

TRIGYNASPIDA (ACARI: MESOSTIGMATA): NEW DIAGNOSIS, CLASSIFICATION, AND PHYLOGENY

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ACARI,
MESOSTIGMATA,
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KEY, HOSTS,
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UPPER TRIASSIC

SUMMARY: A generally accepted view on the superfamilial and familial level evolutionary relationships and the classification of the Trigynaspida (Acari: Mesostigmata) has been reassessed and a new classification scheme has been proposed. A new diagnosis of the Trigynaspida and its superfamilies, and a key to the families and superfamilies were also given. A total of 51 taxa and 55 characters were analyzed based on the principle of maximum parsimony. Results supported bifurcating lineages of Cercomegistina and Antennophorina within the monophyletic Trigynaspida. However, the current superfamily Fedrizzioidae, which contains four families that are mainly associated with passalids (Fedrizziidae and Klinckowstroemiidae), carabids (Promegistidae), and diplopods or squamates (Paramegistidae), is separated into three groups. While the Fedrizziidae and Klinckowstroemiidae have been remained in the current superfamily Fedrizzioidae, the Promegistidae have been assigned to Parantennuloidea, a taxon that displays an association with carabids and tenebrionids. The remaining family Paramegistidae now stands alone as a new superfamily Paramegistoidea. The phylogenetic position of Parantennuloidea was basal within the Antennophorina. The ant associated Antennophoroidea and Aenictequoidea are considered as sister groups. This new classification is supported by host correlation. Plate tectonics and global biogeographic patterns among trigynaspid mites and hosts suggest that the origin of the Trigynaspida is linked, at the latest, to the early Mesozoic (Upper Triassic).

ACARI,
MESOSTIGMATA,
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CLÉ, HÔTES,
MÉSOZOÏQUE,
TRIAS SUPÉRIEUR

RÉSUMÉ: Une re-évaluation des relations évolutives généralement acceptées au niveau supra familial et familial ainsi que de la classification des Trigynaspida (Acari: Mesostigmata) est effectuée et un nouveau schéma de la classification est proposé. Une nouvelle diagnose des Trigynaspida et des superfamilles, une clé d'identification des familles et des sous familles est aussi fournie. 51 taxa et 55 caractères sont analysés selon le principe du maximum de parcimonie. Les résultats montrent au sein du groupe monphylétique des Trygynaspida les lignées bifurcantes des Cercomegistina et des Antennophorina. Cependant, les familles actuelles de la superfamille des Fedrizzioidae, avec quatre familles associées principalement aux passalides (Fedrizziidae et Klinckowstroemiidae), carabides (Promegistidae), et diplopodes ou aux reptiles (Paramegistidae), sont regroupées

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en trois ensembles : les Fedrizziidae et les Klinckowstroemiidae sont conservées dans les Fedrizzioidea, les Promegistidae sont rattachés aux Parantennuloidea, un taxon qui montre l'association avec les carabidés et les ténébrionides, et la famille des Paramegistidae est la seule de la nouvelle superfamille des Paramegistoidea. Les Parantennuloidea sont situés phylogénétiquement à la base des Antennophorina. Les Antennophoroidea et les Aenictequoidea sont considérés comme des groupes frères. La nouvelle classification est confortée par le lien avec l'hôte. La tectonique des plaques et le schéma biogéographique global des Trigynaspides et des hôtes suggèrent que l'origine de ce groupe pourrait dater au moins du mésozoïque moyen (Trias supérieur).

INTRODUCTION

Mites (Subclass Acari) represent the most diverse group of arachnids and are second only to the insects in terms of the number of animal species (JOHNSTON, 1982; LINDQUIST, 2000; WHEELER, 1990). They are critical ecological elements in the process of ecosystem succession and are important to agriculture and to human and animal hygiene. The mite order Mesostigmata, which occupies diverse habitats in the ecosystem, is often divided into two subgroups, known as Trigynaspida and Monogynaspida. The Trigynaspida, first named by CAMIN & GORIROSSI (1955), is composed of 315 described species in 105 genera in 27 known families. The name Trigynaspida was based primarily on morphological features of the female genital area, which usually features a tripartite genital ('tri-gynaspid') shield, whereas females of the Monogynaspida usually have a single, coalesced genital shield. The typical 'trigynaspid' genital system comprises a mesogynial shield flanked by a pair of latigynial shields. In monogynaspid mites, discrete latigynial elements are typically absent and are thought to be fused with adjacent endopodal elements or with the mesogynial shield.

This tripartite genital system of Trigynaspida is not unique to the members of this group as some early derivative Uropodina (*e. g.*, *Trachytes*) also show 'trigynaspid-like' genital structure. On the other hand, some trigynaspids, such as Celaenopsoidea, often have latigynial or mesogynial shields, or both, fused to the ventral shield elements, resulting in a more or less monogynaspid condition. Accordingly, more detailed and generalized characters that are not restricted to the female genital shields are required to define the Trigynaspida.

Diagnosis of Trigynaspida : Although the Trigynaspida can be identified *prima facie* on the basis of female genital structures, with an exception of the paedomorphic millipede associate *Neotenogynium malkini* Kethley, the group Trigynaspida is diagnosed by the following combination of characters in the adults (Except for the character number 1 below, these characters are also useful in identifying the deutonymphs.):

1. Presence of 'trigynaspid' and derivative genital structures in female (shared with some Uropodina)
2. Presence of 8 setae on femora IV (shared with Diarthrophallina)
3. Absence of an unpaired postanal seta (shared with Diarthrophallina and some Uropodina)
4. Presence of the setae *av4* and *pv4* on tarsi IV (shared with Sejina)
5. Presence of 4 anterolateral setae (*al*) on tarsi II-IV (shared with a certain Sejina)
6. Absence of salivary styli in gnathosoma (shared with Sejina and Zerconina)
7. Presence of hypopharyngeal styli in gnathosoma (shared with Diarthrophallina, Uropodina, and Heterozerconina)

Trigynaspids, along with the Diarthrophallina *sensu* TRÄGÅRDH (1946b), carry 8 rather than 7 setae on femora IV in that a posterolateral seta (*pl*) is present (1, 2/1, 2/1, 1). This simple character, which can be applied to both males and females, differs from that of Sejina (including *Sejus*, *Epicroseius*, *Uropodella*) and some Uropodina, which lack a *pl* seta on femora IV (1, 2/1, 2/1, 0) (FIG. 1).

Unlike the majority of mesostigmatid mites, trigynaspids do not retain an unpaired postanal seta (*pon*:

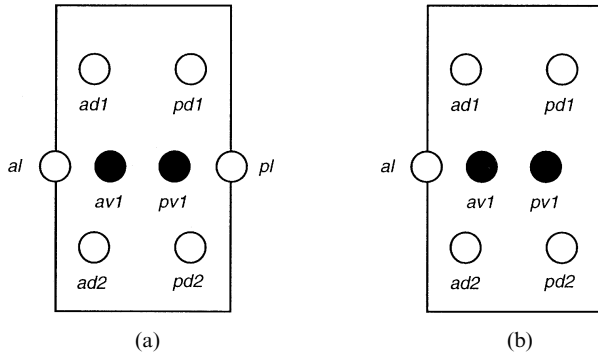


FIG. 1: Schematic diagram of the chaetotaxy of femur IV of (a) Trigynaspida and Diarthrophallina, and (b) Sejina. Open circles represent for the dorsal setae and the filled circles represent for the ventral setae.

sensu EVANS & TILL, 1965: 272; FIGS. 2 & 3) posterior to the anal opening in the adult. This seta appears in the larva, but is absent in subsequent stases. This character is shared by the Diarthrophallina and some Uropodina (such as *Trachytes*, *Polyaspinus*, and *Uro-seius*). In contrast, the Sejina (including *Sejus*, *Epicroseius*, *Asternolaelaps*, and *Uropodella*), the remaining Uropodina (such as *Oplitis* and *Polyaspis*), and

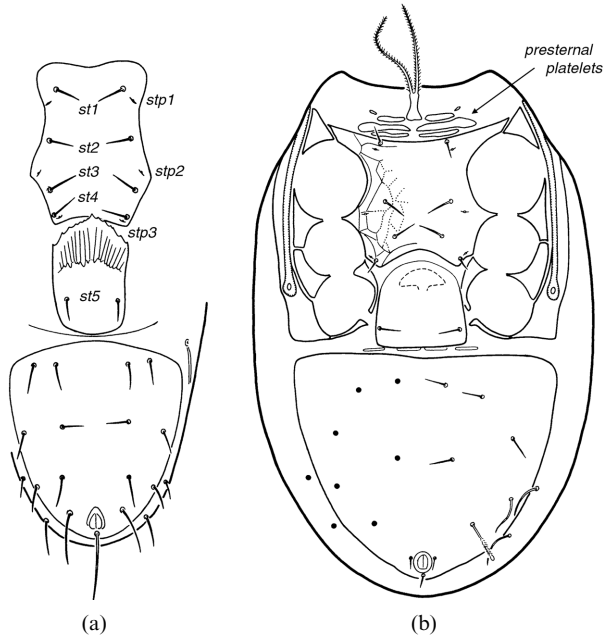


FIG. 2: (a) *Rhodacarus roseus* Oudemans (Rhodacaridae) and (b) *Gamasellus vibrissatus* Emberson (Gamasellidae), showing presternal platelets and postanal seta (*pon*). Note the presence of 3 pairs of *stp* and 4 pairs of *st* on sternal shield. Presternal and metasternal shields are absent. (modified from JOHNSTON, 1968)

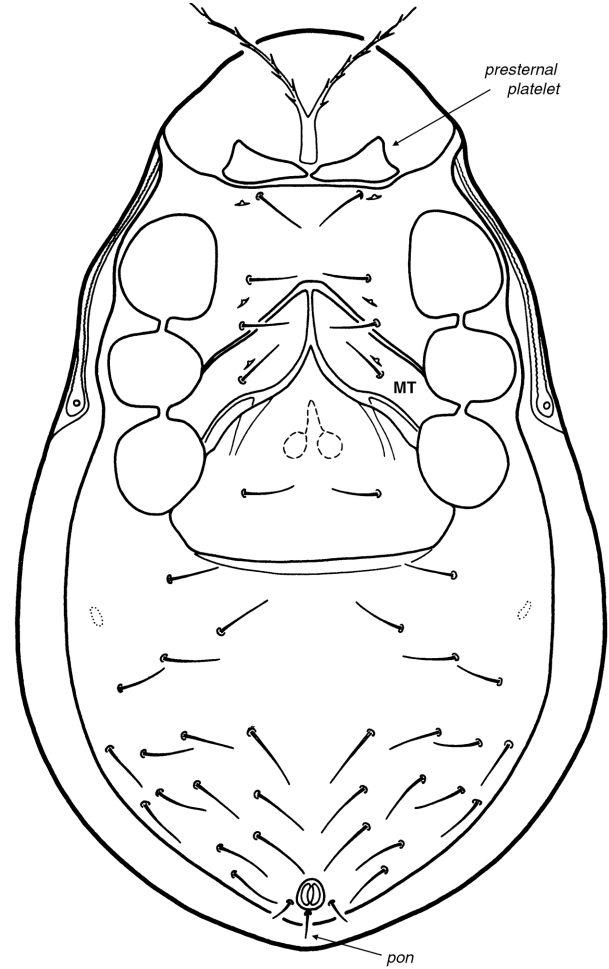


FIG. 3: *Pergamasus crassipes* (Linnaeus) (Parasitidae), showing presternal platelets, metasternal shields (MT), and postanal seta (*pon*). For the difference between latigynial and metasternal shields, see the text. (modified from JOHNSTON, 1968)

other mesostigmatid mites (including Epicriina, Zeronina, Dermanyssina, Parasitina, *etc.*) retain this seta throughout all the stases.

Trigynaspids share the presence of ventral setae *av4* and *pv4* on tarsi IV with the Sejina (EVANS, 1969). These setae, often very minute, usually occur on a free ventral intercalary sclerite in the deutonymph and adult. In the protonymph, the same paired *av* and *pv* setae appear on a free intercalary sclerite. In the absence of the fourth pair of ventral setae on tarsi IV in the protonymph, these setae are referred to as *av3* and *pv3*. They are, however, thought to be homologous to *av4* and *pv4* appearing on such sclerite in the

deutonymph and adult. The intercalary sclerite is fused to the telotarsus in Celaenopsoidea.

Trigynaspids, along with an undescribed species of Uropodellidae (Sejina), carry 4 anterolateral setae (*al*) on tarsi II-IV (EVANS, 1965, 1969), while other Mesostigmata have a maximum of 3 anterolateral setae. With the additional *al* seta, trigynaspids typically carry 19 setae on tarsi II-III (4, 4/3, 4/2, 2), and 21 on tarsi IV (4, 4/4, 4/3, 2). Other mesostigmatid mites have a maximum of 18 setae on tarsi II-III and 20 on tarsi IV (typical number is 18 on tarsi II-IV).

Trigynaspids do not carry salivary styli while most other groups of Mesostigmata do. This character is shared with the Sejina and Zerconina. (BOURDEAU-GORIOSSI, 1989; CAMIN & GORIOSSI, 1955; EVANS, 1992). When they are present, they often appear parallel to the labrum and are often associated with the corniculi. Along with Uropodina, Diarthrophallina, and Heterozerconina, trigynaspids have hypopharyngeal styli (BOURDEAU-GORIOSSI, 1989; CAMIN & GORIOSSI, 1955; EVANS, 1992).

In addition, many trigynaspids have paired eugenital setae on the male genital valves (FIG. 4), a character shared with some Uropodina, such as *Phaulodinychus repletus* (Berlese), *Clausiadinychus*, *Cillibacassidea* (Hermann), *Trachytes*, *Polyaspis*, and *Polyaspinus*. This is compared with the Sejina and Diarthrophallina, which lack male eugenital setae. Most, if not all, trigynaspids do not carry pilus dentilis on the movable digit of chelicerae.

Biology and Distribution: Trigynaspid mites are typically 'large' animals, with adults ranging in size from 0.5 to 5 mm. Despite their large body size, however, they are rarely seen (WALTER, 1997). Approximately 40 species of trigynaspid mites have been reported from temperate Europe and North America, but the vast majority of species have been described from tropical and subtropical realms. More than 200 species have been reported from the neotropics (FUNK, 1980; HUNTER, 1993a; HUNTER & BUTLER, 1966; HUNTER & ROSARIO, 1988; HYATT, 1964; TRÄGÅRDH, 1950; TURK, 1948). Trigynaspid mites in Africa have been reported from Algeria, Ivory Coast, Ghana, Cameroon, Congo, Zaire, Rwanda, Uganda, Zambia, South Africa, and Madagascar (ATHIAS-HENRIOT, 1959; BERLESE, 1903, 1916; ELSÉN, 1974, 1975, 1981; EVANS, 1958; FUNK, 1970, 1974, 1975,

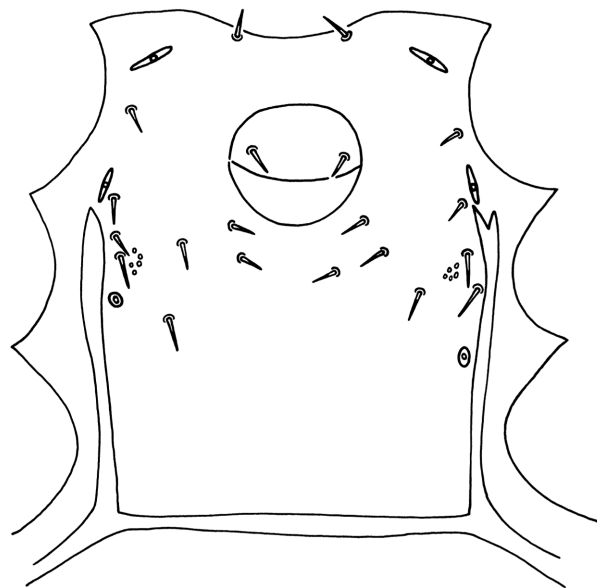


FIG. 4: *Ptochacarus* sp. (Ptochacaridae), male sternogenital region showing paired eugenital setae.

1977, 1980; HUNTER & COSTA, 1970; HUNTER & ROSARIO, 1987; KIM & KLOMPEN, 2002; KRAMER, 1895, 1898; OUDEMANS, 1926; RYKE, 1957; SELNICK, 1951; TRÄGÅRDH, 1906, 1907, 1950; WASMANN, 1902; WIŚNIEWSKI & HIRSCHMANN, 1992, 1993), and several undescribed species have been collected from Kenya and Tanzania. Ten trigynaspid species from India and Sri Lanka (Ceylon) have been reported by BHATTACHARYYA (1969), DATTA (1984a, 1984b), PRAMANIK & RAYCHAUDHURI (1979), SELNICK (1954), and TRÄGÅRDH (1950); and the species from Australia have been summarized in HALLIDAY (1998). Although several species have been reported from former Laurasian continents, it is believed that the origin (*i. e.*, ancestral distribution) of the group Trigynaspida is linked to the former Gondwanaland, because they are predominantly collected from the territories of that ancient landmass, including the Antarctic islands.

The Trigynaspida is generally considered to comprise two lineages that represent the suborders Cercomegistina and Antennophorina (CAMIN & GORIOSSI, 1955). At present, the Cercomegistina contains 19 described species in 10 genera in 6 known families (*i. e.*, Asternoseiidae, Cercomegistidae, Davacaridae, Pyrosejidae, Saltiseiidae, and Seiodidae) within a sin-

gle superfamily, the Cercomegistoidea. With few exceptions; *i. e.*, species of Cercomegistidae associated with scolytids (as in *Cercomegistus* and *Cercoleipus*; KINN, 1971), social spiders (*Holocercomegistus*; EVANS, 1958), or pagurid crabs (*Vitzthumegistus*; ANDRÉ, 1937), both immature and adult cercomegistines are free-living (saprophagous to predaceous) in moist and decaying vegetation, and are found primarily in the Southern Hemisphere.

