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Genus-level revision of the Heterozerconoidea (Parasitiformes: Mesostigmata)

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Abstract

The genera of Heterozerconoidea are revised based on a species-level analysis of relationships in the group. The family Discozerconidae in its current state may be paraphyletic. Diagnoses for the genera are updated, and a catalog of all described species is provided. As part of this re-analysis two new genera, *Amyzozercon* and *Ecuazercon*, and four new species are described, and a key to the genera is provided. Possible evolutionary implications of the proposed set of relationships in terms of biogeography and the evolution of podospermy are discussed.

Key words: Heterozerconidae, Discozerconidae, phylogeny, Myriapoda, mating system

Introduction

The mite superfamily Heterozerconoidea currently includes two families, Heterozerconidae Berlese and Discozerconidae Berlese (Lindquist *et al*. 2009a). Members of both families are generally associated with Myriapoda, although with different subclasses: Discozerconidae mostly with centipedes (Chilopoda), Heterozerconidae mostly with millipedes (Diplopoda). Within Heterozerconidae, the two species of *Amheterozercon* Fain are exceptional in that they are parasitic on vertebrates (snakes, amphisbaenids). Some additional records are from soil and litter or termite nests. Morphologically the two families share the presence of a pair of large opisthogastral suckers, although the structure of these suckers appears to be different among the two families (Domrow 1956; Trägårdh 1911).

Described taxonomic diversity in the Heterozerconoidea is small. The family Discozerconidae currently contains four species in three genera. *Discozercon* Berlese, with two described species, has been collected from scolopendrid centipedes in Indonesia (Berlese 1910a;1914), Australia (Domrow 1956), and the Philippines (Raros pers. comm.), while the single described species of *Discomegistus* Trägårdh is found on similar hosts from the Caribbean (Trägårdh 1911). The third genus, *Berzercon* Seeman & Baker, was recently described from a species associated with carabid beetles in New Zealand (Seeman & Baker 2013). The Heterozerconidae are more diverse. In the most recent revision of the family, Fain (1989) recognized five genera: *Heterozercon* Berlese from South and Central America (Berlese 1888; 1892; Fain 1989; Silvestri 1903) (3 described species), *Amheterozercon* from South America (Fain 1989; Finnegan 1931; Flechtmann & Johnston 1990; Lizaso 1979) (2 species), *Afroheterozercon* Fain from Africa (Berlese 1924; Fain 1988; 1989; Klompen *et al*. 2013) (10 species), *Asioheterozercon* Fain from southeast Asia (Fain 1989) (1–2 species), and *Maracazercon* Fain from South America (Fain 1989) (1 species). Not included in this list is the genus *Allozercon* Vitzthum described from a single specimen collected on Java (Vitzthum 1926). The specimen is lost, and Fain (1989) listed the genus as unrecognizable. This seems excessive, given that the available characters for this genus correspond with those listed as diagnostic for *Asioheterozercon*. *Asioheterozercon* has therefore been synonymized with *Allozercon* (Gerdeman *et al*. 2018). In addition, two genera have been added since Fain's revision, *Narceoheterozercon* Gerdeman & Klompen from North America (Gerdeman & Klompen 2003) (1 species), and *Philippinozercon* Gerdeman *et al*. from the Philippines (Gerdeman *et al*. 2018) (1 species).

Heterozerconidae are of some general interest because of the presence of podospermy. Podospermy and tocospermy are the two main sperm transfer modes in Mesostigmata (Athias-Henriot 1969). In tocospermy, the presumed basal condition, males have unmodified chelicera which they use to transfer a discrete spermatophore to the primary genital opening (ovipore) of the female, in podospermy male chelicera are modified to include a sperm transfer organ, the spermatodactyl. Associated with this modification in the male, females may have secondary genital openings or sperm induction pores (solenostomes). Sperm transfer involves males using their spermatodactyl to transfer sperm to the sperm induction pores rather than to the ovipore (Krantz & Wernz 1979). Both Discozerconidae and Heterozerconidae were listed as having a spermatodactyl (Di Palma *et al*. 2008; Evans 1992) but this is incorrect (Lindquist *et al*. 2009; Seeman & Baker 2013). The so-called spermatodactyl on the movable digit of discozerconid males (and females!) consists of thin strap-like cheliceral excrescences (Figs 1–3, red arrow), unlikely to function in sperm transfer. Similar excrescenses are present in adult Heterozerconidae.

Modification of the chelicera in the male to a spermatodactyl has evolved at least three times in Mesostigmata, in Trigynaspida (Diplogyniidae, Schizogyniidae), in Gamasina (Dermanyssina), and in Sejina *s.l.* (Heterozerconidae) (Walter & Proctor 2013). The three syndromes are distinct: in the Trigynaspida the spermatodactyl appears to be a modification of complex structures already present on the chelicera of the female, while in Heterozerconidae and Dermanyssina the females show no distinct cheliceral outgrowths or modifications. In both Trigynaspida and

Dermanyssina the spermatodactyl is situated on the movable digit, while in Heterozerconidae it is on the fixed digit. Third, and most relevant for this study, secondary genital systems in the females have only been observed in Dermanyssina and Heterozerconidae.

To study the origin and evolution of the syndromes it would be helpful to have intermediate conditions. Mites in the family Heterozerconidae may provide such a system for at least one aspect, the presence or absence of the secondary genital openings in the females. All heterozerconid males have a spermatodactyl but females do not always have secondary genital openings. Di Palma *et al*. (2015) showed that *Narceoheterozercon ohioensis* Gerdeman & Klompen and an unidentified species of *Heterozercon* had secondary genital openings in the female, but an unidentified species of *Allozercon* did not. This raises the question whether the absence of secondary genital openings in *Allozercon* females concerns an early stage in the evolution of podospermy or whether it is a loss from a more "complete" version of podospermy. In this context it is worth considering a hypothesis by Walter & Proctor (2013) who proposed that evolution of secondary genital openings in females might be the result of intersexual conflict. In this view, secondary genital openings might have evolved to help restore female control over fertilization. Implicit in this hypothesis is the idea that males, in the absence of secondary genital openings in females, may use their spermatodactyls to e.g. pierce the female vaginal wall and thus gain a shortcut to the ovaries. To test this hypothesis an adequate understanding of systematics of the group in question is required, an understanding currently not available for Heterozerconoidea. Another issue requiring a good phylogeny concerns evolution of the considerable diversity in spermatodactyl structure within Heterozerconidae.

Availability of new collections from India, Laos, Malaysia, the Philippines, Thailand, Belize, Brazil, Colombia, Costa Rica, Cuba, Ecuador, Honduras, Mexico, Nicaragua, and the United States allowed a re-evaluation of existing generic concepts in the Heterozerconoidea with description of two new genera, and second, the first comprehensive analysis of genus level relationships within that lineage. The latter analysis allows some preliminary hypotheses on the evolution of the spermatodactyl and of podospermy in Heterozerconidae.

