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OBSERVATIONS ON FIVE RARELY COLLECTED GENERA OF MACROCHELIDAE (ACARI: MESOSTIGMATA) ASSOCIATED WITH INSECTS

by G. W. KRANTZ *

SUMMARY: Recent reexamination of specimens representing five rarely collected genera of Macrochelidae that I described in 1961 and 1962 has provided valuable supplemental information on their morphology and has uncovered errors in some of the original descriptions. I have incorporated previously unrecognized or misinterpreted features into revised generic diagnoses and have supplemented these with new or corrected illustrations as deemed appropriate. Finally, I present a description of the heretofore undescribed male of Lordocheles desaegeri Krantz, 1961, and synonymize the genus Grafia Krantz, 1962 with Trigonholaspis Vitzthum, 1930.

INTRODUCTION

The mesostigmatic family Macrochelidae currently comprises some 15 genera of predatory mites, most of which have well established phoretic associations with insects (KRANTZ, 1998). Representatives of certain of these genera have appeared only occasionally in general collections, presumably because their insect hosts or the habitats that support them have not been adequately sampled. During the early years of my tenure at Oregon State University, I erected five new genera to accommodate some of these elusive species, viz. Lordocheles and Synaphaspis (KRANTZ, 1961), Aethosoma (KRANTZ, 1962a), and Ancistrocheles and Grafia (KRANTZ, 1962b). Limited prior experience with the Macrochelidae led to my committing a number of errors—both of omission and commission—in framing their descriptions. It is my intention to rectify these errors in the pages to follow, and to present additional information on the morphology and possible intergeneric relationships of these unusual taxa.

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SYSTEMATICS

Lordocheles Krantz, 1961
(Figs. 1–11)


Revised generic diagnosis

With general characteristics of the family. Dorsal shield (Fig. 8) strongly ornamented throughout, scalloped marginally, with a distinctive submarginal cell pattern and an anteromedian depression bordered in its posterior portion by two or more pairs of strongly sclerotized pits which appear to be glandular openings; with 28 pairs of smooth spinose setae and an unpaired seta 12. Sternal shield (Fig. 10) reduced laterally, endopodal elements free in the soft integument; metasternal shields absent, sternal pores present or absent, when present situated in the soft integument behind the sternal shield. Anal opening posteriorly placed in a small triangular anal shield, cribleum (Fig. 5) extends anterolaterally to anterior shield margin, cribleal gland openings on prominent posterolateral angles of the shield; opisthogaster with few to many smooth setae. Peritremes extend anteriorly and dorsally beyond insertions of coxae I. Vent of gnathosoma (Figs. 1, 10) with or without deutosternal denticles; corniculi narrow and extending to a point level with femoral/genual articulation of the palpi; chelicera of female flexed dorsad (Fig. 7), with few to many teeth on each digit; chelicera of male (L. desaegeri) not flexed, with recurved spermatodactyl on movable digit (Fig. 2). Tritosternum (Figs. 1, 10) reduced to the point of being non-functional (see WERNZ & KRANTZ, 1976 for discussion of tritosternal function). Leg chaetotaxy normal for genus; genu IV with seven setae; femur II of male (L. desaegeri) with a strong ventral spur, setae av1 of genu and tibia II modified as shown in Fig. 6, femur I of both male and female L. desaegeri with a rounded, bilobed ventridistal seta (v27) and a flanking setigerous spur (v1) (Fig. 3).

Immature stages: Unknown.

Species currently included in the genus: Lordocheles desaegeri Krantz (type species), L. rykei Krantz.

Description of the male of Lordocheles desaegeri

The original descriptions of L. desaegeri and L. rykei (KRANTZ, 1961) were based only on females. Following publication of the original description, three males of L. desaegeri were recovered from alcohol-stored collections, numbers 2231 and 3740, from Mission H. DESAEGER, Garamba Park, Congo (Zaire) (1949–1952). A description of the male is presented below. Measurements are in micrometers.

