refers to the new position of the genus and not to a recombination of the species with another genus. Species and their genera not included in the present study, are not dealt with, and remain classified according to Amrine *et al.* (2003). The classificatory structure and position of the Phyllocoptinae and placement of its genera remain as presented in Amrine *et al*. (2003). Despite the inclusion of their presumably deutogyne females in the present phylogenetic study, *Aceria kenyae* (= *Cisaberoptus kenyae*) and *A. pretoriensis* (= *C. pretoriensis*) are not included in the classification proposed here, and they remain within *Aceria* (Eriophyidae: Eriophyinae) as proposed by Amrine *et al*. (2003).

Superfamily: Eriophyoidea Nalepa, 1898

Family: Nalepellidae Roivainen, 1953
= Nalepellinae Roivainen, 1953
= Trisetacini Farkas, 1968
= Nalepellini Roivainen, 1953

Boczekella **comb. nov.**
Nalepella
Pentaporca
Phantacrus
Setoptus **comb. nov.**
Trisetacus ehmanni **comb. nov.**
T. pini **comb. nov.**

Family: Pentasetacidae Shevchenko, 1989 (*in* Boczek, Shevchenko & Davis, 1989)
= Pentasetacini Shevchenko, 1989 *sensu* Amrine *et al.* (2003)

Pentasetacus

Family: Phytoptidae Murray, 1877
Subfamily: Phytoptinae Murray, 1877
= Sierraphytoptinae Keifer, 1944
= Phytoptini (= Sierraphytoptini Keifer, 1944)
= Mackiellini Newkirk & Keifer, 1971
Acathrix
Austracus
Fragariocoptes
Mackiella
Oziella
Phytoptus (= *Anchiphytoptus*) genus synonymy by Chetverikov *et al*. (2009)
Sierraphytoptus

Subfamily: Propilinae Keifer, 1975 **(new subfamily)**
Type genus/species: *Propilus gentyi* Keifer, 1975
= Prothricinae Amrine, 1996 **syn. nov.**

Diagnosis.
The fusion of dorsal annuli caudad *f*, is the synapomorphy supporting this subfamily, and distinguishing it from other Eriophyoidea. The body is fusiform, flattened dorsoventrally, with annuli differentiated into relatively narrow ventral annuli with microtubercles and fewer, broader dorsal annuli, without microtubercles, and when annuli are subequal dorsoventrally, the annuli are slightly broader than usually found in vermiform species, and the ventral annuli are without microtubercles. The prodorsal shield with a roughly similar shape in all species is broadly rounded or square, and anteriorly in lateral view characteristically dorsally elevated before the gnathosoma. Frontal lobe is present. Seta *ve* present, positioned anteriorly on the vertical prodorsum anterior edge, almost on the lateral angle of the broad prodorsal shield, and is projected anteriad. Single *vi* is absent. Seta *sc* as well as the scapular tubercle are present or absent. When present, *sc* may be positioned far forward, directed anteriad (e.g., *Prothrix*), or closer to the rear shield margin, and directed posteriad (e.g., *Retracrus*). Some species with wax. All species for which host plants were recorded, were collected from palms (Arecaceae).

Neopropilus Huang, 1992 **comb. nov.**
Propilus Keifer, 1975 **comb. nov.**
Retracrus Keifer, 1965 **comb. nov.**
Prothrix Keifer, 1965 **comb. nov.**

Family: Eriophyidae Nalepa, 1898
Subfamily: Novophytoptinae Roivainen, 1953 **comb. nov.**
Novophytoptus rostratae **comb. nov.**
Nov. stipae **comb. nov.**

Subfamily: Aberoptinae Keifer, 1966
Aberoptus

Subfamily: Nothopodinae Keifer, 1956
= Colopodacini Mohanasundaram, 1984
= Nothopodini Keifer, 1956
Adenocolus
Anothopoda

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Apontella
Colopodacus\
Cosella
Disella
Floracarus
Neocosella
Nothopoda
Pangacarus

Subfamily: Ashieldophyinae Mohanasundaram, 1984
Ashieldophyes

Subfamily: Cecidophyinae Keifer, 1966
Tribe: Cecidophyini Keifer, 1966
Achaetocoptes
Bariella
Cecidophyes
Chrecidus
Coptophylla
Epicecidophyes **comb. nov.**
Glyptacus
Johnella
Neocecidophyes **comb. nov.**

Tribe: Colomerini Newkirk & Keifer, 1975
Afromerus
Circaces
Colomerus
Cosetacus
Ectomerus
Gammaphytoptus
Indosetacus

Subfamily: Eriophyinae Nalepa, 1898
= Diphytoptini Amrine & Stasny, 1994
= Eriophyini Nalepa, 1898
= Aceriini Amrine & Stasny, 1994
Acalitus
Aceria
Acerimina
Acunda
Asetilobus
Baileyna
Brachendus
Cenaca
Cercodes
Cymoptus
Dechela **comb. nov.**
Diphytoptus
Eriophyes pyri
E. quadrifidus
Keiferophyes
Nacerimina

Neserella **comb. nov.**
Notaceria
Palmiphytoptus **comb. nov.**
Paracolomerus **comb. nov.**
Paraphytoptella
Pareria
Proartacris
Ramaculus
Schizoempodium
Scoletoptus
Stenacis
Trimeracarus

Subfamily: Phyllocoptinae Nalepa, 1892
Classificatory structure remains as in Amrine *et al.* (2003)

Family: Diptilomiopidae Keifer, 1944
Subfamily: Diptilomiopinae Keifer, 1944
Acarhis diospyrosis
Acarhi. lepisanthis
Acarhi. siamensis
Africus
Dacundiopus
Davisella
Diptilomiopus
Diptilorhynacus dioscoreae
Diptilor. sinusetus
Diptilostatus
Kaella
Lambella
Levonga caseariasis
Le. litseae
Le. papaitongensis
Lithocarus
Mediugum
Neoacarhis
Neodiptilomiopus
Neolambella
Neorhynacus
Norma
Prodiptilomiopus
Rhynacus
Sakthirhynchus **comb. nov.**
Suthamus
Thailandus
Vimola

Subfamily: Rhyncaphytoptinae Roivainen, 1953
Acarhynchus **comb. nov.**
Apodiptacus **comb. nov.**
Areekulus
Asetacus
Asetadiptacus **comb. nov.**

Brevulacus
Bucculacus **comb. nov.**
Catarhinus
Chakrabartiella
Cheiracus
Chiangmaia **comb. nov.**
Dialox **comb. nov.**
Diptacus pandanus **comb. nov.**
Dipta. sacramentae **comb. nov.**
Diptiloplatus **comb. nov.**
Duabangus **comb. nov.**
Hoderus
Hyborhinus
Konola
Neocatarhinus
Neodialox **comb. nov.**
Pararhynacus **comb. nov.**
Peralox
Quadracus mangiferae
Quadra. urticarius
Quadriporca indicae
Quadri. mangiferae
Rhinophytoptus
Rhinotergum
Rhyncaphytoptus
Stenarhynchus
Steopa **comb. nov.**
Trimeroptes **comb. nov.**

Phytoptinae and Sierraphytoptinae

These are the two main Phytoptidae subfamilies with species with single *vi* absent, *ve* present, and the spermathecal tube moderately short. Seta *c1* is present in the Phytoptinae and present or absent in the Sierraphytoptinae (Keifer, 1944; Roivainen, 1953; Keifer, 1956, 1964a). Body shape differentiates the two subfamilies: Phytoptinae have a vermiform body shape with annuli subequal, and Sierraphytoptinae a fusiform body shape with dorsal annuli longer (Fig. 3.2b) than ventral annuli (Keifer, 1944). The Sierraphytoptinae have two tribes: the Sierraphytoptini (*c1* present) (Keifer, 1944; Roivainen, 1953; Keifer, 1956, 1964a; Channabasavanna, 1966; Newkirk & Keifer, 1971), and Mackiellini (*c1* absent) (Channabasavanna, 1966; Newkirk & Keifer, 1971).

