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# A cladistic analysis of the Eriophyoidea (Acari: Prostigmata): tests of monophyly of families

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## Abstract

A cladistic analysis of relationships at the generic level was carried out for the Eriophyoidea. The analysis was based on a total of thirty-five characters drawn from the examination of investigated specimens and original descriptions of species in 17 genera examined. These characters were polarized by comparison with the generalized Tydeidae, which was chosen as the outgroup. Three equally parsimonious trees were produced using branch and bound procedure of PAUP after successive character weighting. Three distinct clades were revealed in the strict consensus tree: clade A (*Pentasetacus*, (*Novophytoptus*, *Mackiella*)), clade B (*Phytoptus*) and clade C (*Trisetacus*, (*Nalepella*, ((((*Sierraphytoptus*, *Ashieldophyes*), *Phyllocoptes*), ((*Aberoptus*, *Cecidophyes*), (*Nothopoda*, *Eriophyes*))), (((*Diptacus*, *Diptilomiopus*), *Rhinophytoptus*), *Rhyncaphytoptus*)))). The Phytoptidae is paraphyletic, whereas the Eriophyidae (+ *Sierraphytoptinus*) and the Diptilomiopidae are both monophyletic. The current classification systems within the Eriophyoidea are appraised, with suggestions on further study on the phylogeny of the superfamily, and on the revision of the classification systems to reflect the natural relationships at the familial and generic levels.

**Key words**: Eriophyoidea, monophyly, phylogeny, classification

## Introduction

The cladistic analysis of the Eriophyoidea (Acari: Prostigmata) is discussed as part of a research project on the systematics and phylogeny of the genera of the superfamily Eriophyoidea.

The important role of eriophyoid mites in damaging plants, transmitting plant diseases, and controlling weeds has led to extensive research on various aspects of this group, including taxonomy, morphology, physiology, cytogenetics and ecology (Nault *et al.* 1967; Jeppson *et al.* 1975; Easterbrook 1978, 1979; Andrés 1982; Keifer *et al.* 1982; Helle & Wysoki 1983; Krantz & Ehrensing 1990; Kuang *et al.* 1992; Amrine & Stasny 1994; Kuang *et al.* 1995;). The major problem has been the lack of well-corroborated hypotheses of relationships in the Eriophyoidea.

The concept of the Eriophyoidea or Tetrapodili as a natural group within the suborder Prostigmata is virtually uncontested. The superfamily is well defined by a number of synapomorphies: two pairs of legs with few setae; feathered or rayed empodia; absence of stigmata; peritremes, or tracheae; transverse genital opening (Krantz 1978). In contrast, considerable disagreement exists regarding the relationships within the Eriophyoidea. Four main classification systems of eriophyoid mites have been proposed. Shevtchenko (1974) suggested three superfamilies within the Tetrapodili: Phytoptoidea, including the families Phytoptidae and Sierraphytoptidae; Trisetoidea, including Trisetidae and Nalepellidae; Eriophyoidea, including Eriophyidae, Phyllocoptidae and Rhyncaphytoptidae. This system has been used by some acarologists in the former Soviet Union and other eastern European countries (Kuang 1986). Boczek *et al.* (1989) divided the Eriophyoidea into 6 families, namely the Ashieldophyidae, Pentasetacidae, Nalepellidae, Phytoptidae, Eriophyidae and Diptilomiopidae. The most widely used system was devised by Newkirk & Keifer (1975), who divided the Eriophyoidea into three families: Nalepellidae, Eriophyidae and Rhyncaphytoptidae. Recently Amrine & Stasny (1994) divided the Eriophyoidea into three families: Phytoptidae, Eriophyidae and Diptilomiopidae; their much more detailed system is quite similar to Newkirk & Keifer's in terms of the taxonomic structure. All the classification systems were established largely by character differentiation; their primary purpose is to provide identification guides, not to reflect the evolutionary history. A few analyses of relationships between different families in the Eriophyoidea (Huang & Huang 1990; Kuang *et al.* 1992; Sukhareva 1994; Kuang *et al.* 1995) have failed to provide strong support for any of the existing classification systems or to reinforce the notion that the existing classifications do not reflect natural relationships.

In view of these problems, the goal of the present study is to report the results of a cladistic analysis of relationships at the generic level in the Eriophyoidea, and to appraise the current classification system at the familial level.

## Selection of taxa

The Eriophyoidea consist of ca. 240 described genera (Amrine & Stasny 1994). Limited by the computer power to find the most parsimonious cladogram in a reasonable amount of time and our own research budget and time, we selected 16 typical genera; six are type genera of the six tribes in the Phytoptidae (*Pentasetacus* Schliesske, *Trisetacus* Keifer and *Nalepella* Keifer; *Novophytoptus* Roivainen, *Phytoptus* Dujardin, *Mackiella* Keifer); six are type genera of the six subfamilies of the Eriophyidae (*Aberoptus* Keifer, *Nothopoda* Keifer, *Ashieldophyes* Mohanasundaram, *Cecidophyes* Nalepa, *Eriophyes* von Siebold, *Phyllocoptes* Nalepa); two genera each from the two subfamilies of the Diptilomiopidae (*Diptacus* Keifer, *Diptilomiopus* Nalepa, *Rhinophytoptus* Liro and *Rhyncaphytoptus* Keifer). The generalized Tydeidae was chosen as the outgroup, because the Tydeoidea was recently shown to be a sister group of the Eriophyoidea (Norton *et al.* 1993).

## Character analyses

This section presents a survey of the characters used in the cladistic analysis of the Eriophyoidea. Terminology and notation follow those of Grandjean (1939, 1947), which were applied to the Eriophyoidea by Lindquist (in press, not seen by us; cited by Flechtmann 1995), and Newkirk and Keifer (1975) in parentheses. Some characters are illustrated in Figs. 1-7. The character states recognized are briefly outlined, accompanied by their respective codes, after which a more detailed discussion follows. The data are summarized in the character state matrix of Table 1. Amrine's classification system (Keifer's classification system), which is familiar to many acarologists, is used in the following character discussion to facilitate understanding.