Members of Antennophorina are more diverse than those of Cercomegistina, containing 21 known families in 7 superfamilies (KIM, 2001) (KETHLEY (1977b) proposed 6 superfamilies of Antennophorina.). Unlike cercomegistines, the adult stage of most of antennophorines exhibits associations with passalids, scolytids, formicids, or with diplopods, most of which display gregarious or social behavior. Twenty-two species in three antennophorine genera (*i. e.*, 20 species of *Ophiomegistus* (Paramegistidae), *Ophiocelaeno sellnicki* Johnston & Fain (Diplogyniidae), and *Indogynium lindbergi* Sellnick (Schizogyniidae)) are associated with lizards or snakes (squamates). Two species (*i. e.*, *Celaenopsis xinjiangensis* Ma & Ye (Celaenopsidae), and *Funkotriplogynium vallei* (Fox) (Triplogyniidae)) have been known from rodents or rodents' nest. In addition, some diplogyniids are associated with carabids, scarabaeids, tenebrionids, brentids, curculionids, scoliids, sphecids, apids, anthophorids, termites, or cockroaches in mostly tropical or subtropical realm. Among these various hosts, passalids serve as the major host group for trigynaspids, including diplogyniids (HUNTER, 1993a; HUNTER & ROSARIO, 1988). A few species of the Antennophorina, such as most Triplogyniidae, Megacelaenopsidae, some Diplogyniidae (*Diplogynium marquesana* (Vitzthum), *Heveacarus*, *Pyramidogynium*, *Spatulosternum*), and some Schizogyniidae (*Mixogynium proteae* Ryke, *Schizogynium africanum* Trägårdh) are known to be free-living or associated with plants, such as banana leaves (Musaceae), *Cheirodendron* (Araliaceae), *Hevea* (Euphorbiaceae), or *Protea* (Proteaceae) as adults.

While adult antennophorines are often found on animal hosts, nearly all known immatures, except for *Micromegistus* (Parantennulidae), are free-living. These immatures feed on nematodes, collembolan eggs, fungal hyphae, and other organic debris in the

habitats frequented by the hosts of adult mites (BUTLER & HUNTER, 1968; HUNTER & DAVIS, 1965; KINN, 1971). All of the postembryonic stages of *Micromegistus* are found on carabids (JOHNSTON *et al.*, 1957). Unlike other arthropods that serve as the hosts for Antennophorina, carabids are not gregarious and often move rapidly through a wide range of habitats. Although such behavior of the host beetle could offer a higher chance of wider dispersal for associated *Micromegistus*, the mites probably would not survive if they were to leave their host. Instead of feeding on organic detritus in the host habitat, immature *Micromegistus* feeds on fungal hyphae or other organic debris on the beetle, presumably acquired in the moist and decaying habitats that carabids prefer (NICKEL & ELZINGA, 1970; personal observation).

It should be noted that the mite-host relationships involving most Antennophorina are not parasitic but phoretic, paraphagic (utilizing body secretions from the hosts), or commensal (BUTLER & HUNTER, 1968; HUNTER, 1993a; HUNTER & DAVIS, 1965; JOHNSTON *et al.*, 1957; KINN, 1971; NICKEL & ELZINGA, 1970; TRÄGÅRDH, 1907). FRANKS *et al.* (1991) argued that the antennophorid *Antennophorus grandis* Berlese was an obligate ectoparasite on *Lasius* ants. Although imitating ants' trophallactic behavior by mites to take liquid foods as observed by FRANKS *et al.* (1991) was also reported in previous literature (BANKS, 1915; DONISTHORPE, 1927; JANET, 1897a, 1897b; WHEELER, 1910), there is no clear evidence indicating that *Antennophorus* is truly parasitic on the host ant or that it exploits the host colony. While the mite may not mimic ants' colony odor, any roaming mite is picked up by the ant from any colony. Furthermore, when the mite's antenniform legs I are artificially amputated, the mite is picked up by an ant and delivered to the ants' brood pile, where it is placed among the larvae or in the adjacent soil debris (FRANKS *et al.*, 1991: 66). More detailed research is necessary to understand the subtle and enigmatic relationships between these mites and their host ants. Perhaps, like many antennophorine mites, *Antennophorus* might be mutualistic, attacking the hosts' natural enemies in or around the nest. Referring to another antennophorid species, *Antennophorus donisthorpei* Wheeler, HUNTER & ROSARIO (1988) also stated, "direct harm [from the mite] to the host [ant]

does not occur” (emphases in bracket added by the author). TRÄGÅRDH (1907) speculated paraphagy by *Neomegistus julidicola* Trägårdh (Paramegistidae) on its host millipede. Despite the known and empirical facts relating to adult trigynaspids and their various host groups, the biology of these mites is generally poorly known (WALTER, 2000).

Systematics, Higher Classification, and the Problem *status quo*: Trigynaspid taxonomy is in a state of chaos. Many groups, such as Antennophoridae, Celaenopsidae, Diplogyniidae, and Megisthanidae, are in need of revisionary studies (see BHATTACHARYYA, 1969; HYATT, 1964; JOHNSTON & FAIN, 1964; SAMŠINÁK, 1962).

The evolutionary relationships of higher categories of trigynaspid mites were first explored by TRÄGÅRDH (1907, 1937, 1946a) in a series of studies on systematics of Mesostigmata. His works were based on the premise of grouping taxa with diagnostic characters that are often autapomorphic to the taxon (*i. e.*, evolutionary taxonomy). Many new taxa have been described since the appearance of his work, and many of his major groups were found to contain a mixture of species from apparently different superfamilies. FUNK (1968) later hypothesized the relationships among the families of Celaenopsoidea based on numerical phenetic UPGMA (SOKAL & SNEATH, 1963) by using discrete and continuous characters, such as measurements of setae, appendages, and the body. Although UPGMA (and other distance methods) may have superiority of algorithmic unambiguity to other phylogenetic methodologies, it has no relationship with the organisms’ ancestry (see FELSENSTEIN, 2001). UPGMA has the additional defect of always assuming equal rates of evolution along sister branches. In nature, the rate of evolution in sister taxa is not necessarily equal (AYALA, 1997; LI, 1997).

The latest published scheme of higher-level relationships and the classification of trigynaspid mites was proposed by KETHLEY (1977b), in which he suggested 24 families in 7 superfamilies based on his study of patterns of the distribution of setae (*i. e.*, chaetotaxy) on the legs. In his study, KETHLEY assumed that the Trigynaspida is a natural group, with all of its members having a single ancestor (FIG. 5). His results also confirmed bifurcating internal lineages of

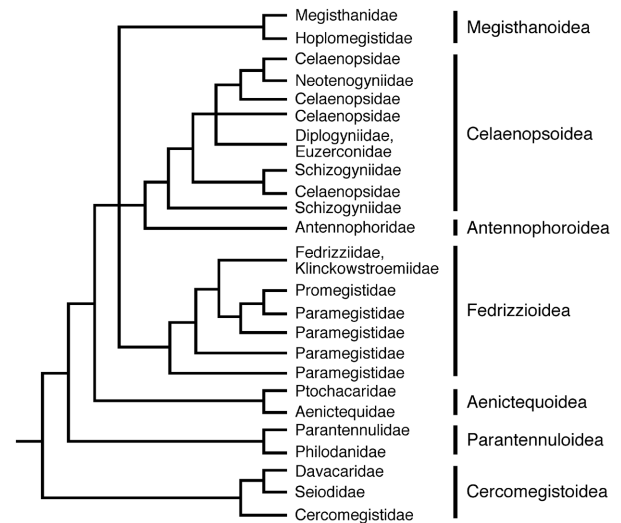


FIG. 5: Phylogenetic tree re-drawn from KETHLEY (1977b). Note that two ant associates of Antennophoroidea and Aenictequoidea are not sisters to each other. Paramegistidae, Celaenopsidae, and Schizogyniidae are not monophyletic.

Cercomegistina and Antennophorina within Trigynaspida, proposed earlier by CAMIN & GORIROSSI (1955). However, despite the general fact that his classification has been widely used (*e. g.*, KRANTZ, 1978; EVANS, 1992; ALBERTI & COONS, 1999), it should be noted that KETHLEY’s methodology is subject to question.

First, although leg chaetotaxy is often useful in acarine systematics as these patterns are often conserved within a group, almost invariable between male and female, and often variable between groups (EVANS, 1963a, 1963b, 1964, 1965, 1969, 1972), interpretation of setal homology can often be controversial when setal bases migrate (EVANS, 1969; EVANS & TILL, 1965; also see LINDQUIST & MORAZA, 1993). For example, EVANS (1965) once recognized the anteroventral (*av*) seta appearing on tarsi II-IV of Antennophorina as ‘medioventral hair (seta)’. This interpretation, which he later revised (Evans, 1969), implies a 7-setae whorl (verticil) system, an aberration of the standard 6-setae whorl in Mesostigmata. These setae are actually *av2* on tibiae IV and *av3* on tarsi II-IV in the adult. While the trigynaspids bear 8 setae on femora IV, resulting in a characteristic chaetotactic formula of (1, 2/1, 2/1, 1), KETHLEY (1977b) recognized that the setae on femora IV are variable among trigynaspid taxa (see TABLE 1 & 2 in KETHLEY, 1977b).

Second, relying only on one or a limited set of morphological characters in systematics is somewhat equivalent to using a small set of a single gene to deduce phylogenetic relationships that may only yield a gene tree rather than a species tree (DOYLE, 1992; PAMILO & NEI, 1988). No single morphological attribute should be used in inferring evolutionary relationships at the higher level (EVANS, 1972). Instead, morphological analyses should rely on multiple sets of attributes that are important for survival (reproductive and feeding structures, for example) and that usually are conserved in the course of evolution. As the members of Trigynaspida have, for example, very peculiar genital structures along with sternal and often anal shield structures in the female, these characteristics should not be disregarded in phylogenetic analyses.

Third, there is no information on rooting the cladogram in KETHLEY's analyses. Although rooting of the tree can be achieved by one of the methods of outgroup, ontogeny, midpoint rooting, or Lundberg rooting (see KITCHING *et al.*, 1998), KETHLEY's approach did not include any outgroups other than Trigynaspida *per se*, and there is no information regarding this question. Without including closely related outgroup taxa that allow the test of monophyly of Trigynaspida, he implicitly assumed that the group Trigynaspida is monophyletic, leaving his systematic results untenable. The test of ingroup monophyly through inclusion of one or more outgroups is fundamental in phylogenetic systematics, as the outgroups serve as the 'control groups' in phylogenetic systematics. It should be noted that, in the cladogram of Trigynaspida presented by KETHLEY (1977b), the Paramegistidae, Celaenopsidae, and Schizogyniidae are not monophyletic (KETHLEY, 1977b: FIGS. 1 & 2; also see FIG. 5).

Finally, KETHLEY's classification fails to conserve host association data as an indicator of group relationships. For example, his two ant-associated superfamilies Antennophoroidea and Aenictequoidea show disparate separation in his cladogram. Species of *Micromegistus* (Parantennulidae) and *Promegistus* (Promegistidae) associated with carabids are also distantly related. Although co-evolution between the hosts and associates does not necessarily have to follow Fahrenholz's rule of mirrored topologies of

evolutionary trees (BROOKS & MCLENNAN, 1993; MITTER & BROOKS, 1983), it is worthwhile to explore the possibility of conserved relationships among mites and their hosts at the higher level.

Goal of the Study: Although KETHLEY's classification of Trigynaspida offers many insights as to relationships within the group, higher-level relationships of Trigynaspida need to be re-examined from a phylogenetic perspective. Comparative morphological studies utilizing a broad range of taxa and morphological characters have been conducted to examine the monophyly of Trigynaspida and the higher-level relationships among its members. Although good diagnostic characters to define the group Trigynaspida were empirically given above, global test of monophyly is required. These studies have also allowed the examination of the higher-level phylogenetic relationships among superfamilies and families of trigynaspid mites.

The scope of this study has been expanded to address the relationships among trigynaspid mites and their hosts. That is, by adding the information of the hosts to the estimated phylogeny, the evolutionary patterns among these mites and their hosts have been introduced. Parallel to this approach, biogeographic patterns of global distribution of these mites have been explored. With an aid from plate tectonics, this approach allows the estimation of the age of Trigynaspida in geological time.

This is the first interpretation on the Trigynaspida based on phylogenetic systematics. Higher-level relationships, diagnoses of the superfamilies, and a revised key to families have been proposed.

MATERIALS AND METHODS

Taxon Sampling: Representatives from all the currently-known superfamilies were included to the study. This includes a total of 51 species, including 40 species in 23 families of Trigynaspida along with 11 species in 9 families of their monogynaspid outgroup taxa (TABLE 1). Selection of outgroup taxa was based on the proposed phylogeny of D. E. Johnston in NORTON *et al.* (1993: Fig. 1. 2).

To test KETHLEY's (1977b) hypothesis of the relationships between the two superfamilies of ant

Superfamily & Family	Species
SUBORDER CERCOMEGISTINA S.F. Cercomegistoidea Asternoseiidae Cercomegistidae Davacaridae Pyrosejidae Saltiseiidae Seioididae	<i>Asternoseius</i> sp. <i>Cercoleipus coelonotus</i> <i>Cercomegistus evonicus</i> <i>Davacarus gressitti</i> <i>Pyrosejus</i> sp. <i>Pyrosejidae</i> n. sp. <i>Saltiseius hunteri</i> <i>Seiodes</i> sp.
SUBORDER ANTENNOPHORINA S.F. Parantennuloidea Parantennulidae Philodanidae	<i>Micromegistus bakeri</i> <i>Micromegistus gourlayi</i> <i>Philodana johnstoni</i>
S.F. Aenictequoidea Aenictequidae Ptochacaridae	<i>Aenictes chapmani</i> <i>Ptochacarus sylvestrii</i>
S.F. Antennophoroidea Antennophoridae	<i>Antennophorus wasmanni</i>
S.F. Fedrizzioidae Fedrizziidae Klinckowstroemiidae Paramegistidae Promegistidae	<i>Fedrizzia</i> sp. <i>Neofedrizzia leonilae</i> <i>Klinckowstroemia starri</i> <i>Klinckowstroemia victoriae</i> <i>Antennomegistus caputcarabi</i> <i>Echinomegistus wheeleri</i> <i>Meristomegistus vazquezus</i> <i>Neomegistus julidicola</i> <i>Ophiomegistus</i> sp. <i>Paramegistus confrater</i> <i>Promegistus armstrongi</i>
S.F. Megisthanoidea Hoplomegistidae Megisthanidae	<i>Stenosternum truitae</i> <i>Stenosternum</i> sp. <i>Megisthanus floridanus</i>
S.F. Celaenopsoidae Celaenopsidae Diplogyniidae Euzerconidae Megacelaenopsidae Schizogyniidae Tripllogyniidae	<i>Pleuronectocelaeno drymoecetes</i> <i>Cryptometasternum</i> sp. <i>Ophiocelaeno sellnicki</i> <i>Passalacarus sylvestris</i> <i>Trichodiplogynium</i> sp. <i>Euzercon latus</i> <i>Neoeuzercon</i> sp. <i>Megacelaenopsis oudemansi</i> <i>Megacelaenopsis</i> sp. <i>Paraschizogynium odontokeri</i> <i>Funkotripllogynium vallei</i> <i>Tripllogynium</i> sp.
SUBORDER UROPODINA Thinozerconidae Trachyuropodidae Polyaspididae	<i>Thinozercon michaeli</i> <i>Oplitis</i> sp. <i>Polyaspis lamellipes</i> <i>Trachytes</i> sp.
SUBORDER SEJINA Sejidae Ichthyostomatogasteridae Uropodellidae	<i>Sejus</i> sp. <i>Epicroseius</i> sp. <i>Asternolaclaps</i> sp. <i>Uropodella</i> sp.
SUBORDER MICROGYNIINA Microgyniidae	<i>Microgynium rectangulatum</i>
SUBORDER HETEROZERCONINA Discozerconidae Heterozerconidae	<i>Discozercon</i> sp. <i>Narceoheterozercon ohioensis</i>

TABLE 1. List of taxa used for the study. S.F. = Superfamily

associates, species of *Aenictes* and *Ptochacarus* (Aenictesquidea) along with *Antennophorus* (Antennophoroidea) were included. For the investigation of the monophyly of Paramegistidae, species from all the known genera (*i. e.*, *Antennomegistus*, *Echinomegistus*, *Meristomegistus*, *Neomegistus*, *Ophiomegistus*, and *Paramegistus*) were included. Finally, to examine the relationships among the associates of carabids, *Micromegistus* (Parantennulidae) and *Promegistus* (Promegistidae) were included.

In addition to the above sampling scheme focused directly on the testing of KETHLEY's cladogram, *Fedrizzia* and *Neofedrizzia* (Fedrizziidae), passalid associates from Australia, were included to examine the relationships among the species within the same family from the same continent. As a possible back up of investigating this relationship, two species of Klinckowstroemiidae (*Klinckowstroemia*) from Central America, another passalid-associated sister family to Fedrizziidae, were also included. Although these two families are very similar to each other in terms of morphology, their biogeographic distribution is quite peculiar, showing no overlap in the global distribution (HUNTER, 1993a).

In an expansion of this sampling scheme, *Micromegistus bakeri* (Parantennulidae) from North America and *M. gowrayi* from Australia were included to investigate the relationships within a same genus (family) but from different continents. In addition, to examine the relationships between two closely related species (genera) that are associated with two different host groups, passalid-associated *Euzercon latus* (Euzerconidae) and millipede-associated *Neoeuzercon* sp. (Euzerconidae) were included to the study.

Analyses: All the characters were coded with equal weight. Multistate characters were coded as multistate. Heuristic searches with TBR (tree-bisection-reconnection) branch-swapping along with random addition of taxa with 100 replicates were performed to avoid local optima. Maximum parsimony, which seeks the minimum number of steps of evolutionary change within the data, implemented in PAUP* 4.0b10 (SWOFFORD, 2002) was used as the optimality criterion. Branches were collapsed if the maximum branch length is zero. To assess the confidence level on the deduced phylogeny, 'branch support' (BRE-

MER, 1988) (= 'decay index' *sensu* DONOGHUE *et al.*, 1992; 'Bremer support' *sensu* KÄLLERSJÖ *et al.*, 1992) was calculated by AutoDecay 4.0.2 (ERIKSSON, 1999) using global reverse constraints of topologies, and the values were added onto the nodes.

For the character numbers of 17, and 28 through 31, 100X differential interference contrast (DIC) objective lens (Zeiss Plan-Neofluar) with oil immersion was applied for the all taxa for the consistency in the character coding. Terminologies used here follow EVANS (1992), otherwise specified.