MALE: Length of idiosoma averages 645 (range=640–648), width at level of coxae III averages 465 (range=455–477) (n=3). Dorsal shield ornamentation and setation similar to those of female (see KRANTZ, 1961). Sternal shield (Fig. 10) reduced laterally, with evanescent reticulation as illustrated and carrying sternal setae 1–4 and the epigynials; sternals 4 distinctly longer than sternals 1–3 and slightly longer than epigynials, shield with three pairs of pores, pores 2 inserted on excavated lateral margins of the shield; endopodal elements free in integument; genital opening beneath an anterior flap of the sternal shield. Peritreme as in female, with a seta inserted just behind peritrematic loop. Tritosternum greatly reduced, no longer than deutosternal setae, laciniae weakly pilose and emanating directly from base. Gnathosoma similar to that of female (Fig. 1, see additional notes below), hypostomatic setae 1 greatly reduced relative to other hypostomastics, deutosternum with five rows of denticles in a poorly defined depression; corniculi with strong siphuncular grooves, with a distinctive proximoventral step series of 12–15 narrow corrugations lying adjacent to and laterad from
FIGS. 1–6: Lordocheles desaegeri Krantz


FIG. 7: Lordocheles rykei Krantz, female chelicera (modified from Krantz, 1961)
hypostomatic setae 1; epistome without lateral processes, forked and weakly divided distally. Chelicerae (Fig. 2) without dorsal flexion as in female; fixed digit with a single median tooth and a setate pilus dentilis, dorsal seta slightly broadened; movable digit edentate, with a recurved spermatodactyl as illustrated. Legs with rugose ornamentation as in female, ambulacral paradactyls as long or longer than adjacent claws; seta v1 of femur II (Fig. 6) a strong setigerous spur; setae av1 of genu and tibia II modified as shown in the enlarged detail attached to Fig. 6, possibly for the purpose of clamping individual setae of the female during sperm transfer.

SPECIMENS. All three male specimens were collected during the Mission H. DESAEGER to Garamba National Park, Congo, (1949–52). Two males were taken from a coprophagous insect (probably a scarabaeine beetle) in fresh elephant dung on a swampy plain, 4 July 1952 (Coll. No. 3740). The remaining specimen was collected from a “diverse” substrate in a grassy savanna, under rhinoceros dung, 28 July 1954 (Coll. No. 2231). Two males will be deposited in the collection of the Musée Royal de l’Afrique Centrale, Tervuren, Belgium, and one will be retained in the acarology collection, Oregon State University, Corvallis, Oregon, USA.

Remarks on the original generic description

Examination of the slide series of L. desaegeri confirmed that hypostomatic setae 1 in both sexes are greatly reduced relative to the other hypostomatic setae (Fig. 1, h1). The singular ornamentation of the adjacent proximoventral surfaces of the corniculi may relate to a functional role normally assumed by hypostomastics 1. Neither the corniculi nor the first pair of hypostomatic setae of L. rykei, the second described species of the genus, display such modification (Fig. 10). It should also be noted in the figure that setae av are present on coxae II–III of L. rykei, as is a distinct deutosternal groove; the setae were omitted in the original illustration and the deutosternal groove was merely suggested. My reexamination of the holotype confirmed that denticles are absent, a possible functional concomitant of radical tritosternal reduction. Finally, I have added both the epigynial pores and the inguinal solenostomes associated with coxae IV to the revised figure, along with the evanescent reticulation noted on the sternal shield. Absence of metasternal pores in the holotype was confirmed, as suggested in the original illustration of the venter (KRANTZ, 1961).

Reexamination of the dorsal shield of the holotype of L. rykei showed that dorsal setae j2 are indeed present, smaller than setae j3 and somewhat obscured in the ornamentation pattern of the shield margin (Figs. 8, 9). I identified the epistome within the distorted gnathosoma of the holotype specimen (Fig. 11) and found that it lacks lateral processes and is distally divided, as in L. desaegeri.