1. Setae *vi* ( median anterior setae) (Fig. 1): (0) present; (1) absent.

*Vi* are a pair of setae in the outgroup Tydeidae, but there is only a single seta on the median anterior part of prodorsal shield in some eriophyoid mites. It only occurs in some genera of the Phytoptidae. It is present in *Pentasetacus*, *Trisetacus* and *Nalepella*, but is absent in *Novophytoptus*, *Phytoptus*, *Mackiella*, *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus*, and *Rhyncaphytoptus*.

2. Setae *ve* (anterior pair of prodorsal shield setae) (Fig. 1): (0) present; (1) absent.

*Ve* are the second pair of setae on the prodorsal shield. They occur in the Phytoptidae (except *Boczekella* Farkas, *Trisetacus*, *Nalepella*, *Phantacrus* Keifer and *Setoptus* Keifer), but are absent in the families Eriophyidae and Diptilomiopidae.

3. Dorsal tubercles: (0) absent; (1) present.

Dorsal tubercles are located on the posterior part of the prodorsal shield. Their presence, absence, location (on rear margin, ahead of rear margin, at lateral margins), orientation (longitudinal, transverse or oblique) and shape (cylindrical, on tapered flange) are often used to differentiate the subfamilies, tribes, genera and species. The dorsal tubercles are absent in the Tydeidae but present in most genera of the superfamily Eriophyoidea, except *Ashieldophyes* and *Cecidophyes*.

4. Setae *sc* (prodorsal setae) (Fig. 1): (0) present; (1) absent.

*Sc* setae are located on the dorsal tubercles in the genera of the Eriophyoidea; exceptions are: *Asetacus* Keifer, *Asetadiptacus* Carmona, *Diptilomiopus*, *Neodialox* Mohanasundaram, *Neodiptilomiopus* Mohanasundaram, *Rhynacus* Keifer, *Vilaia* Chandrapatya & Boczek and *Vimola* Chandrapatya & Boczek. In genera that do not have dorsal tubercles such as those in the tribe Cecidophyini Keifer, *sc* are absent. *Sc* setae are present on the prodorsal shield in the Tydeidae. The direction of *sc* is often used to differentiate the subfamilies, tribes, genera and species in the Eriophyoidea. The length of *sc* is used by some acarologists to separate different species.

As for *sc* in the genus *Ashieldophyes*, Mohanasundaram (1984) stated that the genus is characterised by the absence of dorsal shield and setae. Recent careful examination of the specimens of this genus by Dr. Amrine (personal communication) reveals that prodorsal setae *sc* are present, and they are located on the outer margins of the shield, about 1/3 back from the front margin.

5. Naso (anterior lobe of prodorsal shield): (0) absent; (1) present. (unordered).

Naso shows a variety of forms in the Eriophyoidea. Many genera in the family of Phytoptidae do not have this character, while most Phyllocoptinae mites of the Eriophyidae have the lobe. Among the genera studied, the naso is present in *Pentasetacus*, *Nalepella*, *Sierraphytoptus*, *Mackiella*, *Cecidophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*, but absent in *Trisetacus*, *Novophytoptus*, *Phytoptus*, *Aberoptus*, *Nothopoda*, *Ashieldophyes* and *Eriophyes*.

6. Spine(s) on the naso: (0) absent; (1) present.

Not all the nasos have spines. The spines are present in nasos of *Acadicrus* Keifer, *Acarhynchus* Keifer, *Aculus* Keifer, *Dicruvasates* Abou-Awad & El-Borolossy, *Neoepitrimerus* Kuang & Li, *Neoshevtchenko* Kuang & Zhuo, *Sierraphytoptus* and *Tetraspinus* Boczek. Among the genera studied, only *Sierraphytoptus* shows a spine on the naso.

7. Location of setae *sc*: (0) ahead of the rear margin; (1) at the rear margin.

*Sc* setae are located ahead of rear margin in the genera of *Pentasetacus*, *Trisetacus*, *Nalepella*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Nothopoda*, *Ashieldophyes Eriophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*; and at the rear margin in the genera *Novophytoptus* and *Aberoptus*. They are absent in *Cecidophyes*. There are often two pairs of *sc* setae in the Tydeidae and other prostigmatid families. Setae *sc* of *Ashieldophyes* are located on the outer margins of the shield, about 1/3 back from the front margin (Amrine, personal communication).

8. Direction of setae *sc*: (0) forward; (1) backward; (2) upward or inward.

The prodorsal setae *sc* in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Phytoptus*, *Mackiella*, *Diptacus*, *Rhinophytoptus* and *Rhyncaphytoptus* are directed forward; and those in *Novophytoptus*, *Aberoptus* and *Nothopoda* are directed backward. Setae *sc* in *Ashieldophyes* are directed upward and laterally (Amrine, personal communication). Usually setae *sc* directing forward or backward are long, whereas those directing upward or inward in *Sierraphytoptus* and *Phyllocoptes* are short.

The different understanding of the location and direction of setae *sc* has caused turmoil in the taxonomy of the Eriophyoidea. In their publication of "Revision of types of *Eriophyes* and *Phytoptus*", Newkirk and Keifer (1971) removed species from *Aceria* and reassigned them to the genus *Eriophyes*; the genus *Aceria* discontinued. Mites previously assigned to *Phytoptus* were assigned to the new genus, *Phytocoptella* (Newkirk & Keifer 1971). Their work was based on careful library research and the discovery of older species names, having priority, which resulted in the designation of types and thus the redefinition of generic concepts (Amrine & Stasny 1994). Shevtchenko (1974b), Lindquist *et al.* (1977), and Lindquist and Manson (1987) objected to the designation of the new types for *Eriophyes* and *Phytoptus* because of long established usage, and began petitions to the International Commission of Zoological Nomenclature for the restoration of the types for *Aceria*, *Eriophyes* and *Phytoptus*. In March 1989, the Commission published Opinion 5721 which restored the former uses of the disputed genera and set the types for each genus as follows: 1. *Eriophyes* von Siebold, type species *Phytoptus pyri* Pagenstecher; 2. *Phytoptus* Dujardin, type species *Phytoptus avellanae* Nalepa; 3. *Aceria* Keifer, type species *Eriophyes tulipae* Keifer; and 4. *Colomerus* Newkirk & Keifer, type species *Eriophyes gardeniella* Keifer. As a direct result of this confusion, many acarologists since 1971 have placed eriophyoid mites into the wrong genus (especially the confusion of *Eriophyes* and *Aceria*) and sometimes, in the wrong family (Amrine & Stasny 1994). It is hoped that researchers working on eriophyoid mites will now be able to correctly assign species due to the Opinion 5721 of International Commission of Zoological Nomenclature (1989), and Catalog of the Eriophyoidea (Acarina: Prostigmata) of the world by Amrine and Stasny (1994).

