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Morphological support for a clade comprising two vermiform mite lineages: Eriophyoidea (Acariformes) and Nematalycidae (Acariformes)

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Abstract

A morphology-based parsimony analysis (50 taxa; 110 characters) focused on relationships among basal acariform mites places Eriophyoidea (formerly in Trombidiformes) within Nematalycidae (Sarcoptiformes). Although both taxa have worm-like bodies, this grouping is unexpected because it combines obligate plant inhabitants (Eriophyoidea) with obligate inhabitants of deep-soil or mineral regolith (Nematalycidae sensu stricto). The Eriophyoidea + Nematalycidae clade, which is strongly supported (Bremer =5; bootstrap =85%), retains moderately good support (Bremer=3; bootstrap=66%) when three ratio-based characters pertaining to body shape are excluded. A total of eleven unambiguous synapomorphies unite all or some of Nematalycidae with Eriophyoidea. These include an annulated opisthosoma, an unpaired *vi* seta on the prodorsum, fusion of the palp trochanter with the palp femur, and a large relative distance between the anus and the genitalia. Three of the four Triassic genera of eriophyoid-like mites were also included in our analysis. Although all four genera have been tentatively placed within a new superfamily, we found no support for the monophyly of this group. One other interesting result of the analysis is the placement of a "living fossil", *Proterorhagia oztotloica* (Proterorhagiidae), as sister to the rest of Acariformes. However, support for this relationship is weak.

Keywords: Phylogeny, Sarcoptiformes, Trombidiformes, *Proterorhagia*

Introduction

Eriophyoidea are highly unusual mites that have a worm-like body, only two pairs of legs (I and II), and mouthparts that include a stylet bundle enveloped within a sheath (Nuzzaci 1979; Nuzzaci & de Lillo 1991). This lineage contains the largest family of mites (Eriophyidae >3,500 species), with new species being described at a much faster rate than for any other mite family (Liu *et al.* 2013). Their species richness is explained, at least in part, by their high level of host specificity, but the relatively great age of this group may also be a contributing factor (Schmidt *et al.* 2012; Sidorchuk *et al.* 2015). All Eriophyoidea feed on the fluid contents of vascular plants. Most species feed on only one, or a few, plant host species (Skoracka *et al.* 2010), and individual plant species may have more than one associated eriophyoid species. Given that these mites feed on most vascular plants, which comprise approximately 300,000 species (Christenhusz & Byng 2016), the true species number of Eriophyoidea is likely to be many times that of the roughly 5,000 species that have already been described (Amrine & Stasny 1994; Amrine *et al.* 2003).

Almost all known species of Eriophyoidea are extant. However, a small number of eriophyoid-like fossils have been recovered from Triassic amber (Schmidt *et al.* 2012; Sidorchuk *et al.* 2015). Like extant Eriophyoidea, these mites have styliform chelicerae for feeding on the fluid contents of

plants. All four fossil species of these eriophyoid-like fossils have been placed in a distinct superfamily, Triasacaroidea, on the basis of characters that are transitional and plesiomorphic with respect to all of extant Eriophyoidea (Sidorchuk *et al.* 2015); the name Tetrapodili was proposed for the grouping Triasacaroidea+Eriophyoidea. Because data on this topic is still preliminary, and there are no robust synapomoprhies for Triasacaroidea, we suggest it is too soon to erect a new superfamily. Throughout this paper we therefore treat Tetrapodili and Eriophyoidea as synonyms and only use the term "Eriophyoidea"; Triasacaroidea are simply referred to as Triassic Eriophyoidea.

Although we are beginning to resolve relationships within Eriophyoidea (Lewandowski *et al.* 2014; Li *et al.* 2014; Chetverikov *et al.* 2015), the phylogenetic position of Eriophyoidea has received less attention. And yet this topic is of great interest, not only relative to the evolution of plant feeding, but also because of their unusual morphology, high species diversity, and economic importance as plant pests and vectors of plant diseases (Lindquist et al. 1996; Oldfield & Proeseler 1996). Over the past sixty years or so, Eriophyoidea has usually been hypothesized as related to trombidiform taxa (Table 1), such as spider mites (Eleutherengona: Tetranychoidea) (Baker & Wharton 1952; Evans 1992) or Tydeoidea ("Eupodina") (Hong & Zhang 1996; Lindquist 1996a; Norton *et al.* 1993; Lindquist *et al.* 2009; Zhang *et al.* 2011). The early hypothesis of association with spider mites was poorly supported, and appears to have been based largely on shared plant feeding, but a large number of morphological characters was considered when proposing the move from association with Tetranychoidea to one with Tydeoidea (Lindquist 1996a). Even so, no formal cladistic analysis was conducted. The hypothesized association of Eriophyoidea with Tydeoidea raises some questions on character transitions (acknowledged by Lindquist), for example the difference in the mode of cheliceral attenuation (Lindquist 1998). In all Trombidiformes with styliform chelicerae (excluding Eriophyoidea) the fixed digit of the chelicera is reduced, whereas the movable digit is modified as a stylet. But in Eriophyoidea both fixed and movable digits appear styliform (Chetverikov & Petanović 2016: fig. 5B). In addition, Eriophyoidea lack prosomal stigmata, a characteristic for Trombidiformes (although secondary losses of prosomal stigmata are known for this group).

Acariformes
Sarcoptiformes
Endeostigmata* (including Nematalycidae, Alycidae, and Proteonematalycidae)
Oribatida
Trombidiformes
Sphaerolichida
Prostigmata
Labidostommatina
Eupodina* (including Tydeoidea)
Anystina
Eleutherengona* (including Tetranychoidea)

TABLE 1. Summary of currently recognized classification of Acariformes (Lindquist *et al.* 2009; Zhang 2011**).** Asterisks denote possible placements of Eriophyoidea discussed herein.

One alternative placement to Trombidiformes is "Endeostigmata", a paraphyletic group at the base of Sarcoptiformes (OConnor 1984). Lindquist (1998) suggested the possibility that Eriophyoidea is related to Alycidae ("Endeostigmata") based on the shape of the chelicerae. Cheliceral attenuation in some Alycidae, specifically Bimichaeliini, is similar to that of

Eriophyoidea insofar as they are attenuated into styliform structures, and without reduction of the fixed digits. Ultimately, Lindquist (1998) proposed the placement of Eriophyoidea with Tydeoidea in Trombidiformes based on a greater number of perceived similarities.

The placement of Eriophyoidea within Trombidiformes has also been questioned by recent DNA based phylogenetic studies (Xue *et al.* 2016; Xue *et al.* 2017). Interestingly, one of them shows some support for a sister relationship between Eriophyoidea and Alycidae, albeit with an unusual placement of Astigmata as sister to these two taxa (Xue *et al.* 2017). However, this study does not include any other "Endeostigmata".

One other potential grouping of Eriophyoidea is with the Nematalycidae (5 described species), which has also been placed in "Endeostigmata" (Lindquist *et al.* 2009; Walter *et al.* 2011). Both Eriophyoidea and Nematalycidae have a worm-like body lined with annuli. Interestingly, Nematalycidae were also thought to be within or closely related to Tydeoidea (Cunliffe 1956; Wainstein 1965; Krantz 1970; Kethley 1982; Evans 1992), but by the time Tydeoidea were considered to be the probable sister group of Eriophyoidea (Nuzzaci & de Lillo 1991; Norton *et al.* 1993; Lindquist 1996a), Nematalycidae had already been informally reclassified as "Endeostigmata" in light of the discovery of *Proteonematalycus* (Kethley 1989).

The mouthparts of Nematalycidae provide additional evidence for a close relationship between this family and Eriophyoidea (Bolton *et al.* in prep.). In both taxa, the chelicerae are integrated with the rest of the gnathosoma via membranous extensions of the subcapitulum. In the case of Eriophyoidea, membranous extensions take the form of a stylet sheath (Nuzzaci 1979; Nuzzaci & de Lillo 1991). In Nematalycidae, membranous extensions have been discovered in two different genera: 1) *Cunliffea* appears to have a rudimentary form of the sheath of Eriophyoidea (Bolton *et al.* in prep.); 2) *Osperalycus* has a membranous pouch for the insertion of cheliceral digits (Bolton *et al.* 2015a). By comparison, in Trombidiformes the movable digits of the chelicerae appear to have sunken into a preoral groove in the subcapitulum (de Lillo *et al.* 2001; di Palma *et al.* 2009); membranous extensions have not been observed. Eriophyoidea and Nematalycidae also share another unusual feature: they have anal valves (modified into lobes in Eriophyoidea) that are used to anchor the idiosoma in place (Baker *et al.* 1987; Lindquist 1996b; Bolton *et al.* 2015b).

A close relationship between Eriophyoidea and Nematalycidae would be unexpected because the habitats of these two groups are strikingly different: all known Eriophyoidea live aboveground and on plants, whereas all known Nematalycidae live in deep-soil or mineral regolith, e.g. sand. The combination of dramatically different ecologies and some important morphological differences (e.g. Nematalycidae lack styliform chelicerae) have caused similarities in general morphology (e.g. an elongated body lined with annuli) to be attributed to convergence (Lindquist 1996a).

The primary goal of this study was to use morphological data to test current and new hypotheses on relationships of Eriophyoidea, especially with respect to "Endeostigmata". However, very little is known about basal relationships within "Endeostigmata"; molecular-based studies tend to include only a few token representatives (e.g. Dabert *et al.* 2010). Pepato and Klimov (2015) include a relatively wide range of "Endeostigmata", but they do not sample all families. For this reason, another goal of this study was to use morphological data to re-examine relationships in basal Acariformes, including both "Endeostigmata" and basal Trombidiformes.

Methods

Taxon selection

Fifty taxa were selected for the analysis. Ingroup taxa include representatives of all extant families of "Endeostigmata" and Eriophyoidea. Fossil Endeostigmata were excluded because of their poor

state of preservation, but three of the four species of Triassic Eriophyoidea were included because they are in relatively good condition, allowing most of their characters to be coded.

Ingroup taxa also included representatives of most recognized lineages of Trombidiformes. The focus was on those lineages that at any time have been phylogenetically linked with Eriophyoidea, and on the various taxa of "Eupodina" (Eupodides sensu Lindquist *et al.* 2009). Lineages of Trombidiformes that are usually considered to be relatively derivative (e.g. Heterostigmata and Parasitengona (see Dabert *et al.* 2016)) were excluded. Although Demodecidae somewhat resembles Eriophyoidea and Nematalycidae, this lineage was not included because there is high molecular support for the placement of Demodecidae in Eleutherengona (Palopoli *et al.* 2014; Dabert *et al.* 2016), a relatively derivative lineage of Trombidiformes.

Sampling of Oribatida s.l. was much sparser (1 basal taxon) because Eriophyoidea has never been associated with an oribatid lineage. A solifugid and a ricinuleid—*Mummucia ibirapemussu* Carvalho *et al.* and *Cryptocellus iaci* Tourinho *et al.*—were selected as outgroup taxa. Ricinulei have traditionally been suggested as close relatives of Acari in general (Lindquist 1984; Evans 1992; Shultz 1990, 2007), whereas Solifugae are the sister taxon of Acariformes in several nuclear rDNA based analyses (Dabert *et al.* 2010; Pepato *et al.* 2010; Pepato & Klimov 2015). Grandjean (1954) also suggested a sister relationship between Solifugae and Acariformes.

Character selection and measurement

A total of 110 characters (throughout the text, specific characters are abbreviated to "ch. #") were included in the character matrix (Tables 2 & 3), but 7 uninformative characters (ch. 18, 27, 29, 35, 63, 101 and 102) were excluded from the analysis. Of the remaining 103 characters, only 10 are multistate; the rest are binary.

We included as many characters as possible that could be homologized confidently across taxa. Characters lacking a good basis for homology, e.g. setal counts, were excluded. Individual sensilla (setae, solenidia) were included as separate characters if, and only if, they could be homologized across taxa with a good degree of confidence. In the case of prodorsal setation, we used the chaetotaxic scheme of Kethley (1990), which is the only one to combine major homology schemes across Acariformes. Finally, a number of characters have been used to support a sister relationship between Tydeoidea and Eriophyoidea (Lindquist 1996a). An attempt was made to include as many of these as possible. A decision to exclude a few was again based on difficulties associated with the homology of those characters across taxa (see final section of Character Coding).

Membranous extensions of the subcapitulum, present in Eriophyoidea and some Nematalycidae (see Introduction), were excluded from the analysis because this character is very difficult to discern with a light microscope, and so its absence cannot be confidently demonstrated in Trombidiformes. However, this character appears to be absent in all cases where the mouthparts of Trombidiformes have been observed using electron microscopy (e.g. de Lillo *et al.* 2001; di Palma *et al.* 2009).

Character data were obtained by combining examination of specimens (see Appendix) and study of descriptions. Specimens were observed using a compound microscope equipped with phase contrast (Zeiss Axioskop 3) and/or differential interference contrast (Nikon Eclipse 90i).

Three of the multistate characters are based on ratios (ch. 1–3). These characters, which capture basic information about body shape and the relative distance between certain structures, are ratios that are based on two of the four following measurements: 1) idiosomal length—measurement along the midline (including anus); 2) maximal idiosomal width; 3) distance between the anal opening (most anterior point along the venter) and genital opening (most posterior point)—measurement along the midline; 4) minimum distance between coxal fields I (as determined from the inner margin of the integumental boundary). Measurements were made with the NIS-Elements BR software, version 3.22.01 (Nikon). Measurements were only taken from adult females. In cases where there

were no specimens available for measurements, data were obtained from measurements of figures from the descriptions. The ratios were log transformed and then discretized into integers from 0 to 3 in accordance with Thiele (1993).

Maximum parsimony (MP) analysis

MP was undertaken using PAUP*, version 4.0a146 (Swofford 2002). All of the analyses used the following settings: all characters unweighted; uninformative characters excluded; stepwise addition = random; heuristic algorithm = tree-bisection-reconnection (reconnection limit = 8). An unconstrained heuristic search of the complete morphological dataset was undertaken (stepwise addition = 50 reps; maximum number of saved trees = limitless). A strict consensus tree was generated from the equally most parsimonious trees, which was used to interpret the results. Therefore, unless otherwise stated, the results section highlights congruent relationships across all optimal trees. Strict consensus was used to determine synapomorphies and their associated consistency (CI), retention (RI) and rescaled consistency (RC) indices.