Materials and Methods

Specimens were cleared in 55% lactic acid and slide mounted in Hoyer's medium (Walter & Krantz 2009). Specimens in more recent collections were imaged in cavity slides before dissection of the mouth parts and slide mounting. Specimens were studied with phase contrast (PC) and differential interference contrast (DIC) microscopy. Descriptive drawings were made with a camera-lucida on a Zeiss Axioskop® (White Plains, NY) compound microscope or based on images generated using the automated Z-stacking feature of the Nikon NIS Elements package on a Nikon Eclipse 90i® (Melville, NY) compound microscope with a PC controlled Ds-5M-U1 digital camera. Line drawings were created using Adobe Illustrator 2023® (Adobe Systems Incorporated, San Jose) based on scans of the drawings or on the photographs. Measurements were made using the Nikon NIS Elements package. All measurements are presented in micrometers (μm) in the format: average (standard deviation) and are summarized in Tables 3 and 4.

Idiosomal chaetotaxy follows the system of Lindquist & Evans (1965), with modifications for the caudal region as presented by Lindquist (1994) and Lindquist & Moraza (1998). Setal nomenclature for non-tarsal leg segments follows Evans (1963a), for tarsi II–IV Evans (1969), and for the pedipalps Evans (1963b). Where relevant, states for particular characters are indicated in the format character x.y, where "x" and "y" refer to, respectively, the character number and the state number as listed in Table 1.

Abbreviations for specimen depositories: BMNH: Natural History Museum, London, United Kingdom; BUW: Biozentrum der Universität Würzburg, Würzburg, Germany; CASEnt: California Academy of Sciences, San Francisco, California, U.S.A.; CNAC: Colección Nacional de Ácaros, Instituto de Biología, Universidad Nacional Autoìnoma de Mexico, Mexico City, Mexico; FMNH: Field Museum of Natural History, Chicago, Illinois, U.S.A.; IBSP: Instituto Butantan, São Paulo, São Paulo, Brazil; ICN: Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Bogotá, Colombia; IRSNB: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; ISZA: Berlese collection, Istituto Sperimentale per la Zoologia Agraria, Firenze, Italy; OSAL: Ohio State University Acarology Collection, Columbus, Ohio, U.S.A.; RMCA: Royal Museum for Central Africa, Tervuren, Belgium; UPLBMNH: Museum of Natural History, University of the Philippines Los Baños, College, Laguna, Philippines.

Listing of material examined for new species follows the following format: locality, collecting date, collectors, source, and collection event number, followed by a listing of the number and instar of specimens on a given slide

and the unique slide identification number (usually, but not always, OSAL). Host identification data, when available, are included in "source".

The data matrix was constructed in vSysLab (Johnson 2010) and data were analyzed using TNT (Goloboff & Morales 2023) and PAUP* vs 4.0a 169 (Swofford 2002) For each analysis uninformative characters were removed. Analyses were conducted using heuristic searches, in TNT using New Technology Search with Tree Fusing (set to find the minimum tree length at least 10 times), in PAUP with a minimum of 10 reps, and no limits on the MaxTrees setting. Lineage support was measured by jackknife (JK) analysis (Lanyon 1985), in TNT with 100 replicates and symmetric resampling (P=33) (default settings), in PAUP using the settings: 37% deletion, emulate "JAC" resampling, 1,000 replications, "random addition sequences" = 1, and "hold trees" = 2 (Freudenstein *et al*. 2004). The complete data matrix can be accessed at https://morphobank.org/permalink/?P4664.

Phylogenetic analysis

Taxa

Outgroup selection. Heterozerconoidea are fairly easy to recognize (see below), but an assessment of relationships with other Mesostigmata based on morphology has proven to be more elusive (see e.g. Lekveishvili & Klompen 2004). As a result, our understanding of relationships between the Heterozerconoidea and other Mesostigmata is in flux. Early studies placed them with Trigynaspida (Johnston in Norton *et al*. 1993), or, more commonly, ignored the group. In contrast, limited molecular analyses of relationships among the main lineages of Mesostigmata consistently group Heterozerconoidea with or within Sejina (families Ichthyostomatogasteridae, Reginacharlottiidae, Sejidae, Uropodellidae) (Klompen 2000; Klompen *et al*. 2007; Lekveishvili & Klompen 2004), and in the absence of convincing evidence to the contrary, we will accept that arrangement for this study. Therefore, a sejid, *Sejus carolinensis* Lekveishvili & Klompen, and an ichthyostomatogasterid, *Asternolaelaps* sp., were used as primary outgroups, with representatives of the Uropodina (*Uropoda orbicularis* Müller), Trigynaspida (*Asternoseius* sp.), and Gamasina (*Gamasiphis* sp.) added as secondary outgroups in some analyses.

Ingroup selection. All 20 species of Heterozerconoidea described after 1940 are included. In the absence of actual specimens, the older Berlese species could not be coded for more than a handful of characters, making inclusion in the analysis unproductive. Descriptions of the Vitzthum species (*Allozercon fecundissimus* Vitzthum, *Heterozercon elapsus* Vitzthum) are slightly more complete, and were included, with the added goal of testing the hypothesis that these species cluster with other specimens from S.E. Asia, and that the generic designation *Allozercon* can therefore be applied to the entire lineage. Even so, the amount of missing data for these two "older" species is substantial, and analyses were executed with and without the Vitzthum species. In addition to previously described species, 26 undescribed taxa are included in the analysis to make sure results are as general as possible. The working hypothesis is that specimens from different areas / islands represent different species and are thus included as separate OTU's. This hypothesis will of course require follow-up testing.

Character selection and discussion

The analysis presented is based solely on morphological data. Some DNA sequence data for Heterozerconoidea are available, but that data set is still very incomplete, and insufficient to assess genus level relationships in the families. Similarly, unless stated otherwise, all characters refer to states in the adults. The immatures are likely to provide a rich source of characters (Gerdeman *et al*. 2018), but the number of taxa with known immatures (four, with data for two of these incomplete) is once again quite small and unlikely to help in this analysis.
The complete list of characters scored is presented in Table 1. The discussion in this section is limited to clarifications of state designations and explanations of hypotheses of homology.

Gnathosoma

Spermatodactyl shape (characters 6–7). The spermatodactyl in Heterozerconidae is quite variable in shape but shows several similarities across the family. 1) It is always situated on the fixed digit; 2) it is often quite large rela-

tive to the size of the remaining fixed digit (possible exception in most species of *Afroheterozercon*); 3) it includes distinct coiling elements (Di Palma *et al*. 2008), usually in both the sperm duct and the external structure, but sometimes (e.g. *Narceoheterozercon*) appearing to be limited to the sperm duct. If external, the most common condition seems to be three coils, with the two basal coils somewhat compressed and the terminal coil stretched and often highly modified. In *N. ohioensis*, the only species for which the spermatodactyl has been studied in detail, the sperm duct consists of a groove / gutter closed off by overlapping flaps, rather than an internal tube (Di Palma *et al*. 2008). Comparison of structures across the family suggest a few relatively distinct types:

- Straight (character 7.0). With a strong external coil, straight or slightly curved, and a pointed, well-sclerotized tip (*Amyzozercon* n. gen., *Ecuazercon* n. gen., *Maracazercon*, *Al*. (*Allozercon*), *Al*. (*Philippinozercon*), *Afroheterozercon spirostreptus* Fain, *Narceoheterozercon* ex Alabama-C) (Figs 4–7, 16–19). There can be strong variability within this group in e.g., the length of the cheliceral digits (compare Figs 16–17 with Figs 18–19).
- Flaccid (character 7.1). Like the straight type, but terminal coil with a thin flap-like roundish tip (*Amheterozercon*, most *Heterozercon*) (Figs 8–9, 14–15).
- Recurved (character 7.2). Elongate, hooked backward, and with indistinct external coiling (most *Narceoheterozercon*) (Figs 10–11).
- Compressed (character 7.3). Highly coiled but also highly compressed (length often subequal to, or less than, the length of the remaining fixed digit (most *Afroheterozercon*, *Heterozercon* ex Cuba) (Figs 12–13).