BAUPLAN OF TRIGYNASPIDA

As the word 'Trigynaspida' indicates, the structures of female genital region of trigynaspid mites are crucial in recognizing/identifying this group of mites. However, as the female genital structures, which are often unique to each trigynaspid superfamily, are contiguous with sternal structures along the venter of the body, standardized criteria to distinguish genital structures from those of sternal are required as the first step of homology assessment among these structures.

Definition of Sternal Region : In Mesostigmata, including Trigynaspida, the venter of the female is composed of four major regions. From anterior to posterior, they are referred to as sternal, genital, ventral, and anal region. In males, shields in these regions are quite often fully fused to form a single hologastric shield. Although sexual dimorphism of the venter of mesostigmatid mites is often remarkable, the sternal region in both sexes is easily identified as the area posterior to (or around) the base of tritosternum.

The sternal region in the female is defined as the area, posterior to (or around) the tritosternum, carrying 4 pairs of setae (*st1-st4*) and/or 3 pairs of lyrifissures (or lyriform pores; *stp1-stp3*). In males, which usually have more than 4 pairs of setae on the fused sternogenital or hologastric shield, the area bearing *st1-st4* and/or 3 pairs of lyrifissures is regarded as sternal in origin. In fact, the setae *st5* (and often *st6*) in the male is thought to be homologous to the setae appearing in the genital shield of the females (*i. e.*, latigynial in Trigynaspida or epigynial shield in

most of Monogynaspida, including Dermanyssina), which bear these fifth or sixth setae. Subsequently, the area posterior to this sternal region becomes the beginning of the genital region in female.

The sternal region is often occupied by a single large shield (*i. e.*, sternal shield), but in many cases, especially in Trigynaspida, this region is fragmented to three different kinds of shields based on the distribution of the setae and lyrifissures. From anterior to posterior, they are referred to as presternal, sternal, and metasternal shields.

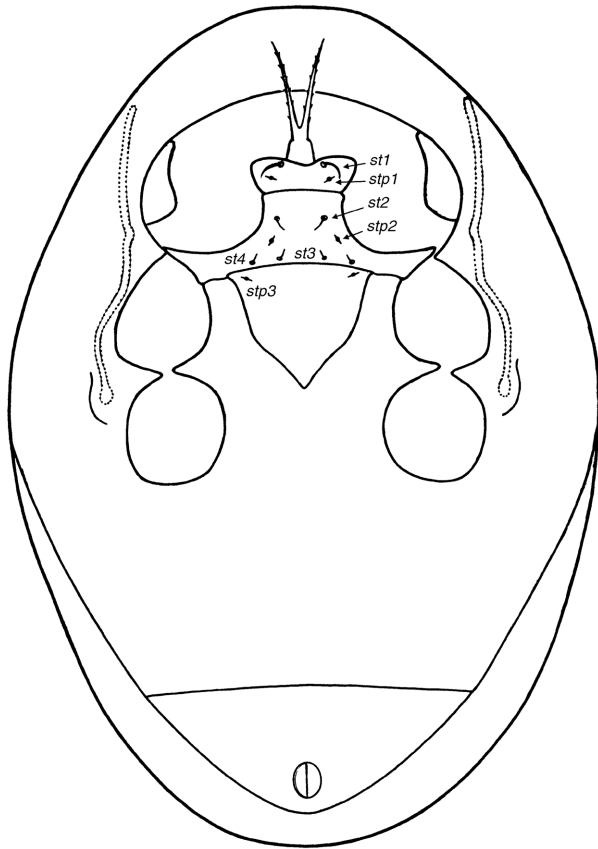


FIG. 6: *Fedrizzia* sp. (Fedrizziidae). Note entire presternal, bearing *st1* and *stp1*, and sternogynial shield, bearing *stp3*. (modified from JOHNSTON, 1968)

Presternal shields, often paired, are defined as the shield(s) carrying *st1* and/or *stp1* (FIG. 6). Often, *st1* are located off the shield(s) but *stp1* are positioned onto the shield(s), allowing recognition of the presternal shield(s). This interpretation includes previous terms of 'presternal shield(s)' (KETHLEY, 1977b;

KRANTZ, 1978), 'jugular shield(s)' (CAMIN & GORI-ROSSI, 1955; HUNTER, 1993b; KRANTZ, 1978; TRÄGÅRDH, 1943), 'jugularium' or 'jugularia' (EVANS, 1992; HYATT, 1964), 'tetartosternum' (KETHLEY, 1974, 1977b; KRANTZ, 1978; ROSARIO & HUNTER, 1987), or 'tetrasternum' (HUNTER, 1993b). Any small sclerotized platelets appearing in the presternal area, but lacking both setae and lyrifissures, are designated as 'presternal platelets' (KIM, 2001; KIM & KLOMPEN, 2002) (FIGS. 2b & 3).

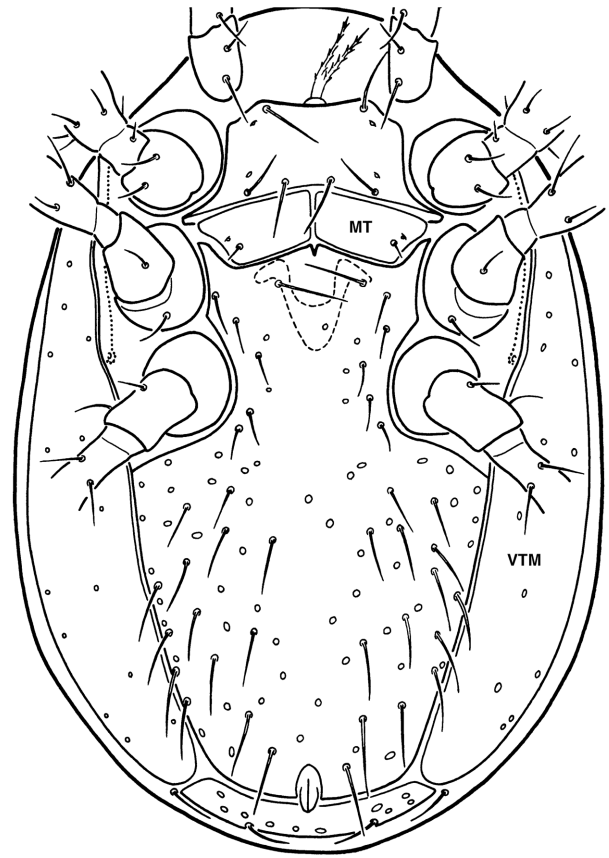


FIG. 7: *Celaenopsis badius* (C. L. Koch) (Celaenopsidae), showing paired metasternal (MT) and ventromarginal (VTM) shields. Postanal seta is absent in all the postlarval Trigynaspida. (modified from JOHNSTON, 1968)

Similarly, metasternal shields, usually paired, are defined as the shield(s) carrying both *st4* and *stp3*. Metasternal shields are commonly found in Celaenopsoidea of Trigynaspida (FIG. 7), Dermanyssina and Parasitina (FIG. 3). Although these metasternals

often resemble the latigynial shields *prima facie*, it should be noted that the latigynials, which are not sternal but genital in origin, do not carry *st4* and *stp3* (but often bear *st5* and *st6*). They should, therefore, not be confused or homologized with metasternal shields.

Often, in the females of Asternoseiidae, Seiodidae, Fedrizziidae, Klinckowstroemiidae, and Paramegistiidae, there appears a shield, bearing only a paired *stp3* (but with no seta), in the midsternal or seeminglypregenital region (FIG. 6). This type of shield is referred to as the sternogynial shield (= sternogynium),

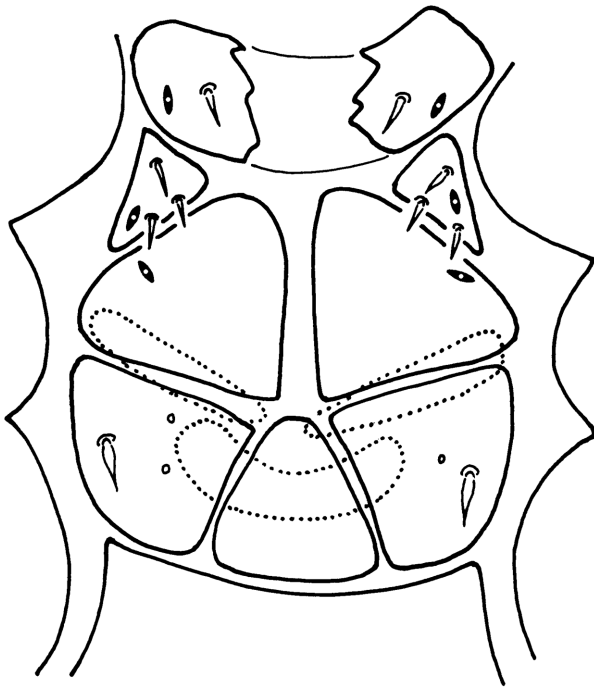


FIG. 8: *Paramegistus confrater* Trägårdh (Paramegistiidae). Weakly-developed (or vestigial) claviform vaginal sclerites are shown in dotted line. Sternogynial shields are paired.

and appears as a pair in Paramegistiidae (FIG. 8) and Hoplomegistiidae. A similar structure, but lacking any seta or lyrifissure, is found in Aenictesquidea, Promegistiidae, and Parantennulidae, and is called pseudosternogynium (= pseudosternum) (FIG. 9). I assume that pseudosternogynium may often be fused with sternogynial shield bringing an elongated sternogynial-pseudosternogynium complex. However, when the pseudosternogynium (= pseudoster-

num) is present alone, its origin is thought to be genital rather than sternal (because of the lack of setae or lyrifissure). This pseudosternogynium is thought to be homologous to the pregenital shield *sensu* VAN DER HAMMEN (1983) in Holothyrida. Both of these structures (*i. e.*, sternogynial shield and pseudosternogynium) lack any form of setae and, therefore, are distinguished from metasternal shield(s), bearing *st4* and *stp3*.

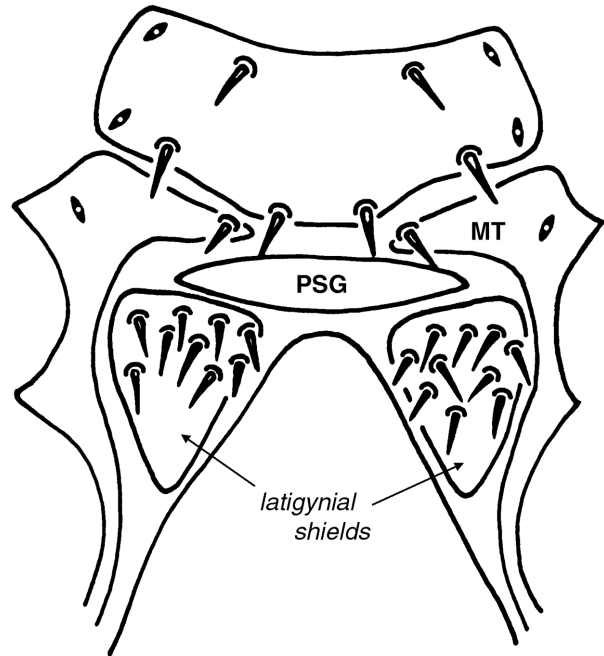


FIG. 9: *Promegistus armstrongi* Womersley (Promegistiidae), showing pseudosternogynium (PSG; = pseudosternum). Each metasternal shield (MT) is fused to the endopodal element.

From this new interpretation on the sternal region of the female Mesostigmata, with a few exceptions, such as the hypertrichy or hypotrachy (as in some Diplogyniidae) in sternal region, or highly modified sternal region of the female (as in some Uropodina or Heterozetconina, where sternal elements are fractured and/or fused with endopodal elements), the followings are generalized throughout the Mesostigmata.

1. Sternal 'region' is composed of the combination of three different sclerotized shields. From anterior to posterior they are, presternal, sternal, and metasternal shields.

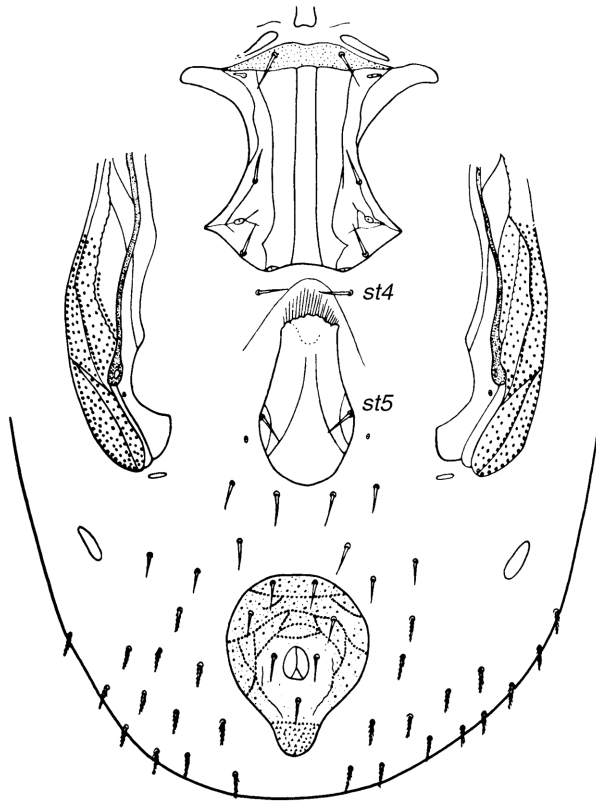


FIG. 10: *Antennoseius delicatus* Berlese (Ascidae). *st4* are on the soft cuticle. (modified from JOHNSTON, 1968)

2. Sternal 'region' carries 4 pairs of setae (*st*) and/or 3 pairs of lyrifissures (or lyriform pores; *stp*).
3. If sternal 'shield' has 4 pairs of setae and/or 3 pairs of lyrifissures, then neither presternal nor metasternal shield(s) is present (FIG. 2). Presternal or metasternal platelets, devoid of any seta or lyrifissure, however, may be found. (*e. g.*, Arctacaridae, Zerconidae, Rhodacaridae, Ologamasidae, *etc.*)
4. If sternal shield has 3 pairs of setae and/or 2 pairs of lyrifissures, then either presternal or metasternal shield(s), bearing additional pair of setae and/or lyrifissures, is present (FIGS. 3 & 7). However, in this case, if neither presternal nor metasternal shield(s) is present, then *st1* or *st4* may be on soft cuticle (FIG. 10).
5. If sternal shield has 3 pairs of setae along with 1 pair of lyrifissures, then both presternal, bearing *st1* and *stp1*, and a sternogynial shield, bearing *stp3*, are present (FIG. 6).

6. If sternal shield has 2 pairs of setae and/or only 1 pair of lyrifissures, then both presternal and metasternal shields are expected to be present. Rare exceptions may be found when *st1*, *stp1*, *st4*, and *stp3* are located on the soft cuticle.

In the case of the situation of hypotrachy, in which the sternal region has less than 4 pairs of setae, often the presence of more than 3 pairs of lyrifissures is observed. The most common form of such aberration is the presence of 3 pairs of setae with 4 pairs of lyrifissures as found in some Diplogyniidae. Although tactile setae and lyrifissures are seemingly different in shape, they are both mechanoreceptors, and accordingly, these aberrations may indicate that the tactile setae and lyrifissures might have been derived from the same origin. Similar transformation between tactile setae and lyrifissures is found in the euanal setae-euanal lyrifissures observed through the ontogenetic stases (see below).

Definition of Genital Region: The area posterior to the sternal structures constitutes the beginning of the genital region of the female, which is often identified by the presence of *st5* (and often *st6*). Like the sternal region, the genital region is also composed of several shields that collectively cover the genital orifice. In male, circular genital orifice, covered by a single or two valves, is either midsternal (*i. e.*, located between coxae II-IV; FIG. 4) or presternal (*i. e.*, located beneath the base of tritosternum) in position.

In female Mesostigmata, three major types of genital shield system are present based on the structure of the genital shields. The first system, which I tentatively call 'hologynaspid' system, appears in Diarthrophallina and Uropodina. In this system, females have one complete horseshoe- or often inverted U-shaped genital shield (currently known as epigynial shield) that covers the female genital orifice (FIG. 11). The whole shield itself is hinged at the posterior margin and is opened when the female delivers her eggs. Although this type of hologynaspid shield is easily identified by its unique shape, it is also recognized by the lack of any sternal setae (*st1-st4*) and lyrifissures (or lyriform pores, *stp1-stp3*) on this shield, which are confined to the sternal region. Setae *st5*, defining the genital area, are located mostly on endopodal elements or rarely on the epigynial shield (as in *Protodi-*

nychus). In *Trachytes* (Polyaspidioidea: Trachytidae) of Uropodina, each lateral margin of epigynial shield can be folded and opened during the oviposition, a condition similar to that in Trigynaspida. In the hologynaspid system, metasternal shields are not present.