Species of the Prothricinae (*Prothrix*), Sierraphytoptini (*Neopropilus*) and Mackiellini (*Propilus* and *Retracrus*) were recovered as a clade [**Dorsal-rear-fused clade (7)**] supported by one synapomorphy: fusion of rear dorsal annuli caudad *f*. This clade is proposed as a new subfamily, Propilinae, in the Phytoptidae *sensu* the present study, and the type genus and species is designated as *Propilus gentyi* Keifer, 1975 (Table 4.10). Morphologically, particularly in body shape, the species are roughly similar, and may also be defined as a new suprageneric taxon when evaluated according to conventional morphological criteria. There are, however, also differences between the genera which are conventionally regarded as being important at suprageneric and generic level, e.g., tibial solenidion, *c1*, *sc*, *l'*, *d*, and/or wax secretion is present or absent; and the shape of setal tubercles, dorsoventral differentiation in annuli, modifications such as ridges and lateral lobes, and detail in the coxigenital area, its position, and possibly shape of the internal genitalia vary between the taxa.

Under most parameters the Phytoptinae and Sierraphytoptinae as well as the two Sierraphytoptinae tribes, were found to be paraphyletic. All Phytoptinae, Sierraphytoptinae and the **Dorsal-rear-fused clade (7)**, and probably *Pentasetacus*, may constitute a clade. They were recovered as the **Phytoptinae-Sierraphytoptinae group (9)** (Fig. 4.11). When the majority of the species in this group are excluded from the smaller data sets, the **Phytoptinae-Sierraphytoptinae group (9)** is not supported in its entirety, although part of this group, the **Smaller-Phytoptinae-Sierraphytoptinae group (8)** (Fig. 4.11) is supported by the 66tax-k20 tree. In the smallest (18tax) data set, the Phytoptinae, and the Sierraphytoptinae tribes, Sierraphytoptini and Mackiellini, are each represented by one species. The two sierraphytoptine tribes particularly are again found to be paraphyletic, and were recovered as sisters [**Sierraphytoptinae group 11b**] under some parameters.

Lindquist & Amrine (1996) considered the Phytoptinae and Sierraphytoptini as monophyletic taxa problematic, because they are not supported by any synapomorphies. They regarded the Sierraphytoptinae to be supported by their fusiform body shape, which they regarded a homoplasious

apomorphy *a priori* phylogenetic analyses, and proposed that the Mackiellini may be monophyletic, supported by the homoplasious apomorphy, loss of *c1*.

In particular, the present results do not support the monophyly of the Sierraphytoptinae tribes, and they are not included in the proposed classification (Table 4.10). This partly supports the hypotheses by Lindquist & Amrine (1996), and it agrees with the classification proposed by Boczek *et al.* (1989) which did not include these tribes in their Eriophyoidea classification, implying they did not regard them to be monophyletic. Although not conclusively found by the present study, the indication that the Phytoptinae and Sierraphytoptinae may be paraphyletic was the strongest hypothesis, and the species that do not belong to the new subfamily, Propilinae, are all placed in the Phytoptinae, rendering the Sierraphytoptinae a junior synonym of this subfamily (Table 4.10). These are subfamilies of the Phytoptidae which constitutes all Phytoptidae species with single *vi* absent, but *ve* present, excluding the Novophytoptinae. The Phytoptinae is probably not a monophyletic taxon and the positions of particularly species of the Sierraphytoptinae *sensu* Amrine *et al*. (2003) are not certain. The Phytoptidae, or similar taxon, may eventually be subdivided into more clades, some of which may possibly also include Eriophyidae, and particularly the Sierraphytoptinae may be reinstated. The species is grouped in the same subfamily, though, until more conclusive results regarding the relationships between the Phytoptidae taxa *sensu* the present study, are found.

Nalepellinae

This subfamily comprises Phytoptidae species with single *vi* present anteromedially on the prodorsal shield, and with spermathecal tubes elongated. Seta *ve*, *sc* and *c1* are present or absent and the opisthosoma is vermiform with subequal annuli or fusiform with annuli differentiated dorsoventrally (Roivainen, 1953; Newkirk & Keifer, 1971; Lindquist & Amrine, 1996). The presence of single *vi* is correlated with long spermathecal tubes and with the Nalepellinae exclusively living on conifers. The Nalepellinae being a natural lineage deeply separated from other eriophyoid lineages with single *vi* absent was regarded by several eriophyoid systematists (e.g., Farkas, 1968b; Shevchenko, 1971) to be particularly important and well-supported. Lindquist & Amrine (1996) proposed the Nalepellinae might be monophyletic, and the elongated spermathecal tubes may be a synapomorphy for the subfamily.

The monophyly of the Nalepellinae is largely not supported by the present study, but the results were not conclusive. The Nalepellinae was recovered as a clade [see **Nalepellinae group and clade (5)**], when only one species of each of the three Nalepellinae tribes were included in the data set (the 18tax data set) and when character states from Hong & Zhang (1996a) were modified. This clade was supported by two synapomorphies: single *vi* present and spermathecal tubes long. When

more taxon and character data, and thus variation, were added in the larger data sets, however, the Nalepellinae species were not recovered as a monophyletic group anymore, and the latter results are more defendable.

The Nalepellinae *sensu* Amrine *et al*. (2003) comprise three tribes: Pentasetacini, Trisetacini (*c1* present), and Nalepellini (*c1* absent). Particularly the monospecific Pentasetacini was not recovered in the same clade or exclusive group with the remainder of the Nalepellinae, and will be discussed separately later on. The monophyly and relationships between the other Nalepellinae taxa are as follows.

The Nalepellinae tribes (Trisetacini and Nalepellini) were not recovered as monophyletic groups. Species from both tribes were recovered in broadly two groups. The one group comprises *Nalepella*, *Phantacrus* and *Pentaporca* of the Nalepellini [***Nalepella* groups (1)**]. Particularly when *Setoptus* (Nalepellini) was included in the data set, however, it was recovered in a group with the Trisetacini species [**Trisetacini-Nalepellini group 3a**], and when it was excluded, *Trisetacus* and the other Nalepellini species were recovered in the same group [**Trisetacini-Nalepellini groups 3b and 3c**]. The position of *Trisetacus* still remains particularly uncertain and plastic, though. Some analyses recovered it in a weakly supported sister relationship with *Acathrix* (Phytoptinae) [**Trisetacini-Phytoptinae group (4)**]. It, however, seems more likely that it has a close relationship with other Nalepellinae species [***Trisetacus* group (2)**, and **Trisetacini-Nalepellini groups (3)**], but its relationships with different Nalepellinae taxa are also uncertain. Overall, the groups with Nalepellinae species largely did not include Phytoptidae species with single *vi* absent.

In conclusion, the Nalepellinae, excluding *Pentasetacus*, may be monophyletic, the Trisetacini polyphyletic and the Nalepellini paraphyletic. The relationships between Trisetacini and Nalepellini species are not conclusive, and the amalgamation of the species of these two tribes (Table 4.10), is proposed pending more robust results regarding the relationships of the Nalepellidae taxa *sensu* the present study. These results partly support Lindquist & Amrine (1996) who proposed the Trisetacini may not be monophyletic, and that the Nalepellini is weakly supported by a homoplasious apomorphy: the loss of *c1*. The classification proposed in the present study (Table 4.10) agrees with the classification of Boczek *et al.* (1989) who did not divide their Nalepellinae (excluding *Pentasetacus*) in tribes.

Position of *Pentasetacus*

The Nalepellinae tribe Pentasetacini sensu Amrine *et al*. (2003) is monospecific, holding *Pentasetacus araucaria* described by Schliesske (1985), a species with five prodorsal setae (unpaired *vi*, *ve* and *sc*) – the maximum number of prodorsal setae in the Eriophyoidea, *c1*[1] present, a vermiform, but more vagrant-like body, with broad annuli subequal dorsoventrally, frontal lobe present, and divided empodium. It causes galling on an ancient relict coniferous species, *Araucaria araucana* (Araucariaceae), in the Chilean Andes of South America (Schliesske, 1985). *P. araucaria* is regarded to be the most primitive or early derived eriophyoid species (Sukhareva, 1994), and became central to most hypotheses regarding the phylogeny and evolution of the Eriophyoidea since its description, and the placement of this species is of particular importance.