Some taxa show intermediate conditions and were coded as a mix of more than one type.

Axial outgrowths of the palp trochanter (characters 8–9). Axial outgrowths of the palp trochanter are found in many Mesostigmata, but development of such structures in some Heterozerconidae is especially strong. If present, palp trochanter seta *v2* is always included on the outgrowths, but it is often reduced in size, with the base almost disappearing (Figs 22, 37). While usually membranous, the outgrowths are solid in females of *Amheterozercon* (Fig. 29; red arrow) and males of *Al*. (*Allozercon*) (Fig. 40; red arrow). Development of the palp trochanteral outgrowths often differs between females and males.

Palp setation (characters 10–14). The setal addition pattern in Heterozerconidae generally follows the pattern outlined by Evans (1963b) for Gamasina and Sejina for most segments. Exceptions include the femora and tarsi, and in the Asian taxa, the genua. The larval setal complement of each femur is standard, with setae *al*, *ad1*, *pd2*, and *pl*, but two setae are added in the protonymph, *ad2* (an acceleration of a seta added in the deutonymphs of Gamasina) and *pd1* (character 10) a unique addition for Heterozerconidae) (Gerdeman *et al*. 2018; Gerdeman & Klompen 2003). Notably, *pd1* is not added in Discozerconidae (Fig. 20). The femoral setae in adult Heterozerconidae are often thick and spine-like (not in *Amyzozercon*) (Fig. 21 vs. 22; character 11)). The genual setation of the larva includes setae *al1*, *ad1*, *ad2*, *pd1*, and *pl*, with seta *al2* added in the deutonymph (Fig. 21), the standard pattern for many Mesostigmata. However, in many *Allozercon* specimens from the Philippines and S.E. Asia, seta *al2* is never added (character 12), resulting in an adult setal complement of five. A further reduction is seen in *Al*. (*Philippinozercon*) which is diagnosed by the absence of seta *pl* on the palp genu of the adults reducing the setal complement to four (Fig. 22, character 13)). In Gerdeman *et al*. (2018) we were incorrect in noting a reduction to three setae. Seta *ad2* was mistakenly assumed to be absent. This seta is present, although often hidden behind the large palp femoral setae *ad1* and *pd1*. Interestingly, deutonymphs of *Al*. (*Philippinozercon*) have five setae on that segment (seta *pl* present), suggesting a loss of a previously present seta rather than loss of an addition (Gerdeman *et al*. 2018). The tibial setal complement in adults is 14 (same as the basic pattern for Gamasina and Sejidae), but the palp tarsal setation is often reduced relative to that in Gamasina and Sejina, in some taxa down to 9–12 (vs. 14–15) sensilla (character 14).

Subcapitulum (characters 19–25). The gnathosoma shows a few unique or at least highly unusual modifications. The lateral lips in Heterozerconidae (not Discozerconidae) are modified into somewhat trough-like structures, extending both anterior and posterior of the origin of the lateral lips (Figs 30, 32 LL, character 19), forming what Evans (1992) referred to as the "labella-like hypostomatic lobe". While the size of these "troughs" varies among heterozerconid genera, their presence appears constant, and constitutes an apomorphy for the family. Second, except for *Berzercon*, the cornicula in all Heterozerconoidea are entirely membranous (character 23), and often difficult to identify because elements of the membranous cornicula overlap with the large membranous extensions of the palp trochanters. A possibly related character in Heterozerconidae involves a pair of small structures on the hypostome

resembling setal bases (character 25), occasionally with some structure inside (e.g., Fig. 35, red arrow). Presence of an additional pair of setae on the hypostome would be highly unusual, but they may be associated with the cornicula, the bases of which are otherwise invisible. Salivary styli generally well developed (e.g., Fig. 38, inset).

Idiosoma

Dorsum, sclerotization. Dorsal sclerotization patterns in e.g. Sejina provide a wealth of characters (Lekveishvili & Klompen 2004), but in Heterozerconidae these patterns are largely invariant, with a single holodorsal shield covering a large part of the dorsum in most females (Figs 45–46), and all of it in most males (Fig. 47). The dorsal cuticle shows reticular patterning (Figs 48–50), although this can be indistinct in some individuals. Reticulation tends to be less prominent in the mid-dorsal region. Secondary sclerotization of areas not covered by the shields is common in older Heterozerconidae, with older adults often appearing to be fully encased in sclerotized cuticle. Notably, this secondary sclerotization appears in a distinct sequence following a fixed pattern. Structurally, primary shields and secondary sclerotization differ somewhat (secondary sclerotization tends to be "rougher" in appearance). The peritrematal shield may extend onto the dorsum but is never fused with the dorsal shield (Figs 46–47).

Setation (characters 28–32). The dorsal setal complement in Heterozerconoidea tends to be hypertrichous, with most or all setae minute (e.g., Figs 44, 47). Some Discozerconidae (e.g., Figs 43, 53–54), show a continuous row of highly modified, flattened, lateral setae and / or a number of very long, lateral, setiform setae (e.g., *Berzercon*, *Discomegistus*). Development of the lateral setae in Heterozerconidae is never that extensive. Within Heterozerconidae, variability appears restricted to three character systems: 1) the level of development of a single pair of median, antero-marginal setae, tentatively designated as *j1*; 2) the multiplication of medium to long setae in the *j1* position (both sexes) and development of a large number of antero-lateral margin setae into hooked spines (males only); 3) the presence of elongate setae postero-lateral on the opisthosoma.

System 1: several populations / species of Heterozerconidae show a pair of medium to long setae inserted anteriorly, either on the dorsal shield or anterior to it on unsclerotized cuticle (Figs 45–46). The designation of these setae as *j1* does not match the designation of any of the elongate setae in immature *Narceoheterozercon* (*j3*, *z4*, *z5*, *s4*, *s6* in Gerdeman & Klompen (2003)). Whether this mismatch suggests a true lack of homology or incorrect designations in either immatures or adults (or both) is unclear. Resolving that issue will require the study of immature development in additional genera of Heterozerconidae. Anterior dorsal setae *j1* in adults are often distinct, and of medium (10–30 μm) to long (>35 μm) length, but they are minute in other populations / species (character 28).

System 2. Fain (1989) listed the presence of a number (7–12) of medium to long setae in the *j1* position (Figs 48–49, character 29) and the presence of multiple (20–30) small, almost hook-like spines on the antero-lateral margin of the dorsal shield in males (Fig. 50, character 30) as diagnostic characters of his genus *Asioheterozercon*, all based on material from Malaysia. Both characters were observed in a few populations of *Allozercon* from the Visayas islands in the Philippines (Bohol, Leyte, Negros, Samar). However, they are absent in the remaining *Allozercon* populations examined and in all other genera. If present, the multiple medium to long setae setae in the *j1* position are much longer in females than in the corresponding males (Tables 3–4), and they are inserted anterior to the dorsal shield, not on the anterior margin of the shield as in males (see Fig. 48 vs. Fig. 49).