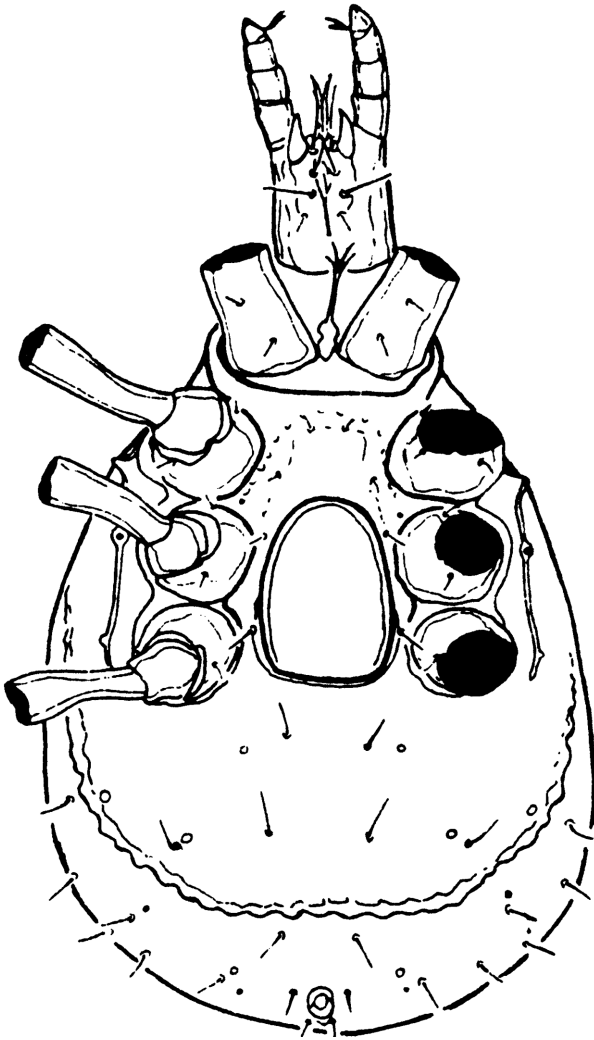


FIG. 11: *Dinychus* sp. (Uropodidae), showing 'hologynaspid' genital system. (after KRANTZ, 1978)

The second type of genital shield system is known as the 'trigynaspid' system, which is found in Trigynaspida and *Trachytes*. In this case, females typically have three genital shields, *i. e.*, a mesogynial and paired latigynial shields. In a typical trigynaspid condition, mesogynial shield, hinged to its posterior margin, is often large and triangular and the latigyn-

nials hinged to their outside lateral margin, are elongate triangular or often bar-shaped. Similar to the hologynaspid genital system, these meso- and latigynial shields do not carry *st1-st4* or *stp1-stp3*. Except for *Micromegistus* (Parantennulidae), genital setae *st5* (and often *st6*) are located on the latigynial shields. Variations from this ancestral trigynaspid condition, however, commonly occur throughout Trigynaspida.

The third type of genital shield system – females have rather a small elastic membranous and often slit- or chute-like genital orifice formed by the anterior extension of a single epigynial shield – is tentatively called 'agynaspid' system, and is common in the remaining groups of Mesostigmata (FIGS. 2a & 10). In Parasitina and in some Dermanyssina, such as Macrochelidae, the epigynial shield is opened during oviposition, rendering retrogressive hologynaspid genital system (FIG. 3). (Along with Parasitina's ribbon-type sperm cells (ALBERTI, 1980) and tocospermic mode of sperm transfer (ATHIAS-HENRIOT, 1969), this genital system may imply the peculiar position of Parasitina in the evolution of Mesostigmata.) In these cases, however, agynaspid system is easily distinguished by the presence of paired metasternal shields, which are usually absent in hologynaspid system. Setae *st5* are usually located on the epigynial shield. Along with the hologynaspid system described above, the agynaspid system constitutes the current concept of 'Monogynaspida'.

It is thought that the agynaspid system is the most derived condition, as it may allow the least amount of loss of water (or body fluid) and it might be the least vulnerable to the potential attacks from parasites during the oviposition. In all of these genital systems described above, oviposition occurs at the anterior end of mesogynial or epigynial shield.

In hologynaspid system, the latigynial shields of the trigynaspid system are thought to be fused mostly with the endopodal elements, but in agynaspid system, these latigynial shields are thought to be fused mostly with the mesogynial shield to form an epigynial shield. This is evidenced by the presence of *st5* on endopodal elements in hologynaspid system, and on the epigynial shield in agynaspid system. In the context of evolution, as the epigynial shield of agynaspid system is thought to be the fusion of mesogynial

and latigynial shields, the epigynial shield of agynaspid system cannot be homologized with the mesogynial shield of trigynaspid system (see CAMIN & GORI-ROSSI, 1955). Based on this point of view, the following criteria to assess the homology are generalized.

1. The mesogynial shield of Trigynaspida is not always considered to be homologous to the epigynial shield of traditional concept. Hence, the presence of mesogynial shield is not always the same as the presence of epigynial shield, and *vice versa*.
2. If the latigynial shields are present, an epigynial shield carrying *st5* can be treated as homologous to the mesogynial shield (as in *Micromegistus*). However, the presence of latigynial shields does not dictate the presence of free mesogynial shield, and *vice versa*.
3. If latigynial shields are not present, an epigynial shield that carries *st5* cannot be treated as homologous to the mesogynial shield. In this case, on the other hand, an epigynial shield with no *st5* can be homologized to mesogynial shield (as in many Uropodina). The absence of latigynial shield does not dictate the presence of epigynial shield (as in fedrizziids and many celaenopsoids). Also, the absence of latigynial shield does not dictate the absence of mesogynial shield.

With regard to these interpretations on the genital systems of Mesostigmata, it should be mentioned that it was the Swedish acarologist IVAR TRÄGÅRDH (1946a) who first applied the terms of 'Agynaspida' and 'Eugynaspida' into the classification of Mesostigmata. Indeed, he speculated that the Mesostigmata is composed of dichotomous lineages, each represented by the members that belong to one of these two groups. However, his interpretation is different from what I present herein, as his Agynaspida does not include any of Dermanyssina, the very typical agynaspid mite group. In addition, he assigned Megisthanidae of Trigynaspida into Agynaspida, while assigning current Celaenopsoidea (Celaenopsina *sensu* TRÄGÅRDH, 1946a), Cercomegistidae, Paramegistidae, Antennophoridae, and Fedrizziidae into Eugynaspida. If his interpretation on genital system had been correct, all of these 'Trigynaspids' should have belonged into the one same grouping of, possibly, his Eugynaspida.

Throughout her intensive study on the gnathosoma of the Mesostigmata, BOURDEAU-GORIROSSI (1989) grouped Mesostigmata into three groups. Despite the fact that the characters she employed are different from those of genital systems that I am describing here, it is interesting to note that, if the group Cercomegistina that she did not include into her study joins with the Antennophorina (*i. e.*, her Group III), the resultant groupings of Mesostigmata out of two studies are basically the same.

Definition of Ventral or Ventrianal Region: The area posterior to the genital region constitutes the ventral or ventrianal region. In the Trigynaspida, the posterior margins of the latigynial shields or mesogynial shield are often fused to the ventral shield. In the Heterozetconina, paired disc-like structures appear in this region. Interestingly, each side of these discs in Heterozetconidae carries a small shield, bearing at least *st4* along with *st5* and *st6*, implying that the sternal and genital regions of this group of mites may have been extended to posterior region compared with other mesostigmatid mites.

Parallel to the ventral shield, strap-like ventromarginal shields are often present along the length of the venter in Celaenopsoidea (FIG. 7) and some Uropodina. Free metapodal shields, located posterior to the coxae IV, often appear in this region.

While cercomegistines have a ventrianal shield in the adult stage, some antennophorines, such as Megisthanoidea, Fedrizziidae, Klinckowstroemiidae, Parantennulidae, Euzetconidae, and Triplogyniidae, have a free anal shield, separated from the ventral shield. In Fedrizziidae and Klinckowstroemiidae, the separation is weak and only a thin line of separation is often observed (FIG. 6).

The anal opening, composed of two anal valves, carries a pair of euanal setae in the larvae in most Parasitiformes *sensu lato* (= Anactinotrichida), including Opilioacarida (= Notostigmata), Ixodida, Holothyrida, and Mesostigmata. These setae are lost in subsequent stases in Trigynaspida, but often the same area is occupied by a pair of lyrifissures. While most mesostigmatid mites carry an unpaired postanal seta (*pon*) posterior to the anal opening throughout all the stases (FIG. 2), all the members of Trigynaspida, along with Diarthrophallina and some Uropodina, retain this seta only in the larval stage.

CHARACTER SELECTION, DESCRIPTION, AND CODING

A total of 55 morphological features drawn from all the different body parts, which allow the assessment of structural homologies, were selected as the characters. These include the characters from dorsum, mouthparts, legs, and those from the venter, such as sternal, genital, ventral, and anal regions. In using body and leg chaetotaxy, each seta was regarded as a single character. Character descriptions and their coding schemes are as follows. Characters are based on females, otherwise specified. Definitions of the terminologies for the sternal and genital regions are given in the section, BAUPLAN OF TRIGYNASPIDA, described above. A Taxon-Character matrix for the analyses is shown in the TABLE 2.

1. Number of dorsal shields (in adult)

- [0] 3 or more (podonotal, mesonotal, pygidial shields);
- [1] 2 (podonotal, opisthonotal shields);
- [2] 1 (holodorsal shield)

Among the members of Trigynaspida, antennophorines usually have a holodorsal shield, while most cercomegistines, excluding Asternoseiidae and Saltiseiidae, carry two or more shields in the adult. More than two dorsal shields in the adult are found in Davacaridae, which retain four (single podonotal, weakly paired mesonotal, and a pygidial shield) and in *Neotenogynium malkini* (Neotenogyniidae), a paedomorphic trigynaspid that shows 3 dorsal shields in the female (KETHLEY, 1974). It should be noted that an undescribed new genus of Neotenogyniidae from Brazil carries a holodorsal shield in the female. Outside of the Trigynaspida, presence of more than two dorsal shields is found in Sejina, Microgyniina, and some Uropodina (*i. e.*, *Trachytes* has four dorsal shields).

KETHLEY (1977a) showed two dorsal shields in the antennophorine Philodanidae. However, re-examination of the holotype and paratype specimens revealed that the female philodanid carries a single shield with a vestigial line of fusion. The male shows an immaculate holodorsal shield.

2. Dorsal setae

- [0] non-holotrichy; [1] holotrichy

While holotrichous setation in dorsum allows setal notations in each seta on dorsum (EVANS & TILL, 1965; LINDQUIST & MORAZA, 1998), non-holotrichous setation in dorsum indicates that such identifications are not possible.

With an exception of Pyrosejidae, all the cercomegistines show hypertrichy (*i. e.*, a form of non-holotrichy). This hirsute situation is also found in antennophorine Philodanidae, Antennophoridae, Aenictequoidea, and most Megisthanoidea. Paramegistidae and Celaenopsoidea (excluding *Trichodiplogynium*) show holotrichous (non-hypertrichous) state.

3. Idiosomal setae [unordered]

- [0] dorsal and ventral setae nearly same in shape (and length);
- [1] dorsal setae are longer or stout;
- [2] ventral setae are longer or stout

This is a variable character within the Trigynaspida. Although nearly similar length and shape of setae on the body are found in general, often, especially in early stases, such as larvae or protonymphs, or in the beetle-associated mesostigmatid mites, longer dorsal setae are found. In *Ophiomegistus*, often foliate or stylus-like, or stout subulate setae are found on venter (GOFF, 1979, 1980a, 1980b).

4. Setae on venter

- [0] simple, setiform, smooth;
- [1] barbed, or foliate, lanceolate, stylus-like

5. Spinous marginal setae

- [0] absent; [1] present

Trigynaspid members of Parantennuloidea, Pro-megistidae, Paramegistidae, Aenictequoidea, and Antennophoridae, along with an outgroup Discozerconidae, carry spinous or subulate setae along the membranous margin of the idiosoma. These setae are located in the lateral end of the body, and may not easily be homologized with the setae of dorsum or venter.

Taxon	Character				
	1	2	3	4	5
	0	0	0	0	0
<i>Asternoseius</i>	20100??011110011111010200010000001002020101100000000011				
<i>Cercoleipus</i>	1000001011100011011011010021111000002020101101000000011				
<i>Cercomegistus</i>	101000101110001101111210021111000002020101101000000001				
<i>Davacarus</i>	0000001011110011011010000020000000002020101100000000011				
<i>Seiodes</i>	101001101110001111101020001000000100202010110000000001				
<i>Pyrosejus</i>	111000101110001111111010020000000002120001100000000001				
Pyrosejidae, n. sp.	1110001011100011111111010020000000002120001101000000001				
<i>Saltiseius</i>	2001000011110011001011200111000200102020101101000000001				
<i>Micromegistus bakeri</i>	2100110010201211110010200101000010112120121111000000001				
<i>Micromegistus gourlayi</i>	2100110010201011111010200101000010112120121111000000001				
<i>Philodana</i>	20001010102010111012002000?00000?0011?21111101000000001				
<i>Promegistus</i>	2121111210201011111000200110000210111?20101101000000001				
<i>Antennomegistus</i>	2121111010211011112000100200000020120201011010000?00?1				
<i>Echinomegistus</i>	212111101021101111200010020000002012000101101000000001				
<i>Meristomegistus</i>	2121111110211111112000010020000002011120101101000000011				
<i>Neomegistus</i>	212011111021121012200010020000002011?001011010000000?1				
<i>Ophiomegistus</i>	2121111010211011112200010020000002011020101101000000011				
<i>Paramegistus</i>	2121111110211211112100010020000002012020101101000000011				
<i>Aenictes</i>	2001111110211211112200201010000010112020101111000000??1				
<i>Ptochacarus</i>	2000111110211211112200001020000010112020101111000000011				
<i>Antennophorus</i>	200011111021121012000110020000000011?20101111000000011				
<i>Klinckowstroemia</i>	2120011111210111102000100020000001012021111001000000011				
<i>K. victoriae</i>	2100011111210111102000100020000001012021111001000000011				
<i>Fedrizzia</i>	2100011111210011?02000100020000001010?01111001000000001				
<i>Neofedrizzia</i>	2100011111210011102000100020000001010?01111001000000001				
<i>Megisthanus</i>	200001121111011111201010002000000?020?00121101000000011				
<i>Stenosternum truitae</i>	20000112111101111002000000020000002020?10121101000000011				
<i>Stenosternum</i> sp.	2100011211110111102000000020000002020?10021101000000011				
<i>Pleuronectocelaeno</i>	2100011211100011012000200111000200020?01101101000010101				
<i>Trichodiplogynium</i>	200001121111001101200020011000?100021021001101000010101				
<i>Cryptometasternum</i>	2100011211110011012000200110000100021021001101000010101				
<i>Ophiocelaeno</i>	2100011211110011012000200110000100021021001101000010101				
<i>Passalacarus</i>	2100011211110011012000200110000100021021001101000010101				
<i>Euzercon</i>	212001121111021101200020011110200020?01121101000010101				
<i>Neoeuzercon</i>	212001121111021101200020011110200020?01121101000010101				
<i>Megacelaenops</i> sp.	2100011211100011002010200110000000020?010011010000010?01				
<i>M. oudemansi</i>	2100011211100011002010200010000000020?010011010000010?01				
<i>Paraschizogynium</i>	2120011211100011012000200110000100021101101101000010101				
<i>Funkotriplogynium</i>	2110011211100111012100200110000000021021121101000010101				
<i>Triplogynium</i>	2100011211100111012100200110000000021021121101000010101				
<i>Thinozercon</i>	00000010000?0001101000100000000010002200100100112121011				
<i>Polyaspis</i>	11100010000?0001000001200010000010002200100101112121010				
<i>Trachytes</i>	011000?0000?0001000000200010000010002120101100111121011				
<i>Oplitis</i>	210000?0000?00010000012000100000100022001000001111210?0				
<i>Asternolaelaps</i>	20000110110?01100111002?00100000?0000?00000100111100001				
<i>Epicroseius</i>	0?0?0000110?001001110021001??000?0000?00000100111100000				
<i>Sejus</i>	0?000000110?00100111002100100000?0000?0000010011110000?				
<i>Uropodella</i>	01010100110?00100012002100111000?0000?00000110111100000				
<i>Microgynium</i>	01100010101?00101110002001000000?0000?010001101111210?0				
<i>Discozercon</i>	210011001010000?111000010121000010000?01100100111121101				
<i>Narceoheterozercon</i>	2100010010100001111000010120000010000?00100100111121101				

TABLE 2. Taxon-Character matrix used for the study. ? = not available

6. Gnathotectum

- [0] with anterior projections or serrations;
[1] without anterior projections or serrations

Gnathotectum is the structure covering dorsal area of the gnathosoma, and is also called epistome *sensu* BERLESE (1900) and KRANTZ (1978); supracheliceral limbus *sensu* VAN DER HAMMEN (1964); tectum *sensu* SNODGRASS (1948); tectum capituli *sensu* SNODGRASS (1948) and EVANS & TILL (1965); or tegular tectum *sensu* ATHIAS-BINCHE (1982). While the presence of, often multiple, anterior projections in the gnathotectum is observed in many groups of Mesostigmata, this character was once regarded as a good diagnostic character for the entire Cercomegistina (FIG. 12a) within the Trigynaspida (KETHLEY, 1977b). Within the Cercomegistina, however, Seiodidae lack such projections (FIGS. 12b & 12c). The members of Antennophorina, excluding Philodanidae, do not show multiple anterior projections.

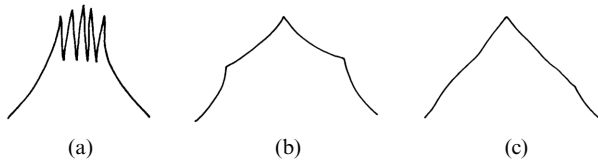


FIG. 12: Gnathotectum of Cercomegistoidea. (a) *Cercoleipus* sp. (Cercomegistidae), (b) *Seiodes ursinus* Berlese (Seiodidae) female and (c) male.

7. Gnathotectum

- [0] not triangular, somewhat roundish; [1] triangular

8. Median keel of gnathotectum

- [0] absent; [1] obscure; [2] conspicuous

Gnathotectum often has a roof-like structure, showing a median keel-like line, which can be seen dorsally and ventrally. Ventral keels are often more prominent than those observed dorsally.

The presence of median keel in gnathotectum was once regarded as a synapomorphy for the Antennophorina. However, detailed observation reveals that this character is variable, and only conspicuous in Celaenopsoidea, Megisthanoidea, and Promegistidae within the Antennophorina. This structure is absent in Parantennulidae, Philodanidae, some Para-

megistidae (*Antennomegistus*, *Echinomegistus*, and *Ophiomegistus*), and the members of Cercomegistina. When it is obscure, it only has a thin longitudinal line as in Klinckowstroemiidae, Fedrizziidae, Aenictequoidea, Antennophoridae, and the remaining Paramegistidae.

9. Chelicerae

- [0] elongate; [1] not elongate

Elongate cheliceral segments are typical to Uropodina, in which all of its members have long and slender cheliceral segments with much shorter and smaller digits (FIG. 13a). In many uropodines, the length of the entire chelicerae is more than a half or close to 3/4 of the idiosomal length. In other groups, including Trigynaspida, Sejina, Heterozerconina, and Microgyniina, their chelicerae are shorter, reaching at best less than the half of the length of the body. In these groups, the cheliceral digits are nearly equal to the length of the cheliceral segments.