9. Body shape: (0) worm-like; (1) fusiform (spindle-shaped).

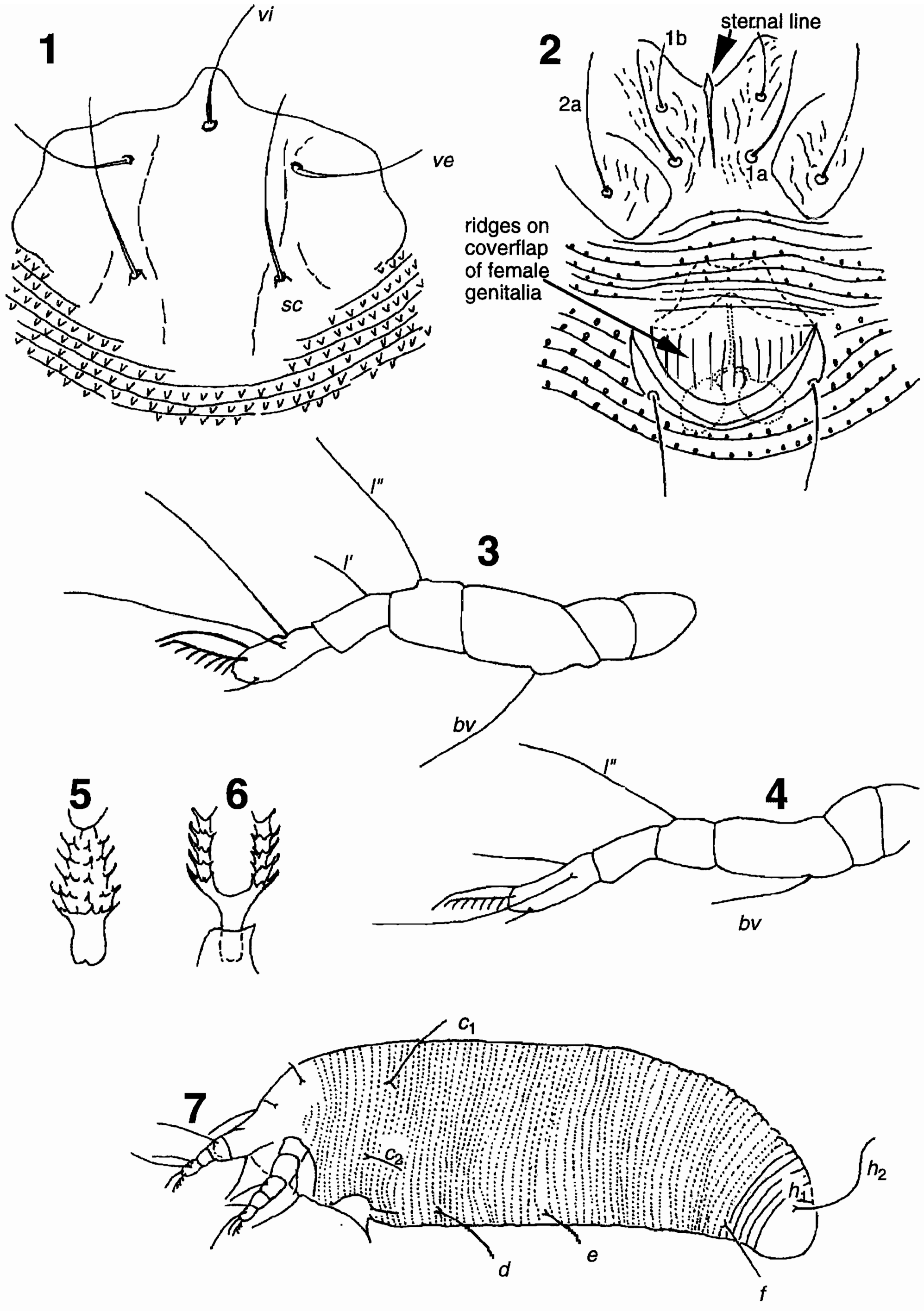
The body shape varies among the Eriophyoidea. *Pentasetacus*, *Trisetacus*, *Novophytoptus*, *Phytoptus*, *Mackiella*, *Nothopoda*, *Ashieldophyes* and *Eriophyes* have the worm-like body; *Nalepella*, *Sierraphytoptus*, *Aberoptus*, *Cecidophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus* have the spindle-shaped body. Many genera in the Phytoptidae and a few genera in the Eriophyidae have the worm-like body, whereas many genera in the Eriophyidae and all genera in the Diptilomiopidae except the genus *Stenarhynchus* Mohanasundaram have the spindle-shaped body.

10. Cheliceral curvature: (0) evenly curved; (1) abruptly curved.

The chelicerae in the families Phytoptidae and Eriophyidae are evenly down-curved, whereas those in the family Diptilomiopidae abruptly bent down near base. Gnathosoma in the Diptilomiopid mites are large in comparison to body, attenuate, and contain long cheliceral stylet. Mites of this family are often called big-rostrum mites. They are leaf vagrants only, rarely causing much damage to their hosts (Jeppson *et al.* 1975). Among the genera examined, the chelicerae curve abruptly in *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*.

11. Location of genital area: (0) not appressed to coxae II; (1) appressed to coxae II.

All the genera in the subfamily Cecidophyinae of the Eriophyidae have a genital area that is appressed to the coxal area. In all the other subfamilies, the genital area is usually not appressed to the coxal area and there are several ventral annuli between the coxal area and the genital area.



**FIGURES. 1-7.** A sample of characters and notations in the Eriophyoidea. 1, prodorsal shield and associated setae of *Pentasetacus araucariae* Schliesske; 2, coxal area of *Aceria tulipae* (Keifer); 3, foreleg of *A. tulipae*; 4, hindleg of *A. tulipae*; 5, simple empodium; 6, divided empodium; 7, lateral view of *Phytoptus avellanae* Nalepa.