The position and relationships of *Pentasetacus* could not be conclusively resolved by the present analyses. When its relationships with other eriophyoid taxa were resolved, *Pentasetacus* is found to be closely related to Phytoptidae, and not to Eriophyidae or Diptilomiopidae species. This relatively strongly supports its current placement in the Phytoptidae, or eventually in a subgroup exclusively with species that previously belonged to the Phytoptidae. In the 318tax- and 66tax trees, contrary to what one would expect, and current hypotheses regarding the species, it has a closer relationship with Phytoptidae with single *vi* absent, and in particular with the Sierraphytoptinae and Phytoptinae, than with Nalepellinae species [see ***Pentasetacus*-Sierraphytoptini groups (6)**, **Smaller-Phytoptinae-Sierraphytoptinae group (8)** and **Phytoptinae-Sierraphytoptinae group (9)**]. This does not support its placement within the Nalepellinae, and it seems from the homoplasies supporting these groups that the presence of *ve*, in combination with other characters, may be more important in determining the relationships of *Pentasetacus* than the presence of single *vi*.

In the 18modify analyses *Pentasetacus* was, however, recovered as part of the Nalepellinae when the subfamily was retrieved as a clade [see **Nalepellinae group and clade (5)**]. Although the trees obtained from data sets with a more comprehensive sampling of taxa and characters are preferred in the present study, the placement of *Pentasetacus* within the Nalepellidae can not be discarded as an alternative hypothesis.

Until evidence that is more conclusive is found regarding the position of *Pentasetacus*, I place it in its own family (Table 4.10) to retain stability of the Eriophyoidea classification in the mean time.

[1] *c1* have been wrongly reported as being absent in this genus by Amrine *et al.* (2003).

This coincides with Shevchenko (in Boczek *et al.*, 1989) who proposed a family rank taxon for *Pentasetacus* Schliesske, 1985, although his proposal was for a different reason. He argued that the family rank is dependent on the number of prodorsal shield setae. Sukhareva (1994) kept *Pentasetacus* in a family of its own, and proposed that it is more closely related to the Nalepellidae (*sensu* Shevchenko, 1976) than to the Phytoptidae (*sensu* Shevchenko, 1976), because it occurs on a conifer, and possesses *vi*. In the present study, it is rather proposed that *Pentasetacus* may be more closely related to the Phytoptidae *sensu* the present study, and may even be recovered to be in the same clade as the latter taxon.

4.7.1.1 A summary and discussion of the proposal to subdivide the Phytoptidae *sensu* Amrine *et al.* (2003) into three separate families (Table 4.10).

The distinction between Phytoptidae species with odd (with single *vi*) and those with even numbers (without single *vi*) of prodorsal setae was central in many arguments and studies regarding the evolution of the Eriophyoidea (e.g., Farkas, 1968b; Shevchenko, 1971, 1974a, 1976; Shevchenko *et al*., 1991). As previously mentioned, Shevchenko (1971, 1974a, b, 1976) and Boczek *et al.* (1989) argued strongly and pertinently that Phytoptidae species with odd and those with even numbers of prodorsal setae are two separate lineages within the Eriophyoidea. Farkas (1968b) and Shevchenko (1971, 1974a, 1976) pointed out that species with odd numbers of prodorsal setae occur exclusively on conifers [Gymnospermae], and those taxa with even numbers of prodorsal setae occurr on a wide range of hosts, including the more recently evolved Angiospermae. The long spermathecal tubes exclusively in species with single *vi* present, which may be another synapomorphy supporting the monophyly of the group (Shevchenko, 1971, 1974a, b, 1976). Lindquist (1996b) and Lindquist & Amrine (1996) also proposed that some Phytoptidae characteristics, such as the long spermathecal tubes and position of the solenidion on tibia I and median position of single *vi* present in some species, may be synapomorphic for clades within the Phytoptidae. On closer inspection, including studying the substructures in more detail, however, particularly the internal genitalia of *Pentasetacus* may not be entirely homologous to the genitalia of other Nalepellinae. The proposal by these authors that the Nalepellinae may be monophyletic is supported by strong arguments and evidence, and although it was not generally supported by the present study, it remains a strong hypothesis which has not been conclusively disputed by the present study.

The present study partly supports the arguments and proposals of the authors above. Generally the Phytoptidae with single *vi* present, and the Phytoptidae with single *vi* absent were found to be in separate clades or exclusive groups, but these two separate groups were generally not particularly

closely related. To express this lack of a close relationship between the two "lineages", they are proposed to be in separate families, Nalepellidae and Phytoptidae (Table 4.10). This agrees with the proposal of the superfamilies **Trisetoidea** and **Phytoptoidea by** Shevchenko (1971, 1974a), which were changed to family level Nalepellidae and Phytoptidae (Shevchenko, 1976; Boczek *et al*., 1989), expressing the proposal that they are two separate, natural lineages.

In the present study, the presence or absence of single *vi* was largely found to be homoplastic, though, and the two groups were not recovered as clades. The Nalepellidae *sensu* the present study, may be polyphyletic and in particular, *Boczekella*, *Setoptus* and *Trisetacus* may belong to other taxa, and possibly even as taxa of the Eriophyidae *sensu* Amrine *et al*. (2003). Even more likely, *Pentasetacus* may have a closer relationship with Phytoptidae without single *vi* than with those with single *vi* (discussed above). Additionally, *Acathrix* (Phytoptinae) and *Trisetacus* (Nalepellinae) were found to be sisters [**Trisetacini-Phytoptinae group (4)**] under some parameters, but as already discussed, this relationship is weakly supported and probably not natural. In the 18modify trees under implied weighting *Mackiella* was recovered as the sister to the **Nalepellinae clade (5)** to constitute the ***Mackiella*-Nalepellinae clade (11c)** and this relationship is supported by the synapomorphy: tibial solenidion *φ* present. If this monophyletic grouping eventually proves to be robust, the Mackiellini *sensu* Amrine *et al*. (2003) is polyphyletic, and the loss or retainment of single *vi* may be even more homoplastic than proposed in the present study.

4.7.1.2 The relationships of the Phytoptidae groups and clades with other eriophyoid taxa

Although some of the clades and groups within the Phytoptidae seem to be robust and stable, the relationships of the Phytoptidae groups and clades with other eriophyoid taxa in the present results are less certain and largely inconclusive. It can be proposed, though, that a large part of the Phytoptidae *sensu* Amrine *et al*. (2003) should be designated to the Eriophyidae or *vice versa*, depending on which taxa were found to be imbedded among the Eriophyidae. At least part of the Phytoptidae, however, is still positioned outside the remainder of the Eriophyoidea as a separate exclusive group or clade.

There are two main tree topologies regarding the Phytoptidae taxa excluded from, and possibly belonging to a separate lineage than the remainder of the Eriophyoidea. The analyses of taxon samples under most parameters recovered some or all Nalepellinae positioned outside a clade or exclusive group with the remainder of the Eriophyoidea including the remaining Phytoptidae (similar to the hypotheses of V.G. Shevchenko and others), and this is the preferred hypothesis. Under another set of parameters, alternatively, some vagrant Phytoptidae species (of the Sierraphytoptinae and Phytoptinae), sometimes including *Pentasetacus*, are positioned outside the remainder of the Eriophoidea, which consists of the Eriophyidae, Diptilomiopidae and a part of the Phytoptidae, including the Nalepellinae (sometimes including and sometimes excluding *Pentasetacus*). Either of these two different

Phytoptidae groups being excluded from the remainder of the Eriophyoidea is not well-supported and conclusive, however, because the group constituting the remainder of the Eriophyoidea was usually not well-supported [see **Eriophyidae groups and clades (13)**]. In general, it was found that *Pentasetacus* has a close relationship with, and is in exclusive groups including Phytoptinae and Sierraphytoptinae, and resultingly, based on the preferred hypotheses, *Pentasetacus* together with its closely related Phytoptidae could be designated to the Eriophyidae. This exclusive group (excluding part of the Nalepellinae) sometimes also includes the **Diptilomiopidae clade or group (27)** (Figs 4.9, 4.28, 4.33, 4.43, 4.51). The position of the Phytoptidae clades and exclusive groups among the Eriophyidae and Diptilomiopidae clades and groups in the different trees can be viewed in Figs 4.6, 4.26, 4.43, 4.55, 4.57, 4.58, 4.59, 4.60 and 4.62.