10. Cheliceral digits

- [0] tapered, often edentate
(or with numerous minute teeth);
[1] robust, often with large proximal tooth on digits

This character is thought to be related to the kinds of food that the mites uptake. In other words, while the tapered and often edentate cheliceral digits are used for the ingestion of liquid or soft food, those of robust and often dentate ones are thought to be used to grab more solid food. The robust and dentate chelicerae are often used for the phoresy by holding the host's body part, such as seta (EVANS & HYATT, 1963). Moreover, it is assumed that the mites with tapered and edentate ones are not predatory but often paraphagic, while those with robust ones are often predatory (KINN, 1971). In Trigynaspida, Parantennuloidea, Promegistidae, Paramegistidae, Aenictequoidea, and Antennophoridae have tapered and edentate digits. All the Cercomegistina along with the antennophorine Megisthanoidea, Fedrizziidae, Klinckowstroemiidae, and Celaenopsoidea have robust and dentate digits.

11. Chelical excrecences

- [0] reduced or absent; [1] dendritic
(or brush-like);
[2] filamentous (hypertrophied)

Chelical excrecences are thought to be homologous to the arthrodial brushes that are often observed at the proximal region of the movable digit of chelicerae in many Mesostigmata, including, but not limited to, Microgyniina, Heterozetconina, Dermanysina, and Parasitina (see EVANS & TILL, 1979). While it is thought that these chelical excrecences in male are used for, among others, handling sperm cells for insemination (BANKS, 1915), assuming their homology with spermatodactyli may not be plausible, because chelical excrecences are also present in the female. Some celenopsoidea, including *Indogynium lindbergi* Sellnick (SELLNICK, 1954), carry both spermatodactyl (or spermatotreme) and chelical excrecences in male chelicerae. In the Trigynaspida, Cercomegistoidea, Megisthanoidea, and Celenopsoidea show dendritic or brush-like forms (FIG. 13b), while the remaining groups, such as Parantennuloidea, Promegistidae, Paramegistidae, Aenictetquoidea, Antennophoridae, Fedrizziidae, and Klinckowstroemiidae show more or less filamentous forms (FIG. 13c). Uropodina and Sejina lack this character on their chelicerae.

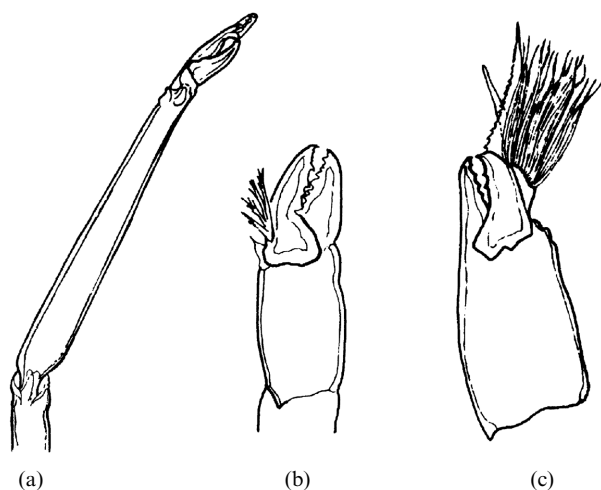


FIG. 13: (a) Long and slender chelicera of Uropodoidea. Chelical excrecences are absent. (b) Short and robust chelicera of Celenopsoidea. Excrecences are dendritic. (c) Short and robust chelicera of *Klinckowstroemia* sp. (Fedrizziidae). Excrecences are filamentous. (after KRANTZ, 1978)

12. Location of chelical excrecences

- [0] proximal; [1] middle or mediolateral

In most Cercomegistoidea, Parantennuloidea, Promegistidae, and Celenopsoidea, the chelical excrecences originate from the proximal region of the movable digit of the chelicera. This contrasts with the condition in Fedrizziidae, Klinckowstroemiidae, and Megisthanoidea, in which they arise from the mediolateral region of the movable digit (FIG. 13c).

13. Corniculi

- [0] strong, stout at base, heavily sclerotized;
[1] not heavily sclerotized, sometimes membranous,
or almost seta-like

Corniculi are also known as the external malae, which are the parts of the endites of the coxae of the pedipalps in the Mesostigmata (EVANS, 1992). Similar structures are the rutella appearing in the acariform Sarcoptiformes. In Trigynaspida, all the members of Cercomegistina along with antennophorine Fedrizziidae, Klinckowstroemiidae, Megisthanoidea, and Celenopsoidea retain strong and heavily sclerotized corniculi (FIGS. 14a & 14e). In contrast, the members of Parantennuloidea, Promegistidae, Paramegistidae, Antennophoridae, and Aenictetquoidea show somewhat membranous or almost setiform corniculi (FIGS. 14b, 14c, & 14d). As typical to the Mesostigmata, all the outgroups have heavily sclerotized corniculi in the adult.

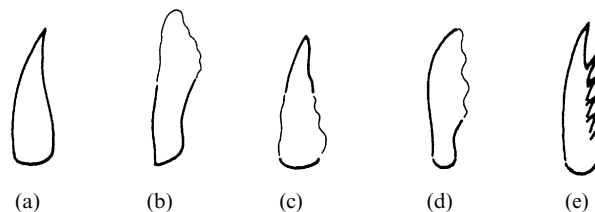


FIG. 14: Corniculi. (a) *Fedrizzia* sp. (Fedrizziidae); (b) *Paramegistus confrater* Trägårdh (Paramegistidae); (c) *Echinomegistus wheeleri* (Wasmann) (Paramegistidae); (d) *Antennophorus* sp. (Antennophoridae); (e) *Euzercon latus* (Banks) (Euzerconidae)

14. Corniculi

- [0] smooth, not branched, horn-like; [1] 2-tined;
[2] 3- or more tined, somewhat serrate

While having smooth and horn-like corniculi is typical to the Mesostigmata, often 2-tined (bifid; as in some Triplogyniidae and *Meristomegistus vazquezus* (Paramegistidae)) or multi-tined (serrate; as in Antennophoridae or Euzerconidae) corniculi are present in Trigynaspida (FIG. 14).

15. Salivary styli

- [0] present; [1] absent

16. Hypopharyngeal styli

- [0] absent; [1] present

17. Palpcoxal setae

- [0] barbed; [1] smooth

Palpcoxal setae *sensu* EVANS (1992) are also known as capitular setae *sensu* EVANS & TILL (1966); subcapitular setae *sensu* EVANS & TILL (1965, 1979) and KRANTZ (1978); gnathosomal setae *sensu* FUNK (1968) and GHILYAROV & BREGETOVA (1977); or deutostomal setae *sensu* NICKEL & ELZINGA (1970). While smooth setae are simple and with no serrations, barbed ones are bipectinate.

18. Hypostomal setae

- [0] form a straight line;
[1] not form a straight line, angled

Linear arrangement of hypostomal setae along the axis of the body has extensively been used to diagnose Uropodina and Diarthrophallina. Trigynaspid families of Saltiseiidae, Philodanidae, Klinckowstroemiidae, Fedrizziidae, Hoplomegistidae, and Megacelaenopsidae also show oblique-linear arrangement of these setae.

19. Palp genua

- [0] with 5 setae; [1] with 6 setae; [2] with 7 setae

With few exceptions, presence of 7 setae on palp genua in Antennophorina is unique in the Mesostig-

mata. These 7 setae are composed of 3 dorsal (*d*), 2 anterolateral (*al*), 1 posterolateral (*pl*), and 1 ventral (*v*) seta. Exceptions to this chaetotaxy in Antennophorina are found in *Micromegistus bakeri* (Parantennulidae), which has only 5 (by lacking a ventral and an anterolateral seta), and in *M. gourlayi* (Parantennulidae), Philodanidae, Promegistidae, *Echinomegistus* (Paramegistidae), and Neotenogyniidae, all of which have 6 setae as in Cercomegistina. In outgroups, while most of Uropodina, excluding Thinozerconidae, carry 5 setae on this palp segment, most mesostigmatids have 6 setae by lacking a ventral seta.

20. Palp tibiae and tarsi

- [0] completely articulated;
[1] slightly (or partially) fused;
[2] (insensibly or completely) fused

When the palp tibiae and tarsi are completely articulated, the diameter of the base of tarsus usually becomes smaller than the diameter of the distal end of tibia, and the intersegmental membrane is observed at the ventral side of the palp. As to the fused tibiae and tarsi, there is no such separation, and the membrane or the line of separation is not present (FIG. 15b). In this case, the presumed area of palp tarsus can be estimated by the location of palptarsal claw (= apotele), which is located in the base of palp tarsus in the Mesostigmata. Often, the separation or fusion between these two palpal segments is obscure, but with a thin line of separation between the two segments (FIG. 15a). When they show this feature, the entire palp tibiae and tarsi become tapered, and no intersegmental membrane is present.

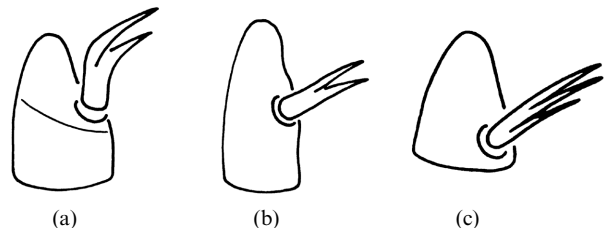


FIG. 15: (a) weakly fused (*Paramegistus*) and (b) completely fused (*Ophiomegistus*) palp tibia and tarsus. (c) Palp tarsus with 3-tined palptarsal claw (*Megacelaenopsis*).

21. Palptarsal claw

[0] 2-tined; [1] 3-tined

Within the group Trigynaspida, all the members of Cercomegistina (Cercomegistoidea) carry a 3-tined palptarsal claw (= apotele), while those of Antennophorina usually have a 2-tined one. Exceptions to this in Antennophorina are observed from *Parantennulus* (not included in this study) and *Micromegistus* (Parantennulidae), Megisthanidae, and Megacelae-nopsidae, all of which have 3-tined palptarsal claw (FIG. 15c). EVANS (1992: 426) described 3-tined palptarsal claw for Heterozerconina, but along with the specimens that have been used for this study, many other heterozerconid and discozerconid specimens that I examined have 2-tined palptarsal claw.

22. Tritosternal laciniae

[0] free, separated

(occasionally fused in the proximal portion;
base of tritosternum often wider than long);

[1] fused (occasionally separated terminally;
base of tritosternum often longer than wide)

In his key to the families of Trigynaspida, KETHLEY (1977b) recognized the fused tritosternal laciniae as one of the main characters for Cercomegistina (FIG. 16). However, exceptions are found in three



FIG. 16: *Cercoleipus* sp. (Cercomegistidae). Fused tritosternal laciniae.

cercomegistine families, such as Asternoseiidae, Davacaridae, and Seiodidae, which retain free tritosternal laciniae (FIG. 17). Along with this character, the Seiodidae also show smooth edge of gnathotectum, which is atypical to the Cercomegistina. All the members of Antennophorina and outgroups, except for *Polyaspis* and *Oplitis*, carry free tritosternal laciniae.

23. Presternal shield

[0] paired; [1] entire (not paired); [2] absent

24. Sternal shield

[0] entire (not fragmented, fused);

[1] fragmented, divided, paired, not entire

As for this character, the presence of presternal or metasternal shield(s) is not regarded as the fragmented, paired, or divided sternal shield. Instead, this character refers symmetric separation (*i. e.*, pairing)

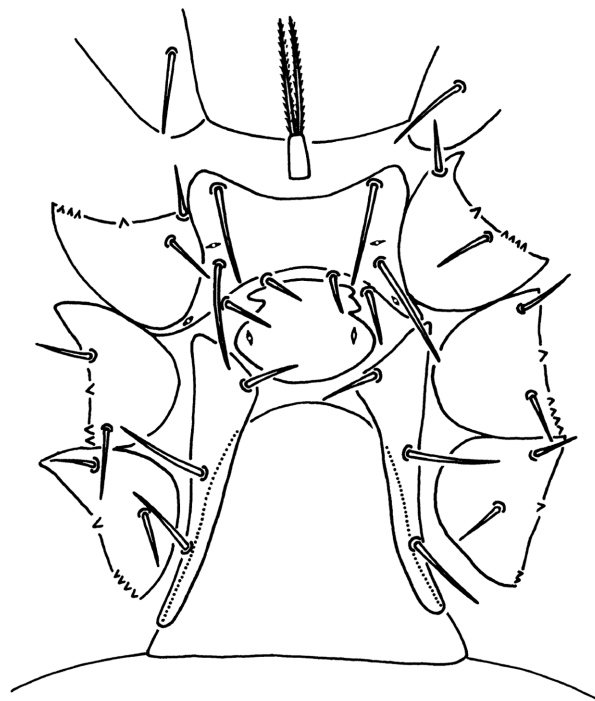


FIG. 17: *Seiodes ursinus* Berlese (Seiodidae), female sternal-genital region. Tritosternal laciniae are free.

of the sternal shields along the median line of the body. Fragmented or paired sternal shields appear in many Cercomegistina, Paramegistidae, Antennophoridae, and in the outgroups of Sejina, Microgyniina, and Heterozerconina.

In Microgyniina, two sternal shields, each bearing two setae of *st1-st2* and *st3-st4*, are separated longitudinally. As each shield carries two pairs of sternal setae, it is assumed that these shields are neither presternal nor metasternal but simply separated sternals. In Heterozerconina, the sternal structures, bearing *st1-st4* and *stp1-stp3*, are separated. While the

bar-shaped sternal shield is located in its original location, the remaining structures, identified by the retention of sternal lyrifissures (*stp*), are fused with the endopodal elements.

25. Sternovaginal sclerites

[0] absent; [1] present

Members of the Aenictquoidea have a pair of posterior internal sternal shield extensions, called the sternovaginal sclerites (FIG. 18). As these internal structures are originated from the sternal elements, they cannot be homologized with the claviform vaginal sclerites.

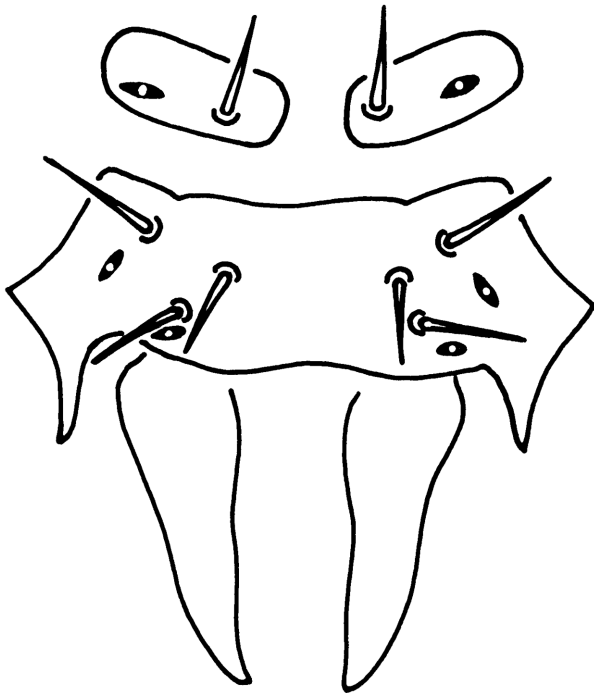


FIG. 18: *Ptochacarus silvestrii* Womersley (Ptochacaridae), showing paired sternovaginal sclerites.

26. Sternal shield

[0] bearing metasternal setae;
[1] not bearing metasternal setae

In the Mesostigmata, metasternal setae refer to the fourth pair of the sternal setae (*st4*). While the setae *st4* on sternal shield is common (FIGS. 2, 6, & 18), often these setae are located on soft integument or on

separate metasternal shields outside the sternal shield (FIGS. 3, 7, 9, 10, & 19). When the setae *st4* are on sternal shield, metasternal shield is expected to be absent. However, presence of the *st4* outside the sternal shield does not necessarily mean that the metasternal shield is present as the *st4* are often located in soft cuticle.

27. Sternal setae 1 (*st1*)

[0] on integument; [1] on sternal shield;
[2] on presternal shield

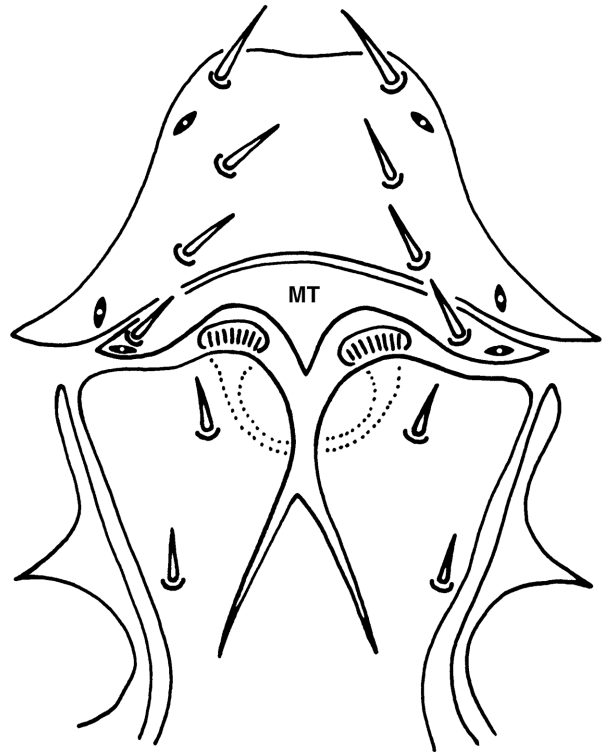


FIG. 19: *Choriarchus reginus* Kinn (Schizogyniidae), showing fused metasternal shield (MT). Heads of claviform vaginal sclerites are well-developed.

28. First sternal setae (*st1*)

[0] smooth; [1] barbed

29. Second sternal setae (*st2*)

[0] smooth; [1] barbed

30. Third sternal setae (*st3*)

[0] smooth; [1] barbed

31. Fourth sternal setae (*st4*)

[0] smooth; [1] barbed

32. Metasternal shields

[0] absent; [1] entire, fused together; [2] paired, divided

In this study, metasternal shields are defined as the shield bearing *st4* and *stp3* in the adult. This is compared with sternogynial shield (sternogynium) that bears *stp3* only, and with latigynial shields, each of which usually bears *st5* (and often *st6*). In many mesostigmatid mites, metasternal shields, if present, usually appear as a pair (FIG. 7). In some Celaenopsoidea, these shields are thin and transversely narrow, and the two shields are often weakly connected together by a bridge (FIG. 19).