The number of ventral annuli between the genital area and the coxae has been used by a few acarologists to describe species. The genital area in *Aberoptus*, *Ashieldophyes* and *Cecidophyes* are appressed to the coxal area; whereas the genital area in the other genera are not appressed to the coxal area. The genital area in the Tydeidae is far away from the second coxae.

12. Setae $c_1$ (subdorsal setae) (Fig. 7): (0) present; (1) absent.

Setae $c_1$ are present only in 10 genera of the Phytoptidae (*Acathrix* Keifer, *Anchiphytoptus* Keifer, *Austracus* Keifer, *Boczekella*, *Fragariocoptes* Roivainen, *Pentasetacus*, *Phytoptus*, *Prothrix* Keifer, *Sierraphytoptus* and *Trisetacus*) and absent in most other genera of the Eriophyoidea. The presence, ring position, length, spacing etc. of $c_1$ are used to describe and differentiate the subfamilies, genera, tribes and species.

13. Setae *d* (first ventral setae) (Fig. 7): (0) present; (1) absent.

With the exception of *Ashieldophyes*, all genera examined have setae *d*. In almost 240 reported genera of the Eriophyoidea, setae *d* are absent in the following 15 genera: *Acamina* Keifer, *Ashieldophyes*, *Cecidodectus* Nalepa, *Diptilorhynchus* Mondal & Chakrabarti, *Hemiscolocenus* Mohanasundaram, *Hornophyes* Mohanasundaram, *Knorella* Keifer, *Neocupacarus* Das & Chakrabarti, *Neodicrothrix* Mohanasundaram, *Neomesalox* Mohanasundaram, *Proneotegonotus* Mohanasundaram, *Retracus* Keifer, *Scolocenus* Keifer, *Schizacea* Keifer and *Tumescoptes* Keifer. The presence, ring position, length and spacing of setae *d* are often used to describe and differentiate genera and species.

14. Setae *e* (second ventral setae) (Fig. 7): (0) present; (1) absent.

With the exception of the genus *Ashieldophyes*, all genera examined have setae *e* which are usually the shortest of the three pairs of ventral setae. Among 240 described genera of the Eriophyoidea, setae *e* are absent in the following 19 genera, namely, *Acamina* Keifer, *Amerineus* Flechtmann, *Asetilobus* Manson, *Ashieldophyes*, *Cecidodectus* Nalepa, *Dicrothrix* Keifer, *Hornophyes* Mohanasundaram, *Knorella* Keifer, *Neocupacarus* Das & Chakrabarti, *Neodicrothrix* Mohanasundaram, *Paracolopodacus* Kuang & Huang, *Paraphytoptella* Keifer, *Phyllocoptacus* Mohanasundaram, *Proneotegonotus* Mohanasundaram, *Prophyllocoptes* Mohanasundaram, *Ramaculus* Manson, *Schizacea* Keifer, *Surapoda* Boczek & Chandrapatya and *Tumescoptes* Keifer. The presence, ring position, length and spacing of setae *e* are often used to describe and differentiate genera and species.

15. Setae *1b* on coxae I (first pair of forecoxal setae) (Fig. 2): (0) present; (1) absent.

Setae *1b* are absent in the forecoxae of *Nothopoda* and *Diptilomiopus*, and present in those of other genera examined. Mohanasundaram (1984) stated that *Ashieldophyes* is characterised by the absence of dorsal shield and setae, first and second ventral setae, and first and second coxal setae. After careful examination of the specimen, Dr. Amrine (personal communication) found that all three coxal setae are present. Usually there are two pairs of setae on the forecoxae and one pair on the hindcoxae. Variation occurs in the forecoxal setae, but not in the hindcoxal setae.

16. Seta *bv* on femur I (forefemoral seta) (Fig. 3): (0) present; (1) absent.

A single seta *bv* is usually located near mid-ventral 1/2 on the forefemur. The presence, length and position are used to describe and differentiate genera and species. It is present in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phyllocoptes*, *Rhinophytoptus* and *Rhyncaphytoptus*, but absent in *Novophytoptus*, *Diptacus* and *Diptilomiopus*.

17. Seta *l''* on genu I (foregenual seta) (Fig. 3): (0) present; (1) absent.

With the exception of the genus *Diptilomiopus* whose seta $l''$ is absent, all the other genera examined have seta $l''$. Seta $l''$ is always dorsal or laterodorsal, and directed upward. The presence and length of seta $l''$ are used to differentiate genera and species.

18. Seta $l'$ on tibia I (foretibial seta) (Fig. 3): (0) present; (1) absent.

Seta $l'$ is usually located at basal 1/3 of tibia I and is a very important character for differentiating tribes and genera. The presence, length and position on tibia are often used to describe genera and species. Among the genera examined, seta $l''$ is absent on tibia I of *Aberoptus*, *Nothopoda* and *Diptilomiopus*, but is present in those of other genera.

19. Seta *bv* on femur II (hind femoral seta) (Fig. 4): (0) present; (1) absent.

The hind femoral seta *bv* is located at mid-ventral 1/2 on the hindfemur. The presence, length and position are used to describe and differentiate genera and species. It is present in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phyllocoptes*, *Rhinophytoptus* and *Rhyncaphytoptus*, but absent in *Novophytoptus*, *Diptacus* and *Diptilomiopus*.

20. Seta $l''$ on genu II (hind genual seta) (Fig. 4): (0) present; (1) absent.

With the exception of the genus *Diptilomiopus*, all the other genera examined have seta $l''$ on genu II. The presence or absence of seta $l''$ on genu II is often used to differentiate tribes and genera in the Eriophyoidea.

21. Tibia: (0) normal; (1) reduced or fused.

In the subfamilies Aberoptinae and Nothopodinae, tibiae are reduced or completely fused with tarsi; foretibiae never bear setae. All the other eriophyoid mites have normal tibiae which are always distinct from tarsi, fortibial seta nearly always present except in a few genera. Among the genera studied, tibiae in the genera of *Aberoptus* and *Nothopoda* are reduced or fused with tarsi, whereas tibiae in other genera do not show this reduction.