Relationships within the family

The two known species of Lordocheles display an unusual combination of morphological traits which, when considered separately, suggest affinities with a variety of macrochelid genera. These traits include lack of discrete lateral epistomatic processes (as in Geholaspis Berlese), strong scalloped marginal and cellular submarginal ornamentation of the dorsal shield (as in certain Holostaspella Berlese), a greatly reduced sternal shield (as in Ancistrocheles Krantz, referred to later in this paper), an anal rather than a ventrianal shield and strong paranal extensions of the cribrum (as commonly seen in the opacus group of the genus Macrocheles Latreille), and lack of a bidentate tooth on the movable cheliceral digit of the female (as in some Holostaspella species and the opacus species group). Structures similar to the sclerotized median pits of the dorsal shield of Lordocheles occur in Macrocheles bilacunatus Krantz, a species taken from a scarab in Natal, South Africa (KRANTZ, 1970), and in an undescribed species of Holostaspella s.lat. from cacao and forest litter in Venezuela, Trinidad, and Costa Rica. An unpaired seta J2 as described for Lordocheles also is found in one species of the genus Glypholaspis Filipponi & Pegazzano and in certain opacus group species. Only the dorsally flexed chelicerae of the female and the greatly reduced tritosternum seen in both sexes are considered unique to Lordocheles. Cladistic analysis may help clarify its phylogenetic relationships within the family.
FIGS. 8–13.

FIGS. 8–11: Lordocheles rykei, female

FIGS. 12–13: Synaphaspis congoensis Krantz, female.
Synaphaspis Krantz, 1961
(Figs. 12, 13)


Revised generic diagnosis (female)

Small heavily sclerotized mites with the general characteristics of the family. Dorsal shield punctate-areolate; with 28 pairs of distally pilose setae, many of which are distally expanded; with 22 pairs of pore-like openings (not shown in original description). Sternal, metasternal, podal, and ventrianal shields fused around the posteriorly truncate epigynial shield to form a completely armored, uropodine-like venter (Fig. 13), peritrematic shields free distally, peritremes curving dorsad beyond coxae I; cribrum narrow and obscure, occupying the posterior opisthogastric margin. Chelicerae weakly dentate, movable digit without bidentate tooth, paraxial arthrodial brush less than half the length of movable digit; epistome with well developed lateral processes. Legs without spurs, genu IV with six setae.

Male and immature stases: Unknown.

Remarks on the original generic description

Reexamination of the paratype series of S. congoensis, the type and only species of Synaphaspis, revealed a number of minor inconsistencies in the original description. The placement of setae av and pv on coxa I in the original figure (KRA NTZ, 1961, Fig. 10) is misleading and probably was based on an atypical specimen. I have redrawn the two setae in the correct position and scale in Fig. 12. Seta pv of coxa II was originally figured as being distally pilose, but only two of the eight specimens of S. congoensis presently available to me give any indication of pilosity. Also, although it does not appear in the original drawing of the venter, a v seta is indeed present on coxa IV. The sternal, epigynial, and many of the leg setae are longer than illustrated in the original figure (for example, compare st1 as shown in Fig. 12 with the original figure in KRA NTZ, 1961), and sternal “pores” 1–3 are present but obscure. Pores 1 and 2 are situated beneath sclerotized folds of the shield laterad from their corresponding sternal setae (Fig. 12, p1), and the metasternal pores are small exposed openings situated medially from the insertions of coxae III. I confirmed that cheliceral teeth of S. congoensis are present but extremely small (KRA NTZ, 1961, Fig. 12), although the nature of the teeth is not made clear in the original description. They appear to be membranous, and often may be found only by first locating their rounded sclerotized bases.

Relationships within the family

There are strong general similarities between S. congoensis and certain other macrochelid genera, primarily Glypholaspi s Filipponi & Pegazzano and Holostaspella Berlese (FILIPPONI & PEGAZZANO, 1960, 1967; KRA NTZ, 1967b, 1998). Holostaspella shares with Synaphaspis (among other characteristics) a weak cribrum and a typically outward-curving peritrematic loop at its juncture with the stigma. Like Holostaspella and Glypholaspi s, and based on its lack of a cheliceral bidentate tooth and otherwise weak cheliceral dentition, Synaphaspis may also prove to be an incidental rather than an obligate phoretic on the insects with which it shares its habitat. However, while it appears to have close derivative ties with a putative Holostaspella/Glypholaspi s clade, I consider the combination of weak cheliceral dentition, fused sternal/podal/ventrianal elements, and obscure cribrum to be unique for Synaphaspis.