Using the same settings as the original heuristic search, Bremer support was determined through searches for trees that are suboptimal, and through searches in which constraints were imposed against monophyly of specified groupings. In addition, bootstrap support analyses were undertaken using the following settings: number of bootstrap replicates = 5000; stepwise addition = 1 rep; maximum number of saved trees = 1000. Additional analyses for support (Bremer and bootstrap) were undertaken using the same settings, but with the three ratio characters (ch. 1–3) pertaining to body shape excluded in order to determine if this would remove support for the Eriophyoidea + Nematalycidae clade.

A number of additional heuristic searches (settings were identical to the unconstrained heuristic search) were undertaken enforcing monophyly of: 1) Eriophyoidea + Nematalycidae + Trombidiformes; 2) Eriophyoidea + Trombidiformes; 3) Eriophyoidea + Rhaphignathina; 4) Eriophyoidea + Tydeoidea; 5) Nematalycidae + *Micropsammus* + *Proteonematalycus*. These groupings, although incongruent with the results of our analysis, reflect current or previously held hypotheses on phylogeny (Kethley 1989; Evans 1992; Lindquist 1996a; Lindquist *et al.* 2009). The goal was to examine how much worse these hypotheses were relative to the most parsimonious solution. Note that for the constraints involving Trombidiformes (hyp. 1 & 2), *Hybalicus* was excluded from Trombidiformes (in contrast with Pepato & Klimov 2015) because this taxon falls outside of Trombidiformes in the unconstrained analyses. Therefore, retaining *Hybalicus* in Trombidiformes would have added extra steps for these alternative hypotheses. The constraint for the monophyly of Nematalycidae + *Micropsammus* + *Proteonematalycus* was included in order to address the feasibility of Nematalycoidea as hypothesized by Kethley (1989), although it is worth noting that a close relationship between Nematalycidae and Micropsammidae has already been undermined by the results of the phylogenetic analysis undertaken by Pepato and Klimov (2015). The constraint for the monophyly of Eriophyoidea + Raphignathina is consistent with the older and now widely disregarded hypothesis of Eriophyoidea as sistergroup to Tetranychoidea (Krantz & Lindquist 1979). The lengths (total number of steps) of trees from these constrained heuristic searches were compared with the tree from the unconstrained heuristic search using KH tests (Hasegawa & Kishino 1994).

The Eriophyoidea + Nematalycidae clade is abbreviated to EN throughout the results, discussion and conclusion.

Character coding

General character treatment

Where characters did not appear independent, due to identical patterns of expression across the taxa included in the matrix, they were amalgamated into a single character. For example, the pattern of empodial expression (ch 73) is identical for legs II to IV across all of the taxa considered. Each of the legs is not, therefore, treated as a single character with respect to the presence/absence of empodia. Some characters are associated with structures that may be present or absent (e.g. legs). When these structures are absent, we coded the associated characters as inapplicable.

All of the multistate characters are unordered except the three ratio characters, which were discretized into four character states (Thiele 1993). The ratio characters are ordered because the integers (0–3) are arbitrary divisions along a continuum. The seven other multistate characters are unordered because this forces no prior assumptions with respect to their transition between states. Some of these characters represent probable ontogenetic sequences, e.g. identity of the terminal segment (ch. 42), no. of genital papillae (ch. 47), fusion of femora (ch. 104–107), and therefore they could, in reality, be ordered. But their ontogenetic status also means that the switching off and on of key developmental pathways could allow the sudden loss or recovery of more than one instar along an ontogenetic sequence.

Body measurements (ch. 1 to 3—multistate, ordered)

The three ratio characters are: 1) the degree of elongation (ch. 1) (idiosomal length/maximal width); 2) the proportion of the idiosomal length that is between the anus and genitalia (ch. 2); 3) the distance between coxal fields I relative to the maximal width of the idiosoma (ch. 3). The first of these ratios represents the basic shape of the mite. The second of these ratios corresponds with the relative position of the genitalia along the body (the anus tends to remain in a highly posterior position). The third ratio was included because Lindquist has suggested that the relatively small gap between coxae I in Ereynetidae may be an ancestral trait of Tydeoidea, and might therefore be a synapomorphy that unites Tydeoidea and Eriophyoidea (Lindquist 1996a).

In Eriophyoidea, coxal fields I are consolidated (ch. 3). In Ereynetidae (a family within Tydeoidea) the gap between the coxal fields is often reduced. Coxal fields I therefore appear to be fairly close to a state of consolidation. A raw or absolute measurement of the gap between these plates could mean that similarities are an artifact of having a small or narrow body. In this regard, any resemblance between the Nematalycidae and Eriophyoidea would be inflated; both taxa have narrow bodies. Therefore, in an attempt to exclude this effect, we used a ratio for the size of the gap between coxal fields I relative to the maximal width of the idiosoma. Despite the use of this ratio, Nematalycidae clearly bear a much closer resemblance to Eriophyoidea than Tydeoidea for this character. In Nematalycidae (namely *Cunliffea* and *Gordialycus*), coxal fields I can be fused into a single plate, whereas in Tydeoidea, these plates are always separate and often relatively far apart. Of all the taxa that were included in the morphological character matrix, *Triophtydeus* sp., which falls within Tydeoidea, had the largest gap of any species between coxal fields I relative to the body width.

Note: When continuous characters have a large number of states, those characters can drown out the signal of discrete binary characters. Therefore, the ratio characters have only four states. This means that in cases where the coxae are not consoidated but instead close together (e.g. *Osperalycus*), ch. 3 is scored as 0.

The ratio characters were not consolidated into a single character pertaining to body shape because they pertain to different and largely independent body metrics. For example, body elongation (ch. 1) can arise without any extension of the region between the anus and genitalia (ch. 2), e.g. in Proteonemtalycidae (Kethley 1989). Moreover, the large gap between the anus and the

genitalia in many parasitiform mites does not appear to be the result of elongation, but instead because the genitalia have shifted to a highly anterior position on the body. Likewise elongation does not have to mean a reduction in the gap between coxal fields I (ch. 2). There are relatively round mites (e.g. Labidostommatidae) in which the coxal fields I meet, and there are relatively elongated mites (e.g. Proteonematalycidae) that have a noticeable gap between coxal fields I.

Tritonymph instar (ch. 4—binary)

Among the taxa that were included in the analysis, only the tritonymph stage was coded for absence/presence. Suppression of other instars was either so rare as to be uninformative or homologies are unclear, i.e. it is not clear which instar is being suppressed. In that case, the presence/absence of the tritonymph is also coded as unknown.

It was believed that Eriophyoidea normally suppress the deutonymph and tritonymph. But a detailed study of development in a species of *Phytoptus* found all three nymphal instars (Ozman 2000). However, these findings are inconclusive (one of the figures in this study includes a "nymph" with genital structures). In the absence of detailed studies of development in the selected representatives of Eriophyoidea, it is unclear whether the deutonymph and/or tritonymph might be present. For this reason, the presence of the tritonymph is coded as uncertain throughout Eriophyoidea.

The presence of the tritonymph is sometimes designated as unknown in other taxa when the number of specimens is deemed inadequate to rule out its presence. However, because the number of nymphal instars is usually very stable across taxonomic groups, the presence or absence of this instar can generally be inferred from closely related taxa.

Sexual versus asexual (ch. 5—binary)

Males are unknown for a large proportion of the species included in this analysis. As with the detection of nymphal instars, this may be due to the relatively low numbers of available specimens of many species. It is also due to highly skewed sex ratios or intersexual differences in dispersal behavior. Therefore, the status of those species was sometimes designated as unknown with regard to sexual reproduction. However, the status of a species was not designated as unknown when all known species from the same taxonomic group are either sexual or asexual, and when the few available specimens of the target species do not demonstrate otherwise.

Integument (ch. 6 to 8—binary)

Three integumental characters were used in the analysis: annuli (ch. 6); integumental protrusions (ch. 7); reticulated regions (ch. 8). When present, these features comprise a large proportion of the idiosomal integument. Annuli (ch. 6) are ridges that run completely around the circumference of the opisthosoma. Integumental protrusions (ch. 7) include any projecting structures that are not striae, e.g. protubercles. Reticulation (ch. 8) is present when striae interlink to form a network across the integument; in most mites these striae run parallel but never meet. Striae were not included as a character because they are uninformative (they appear in all sampled taxa).

Prodorsum (ch. 9 to 24)

Non-setal characters (ch. 9 to 13—binary): A number of different prodorsal characters were used for the analysis, including a naso (ch. 9, 11), a central eye (ch. 10), one pair of lateral eyes (ch. 12), and post-ocular bodies (ch. 13). The eyes of solifugids are probably homologous with the central eye (ch. 10) of the acariformes, which is indicated by their anteromedial position. A central eye was therefore coded as present in the single solifugid that was used for the outgroup. Some Eriophyoidea

also have eye-like structures that may be true eyes (Smith 1977). These were therefore coded as unknown for the presence/absence of, in this case, lateral eyes.

Some mites have one pair of post-ocular bodies (ch. 13), which are eye-like structures posterior to the single pair of lateral eyes. These structures have sometimes been treated as an extra pair of eyes (e.g. Uusitalo 2010a, b). However, they do not appear to function as true eyes because they lack the smooth integumental covering that characterizes eye lenses. But although they do not function as true eyes, they are probably homologous with true eyes. For this reason, when two pairs of eyes are present, the posterior pair is treated as post-ocular bodies. Based on their ultrastructure, the pustules of Labidostommatidae are regarded as glands (Alberti & Coons 1999), and are therefore very unlikely to be homologous with eyes or post-ocular bodies. This structure was excluded from the analysis because it is uninformative (it is an autapomorphy for the single labidostommatid that was included in the analysis).

Setae (ch. 14 to 24—binary): Kethley (1990) formulated a prodorsal scheme that homologized the setae of Trombidiformes with Sarcoptiformes. His scheme was adopted for the phylogenetic analysis. Accordingly, *exp* (ch. 20) and *in* (ch. 21) are missing from the prodorsum in most trombidiform mites, and also in Nematalycidae. Eriophyoidea, which are widely regarded as trombidiform mites, are also generally treated as missing *exp* and *in* setae (Lindquist 1996b). We did not deviate from this convention. Eriophyoidea are missing a pair of scapular setae (ch. 18, 19), although the exact seta (*sce* or *sci*) is not usually designated. We treated *sce* (ch. 19) as missing in Eriophyoidea, but this choice would not have made any difference to the outcome of the analysis because both of the scapular setae are present in all of the other mites that were included in the analysis. However, if *sce* have been lost, the *sci* of the Eriophyoidea cannot be trichbothrial (ch. 24), whereas the trichbothrial status of *sci* would be unknown if *sci* were absent. For the sake of caution, the trichbothrial status of *sci* was treated as unknown in Eriophyoidea (it is inapplicable in *Rhynacus* because both scapular setae are absent).

A single deviation from Kethley's scheme occurred in the setal coding of *Labidostomma* sp.; *exp* (ch. 20) and *in* (ch. 21) are treated as present. This is in accordance with Walter *et al.* (2009). This modification arose because *exp*, which was previously treated as opisthosomal, is anterior to the lateral ocellus and must therefore be prodorsal.

Opisthosoma (ch. 25 to 49)

Lyrifissures (ch. 25 to 32—binary): Many acariform mites bear a pair of lyrifissures (cupules) (ch. 25) on their segments. The complete set of lyrifissures is as follows: segment *D—ia* (ch. 26); *E—im* (ch. 27); *F—ip* (ch. 28); *H—ih* (ch. 29); *PS—ips* (ch. 30); *AD—iad* (ch. 31). Proteonematalycidae and Micropsammidae also have an additional pair of lyrifissures on their genitalia (ch. 32).

The presence/absence of each particular pair of lyrifissures is treated as a separate character. (ch. 26–32). Many mites have a complete or near complete set of lyrifissures, or else they tend to be completely absent. This suggests that the absence of any particular lyrifissures could be because the ability to express any lyrifissures has been completely suppressed or lost. Therefore, the presence/absence of any lyrifissures is also used as an additional character (ch. 25), and the presence of any particular lyrifissure is treated as unknown for taxa in which lyrifissures are absent from all segments.

The presence/absence of post-podosomal constriction (ch. 34, binary): Some mites have a constriction in the opisthosoma directly behind the podosoma.

Setae on the segments (ch. 35 to 42, binary): Near the posterior region of the opisthosoma, many of the opisthosomal setae cannot be confidently homologized. For this reason, these setae were excluded from the analysis. But setae from segments C (ch. 34–37), D (ch. 38, 39) and E (ch. 40, 41) were used in the analysis because they are few enough to homologize. These setae have also been

used because some of them have been lost by Trombidiformes (OConnor 1984). They are, therefore, important with respect to synapomorphies that unite that group. The internal setae from some of these segments are uninformative because they are universally present among taxa. They were, therefore, excluded from the analysis.

The identity of the terminal segmental remnant of the adult instar (ch. 42—multistate, unordered): This character comprises five states: 1) *PS*; 2) *AD*; 3) *AN*; 4) *PA*; 5) *PA*+1. The last of these states reflects the existence of an additional terminal body segment in almost all arachnids, and which is therefore needed for the outgroup taxa used in this analysis. The identity of the terminal segmental remnant is usually indicated by the associated setae—the anal shields represent the terminal segment, which may sometimes be nude. In Eriophyoidea, no segmental remnants appear to be added after *PS*. The suppression of anamorphosis has been considered to be possible evidence of a close relationship between Tydeoidea and Eriophyoidea (Lindquist 1996a), but Tydeoidea appear to add segment *AD* even though setae *ad* and lyrifissures *ips* are absent (André 1981; Kazmierski 1989; Kethley 1990).

Structure and shape of opisthosomal setae on the dorsum (ch. 43 and 44—binary): Setae from the dorsum of the opisthosoma were used for characters pertaining to setal shape and structure. This is because they are large and, therefore, it is easy to distinguish the different character states. Two characters were used: presence/absence of branching (Fig. 1B, C) (ch. 43); shape of setal body (thin/swollen) (ch. 45). Any setae that possess setules (short terminal branches) are coded as branched (Fig. 1D–G).

In the case of *Proctotydaeus* (Tydeidae), the length of the setules is highly reduced, causing the profile of the seta to look serrate (Fig. 1E). In all other tydeoids, the setules tend to be more prominent, although in some cases the form is very close to that of *Proctotydaeus*. Across the range of taxa studied, the length of terminal branches varies dramatically. However, the lengths of terminal branches do not fall into readily defined and discrete character states. Characters for branch length were therefore not developed for this analysis.