22. Solenidion $\phi$ on tibia I (solenidion on foretibia): (0) present; (1) absent.

Solenidion $\phi$ is a lateral foretibial spur. The foretibiae in the Phytoptidae usually bear $\phi$, while those of the Eriophyidae and Diptilomiopidae rarely do. Solenidion $\phi$ is present in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Phytoptus* and *Mackiella*, but absent in *Novophytoptus*, *Sierraphytoptus*, *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*.

23. Ridge(s) or trough(s) on the hysterosoma: (0) absent; (1) present.

A slight longitudinal subdorsal furrow is present on the hysterosoma of *Diptacus*. A central ridge is present on hysterosoma in *Diptilomiopus*. The ridge is not stable, and is not very obvious in the genus *Rhyncaphytoptus*; in other words, ridge appear in some species and does not appear in other species of *Rhyncaphytoptus*. Ridge(s) or trough(s) are absent in other genera studied.

24. Empodium (Fig. 6): (0) simple (normal); (1) not normal (divided, palm-shaped etc.).

The length, position, number of rays, configuration (divided or undivided), and shape of empodium are important for distinguishing subfamilies, tribes, genera and species. Empodia in *Pentasetacus*, *Diptacus* and *Diptilomiopus* are divided, those in *Aberoptus* are reduced to a bristle; and those in other genera are normal (undivided). Empodia in the Tydeidae are undivided.

25. Setae $c_2$ (lateral setae) (Fig. 7): (0) present; (1) absent.

With the exception of *Diptilomiopus*, all the other genera examined have setae $c_2$. In the Eriophyoidea, setae $c_2$ are absent in only 15 genera (*Acarhis* Keifer, *Africus* Smith Meyer & Ueckermann, *Amrineus* Flechtmann, *Dacundiopus* Manson, *Diptilorhynacus* Mondal, Ghosh & Chakrabarti, *Diptilomiopus*, *Lambella* Manson, *Levonga* Manson, *Pseudodiptacus* Chakrabarti, Ghosh & Das, *Rhynacus* Keifer, *Thacra* Keifer, *Vilaia* Chandrapatya & Boczek and *Vimola* Boczek). It is interesting that 13 of the above 15 genera belong to the family Diptiliomiopidae; only two genera (*Amerineus* and *Thacra*) belong to the Eriophyidae. The presence, ring position, length and spacing of setae $c_2$ are used to describe genera and species.

26. Ridges of the female genital coverflap (Fig. 2): (0) absent; (1) one longitudinal row; (2) two longitudinal rows or transverse lines.

Scoring or sculpture of female genital coverflap is a very important character which is used to differentiate subfamilies, tribes, genera and species. In the Cecidophyinae, the female genitalia, which noticeably project from hysterosoma venter, are appressed to coxae; longitudinal ridges of female genital coverflap typically are in 2 ranks. In other subfamilies in the Eriophyoidea, genitalia lie more on level with hysterosoma venter, and are not appressed to coxae; female genital coverflap are variably sculptured, and ridges are rarely in 2 ranks. Usually female genital coverflap in the Phytoptidae are without ridges except in *Fragariocoptes* Roivainen.

Among the genera studied, there is no sculpture on the female genital coverflap of *Pentasetacus*, *Trisetacus*, *Nalepella*, *Novophytoptus*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Nothopoda*, *Ashieldophyes*, *Diptilomiopus* and *Rhinophytoptus*. There are 2 ranks of ridges on the female genital coverflap of *Cecidophyes*. On the female genital coverflap of *Eriophyes*, *Phyllocoptes* and *Rhyncaphytoptus*, sculpture varies. Some species have smooth coverflap, while others have one longitudinal row ridge.

27. Spatulate or shovel-shaped projections on legs: (0) absent; (1) present.

In the subfamily Aberoptinae of Eriophyidae, spatulate or shovel-shaped projections are present, either on rostral termen, or on tarsi; legs lacking spatulate appendages are very stout; segments are shortened or combined. With the exception of the genus *Aberoptus*, all the other genera studied and the Tydeidae do not have spatulate or shovel-shaped projections on legs. The location of spatulate or shovel-shaped projections is used to differentiate genera and species within the Aberoptinae.

28. Lateral opisthosomal differentiation: (0) absent; (1) differentiate into dorsal tergites and ventral sternites.

The bodies of mites in *Pentasetacus*, *Trisetacus*, *Novophytoptus*, *Phytoptus*, *Nothopoda*, *Ashieldophyes* and *Eriophyes* are elongate and wormlike, whereas those in *Nalepella*, *Sierraphytoptus*, *Mackiella*, *Aberoptus*, *Cecidophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus*, *Rhyncaphytoptus* are more or less fusiform and are differentiated into dorsal tergites and ventral sternites.

29. Dorsal annuli: (0) not extended laterally; (1) extended laterally or with indentations.

With the exception of *Sierraphytoptus* whose dorsal annuli project a little laterally, all the other genera examined have normal dorsal annuli which do not extend laterally. The extension of dorsal annuli in some eriophyoid mites is seen as a peculiar character, and is used to describe and differentiate genera.

30. Sternal line: (0) absent; (1) present.

Sternal line is absent in *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes* and the

Tydeidae, but is present in the genera *Pentasetacus*, *Novophytoptus*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Phyllocoptes*, *Diptacus*, *Rhinophytoptus* and *Rhyncaphytoptus*. It is unstable in *Trisetacus*, *Nalepella*, *Eriophyes*, *Diptilomiopus* among which some species have sternal line whereas others do not. The presence, development and shape of sternal line are important for differentiating and describing genera and species.

31. Setae $h_1$ (accessory setae) (Fig. 7): (0) present; (1) absent.

Setae $h_1$ are present in the genera *Pentasetacus*, *Trisetacus*, *Nalepella*, *Novophytoptus*, *Phytoptus*, *Sierraphytoptus*, *Mackiella*, *Ashieldophyes* and the family Tydeidae; and absent in the genera *Aberoptus*, *Nothopoda* and *Cecidophyes*. They are present in some species and absent in other species in the genera *Eriophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*. The length, presence and spacing of setae $h_1$ are used to decribe genera and species.