Aethosoma Krantz, 1962
(Figs. 14–19)


Type species: Aethosoma burchellestes Krantz, by monotypy.

Revised generic diagnosis (female)

Idiosoma narrow and elongate (ratio of idiosomatic length vs width of type material averages 2.9:1); dorsal shield (Fig. 14) with distinctive punctate-reticulate pattern, with only 25 pairs of setae (z1, z2,
Figs. 14–20.

Figs. 14–19: *Aethosoma burchelletes* Krantz, female


Fig. 20: *Ancistrocheles bregetovae* Krantz, chelicera of female with tip of fixed digit lacking (antiaxial).
and j3 absent) and 18 clearly defined pore/gland openings; setae j1, z6, s2, s6, S1, and S2 smooth and spinose, shorter than most of the remaining dorsals which are elongate and distally pectinate (see enlarged drawing of seta Z3 attached to Fig. 14), setae J5 minute, palmate, distally divided (see enlarged attachment to Fig. 14), Z5 inserted on posterolateral protuberances of the shield. Stigmata and proximal portion of peritremes dorsolateral, continuing forward in a ventrolateral position to a level beyond coxae II, and then swinging dorsal to terminate laterad from insertions of setae j2. Tritosternum (Fig. 15) with weakly pilose laciniae. Sternal, epigynial and ventrianal shields ornamented as shown in Fig. 17; sternal shield greatly elongated, reflecting the unusually wide separation between coxae I and II, shield fused laterally with podal shields; metasternal setae and pores on small shields located medially from and between coxae II–III. Epigynial shield nearly as broad as long; accessory sclerites beneath the lateral shield margins; ventrianal shield longer than wide, insertions of preanal setae in nearly straight lines and well removed from the shield margins; cribrum obscure, comprising what appears to be a single row of tiny spicules behind the anal field (Fig. 18). Gnathosomatic base with five large deutosternal teeth arranged in single file in a narrow deutosternal groove (Fig. 19), corniculi short and broad, epistome (Fig. 16) a smooth membranous flap narrowing terminally to an attenuate tongue-like projection; movable and fixed digits of chelicerae each with a single median tooth, with a single, reduced arthrodial brush at the base of the movable digit. Ambulacra II–IV without well developed paradactyls, genu IV with six setae.

**Male and immature stages: Unknown.**

### Remarks on the original generic description

Reexamination of paratype material of *A. burchelllestes* associated with the army ant *Eciton burchelli* in Guyana (1935–36), and recent study of additional specimens taken from the nests of *E. hamatum* in Ecuador in 1975, has provided additional information on generic characters and has uncovered a number of omissions in the original description. I have refigured the dorsal shield (Fig. 14) to show setal and "pore" disposition, and have clarified the nature of setae J5. The tritosternum (Fig. 15) was found to be weakly pilose rather than smooth as shown in the original description, and the peculiar membranous, elongate epistome is identified and figured for the first time (Fig. 16). Although they are not shown in the original figure, sternal pores 1 and 2 are present in the heavily ornamented sternal shield (Fig. 17), and a narrow cribrum may be seen on the posterior margin of the ventrianal shield (Fig. 18). I omitted the deutosternal setae from the gnathosomatic base of *A. burchelllestes* in the original description but have added them in the revised illustration (Fig. 19). Likewise, a pilus dentilis was found to be present on the fixed cheliceral digit and is shown in the revised figure, as are some originally omitted palptrochanteral, femoral and genital setae. In addition, the three-tined palpal apotele which was omitted from one of the palpi in the original figure has been added.

Finally, it should be noted that the original designation of *A. burchelllestes* as a phoretic of *Eciton burchelli* (Krantz, 1962a) was based on inference from the type slide data, which refers to the ant as the "host" of *A. burchelllestes*. Collection data from more recently examined material indicates that the mite is in fact a nest associate rather than a phoretic.