The second setal character—shape of setal body (ch. 44)—excludes the setules. The setae of most mites have a thin setal body (Fig. 1B–E). But in some mites the setal body is distinctly swollen (Fig. 1F, G).

Hypertrichy of the setae (ch. 45—binary): Some mites have a dense covering of setae on the opisthosoma that is readily distinguishable from holotrichy. Presence of hypertrichy does not include mites that exceed the holotrichous state by merely a few setae.

Genital papillae in the adult instar (ch. 46—binary; ch. 47 multistate, unordered): As with other characters, if genital papillae are absent (ch. 46), the number of genital papillae (ch. 47), which varies from 1 to 3 pairs, is coded as inapplicable. This is because it is possible that absence is due to the loss of ability to express these structures, i.e. we cannot know that absence represents a count of 0.

Genital setae (ch. n/a): Genital and aggenital setae were not included because it was too difficult to confidently determine the homology of each seta. Furthermore, establishing which setae are genital or aggenital is also often difficult or based on somewhat arbitrary criteria. And in some cases an apparent aggenital seta has migrated to the extreme venter from the dorsum, and should instead be designated as a seta from a segment.

Presence/absence of eugenital setae in females (ch. 48—binary): Eugenital setae are the setae next to the opening of the genitalia, and can be readily distinguished from the genital and aggenital setae. The complete absence of these setae from females was hypothesized as a possible synapomorphy for Nematalycoidea (Kethley 1989). In Oribatida and *Speleorchestes*, the opening of the genitalia is at the tip of an ovipositor, which has setae that appear to be homologous with the eugenital setae of mites in which the ovipositor is vestigial or absent. Accordingly, the coding scheme treats these setae as eugenital.

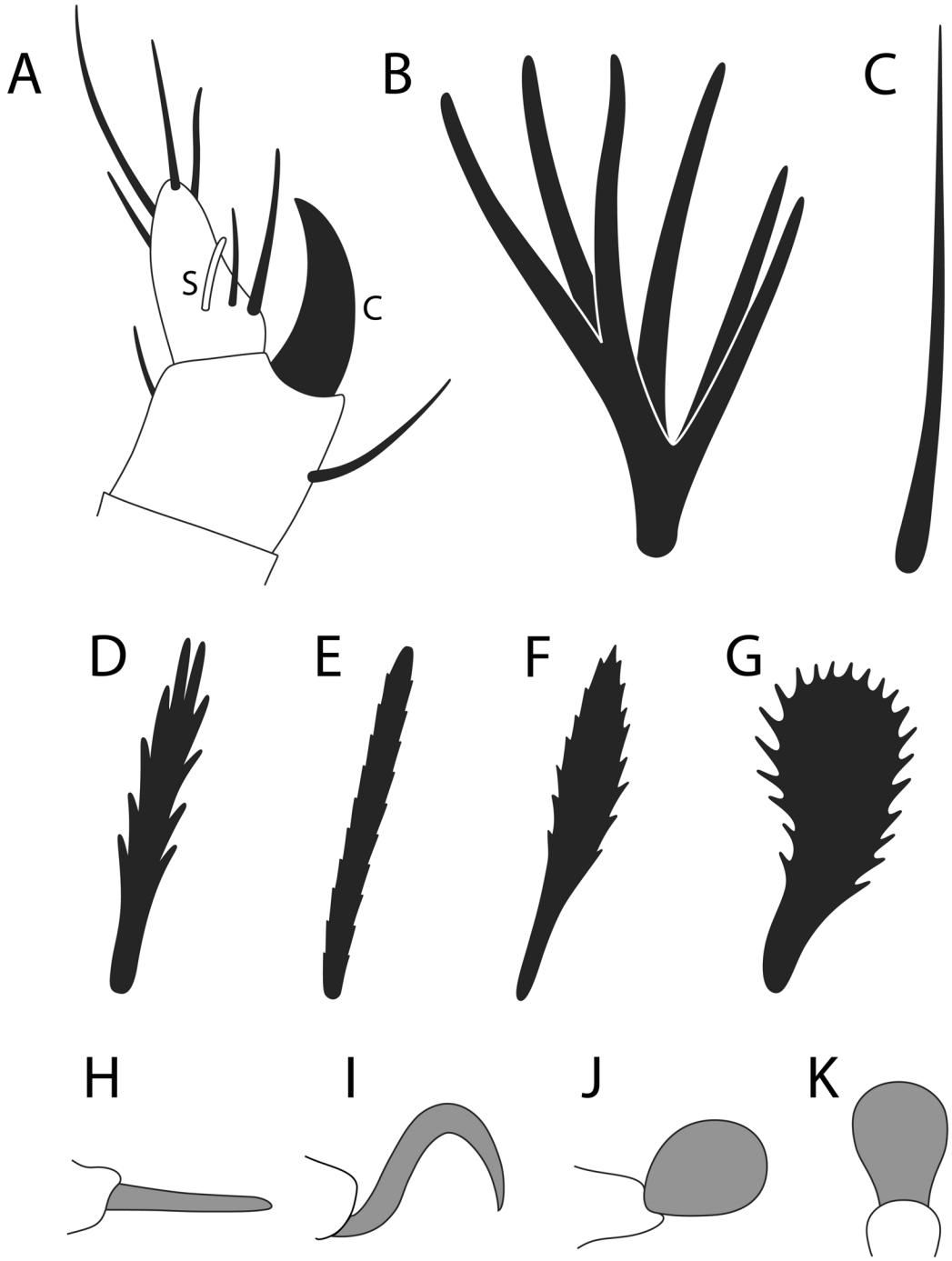

FIGURE 1. Empodia and setae. Palp and setal claw of palp-tibia: **A,** *Apomerantzia kethleyi* Price (copied from Price, 1975). Setae: **B,** branched; **C,** simple; **D,** thin with long setules; **E,** thin with short setules; **F,** swollen - spatulate; **G,** swollen—globose; Empodia (figures exclude setules and claws): **H,** Elongated and straight—lateral view; **I,** Elongated and curved (claw-like)—lateral view; **J,** Bulbous—lateral view; **K,** Flat and rounded (pad-like)—dorsal view. S = solenidion; C = claw-like seta.

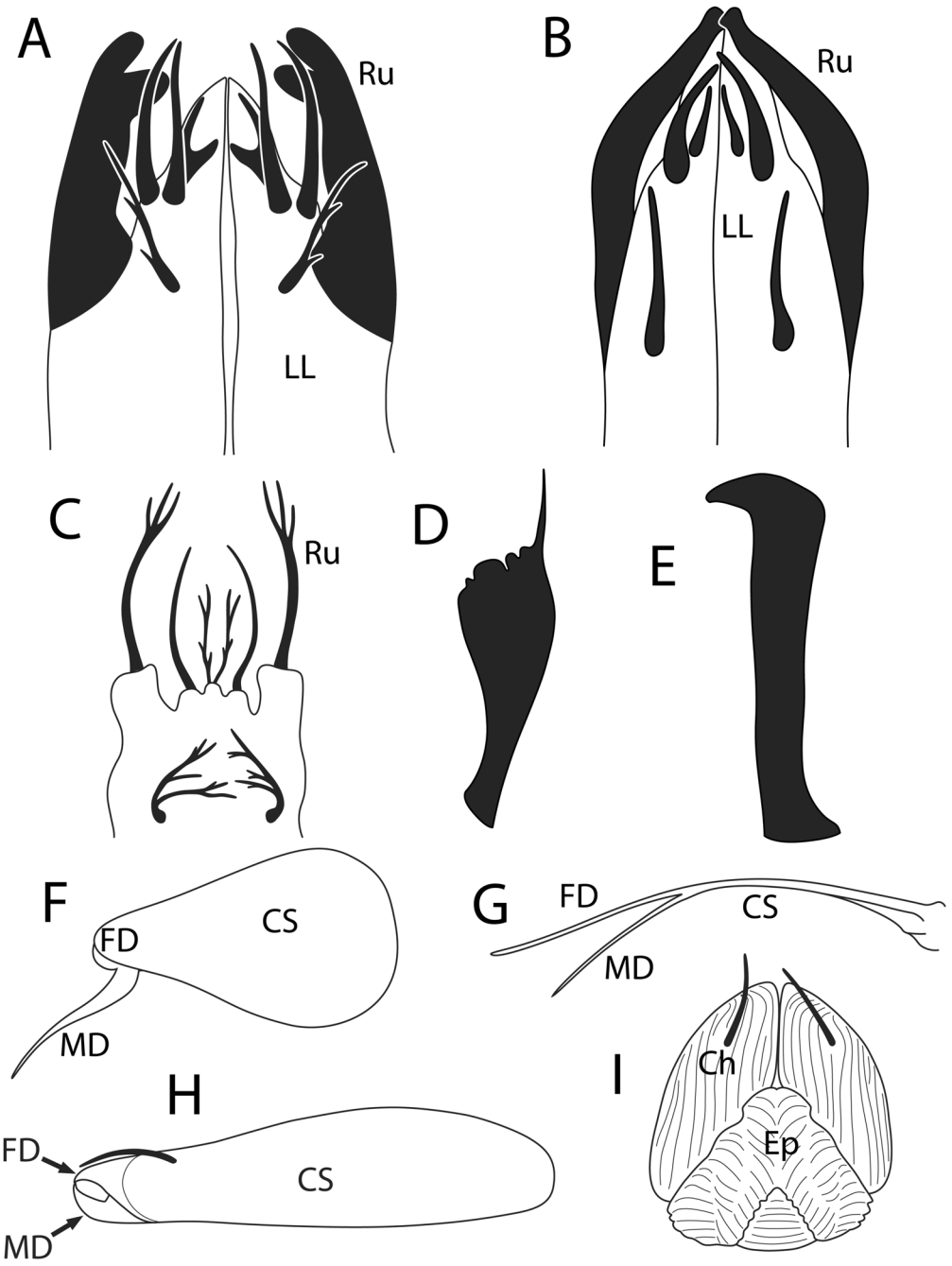

FIGURE 2. Mouthparts. Ventral views of subcapitulum: **A,** *Stigmalychus* nr. *veretrum*; **B,** *Gordialycus* sp. A; **C,** *Nanorchestes globosus* Theron and Ryke (copied from Theron and Ryke, 1969). Lateral views of rutella: **D,** *Petralycus unicornis* Grandjean (copied from Grandjean, 1943); **E,** cf. *Psammolycus* sp. A (Florida, USA). Lateral views of chelicerae: **F,** *Proctotydaeus galapagosensis* Fain and Evans (copied from Fain and Evans, 1966); **G,** Eriophyidae (copied from Lindquist, 1996b); **H,** *Cunliffea strenzkei*. Dorsal view of epistome and chelicerae: **I,** *Neonanorchestes* sp. (Ohio, USA). Ru = rutellum; LL = Lateral lip; FD = fixed digit; MD = movable digit; CS = cheliceral shaft; Ch = chelicera; Ep = epistome.

Gut boluses (ch. 49—binary): A gut bolus can often be observed in the opisthosoma of particulate feeding mites. The results of Walter (1988) were used to help determine which genera contain gut boluses in cases where specimens are unavailable, i.e. where descriptions did not reveal this information. Observations of *Proteonematalycus wagneri* Kethley, which was not included in Walter (1988), showed that this species also often contains gut boluses. Species which are scored as 'absent' have never been shown to contain gut boluses, whereas species that are scored 'present' have boluses in 10% or more of specimens.

Gnathosoma (ch. 50 to 66)

Presence/absence of rutella (ch. 50—binary): The presence/absence of rutella appears to be obvious in almost all cases. Although Sphaerolichida are often regarded as lacking rutella (Walter *et al.* 2009), OConnor (1984) hypothesized that a pair of subcapitular setae on *Hybalicus* may be homologous with rutella. However, given that the number and position of the subcapitular setae vary across both the "Endeostigmata" and the Sphaerolichida, there is no evidence to support this. It is certainly not the case that Sphaerolichida have an extra pair of setae that "Endeostigmata" lack. Rutella are, therefore, treated as absent in all Trombidiformes (excluding Eriophyoidea, where they are treated as unknown—see below).

It is not clear if rutella are present or absent in Eriophyoidea, which contains a number of mouthpart elements of unknown origin, including the "auxiliary" and "infracapitular" stylets. It is possible that some of these structures are derived from the rutella (Lindquist 1998). The "infracapitular" guides and "auxiliary" stylets of some eriophyoids appear to be birefringent (pers. obs.), but this is not necessarily proof that they were once rutella. Because there is not yet a confident basis for homology, the presence of rutella has been coded as unknown in Eriophyoidea.

The single described species of Proterorhagiidae—*Proterorhagia oztotloica* Lindquist and Palacios-Vargas—appears to have a very small, possibly vestigial pair of rutella (Lindquist & Palacios-Vargas 1991). Therefore, this species was also coded as unknown for the presence/absence of rutella.

Rutella shape (ch. 51—binary): Many mites have rutella with teeth. Others have lobes (Fig. 2A) or long spine-like projections. These all represent different types of projections from the main body of the rutellum. They also represent forms that are part of a continuum, and it is therefore not always possible to confidently characterize a projection as one type or another. For example, teeth are very small lobes, and spine-like projections are long and attenuated lobes.

Rutella often have highly complex shapes and may possess all three types of projections (Fig. 2D). Homologizing each of these individual projections is probably not possible across disparate and distantly diverged taxa. Because of this, and because the characterization of shape is not robust, we used a simple character; presence/absence of multiple projections (ch. 51). Projections can include teeth, lobes and spines. Multiple projections include all rutella that branch into two or more projections. The setiform rutella of *Nanorchestes* were, therefore, coded for the presence of multiple projections (Fig. 2C). Multiple projections are present in almost all mites that possess rutella, although they are absent in some Nematalycidae (Fig. 2B, E).

Cheliceral shape (ch. 54 to 57—binary): Four characters pertain to the shape of the chelicerae: 1) reduction of the fixed digits (ch. 52); 2) attenuation of the cheliceral shafts (ch. 53); 3) attenuation of the fixed digits (ch. 54); 4) attenuation of the movable digits (ch. 55). The first of these characters pertains to the dramatic reduction of the fixed digits in some trombidiform mites (Fig. 2F). The other characters address the styliform/substyliform chelicerae of some mites (Fig. 2F, G). In trombidiform mites only the movable digits are styliform (Fig. 2F), whereas both *Bimichaelia* and Eriophyoidea have styliform shafts and digits (Fig. 2G). With respect to Eriophyoidea, it is possible that the movable and fixed digits are really a bifurcation of extremely elongated movable digits. But this

hypothesis is undermined by evidence that both the movable and fixed digits may retain innervated fine elements (Lindquist 1996b; Nuzzaci & Alberti 1996; Lindquist 1998). Furthermore, the attenuation of digits and shafts also seems much more parsimonious. These chelicerae, which appear to be derived from the attenuation of robust chelicerae, represent a slightly more extreme version of the cheliceral attenuation observed in *Bimichaelia* (Lindquist 1998). Therefore, the movable and fixed digits of Eriophyoidea were coded as attenuated.