32. Spermathecal tubes: (0) long; (1) short.

Spermathecal tubes are usually long in the Phytoptidae and short in the Eriophyidae and Diptilomiopidae. They are long in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Novophytoptus*, *Phytoptus*, *Sierraphytoptus* and *Mackiella*, but short in *Aberoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phylllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*. The orientation, length, position of spermathecal tubes and spermathecae are often used to describe species. Due to the techniques of specimen preparation and the limitation of microscope, the spermathecal tubes may not be discernible and therefore not given in the descriptions of some species.

33. Length of setae *sc*: (0) very long; (1) long; (2) short; (3) absent.

Length of *sc* is a relative concept. Very long means that the seta is longer than the distance between 2 tubercles; long means the seta is longer than half the distance; short means the seta is shorter than half the distance. *Sc* setae are very long in *Pentasetacus*, *Trisetacus*, *Nalepella*, *Novophytoptus*, and *Phytoptus*, long in *Aberoptus*, *Eriophyes*, *Phyllocoptes* and *Rhyncaphytoptus*, and short in *Sierraphytoptus*, *Nothopoda*, *Ashieldophyes*, *Diptacus* and *Rhinophytoptus*. They are absent in *Cecidophyes* and *Diptilomiopus*.

34. Microtubercles on dorsal annuli : (0) absent; (1) present.

Microtubercles are absent on the dorsal annuli of *Sierraphytoptus*, *Mackiella* and *Ashieldophyes*, but present on dorsal annuli of *Pentasetacus*, *Trisetacus*, *Novophytoptus*, *Phytoptus*, *Aberoptus*, *Nothopoda*, *Cecidophyes* and *Eriophyes*. They vary among the species in *Nalepella*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus* and *Rhyncaphytoptus*. Taking *Diptacus* as an example, there are microtubercles on dorsal annuli in *D. flocculentus* Keifer, *D. ragarifoliae* Keifer, *D. gigantorubra* Xin & Dong, *D. prunorum* (Keifer), *D. pseudocerasis* Kuang & Hong, *D. rubra* Keifer and *D. swensoni* Keifer; no microtubercles on dorsal annuli in *D. aceris* Kuang & Hong, *D. calicoryli* (Keifer), *D. castaneae* Kuang & Feng, *D. gigantorhynchus* (Nalepa), *D. guangxiensis* Kuang & Hong, *D. liquidambaris* Kuang & Feng, *D. maackiae* Kaung & Feng, *D. sacramentae* (Keifer) and *D. ulmi* Kuang & Huang. When microtubercles are present on dorsal annuli, there are variation in the form (triangle, bead, elongate, blunt, rounded etc.), location (a little ahead of ring margin, on ring margin, reaching ring margin etc.) and density.

35. Location comparison between setae *1a* and *2a* (Fig, 2): (0) *1a* ahead of *2a*; (1) *1a* same line as *2a*; (3) *1a* behind *2a*.

The location of coxal setae (*1b*, *1a* and *2a*) is quite stable, although few acarologists use them in describing the eriophyoid mites. Keifer (1938) was the first to compare coxal setal locations, and Smith Meyer always compares coxal seta locations in her descriptions (e.g. Smith Meyer 1981, 1989; Smith Meyer & Ueckermann 1995). In the genera *Trisetacus*, *Nalepella*, *Phytoptus*, *Sierraphytoptus*, *Nothopoda*, *Ashieldophyes*, *Cecidophyes*, *Eriophyes*, *Phyllocoptes*, *Diptacus*, *Diptilomiopus*, *Rhinophytoptus*, *Rhyncaphytoptus*, setae *1a* are ahead of setae *2a*; in the genera *Pentasetacus*, *Mackiella* and *Aberotptus*, setae *1a* are almost on the same line as setae *2a*; and in the genus *Novophytoptus*, setae *1a* are behind of setae *2a*.

**TABLE 1.** Character state matrix for the outgroup and the examined eriophyoid genera

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 |
| Tydeidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pentasetacus* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Trisetacus* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 |
| *Nalepella* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | 0 | 0 | 0 | ? | 0 |
| *Novophytoptus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 |
| *Phytoptus* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Sierraphytoptus* | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Mackiella* | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Aberoptus* | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Nothopoda* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 |
| *Ashieldophyes* | 1 | 1 | 0 | 0 | 0 | 0 | ? | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| *Cecidophyes* | 1 | 1 | 0 | 1 | 1 | 0 | ? | ? | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 1 | 0 |
| *Eriophyes* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 0 | 0 | ? | ? | 1 | 1 | 1 | 0 |
| *Phyllocoptes* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | ? | 0 | 1 | 0 | 1 | ? | 1 | 1 | ? | 0 |
| *Diptacus* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | ? | 0 | 1 | 0 | 1 | ? | 1 | 2 | ? | 0 |
| *Diptilomiopus* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | ? | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | ? | ? | 1 | 3 | ? | 0 |
| *Rhinophytoptus* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | ? | 1 | 2 | ? | 0 |
| *Rhyncaphytoptus* | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 0 | ? | 0 | 1 | 0 | 1 | ? | 1 | 1 | ? | 0 |

## Analysis and results

Characters of each genus were determined by examining specimens and original descriptions representing as many species as possible. The character state matrix given in Table 1 was analyzed using the parsimony program PAUP 3.0 (Swafford, 1991) on a Macintosh Centris 650 Computer. In Table 1, unknown or unstable character states are coded '?'. All characters are ordered except the character 5 (the prodorsal shield lobe). The family Tydeidae of Tydeoidea, which is the sister group of the Eriophyoidea according to Norton *et al.* (1993), was selected as the outgroup.

The branch and bound procedure produced 33 equally parsimonious trees (length = 79; consistency index = 0.506; retention index = 0.606). According to Farris (1988), successive weighting may have the advantage of providing a means of basing groups on more reliable characters without making prior decisions on weighting. Successive weighting was used to identify if there were more characters in the present character set supporting monophyletic groups. Branch and bound procedure produced 3 equally parsimonious trees after the first and second reweighting. Consensus procedure produced 1 strict consensus tree (Fig. 8).