### Relationships within the family

The unique and oftentimes bizarre morphological modifications seen among Neotropical mesostigmatic associates of doryline army ants (Rettenmeyer, 1962; Elzinga, 1981, 1982a, 1982b) frequently have confounded efforts to resolve their systematic positions within established schema, and have occasionally led to their elevation to family level (Elzinga, 1993). While its singular idiosomatic shape, dorsal setal deficiencies, unusual deutosternal dentition, membranous attenuate epistome, and disposition of coxae I–II relative to the greatly elongated sternal shield offer ample justification for assigning separate generic status to *A. burchelllestes*, the basic morphology remains clearly macrochelid. However, like some unique myrmecophilous genera in other mesostigmatic taxa (e.g. Coxequesoma, Planodiscus, Circocyliliba), the systematic position of *Aethosoma* relative to...
other macrochelid genera is not easily determined (Krantz, 1962a). As suggested earlier for the genus Lordocheles, inclusion of Aethosoma in a broad cladistic analysis of the Macrochelidae may clarify its phylogenetic relationships.

**Ancistrocheles Krantz, 1962**

(Figs. 20–23)


**Revised generic diagnosis (female)**

Large mites (idiosomatic length of type species over 1000 μm) with the general characteristics of the family; dorsal shield (Fig. 23) lightly ornamented and with a dense sclerotized border, with only 26 pairs of smooth and distally pilose setae (z1 and r3 absent) and 20 pairs of “pores” (pz1 and pz5 absent). Sternal shield (Figs. 21, 22) lightly reticulate, weakly produced laterally, with three pairs of setae and two pairs of pores, with tanned posterolateral extensions as illustrated; epigynial shield rounded posteriorly, bordered by four small postepigynial platelets; metasternal shields absent, sternal setae 4 and associated pores in the soft integument behind sternal shield; ventrianal shield (Fig. 21) oblong-ovoid, bordered anteriorly and laterally by a dense sclerotized rim, shield carrying only one pair of preanal setae (Jv3); cribrum marginal, comprising several rows of spicules that extend laterally in a wide band to the cibarial gland openings; with a pair of large, distinctive glandular atria posterior to the stigmata and laterad from the postcoxal solenostomes; metapodal shields small, indistinct; peritrematic shields free, peritremes extend only to the level of coxae I, peritrematic extremities toothed. Chelicerae (Fig. 20) dentate, without a bidentate tooth on the movable digit; paraxial arthrodial brush over half the length of movable digit, dorsal chelical seta simple, tip of fixed digit missing in available material; corniculi narrow, extending well beyond the palp trochanters. Legs without spurs, tarsi II–IV with short, broad paradactyls which may be weakly divided distally; genu IV with six setae.

**Male and immature stages:** Unknown.

**Remarks on the original generic description**

The original description of *A. bregetovae*, the type and only species of Ancistrocheles, was based on two female specimens collected in 1937 from the mouthparts of an adult secondary screwworm Cochliomyia macellaria (Fabr.) in Arizona. The specimens, part of a National Museum of Natural History collection (USNM 37-8263), may have been mounted in polyvinyl alcohol or a similar medium in that they are overly cleared and quite distorted. The redescription above is based almost entirely on a third specimen taken from an unidentified fly intercepted by quarantine officials at the Port of New Orleans (LA) in 1966 from a ship cargo that originated in Brazil. I dissected the specimen and mounted it in Hoyer’s medium, and it proved to be of sufficiently good quality to warrant a reevaluation of the original diagnosis. Verification of the deficient dorsal setal pattern (Fig. 23), addition of postepigynial platelets, missing leg setae, and opisthogastric gland openings (Fig. 21), and the recognition of border sclerotization on the sternal and ventrianal shields (Figs. 21, 22) have provided important adjuncts to the original generic description of Ancistrocheles.

Special mention should be made of the condition of the cheliceral fixed digit which, based on examination of all four chelicerae of the two available specimens, I described as being abbreviated (Krantz, 1962b). The fixed cheliceral digits of the specimen intercepted from Brazil were likewise found to be abbreviated, but their appearance (Fig. 20) strongly suggests accidental breakage at the time of removal from the fly host rather than a natural condition. That identical breakage occurred on all three specimens was coincidental, but it suggests that attachment of Ancistrocheles to its host is so tenacious that forcible removal is likely to damage the chelae.