System 3: In addition to the standard set of many minute dorsal setae, adults of *Amyzozercon* and females of *Ecuazercon* have seven pairs of elongate setae on the posterior lateral part of the dorsum (character 32). Of these, two, designated as *Z2*, Z3, are always inserted on the shield. Setae *Z4* are inserted off the dorsal shield in females of *Amyzozercon*, but on the shield in males of that genus and in adults of *Ecuazercon*. The remaining four pairs of setae are inserted lateral or postero-lateral to the dorsal shield. These setae are tentatively designated as *s6*, *S1*, *S2*, and *S3*, all based on positional considerations (Figs 45, 55). Setae *S3* are generally inserted ventral in position. Notably, males of *Ecuazercon* do not retain the elongate marginal (*S*-) setae observed in the females. Instead, they show a small set of hook-like spines that are absent in females (Fig. 58). Whether these are homologous with the elongate setae in the females is uncertain. None of the remaining heterozerconid genera or any Discozerconidae show elongation of this set of posterior dorsal setae.

Venter (characters 33–79), sclerotization in Heterozerconidae. Ventral shields show considerable variability in Heterozerconidae, although a few characteristics are common. The sternal shield of females is always fragmented, with many characters referring to arrangement of the shield fragments and the distribution of setae across them

(characters 33–40, 42–43, 48–53). The endopodal shields are often well developed, fusing posterior to coxae IV with exopodal, peritrematal, and metapodal elements. The female genital shield is nearly always fused with all (Heterozerconidae) or part of (Discozerconidae) the ventral shield (possible exception *Berzercon*). This genitiventral shield is usually smooth with faint reticulation, rarely with strong cuticular patterning (Fig. 51; character 57). The shield is nearly always adjacent to the anal shield in the area between the suckers (exception *Amyzozercon*). It may or may not be fused to the anal shield, but a separation line is usually retained (character 66). If present, the suckers are inserted on the postero-lateral edges of the ventral shield. A final common element is formed by the presence of a narrow and transverse postero-marginal shield.

Opisthogastral suckers (character 63). The most used morphological character for Heterozerconoidea, the presence of a large pair of membranous suckers on the opisthogaster is coded as two independent changes. The suckers in Discozerconidae (Figs 53–54) are positioned anterior to the ventral shield segments and have a much more membranous structure than the suckers in (most) Heterozerconidae. The suckers in Heterozerconidae are positioned posterior to the ventral shield and are more solid (e.g. Fig. 57, OS). In this we follow Trägårdh (1911). While these two states may be homologous at some level, we currently lack evidence for this.

Chaetotaxy. As with the shield pattern, ventral setation patterns provide more diagnostic characters for genera and for analyzing genus-level relationships than dorsal patterns. Gerdeman & Klompen (2003) proposed the presence in the deutonymph of *N. ohioensis* of *st1–st5*, *Jv1*, *Jv2*, *Jv5*, *Zv2*, *Zv3*, paired paranal (*pa*), and unpaired postanal (*po*) setae. Some of these designations had to be changed based on the more broad-based analysis in this study. Comparison of setal complements across Heterozerconidae suggest that one pair of sternal setae is absent in most Heterozerconidae. We hypothesize that these are the metasternal setae, *st4* (character 41), because setae *st4* are the last ones to be added (in the deutonymph), and because setae *st4* are already very small in e.g., *Discozercon* (Fig. 53). Within Heterozerconidae, only *Amyzozercon* retains the addition of setae *st4* (Fig. 55). Second, the discovery of *Amyzozercon*, which lacks opisthogastral suckers, allowed a study of ventral setation patterns that is not complicated by the distorting effects of the suckers. Based on this we propose the presence of opisthogastral setae *Jv1*, *Jv2*, *Jv5*, *Zv2*, *Sv2*, and *Sv3* in all adult Heterozerconidae. Of these, setae *Jv1* and *Zv2* are positioned antero-lateral to the suckers, *Jv2* and *Jv5* anterior to the anus, and *Sv2* and *Sv3* lateral to the suckers. In the Asian populations (*Al.* (*Allozercon*), *Al.* (*Philippinozercon*)) setae *Jv5* have shifted insertion to a position posterior to the fusion line between the genitiventral and anal shields. We stress that homology with setae of the same designation in Gamasina is tentative, although homology across the Heterozerconidae seems well established. Setae *Zv3* are found exclusively in *Amyzozercon* where they are inserted in the position of the ventral suckers in the other genera (Figs 55–56; character 62). Adults of *Amyzozercon* may also have additional elongate ventral setae assumed to belong to the *S*, *R* or *Rv* series (Fig. 55). Such setae are absent in adults of the other genera. Some genera of Heterozerconidae show hypertrichy in marginal opisthosomal setae, accompanied by distinct modifications of setal shapes (e.g. Figs 59, 63, 65; character 77–78).

Finally, the narrow and transverse postero-marginal shield of Heterozerconidae often shows variable numbers of minute setae and three to four pairs of larger, and often quite distinct, setae. The latter setae are assumed to be dorsal in origin and are designated as *Z5*, *S5*, *R5* (and *R4*). This set of designations is compatible with the pattern and designations of elongate setae proposed for *Narceoheterozercon* deutonymphs (Gerdeman & Klompen 2003). The only differences are that in the deutonymph setae *Z5* remain dorsal, and setae *R5* in this study are designated as *S4* by Gerdeman & Klompen (2003). The shape and relative size of setae *Z5*, *S5* and *R5* (characters 74–75) are variable across Heterozerconidae (e.g., compare Figs 61, 67, 69).

Setal homologies with Discozerconidae are less clear, in part because the development of the opisthogastral shields is strikingly different from that in Heterozerconidae, featuring a long thin posterior extension of the genital shield, a narrow and elongate anal shield which divides the ventral shield in two, and strap-like extensions of the endopodal / peritrematal shield into the metapodal region. As noted above, the suckers differ not only in structure from those observed in Heterozerconidae, but also in position: anterior to the ventral shield remnants, rather than on the posterior edge of those shields. Notably, the sternal shield is fragmented (as in Heterozerconidae), and the number of opisthogastral setae in *Discozercon* and *Discomegistus* is identical to that observed in most Heterozerconidae, even if their distribution is different. The following homologies are proposed. A small pair of shields at the posterior edge of the sternal region, but anterior to the suckers, includes three pairs of setae and a pair of glands / lyrifissures. We designate these setae *st4* (very small), *st5*, and *Jv1*. Each ventral shield carries two pairs of setae whose bases appear largely fused. Given their position slightly anterior to the anus we designate them as *Jv2* and

Jv5. Three additional pairs of setae are situated on (*Zv2*), or near (*Sv2*, *Sv3*), the metapodal extensions of the endopodal/peritrematal shields (Figs 53–54). While these hypotheses can accommodate the ventral setation in *Discozercon* and *Discomegistus*, they fail to accommodate the same in *Berzercon*, a genus carrying two additional pairs of setae on the venter. A possible solution would be the displacement of setae *Z5* from the postero-marginal sclerite to the posterior part of the anal shield (flanking seta *po*) and presence of setae *Zv3* (as in *Amyzozercon*), but this leads to considerable positional inconsistencies. At this point it is not possible to present a well-supported hypothesis of homology for the ventral setation of *Berzercon* vs. Heterozerconidae.