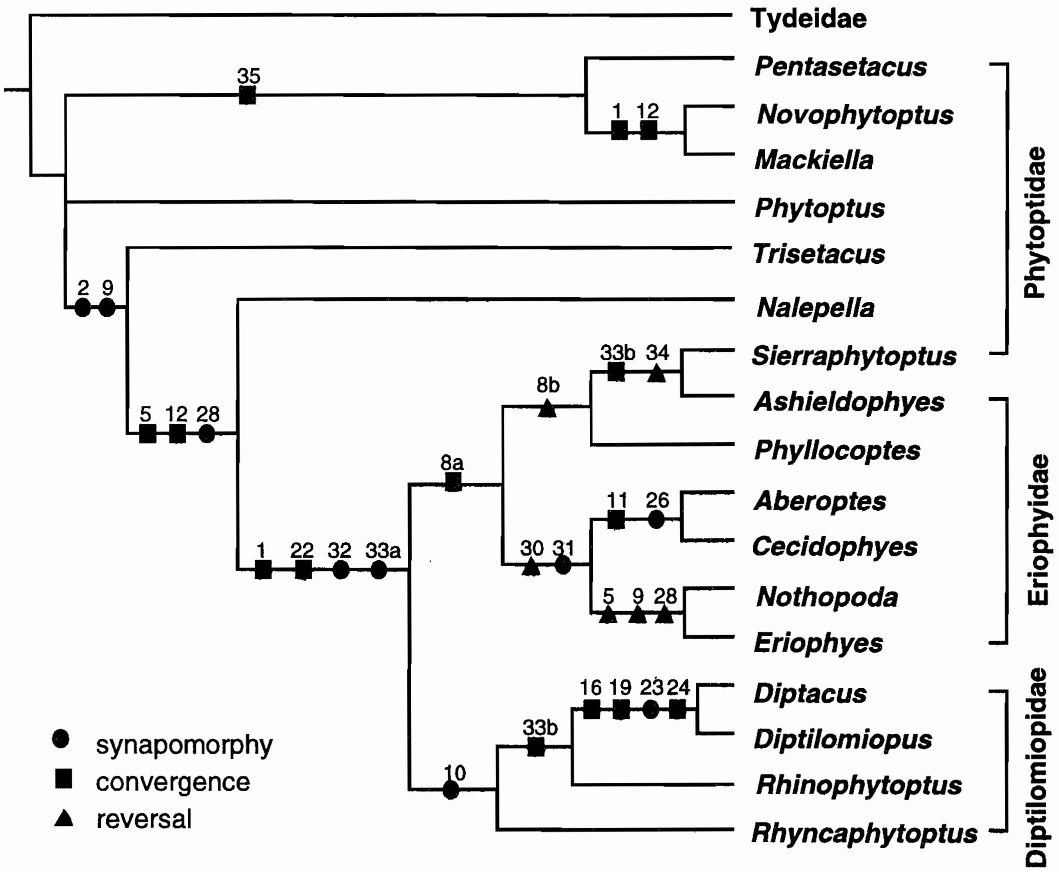


FIGURE 8. A cladogram showing the hypothetical relationships among selected genera of the Eriophyoidea. It is the strict concensus tree of three equally parsimonious trees. 8a = *sc* directing forward; 8b = *sc* directing upward or inward; 33a = *sc* long; 33b = *sc* short. See text for details.

The monophyly of *Novophytoptus* + *Mackiella* is supported by two synapomorphies: the absence of seta *vi* (character 1) and setae $c_1$ (character 12). The monophyly of *Novophytoptus* + *Mackiella* + *Pentasetacus* is supported by one synapomorphy: coxal setae *1a* not ahead of coxal setae *2a*.

*Sierraphytoptus* + *Ashieldophyes* forms a monophyletic group, based on two synapomorphies: short setae *sc* (character 33) on prodorsal shield and presence of microtubercles on dorsal annuli (character 34). The group (*Phyllocoptes*, (*Sierraphytoptus*, *Ashieldophyes*)) is united by upward or inward setae *sc* on the prodorsal shield (character 8). The monophyly of *Aberoptus* +

*Cecidophyes* is supported by two synapomorphies: female genital area close to coxae (character 11) and presence of ridges on female genital coverflap (character 26). The monophyly of *Nothopoda* and *Eriophyes* is based on three synapomorphies: the absence of naso (character 5), worm-like body (character 9) and dorsoventrally subequal opisthosoma (character 28). The sister-group relationship of (*Aberoptus*, *Cecidophyes*) and (*Nothopoda*, *Eriophyes*) is supported by the sternal line (character 30) and setae $h_1$ (character 31).

*Diptacus* and *Diptilomiopus* form a monophyletic group, based on four synapmorphies: the absence of setae *bv* on femur I (character 16), the absence of setae *bv* on femur II (character 19), the presence of ridges on hysterosoma (character 23) and divided empodium (character 24). The group ((*Diptacus*, *Diptilomiopus*), *Rhinophytoptus*) forms a monophyletic group, based on the short *sc* on the prodorsal shield. The Diptilomiopidae, represented by (((*Diptacus*, *Diptilomiopus*), *Rhinophytoptus*), *Rhyncaphytoptus*), forms a monphyletic group, based on the abruptly curved chelicerae (character 10).

All the genera in the Diptilomiopidae + Eriophyidae, and the genus *Sierraphytoptinus* from Phytoptidae form a monophyletic group, supported by four synapmorphies: the absence of setae *vi* (character 1), the absence of solenidion on foreleg (character 22), short spermathecal tubes (character 32) and reduced length of setae *sc* (character 33). The sister group of this large group is *Nalepella*; this is based on two synapmorphies: the absence of setae $c_1$ (character 12) and differentiated opisthosoma (character 28) (with reversal in *Nothopoda* and *Eriophyes*). The monophyly of above genera and *Trisetacus* is supported by two synapmophies: the absence of setae *ve* (character 2) and the fusiform body (character 9) (with reversal in *Nothopoda* and *Eriophyes*).

## Discussion

Studies on the higher level relationships in the Eriophyoidea are few (e.g. Huang & Huang 1990; Kuang *et al.* 1992). Both phenetic and cladistic approaches have been used.