In conclusion, if a classification should be proposed mainly based on the preferred phylogeny recovered in the present study, the Phytoptidae, except *Nalepella*, *Phantacrus* and *Pentaporca*, should be designated to the Eriophyidae. This will cause a huge, probably premature, upset in the nomenclature and suprageneric concepts of the Eriophyoidea. With *Phytoptus* Dujardin, 1851 designated to the Eriophyidae, *Phytoptus* will take precedence over *Eriophyes* von Siebold, 1851 as the type species of the less restricted Eriophyidae, and resultantly Phytoptoidea and Phytoptidae Murray, 1877 will have precedence over Eriophyoidea and Eriophyidae. The Eriophyidae (possibly including the Diptilomiopidae) will be junior synonyms of the Phytoptidae. There may also be other implications which may leave the taxonomy of the Eriophyoidea unstable. Disrupting nomenclatural changes may be prevented, however, by applying to the Commission of the International Code for Zoological Nomenclature (ICZN) to overrule the Principle of Priority (Article 23.1) and give precedence to the taxon names currently in use to promote stability in the classification of the Eriophyoidea (Article 23.2) (ICZN, 1999). The diagnoses and concepts of most suprageneric taxa will, however, still change significantly. Most phylogenetic studies (e.g., Hong & Zhang, 1996a; present study) found that at least part of the Phytoptidae should be in the same clade with at least part of the Eriophyidae. The position, however, of, among others, *Phytoptus*, is still regarded to be uncertain. Taking all these aspects in regard, I propose that the Phytoptidae *sensu* Amrine *et al*. (2003), which should, according to the preferred phylogenetic groupings, be designated to the Eriophyidae, remain classified outside the Eriophyidae for the interim, pending more robust hypotheses. The Phytoptidae *sensu* Amrine *et al*. (2003) are classified into three taxa at the same taxon level as the Eriophyidae, namely the Phytoptidae, Pentasetacidae and the Nalepellidae (Table 4.10). The Novophytoptinae, however, are assigned to the Eriophyidae (Table 4.10). It is proposed that among these taxa, Phytoptidae and Pentasetacidae are closely related, possibly in the same clade, and the Phytoptidae-Pentasetacidae is more closely related to the Eriophyidae, than both are to the Nalepellidae. The reasons for subdividing the Phytoptidae *sensu* Amrine *et al*. (2003) in three families are discussed above.

4.7.2 ERIOPHYIDAE

Eriophyidae are species without anterior prodorsal setae – *ve* and paired or unpaired *vi*, and without the "diptilomiopid" gnathosoma. It is the largest family in the Eriophyoidea, and the classification of this family is in reality the most comprehensive hypothesis of the relationships between Eriophyoidea taxa. In contrast to the Phytoptidae, however, few phylogenetic and evolutionary hypotheses were specifically developed or discussed regarding the relationships between the Eriophyidae taxa, apart from the assumption that the Eriophyidae and most of its subgroupings are probably not monophyletic (including Lindquist & Amrine, 1996). Vagrant forms, living more exposed and tending to have broader host ranges than the non-vagrant species, are proposed to have developed repeatedly and homoplasiously from the usually more specialized non-vagrant species and *vice versa* (Das & Chakrabarti, 1989; Lindquist & Amrine, 1996). This brought about the general vermiform and fusiform body shapes found in the Eriophyoidea, including the Eriophyidae. The Eriophyidae live on a wide variety and range of host plant taxa, ranging from earlier derivitive Gymnospermae to the most recently derived plant taxa in the Angiospermae. It does not seem that there is a close relationship between the phylogeny of the host plants and the phylogeny of the Eriophyidae, similar to that proposed for the Phytoptidae.

The family Eriophyidae was not retrieved as a monophyletic group in any of the analyses and was found to be paraphyletic and possibly polyphyletic [see **Eriophyidae group and clades (13)**]. In the trees found with the 18tax analyses, the "Eriophyidae" clades are more supported (see e.g., **Eriophyidae clade 13e**) than the Eriophyidae groups or clades found by analyses of data sets with more characters and species. The 18tax tree **Eriophyidae clades (13)** include all the Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and all Phytoptidae except the Nalepellinae and are supported by the synapomorphies: single *vi* absent, and spermathecal tubes short. Alternatively, the clade includes all Eriophyidae, the **Diptilomiopidae clade – 18tax trees (27b)** and *Novophytoptus*, but excludes the other Phytoptidae, and the clade is supported by one synapomorphy, *sc* at or near the rear shield margin. The Eriophyidae (including the Diptilomiopidae) was retrieved as a separate group from all the Phytoptidae in one tree, but then the Eriophyidae group is supported by homoplasies. The hypotheses postulated from the 18tax trees can not be totally disregarded before further testing, but are not regarded as reliable, because the extremely small biased data set excluded a large amount of morphological evidence from other taxa in the Eriophyoidea. Results from 18tax analyses, however, are broadly similar to the results from the 318tax and 66tax analyses, as the Eriophyidae was found to be paraphyletic under most parameters, but it may also be polyphyletic, since some groups were only supported by homoplasies. To summarize results from the present study: the most supported recovered Eriophyidae groups or clades generally include all Eriophyidae taxa, include some of the Phytoptidae,

but exclude the ***Nalepella* groups (1)** or **Nalepellinae group or clade (5)** or, alternatively, exclude some of the **Phytoptinae-Sierraphytoptini groups (6),** and may also include the **Diptilomiopidae group or clade (27).** In other words, the **Eriophyidae group or clade (13)** in some trees can essentially be regarded as the same group of species as the monophyletic Eriophyoidea, except in all the trees a few species, usually Phytoptidae species, are not part of it. The **Eriophyidae groups or clades (13)** are not retrieved in analyses under equal weighting of characters, and is not supported by symmetric resampling values, and does not consist of the same species under all parameters, and can not be regarded as a robust grouping. The more restricted Eriophyidae *sensu* Amrine *et al*. (2003) are retained as a family separate from the Diptilomiopidae and Phytoptidae families *sensu* the classification proposed in the present study, largely to preserve the stability of the classification until more conclusive results can be obtained regarding the relationships of these family groupings (Table 4.10).

With the present data sets, less phylogenetic phylogenetic resolution and fewer and less robust groups were recovered from the Eriophyidae taxa, particularly those largely exclusively consisting of Eriophyidae species, than what were found in the Phytoptidae and Diptilomiopidae. It was found that many of the current suprageneric taxa in the Eriophyidae are most likely not monophyletic. Some subfamilies with specific body modifications, e.g., the Cecidophyinae with the genitalia appressed against the coxae, and the genital anterior apodeme folded up to appear as a thick line, and the Nothopodinae with reduced or fused tibiae, were found to be possibly monophyletic, or partly monophyletic, in the present study. Most Eriophyidae are, however, divided between non-vagrant forms (e.g., *Aceria*) (constituting the Eriophyinae) and vagrant forms (e.g., *Aculus*) (constituting the Phyllocoptinae) similar to the way Nalepa constructed the classification of the Eriophyoidea. None of these were found to be monophyletic.

The Eriophyidae have six subfamilies (Amrine *et al*., 2003; Table 1.1), and the appraisal of their monophyly is as follows.

Aberoptinae and Nothopodinae

The leg tibia of some Eriophyidae is entirely or partly fused with the tarsus, resulting in the reduction or apparent absence of the tibia. This is regarded as an important suprageneric character in the classification of the Eriophyidae, and is the key character differentiating the Nothopodinae and Aberoptinae from other Eriophyidae taxa, and additionally *l'* is always absent in these subfamilies (Keifer, 1956: 163; Lindquist & Amrine, 1996). The Aberoptinae is distinguished from the Nothopodinae by having spatulate or shovel-shaped projections on the tarsi (Amrine *et al.*, 2003).

The restricted Aberoptinae *sensu* Amrine *et al*. (2003) only comprise *Aberoptus* spp. In the present study, the subfamily was represented by an *Aberoptus* sp., and two *Cisaberoptus* spp. (Table 4.1).