In all of the other mites that were included in the morphological matrix, the chelicerae, including the digits, are comparatively robust and chelate (Fig. 2H), and are therefore easy to distinguish from styliform mouthparts.

Fusion of the cheliceral shafts (ch. 56—binary): In some cases the chelicerae fuse along their cheliceral shafts. In Tydeoidea and Raphignathina, where this feature is sometimes present, it is easy to identify. Eriophyoidea possess a unique and specialized structure at the base of their stylets, the motivator. It has been suggested that the motivator may be homologous with the cheliceral shafts (sometimes termed cheliceral bases) (Lindquist 1996a, 1996b; Nuzzaci & Alberti 1996). However, the issue of homologizing the motivator is problematical (Lindquist 1996b; Nuzzaci & Alberti 1996). Eriophyoidea possess long and attenuated cheliceral shafts that project from the motivator (Fig. 2G). The motivator would therefore have to be a highly unusual modification at the base of the shafts. In Tydeoidea in which the shafts are fused, fusion takes place along a large proportion of the length of each shaft, and there is no dramatic modification of the shaft base. Furthermore, the motivator of Eriophyoidea functions as a fulcrum, enabling the alternating movement of the cheliceral stylets (Nuzzaci & Alberti 1996). In order to function as a fulcrum the motivator has to articulate with the rest of the chelicerae. The shaft would therefore have to have divided into an additional segment (fusion only occurring between the basal segments). This is a weak basis for homologizing the fused shafts of Tydeoidea with the motivator of Eriophyoidea. Therefore, the chelicerae are coded as separate along the shafts in Eriophyoidea.

Cheliceral setae (ch. 57 and 58—binary): The cheliceral setae can be fairly confidently homologized across the taxa. There is usually only a single seta on each chelicera, which is often near the fixed digit (ch. 57). Sometimes there is an additional seta, which is noticeably posterior relative to the other cheliceral seta (ch. 58). A cheliceral seta may be routinely present in Eriophyoidea. A detailed study of their mouthparts has revealed protuberances (Chetverikov & Craemer 2015—Fig. 1A, Fig. 3ABCD indicated as “a”, Fig. 4 two white arrows) that closely resemble cheliceral setae or perhaps vestiges of setae. These structures may be present on most or all of Eriophyoidea that were included in the dataset. It is not known whether they are true setae, or which particular cheliceral setae they may represent (they are not strongly posterior or anterior). For these reasons, both the anterior and posterior setae were coded as unknown for all Eriophyoidea.

Presence/absence of an epistome (ch. 59—binary): The epistome is the triangular structure between the bases of the chelicerae of Nanorchestidae (Fig. 2I). This triangular structure is not found in any other taxa included in this analysis. It is not clear whether the epistome of Nanorchestidae is a true homologue of the epistome of other arachnids.

Labrum (not coded): In some mites, e.g. Eriophyoidea and *Nanorchestes*, the labrum is styliform whereas in others, e.g. Proteonematalycidae and some Nematalycidae, this structure is relatively broad. However, labral elongation varies along a continuum. Obtaining relatively accurate measurements of such a small structure for the purpose of coding an additional ratio character is not feasible using only light microscopy and descriptions. Therefore, this character was excluded from the analysis.

Palp (ch. 60 to 65—binary): In Acariformes, the palp segments can fuse in a number of different places. Fusions in acariform mites typically appear to involve the femur, genu and trochanter. The first segments to fuse are often the femur and genu (ch. 61). The result is that a relatively long palp

segment—a femurogenu—is directly anterior to a short trochanteral segment at the base of the palp. This is consistent with generally accepted hypotheses on the fusion of the palp segments. For example, Lindquist (1996a) has suggested that the palp femur and genu has fused in Tydeoidea and Eriophyoidea. However, there are also some exceptions to this general pattern (Lindquist & Sidorchuk 2015). For the analysis, the state of consolidation of each pair of adjoining segments is treated as a binary character—fused or separate.

Several palp structures were also incorporated into the character matrix. Some trombidiform mites have a claw-like seta on the palp tibia (Fig. 1A) (ch. 64). Among the taxa included in this analysis, this seta is easy to distinguish from ordinary setae. The trichoid setae of the palp can be numerous, and are therefore difficult to homologize. For this reason, they were excluded from the analysis. Although there are fewer setae on the basal segments of the palp, homology hypotheses appear to be prone to error because they also rest on correctly homologizing the segments, which can fuse in different ways (Lindquist & Sidorchuk 2015). A very large proportion of acariform mites have a single solenidion on the palp tarsus. This is easy to homologize because no additional solenidia are apparent. Therefore, the presence/absence of the palp solenidion was included in the analysis (ch. 65).

Gnathosomal stigmata (ch. 66—binary): The presence of gnathosomal stigmata is considered to be an important synapomorphy for most of Trombidiformes. In some members of this taxonomic group, the stigmata have repositioned onto the prodorsum, but no examples of these mites were included in the matrix.

LEGS (CH. 67 TO 110)

Presence/absence of lateral claws (ch. 67 to 69—binary): The pre-tarsi of mites usually bear lateral claws. But in some or all legs they may be suppressed. The taxa examined showed an identical pattern of suppression in legs II and III (ch. 68). These legs were, therefore, amalgamated into the same character. But legs I (ch. 67) and IV (ch. 69) were kept as separate characters because they can sometimes differ from all of the other legs.

Presence/absence of empodia (ch. 70 and 71—binary): Empodia can also vary in their expression. The taxa showed an identical pattern of empodial suppression in legs II to IV. Therefore, these legs were amalgamated into a single character (ch. 71).

Empodial shape (ch. 72—multistate, unordered; ch. 73 and 74—binary): If the cilia (setules) are excluded, the shape of the empodium can be characterized as four basic character states: elongated and straight (Fig. 1H); elongated and curved—claw-like (Fig. 1I); bulbous (Fig. 1J); flat and rounded—pad-like (Fig. 1K). The shape of the main empodial body (empodium minus cilia) was therefore coded as a separate character (ch. 72) to the presence/absence of cilia/setules (ch. 73). The empodial shape and presence/absence of cilia, including tenent hairs, is always identical across all 4 pairs of legs. The Raphignathina have tenent hairs, which are cilia with distinct T-shaped tips. These are treated as ordinary cilia, but an additional character is also used for the presence/absence of tenent hairs (ch. 74).

Setae (ch. 75 to 86—binary): Among early derivative mites, most leg segments typically have too many setae and too much variation in the number of setae across taxa to confidently determine their homology. A presence/absence scheme for individual setae was, therefore, only undertaken for the trochanteral setae, where numbers of setae per segment remain low enough (3 or fewer) across all taxa to make it possible to fairly confidently determine setal homology between families, infraorders and suborders. These trochanteral setae also appear to occupy a relatively stable position, and numbers of setae vary very little, if at all, within families and superfamilies.

Presence/absence of solenidia (ch. 87 to 103—binary): For each leg segment, the presence/absence of solenidia was coded, but not the number (for the reason mentioned above). These

characters are informative because many leg segments do not have solenidia, and also because it is likely that one or more of the solenidia that are on homologous leg segments of different taxa are also homologous. The presence/absence of rhagidial solenidia was also included as an additional character (ch. 103). Rhagidial solenidia are recumbent structures that lie within tight and shallow integumental depressions on the tarsi of legs I and II.

The fusion of leg segments (ch. 104–107—multistate, unordered; ch. 108 and 109—binary): In many arachnids, the femora comprise two segments (ch. 104–107). These segments often form a single, consolidated segment in Acariformes. Femoral fusion for each pair of legs comprises three character states: 1) no fusion; 2) partial fusion; 3) complete fusion. Partial fusion is indicated by the presence of a suture, which may or may not completely encircle the leg. Complete fusion indicates that no trace of any segmentation could be detected across each femur. The fusion of the femora varies among the legs. Therefore, each pair of legs represents a distinct character with respect to femoral fusion. In *Gordialycus*, another fusion event has arisen – the genua of legs III and IV have fused with the femora. A separate and additional character addresses this synapomorphy (ch. 108). In the non-acarine outgroup taxa, all of the tarsi are divided into two or more segments; this was treated as a single character (ch. 109).

Presence/absence of legs III and IV (ch.110—binary): Legs III and IV are lost in all of Eriophyoidea. This character is therefore an obvious and robust synapomorphy for that group.

Uncoded characters that were previously treated as evidence for a sister relationship between Tydeoidea and Eriophyoidea

Lindquist (1996a) has suggested that a number of similarities between Eriophyoidea and Tydeoidea may be possible synapomorphies that support a sister relationship between these two groups. For this reason, an attempt was made to include those hypothesized synapomorphies in the phylogenetic analysis. However, a small number of those characters were excluded because they are problematical with respect to character coding. There is little reason to suggest that those characters undermine a case for a close relationship between Eriophyoidea and Nematalycidae. In the case of most characters, Eriophyoidea are no more similar to Tydeoidea than they are to Nematalycidae. Characters are generally excluded because of difficulties with respect to determining the character state, e.g. lack of confidence in homology, or because the character is uninformative.

Coxisternal setae: Lindquist (1996a) used coxisternal setae to make a case against a sister relationship between Eriophyoidea and any of the Eleutherengone superfamilies. There is a shared retention of fundamental setae *2a* on coxisternae II in Tydeoidea and Eriophyoidea. However, Lindquist is careful to point out that this is a symplesiomorphy, and therefore not a reliable indicator of a close relationship between Tydeoidea and Eriophyoidea—Nematalycidae also possess a fundamental seta on coxisterna II. We have not coded the coxisternal setae due to issues of homology. These setal characters do not appear to be robust enough for use in a phylogenetic analysis that includes different suborders. Because setae that are on the coxal fields are seldom homologized with intercoxal setae, chaetotaxic schemes applied at the family or superfamily level are not easy to confidently apply across all of Acariformes, where shifts to and from the coxal fields may have occurred due to long periods of divergence (it is not clear that the coxal fields are true segments). Sometimes this appears to be caused by the reduction or movement of the coxal fields. And so unlike the prodorsum, for example, the chaetotaxy of this body region is still very poorly understood.

Sexually dimorphic suppression of eugenital setae: Lindquist also suggests that the suppression of eugenital setae in females is a potential synapomorphy for linking Tydeoidea and Eriophyoidea as sister groups (Lindquist 1996a). However, whereas there is complete suppression of eugenital setae in female eriophyoids (*Loboquintus* Chetverikov & Petanovic. may be an exception

(Chetverikov *et al*. 2013)), there is noticeable variation in this character in Tydeoidea. For example, there is complete suppression in both males and females in the subfamily Pronematinae, and females have fewer pairs of eugenital setae in the Triophtydeinae, but they are not completely suppressed.

But Nematalycidae also show evidence of the dimorphic suppression of eugenital setae. Like the Eriophyoidea, female nematalycids completely lack eugenital setae. Almost all known nematalycids are thelytokous, and spanandric males are, so far, unknown. However, an undescribed sexual species of Nematalycidae from New Mexico clearly shows that the males possess eugenital setae (pers. obs.). There is, therefore, no stronger basis for interpreting this character as a synapomorphy for linking Eriophyoidea with Tydeoidea than there is for interpreting this character as a synapomorphy for linking Eriophyoidea with Nematalycidae.

In this analysis, the presence/absence of eugenital setae in females was coded instead of dimorphic suppression (see above). This is because dimorphic suppression is impossible to determine in thelytokous lineages in which spanandric males are absent. Presence/absence of eugenital setae is also a straightforward character to code compared to dimorphic suppression.

Sex determination mechanisms: This character is based on karyotypic studies, which indicate that both Tydeoidea and Eriophyoidea are haplo-diploid (Helle & Wysoki 1983). This character is excluded because there is no data on the karyotype of any of the traditional Endeostigmata, including Nematalycidae (Helle *et al.* 1984; Norton *et al.* 1993). The status of all of the members of this order is therefore unknown with respect to haplodiplody.

Calyptostatic nymphs: A few Tydeoidea have calyptostatic nymphs. It has been hypothesized that this represents a stage of ontogenetic reduction that is approaching the complete loss of the nymphal instars (Lindquist 1996a). Accordingly, Eriophyoidea have taken this ontogenetic reduction to completion by eliminating some of those nymphal instars altogether. But this argument rests on the assumption that calyptostases are a transitional step towards the loss of a nymphal instar. There does not appear to be evidence to support that argument; none of Eriophyoidea has calyptostatic nymphs. Furthermore, none of the taxa included in the analyses appear to have calyptostatic nymphs. Therefore, this character is uninformative and has been excluded from the analysis.

Suppression of nymphal progenital chamber: In Eriophyoidea and Tydeoidea, a genital chamber does not develop until adulthood (André 1981). This was hypothesized as a synapomorphy for Eriophyoidea and Tydeoidea because in the more early derivative taxa, a progenital chamber is formed in the nymphal instar (Lindquist 1996a). This character was excluded because its presence/absence could not be confidently determined for many of the taxa included in the analysis. It is a relatively soft and internal structure that is not easy to discern using light microscopy, and it is almost always excluded from descriptions.