Huang and Huang (1991) used both phenetic and cladistic methods to investigate the phylogenetic relationships among 15 eriophyoid species which belong to 11 subfamilies. Their results show that phenetic analysis based on morphometric measurements failed to reveal natural groups and the phenograms are inconsistent with classical taxonomy. In their cladistic analysis of the same 15 species, Huang and Huang (1990) did not select an outgroup; character polarization was based on the assumption that the Diptilomiopidae have plesiomorphic states of characters. They used the program "Phylip" to construct the cladogram and reported a tree with length 32. They did not mention what procedure they used and whether the reported tree was the shortest one. We did an analysis of their data (in their Table 5) using PAUP; the branch and bound procedure produced 62 shortest trees of equal length 28. Clearly, their tree of 32 steps is not the shortest. Nevertheless, Huang and Huang (1991) concluded that both Eriophyidae and "Rhyncaphytoptidae" (i.e. Diptilomiopidae) are monophyletic, whereas "Nalepellidae" (i.e. Phytoptidae) is paraphyletic. They did not explain why the five sections of the Phyllocoptinae scattered in different clades within the Eriophyidae.

Kuang *et al.* (1992) used polyacrylamide gel electrophoresis to examine patterns of esterase isozymes of five eriophyoid mites: *Trisetacus juniperus* (Nal.), *Boczekella pseudolaris* Kuang & Shen, *Tegolophus fontanesiae* Kuang & Hong, *Aculus ligustri* Keifer and *Rhyncaphytoptus lonicera* Kuang & Zhuo. Cluster analyses of the isozyme patterns and 18 morphological characters using Euclidean distance and coefficient of similarity showed that the Diptilomiopidae is more similar to the Eriophyidae than to the Phytoptidae. A similar study on karotypes and 18 morphological characters of 10 eriophyoid mite species showed that the Eriophyidae and Diptilomiopidae are more similar to each other than either to the Phytoptidae (Kuang *et al.* 1995).

Our cladistic analysis showed that the Eriophyidae and Diptilomiopidae are closer to each other than to the paraphyletic Phytoptidae (Fig. 1). The Phytoptidae have more plesiomorphous characters than the other two families. The genus *Pentasetacus* has the most plesiomorphous characters in the Eriophyoidea.

A comparison of the current classification systems of the Eriophyoidea is presented in Table 2. The use of numbers of dorsal setae by current classifications for the diagnosis of the Phytoptidae emphasize its differences from the other families; there is a lack of synapomorphies for the Phytoptidae. Huang & Huang (1990) also showed that four subfamilies in Nalepellidae form a paraphyletic group. We feel that it is probably more reasonable to divide the Phytoptidae into several monophyletic families: e.g. Pentasetacidae, Novophytoptidae, Phytoptidae, Trisetacidae, Nalepellidae and Sierraphytoptidae based on the present study. However, before the new system is formally proposed, more detailed research is needed because many more species of the Eriophyoidea remain undescribed and other characters (e.g. DNA data) have not been studied. It seems to us that the system erected by Boczek *et al.* in 1989 is a step toward dividing the paraphyletic Phytoptidae, although their idea on the Ashieldophyidae is incorrect due to the wrong description by Mohanasundaram in which *Ashieldophyes* was diagnosed as not having dorsal shield and setae and coxae setae (Mohanasundaram 1984). In fact, these characters are present (Amrine, personal communication).

**TABLE 2.** Comparison of classifications of the eriophyoid mites

| Shevtchenko (1974a) | Newkirk & Keifer (1975) | Boczek *et al.* (1989) | Amrine & Stasny (1994) |
|---|---|---|---|
| Phytoptidoidea | Nalepellidae | Ashieldophidae | Phytoptidae |
| Phytoptidae | Novophytoptinae | Nalepellidae | Nalepellinae |
| Sierraphytoptidae | Nalepellinae | Phytoptidae | Novophytoptinae |
| | Phytocoptellinae | Sierraphytoptinae | Phytoptinae |
| Trisetoidea | Sierraphytoptinae | Novophytoptinae | Sierraphytoptinae |
| Trisetidae | Eriophyidae | Phytoptinae | Eiophyidae |
| Nalepellidae | Aberoptinae | Eriophyidae | Aberoptinae |
| | Nothopodinae | Aberoptinae | Nothopodinae |
| Eriophyoidea | Cecidophyinae | Nothopodinae | Ashieldophyinae |
| Eriophyidae | Eriophyinae | Cecidophyinae | Cecidophyinae |
| Phyllocoptidae | Phyllocoptinae | Eriophyinae | Eriophyinae |
| Rhyncaphytoptidae | Rhyncaphytoptidae | Phyllocoptinae | Phyllocoptinae |
| | Rhyncaphytinae | Diptilomiopidae | Diptilomiopidae |
| | Diptilomiopinae | Rhyncaphytoptinae | Rhyncaphytoptinae |
| | | Diptilomiopinae | Diptilomiopinae |

Although the genera of Eriophyidae + *Sierraphytoptus* from Phytoptidae form a monophyletic group, based on the direction of dorsal setae *sc* which is backward or upward or inward, there is a lack of apomorphous characters which can be used to define all the genera in the Eriophyidae. The relationships within the family are well defined (Fig. 1). The monophyly of the Diptilomiopidae is supported by a single synapomorpy: abruptly curved chelicerae on the characteristic big gnathosoma. The sister group relationship between the Eriophyidae and Diptilomiopidae are strongly supported (Fig. 1).

The cladistic study on the Eriophyoidea presented here, although tentative and incomplete, identifies the phylogenetic relationships among the families, appraises the current classification systems, and underscores the need for increased study of the families Phytoptidae and Eriophyidae which are poorly defined. The relatively low consistency index in the cladogram indicates a relatively high degree of homoplasy in the morphological characters used in the current classification of the Eriophyoidea.

Most studies on the Eriophyoidea have emphasized finding the differences among taxa and describing new taxa. It is high time that more attention should be paid to critical analyses of characters (morphological, molecular, etc) and more efforts be devoted to finding shared derived characters that define monophyletic groups in the Eriophyoidea.

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*Note added in proof*: The paper by E. E. Lindquist on external anatomy and notation of structures in eriophyoid mites, which was cited in this paper but was not seen by us when this paper was prepared, was published in June 1996. It is added below.

Lindquist, E.E. (1996) External anatomy and notation of structures. In: Lindquist, E.E., Sabelis, M.W. & Bruin, J. (eds.) *Eriophyoid Mites - Their Biology, Natural Enemies and Control.* Amsterdam: Elsevier. pp. 3-31.