Amrine *et al.* (2003) synonymized *Cisaberoptus* with *Aceria*, because the protogyne of *Cisaberoptus* spp. fits into the latter genus, and the generic concept of *Cisaberoptus* is based on the morphology of the supposed deutogyne females. Analyzing the data of *Cisaberoptus* spp. in the current data sets might be flawed, because the characteristics scored were from the supposed deutogyne females, while all other species in the data sets were scored from protogyne females. Nevertheless, the two *Cisaberoptus* spp. were found to be sisters, supported by the two homoplasies: apical palp ends spatulate or with triangular projections, and body flattened fusiform. They were not found to have a close relationship with *Aberoptus*. Lindquist & Amrine (1996) proposed the Aberoptinae might be monophyletic, supported by four synapomorphies: tarsi with projections, legs extraordinary stout, empodium II large with many rays, female genital coverflap abbreviated, and three to four times wider than long. The data set was not designed in such a way that the monophyly of the restricted Aberoptinae could be tested. The relationships of *Aberoptus* with other Eriophyoidea are uncertain. Under the different parameters, it was found to have close relationships with *Cymoptus* (Aceriini) and some Phyllocoptinae, or particularly with some Cecidophyinae species. The latter relationship is primarily supported by the position of its genitalia, and particularly in the small 18tax trees, *Aberoptus* is in the same clade as *Ashieldophyes*-*Cecidophyes*, supported by one synapomorphy: female genitalia appressed to coxae. It never was found to have a close relationship with the Nothopodinae. See the **Aberoptinae groups (16)** for further information. Since the relationships of the Aberoptinae could not be conclusively determined, the subfamily is retained as is (Table 4.10), but it is proposed that *Aberoptus* spp. may be closely related to some Cecidophyinae species.

Lindquist & Amrine (1996) proposed the Nothopodinae to be weakly supported by the reduced leg tibia, which they regarded as a homoplasious apomorphy. The monophyly of the Nothopodinae, although not conclusively, is supported more or less in most of the 318tax and 66tax trees under implied weighting [see the **Nothopodinae groups and clade (14)**]. In particular, in the 66tax-k30 tree, *Colopodacus* and *Nothopoda* are recovered as sister species (Fig. 4.52) well-supported by two synapomorphies: reduction of tibia, which is completely fused with tarsus in legs I and II. It seems that the Nothopodinae may be a well-supported clade, but it still needs testing.

The Nothopodinae are divided into the Colopodacini with *1b* present (Mohanasundaram, 1984; Amrine, 1996), and the Nothopodini with *1b* absent (Keifer, 1956; Amrine *et al*., 2003). The tribes, on the same taxonomic level, are not well-supported by the trees, and they each were found to be paraphyletic and polyphyletic, because the species of these tribes were recovered exclusively in the same groups and clades, and were not found to be separated in two groups that may support

the tribes. Boczek *et al.* (1989) did not include the taxon groups, Colopodacini and Nothopodini, *sensu* Amrine *et al.* (2003) in their classification.

Based on the present results, I do not recognize the new subfamily, Colopodacinae, proposed by Mohanasundaram (1984), and also not the subsequent division of the Nothopodinae into the tribes Colopodacini and Nothopodini by Amrine (1996). The Nothopodinae are potentially monophyletic, but is proposed not to be subdivided into smaller groupings at this stage (Table 4.10).

Ashieldophyinae

Mohanasundaram (1984) placed *A. pennadamensis* in its own monospecific family, Ashieldophyidae, largely based on his erroneous morphological description of the species (Amrine & Stasny, 1994; Amrine, 1996; Lindquist & Amrine, 1996; Amrine *et al.*, 2003) and Boczek *et al.* (1989) concurred with this placement, and retained the taxon for this species at family rank. Amrine & Stasny (1994) lowered the family to subfamily rank, and assigned the Ashieldophyinae to the Eriophyidae. *Ashieldophyes* has a particularly small prodorsal shield, encroached by dorsal annuli-like structures; a minute *sc* without a setal tubercle and located on the lateral prodorsal shield margin; coxisternal plates widely separated, without a prosternal apodeme, and external female genitalia between coxisternal plates II (Amrine & Stasny, 1994; Amrine, 1996; Lindquist & Amrine, 1996; Amrine *et al.*, 2003). Except for the size and position of *sc* and it being without a setal tubercle, the other characters are autapomorphic for this species (Lindquist & Amrine, 1996). The positions of *Ashieldophyes* recovered by the different analyses in the present study, were not well-supported, and its relationships are uncertain. It was recovered imbedded in the Eriophyidae and may be closely related to Phyllocoptinae or Cecidophyinae species. It should probably not be in its own subfamily, but it is retained therein (Table 4.10), since the relationships recovered are inconclusive.

Cecidophyinae

The Cecidophyinae are Eriophyidae species with female genitalia enlarged and the internal female anterior genital apodeme folded up, appearing as a broad line (Fig. 3.5c), in combination with the genitalia being pressed up against the coxisterna, separating the coxisternal plates more than usually found in the Eriophyoidea (Fig. 3.5a, b). In lateral view the genitalia is noticeably projecting from the ventral opisthosomal aspect. The longitudinal ridges on the female genital coverflap are usually in two ranks (Keifer, 1966d: 15, 17; Lindquist & Amrine, 1996; Amrine *et al.*, 2003).

The 19 Cecidophyinae species (Table 4.1) included in the present study, were never recovered as a clade, but strong affinities between most of the species were found, and they are largely positioned close to each other in the trees [see **Cecidophyinae groups (17)**], and an example of this group in the

318tax-k10 tree (Fig. 4.13). Some single species of the Cecidophyinae, however, were not recovered in close association with the bulk of the Cecidophyinae. One such species is *Paracolomerus* which was found in a group with *Keiferophyes*, *Acunda* and *Brachendus* (Eriophyinae), *Palmiphytoptus*, and *Cisaberoptus* deutogynes, constituting the **Broadly-folded-apodeme group (18)**. This group is largely supported by the anterior genital apodeme only broadly folded up, and not forming such a clear straight line as found in other Cecidophyinae, and it is a feasible grouping. *Neserella* and *Dechela* probably should also not be in the Cecidophyinae, but were rather found to have close relationships and may belong to a group of species from the southern hemisphere, including particularly some Eriophyinae [**Extended southern-Aceriini group (19)**]. In some of the 18tax trees, *Cecidophyes* (the only cecidophyine species included) was recovered in a clade with *Aberoptus* and *Ashieldophyes*, supported by the position of the genitalia, and a close relationship between these genera can be investigated.

Lindquist & Amrine (1996) proposed that the Cecidophyinae may be monophyletic, supported by one synapomorphy: enlarged genitalia appressed against coxae. In combination with this characteristic, the genital apodeme is folded up to form a thickened straight line (Fig. 3.5c). Based on the present results it is proposed that a large part of the Cecidophyinae may be monophyletic, but in its entirety, the subfamily was found likely polyphyletic and possibly paraphyletic. The phylogeny of the Cecidophyinae and possibly closely related species from other taxa may be better and more robustly resolved if the genitalia are studied in more exact detail. Descriptive drawings of the same internal genitalia and apodemes by different authors may differ considerably, e.g., the drawing of the internal genitalia of *Cecidophyes rouhollahi* by C. Craemer (Fig. 3.5c) and a drawing of the genitalia of the same species by H.H. Keifer (from his collection) (Craemer *et al*., 1999) as a less clear case. More detailed descriptions will facilitate the identification and more exact definition of primary homologies in the genitalia. The Cecidophyinae is retained, but *Paracolomerus*, *Neserella* and *Dechela*, is re-assigned to other subfamilies.

The Cecidophyinae have two tribes (conceived by Keifer, 1966b): the Cecidophyini with *sc* and its setal tubercle absent (Fig. 3.3), and the Colomerini with *sc* present (Keifer, 1966d; Newkirk & Keifer, 1975). Lindquist & Amrine (1996) did not regard either of these tribes as well-supported groupings. According to them, the Colomerini might not be monophyletic, because it is supported by a plesiomorphic character, and the Cecidophyini are weakly supported by one homoplasious apomorphy: the loss of *sc*.

In the present study, Cecidophyinae species were positioned close to each other in about two groupings coinciding with the tribes [see **Cecidophyinae groups (17)**], but neither formed a single grouping together at one node. They may be monophyletic groupings, being slightly paraphyletic or polyphyletic, e.g., *Neocecidophyes* and *Epicecidophyes* (Colomerini) may rather belong to the

Cecidophyini. Nothing conclusively about the monophyly of these two tribes was found in the present study and neither strongly support or negate the hypotheses. It seems generally more phylogenetic structure is present in the Cecidophyini than in the Colomerini. Boczek *et al.* (1989) only included Cecidophyini genera in the Cecidophyinae, and regarded the absence of *sc* and its setal tubercle as one of the diagnostic characteristics of the subfamily. They designated genera of the Colomerini *sensu* Keifer (1966d) and Newkirk & Keifer (1975) to the Eriophyinae and Phyllocoptinae. This classification is not supported by the present results. The Cecidophyinae tribes are retained (Table 4.10), pending more detailed analyses.