33. Posterior end of sternal element

[0] not fused with endopodal elements;
[1] fused with endopodal elements

In most mesostigmatid mites, sternal elements, including presternal, sternal, or metasternal shields, if present, are free and distinct. Often, sternal or metasternal shields are elongated and fused with endopodal elements as in *Micromegistus* (Parantennulidae), Promegistidae, and Aenictequoidea in Trigynaspida. In Promegistidae, the metasternal shields, bearing *st4*, are extended posteriorly (FIG. 9), and the posterior sides of sternal shield are extended in Aenictequoidea. This external structure is distinguished from the internal sternovaginal elements.

34. Sternogynial shield

[0] absent; [1] entire (not divided, fused); [2] divided, paired

Sternogynial shield (sternogynium) is defined as a shield bearing *stp3* only (FIG. 6). When a shield carries additional *st4*, it is defined as the metasternal shield (FIGS. 3 & 7). A sternogynial shield appears in Asternoseiidae and Seiodidae (FIG. 17) in Cercomegistina, and Klinckowstroemiidae, Fedrizziidae, Paramegistidae, and Hoplomegistidae in Antennophorina. Despite the fact that KETHLEY (1977b) used this character to identify his Fedrizzioidae that includes Klinckowstroemiidae, Fedrizziidae, Paramegistidae, and Promegistidae, it is evident that the family Promegistidae (*Promegistus*) lacks this character.

Paramegistidae and Hoplomegistidae are diagnosed by the presence of paired sternogynial shields (FIG. 8).

35. Pseudosternogynium

[0] absent; [1] present

Pseudosternogynium *sensu* KRANTZ (1978) (= pseudosternum *sensu* KETHLEY, 1977b) is defined as a shield or a sclerite located between sternal and genital region that lacks any seta or lyrifissure. This structure is, therefore, distinguished from sternogynial shield (sternogynium) that retains *stp3*. The pseudosternogynium is rhombic in Promegistidae or rectangular in *Micromegistus* (Parantennulidae). As this structure lacks any seta or lyrifissure, which delimits the sternal region, it is thought to be the genital in origin, and is thought to be homologous to the pregenital shield in Holothyrida. It is found in Saltiseiidae, Parantennulidae, Promegistidae, and Aenictequoidea in Trigynaspida (FIG. 9).

36. Claviform vaginal sclerites

[0] absent; [1] present, but head reduced;
[2] head well-developed

Claviform vaginal sclerites *sensu* TRÄGÅRDH (1950), simply known as the vaginal sclerites, are thought to be the internal genital structures that support egg delivery, and are well developed in the Celaenopsoidea and Megisthanoidea (FIG. 19). Often, the heads are vestigial and arms look like thin straps in other groups of Trigynaspida, including Parantennuloidea, Promegistidae, Paramegistidae, Aenictequoidea, Antennophoridae, Klinckowstroemiidae, and Fedrizziidae (FIG. 8). Similar structures are also found in *Polyaspinus migginsi* Camin (Uropodina). Members of Cercomegistina and other outgroups used in this study lack this character.

37. Mesogynial shield

[0] absent; [1] reduced, obscure;
[2] present (distinct, free, well-developed)

In Cercomegistina, the mesogynial shield is free, usually larger than that of Antennophorina, and mostly triangular. This structure becomes variable in Antennophorina, in which the shield is triangular (as in Aenictequidae or Ptocharidae), rectangular (as

in *Micromegistus* (Parantennulidae)), reduced (as in Philodanidae, Diplogyniidae, or Triplogyniidae), or completely fused to ventral or ventrianal elements (as in Fedrizziidae, Megisthanoidea, Euzerconidae, Celaenopsidae, or Megacelaenopsidae).

38. Mesogynial shield [unordered]

- [0] triangular or subtriangular;
- [1] rectangular, subrectangular, or bar-shaped;
- [2] circular, other

39. Latigynial shields

- [0] reduced or incorporated in other shield elements;
- [1] two shields fused together;
- [2] present, distinct, free, well-developed

Having the functional latigynial shields that are opened during oviposition is often characteristic of female Trigynaspida. These shields are absent in other mesostigmatid mites, excluding *Trachytes* of Uropodina, but are thought to be fused with the endopodal elements in Uropodina (*Protodinychus* is an exception) and Diarthrophallina. In higher mesostigmatids, such as Dermanyssina, latigynial shields are thought to be fused with the epigynial shield. As to this character, however, the presence of endopodal elements, which are not related to oviposition, is not regarded as the same as the presence of latigynial shields, and are coded as 0 state.

When the latigynials are present as free and paired, they are usually triangular in shape (as in most Cercomegistina, Promegistidae, Paramegistidae, Diplogyniidae, etc.), but (sub)rectangular (as in some Aenictequoidea) or rare roundish form (as in Philodanidae) is also present. Often two shields are fused together to form a single shield as in Hoplomegistiidae. In addition, in some Celaenopsoidea, such as Euzerconidae, Celaenopsidae, or Megacelaenopsidae, these shields are completely fused to ventrianal shield (FIG. 7).

40. Ventromarginal shields

- [0] absent (fused with peritrematal plate);
- [1] present (free from peritrematal plate)

41. Anal or ventrianal shield

- [0] fused with dorsal shield; [1] not fused with dorsal shield

42. Anal shield

- [0] (insensibly) fused with ventral shield (ventrianal shield);
- [1] contiguous with ventral shield;
- [2] present, free, not fused with ventral shield

Anal shield is defined as a free shield bearing anal opening. When this shield is not free, it is fused to ventral shield to form a ventrianal shield. In Trigynaspida, all the Cercomegistina lack free anal shield. In Saltiseiidae, weakly developed sclerotization around anal opening is present (WALTER, 2000). This sclerotization, however, is embedded into the ventral element covering the entire ventrianal area. Fedrizziidae and Klinckowstroemiidae often have a thin line between ventral and anal area.

43. Postanal seta (*pon*) (in adult)

- [0] present; [1] absent

44. Pedofossae

- [0] present; [1] absent

Pedofossae (= foveolae pedales *sensu* CAMIN & GORIOSSI, 1955; foveae pedales *sensu* KRANTZ, 1978) are the depression of the cuticle around the base of coxae IV, which are thought to be used for the resting of the legs IV. This character is observed in Klinckowstroemiidae, Fedrizziidae, and Uropodoidea of Uropodina (outgroup).

45. Peritreme

- [0] well-developed;
- [1] (greatly) reduced or peritreme-like groove (pseudoperitreme) present

While normally developed peritremes reach almost to the base of coxae I or to the base of gnathosoma, reduced peritremes reach only to the area around/between coxae II-III. In Trigynaspida, Parantennulidae and ant associates of Aenictequoidea and Antennophoridae show short peritremes.

46. Tarsi I

- [0] with claws; [1] without claws

In Trigynaspida, all the members of Antennophorina lack claws on tarsi I. This character is shared with cercomegistine members of *Cercoleipus* and

Cercomegistus (Cercomegistidae), undescribed new genus of Pyrosejidae, and Saltiseiidae, along with uropodine outgroup, *Polyaspis* (Polyaspididae).

47. *al3* on Tarsi II

[0] present; [1] absent

Unlike most monogynaspid mites, trigynaspids have an additional anterolateral seta (*al*; *alx* in EVANS, 1965, 1969) on tarsi II-IV in the adult, yielding a total of 4 *al* setae on these leg segments. Although this seta is identified as *al3* in the adult, in the context of the sequence of ontogeny this seta appears as the fourth one.

48. *al3* on Tarsi III

[0] present; [1] absent

Although this character is similar to the character number 47, character independence is assumed as the setae (characters) are not located in the same leg. Hence, these are two different characters on two different locations. This character becomes synapomorphic to the Trigynaspida.

49. Femora IV

[0] with 8 setae; [1] with 7 setae; [2] with 6 setae

When the femora IV in the adult bear 8 setae, they form a chaetotaxy of (1, 2/1, 2/1, 1) (FIG. 1). The posterolateral (*pl*) seta becomes absent when this leg segment has a total of 7 setae as in Sejina, Microgyniina, and Heterozerconina; and both *pl* and posteroventral (*pv*) setae are usually absent if the femora IV have 6 setae.

50. Tarsi IV

[0] with 4 *al* setae; [1] with 3 or fewer *al* setae

51. Ventral intercalary sclerite on tarsi IV

[0] free, well-developed; [1] weakly developed; [2] absent

The presence of this sclerite, bearing *av4* and *pv4* on tarsi IV in the adult, is shared by the Sejina and most of the Trigynaspida, excluding Celaenopsoidea. In Celaenopsoidea, the sclerite is partially fused to telotarsus IV. In Epicriidae (not used for this study), a

similar sclerite is present at the circumsegmental region of tarsi IV. It should be noted that this sclerite is not ventral but dorsal in position, and bears *ad3* and *pd3*. In the adult Trigynaspida and Sejina, circumsegmental region of tarsi II-III also bears this sclerite.

52. Proximoventral region of tarsi IV

[0] *av4* and *pv4* present; [1] *av4* and *pv4* absent

All the Trigynaspida, including Celaenopsoidea, and Sejina carry paired setae of *av4* and *pv4* on ventral intercalary sclerite appearing in the circumsegmental fissure between basi- and telotarsus IV in the deutonymph and adult stases. Presence of these setae in the Mesostigmata outside the Trigynaspida and Sejina has not been reported.

53. Male genital orifice

[0] midsternal (= located between coxae II-IV);
[1] presternal (= located beneath the base of tritosternum)

In primitive mesostigmatid mites, the location of male genital orifice is more or less posterior, located in an area between coxae II-IV. Most of the Trigynaspida along with the outgroups of Uropodina and Sejina used in this study retain this ancestral state. In Celaenopsoidea, the orifice is located beneath the base of tritosternum, which is observed in many derived groups of the Mesostigmata, such as Dermanyssina and Parasitina. Along with this character, celaenopoid members of *Indogynium lindbergi* Sellnick and *Choriarchus reginus* Kinn (Schizogyniidae) carry spermatodactyl (or spermatotreme) on movable digit of male chelicerae. Members of Heterozerconina also show presternal position in male genital orifice.

54. Male eugenital setae

[0] absent; [1] present

Some trigynaspids carry paired eugenital setae on the male genital valve, a character shared with some members of Uropodina, such as *Thinozercon*, *Trachytes*, and *Polyaspis*. In Trigynaspida, this character is found in the cercomegistine groups of Asternoseiidae, *Cercoleipus* (Cercomegistidae), and Davacaridae, and in the antennophorine groups

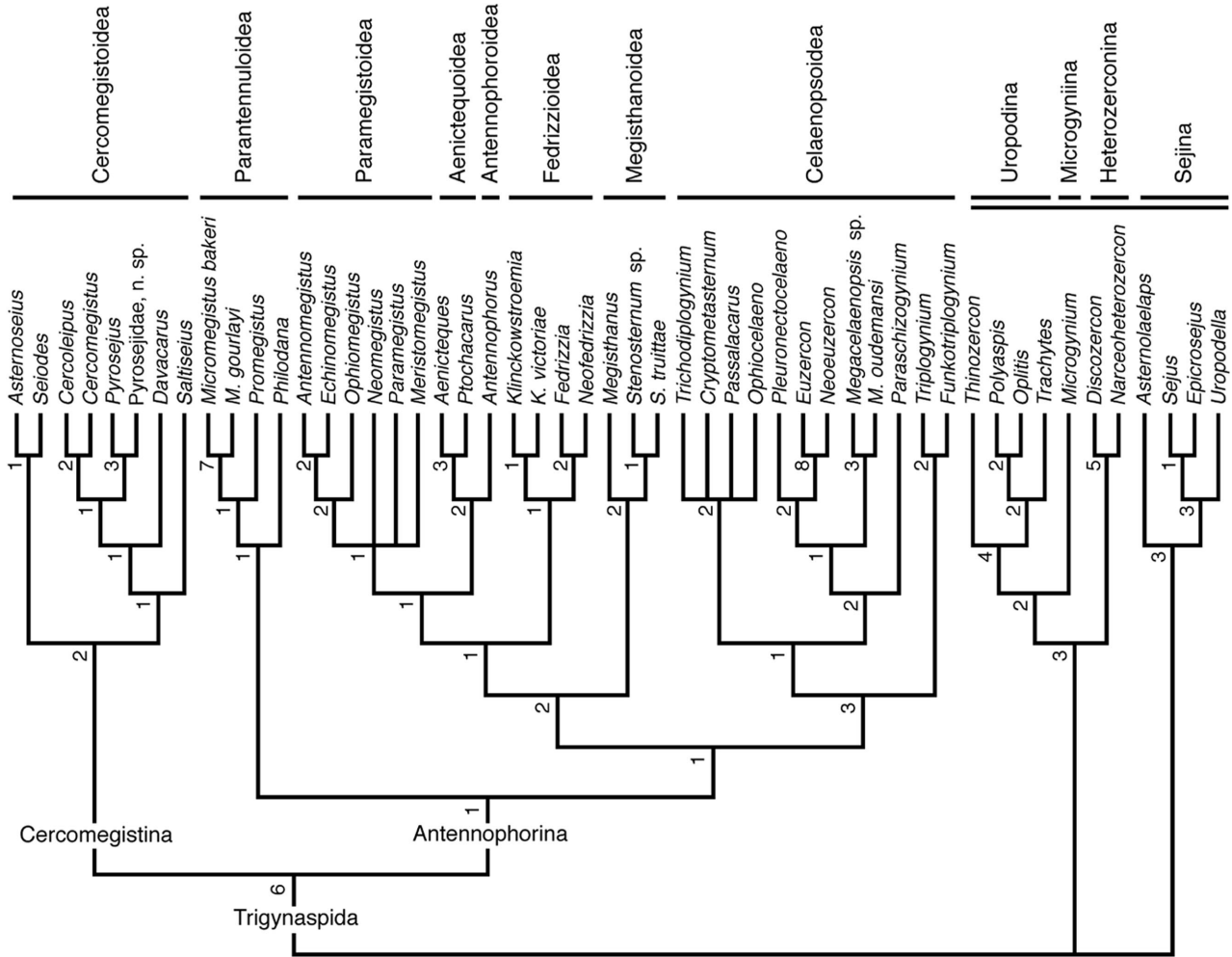


FIG. 20: Strict consensus tree from 3 equally most parsimonious trees under no topological constraints. Numbers shown are the values of branch support *sensu* BREMER (1988). Names of the superfamilies are from this study.

of Paramegistidae (excluding *Echinomegistus wheeleri*), Aenictequoidea, Antennophoridae, Klinckowstroemiidae, and Megisthanoidea (FIG. 4). Members of Sejina used in this study lack male eugenital setae.

55. Phoretic deutonymph

[0] present; [1] absent

In the Mesostigmata, phoretic deutonymphs are found in certain Uropodina (Uropodinae), some Sejina, Microgyniina, certain Parasitina (Parasitinae) and some Dermanyssina. The phoretic deutonymph often entails a specialized body form, such as anal pedicel and anal gland in Uropodinae (Uropodina) or modified anal region in *Microsejus* (Microgyniina)

(EVANS & TILL, 1979) or *Uropodella laciniata* (Sejina) (KETHLEY, 1983), all of which offer the function of an attachment to the host. When these phoretic deutonymphs are associated with their host for dispersal, they are sessile and probably non-feeding. In *Micromegistus* (Parantennulidae) of Triginaspida, all the postembryonic stages are found on a single beetle host. Although its deutonymphal stage is associated with its host, it is not regarded as the phoretic deutonymph, because, along with other stases, those deutonymphs are always active and feed on fungi or other organic debris. Unlike phoretic monogynaspid mites that have a deutonymphal dispersal stage, triginaspids, including *Micromegistus*, disperse as adults (HUNTER, 1993a).

RESULTS AND DISCUSSION

Tree Topology and Systematics

From the data set, three equally most parsimonious trees ($L = 273$ steps; $CI = 0.27$; $RI = 0.75$) were deduced under no topological constraints. A strict consensus tree recognized monophyletic Triginaspida, carrying the bifurcating lineages of Cercomegistina and Antennophorina (FIG. 20). Global branch support scores for this strict consensus tree deduced from AutoDecay 4.0.2 (ERIKSSON, 1999) were rather low throughout the phylogeny, having 1 to 3 in most cases. It should be mentioned that, however, these numbers are not objective, and often are reflected by the number of characters included. In fact, when the taxon: character ratio is close to 1:1 in a well-resolved strict consensus tree, low scores of global branch support do not necessarily indicate poor support of the branches (nodes), as the support for a branch cannot exceed its branch length.

Removal of potentially subjective characters, such as the characters of numbers 5 and 28 through 31, yielded nine trees ($L = 256$ steps; $CI = 0.27$; $RI = 0.76$). Except for having a polytomy in a cercomegistine node, showing (*Cercoleipus*, *Cercomegistus*, *Davacarus*, (*Pyrosejus*, *Pyrosejidae* n. sp.)) relationship, this treatment did not influence the change of topology (*i. e.*, branching order) of the strict consensus tree shown in the FIG. 20.

As to the higher relationships within the Triginaspida, KETHLEY's (1977b) grouping of the superfamily Fedrizzioidea, containing Fedrizziidae, Klinckowstroemiidae, Promegistidae, and Paramegistidae, was not supported, as this superfamily is not monophyletic. In addition, the phylogeny showed that the two ant associates, Antennophoroidea and Aenictequoidea, are not distantly related but monophyletic sister groups.

Regarding the status of Fedrizzioidea *sensu* KETHLEY (1977b), while two sister families of Fedrizziidae and Klinckowstroemiidae, passalid associates, formed a monophyletic group, Promegistidae and Paramegistidae turned out to be more closely related to the members of other superfamilies. Promegistidae, represented by a single known species, *Promegistus armstrongi* Womersley, associated with *Pamborus* (Coleoptera: Carabidae) in Australia, became the sister to the two species of *Micromegistus* (Parantennuloidea: Parantennulidae), carabid associates from North America and Australia-New Zealand. This new group, along with another known parantennuloid, *Philodana johnstoni* (Philodanidae), formed a clade, suggesting the re-definition of the superfamily Parantennuloidea. Unlike Fedrizziidae and Klinckowstroemiidae that have entire (= unpaired) sternogynial shield, heavily sclerotized corniculi, robust dentate cheliceral digits, and 7 setae on palp genua, Promegistidae carry no sternogynial shield, and carry membranous base of corniculi, tapered edentate chelicerae, and 6 setae on palp genua, which are characteristic of the members of Parantennuloidea.