Legs

Segmentation and shape (characters 81–82). Leg segmentation in Heterozerconoidea is similar to that in other Mesostigmata, with one exception: Heterozerconoidea show a distinct acrotarsus on legs I (Fig. 73), a phenomenon that is uncommon in other groups (present in deutonymphs of Parasitidae as well as in Ixodidae and Holothyrida, and some Sejina (Moraza 2005)). In terms of the shape of the leg segments, the character of tarsus and tibia I much narrower than the other segments of the leg, listed as diagnostic for *Asioheterozercon* by Fain (1989), proved to be inconsistent. Some *Allozercon* clearly show this state, but it is indistinct in many others.

Chaetotaxy (characters 83–101). Compared to Sejina, the setal complement in Heterozerconidae is notably reduced, especially for the anterior legs. Interestingly, *Berzercon* (Discozerconidae) retains seven leg setae that are lost in all other Heterozerconoidea. Within Heterozerconidae the leg setal complement is largely invariant, with only two setae on legs I and one each on legs II–IV variable among taxa examined (Table 2). On first glance, arrangements of these setae on a given segment may appear to be variable but they can easily be reconciled with the standard pattern.

Setal shapes (characters 102–114). In contrast to presence / absence of leg setae in Heterozerconidae, shape (and occasionally positional) changes are common. All genera of Heterozerconidae show a transformation on femora I of setae *av* from setiform to spines: large, curved spines in males of *Amyzozercon* and *Ecuazerccon* (Figs 73, 79) , straight spines in females of those genera and adults of all other genera (Figs 74, 80–86). Setae *pv* on femora I are usually smaller, but commonly spinose. Except for *Amyzozercon* and *Ecuazercon* femora I also show a shape change of setae *al1* and *al2* from from setiform to distinct spines and positionally from anterolateral to almost ventral (e.g. Fig. 84) . All these changes are found in both males and females, although they may be slightly less pronounced in females (see Figs 73 vs. 74).

The most spectacular changes relative to e.g., *Sejus* or *Discozercon* are found on femora II of the males. Changes on femora II are most prominent in *Afroheterozercon*, *Allozercon* (incl. *Al.* (*Philippinozercon*)), *Heterozercon*, and *Maracazercon*. In these males some ventral and lateral setae tend to be inflated into strong spines, setae *pv1* only in *Afroheterozercon* (Fig. 92), setae *av1*, *pv1*, *al1* and *pl1* in the other three genera (Figs 93–96; characters 105–108). Interestingly, inflation of *al1* and *pl1* coincides once again with a shift of these setae to a more ventral position, a change resembling that of the *al* setae on femora I. These shape modifications are absent in the females. Independently, *Amheterozercon*, *Ecuazercon*, *Heterozercon*, and *Maracazercon* all show a transformation of seta *pl1* on tarsi II to a spine (Figs 89–90, 93–94, black arrows; character 111). This transformation is present in both sexes, but spines in males tend to be distinctly larger than in females (Tables 3–4). Shape variability of setae on legs III–IV is very limited, except for some setae on trochanters III.

Systematic relationships

The character matrix included 51 taxa (including 5 outgroups) and 114 characters (listed in Table 1). All multi-state characters were treated as unordered. The initial analysis used *Sejus* as primary outgroup and included *Asternolaelaps*, *Asternoseius*, *Uropoda*, and *Gamasiphis* as additional outgroups. It excluded the Vitzthum species *Al. fecundissimus* and *H. elapsus* and resulted in multiple trees of length (L) 331 (CI= 0.40; RI=0.75). A strict consensus tree featured a basal polytomy of four lineages: the three genera of Discozerconidae and the family Heterozerconidae. Closer examination revealed multiple possible arrangements of the discozerconid genera among the equally most parsimonious trees, including a minority of trees featuring a monophyletic Discozerconidae.

TABLE 1. Characters and character states in phylogenetic analysis of relationships in Heterozerconoidea.

Char. #	Character description and states
	GNATHOSOMA
1	Basal part of fixed digit in female: 0, stout, length width ratio 1–2 (Figs. 1, 3); 1, elongate, length width ratio 4–6 (Fig. 2).
2	Movable digit in adults: 0, without thin, strap-like extensions; 1, with thin, strap-like extensions (Figs. 1–3, red arrows).
3	Movable digit in female: 0, stout, digit length ~3 times basal width (Fig. 1); 1, elongate, digit length >6 times basal width (Figs. 2–3).
4	Inside movable digit female: 0, with distinct teeth; 1, with brush-like structure (Fig. 3, blue arrow).
5	Excrescences on male chelicera: 0, absent; 1, present, on movable digit; 2, present, interdigital.
6	Spermatodactyl on chelicera male: 0, absent; 1, present, on movable digit; 2, present, on fixed digit.
7	Spermatodactyl shape: 0, straight (Figs. 4–7, 16–19); 1, flaccid (Figs. 8–9, 14–15); 2, recurved (Figs. 10–11); 3, compressed (Figs. 12–13).
8	Axial outgrowth of palp trochanter in female: 0, absent; 1, small and membranous; 2, distinct and membranous (e.g., Figs. 22, 37); 3, distinct and sclerotized (Fig. 29, red arrow).
9	Axial outgrowth of palp trochanter in male: 0, absent; 1, small and membranous; 2, distinct and membranous (e.g., Fig. 42); 3, distinct and sclerotized (Fig. 40).
10	Seta *pd1* on palp femur: 0, absent; 1, present.
11	Setae on palp femur: 0, relatively thin, setiform (Fig. 21); 1, thick, spine-like (Fig. 22).
12	Seta *al2* on palp genu: 0, present; 1, absent.
13	Seta *pl* on palp genu: 0, present; 1, absent (Fig. 22).
14	Number of sensilla on palp tarsus: 0, 13–15; 1, 10–12; 2, 9.
15	Gnathotectum: 0, without prominent points; 1, with prominent points.
16	Anterior margin gnathotectum: 0, serrate 1, not serrate.
17	Overall shape of gnathotectum: 0, triangular; 1, curved; 2, blunt.
18	Sexual differentiation in gnathotectum shape: 0, absent; 1, present.
19	Lateral lips: 0, independent small flaps; 1, enlarged to form a trough (Figs. 23–42).
20	Posterior extension of lateral lips: 0, short, not extending beyond insertions of setae *hyp2* (Fig. 30); 1, long, extending distinctly past insertions of setae *hyp 2* (Fig. 32).
21	Distance from setae *hyp3* to *sc* vs. *hyp3* to *hyp2*: 0, distinctly smaller; 1, subequal; 2, distinctly larger.
22	Length setae *hyp2* relative to *hyp 3*: 0, subequal or slightly longer; 1, at least twice as long.
23	Cornicula: 0, solid; 1, membranous.
24	Membranous cornicula: 0, without a distal notch; 1, with a distal notch (Fig. 34, arrow).
25	Additional setal base-like structure on hypostome: 0, absent; 1, present (Fig. 35, arrow).
	IDIOSOMA
26	Pygidial shield in larva: 0, present; 1, absent.
27	Pygidial shield in protonymph: 0, present; 1, absent.
28	Anterior dorsal setae *j1* (Figs. 45–46): 0, long (> 35 μm); 1, medium long (10–30 μm); 2, minute (<5 μm)
29	Anterior dorsal margin in female: 0, with at most a single pair of elongate setae (*j1*); 1, with multiple medium to long setae in *j1* position (Fig. 48).
30	Antero-lateral margin of dorsal shield in males. 0, without distinct spines; 1, with small, hook-like spines (Fig. 49).
31	Median dorsal setae. 0, distinct; 1, minute
32	Posterior dorsal setae *Z2–Z4*. 0, elongate (Figs. 45–46); 1, minute (Fig. 47).
33	Areas near sternal seta *st1* in female. 0, sclerotized; 1, with soft cuticle.