Eriophyinae and Phyllocoptinae

The largest Eriophyidae subfamilies – Eriophyinae and Phyllocoptinae – are essentially differentiated from each other by vagrant (Phyllocoptinae) and non-vagrant (Eriophyinae) body shape characteristics (Amrine *et al*., 2003). This division corresponds with the original division of the Eriophyoidea by Nalepa (1892, 1898b), which prevailed, despite the splitting of new taxa from these two major groupings. The Eriophyinae and Phyllocoptinae, and particularly their tribes, had the least phylogenetic signal of all the Eriophyoida suprageneric taxa, and none were recovered as monophyletic groupings in the present study. Particularly the Eriophyinae and Phyllocoptinae tribes were found to be highly polyphyletic. This supports Lindquist & Amrine (1996) who regarded these two subfamilies and their tribes as natural groupings problematic.

Eriophyinae

The Eriophyinae *sensu* Roivainen (1953), Newkirk & Keifer (1971) and Amrine *et al*. (2003) have a vermiform body, albeit sometimes slightly fusiform. The dorsal and ventral annuli are entirely or for most part of the opisthosoma subequal dorsoventrally, the prodorsal shield is typically without a frontal lobe, and if present, and particularly when it stretches across the gnathosoma, it is flexible and narrow and is present in combination with subequal annuli. Most species do not have body modifications, including ridges and furrows. This taxon is similar to the Eriophyinae defined by Nalepa (1898b: 5) but with the exclusion of species with a similar vermiform body shape now classified as the Aberoptinae, Nothopodinae, Cecidophyinae and Ashieldophyinae. The Eriophyinae body shape (Fig. 3.2a) is usually associated with non-vagrant[2] eriophyoid mites living a more sheltered life. They live in natural plant microhabitats e.g., in buds, underneath needle and leave sheaths, and between bulb scales (refuge-inhabiting[1] mites), or in microhabitats created by symptomatic growth caused by their feeding, such as galls (gall-inhabiting[1] mites). This life style and concurrent body shape probably developed homoplasiously and repeatly within the Eriophyoidea (Lindquist & Amrine, 1996). The present study supports this hypothesis, and characters describing body shape were found to be

[2] This terminology is used as it has been defined in Sabelis & Bruin (1996).

homoplastic, and were sometimes found as homoplasies, but never as synapomorphies, supporting clades.

The Eriophyinae are divided into three tribes: Diphytoptini (with divided empodia) (Amrine & Stasny, 1994), Eriophyini (scapular setal tubercles about ahead of the rear shield margin, with *sc* directed forward or up) (Fig. 3.3c), and the Aceriini (scapular setal tubercles on or very near the rear shield margin, with *sc* always directed to the rear) (Fig. 3.3b) (Amrine & Stasny, 1994; Amrine *et al.*, 2003). The tribes are thus differentiated by the empodial shape, and the position of *sc*, in combination with the direction into which *sc* is projected.

The species of the Eriophyinae and the Eriophyinae tribes are mostly scattered as single species in the trees found for the 318tax and 66tax data sets. Few supported groups and close relationships between them and other eriophyoid taxa were found by the analyses. Only one weakly supported group [**Extended Southern-Aceriini group (19)**] with an appreciable number of Eriophyinae species was identified from the recovered relationships. The positions and relationships of some of the single Eriophyinae species were, however, additionally evaluated to explore the type and quality of information that can be extracted from these. Some useful hypotheses can be proposed, and are presented and chronologically numbered: **Eriophyini species positions (20)** and **Aceriini species positions (21)**.

Lindquist & Amrine (1996) argued that the Diphytoptini and Aceriini might be supported by homoplasious apomorphies: divided empodium, and position and projection of *sc*, alternatively. They, however, proposed that the Eriophyini is probably not monophyletic, because it is not supported by any apomorphies. All three tribes were, however, found to be highly polyphyletic in the present study. Although the Eriophyinae was found to be polyphyletic as well, it has been decided for practical classification and identification, and for retaining the stability of the classification, to retain this subfamily pending more detailed analyses of particularly the large genera such as *Aceria*, and pending the recovery of improved, more robust monophyletic groupings in the Eriophyidae. It has been decided, based on the high polyphyly of the Eriophyinae tribes, to leave the Eriophyinae undivided (Table 4.10). It is believed this is the step in the right direction towards entirely restructuring and reclassifying the Eriophyidae according to the phylogeny of the group. Boczek *et al.* (1989) also did not recognize the tribes of the Eriophyinae, but they divided the Eriophyinae into two unnamed subgroups based on the presence of the frontal lobe, which is laterally thin and with a narrow base if present in the Eriophyinae. This subdivision is not supported by the present results either. The scoring of this character from slide-mounted

specimens is also difficult, subjective and ambiguous, and it is also not a good differentiating character in practical taxonomy.

Phyllocoptinae

The Phyllocoptinae *sensu* Newkirk & Keifer (1971) and Amrine *et al*. (2003) typically have a fusiform body, which is widened anteriorly. Their annuli are characteristically differentiated dorsoventrally with the dorsal annuli longer (length parallel to the body axis) than the ventral annuli, and they are usually smooth. The prodorsal shield generally has a rigid frontal lobe with a broad base (Nalepa, 1898b: 45; Roivainen, 1953). This general body shape (Fig. 3.2b) is usually associated with species living a more exposed life-style (vagrant[1] mites), e.g., on the leaf surface.

In the present study, the Phyllocoptinae was found to be polyphyletic and possibly also paraphyletic and agrees with Lindquist & Amrine (1996) which proposed that the Phyllocoptinae are not based on any apomorphy and are probably not monophyletic.
Farkas (1969) proposed that the Phyllocoptinae originated from two lineages, Eriophyinae species with *sc* on or near the rear shield margin, with these projected to the rear (e.g., *Vasates* originated from *Aceria*); and likewise *Phyllocoptes* originated from *Eriophyes*. This was not supported by the present study.

Newkirk & Keifer (1975) divided the Phyllocoptinae, which was perceived to have little classificatory structure, into five groups to simplify the identification and classification process. They noted it was for convenience, and that only some may indicate relationships. These informal groups were proposed as tribes by Amrine & Stasny (1994). Two of the phyllocoptine tribes (Acaricalini and Tegonotini) are defined by body structure shapes (empodia and annuli, respectively), while the others are largely defined by the presence, position or other characteristics of *sc* and its setal tubercle. Boczek *et al.* (1989) supported Newkirk and Keifer (1975) in creating subgroups for the Phyllocoptinae. They divided the Phyllocoptinae into ten subgroups with about the same morphological criteria than Newkirk & Keifer (1975), but subdivided the groups further on basis of the presence of the frontal lobe, and body shape in regard the presence of ridges and/or troughs.

The five Phyllocoptinae tribes, and the hypotheses of their monophyly by Lindquist & Amrine (1996), are as follows.

- The Acaricalini have a divided empodium (Newkirk & Keifer, 1975; Amrine & Stasny, 1994), which is a homoplasious apomorphy supporting the tribe.

- The Calacarini have *sc* vestigial or absent, and its setal tubercle may be present or absent (Newkirk & Keifer, 1975; Amrine & Stasny, 1994). This tribe is based on a homoplasious apomorphy: the loss of *sc*.
- The Tegonotini have lateral lobes or pointed projections from all or some opisthosomal annuli, or have a plate behind the prodorsal shield with lateral extensions (Newkirk & Keifer, 1975; Bagdasarian, 1978; Amrine & Stasny, 1994). This tribe is weakly supported by one homoplasious apomorphy: dorsoventral differentiation of opisthosomal annuli.
- The Phyllocoptini have *sc* present, with its setal tubercle ahead of rear shield margin, directing *sc* forward, up or medially. If the scapular setal tubercle is near the rear shield margin, the alignment of its base is longitudinal or diagonal to the body's long axis, and when the tubercle is subcylindrical it is bent forward (Newkirk & Keifer, 1975; Amrine & Stasny, 1994). The Phyllocoptini is not based on any apomorphy and is probably not monophyletic.
- The Anthocoptini have *sc* present, with its setal tubercle on or near the rear shield margin, directing *sc* to the rear. Alternatively, the tubercle is either subcylindrical, or the alignment of its base is transverse to the long axis of the body (Newkirk & Keifer, 1975; Amrine & Stasny, 1994).