24 — Epistome of female. 25 — Chelicera of male (antiaxial).
Relationships within the family

Like Aethosoma and other genera discussed earlier, the intergeneric relationships of Ancistrocheles are not clear. Aside from the genus Aethosoma (with which Ancistrocheles shares few other characters), pronotal setal deficiencies are unknown in the Macrochelidae. Postepigynial platelets (Fig. 21) are typical of both the opacus and carinatus species groups of Macrocheles (Hyatt & Emerson, 1988), but only the opacus group also shares with Ancistrocheles a posteriorly rounded epigynial shield, a greatly reduced ventrianal shield and, in most known species, paranal setal deficiencies. Unlike A. bregetovae, however, the cribrum of opacus-group species has distinctive paranal extensions, typical of many edaphic and mammal-associated macrochelids. The presence of sclerotized borders on the posterolateral angles of the sternal shield of A. bregetovae (Fig. 22) is singular, but the dense, tanned margins of the ventrianal shield are reminiscent of those in some species of Holostaspella (Krantz, 1967) and of Trigonholaspis (see below), in which the extent of extrashield tanning (Fig. 26) may be related to the age of the specimen.

Based on the original collection of A. bregetovae from a muscoid dipteran (Krantz, 1962b), and the more recently acquired specimen from “a fly” in Brazil, it may be that A. bregetovae, like M. muscaedomesticae (Scop.) and certain members of the subbadius and glaber species groups of Macrocheles, has established phoretic ties with dipteran rather than coleopteran or vertebrate hosts (Petrova, 1964). However, there is little evidence suggesting that Ancistrocheles shares either of the phylogenetic lineages hypothesized for these groups (Krantz, 1998). A broader analysis will be necessary to reveal its true relationships.

Trigonholaspis Vitzthum, 1930
(Figs. 24–27)

Trigonholaspis Vitzthum, 1930: 300. Type species: Trigonholaspis salti Vitzthum, by original designation.

Revised generic diagnosis

Female with general characteristics of the family. Pronotum thickened and appearing strongly gibbous in lateral view; dorsal shield (Fig. 27) smooth or variously ornamented, often with crenulated margins, generally abbreviated and not covering the lateral and posterior portions of the dorsum (T. amalthaeae Vitzthum is an exception), rounded or weakly truncate posteriorly; with 30 pairs of setae which may be simple, distally spatulate, broadly spinose, cylindrical or stubby, with four pairs of J setae (J1, J2, J3, J5), J1–3 inserted more or less behind one another; dorsal pore pattern mostly obscure in available material. Sternal shield (Fig. 26) broader than long, typically with an anteromedian notch to accommodate the tritosternal base, variously ornamented, anterolateral angles of shield extend well beyond insertions of coxae I; metasternal shields free, ventrianal shield often with distinctive sclerotized perianal extensions on which numbers of opisthogastric setae may be inserted; anal opening medially or posteriorly situated in shield, cribrum marginal, well developed; peritremes free, extending anteriorly and laterally to the level of setae j2. Deutosternal groove of gnathosomatic base broad, shallow, with five rows of small teeth; proximal apotelic tine of palptarsus usually reduced in size, corniculi conical and extending to level of palpfemora; movable cheliceral digit with one or two medial teeth, bidentate tooth absent; epistome trifid, base with serrated margin, lateral flags long and narrow, ornamented with spikes or spines on the internal angles as illustrated (Fig. 24). Legs I shorter than or subequal in length to the thickened and strongly sclerotized legs II–IV; ambulacral paradactyls subequal in length to claws, undivided distally, genu IV with seven setae.

Male similar to female except for the following: dorsal shield more or less covers the entire dorsum; with a holoventral shield that may have a weak suture between the genitiventral and ventrianal portions; seta v1 of femur I modified into a strong spur, movable cheliceral digit (Fig. 25) with a sigmoid spermadactyl.