.....Continued on the next page

TABLE 1. (continued)

Char. #	Character description and states
34	Sclerotized areas around sternal setae *st1* in female. 0, fused to each other (sometimes as a sternal shield); 1, fused to endopodal shields; 2, separate platelets. Inapplicable if area not sclerotized.
35	Sclerites of sternal setae *st1* and *st2* in female. 0, fused; 2, not fused. Inapplicable if area not sclerotized.
36	Sternal setae *st1* and lyrifissures *iv1* in female. 0, on separate shields or inserted in soft cuticle; 1, inserted on same shield.
37	Areas near sternal setae *st2* in female. 0, sclerotized; 1, with soft cuticle.
38	Sclerotized areas near sternal setae *st2* in female. 0, fused to genitiventral shield; 1, fused to endopodal shield; 2, separate platelets. Inapplicable if area not sclerotized.
39	Areas near sternal setae *st3* in female. 0, sclerotized; 1, with soft cuticle.
40	Sclerotized areas near sternal setae *st3* in female. 0, fused to genitiventral shield; 1, fused to endopodal shield; 2, separate platelets. Inapplicable if area not sclerotized
41	Metasternal setae *st4,* 0, present; 1, absent
42	Areas near sternal setae *st5* in female. 0, sclerotized; 1, with soft cuticle
43	Sclerotized areas near sternal setae *st5* in female. 0, fused to genitiventral shield; 1, separate from genitiventral shield. Inapplicable if area not sclerotized.
44	Sternal lyrifissures *iv1* in adults. 0, present; 1, absent.
45	Sternal lyrifissures *iv3* in female. 0, present; 1, absent.
46	Distinct curved, sclerotized ridge on anterior margin of genitiventral (or genitiventrianal) shield in the female. 0, absent; 1, present (Figs. 51, 67, 71).
47	Areas near sternal setae *st1* in male. 0, sclerotized shields or platelets; 1, dentate; 2, with soft cuticle.
48	Sclerotized areas near sternal setae *st1* in male. 0, fused to sternitiventral shield; 1, fused to endopodal shield; 2, separate platelets. Inapplicable if area not sclerotized.
49	Sternal setae *st1* and lyrifissures *iv1* in male. 0, on separate shields or inserted in soft cuticle; 1, inserted on same shield.
50	Sclerotized areas near sternal setae *st2* in male. 0, fused to sternitiventral shield; 1, fused to endopodal shield; 2, separate platelets or area not sclerotized.
51	Sclerotized areas of sternal setae *st2* and *st3* in male. 0, completely fused; 1, partially fused; 2, not fused.
52	Sclerotized areas near sternal setae *st3* area in male. 0, fused with sternitiventral shield; 1, fused with endopodal shield; 2, separate platelets or no shield.
53	Sclerotized areas near setae *st5* in male. 0, fused to sternitiventral shield; 1, not fused to sternitiventral shield.
54	Sternal lyrifissures *iv3* in male: 0, present; 1, absent.
55	Male genital opening: 0, mid-sternal, between coxae III; 1, anterior sternal, between coxae II; 2, presternal.
56	Male genital shields relative to tritosternum: 0, distant; 1, overlaying.
57	Sternitiventral area in male: 0, smooth; 1, with distinct ridges (Fig. 51).
58	Endopodal and sternitiventral shields in male: 0, not fused; 1, fused.
59	Metapodal and sternitiventral shields in male: 0, not fused; 1, fused (Fig. 64).
60	Level of fusion between metapodal and sternitiventral shield. 0, partial; 1, complete.
61	Posterolateral margin of metapodal shields in adults. 0, rounded; 1, “cut off”, with sharp angles (Figs. 71–72).
62	Setae *Zv3* in adults: 0, present; 1, absent.
63	Opisthogastral suckers in adults: 0, absent; 1, present, posterior to ventral shield, heterozerconid type; 2, present, anterior to ventral shield, discozerconid type.
64	Apodemes extending from opisthogastral suckers. 0, absent; 1, present, small but distinct knobs in posterior position (both sexes); 2, present, distinctly hook-shaped in anterior position (female only; Fig. 61).
65	Ventral shield area in adults: 0, with a single shield (e.,g. Fig. 59); 1, split into two or three shields (Figs. 53–54).

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TABLE 1. (continued)

Char. #	Character description and states
66	Sternitiventral and anal shields in male: 0, not fused; 1, fused, but line of fusion still visible; 2, fused, line of fusion not visible.
67	Setae *Sv2* in female: 0, inserted on genitiventral shield; 1, not inserted on genitiventral shield.
68	Setae *Sv2* in male: 0, inserted on sternitiventral shield; 1, not inserted on sternitiventral shield.
69	Setae *Sv3* in female: 0, inserted on genitiventral shield; 1, not inserted on genitiventral shield
70	Setae *Sv3* in male: 0, inserted on sternitiventral shield; 1, not inserted on sternitiventral shield
71	Insertion of setae *Jv5*: 0, anterior to ventrianal fusion line (Fig. 57); 1, posterior to ventrianal fusion line (Fig. 69).
72	Insertion paranal setae (*pa*): 0, at level of anus; 1, posterior to the anus; 2, anterior to the anus.
73	Postanal (*po*) seta: 0, of similar length as paranal (*pa*) setae; 1, less than 1/3 the length of paranal (*pa*) setae.
74	Setae *Z5* in male: 0, elongate (>40 μm); 1, medium but distinct (15–40 μm); 2, small to minute (<15 μm).
75	Setae *S5* in male: 0, elongate (>40 μm); 1, medium but distinct (15–40 μm); 2, small to minute (<15 μm).
76	Equally spaced long marginal setae: 0, absent; 1, present (Fig. 43).
77	Marginal opisthosomal setae: 0, all setiform; 1, some spine-like; 2, some flattened (Figs. 43, 53–54).
78	Shape of spine-like marginal opisthosomal setae: 0, peg-like (Figs. 59–60); 1, hook-like (Figs. 65–66); 2, anchor-like (Figs. 63–64). Inapplicable if setae not spine-like.
79	Lyrifissures *iv5* in male: 0, inserted near anterior margin of sucker; 1, absent.
80	Postero-marginal shields in female: 0, small, not extending lateral to opisthogastral suckers (Fig. 57); 1, wide, extending lateral well beyond opisthogastral suckers.
	LEGS
81	Tibiae and tarsi of legs I: 0, of similar width as the rest of the leg; 1, somewhat narrowed relative to the rest of the leg; 2, distinctly narrowed relative to the rest of the leg (Fig. 85).
82	Acrotarsus on legs I: 0, present (Fig. 73); 1, absent.
83	Femora I seta *ad3*: 0, absent; 1, present.
84	Femora I setae *v3*, *v4*: 0, present; 1, absent.
85	Femora I seta *pl2*: 0, absent; 1, present.
86	Genua I seta *ad3*, *pd3*: 0, present; 1, absent.
87	Tibiae I seta *ad2*: 0, present; 1, absent.
88	Tibiae I seta *ad3, pd3*: 0, present; 1, absent.
89	Tibiae I setae *av2*, *pv2*: 0, present; 1, absent.
90	Femora II seta *av2*: 0, present; 1, absent.
91	Femora II seta *pv2*: 0, present; 1, absent.
92	Genua II–III seta *ad3*: 0, present; 1, absent.
93	Genua II seta *pd3*: 0, present; 1, absent.
94	Genua II seta *pl2*: 0, present; 1, absent.
95	Tibiae II–IV seta *ad2*: 0, present; 1, absent. .
96	Tibiae II–IV seta *pd3*: 0, present; 1, absent.
97	Tibiae II–IV seta *pl2:* 0, present; 1, absent.
98	Femora III seta *v3*: 0, present; 1, absent.
99	Genua IV seta a*d3*: 0, present; 1, absent.
100	Genua III–IV seta *pd3*: 0, present; 1, absent.
101	Tarsi IV setae *av4*, *pv4*: 0, present; 1, absent.
102	Coxae I setae in male. 0, setiform; 1, distinct spines (Figs. 67–68).