In the present study, none of the Phyllocoptinae tribes were found to be monophyletic. The phylogenetic structure recovered for the group was meager and was weakly supported, but more structure was found than in the Eriophyinae. Some Phyllocoptinae were, however, positioned in proximity to each other, e.g., Figs 4.10, 4.12 and 4.15. Groups identified which can be proposed as potential monophyletic groupings pending further studies are: ***Schizacea-Knorella* group (22)** (Acaricalini); **Flat-monocot group (23)** (some Acaricalini and some Phyllocoptini); **One-Phyllocoptini group (24)** (some Phyllocoptini); ***Tetra-Ursynovia* group (25)** (some Anthocoptini); and ***Abacarus* groups (26)** (Anthocoptini and other taxa).

No robust alternative hypotheses for groupings within this family were retrieved in the present study, except for a few that are good hypothetical groupings to study. Additional analyses including more detailed characteristics of ridges and furrows and other modifications of the body may aid in the phylogenetic phylogenetic resolution of the Phyllocoptinae, but this is not sure. The entire classificatory structure of the Eriophyidae (apart from the Nothopodinae and Cecidophyinae) (particularly the Eriophyinae, the Phyllocoptinae and the tribes of both families) can, however, not be dissolved. It will make the classification awkward and development of keys and identification difficult. One could consider to dissolve the tribes of the Eriophyinae and not to subdivide this subfamily, to possibly group more related species together that are currently in the different tribes, but even this may be too preliminary and complicate identification. A team of researchers in the USA is currently

undertaking a phylogenetic analysis of the Eriophyoidea with molecular research, and included some species of the Eriophyidae, as well as more than one *Aceria* spp. This is a step in the right direction.

4.7.2.1 Conclusion: monophyly of the Eriophyidae

In conclusion, the Eriophyidae (without the Diptilomiopidae) being one clade is unlikely, but this aspect has not been resolved by the present analyses. It is broadly hypothesized the suprageneric taxa within the Eriophyidae are probably highly polyphyletic, including larger genera such as *Aceria*. The Cecidophyinae and Nothopodinae, may however, be more or less natural groupings, but the remainder of the Eriophyidae species will eventually "mix up" and be retrieved as totally new groups, different from the taxa in the existing Eriophyoidea classification.

4.7.3 DIPTILOMIOPIDAE

The diagnosis and delimitation of the Diptilomiopidae stayed more or less unchanged since its conception by Keifer (1944). The family is largely defined by the distinctive shape of the gnathosoma and its complex of structures (Keifer, 1944; Fig. 3.22), including strong and robust chelicerae projecting ahead and then abruptly downwards, and a "long-form" oral stylet (Fig. 3.22b, d, e) (Keifer, 1944; Roivainen, 1953; Keifer, 1964a). The Diptilomiopidae is probably a monophyletic taxon supported by synapomorphic gnathosomal characteristics (Lindquist & Amrine, 1996). It was also found as a monophyletic taxon in the empirical studies by Huang & Huang (1990) and Hong & Zhang (1996a). These studies included very few Diptilomiopidae species, but the Diptilomiopidae clades found were well-supported by one synapomorphy: chelicerae abruptly curved downwards.

The taxon sample from the Diptilomiopidae was significantly increased in the present study and species of 53 genera were included (Table 4.1), as well as 83 *Diptilomiopus* spp. The monophyly of the Diptilomiopidae was largely supported [see **Diptilomiopidae groups and clades (27)**], although not conclusively. Despite a complicated, and frequently ambiguous data set, with a very low characters:taxa ratio, and with obvious conflict and high levels of homoplasy, the congruence and phylogenetic information in the Diptilomiopidae taxa was robust enough for the group to be retrieved as a clade under some parameters [e.g., **Diptilomiopidae clade – 318tax trees (27a)**] after relatively light implied weighting against the influence of homoplasy and after finding the best overall fit for the characters. With all evidence in the present study it is again proposed that the Diptilomiopidae is monophyletic, despite lack of support by resampling methods, and analyses under equal weighting, and lack of consistent retrieval of the Diptilomiopidae as a single clade in the present study. Gnathosomal character states typical to the Diptilomiopidae remain the only synapomorphies supporting the group.

The gnathosoma is a complex organ in the Eriophyoidea and future data sets will be improved if its structure is studied in more detail, and smaller, independent gnathosomal substructures are proposed as

primary homologies. In this process, one should be cautious though, that character sampling for parsimony analyses should be random, and not to artificially weigh the importance of the exact same character. The variation in its complexity should not be masked either, though. This improvement may strengthen the robustness of the recovery of the Diptilomiopidae as a clade.

The structure and hierarchical position of the Diptilomiopidae proposed by Keifer (1944) and Roivainen (1953) and presented in Amrine *et al.* (2003) classifies the Diptilomiopidae on the same taxonomic level as the Phytoptidae and Eriophyidae, and they thus did not imply specific relationships between the families, apart from being part of one superfamily. Shevchenko (1971, 1974a), however, implied that the Eriophyidae are more closely related to the Diptilomiopidae than the Phytoptidae (Shevchenko, 1971) in his proposed classification. This has been supported in some of the preliminary empirical studies including Kuang *et al.* (1992) and Hong & Zhang (1996a). The close relationship between the Diptilomiopidae and Eriophyidae is also expressed in the classification proposed by Boczek *et al.* (1989) in which the Eriophyidae *sensu* Amrine *et al.* (2003) includes the Diptilomiopidae. Whether the Diptilomiopidae is a separate clade from the **Eriophyidae group or clade (13)**, or imbedded within the latter group in the present study, is inconclusive, but it was found to have a closer relationship with the extended Eriophyidae group, than with part of the Phytoptidae excluded from the latter group [see **Eriophyidae groups and clades (13)** and **Diptilomiopidae groups and clades (27)**].

The Diptilomiopidae have two subfamilies (Newkirk & Keifer, 1971: 9): Diptilomiopinae with a divided empodium (Keifer, 1944), and Rhyncaphytoptinae with a simple, undivided empodium (Roivainen, 1953). Lindquist & Amrine (1996) proposed Diptilomiopinae are weakly supported by the divided empodium, which they regarded a homoplasious apomorphy on which the subfamily is based, and Rhyncaphytoptinae are probably not monophyletic. These proposals are partly supported by the present study. Monophyly of the subfamilies was not retrieved, and they were found to be polyphyletic, and at the same time, particularly the Rhyncaphytoptinae, is probably also paraphyletic (Figs 4.19, 4.35 and 4.43). The character, the empodial shape and in particular, whether it is divided or not, differentiating the subfamilies, was found to be highly homoplasious within the Eriophyoidea.

The Diptilomiopidae species were recovered largely in two groupings, broadly corresponding to the Rhyncaphytoptinae [**"Rhyncaphytoptinae" part (28)**] and the Diptilomiopinae [**"Diptilomiopinae" group (29)**] (e.g., Figs 4.19, 4.35).

4.7.3.1 **"Diptilomiopinae" group (29)**

"Diptilomiopinae" group (29) was largely found to be monophyletic. It was retrieved as a group (318tax-k10 tree), and as a clade (318tax-k20). The monophyly of the group was supported by five exemplar species which were recovered as a relatively robust clade [**66-Diptilomiopinae clade (40)**] by all the 66tax analyses. When only two species of the Diptilomiopinae was included (the 18tax data set), they were recovered as sisters, although not as a clade. The **"Diptilomiopinae" group (29)** includes all *Diptilomiopus* spp. included in the respective data sets. It also includes species of about 65% of the genera currently in the Diptilomiopinae included in the 318tax data set, as well as one Rhyncaphytoptinae species, *Sakthirhynchus*.