Immature stases: Inadequate material on which to base a description.
Species currently included in the genus: *Trigonholaspis salti* Vitzthum (type species), *columbiana* Vitzthum, *trigonarum* Vitzthum, *amaltheae* Vitzthum.

Remarks on the original generic description

Vitzthum (1930) erected the genus *Trigonholaspis* to accommodate four new species of New World macrochelid nest associates of meliponine bees that share the following characters: 1) legs I shorter than legs II; 2) coxae I in close contact with the anterolateral margins of the sternal shield; and 3) with an anteromarginal excavation of the sternal shield. Krantz (1962b) redefined the genus on the basis of dorsal shield configuration and dorsal/ventral setal condition, erecting the genus Grafia to accommodate Vitzthum’s *T. columbiana*, *trigonarum*, and *amaltheae*. Recent acquisition of specimens identified as *T. salti* and *G. trigonarum* and recovery of some five new species referable to *Trigonholaspis* or Grafia from stingless bee nests in Brazil and Panama has provided a basis for reevaluation of these genera.

While clear setal and shield differences exist between *Trigonholaspis salti* and the three species of *Trigonholaspis* assigned to the genus Grafia (Krantz, 1962b), a variety of intermediate conditions (especially in setal form) have been found in the newly discovered material that cloud the separation between the two taxa. At the same time, I found that *Trigonholaspis* and Grafia share two highly unusual morphological traits: the presence of setae J1, J2, and J3 on the dorsal shield, and a strongly gibbous (humped) dorsum. It is on the strength of these characters that I have relegated the genus Grafia to synonymy with *Trigonholaspis* in the present treatment.

Relationships within the family

Members of the genus *Trigonholaspis* possess a number of morphological characters typical of *Macrocheles* s. lat., but they lie well outside the spec-
trum of species groups currently considered referable to that genus (Hyatt & Emerson, 1988; Krantz, 1998). Like Aethosoma, another nidicolous macrochelid taxon with strong ties to eusocial Hymenoptera (see above), Trigonholaspis species display a set of unusual morphological traits that are of uncertain functional significance and offer little or no intuitive information as to its phylogenetic position. Like Aethosoma, another nidicolous macrochelid taxon with strong ties to eusocial Hymenoptera (see above), Trigonholaspis species display a set of unusual morphological traits that are of uncertain functional significance and offer little or no intuitive information as to its phylogenetic position. Other characters are less bizarre but likewise of questionable value in establishing affinities; e.g. development of tanned shield borders and the state of cheliceral dentition/cribral development. The similarities between certain Trigonholaspis species, some nidicolous Holostaspella (e.g. H. sculpta Berlese), and Ancistrocheles bregetovae in development of a dense rim around the ventrianal shield is likely a convergence in which the degree of tanning may be a function of aging. Lack of a well developed bidentate tooth on the movable cheliceral digit (common to early derivative free-living macrochelid genera) coupled with lack of paranal cribral extensions (common to highly derived phoretic genera) is a dual deficiency seen in Trigonholaspis and certain other phoretic and non-phoretic macrochelid genera, including some Holostaspella species and three of the taxa treated above (Aethosoma, Synaphaspis, and Ancistrocheles). Cribral reduction in non-phoretic nidicolous taxa like Trigonholaspis and Aethosoma suggests that the intimacy of a eusocial nest situation equals or surpasses that of an insular non-nest field habitat such as dung, where the need for pheromonal signaling between sexes of phoretic macrochelid species is thought to be minimal (Krantz & Redmond, 1988). However, confirmation that Trigonholaspis shares an atypical cribral/cheliceral character state combination with a number of other macrochelid genera provides no obvious clues as to its broader relationships with these taxa.