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TABLE 1. (continued)

Char. #	Character description and states
103	Femora I setae *al1* and *al2* in male. 0, setiform, in anterolateral position; 1, spinose, in anteroventral position (Fig. 84).
104	Femora I seta *av* in male. 0, setiform; 1, large, curved spine (Figs. 73, 79); 2, large straight spine (Figs. 80–86).
105	Femora II seta *al* in male. 0, setiform; 1, spine and ventral in position (Figs. 93–96).
106	Femora II seta *pl* in male. 0, setiform; 1, spine and ventral in position (Figs. 93–96).
107	Femora II seta *av* in male. 0, setiform; 1, spine (Figs. 93–96).
108	Femora II seta *pv* in male. 0, setiform; 1, spine (Figs. 93–96).
109	Genua II seta *pv* in male. 0, setiform; 1, spine (Figs. 94–95).
110	Tibiae II seta *pv* in male. 0, setiform; 1, spine (Figs. 94–95).
111	Tarsi II seta *pl1*. 0, setiform; 1, spine (Figs. 89–90, 93–94).
112	Trochanters III seta *al* in male. 0, setiform; 1, distinct spine.
113	Trochanters III seta *av* in male. 0, setiform; 1, distinct spine.
114	Trochanters III seta *pl* in male. 0, setiform; 1, short, thick, rounded spine; 2, distinct spine, with pointed tip.

The lack of resolution for Discozerconidae prompted a second set of analyses with the sejine genera *Sejus* and *Asternolaelaps* as the only outgroups, thus enforcing the close relationship of Sejoidea and Heterozerconoidea recovered previously in molecular based analyses (Klompen 2000; Klompen *et al*. 2007; Lekveishvili & Klompen 2004). The various equally most parsimonious trees had a length of 296 (CI= 0.43, RI 0.75). A strict consensus tree strongly supported one of the solutions for relationships among the discozerconid genera recovered in the previous analysis. As the best option given the data this consensus tree (Fig. 97) is used as the basis for all following discussions.

At the family level, the family Discozerconidae sensu Seeman & Baker (2013) (= Discozerconidae *s.l.*), does not appear to be monophyletic, with *Berzercon* the sistergroup to a lineage including Discozerconidae *s.s*. and Heterozerconidae. Support for this arrangement was substantial (78–88% jackknife (JK) support) but it is worth noting again that alternative arrangements, including monophyly of Discozerconidae *s.l*., were among the optimal trees in the analyses including more outgroups. For that reason, we refrain from proposing a new family for *Berzercon* at this time. Additional data will be required to confidently differentiate between the alternative hypotheses of relationships among the discozerconid genera. In contrast to Discozerconidae, the family Heterozerconidae was monophyletic and well supported (92–96% JK). Finally, the status of the superfamily Heterozerconoidea showed some similarity with that of Discozerconidae *s.l.*: well supported in the analysis using only Sejina as outgroups (86–94% JK), less so (but still monophyletic) in analyses including more outgroups. In this case additional (molecular) data are available and, as noted above, the grouping of Discozerconidae and Heterozerconidae was well supported in DNA sequence-based analyses. One caveat to those molecular data, the number of taxa included in the molecular analyses was small, and these analyses did not include *Berzercon*. Still, overall support for monophyly of Heterozerconoidea is relatively strong.

At the generic level, most taxa examined grouped into lineages for which generic names are available. A few OTU's (e.g., *Narceoheterozercon* ex Alabama-C and *Heterozercon* ex Cuba) did not fit well within the previously defined concept of these genera, but they were closely related, and the generic concepts can be slightly broadened to accommodate these "oddities". However, two taxa in the family Heterozerconidae could not be accommodated in existing genera at all, and new generic concepts, *Amyzozercon* n. gen. and *Ecuazercon* n. gen, are proposed for these lineages (description below). Support for the individual generic groupings was quite variable. There was strong (>80% JK) support for the genera *Afroheterozercon*, *Amheterozercon*, *Allozercon*, *Al*. (*Philippinozercon*), and the core of the genus *Narceoheterozercon*. Support for the remaining species-rich genus, *Heterozercon*, was weaker (<50–62% JK), possibly affected by the fact that many terminal taxa in this genus were represented by very few specimens and / or a single sex (= high levels of missing data). Concerning the grouping of *Allozercon* and *Philippinozercon*, *Philippinozercon* itself was very well supported, but its recognition makes *Allozercon* paraphyletic. As a compromise we propose to re-classify *Philippinozercon* as a subgenus of *Allozercon*, *Allozercon* (*Philippinozercon*) n. comb.

TABLE 2. Leg chaetotaxy in adult Heterozerconoidea.