Of the two parts, more phylogenetic structure was found in the **"Diptilomiopinae" group (29)** and it is also more robust. Several groups could be identified in the 318tax trees. Eleven Diptilomiopinae species were recovered as the **One-Diptilomiopinae group (34)**, where the species were positioned close to each other, but were not necessarily found as an exclusive group one node. These species are morphologically similar, except *Diptilostatus* and *Davisella* which may eventually be found not to be part of the group. Within the **One-Diptilomiopinae group (34)**, a smaller potential clade was recovered consisting of three morphologically similar Diptilomiopinae species from the Oriental Region [***Lithocarus* group (35)**]. Three species from New Zealand, with the tarsus divided into two segments, were recovered as a clade [***Dacundiopus* clade (36)**]. The **Separate-coxae group (37)** consists of three species (a *Levonga* and two *Diptilomiopus* spp.) that are not correctly placed in these genera [according to Amrine *et al*. (2003)], and this is only one of many examples where the present analyses retrieved groupings that confirms either mistakes in interpretation of structures, or obviously wrong generic placements of species. *Africus* is a monospecific genus described from South Africa (Meyer & Ueckermann, 1995). It had a close affinity with *Diptilomiopus* spp., and most definitely is correctly placed in the Diptilomiopinae. It was recovered in a clade with *Neodiptilomiopus* and *D. ervatamiae*, pending confirmation of the correctness of the description of the latter species. *Africus* may alternatively or additionally be closely related to *D. knorri* [see the ***Africus* group and clade (38)**]. Three new *Diptilomiopus* spp. are described from South Africa in the present study. They were retrieved as one group [**SA *Diptilomiopus* group (39)**] under many different parameters from the outset of the present study. The latter may be a case where correctness and detail of description (including SEM study) may have contributed to the recovery of the group, rather than real morphology and particularly the recovered relationships of these three *Diptilomipus* spp. may change with improved description of other *Diptilomiopus* spp., and additional data from molecular studies.

Very little phylogenetic resolution was found of the relationships between the *Diptilomiopus* spp., but this was expected, since the character sample was focused on including all characteristics used on suprageneric and generic level. Some species level characters were included, but possibly many

additional well-defined characters must be found on species level for the phylogenetic resolution of species in one Eriophyoidea genus. The little phylogenetic resolution in *Diptilomiopus* also confirms that the character sample was largely informative regarding genus and suprageneric groupings. A phylogenetic analysis of *Diptilomiopus* and closely related genera is in progress (C. Craemer, *unpubl. data*). In general, the *Diptilomiopus* spp. that were retrieved in relationships with species from other genera in the Diptilomiopinae in the present study were wrongly placed in *Diptilomiopus* according to the conventional classification and diagnosis of *Diptilomiopus*.

4.7.3.2 **"Rhyncaphytoptinae" part (28)**

"Rhyncaphytoptinae" part (28) (Figs 4.19, 4.20) as an exclusive grouping is not as robust as **"Diptilomiopinae" group (29)**, and was found to be paraphyletic, because it is at the base of the **Diptilomiopidae clade – 318tax trees (27a)** (Fig. 4.19) in an exclusive group at one node in the 318tax-k10 tree (not confirmed by the topology in the 318tax-k20 tree). The position of some species is uncertain, e.g., in the 66tax-k999 tree (Fig. 4.19) *Catarhinus* and *Cheiracus* were found as sisters, imbedded among the Phyllocoptinae, and outside the Diptilomiopidae group in the tree. Some groupings were, however, identified within **"Rhyncaphytoptinae" part (28)**. The position of the Diptilomiopinae which were recovered as part of this part is feasible and defendable. The ***Apodiptacus* groups (32)** largely constitute Diptilomiopinae species. They are generally morphologically different from the "general morphology" of the species in **"Diptilomiopinae" group (29)**. Species of the latter are morphologically more similar to *Diptilomiopus* spp. The phylogeny of the larger genera, such as *Diptacus*, in ***Apodiptacus* groups (32)** should be studied before one can propose strong hypotheses about their position. For example, *Diptacus gigantorhynchus* (Nalepa, 1892) (Keifer, 1952b), is morphologically more similar to *Diptilomiopus* spp., than some of the other *Diptacus* spp., including *Diptacus sacramentae*, are. The ***Apodiptacus* groups (32)** are not well-supported, but relationships between them and their placement in the Rhyncaphytoptinae are usable hypotheses. The other identified groupings within **"Rhyncaphytoptinae" part (28)** are ***Cheiracus* groups (30)**, **Long-tibia groups (31)**, and ***Rhyncaphytoptus* groups (33)** (Fig. 4.20) are all potential clades.

The monophyly of the Diptilomiopidae is likely. Although the family may be placed within the extended Eriophyidae *sensu* the present study, it is a relatively robust larger clade, and well-defined and differentiated from the remainder of the Eriophyoidea. It is retained as a separate family *on par* with the Eriophyidae (Table 4.10), but is proposed to have a close relationship with the extended Eriophyidae *sensu* the present study.

The Rhyncaphytoptinae are paraphyletic, and possibly polyphyletic, and the Diptilomiopinae is polyphyletic and paraphyletic, but a large part of the Diptilomiopinae *sensu* Amrine *et al*. (2003), may constitute a clade. The Diptilomiopidae subfamilies are currently defined and differentiated on the basis

of one character, having a divided or undivided empodium (Amrine *et al*., 2003). This character was found to be homoplasious within the Eriophyoidea and was not retrieved as a synapomorphy. It is quite conclusive that the Rhyncaphytoptinae and Diptilomiopinae are not monophyletic, and only confuse the real relationships within the Diptilomiopidae. It is proposed that the two subfamilies are retained (Table 4.10) pending more robust hypotheses about the Diptilomiopidae phylogenetic structure, but they are redefined in concordance with the two Diptilomiopidae groupings found in the present study implied by new combinations of the Diptilomiopidae species which were included in the present study. A series of phylogenetic analyses of smaller hypothetical potential clades, as well as the two larger groupings within the Diptilomiopidae are currently undertaken (C. Craemer, *in prep.*).

4.8 CONCLUSIONS

Phylogenetic analyses were undertaken to test the monophyly of suprageneric Eriophyoidea taxa. The analyses were designed to be exploratory, and a large number of taxa were included to sample variation at generic level comprehensively. Additional analyses under different parameters and of data matrices with fewer exemplar taxa were included to test the robustness of groups found, and to alleviate the problem of a small characters:taxa ratio. The hypothesis that the families, subfamilies and tribes of the Eriophyoidea are not monophyletic, with the possible exception of the Diptilomiopidae, was successfully appraised, but not conclusively proven to be true in all regards. Additionally, alternative feasible hypotheses about relationships between Eriophyoidea taxa, and some consequent changes to improve the suprageneric classification of the Eriophyoidea, were proposed. Previous phylogenetic analyses, and their results, were also appraised and compared with the results found in the present study.

The characters and character states for the analyses were scored and coded from published descriptions, and many descriptions were found to be faulty, and some characters were sometimes described in so little detail, that it was hardly possible to define primary homologies from them. Some of the chosen characters could not be scored for all species, or were scored ambiguously, because they were not included in all descriptions, although species descriptions were found to be largely standardized in content. It was confirmed that alpha taxonomic descriptions need to be improved and brought up to standard, otherwise both conventional and more comprehensive systematic studies will suffer the consequences.

The area primarily identified for future improvement in the systematics of the Eriophyoidea, is the improvement of morphological and other systematically useful character data. Descriptions should be standardized, and more systematically informative characters should be found, and this can mostly be achieved by incorporating more modern technologies, such as SEM and molecular studies more extensively and on a routine basis.

There is no doubt that the present phylogenetic study contributed a large amount of data that will be useful and improve the systematics of the Eriophyoidea, quantitatively and qualitatively superior to what a traditional, manual review of the classification would have been able to contribute. The study is also repeatable and testable, which places it on sound scientific ground. As result of the present study I became convinced that phylogenetic analyses should not be seen as a separate process from traditional taxonomy, but rather as a useful tool to be used concurrently with alpha taxonomy. The most important step in phylogenetic studies is the description of primary homologies in alpha taxonomic studies, and the preparation of a good quality data set for the analyses. This should also be the goal for traditional taxonomy, and should not entail extra, unnecessary work. The empirical analyses are used to test the taxonomist's hypotheses of primary homologies and classificatory placements and aid with the development of a natural classification as far as the data allow. Programs (e.g., TNT) are now freely available same as the know-how for undertaking phylogenetic analyses. It should be considered standard by eriophyoid systematists that description of new supraspecific taxa should incorporate phylogenetic analyses.