The family Paramegistidae, displaying the associations with diplopods, squamates, or carabids, became monophyletic and shared sister group relationships with the ant-associates, Antennophoroidea and Aenictequoidea. This result is compared with the KETHLEY's (1977b) non-monophyly of Paramegistidae, and the new relationship suggests the removal of Paramegistidae from current Fedrizzioidea to form a new superfamily, Paramegistoidea. The breakdown of Fedrizzioidea and the new status for its members are summarized in the TABLE 3.

When the monophyletic Fedrizzioidea *sensu* KETHLEY (1977b) was enforced from the data set, 10 additional steps ($L = 283$) were required. A strict

Current Fedrizzioidea	Host	Proposed Superfamily
Fedrizziidae	passalids	Fedrizzioidea
Klinckowstroemiidae	passalids	Fedrizzioidea
Paramegistidae	squamates, diplopods, carabids	Paramegistoidea, NEW
Promegistidae	carabids	Parantennuloidea

TABLE 3. Proposed classification for the Fedrizzioidea.

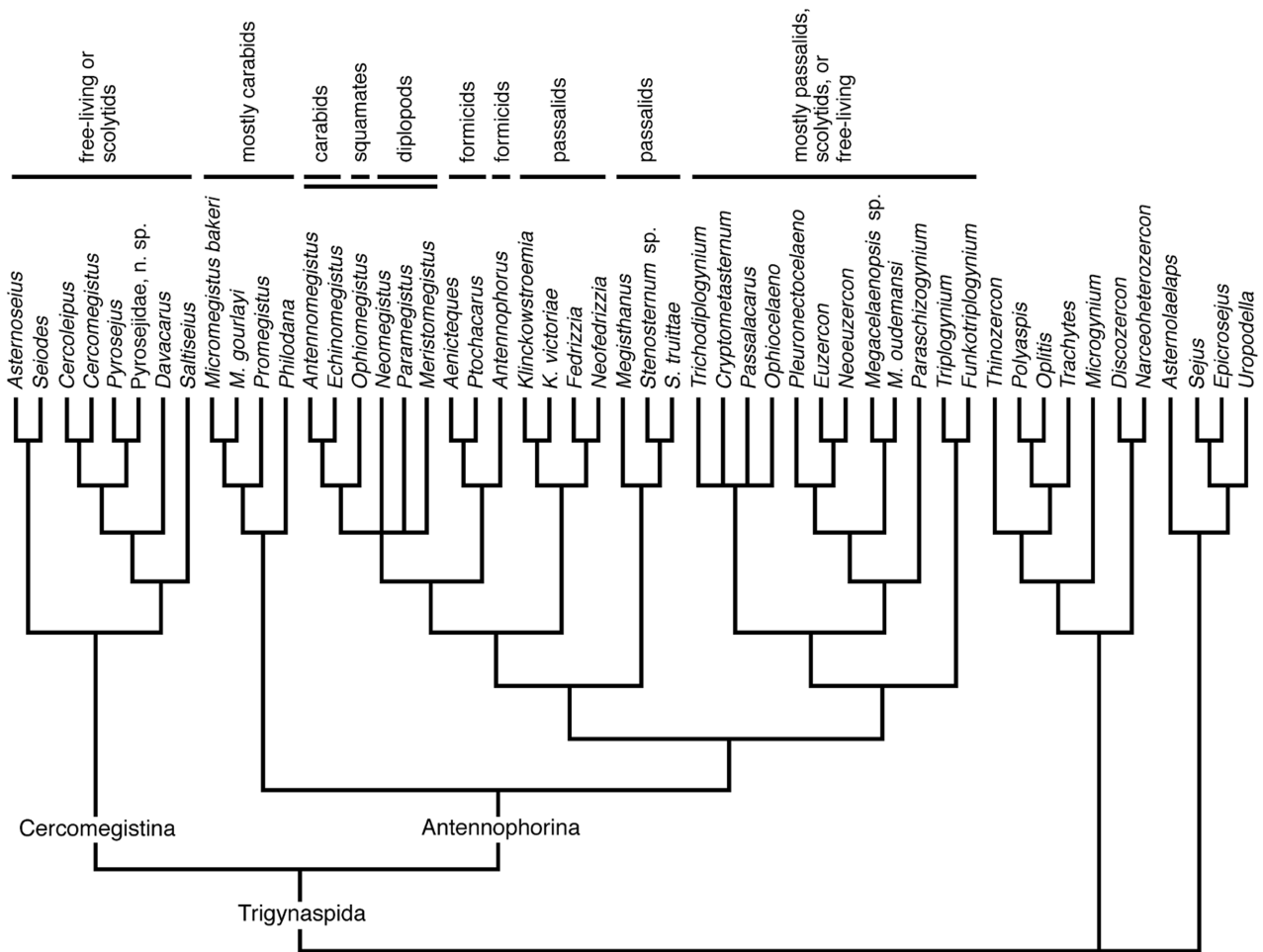


FIG. 21: Strict consensus tree with host associations. See the text for the deviations of association.

consensus tree from these enforced trees recognized the monophyly of Trigynaspida, but it failed to recognize the monophyletic Cercomegistina and Antennophorina as the tree loses the hierarchy within the Trigynaspida. Similarly, when the monophyletic (Parantennuloidea, Paramegistoidea) was enforced from the data set, 4 additional steps ($L = 277$) were required. A strict consensus tree from these non-parsimonious trees, however, yielded non-monophyletic Parantennuloidea, and the relationships within the Antennophorina were not resolved. In addition, this enforced tree failed to recognize the monophyly of (Klinckowstroemiidae, Fedrizziidae) relationship.

This study showed that the two current superfamilies of ant-associates, Antennophoroidea and Aenic-

tequoidea, are not as distantly related as suggested by KETHLEY (1977b). Instead, they are the sister groups, suggesting either uniting them in a single superfamily (of Antennophoroidea), or retaining two superfamilies as is by keeping their current names. These ant-associates are not that different in terms of morphology, as they share several characters, such as the presence of short peritremes, paired eugenital setae on male genital valve, and non-sclerotized corniculi.

Within the Antennophorina, reshuffled Parantennuloidea, now including Promegistidae, branched first. Although the phylogeny from this study is different from that of KETHLEY's, this initial branching of Parantennuloidea within the Antennophorina is consistent with the KETHLEY's. This group is supported by the characters, such as the presence of 5 or 6

setae (not 7) on palp genua, presence of a pseudosternogynium, absence of presternal shield, and absence of paired male eugenital setae. The diagnosis for each superfamily from this study has been shown in the diagnosis section below.

Systematics and Host Association

Based on the information from ontogeny and phylogeny (FIG. 21), I assume that the ancestral Trigynaspida was a free-living predator, dwelling in moist and decaying environment feeding on nematodes, collembolans, or other insects' eggs. From this environment, evolution of phoretic associations that may allow dispersal is thought to be established.

Among the 8 superfamilies proposed in this study, nearly all the members of Cercomegistoidea are free-living in both immature and adult stages (A few exceptions were given in the INTRODUCTION.). All the cercomegistoids have robust and dentate chelicerae, supporting their predatory feeding behavior.

The patterns of host association become more diverse in the remaining 7 superfamilies that collectively constitute Antennophorina. The first branched group Parantennuloidea, revised herein to include Promegistidae, is associated mostly with carabids. *Philodana johnstoni* Kethley (Philodanidae) associated with tenebrionid was an exception in this study.

Except for a few free-living groups (*i. e.*, Triplogyniidae, Megacelaenopsidae, some Diplogyniidae, and some Schizogyniidae), nearly all the adults of Celaenopsoidea display the associations with their hosts, mostly with the passalids. In fact, among the 159 known species of Celaenopsoidea, at least 75 species show the associations with passalids at the adult stage. From the free-living and mostly passalid associations, multiple independent associations toward non-passalids are thought to be evolved within the Celaenopsoidea. In fact, the highest degree of diversification of trigynaspids appearing in Celaenopsoidea is thought to be triggered by the shifts of their phoretic host, dwelling in moist and decaying habitats.

Two superfamilies of Megisthanoidea (containing Megisthanidae and Hoplomegistidae) and Fedrizioidea (now only containing Fedrizziidae and Klinkowstroemiidae) are also associated mostly with passalids. Rare exceptions are found in *Megisthanus lamellicornium* Kramer (Megisthanidae) associated

with scarabaeids, and *Fedrizzia carabi* Womersley (Fedrizziidae) associated with carabids. Along with Celaenopsoidea, these two superfamilies display passalid associations within the Antennophorina in the phylogeny (FIG. 21).

The pattern of strict association applies to the Antennophoroidea and Aenictequoidea, which are the associates of formicids. The associations in the remaining superfamilies, *i. e.*, Paramegistoidea and Parantennuloidea, were discussed above and summarized in the TABLE 3. Although there are minor exceptions of *Echinomegistus* and its close sister *Antennomegistus* (Paramegistidae) that are associated with carabids, it needs to be noted that the members of Paramegistoidea do not share the same host range with those of Parantennuloidea in general.

Biogeography and Origin

The facts that most trigynaspids are found in the continents of former Gondwanaland and that they are either free-living (as in most Cercomegistoidea, and some Celaenopsoidea) or associated with mostly non-volant gregarious hosts indicate that the origin (age) of trigynaspids is linked to the age of the southern continents and global distribution of the hosts, which are primarily passalids. Passalids, which serve as the major hosts for antennophorine lineages in the phylogeny (FIG. 21), are also thought to be former Gondwanaland in origin (PEDRO REYES-CASTILLO, ALAN GILOGLY, CHRIS MARSHALL, personal communication).

Accordingly, without having a direct evidence of fossil record of Trigynaspida, it is possible to estimate the age of these mites based on the information from the plate tectonics and the biogeography (vicariance) of trigynaspids and their hosts. Based on the information on biology, biogeography, and the phylogeny of these mites, I assume that the origin of free-living Cercomegistina is in, at the latest, Upper Triassic period of Mesozoic era (*ca.* 200-225 million years ago) when the supercontinent Pangaea broke into northern Laurasia and southern Gondwanaland (KIOUS & TILLING, 1994). By Jurassic, when this former Gondwanaland became separated into South America, Africa, India, and Antarctica-Australia complex, the evolution of the major groups in Cercomegistina and Antennophorina that display the

host associations is thought to be already established. Although it is almost certain that the free-living trigynaspids appeared earlier than those showing the associations, there is no direct evidence on the starting point of the acquisition of host association or the evolution of phoresy found in most Antennophorina. However, as the host associations occur in the adult stage, and are thought to be obligatory, the appearance of phoretic trigynaspid groups should address the initiation of host association.

Although the only known passalid fossil is from the Cenozoic Oligocene deposits (REYES-CASTILLO, 1977), the paleogeography of this period shows the complete separation of the Gondwanaland (KIOUS & TILLING, 1994; MINTZ, 1977). Accordingly, assuming the acquisition of passalid association at this period requires multiple independent associations toward passalids on these already separated continents. In other words, it is more plausible to speculate the starting point of the evolution of phoresy in, at the latest, the Jurassic, when the continents and these flightless animals are still combined together. Furthermore, the passalids are also thought to be at the latest Mesozoic (P. REYES-CASTILLO, personal communication) or even Paleozoic (A. GILOGLY, personal communication) in origin.

Another support to the speculation of the Jurassic origin of Antennophorina comes from the stenoxenic ant associates, Antennophoroidea and Aenictequoidea. Although these two superfamilies are closely related in the phylogeny (FIGS. 20 & 21), they do not share the same distribution area in the globe. While the members of Aenictequoidea appear in the Philippines, Papua New Guinea, eastern Australia, and South Africa, those of Antennophoroidea appear in Europe and North America, better supporting vicariance than dispersal. Information on the Jurassic (CROZIER *et al.*, 1997) or the Cretaceous (GRIMALDI *et al.*, 1997) origin of ants along with the time of separation of Europe and North America (*ca.* 65-135 mya) also supports, at the latest, the Jurassic origin of these mites.

Current biogeographic distributions of the three known species of *Micromegistus* (Parantennuloidea: Parantennulidae) that exhibit the association with carabids, *i. e.*, *M. bakeri* from North America, *M. viduus* from South America (not included in this study), and *M. gourlayi* from Australia and New

Zealand, may also support the above speculation on the origin. Although carabids are more active than passalids, the peculiar global distribution patterns of these mites on carabids in three different continents still prefers passive vicariance over active dispersal, allowing the estimation of the age of these mites at the latest to the Jurassic.

This effort to estimate the origin and the age of trigynaspid mites is important as this estimation reduces the significant gap of the origin (age) between two different acarine lineages: Acariformes (= Actinotrichida) and Parasitiformes (= Anactinotrichida). Although the formation, preservation, and discovery of fossils are the rare events of chance, and although this is especially true for the tiny mites, there is a huge gap of time in terms of the oldest fossil records between the Acariformes and Parasitiformes. That is, while there are several fossil records of acariform mites beginning from the Devonian (*ca.* 400-405 mya) (BERNINI, 1991; HIRST, 1923; NORTON *et al.*, 1988; SELDEN, 1993), the earliest known fossil of Parasitiformes is only from the Upper Cretaceous (*ca.* 90-94 mya) (KLOMPEN & GRIMALDI, 2001), leaving the gap of time of about 306-315 million years. It would be natural to have the same or close time of origin between Acariformes and Parasitiformes, if the group Acari is monophyletic (see ATHIAS-HENRIOT, 1975; LINDQUIST, 1984; SHULTZ, 1990; VAN DER HAMMEN, 1977, 1989; WEYGOLDT & PAULUS, 1979; ZACHVATKIN, 1952). Accordingly, if the estimation of the age of Trigynaspida proposed herein, based on the information from the biogeography of mites and their hosts, phylogeny, and the plate tectonics, is legitimate, the origin of the Parasitiformes, including mesostigmatic Trigynaspida, goes back to the Upper Triassic period (*ca.* 200-225 mya) and the gap of time between the two acarine lineages is much narrowed by only about 175-205 million years.

A KEY TO THE FAMILIES OF TRIGYNASPIDA (BASED ON FEMALE)

1. Often with two or more dorsal shields (if one, then often a line of fusion exists between anterior podonotal and posterior opisthonotal shields). Gnathotectum usually with anterior projections or serrations, and without ventral median keel (if edge of gnathotectum smooth with pointed

anterior end, then tritosternum with 2 distinct laciniae as in Seiodidae). Palp genua usually with 6 setae. Palptarsal claw (= apotele) 3-tined. Chelicerae usually robust, dentate or with large proximal teeth. Cheliceral excrescences dendritic, originating from proximal or medioproximal region of movable digit. Tritosternal laciniae usually fused for half or more of length, often rod-like, occasionally separated terminally, OR laciniae not fused to each other, often completely separated at base (as in Seiodidae (FIG. 17), Asternoseiidae, and Davacaridae). Claviform vaginal sclerite absent. Mesogynial shield often large and triangular. Latigynial shields usually well-developed. Anal opening on ventrianal shield. Tarsi I with or without claws.....

..... **Cercomegistina, Superfamily Cercomegistoidea — 2**

1'. With a single dorsal shield (sometimes a line of fusion exists as in Philodanidae; if more than one shield, then palp genua with 6 setae, and well-developed claviform vaginal sclerites present as in Neotenogyniidae). Gnathotectum more or less triangular or rounded, smooth, often with a ventral median keel. Palp genua usually with 7 setae (rarely with 5-6 setae). Palptarsal claw (= apotele) usually 2-tined (rarely 3-tined). Chelicerae often tapered, edentate or with minute teeth, OR robust, dentate. Cheliceral excrescences filamentous or rarely dendritic, originating from various region of movable digit. Tritosternal laciniae free. Claviform vaginal sclerites or sternovaginal processes often present, sometimes head of claviform vaginal sclerites reduced. Anal opening on ventrianal or free anal shield. Tarsi I without claws.....

..... **Antennophorina — 7**

2. Sternogynial shield, bearing third sternal lyrifissure (*stp3*), present (FIG. 17). Tritosternal laciniae free, not fused to each other. Tarsi I with claws. Chaetotactic formula of dorsal setae on genua I-IV, 5-5-6-6..... **3**

2'. Sternogynial shield, bearing third sternal lyrifissure (*stp3*), absent. Tritosternal laciniae usually fused for half or more of length, rarely free (as in Davacaridae). Tarsi I with or without claws. Chaetotactic formula of dorsal setae on genua I-IV not as above..... **4**

3. Holodorsal shield. Presternal shields paired. Sternal shields paired. Sternal setae 1 (*st1*) on integument posterior to paired presternal shields. Male genital valve with paired eugenital setae..... **ASTERNOSEIIDAE**

3'. 2 dorsal shields. Presternal shield absent. Sternal setae 1 (*st1*) on an entire sternal shield. Gnathotectum more or less triangular, with smooth edge (FIGS. 12b & 12c). Latigynial and mesogynial shields not distinctly separated (FIG. 17). Peritreme reduced. Male genital valve with no eugenital setae..... **SEIODIDAE**

4. Holodorsal shield. Gnathosoma strongly prognathous. Tarsi I without claws. Legs IV hypertrophied, modified for jumping. Peritrematal shield with longitudinal groove behind coxae IV. (WALTER, 2000: FIG. 2)..... **SALTISEIIDAE**

4'. Dorsum with 2 or more shields. Tarsi I with or without claws..... **5**

5. With four dorsal shields. Metapodal shields free. Mesogynial shield well-developed, elongate-subrectangular. Tritosternal laciniae free, not fused to each other. Tarsi I with claws. Male genital valve with paired eugenital setae. Chaetotactic formula of dorsal setae on genua I-IV, 6-5-6-6.....