Table 2. Characters and states (ch. 1–55)

Ch. #	Character and states
1	Idiosomal elongation (length/maximal width): [0–3]
2	Distance between anus and genitalia as proportion of idiosomal length: [0–3]
3	Distance between coxae I as a proportion of maximal width: [0–3]
4	Tritonymph: [0] not suppressed; [1] suppressed
5	Mode of reproduction: [0] sexual; [1] asexual
6	Annuli: [0] absent; [1] present
7	Integumental protrusions/microturbercles: [0] absent; [1] present
8	Reticulation of the integument: [0] absent; [1] present
9	Naso: [0] absent; [1] present
10	Central eye: [0] absent; [1] present
11	Naso position: [0] naso anterior and proximal to chelicerae; [1] naso receded back
12	Lateral eyes: [0] absent; [1] present
13	Postocular bodies: [0] absent; [1] present
14	Seta(e) *vi*: [0] absent; [1] present
15	Number of *vi* setae: [0] paired; [1] unpaired
16	Seta(e) *vi* and naso: [0] if *vi* and naso present, naso without *vi*; [1] if *vi* and naso present, naso bearing *vi*
17	Setae *ve*: [0] absent; [1] present
18	Setae *sci*: [0] absent; [1] present
19	Setae *sce*: [0] absent; [1] present
20	Setae *exp*: [0] absent; [1] present
21	Setae *in*: [0] absent; [1] present
22	Trichobothria 1: [0] *vi* is trichobothrial; [1] *vi* is not trichobothrial
23	Trichobothria 2: [0] *ve* is trichobothrial; [1] *ve* is not trichobothrial
24	Trichobothria 3: [0] *sci* is trichobothrial; [1] *sci* is not trichobothrial
25	Opisthosomal lyrifissures; [0] absent; [1] present
26	Lyrifissures *ia*: [0] absent; [1] present
27	Lyrifissures *im*: [0] absent; [1] present
28	Lyrifissures *ip*: [0] absent; [1] present
29	Lyrifissures *ih*: [0] absent; [1] present
30	Lyrifissures *ips*: [0] absent; [1] present
31	Lyrifissures *iad*: [0] absent; [1] present
32	Lyrifissures *ig*: [0] absent; [1] present
33	Body constriction: [0] body not constricted behind podosoma; [1] body constricted behind podosoma
34	Setae *c*1: [0] absent; [1] present
35	Setae *c*2: [0] absent; [1] present
36	Setae *c*3: [0] absent; [1] present
37	Setae *c*4: [0] absent; [1] present
38	Setae *d*2: [0] absent; [1] present
39	Setae *d*3: [0] absent; [1] present
40	Setae *e*2: [0] absent; [1] present
41	Setae *e*3: [0] absent; [1] present
42	Identity of terminal segment in adult: [0] PS; [1] AD; [2]; AN; [3] PA; [4] PA+1
43	Setal branching: [0] absent; [1] present
44	Shape of body of setae: [0] thin; [1] swollen
45	Hypertrichy of the opisthosoma [0] absent; [1] present
46	Genital papillae in the adult stage: [0] absent; [1] present
47	Number of pairs of genital papillae in the adult stage: 1–3
48	Eugenital setae: [0] absent; [1] present
49	Gut boluses: [0] absent; [1] present
50	Rutella: [0] absent; [1] present
51	Rutella structure: [0] rutella without multiple projections; [1] rutella with multiple projections
52	Fixed digit reduction: [0] fixed digit not reduced relative to movable digit; [1] fixed digit reduced relative to movable digit
53	Cheliceral shaft attenuation: [0] cheliceral shaft robust; [1] cheliceral shaft styliform/substyliform
54	Fixed digit attenuation: [0] fixed digit robust and chelate; [1] fixed digit styliform/substyliform
55	Movable digit attenuation: [0] movable digit robust and chelate; [1] movable digit styliform/substyliform

.....continued on the next page

Table 2 (continued). Characters and states (ch. 56–110)

Ch. #	Character and states
56	Fusion of cheliceral shafts: [0] separate; [1] fused
57	Anterior cheliceral seta: [0] absent; [1] present
58	Posterior cheliceral seta: [0] absent; [1] present
59	Epistome: [0] absent; [1] present
60	Palp segmental fusion 1: [0] trochanter separate from femur; [1] trochanter fused with femur
61	Palp segmental fusion 2: [0] femur separate from genu; [1] femur fused with genu
62	Palp segmental fusion 3: [0] genu separate from tibia; [1] genu fused with tibia
63	Palp segmental fusion 4: [0] tibia separate from tarsus [1] tibia fused with tarsus
64	Claw-like seta on tibia: [0] absent; [1] present
65	Solenidion on palp tarsus: [0] absent; [1] present
66	Gnathosomal stigmata: [0] absent; [1] present
67	Legs I lateral claws: [0] absent; [1] present
68	Legs II–III lateral claws: [0] absent; [1] present
69	Legs IV lateral claws: [0] absent; [1] present
70	Legs I empodia: [0] absent; [1] present
71	Legs II–IV empodia: [0] absent; [1] present
72	Empodial shape (excluding setules/cilia): [0] elongated and straight; [1] elongated and curved—claw-like; [2] flat and rounded—pad-like; [3] bulbous
73	Empodial ciliation: [0] nude; [1] ciliated (covered in setules—fine hairs)
74	Empodial tenent hairs: [0] cilia, if present, are not tenent hairs; [1] cilia, if present, are tenent hairs
75	Setae *v'* on trochanters I: [0] absent; [1] present
76	Setae *l'* on trochanters I: [0] absent; [1] present
77	Setae *v"* on trochanters I: [0] absent; [1] present
78	Setae *v'* on trochanters II: [0] absent; [1] present
79	Setae *l'* on trochanters II: [0] absent; [1] present
80	Setae *v"* on trochanters II: [0] absent; [1] present
81	Setae *v'* on trochanters III: [0] absent; [1] present
82	Setae *l'* on trochanters III: [0] absent; [1] present
83	Setae *v"* on trochanters III: [0] absent; [1] present
84	Setae *v'* on trochanters IV: [0] absent; [1] present
85	Setae *l'* on trochanters IV: [0] absent; [1] present
86	Setae *v"* on trochanters IV: [0] absent; [1] present
87	Solenidia on tarsi I: [0] absent; [1] present
88	Solenidia on tarsi II: [0] absent; [1] present
89	Solenidia on tarsi III: [0] absent; [1] present
90	Solenidia on tarsi IV: [0] absent; [1] present
91	Solenidia on tibiae I: [0] absent; [1] present
92	Solenidia on tibiae II: [0] absent; [1] present
93	Solenidia on tibiae III: [0] absent; [1] present
94	Solenidia on tibiae IV: [0] absent; [1] present
95	Solenidia on genua I: [0] absent; [1] present
96	Solenidia on genua II: [0] absent; [1] present
97	Solenidia on genua III: [0] absent; [1] present
98	Solenidia on genua IV: [0] absent; [1] present
99	Solenidia on femora I: [0] absent; [1] present
100	Solenidia on femora II: [0] absent; [1] present
101	Solenidia on femora III: [0] absent; [1] present
102	Solenidia on femora IV: [0] absent; [1] present
103	Rhagidial solenidia: [0] absent; [1] present
104	Femur I subdivision: [0] not subdivided; [1] partially subdivided; [2] completely subdivided
105	Femur II subdivision: [0] not subdivided; [1] partially subdivided; [2] completely subdivided
106	Femur III subdivision: [0] not subdivided; [1] partially subdivided; [2] completely subdivided
107	Femur IV subdivision: [0] not subdivided; [1] partially subdivided; [2] completely subdivided
108	Fusion state of femora III and IV with genu III and IV: [0] femora III and IV distinct segments from genua III and IV; [1] femora III and IV fused with genua III and IV
109	Leg tarsi subdivision: [0] not subdivided; [1] subdivided
110	Legs III and IV of adults: [0] absent; [1] present

TABLE 3. Character matrix. Inapplicable characters denoted with hyphen; unknown characters denoted with question mark.

Character matrix: Part 1 (Ch. 1–22)	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	1	1	1	1	1	1	1	1	1	1	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Mummucia ibirapemussu	1	?	?	0	0	0	?	?	0	1	-	0	0	1	?	-	1	1	1	1	1	1
Cryptocellus iaci	0	3	2	0	0	0	?	?	0	0	-	1	0	1	?	-	1	1	1	1	1	1
Metatydaeolus sp.	1	0	1	?	?	0	1	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Brachytydeus sp.	0	0	3	0	?	0	1	1	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Riccardoella triodopsis	0	0	1	?	0	0	1	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Triophtydeus sp.	0	1	3	?	?	0	1	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Proctotydaeus sp.	0	1	2	?	0	0	1	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Halotydeus destructor	0	1	2	0	0	0	1	0	0	0	-	1	0	1	0	-	1	1	1	0	0	1
Stereotydeus sp.	0	1	0	0	?	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	1
Arhagidia monothrix	1	0	0	0	?	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	1
Claveupodes sp.	0	1	2	0	?	0	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	1
Neoscirula reticulata	0	0	0	0	?	0	1	0	0	0	-	0	0	1	0	-	1	1	1	0	0	0
Trachymolgus purpureus	0	0	0	0	0	0	0	0	0	0	-	1	1	1	0	-	1	1	1	0	0	0
Apomerantzia kethleyi	1	0	1	0	1	0	0	0	0	0	-	0	0	0	-	-	1	1	1	0	0	-
Neognathus ozkani	0	?	3	1	?	0	0	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Stigmaeus cariae	0	0	2	1	?	0	0	0	0	0	-	0	0	1	0	-	1	1	1	0	0	1
Aegyptobia pirii	0	0	1	1	?	0	0	1	0	0	-	1	1	0	-	-	1	1	1	0	0	-
Labidostomma sp.	0	0	0	0	?	0	1	1	0	0	-	0	0	1	0	-	1	1	1	1	1	0
Sphaerolichus lekprayoonae	0	1	?	?	0	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	0
Hybalicus multifurcatus	0	0	2	?	1	0	1	0	1	0	0	0	0	0	-	-	1	1	1	0	0	-
Loboquintus subsquamatus	1	3	0	?	0	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	1
Pentasetacus araucariae	1	3	0	?	0	1	1	0	1	0	0	0	0	1	1	0	1	1	0	0	0	1
Oziella sibirica	1	3	0	?	0	1	1	0	0	0	-	?	0	0	-	-	1	1	0	0	0	-
Notostrix macrothrix	1	3	0	?	0	1	?	0	1	0	0	0	0	0	-	-	0	1	0	0	0	-
Rhynacus acerioides	1	3	0	?	0	1	1	0	0	0	-	0	0	1	1	-	0	0	0	0	0	1
Triasacarus fedelei	1	3	?	?	?	1	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	1
Ampezzoa triassica	0	2	?	?	?	1	1	0	0	0	-	0	0	0	-	-	0	1	0	0	0	-
Minyacarus aderces	?	?	?	?	?	1	1	0	?	?	?	?	?	1	1	?	0	1	0	0	0	1
Gordialycus sp. A	3	3	0	?	1	1	1	0	0	0	-	0	0	1	1	-	1	1	1	0	0	1
Gordialycus sp. B	3	3	0	?	1	1	1	0	0	0	-	0	0	0	-	-	1	1	1	0	0	-
Osperalycus tenerphagus	2	2	0	0	1	1	1	0	0	0	-	0	0	1	1	-	1	1	1	0	0	1
Cunliffea cf. strenzkei	1	2	0	0	1	1	1	0	0	0	-	0	0	0	-	-	1	1	1	0	0	-
cf. *Psammolycus* sp. A	1	2	?	?	1	1	1	0	0	0	-	0	0	1	1	-	1	1	1	0	0	1
cf. *Psammolycus* sp. B	2	2	1	0	1	1	1	0	0	0	-	0	0	1	1	-	1	1	1	0	0	1
Alycus cf. *denasutatus*	0	0	2	0	0	0	1	0	0	0	-	1	1	1	0	-	1	1	1	1	1	1
Pachygnathus sp.	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1
Bimichaelia nr. *campylognatha*	0	0	2	?	?	0	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1
Petralycus sp.	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	1	0	1	1
Nanorchestes globosus	0	1	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1
Speleorchestes nylsvleyensis	1	?	?	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1	1
Speleorchestes potchefstroomensis	0	1	?	0	?	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1	1
Proterorhagia oztotloica	1	1	2	?	?	0	1	0	0	1	-	0	0	1	0	-	1	1	1	1	1	1
Proteonematalycus wagneri	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1
Micropsammus sp.	1	0	2	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	1	1
Terpnacarus glebulentus	0	0	2	0	1	0	1	0	1	1	0	1	0	1	0	1	1	1	1	1	1	1
Alicorhagia usitata	0	0	2	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1
Stigmalychus veretrum	1	1	2	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1
Grandjeanicus uncus	?	?	?	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	1	1
Oehserchestes humicolus	0	0	2	0	1	0	1	0	1	0	1	0	0	1	0	1	1	1	1	0	1	1
Aphelacarus acarinus	1	1	2	0	?	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1

.....continued on the next page

TABLE 3 (continued). Character matrix.

Character matrix: Part 2 (Ch. 23–44)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
Mummucia ibirapemussu	1	1	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	4	0	0
Cryptocellus iaci	1	1	?	?	?	?	?	?	?	?	0	1	1	1	1	1	1	1	1	4	0	0
Metatydaeolus sp.	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Brachytydeus sp.	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0
Riccardoella triodopsis	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Triophtydeus sp.	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Proctotydaeus sp.	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Halotydeus destructor	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Stereotydeus sp.	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Arhagidia monothrix	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Claveupodes sp.	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Neoscirula reticulata	1	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Trachymolgus purpureus	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0
Apomerantzia kethleyi	1	1	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0	0
Neognathus ozkani	1	1	1	1	1	1	1	?	?	?	0	1	1	0	0	0	0	0	0	0	0	0
Stigmaeus cariae	1	1	0	-	-	-	-	-	-	-	0	1	1	0	0	1	0	1	0	0	0	0
Aegyptobia pirii	1	1	0	-	-	-	-	-	-	-	0	1	1	1	0	1	1	1	1	0	1	1
Labidostomma sp.	1	0	0	-	-	-	-	-	-	-	0	1	1	0	0	1	0	1	0	1	0	0
Sphaerolichus lekprayoonae	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0
Hybalicus multifurcatus	0	0	0	-	-	-	-	-	-	-	0	1	1	1	0	1	0	1	0	1	1	0
Loboquintus subsquamatus	1	?	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0	0
Pentasetacus araucariae	1	?	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0	0
Oziella sibirica	1	?	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	0	0	0	0	0
Notostrix macrothrix	-	?	0	-	-	-	-	-	-	-	0	0	1	0	0	0	0	0	0	0	0	0
Rhynacus acerioides	-	-	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Triasacarus fedelei	-	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0	0	0	0	0
Ampezzoa triassica	-	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0	0	0	0	0	0	0
Minyacarus aderces	-	?	?	?	?	?	?	?	?	?	0	1	1	0	0	0	0	0	0	0	0	0
Gordialycus sp. A	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	0	0	1	0	?	1	0
Gordialycus sp. B	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	0	0	1	0	?	1	0
Osperalycus tenerphagus	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	0	3	1	0
Cunliffea cf. strenzkei	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	?	3	1	0
cf. *Psammolycus* sp. A	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	?	?	1	0
cf. *Psammolycus* sp. B	1	1	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	?	3	1	0
Alycus cf. *denasutatus*	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	3	1	0
Pachygnathus sp.	0	0	1	1	?	1	1	1	?	0	0	1	1	1	1	1	1	1	1	3	1	0
Bimichaelia nr. *campylognatha*	0	0	?	?	?	?	?	?	?	0	0	1	1	1	1	1	1	1	1	3	1	0
Petralycus sp.	0	0	1	?	?	?	1	1	?	0	0	1	1	1	1	1	0	1	0	3	1	0
Nanorchestes globosus	0	0	0	-	-	-	-	-	-	-	0	1	1	1	1	1	1	1	1	?	1	0
Speleorchestes nylsvleyensis	0	0	0	-	-	-	-	-	-	-	1	1	1	1	1	1	0	1	0	?	1	1
Speleorchestes potchefstroomensis	0	0	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	0	?	1	1
Proterorhagia oztotloica	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	2	1	0
Proteonematalycus wagneri	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	2	1	0
Micropsammus sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	3	1	0
Terpnacarus glebulentus	1	0	1	?	?	?	?	?	1	0	0	1	1	1	1	1	0	1	0	3	1	0
Alicorhagia usitata	1	0	0	-	-	-	-	-	-	-	0	1	1	1	1	1	0	1	0	2	1	0
Stigmalychus veretrum	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	2	1	0
Grandjeanicus uncus	1	0	0	-	-	-	-	-	-	-	0	1	1	?	?	?	?	?	?	?	1	0
Oehserchestes humicolus	1	0	0	-	-	-	-	-	-	-	0	1	1	1	0	1	0	1	0	2	1	1
Aphelacarus acarinus	1	0	0	-	-	-	-	-	-	-	1	1	1	1	1	1	0	1	0	2	0	0

.....continued on the next page

Table 3 (continued). Character matrix.