GENERAL COMMENTS

The genera discussed in this paper share two interesting attributes: 1) all have singular morphologies that tend to cloud their genealogical relationships with other macrochelid taxa and with each other, and 2) all have been collected only rarely and (with the possible exception of Ancistrocheles) in highly specialized and restricted habitats. How specialized are these habitats? Aethosoma and Trigonholaspis are restricted respectively to the nests of army ants and stingless bees, eusocial insects whose nests do not invite casual invasion (or inspection) by non-residents. Known species of Lordochelus and Synaphaspis have been found only in association with elephant or rhinoceros dung and usually in association with insects, presumably scarabaeine beetles (DeSaeger, 1956). Dung is an insular substrate, in some ways as specialized as the nest habitat but presumably not as restrictive. While Frey (1961) found that crossover of onthophagine scarab species occurs between elephant, rhinoceros, and buffalo excrement in the Congo, Halfifier & Matthews (1966) observed that there is considerable specialization for particular animal excrements among coprophagous Scarabaeinae. For example, distribution of certain Heliocoris species in the Ethiopian and Oriental regions is closely linked to that of the animals on whose dung they specialize. Macrochelid mite associates of these and other scarabaeine dung beetles tend to be similarly restricted, especially in warm temperate and tropical realms (Krantz, 1967a, 1991; Krantz et al., 1991).

The two specimens of Ancistrocheles bregetovae in the type series were taken from the mouthparts of Cochliomyia macellaria, in Arizona, and an additional specimen was later collected from an unidentified fly during quarantine inspection of a ship from Brazil. C. macellaria is a New World pest of man and animals whose larva feeds in carrion or excrement and has been implicated in the transmission of diseases to man and animals (Harwood & James, 1979). The presumption would be that A. bregetovae is a predator in the larval habitat and utilizes the adult fly for phoretic dispersal. However, the fact that C. macellaria is commonly collected while the mite is virtually unknown suggests that A. bregetovae is not normally phoretic on C. macellaria or on other fami-
liar New World fly species. Its rarity suggests that it may be an incidental phoretic in a specialized habitat—perhaps in soil and litter beneath large animal carcasses—or that it may have a preference for a phoretic host other than synanthropic flies.

In an earlier paper (1991), I noted that dung beetles occupy insular multidimensional niches, or hypervolumes, that may provide the mechanism for isolation of their phoretic mite associates. This assumption also would apply to the macrochelid genera *Aethosoma*, *Trigonholaspis*, *Lordocheles*, and *Synaphaspis*, whose circumscribed universes reflect the high degree of niche specialization of their insect associates. The nature of the habitat and host relationships of the genus *Ancistrocheles* remains moot pending additional collections of *A. bregetovae*.

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**References**


Due to a printing error, a portion of text was inadvertently lost from the description of *Proctotydaeus* (*Oriolella*) *polonicus*. The first paragraph of page 39 should be replaced by:

Ventral surface (Fig. 2A) more strongly striated than dorsal surface; striae run longitudinally between setae (1a)=(pt), (3a)=(mta), (4a)=(mtb) and (agl); striae form a circle anterior to longitudinal genital opening. All ventral setae, together with aggenital ones, similar in shape (slender, slightly serrate), but different in length: ag2, ag3 and ag4 longer (19–22) than 1a, 3a, 4a and ag1 (about 16).

Legs. Tarsus I (Fig. 3A, 3B): length 18, width 12. Setae: ft 9.5, ft' 67, (tcζ) 87, pζ 60, p''ζ 64, (u) 3.5, ωI 6. Seta ft relatively small, slender and slightly serrate. Setae: ft''ζ, (tcζ) and (pζ) distinctly serrate, but their tips without serration for about 1/10 of total length. Setae (u) minute and cleft, inserted close to (pζ). Solenidion ωI shorter than half length of tarsus I, not protruding beyond anterior margin of segment. Tibia I (Fig. 3A). Length: 23, width: 12. Setae: ft 17, ft' 18, v' 52, k'' 2.8. Solenidion ωI 4. Seta v' visibly serrated, (l) slightly serrated, famulus k'' forked. Tarsus II (Fig. 4A): solenidion ωII 3.5. All leg setae distinctly serrate. Genu III, genu IV and femur IV each with apophysis. Apophysis on femur IV broad and blunt (Fig. 1), situated in dorso-paraxial position. Genual apophyses spur-like and situated dorso-antiaxially.

On page 105 (first paragraph, last sentence), the generic name *Holostaspella* was inadvertently used in place of *Holocelaeno*, and the reference citation that immediately follows should read 1967a, rather than 1967.