..... **DAVACARIDAE**

5'. With two subequal dorsal shields. Free metapodal shields absent. Mesogynial shield reduced or lost, or triangular in shape. Tritosternal laciniae usually fused for half or more of length. Tarsi I with or without claws. Male genital valve usually without paired eugenital setae. Chaetotactic formula of dorsal setae on genua I-IV not as above... **6**

6. Dorsal shields with relatively few setae. Lateral idiosomal setae on marginal shields (LINDQUIST & MORAZA, 1993: FIG. 2), not on platelets in soft cuticle. Ventrianal shield fused posteriorly to opisthonotal and marginal shields. Tarsi I with or without claws. Paralacinae present. Chaetotactic formula of dorsal setae on genua I-IV, 5-5-6-6.....

..... **PYROSEIIDAE**

6'. Dorsal shields hypertrichous. Lateral idiosomal setae on platelets in soft cuticle. Ventrianal shield free posteriorly and posteromarginally, not fused with dorsal shield. Tarsi I without claws. Paralacinae absent. Chaetotactic formula of dorsal setae on genua I-IV, 6-6-6-6.....

..... **CERCOMEISTIDAE**

7. Palp genua with 5-6 setae. Sternogynial shield absent. Pseudosternogynium often present. Claviform vaginal sclerite absent or head greatly reduced. Median keel of gnathotectum reduced or absent. Chelicerae tapered, edentate, digits reduced with filamentous excrescences. Corniculi setiform or multi-tined. Setae *av4* and *pv4* on tarsi IV often short. Paired male eugenital setae absent.....

..... **Superfamily Parantennuloidea — 8**

7'. Palp genua with 7 setae (if 6, then paired sternogynial shield present as in *Echinomegistus* (Paramegistidae), or dorsum with 3 dorsal shields as in *Neotenogynium malkini* (Neotenogyniidae)). Claviform vaginal sclerite present, or head often reduced. Median keel of gnathotectum often present. Chelicerae dentate or edentate. *av4* and *pv4* on tarsi IV variable. Paired male eugenital setae present or absent..... **10**

8. Palp tibiae and tarsi fused. Palptarsal claw 2-tined. Mesogynial shield vestigial or absent. Anal shield wide, strap-like, with more than 5 pairs of setae. Dorsal shield hypertrichous, with more than 50 pairs of setae. Associated with tenebrionids. (KETHLEY, 1977a: FIG. 2).....

..... **PHILODANIDAE**

8'. Palp tibiae and tarsi normally articulated. Palptarsal claw 2 or 3-tined. Mesogynial shield well-developed or fused to ventrianal shield. Pseudosternogynium often present. Anal area with 2 pairs of setae. Dorsal shield not as above..... **9**

9. Sternal shield paired or fragmented. Mesogynial shield free, not fused to ventral shield. Anal shield separated from

ventral shield with no more than 2 pairs of setae. Peritreme more or less reduced, not reaching to the base of coxae I. Chaetotactic formula of dorsal setae on genua I-IV, 5-5-6-6. Associated with carabids or rarely with myriapods.

..... **PARANTENNULIDAE**

9°. Sternal shield entire, not fragmented (FIG. 9). Mesogynial shield fused to ventrianal shield. Metasternal shields fused to endopodal elements. Pseudosternogynium ellipsoid. Peritreme not reduced, reaching to the base of coxae I. Chaetotactic formula of dorsal setae on genua I-IV, 4-4-4-4. *av4* and *pv4* on tarsi IV short. Corniculi membranous with horned tip. Associated with carabid (or very rarely with passalids)

..... **PROMEGISTIDAE**

10. Presternal shield(s) usually present (if absent, then pseudosternogynium or triangular mesogynial shield well-developed as in Physalozzerconidae and Aenictequidae). Sternal shield entire, or paired, or rarely fragmented. Metasternal shield, bearing *st4* and *stp3*, absent. Mesogynial shield well-developed or fused to ventral element. Head of claviform vaginal sclerites often vestigial. Sternogynial or sternovaginal elements often present. Gnathotectum smooth, triangular, or more or less roundish, median keel often obscure or absent. Chelicerae robust or tapered; with dendritic or filamentous cheliceral excrescences. Palp genua with 6-7 setae. Ventral intercalary sclerite on tarsi IV free, not fused to tarsi. Male genital orifice located in intercoxal region II-IV, not above base of tritosternum..... **11**

10°. Presternal shield absent (if present, then dorsum with 3 dorsal shields as in *Neotenogynium malkini* (Neotenogyniidae)). Sternal shield entire, not paired. Free metasternal shield(s), bearing *st4* and *stp3*, often present. Mesogynial shield, if present, small or vestigial, often fused to ventral element. Sternogynial or sternovaginal elements absent. Claviform vaginal sclerites well-developed, head well-developed. Dorsal shield with an unpaired median seta at anterior margin. Gnathotectum smooth, triangular, median keel present. Chelicerae robust, with large proximal tooth on movable digit; with dendritic or brush-like cheliceral excrescences. Palp genua with 7 setae (if 6, then dorsum with 3 dorsal shields as in *Neotenogynium malkini* (Neotenogyniidae)). Ventral intercalary sclerite on tarsi IV absent or fused to telotarsi. Spermatodactyl (or spermatotreme) often present on movable digit of male chelicerae. Male genital orifice located above base of tritosternum.

..... **Superfamily Celaenopsoidea — 20**

11. Chelicerae tapered, edentate. Movable digit with filamentous excrescences. Corniculi membranous or setiform, often with small protuberance(s). Anal shield fused with ventral shield. Associated with formicids, carabids, diplopods, or squamates

12

11°. Chelicerae robust, dentate. Movable digit with filamentous or dendritic excrescences. Corniculi sclerotized, horn-like. Anal shield free from or contiguous to ventral shield. Associated with passalids

17

12. Sternogynial shield bearing sternal lyrifissures 3 (*stp3*)

present. Sternovaginal elements absent. Peritreme normal. Pseudoperitreme absent. Corniculi membranous. Associated with arthropods or reptiles

..... **Superfamily Paramegistoidea**

..... **— PARAMEGISTIDAE**

12°. Sternogynial shield absent. Latigynial shield each usually with many setae. Sternovaginal element often present. Peritreme short, often with pseudoperitreme. Corniculi often setiform, often with small protuberance(s). Strictly associated with formicids

13

13. Palp tibiae and tarsi normally articulated. Mesogynial and ventral elements fused narrowly

..... **Superfamily Antennophoroidea**

..... **— ANTENNOPHORIDAE**

13°. Palp tibiae and tarsi insensibly fused. Sternal shield with paired posterior extensions devoid of setae and pores (= sternovaginal elements), and usually (or often) covered by latigynial shields. Mesogynial shield usually well-developed (if obscure or absent, then presternal shields present as in Messoracaridae).....

..... **Superfamily Aenictequoidea — 14**

14. Presternal shields paired. Latigynial shields elongate, subrectangular, with parallel mesal margins. Mesogynial shield obscure or absent

..... **MESSORACARIDAE**

14°. Presternal shield absent. Latigynial shields subtriangular, mesal margins not parallel. Mesogynial shield triangular.....

15

15. Latigynial shields each with two setae. Peritreme-like groove (= pseudoperitreme) present

..... **AENICTEQUIDAE**

15°. Latigynial shields each with more than 8 setae. Pseudoperitreme absent

16

16. Sternal setae 1 (*st1*) on paired presternal shields. Latigynial shields each with less than 12 setae.....

..... **PTOCHACARIDAE**

16°. Sternal setae 1 (*st1*) on entire sternal shield. Presternal shield absent. Latigynial shields each with more than 30 setae.....

..... **PHYSALOZERCONIDAE**

17. Chelicerae with dendritic excrescences. Anal shield completely separated from ventral shield. Sternogynial shield entire or divided. Pedofossae (= foveae pedales) absent. Large mites, ranging over 3 mm long

..... **Superfamily Megisthanoidea — 18**

17°. Cheliceral digits short with filamentous excrescences. Anal shield fused with or contiguous to ventral shield. Sternogynial shield entire, inversely triangular. Pedofossae (= foveae pedales) to accommodate folded legs often present. Turtle-like mites, ranging about 1 mm long

..... **Superfamily Fedrizzioidea — 19**

18. Presternal shields paired, each with *st1*. Latigynial shield fused together, free from ventral shield. Claviform vaginal sclerites well-developed

..... **HOPLOMEGISTIDAE**

- 18'. Presternal shield, bearing *st1*, usually entire, rarely paired, weakly sclerotized. Latigynial and mesogynial shields lost, represented by a ridge bordering the sternogynial elements posteriorly. Sternogynial shield divided or entire, completely covering the genital orifice. Claviform vaginal sclerites reduced, without heads but often with thickened arms. **MEGISTHANIDAE**
19. Latigynial and mesogynial shields well-developed. Claviform vaginal sclerites present but head reduced. Male genital orifice ellipsoid, located between coxae III. Paired male eugenital setae often present **KLINCKOWSTROEMIIDAE**
- 19'. Latigynial and mesogynial shields reduced or lost, covered by enlarged sternogynial shield. Claviform vaginal sclerites absent or obscure. Male genital orifice circular or only slightly wider than long, located between coxae II-III. Paired male eugenital setae absent **FEDRIZZIIDAE**
20. Palp genua with 6 setae. With 3 dorsal shields plus with presternal shield (if holodorsal shield present, then presternal shield absent.). Peritremes greatly reduced. Associated with Neotropical diplopods. **NEOTENOGYNIIDAE**
- 20'. Palp genua with 7 setae. With holodorsal shield. Sternal setae 1 (*st1*) on an entire sternal shield **21**
21. Latigynial shields well-developed, free from ventral elements. Mesogynial shield usually small, flanked by latigynial shields or reduced **22**
- 21'. Latigynial shields rarely free, usually fused to ventral elements posteriorly. Mesogynial shield usually vestigial or fused to ventral elements. **24**
22. Anal shield fused to ventral shield (*Neodiplogynium* is exception). Mesogynial shield, if present, usually less than 1/3 length of the latigynial shields. Associated with arthropods or rarely with squamates **DIPLOGYNIIDAE**
- 22'. Free anal shield present. Mesogynial shield usually longer than 1/3 length of latigynial shields. Free-living or associated with insects or diplopods **23**
23. Metasternal shield fused to sternal shield. *st4* and *stp3* on sternal shield. Mesogynial shield at least 1/2 length of latigynial shields. Latigynial shield each with 1 seta. Ventromarginal shields present. Corniculi often weak, seta-like, or bifurcated. Free-living in soil-litter, on bark, in bark beetle galleries, or in the nests of stingless bees. (FUNK, 1977: Fig. 1) **TRIPLOGYNIIDAE**
- 23'. Metasternal shield, bearing *st4* and *stp3* present. Mesogynial shield very small or vestigial. Latigynial shield each with 2 setae. Ventromarginal shields absent. Corniculi horn-like. Associated with diplopods. (HUNTER, 1993b: Fig. 4). **COSTACARIDAE**
24. Anal shield free or fused with ventral shield. Often multi-tined paralaciniae present. Latigynial and mesogynial elements free from each other mesally, fused with ventral element posteriorly. Metasternal shield(s), bearing *st4*,

- narrow, strap-like (absent in *Karkinoeuzercon*). Associated with a variety of arthropods, rarely with squamates, or free-living **25**
- 24'. Anal shield fused with ventral shield. Free, narrow postanal shield, not bearing anal opening, often present. Latigynial-mesogynial complex insensibly fused, with at most a small median notch present on anterior margin of genito-ventral element. *st4* on sternal shield or on well-developed metasternal shields. Free-living or associated with scolytids **26**
25. Anal opening on free anal shield, bearing 2 pairs of setae. Median separations between mesogynial and latigynial elements not extending past level of coxae III. Corniculi serrate. Hypostomal setae *hs1* on anteriorly extended projection or lobe. Associated with passalids or rarely with diplopods. **EUZERCONIDAE**
- 25'. Free anal shield often present. Latigynial shields elongate, often extending posteriorly to and often beyond coxae IV. Corniculi horn-like. Hypostomal setae *hs1* not on anteriorly extended projection. Male chelicerae often with spermatodactyl or spermatotreme on movable digit. Free-living or associated with passalids, scolytids, or rarely with squamates. **SCHIZOGYNIIDAE**
26. Metasternal shield, bearing *st4* and *stp3*, well-developed, paired. Free, narrow postanal shield, not bearing anal opening, often present. Fused endopodal-metapodal-peritrematal elements fused with ventrianal shield. Associated with bark and beetles burrowing under bark. **CELAENOPSIDAE**
- 26'. Metasternal shield absent, fused to sternal shield. Setae *st4* on sternal shield. Postanal shield absent. Endopodal-peritrematal shields fused, but free from ventrianal shield. Large mites with body over 1 mm in length. Free-living. **MEGACELAENOPSIDAE**

DIAGNOSES OF THE SUPERFAMILIES OF TRIGYNASPIDA

Superfamily Cercomegistoidea

DIAGNOSIS: Body often with moderate hypertrichy; often with two or more dorsal shields (if one, then often a line of fusion present between anterior podonotal and posterior opisthonotal shields). Tritosternal laciniae usually fused for half or more of length, often rod-like, occasionally separated terminally, or separated at base. Sternal shield well-developed (entire) or fragmented. Sternogynial shield, if present, entire. Mesogynial shield often large and triangular; latigynial shields usually well-developed. Claviform vaginal sclerites absent. Anal opening on ventrianal shield. Free anal shield absent. Gnathotectum usually with anterior projections or serrations, without median keel (if edge of gnathotectum

smooth with pointed anterior end, then tritosternum with 2 distinct laciniae.) Palp genua with 6 setae. Palptarsal claw (= apotele) 3-tined. Chelicerae robust, dentate, or with large proximal teeth. Cheliceral excrescences dendritic, originating from proximal or medioproximal region of movable digit. Tarsi I with or without claws. Tarsi IV with setae *av4* and *pv4* on free ventral intercalary sclerite. Male genital orifice on intercoxal area, usually between coxae II-IV, covered by 1 or 2 transverse valves.

Superfamily Parantennuloidea

DIAGNOSIS: Oval, flattened mites often with minute dorsal setae with marginal fringe of enlarged, flattened setae. Presternal shield absent. Sternal shield variously fragmented. Sternogynial shield bearing *stp3* absent. Pseudosternogynium often present. Mesogynial shield free from or fused to large ventral or ventrianal shield; latigynial shields generally well-developed. Palp tibiae and tarsi fused, or distinct, unfused; palp genua with 5 or 6 setae. Chelicerae not robust, tapered, edentate; often digits reduced; movable digit with filamentous excrescences located in proximal region; fixed digit with membranous distal processes or fimbriate dorsal excrescence. Corniculi often setiform or rarely multi-tined. Paired male eugenital setae absent.

Superfamily Paramegistoidea, NEW

DIAGNOSIS: Oval, flattened mites with minute dorsal setae and distinctly larger stylus-like, spinous, or foliate ventrianal setae. Presternal shield present. Sternal shield paired or two shields connected by narrow bridge. Sternogynial shields, bearing *stp3*, paired. Mesogynial shield free from or fused to large ventrianal shield; latigynial shields generally well-developed. Palp tibiae and tarsi fused or rarely unfused; palp genua with 7 setae (*Echinomegistus* with 6 setae). Chelicerae edentate; movable digit with filamentous or more or less dendritic excrescences. Corniculi membranous, often with sclerotized tip. Paired male eugenital setae often present.

Superfamily Antennophoroidea

DIAGNOSIS: Sternal setae 1 (*st1*) on entire presternal shield. Mesogynial shield reduced, with anterior

pedicellate ventrianal element dividing narrow latigynial shields; latigynial shields each with more than two pairs of setae. Peritremes short. Palp tibiae and tarsi distinct, unfused; palp genua with 7 setae. Chelicerae with minute teeth; movable digit with filamentous excrescences. Corniculi with small protuberance(s) or more or less serrate. Paired male eugenital setae present.

Superfamily Aenictequoidea

DIAGNOSIS: Sternal setae 1 (*st1*) on separate presternal shields or on entire sternal shield. Sternal shield with a pair of posterior projections lying under latigynial shields (= sternovaginal processes). Pseudosternogynium present. Mesogynial shield subtriangular, separate from ventrianal shield, and overlapped or covered by latigynial shields each bearing 2 to numerous setae. Peritremes short, often associated with additional peritreme-like groove (= pseudoperitreme). Palp tibiae and tarsi insensibly fused; palp genua with 7 setae. Chelicerae tapered, edentate. Corniculi with small protuberance(s).

Superfamily Megisthanoidea

DIAGNOSIS: Sternal setae 1 (*st1*) on paired or entire presternal shield(s) often weakly sclerotized. Sternal shield entire, with 3 pairs of setae (*st2-st4*). Mesogynial shield obscure; latigynial shields insensibly fused to each other or weakly separated, free from ventral shield. Sternogynial shield entire or divided. Anal shield free, not fused with ventral shield. Palp tibiae and tarsi distinct, unfused; palptarsal claw 2- or 3-tined; palp genua with 7 setae. Chelicerae robust, strongly toothed, movable digit with dendritic excrescences.

Superfamily Fedrizzioidea

DIAGNOSIS: Sternal setae 1 (*st1*) on entire presternal shield, sternal shield with 3 pairs of setae (*st2-st4*). Sternogynial shield entire, hinged along posterior margin of sternal shield. Mesogynial and latigynial shields well-developed, or reduced and withdrawn under ventral plate. Pedofossae often present. Anal shield subtriangular, fused with or contiguous to ventral shield. Palp tibiae and tarsi distinct, unfused; palp genua with 7 setae. Chelicerae robust, with short

digits and dense, mop-like mass of filamentous excrescences. Corniculi horn-like.

Superfamily Celaenopsoidea

DIAGNOSIS: Presternal shield absent (except for *Neotenogynium malkini*). Sternal shield entire, bearing 3-4 pairs of setae; free metasternal shield bearing *st4* and *stp3* often present. Mesogynial shield small, triangular, free, or fused with latigynial or ventral elements; latigynial shields free or fused to ventral shield. Claviform vaginal sclerites well-developed. Dorsal shield with an unpaired median seta at anterior margin. Palp tibiae and tarsi distinct, unfused; palp genua with 7 setae (except for *Neotenogynium malkini* carrying 6 setae). Chelicerae robust, dentate; movable digit with large proximal tooth with dendritic excrescences. Corniculi horn-like, setiform, or serrate. Ventral intercalary sclerite fused to telotarsi IV. Male genital orifice on anterior margin of sternal shield.

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