Character matrix: Part 3 (Ch. 45–66)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Mummucia ibirapemussu	1	0	-	?	?	0	-	0	0	0	0	0	1	1	0	0	0	0	0	0	?	0
Cryptocellus iaci	1	0	-	?	0	0	-	1	0	0	0	0	1	1	0	0	0	1	0	0	?	0
Metatydaeolus sp.	0	1	0	0	0	0	-	1	0	0	1	1	0	0	0	0	1	0	0	0	1	1
Brachytydeus sp.	0	1	0	0	0	0	-	1	0	0	1	1	0	0	0	0	1	0	0	0	1	1
Riccardoella triodopsis	0	1	1	0	0	0	-	1	0	0	1	0	0	0	0	0	1	?	?	0	1	1
Triophtydeus sp.	0	1	0	1	0	0	-	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1
Proctotydaeus sp.	0	1	0	0	0	0	-	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1
Halotydeus destructor	0	1	1	1	0	0	-	1	0	0	1	0	0	0	0	0	1	0	0	0	1	?
Stereotydeus sp.	0	1	1	1	0	0	-	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1
Arhagidia monothrix	0	1	1	1	0	0	-	0	0	0	0	0	1	0	0	0	1	0	0	0	1	?
Claveupodes sp.	0	1	1	1	0	0	-	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Neoscirula reticulata	0	1	1	?	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Trachymolgus purpureus	0	1	2	1	0	0	-	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1
Apomerantzia kethleyi	0	1	2	1	0	0	-	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1
Neognathus ozkani	0	0	-	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1
Stigmaeus cariae	0	0	-	0	0	0	-	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Aegyptobia pirii	0	0	-	0	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Labidostomma sp.	0	1	1	0	0	0	-	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1
Sphaerolichus lekprayoonae	0	1	1	0	?	0	-	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Hybalicus multifurcatus	0	1	2	0	?	0	-	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Loboquintus subsquamatus	0	0	-	?	0	?	?	0	1	1	1	0	?	?	0	1	1	0	0	0	0	0
Pentasetacus araucariae	0	0	-	0	0	?	?	0	1	1	1	0	?	?	0	1	1	0	0	0	0	0
Oziella sibirica	0	0	-	0	0	?	?	0	1	1	1	0	?	?	0	1	1	0	0	0	0	0
Notostrix macrothrix	0	0	-	0	0	?	?	0	1	1	1	0	?	?	0	1	1	0	0	0	0	0
Rhynacus acerioides	0	0	-	0	0	?	?	0	1	1	1	0	?	?	0	0	1	0	0	0	0	0
Triasacarus fedelei	0	0	-	?	0	?	?	?	1	?	?	0	?	?	0	1	1	0	0	0	?	?
Ampezzoa triassica	0	0	-	?	0	?	?	?	?	?	?	0	?	?	0	1	1	0	0	0	?	?
Minyacarus aderces	0	?	?	?	0	?	?	?	1	?	?	0	?	?	0	?	1	?	?	0	?	?
Gordialycus sp. A	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Gordialycus sp. B	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Osperalycus tenerphagus	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Cunliffea cf. strenzkei	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0
cf. *Psammolycus* sp. A	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
cf. *Psammolycus* sp. B	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Alycus cf. *denasutatus*	1	1	2	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Pachygnathus sp.	1	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bimichaelia nr. *campylognatha*	1	1	2	1	0	0	-	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Petralycus sp.	0	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nanorchestes globosus	1	1	1	1	0	1	1	0	0	0	0	0	?	1	1	0	0	0	0	0	0	0
Speleorchestes nylsvleyensis	1	1	2	1	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Speleorchestes potchefstroomensis	1	1	2	1	0	1	?	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Proterorhagia oztotloica	0	1	2	0	0	?	?	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Proteonematalycus wagneri	0	1	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Micropsammus sp.	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Terpnacarus glebulentus	0	1	2	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Alicorhagia usitata	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Stigmalychus veretrum	0	1	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Grandjeanicus uncus	0	1	2	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Oehserchestes humicolus	0	1	2	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Aphelacarus acarinus	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0

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TABLE 3 (continued). Character matrix.

Character matrix: Part 4 (Ch. 67–88)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	6	6	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8
	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Mummucia ibirapemussu	1	1	1	?	?	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1	?	?
Cryptocellus iaci	1	1	1	0	0	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1	?	?
Metatydaeolus sp.	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1
Brachytydeus sp.	1	1	1	1	1	2	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1
Riccardoella triodopsis	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1
Triophtydeus sp.	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0
Proctotydaeus sp.	0	1	1	0	1	-	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1
Halotydeus destructor	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Stereotydeus sp.	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Arhagidia monothrix	1	1	1	1	1	2	1	0	1	0	0	1	1	0	1	1	0	1	1	0	1	1
Claveupodes sp.	1	1	1	1	1	2	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Neoscirula reticulata	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Trachymolgus purpureus	1	1	1	1	1	2	1	0	1	1	0	1	1	0	1	1	0	1	1	0	1	1
Apomerantzia kethleyi	1	1	1	0	0	-	-	-	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Neognathus ozkani	1	1	1	1	1	0	1	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Stigmaeus cariae	1	1	1	1	1	0	1	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Aegyptobia pirii	1	1	1	1	1	3	1	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Labidostomma sp.	1	1	1	0	1	-	0	-	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Sphaerolichus lekprayoonae	1	1	1	0	1	-	0	-	0	0	0	1	0	0	1	0	0	1	0	0	1	1
Hybalicus multifurcatus	1	1	1	1	1	2	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1
Loboquintus subsquamatus	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Pentasetacus araucariae	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Oziella sibirica	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Notostrix macrothrix	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Rhynacus acerioides	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Triasacarus fedelei	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Ampezzoa triassica	0	0	-	1	1	0	1	0	?	?	?	?	?	?	-	-	-	-	-	-	1	1
Minyacarus aderces	0	0	-	1	1	0	1	0	0	0	0	0	0	0	-	-	-	-	-	-	1	1
Gordialycus sp. A	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Gordialycus sp. B	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Osperalycus tenerphagus	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cunliffea cf. strenzkei	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
cf. *Psammolycus* sp. A	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
cf. *Psammolycus* sp. B	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Alycus cf. *denasutatus*	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	1	0	0	1	1
Pachygnathus sp.	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1
Bimichaelia nr. *campylognatha*	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1
Petralycus sp.	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	1	0	1	1	1	1	1
Nanorchestes globosus	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Speleorchestes nylsvleyensis	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Speleorchestes potchefstroomensis	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterorhagia oztotloica	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	1	1	0	1	1
Proteonematalycus wagneri	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Micropsammus sp.	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1
Terpnacarus glebulentus	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Alicorhagia usitata	0	0	0	1	1	1	0	-	0	0	0	0	0	0	1	1	0	1	0	0	1	1
Stigmalychus veretrum	0	0	0	1	1	1	0	-	0	0	0	0	0	0	1	1	0	1	0	0	1	1
Grandjeanicus uncus	0	1	1	0	1	-	0	-	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Oehserchestes humicolus	0	1	1	1	1	1	0	-	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Aphelacarus acarinus	1	1	1	1	1	1	0	-	0	0	0	1	0	0	1	1	0	1	1	0	1	1

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Table 3 (continued). Character matrix.

Character matrix: Part 5 (Ch. 89–110)	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
	8	9	9	9	9	9	9	9	9	9	9	0	0	0	0	0	0	0	0	0	1
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Mummucia ibirapemussu	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	2	2	0	1	0
Cryptocellus iaci	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0
Metatydaeolus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachytydeus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Riccardoella triodopsis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Triophtydeus sp.	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Proctotydaeus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Halotydeus destructor	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	2	2	2	2	0	0	0
Stereotydeus sp.	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Arhagidia monothrix	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	2	2	2	2	0	0	0
Claveupodes sp.	0	0	1	?	0	0	1	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0
Neoscirula reticulata	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	2	2	2	2	0	0	0
Trachymolgus purpureus	0	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	2	2	0	0	0
Apomerantzia kethleyi	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0
Neognathus ozkani	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stigmaeus cariae	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aegyptobia pirii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Labidostomma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0
Sphaerolichus lekprayoonae	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0
Hybalicus multifurcatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	2	0	0	0
Loboquintus subsquamatus	-	-	1	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Pentasetacus araucariae	-	-	1	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Oziella sibirica	-	-	1	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Notostrix macrothrix	-	-	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Rhynacus acerioides	-	-	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Triasacarus fedelei	-	-	1	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Ampezzoa triassica	-	-	1	?	-	-	0	0	-	-	0	0	-	-	0	?	0	-	-	-	0	1
Minyacarus aderces	-	-	1	0	-	-	0	0	-	-	0	0	-	-	0	0	0	-	-	-	0	1
Gordialycus sp. A	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Gordialycus sp. B	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Osperalycus tenerphagus	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cunliffea cf. strenzkei	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cf. *Psammolycus* sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cf. *Psammolycus* sp. B	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alycus cf. *denasutatus*	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0
Pachygnathus sp.	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0
Bimichaelia nr. *campylognatha*	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Petralycus sp.	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	2	0	0	0
Nanorchestes globosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Speleorchestes nylsvleyensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0
Speleorchestes potchefstroomensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0
Proterorhagia oztotloica	0	0	1	1	1	1	?	1	1	0	0	0	0	0	0	2	2	2	2	0	0	0
Proteonematalycus wagneri	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	2	2	2	2	0	0	0
Micropsammus sp.	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
Terpnacarus glebulentus	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	2	0	1	2	0	0	0
Alicorhagia usitata	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	2	2	2	2	0	0	0
Stigmalychus veretrum	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0
Grandjeanicus uncus	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	1	1	2	0	0	0
Oehserchestes humicolus	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	2	0	2	2	0	0	0
Aphelacarus acarinus	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	2	2	2	2	0	0	0

Results

The heuristic search using the full character set generated 480 equally most parsimonious trees (tree length, 447 steps; CI= 0.27; RI= 0.70; RC= 0.19). In common with the results of Pepato and Klimov (2015), Sarcoptiformes came out as paraphyletic with respect to Trombidiformes (Fig. 3). Our results also recovered a large clade that includes all of Acariformes except *Proterorhagia oztotloica* Lindquist and Palacios-Vargas, which was not included in the analysis undertaken by Pepato and Klimov (2015). However, this clade has weak support (Bremer =1; bootstrap <50%).

Some traditional taxa were recovered with moderate or strong support (Bremer >1; bootstrap >50%), namely Nanorchestidae, Alycidae and Eriophyoidea. As expected, the heuristic search did not recover Eupodina (Eupodides) as a clade. Some of the commonly accepted members of Eupodina form a grade with respect to Raphignathina, whereas Eriophyoidea falls outside of Trombidiformes, a result that is consistent with the results of Xue *et al*. (2016, 2017). Aside from these features and the placement of *Hybalicus* (Lordalycidae) with several sarcoptiform mites (*Grandjeanicus*, *Oehserchestes* and *Aphelacarus*), the structure and composition of Trombidiformes largely accords with current classification schemes (Lindquist *et al*. 2009; Zhang *et al*. 2011). However, support for the Trombidiformes clade is weak (Bremer =1; bootstrap <50%).

Triassic Eriophyoidea ("Triasacaroidea") do not form a monophyletic group. Specifically, *Ampezzoa* falls into a clade with some of the extant Eriophyoidea, namely *Rhynacus* and *Notostrix*. All other fossil Eriophyoidea fall outside that clade. Eriophyoidea was found nested within Nematalycidae. A larger clade unites Eriophyoidea + Nematalycidae (EN) with Nanorchestidae (Bremer =4; bootstrap <50%). This clade is nested within Sarcoptiformes, but support for the more basal clades of that order are weak (Bremer=1; bootstrap <50%).

EN is one of the strongest supported clades across the whole tree (Bremer =5; bootstrap =85%), along with Nanorchestidae (Bremer =8; bootstrap =99%), *Speleorchestes* (Bremer =3; bootstrap =92%) and Eriophyoidea (Bremer =7; bootstrap =99%). Alternative hypotheses to EN (hypotheses 2 to 5 of table 4) cannot yet be dismissed becaue the K-H tests resulted in p-values above 0.05 (Table 5). However, p-values are relatively low (<0.15) with respect to the previously hypothesized placement of Eriophyoidea with Raphignathina (hypothesis 3), Tydeoidea (hypothesis 4), or Proteonematalycidae and Micropsammidae (Hypothesis 5).

Support for EN was still relatively good after the ratio characters were removed (Bremer=3; bootstrap=66%). Therefore, not all the support for this clade arises from synapomorphies pertaining to body shape and proportions. Body elongation (ch. 1) is an ambiguous synapomorphy for EN (note its exclusion from Table 5). Instead, an elongated body (ch.1 >0) may be a synapomorphy for a larger clade that also includes *Micropsammus* and *Proteonematalycus*.

Eleven unambiguous synapomorphies unite some or all members of Nematalycidae with Eriophyoidea (Table 5). Additionally, five unambiguous synapomorphies unite Nanorchestidae, Nematalycidae and Eriophyoidea: 1) increased relative distance between anus and genitalia (ch. 2–character states 1 to 3); 2) absence of opisthosomal lyrifissures (ch. 25); 3) gut without boluses (ch. 49); 4) absence of solenidia from palp tarsus (ch. 65); 5) absence of solenidia from tibiae II (ch. 92). Note that in the description of the nematalycid *Psammolycus delamarei* Schubart (no specimens were available for this study) a solenidion is drawn on the palp tarsus (Schubart 1973). However, detailed observations using SEM have not revealed a solenidion on the palp tarsus of any of the Nematalycidae, including cf. *Psammolycus* (pers. obs.). Therefore it is possible that a structure on the palp tarsus was misinterpreted as a solenidion. Alternatively, the palp-tarsal solenidion re-evolved in this species.

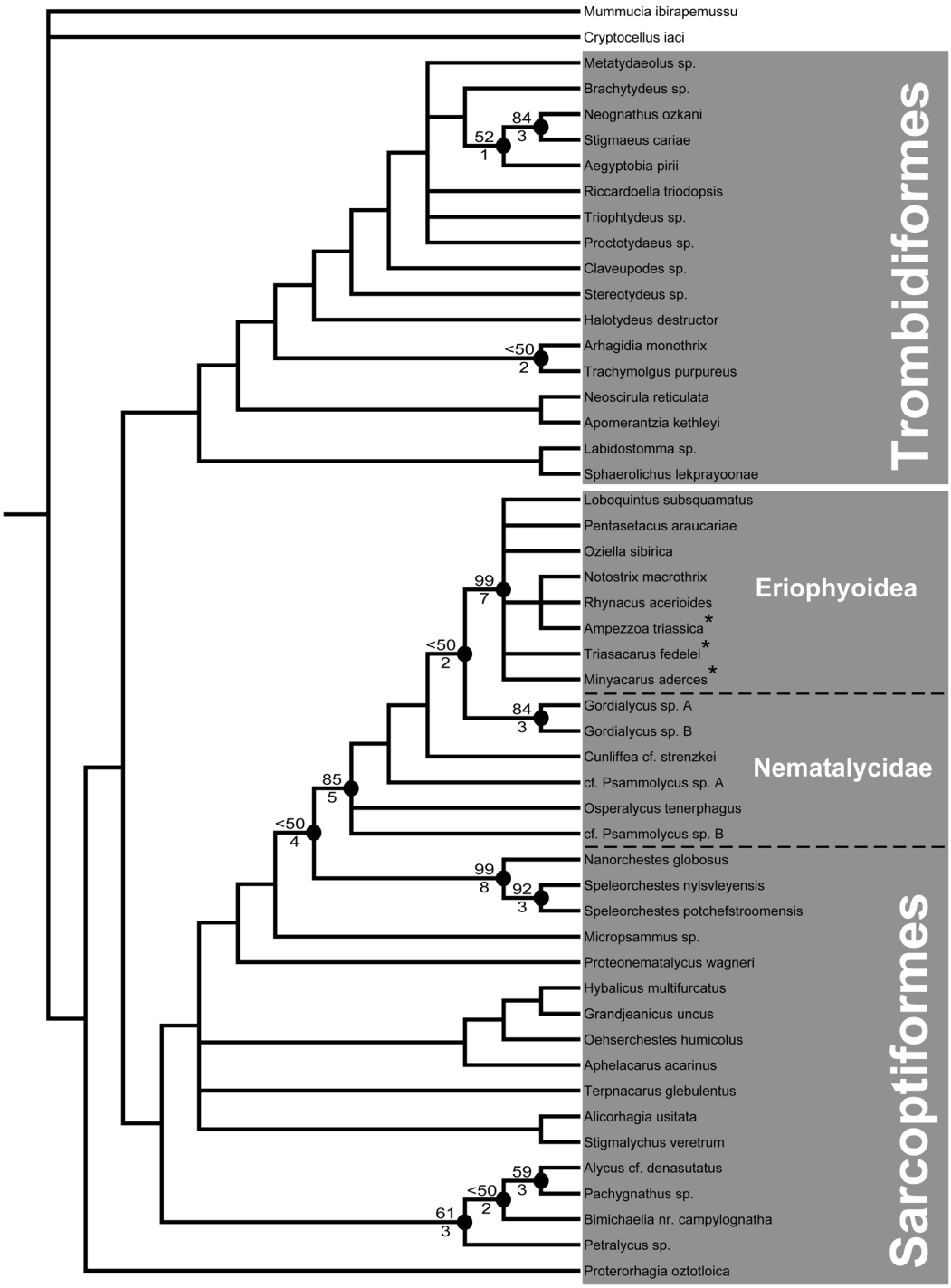

FIGURE 3. Strict consensus tree of the 480 equally most parsimonious trees (heuristic search using all characters). Nodes with opaque, black circles have bootstrap >50% and/or Bremer >1: bootstrap above; Bremer below. Asterisks denote Triassic Eriophyoidea. All other species of Eriophyoidea are extant. The results of this tree deviate from the current classification (Lindquist *et al.* 2009; Zhang 2011) with respect to Eriophyoidea and *Hybalicus*, which both fall outside Trombidiformes and into Sarcoptiformes.

TABLE 4. Scores of optimal trees in constrained analyses (heuristic analysis—characters unweighted). Numbers in brackets indicate the additional number of steps relative to the optimal unconstrained trees (length 447). The p-values (two-tail tests) indicate whether the length of trees from the constrained search is significantly different from the length of trees from the unconstrained search. Note that *Hybalicus* was excluded from Trombidiformes (see Method).

Hypothesis #	Constraint	Score of optimal tree(s)	p-value (KH test)
1)	(Eriophyoidea, Nematalycidae, Trombidiformes)	451(+4)	0.57
2)	(Eriophyoidea, Trombidiformes)	456 (+9)	0.27
3)	(Eriophyoidea, Raphignathina)	457 (+10)	0.10
4)	(Eriophyoidea, Tydeoidea)	460 (+13)	0.13
5)	(Nematalycidae, *Proteonematalycus*, *Micropsammus*)	461 (+14)	0.06

TABLE 5. Unambiguous synapomorphies that unite some or all of Nematalycidae with Eriophyoidea. CI = consistency index; RI = retention index; RC = rescaled consistency index. Note that the values in the left column associated with two of the ratio characters (2 & 3) refer to discretized ratios (Thiele, 1993) that range from 0 to 3. (G) or (GC) indicates that the synapomoprhy unites only more derivative members of Nematalycidae with Eriophyoidea (G=only *Gordialycus*; GC = only *Gordialycus* and *Cunliffea*). (R) indicates that the trait has reversed to the plesiomorphic state among some members of the clade. Asterisk means the exact point of origin is ambiguous; it may instead be a synapomorphy for all EN.

Synapomorphy	**Ch #**	**CI**	**RI**	**RC**
Relative distance between anus and genitalia = 2 to 3	2	0.231	0.744	0.172
Relative distance between coxal fields I = 0 (R) (GC)*	3	0.158	0.500	0.079
Annuli present	6	1.000	1.000	1.000
Unpaired *vi* seta	15	0.333	0.800	0.267
Setae *exp* absent	20	0.250	0.813	0.203
Setae *in* absent	21	0.333	0.895	0.298
Setae *d2* absent (G)	38	0.250	0.857	0.214
Palp trochanter fused with palp femur (R)	60	0.250	0.700	0.175
Legs II lacking lateral claws (R) (GC)	68	0.250	0.786	0.196
Empodia elongated and straight (G)	72	0.333	0.750	0.250
Femur I not subdivided	104	0.200	0.556	0.111

Discussion

The Eriophyoidea + Nematalycidae clade

The results of the analysis are inconsistent with the view that similarities between the unusual morphologies of Eriophyoidea and Nematalycidae are the result of convergent evolution. Instead there is strong support for the hypothesis that these two taxa belong in the same clade. A number of the synapomorphies are interesting because they are somewhat unusual among most acariform mites. These include a large relative distance between the anus and genitalia (ch. 2), opisthosomal annuli (ch. 6), an unpaired seta *vi* on the prodorsum (ch. 15), and fusion of the palp trochanter and femur (ch. 60). Notably, body elongation (ch. 1) is an ambiguous synapomporphy for this group; there are similar degrees of elongation in other Endeostigmata, e.g. *Proteonematalycus*.

Because Eriophyoidea and Nematalycidae both have a highly elongated body, they may also share other features associated with body elongation. These may include characters such as a small intercoxal gap (ch. 3) (associated with the body narrowing) and a large relative distance between the anus and the genitalia (ch. 2) (associated with posterior body elongation). Therefore, it could be argued that support for EN is elevated by a suite of convergences associated with body elongation. However, even when the three ratio characters pertaining to body shape (ch. 1 to 3) are excluded, support for EN is still relatively strong (Bremer=3; bootstrap=66%). Moreover, much of the support for EN and EN + Nanorchestidae can be attributed to synapomorphies that appear to bear no relationship with body elongation. These include absence of opisthosomal lyrifissures (ch. 25), fusion of the palp trochanter and femur (ch. 60), loss of palp solenidia (ch. 65), loss of lateral claws from legs II (ch. 68), loss of claw-like empodia (ch. 72), and lack of subdivision of femur I (ch. 104). Therefore, it seems more likely that EN is a true clade.

The results of the analyses do not support the monophyly of Nematalycoidea sensu Kethley (1989) (hypothesis 5 of Table 4), although this hypothesis cannot yet be rejected with a high degree of confidence because the constrained tree is not quite significantly different in length from the unconstrained tree (p=0.06: K-H test). Lack of support for Nematalycoidea sensu Kethley (1989) is unsurprising. Although all of the members of this group share a relatively elongated body, *Proteonematalycus* and *Micropsammus* share relatively few features with Nematalycidae. They lack annuli (ch. 6)—their opisthosomal striations are predominantly longitudinal, which prevents the extension or contraction of their bodies. Furthermore, they have a genital region that is near to their anus (ch. 2), and they have a prodorsum that has either a complete or near-complete set of setae (ch. 14–21). They also have opisthosomal lyrifissures (ch. 25) and at least one post-podosomal constriction (ch. 33), both features that are completely absent from Nematalycidae and Eriophyoidea. Furthermore, *Proteonematalycus* and *Micropsammus* are particulate feeding mites (ch. 49), like most other Sarcoptiformes, whereas Nematalycidae and Eriophyoidea are fluid feeding mites.

A Tydeoidea-Eriophyoidea clade (hypothesis 4 of Table 4) cannot yet be confidently rejected either (p=0.13: K-H test), but our results provide no support for this relationship. Lindquist based his argumentation for a sister relationship between Tydeoidea and Eriophyoidea on a relatively large number of different characters (Lindquist 1996a). Despite the inclusion of the majority of these characters in our analysis, the results do not support a close relationship between the two taxa. Notably, the majority of the characters that were highlighted by Lindquist (1996a), but are not included in the analysis, do not show a greater resemblance between Eriophyoidea and Tydeoidea than between Eriophyoidea and Nematalycidae (see section on Character coding).

Tydeoidea and Eriophyoidea are clearly very different with respect to body proportions. A number of similarities between these taxa, including cheliceral attenuation (ch. 53–55) and reduced segmental anamorphosis (ch. 42), are assumed to be the result of convergence (based on the results of the current analysis). As mentioned above, cheliceral attenuation of Tydeoidea has occurred in a completely different way in Tydeoidea than in Eriophyoidea. In Eriophyoidea, the entire chelicerae are attenuated whereas in Tydeoidea, like other members of Trombidiformes, only the movable digits have undergone attenuation. Sexually dimorphic suppression of eugenital setae has been used as an argument for linking Eriophyoidea and Tydeoidea as sister groups (Lindquist 1996a), but this feature is also present in Nematalycidae (see section on Character coding).

Finally, two other features, fusion of palp segments (ch. 60–63) and the small size of the gap between coxae I (ch. 3), both suggested as possible evidence of a sister relationship between Eriophyoidea and Tydeoidea (Lindquist 1996a), show much greater similarity between Eriophyoidea and Nematalycidae. In both of the latter taxa, coxae I (ch. 3) are adjoined or close together (character state = 0 to 1). In Tydeoidea, this character is usually higher and never as low as

0. With regard to the palps, the palp trochanter (ch. 60) of Eriophyoidea and Nematalycidae is usually fused with the palp femur. But in Tydeoidea the palp trochanter is never fused with the palp femur.

Eriophyoidea are a very strongly supported monophyletic group; bootstrap values are 99% and Bremer support is 7. In contrast, the monophyly of Triassic Eriophyoidea (Triasacaroidea) has no support. But this is perhaps to be expected because no morphological synapomoprhies have been found for this group, although blunt cheliceral stylets are regarded as a putative syanpomorphy (Sidorchuk *et al.* 2015). However, this character can no longer be a putative synapomorphy if Eriophyoidea is derived from within "Endeostigmata", which have chelate chelicerae. If the styliform chelicerae of Eriophyoidea evolved through the attenuation of chelate chelicerae, blunt stylets would appear to represent a transitional state before the evolution of fine stylets.

Nematalycidae has no support either. In all of the optimal trees from the main heuristic search, Nematalycidae are paraphyletic with respect to Eriophyoidea. In that arrangement, *Gordialycus* is the presumed sister taxon to Eriophyoidea (Bremer = 2; bootstrap =53%). Interestingly, this result is consistent with an older idea by Keifer (1975), suggesting that the disappearance of the rear pairs of legs of Eriophyoidea may be attributed to the anterior movement of the genitalia, a phenomenon which is evident in *Gordialycus* (ch. 2; character state 3 is a synapomorphy for both taxa). According to Keifer's hypothesis, the dramatic reduction of the rear legs in *Gordialycus* may be a synapomorphy that Eriophyoidea took to completion with the total loss of those legs.

Another synapomorphy that unites *Gordialycus* and Eriophyoidea is the loss of claw-like empodia (ch. 72). These two taxa also share a reduced opisthosomal chaetome compared to other nematalycids; e.g. both share an absence of setae *d2* (Ch. 38). But most opisthosomal setae were not included in this analysis due to difficulties pertaining to their homology. There are also two characters that unite the most derivative members of Nematalycidae, *Gordialycus* and *Cunliffea*, with Eriophyoidea: 1) the adjoinment of coxae I (ch. 3); 2) the loss of lateral claws from legs II (ch. 68).

One final but more tentative piece of evidence for paraphyly comes from the shape of the rutella (ch. 51), which possess multiple projections in other mites. In *Gordialycus*, *Cunliffea* and cf. *Psammolycus* sp. A, but not more basal members of Nematalycidae, there is no furcation of the rutella and so they are more styliform in their basic structure (Fig. 2B, E). This is consistent with the hypothesis that some of the additional styliform elements in the mouthparts of Eriophyoidea are homologous with rutella (Lindquist 1998). Note that both the presence and shape of rutella was coded as unknown for Eriophyoidea, and therefore rutella provided no actual support for any clade that includes Eriophyoidea and some or all of Nematalycidae.

When heuristic searches are constrained for the monophyly of Nematalycidae, the resulting trees are only 2 steps longer (p=0.62: KH test) than trees resulting from the unconstrained search. Therefore, the paraphyletic status of Nematalycidae is tentative. But if Nematalycidae are paraphyletic, they would have to be older than the Eriophyoidea, which originated no later than the Triassic (c. 230 Ma) (Schmidt *et al.* 2012; Sidorchuk *et al.* 2015). Accordingly, the highly elongated body and unusual modes of locomotion (Bolton *et al.* 2015b) of Nematalycidae would represent a relatively early departure from the primitive body form and mode of locomotion of Acariformes.

The phylogenetic position of the Eriophyoidea + Nematalycidae clade

The EN lineage falls consistently outside of Trombidiformes, and into Sarcoptiformes. This is concordant with the results of recent molecular based studies, which place Nematalycidae or Eriophyoidea outside of Trombidiformes (Pepato & Klimov 2015; Xue *et al.* 2016; Xue *et al.* 2017). But note that the constraint for the placement of EN within Trombidiformes (hypothesis 1 of table 4) results in a tree length that is not significantly different to the tree resulting from the unconstrained search (p=0.57: K-H test), and so the position of EN is not yet known. However, placement of EN

within Trombidiformes would mean that Nematalyicdae would be unique among Trombidiformes with respect to the possession of rutella (ch. 50). Indeed, the presence or absence of rutella, a pair of modified setae on the gnathosoma, is the main diagnostic character used to differentiate Sarcoptiformes from Trombidiformes (OConnor 1984). Modified rutella may also be present in Eriophyoidea (see above).

Notably, placement of Eriophyoidea outside of Trombidiformes is not a new idea, as several older classification schemes, e.g. Oudemans (1923), Thor (1928), Vitzthum (1931) and André (1949), did the same. Of course those authors based this decision on "degree of difference", whereas the current analysis achieved the same result based on shared derived character states.

Evolutionary considerations

Whereas the current results solve a number of existing questions and contradictions, they do raise some new ones. For example, Eriophyoidea and Nematalycidae live in completely different habitats and have strongly differing life styles. Eriophyoidea live and feed on vascular plants, dispersing by air currents, whereas Nematalycidae are extremophiles that inhabit deep soil or mineral regolith, e.g. sand. In this respect, Nematalycidae are not so unusual among "Endeostigmata", which typically live in soil, mineral regolith or leaf litter. Plant-feeding is therefore an apomoprhic condition that appears unique to Eriophyoidea among "Endeostigmata".The feeding habits of most Nematalycidae are not known, but *Osperalycus* and *Gordialycus* appear to be adapted for feeding on single-celled microorganisms such as yeasts and/or bacteria (Bolton *et al.* 2015a).

In the absence of hard data, we can only suggest a scenario that would be consistent with available data. If Nematalycidae are ancestral to Eriophyoidea (Fig. 3), then it is possible that Eriophyoidea originated in mineral regolith. They may have originally used their chelate chelicerae for piercing thin-walled organisms in this habitat (fungi and/or bacteria) before they became modified into styliform structures for piercing vascular plants. It may be that they transitioned to feeding on plant roots by first feeding on the mycorhyza or bacterial colonies associated with those roots. This is consistent with recent hypotheses that some Nematalycidae feed on fungi and/or bacteria (Bolton *et al.* 2015a). Once Eriophyoidea switched to feeding on plants, their diversification was possibly driven by a symbiotic relationship with plants. Evidence for this is provided by the high levels of host specificity of Eriophyoidea (Skoracka *et al.* 2010). It may even be that Eriophyoidea were already somewhat preadapted for plant feeding while they still lived in the mineral regolith as nematalycids. Their narrow bodies could have allowed them to exploit very tight spaces within plants (e.g. underneath the epidermis). This is consistent with a recent hypothesis that endoparasitism is the ancestral state for all Eriophyoidea (Chetverikov 2015).

Preadaptation for plant-feeding is also evident with respect to the gnathosoma. In Acariformes, feeding on the fluids of plants usually involves a large degree of gnathosomal integration because this allows the chelicerae to run through the preoral cavity. Consequently, fluid can pass into the mouth via a puncture, made by the chelicerae, without requiring the gnathosoma to move position. But gnathosomal integration also arises in mites that feed on the fluids of animals, fungi, etc. The gnathosomas of Nematalycidae and Eriophyoidea are unusually compact (the palp trochanter and femur are often fused in both taxa) and in some cases the chelicerae have become tightly intergrated with the subcapitulum (Introduction; Bolton et al. 2015a). In Nematalycidae these modifications could have originally arisen for feeding on fungi or possibly bacteria. Eriophyoidea has undergone additional gnathosomal integration: their stylet bundle is completely enveloped within a subcapitular sheath (Nuzzaci 1979; Nuzzaci & de Lillo 1991).

Therefore, the results of this analysis provide a possible explanation for the unusual mouthparts of Eriophyoidea. However, some gnathosomal apomorphies are still poorly understood with respect to their origin and/or homology. These include the suboral fork (Chetverikov and Bolton, 2016) and

the motivator. And it is also uncertain if rutella are homologous with any of the components of the stylet bundle (Lindquist, 1998).

Another interesting and unusual feature of the mouthparts of Eriophyoidea is the styliform labrum. A styliform labrum is also present in *Nanorchestes*, which is noteworthy because this genus belongs to a family that may be sister to EN (Fig. 3). However, the labra of *Speleorchestes* (sister to *Nanorchestes*) and basal Nematalycidae (cf. *Psammolycus* and *Osperalycus*) are relatively broad. Therefore, if the tree in Fig. 3 is correct, the styliform labrum of Eriophyoidea almost certainly arose independently of the one in *Nanorchestes*.

Basal phylogeny of Acariformes

Relationships in basal Acariformes are only partially resolved in this analysis due to weak support. However, this is the first formal phylogenetic analysis to include representatives of all families within "Endeostigmata"; note that Proterorhagiidae was not yet discovered when OConnor (1984) undertook his phylogenetic analysis. Aside from the strongly supported relationship between Nematalycidae and Eriophyoidea (see above), the most interesting result is the sister relationship between *Proterorhagia oztotloica* and the rest of Acariformes, although support values for the clade that excludes *Proterorhagia* are weak (Bremer =1; bootstrap <50%).

Interestingly, *Proterorhagia* does have a number of primitive character states that are consistent with that phylogenetic position (Lindquist & Palacios-Vargas 1991). It is the only acariform taxon to retain a distinct labium, and it also has unusually large chelicerae, a feature shared with Solifugae (note that cheliceral size was not included among the coded characters), a possible sister taxon to Acariformes (Grandjean, 1954; Dabert *et al.* 2010; Pepato *et al.* 2010; Pepato & Klimov 2015). So far, specimens of this highly distinctive mite have not been obtained for molecular phylogenetic analysis.

Assuming our strict consensus tree is correct (Fig. 3), the exclusion of *Proterorhagia* from Sarcoptiformes would make Trombidiformes sister to Sarcoptiformes (sensu OConnor 1984), providing that *Hybalicus* (Lordalycidae) is also relocated to Sarcoptiformes. However, this is inconclusive due to the weak support for all basal relationships. One final and perhaps noteworthy finding is that Nematalycoidea (sensu Kethley 1989) is monophyletic if Nanorchestidae and Eriophyoidea are also included within this group. But again, support for this clade is weak (Bremer =1; bootstrap <50%).

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Appendix: Collection data for specimens examined

Metatydaeolus sp.—USA, Ohio, Hocking Co., Deep Woods Farm, 39.4088 N, 82.5766 W, loam, 20-30 cm deep; collector: Samuel Bolton, May, 2010, (SB10-0516-III), 1 female (OSAL 0116344).

Brachytydeus sp.—USA, Ohio, Fairfield Co., Carroll, 39.7986 N, 82.70709 W, ex under apple bark; collector: D. W. Davis, 8 April 1966, 1 female (OSAL 0065954).

Riccardoella triodopsis—U.S.A. Alabama, Lawrence Co., Bankhead National Forest, 34.1334 N, 87.2583 W, ex *Triodopsis obstricta*; collector J. Petranka, 27 Sep 1984 (HK 85-0205-2) 2 males, 1 larva (OSAL 0065202, 0065203, 0065204).

Triophtydeus sp.—USA, Ohio, Fairfield Co., Carroll, 39.7986 N, 82.70709 W, ex under apple bark; collector: D. W. Davis, 8 April 1966, 1 female (OSAL 0065963)

Proctotydaeus sp.—Mexico, Yucatan, 30 km north of Santa Elena, 20.3279 N, 89.64409 W, ex *Schistocerca*; collector: Mario Poot, 10 Sept 2009, 1 female (OSAL 0103884).

Stereotydeus sp.—unknown location; collector J. Robillard, 5 Sep 1968, 1 female (OSAL 0065522)

Claveupodes sp.—Italy, Tuscany, Florence, Boboli Gardens, 43.7627 N, 11.2481 E; collector: D. Wrensch, 2 Nov 1974, 1 female (OSAL 0065214).

Neoscirula reticulata—USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf transect, 35°52.040 N 93°24.099W, ex litter old growth beech, flag 7; collectors: J.R. Fisher and M. J. Skvarla, 5 May 2010, 1 female (OSAL 0104763) (APGD 10-0506-011).

Trachymolgus purpureus—USA, Arkansas, Newton Co., Rock Bridge Creek, 2.5km N of Mount Sherman, N36.0566 N, 93.2570 W, ex litter in and near rotten stumps; collectors: W. C. and J. M. Welbourn, 20 July 1986, 1 protonymph (measurements based on description) (OSAL 0061852).

Apomerantzia kethleyi—USA, Ohio, Hocking Co., Deep Woods Farm, 39.4088 N, 82.5766 W, 20-30 cm deep; collector: S.J. Bolton, 1 May 2010, 1 female (OSAL 0116332).

Labidostomma sp.—Guatemala, El Progresso, Cerro Pinalón, 15.0847 N, 89.9499 W, ex: sifted leaf litter, cloud forest; collector: LLAMA, 02 May 2009, 1 male (measurements based on SEM images) (OSAL 0116345).

Gordialycus sp. A—USA, New Mexico, 45-60 cm deep; collector, J.B. Kethley, 1985 (FMHD 85-289), 1 female (OSAL 0116330).

Gordialycus sp. B—USA, New Mexico; collector, J.B. Kethley, 1983 (FMHD 83-586), 1 female (OSAL 0116331).

Osperalycus tenerphagus—USA, Ohio, Franklin Co., Kinnear Road, 39.9990 N, 83.0468 W, silty clay loam from suburban prairie (including shrubs, grasses and small trees), 40 cm deep; collector: Samuel Bolton, May 2011, (SB11-05-I), 3 females (OSAL 015134, 0103239, 0105138).

Cunliffea cf. *strenzkei*—USA, Indiana, Lake Co., Marquette Park, 41.6175 N, 87.2711 W; collector, S.J. Bolton, 25 May 2013, 2 females (OSAL 0114124, 0116329)

cf. *Psammolycus* sp. A—USA, Florida, Highlands Co., Highlands Hammock State Park, 27.4713 N 81.5646 W, sand, 30 to 40 cm deep; collector: S.J. Bolton, April 2011, 1 female (OSAL 0116328).

cf. *Psammolycus* sp. B—USA, Indiana, Lake Co., Marquette Park, 41.6175 N, 87.2711 W; collector, S.J. Bolton, 25 May 2013, 1 female (OSAL 0114146).

Alycus cf. *denasutatus*—USA, Illinois, Carroll Co., Miss. Palisades St. Pk., 2 mi N Savanna, ravine litter with interrupted fern; collectors: J. Wagner and J. Kethley, 11 April 1983 (FMHD 83-61), 1 female, 1 male (OSAL 0116334, 0116395).

Pachygnathus sp.—USA, Nebraska, Washington Co., N. Fort Calhoun, Desoto Natl. Wildlife | Refuge, floodplain litter; collector: W. Suter, 15 May 1982 (FMHD 82-144), female (OSAL 0116337).

Bimichaelia nr. *campylognatha*—USA, Wisconsin, Kenosha Co., Silver Lake Bog, Sphagnum, u. Larix and poison sumac; collector: W. Suter, 28 April 1985 (FMHD 85-173), 1 female (OSAL 0116338).

Petralycus sp.—USA, Florida, Franklin Co., Ochlockonee Bay, algal drift near river; collector: W.S. Suter (FMHD 82-105), 27 March 1982, 1 female, 1 male (OSAL 0116335, 0116336).

Proteonematalycus wagneri—USA, Indiana, Indiana Dunes State Park, Marquette Park, sand, upper 10 cm; collector: J.B. Kethley, 14 May 1986 (FMHD 86-203), 1 female (OSAL 0116343).

Micropsammus sp.—1) USA, Florida, Pinellas Co., Clearwater Beach Island, 27.9845 N, 82.8280 W, sand among marram grass, upper 10 cm; collector: S.J. Bolton, April 2011, 1 female, 2 males (OSAL 0116339, 0116340, 0116341). 2) USA, Florida, Archer; collector: J.B. Kethley, 1987 (FMHD 87-129), 1 female (OSAL 116342).

Oehserchestes humicolus (=spathatus)—unknown location and collector, 1985 (FMHD 85-7), 1 female (OSAL 0116333).