Taxon name	Leg I	Leg II	Leg III	Leg IV
Femur				
Sejus carolinensis	2 5/4 2	2 5/4 1	1 4/3 0	1 4/2 0
Berzercon	2 2/1 3/1 2	1 2/2 3/2 1	1 2/1 2/2 0	1 2/1 2/1 0
Discozercon	2 2/1 2/1 2	2 3/1 2/1 1	1 2/1 2/1 0	1 2(3)/1 2/1 0
Discomegistus	2 3/1 2/1 1	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Amyzozercon	2 3/1 2/1 1	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Ecuazercon	2 3/1 2/1 1	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Amheterozercon	2 3/1 2/1 2	2 3/1 2/1 1	1 2(1)/1 2/1 0	1 2/1 2/1 0
Heterozercon	2 3/1 2/1 2	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Narceoheterozercon	2 3/1 2/1 1	2 3/1 2/1(2) 1	1 2/1 2/1 0	1 2/1 2/1 0
Maracazercon	2 3/1 2/1 2	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Afroheterozercon	2 3/1 2/1 2(1)	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Allozercon	2 3/1 2/1 2	2 3/1 2/1 1	0 1/1 3/2 0	0 2/1 2/2 0
A. (Philippinozercon)	2 3/1 2/1 2	2 3/1 2/1 1	1 2/1 2/1 0	1 2/1 2/1 0
Genu				
Sejus carolinensis	2 3/1 3/1 2	2 3/1 3/1 2	2 3/1 3/1 2	2 3/1 3/1 1
Berzercon	2 3/1 3/1 2	2 2/1 2/0 2	2 3/1 2/0 2	2 3/1 3/0 2
Discozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 2/1 1(0)	2 2/1 2/1 1
Discomegistus	2 2/1 2/1 1*	2 2/1 2/1 1	2 2/1 2/1 (01)	2 2/1 2/1 1
Amyzozercon	2 3/1 2/1 1	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Ecuazercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Amheterozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Heterozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 2/1 2	2 2/1 3/1 1
Narceoheterozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Maracazercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Afroheterozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Allozercon	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
A. (Philippinozercon)	2 2/1 2/1 2	2 2/1 2/1 1	2 2/1 3/1 1	2 2/1 3/1 1
Tibia				
Sejus carolinensis	2 3/2 3/2 2	2 2/1 3/1 2	2 2/1 3/1 2	2 2/1 3/1 2
Berzercon	2 3/1 3/1 2	2 2/1 2/1 2	2 2/1 2/1 2	2 2/1 2/1 2
Discozercon	2 2/1 2/1 2	2 1/1 2/1 1	1(2) 1/1 2/1 1	1(2) 1/1 2/1 1
Discomegistus	2 2/1 2/1 1*	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Amyzozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Ecuazercon	2 2/1 2/1 2	2 1/1 2/1 2*	2 1/1 2/1 2*	2 1/1 2/1 2*
Amheterozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Heterozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Narceoheterozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Maracazercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Afroheterozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
Allozercon	2 2/1 2/1 2	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1
A. (Philippinozercon)	2 1/1 2/1 2*	2 1/1 2/1 1	2 1/1 2/1 1	2 1/1 2/1 1

() indicates an alternative (usually rare) condition in some specimens/species of the taxon.

* indicates a deviation from the "standard" pattern in Heterozerconidae.

TABLE 3. Comparative measurements (in µm) of newly described Heterozerconidae: females.

	Amyzozercon chocoensis average N=5	SD	*Ecuazercon cushuimensis* average N=5	SD	*Heterozercon calakmulensis* N=1	*Allozercon leytensis* average N=5	SD
Idiosoma: length	**652.4**	43.0	**819.4**	52.2	**834**	**1530.2**	152.4
Idiosoma: width	**560.2**	56.6	**807.6**	61.8	**698**	**1287.0**	185.6
Chelicera: length base of fixed digit	**281.0**	14.7	**160.6**	11.2	**176**	**346.4**	6.0
Movable digit: length	**62.6**	3.4	**118.4**	1.7	**100**	**208.6**	10.4
Movable digit: width	**8.8**	0.4	**8.4**	0.7	**7.5**	**18.3**	0.6
Palp: length	**179.6**	21.3	**209.4**	2.3	**216**	**395.8**	10.3
Palp: width at femur	**45.6**	4.0	**50.6**	0.9	**40**	**77.2**	9.4
Setae *j1*	**139.4**	8.2	**29.8**	3.1		**99.8**	15.4
Elongate setae nr *j1*						**96.4**	7.5
Seta *Z2*	**132.6**	8.6	**119.0**	6.0		**5.6**	0.9
Seta *Z3*	**128.0**	7.1	**103.2**	4.1		**8.6**	3.2
Seta *Z4*	**120.7**	5.0	**80.8**	1.9			
Seta *Z5*	**81.6**	10.5	**38.8**	4.1	**27**	**267.0**	17.1
Seta *s6*	**116.0**	11.6	**102.4**	4.4			
Seta *S1*	**123.8**	7.4	**84.4**	6.1			
Seta *S2*	**123.6**	19.4	**81.0**	8.0		**6.7**	1.5
Seta *S5*	**110.0**	5.1	**23.4**	2.3	**27**	**31.6**	5.1
Seta *R5*	**81.6**	4.8	**37.0**	5.1	**23**	**25.6**	3.0
Seta *st1*	**85.0**	8.9	**43.4**	1.5	**29**	**83.8**	11.3
Seta *st2*	**81.0**	4.0	**33.4**	2.1	**40**	**61.5**	3.4
Seta *st3*	**63.6**	3.0	**32.8**	2.6	**32**		
Seta *st4*	**54.0**	4.7	**NA**		**NA**	**NA**	
Seta *st5*	**45.8**	4.3	**18.0**	1.2	**32**		
Seta *pa*	**55.8**	9.1	**42.2**	2.0	**67**	**92.6**	21.1
Seta *po*	**57.6**	8.6	**31.3**	0.5	**49**	**54.4**	9.0
Sucker cavity, maximum width	**NA**		**138.2**	5.1	**133**	**246.0**	23.4
Sucker, maximum width	**NA**		**110.8**	8.5	**92**	**163.8**	28.6
Leg I: length	**969.4**	56.1	**995.2**	46.7	**995**	**2191.6**	103.8
Leg II: length	**655.6**	59.9	**661.0**	20.5	**658**	**1345.6**	74.2
Leg III: length	**666.4**	70.2	**682.2**	5.2	**699**	**1303.0**	71.0
Leg IV: length	**672.4**	64.6	**717.8**	24.1	**724**	**1369.0**	95.7
Femur I seta *al1*	**115.0**	7.6	**7.0**	2.4	**129**	**219.4**	11.7
Femur I seta *al2*	**74.6**	6.4	**6.3**	0.5	**74**	**229.8**	9.9
Femur I seta *v1*	**51.8**	4.4	**71.4**	2.8	**93**	**153.8**	11.8
Femur I seta *v2*	**38.2**	1.6	**99.0**	4.2	**89**	**112.3**	9.9
Genu I seta *av*	**109.8**	5.4	**108.8**	6.2	**137**	**179.0**	27.1
Genu I seta *pv*			**50.4**	3.3	**32**		
Femur II seta *al*	**30.0**	7.7	**32.4**	1.5	**34**	**45.0**	3.0
Femur II seta *pl*	**40.0**	3.1	**22.8**	3.0	**34**	**51.3**	5.7
Femur II seta *av1*	**56.4**	5.7	**49.0**	1.9	**45**	**75.0**	4.8
Femur II seta *pv1*: length	**63.6**	4.6	**54.6**	2.1	**51**	**75.4**	5.7
Femur II seta *pv1*: width			**4.5**	0.4	**5**	**9.3**	0.6
Genu II seta *av1*	**60.8**	5.3	**49.4**	1.9	**46**	**71.6**	2.9
Genu II seta *pv1*	**55.8**	5.4	**46.8**	3.3	**51**	**71.2**	4.3
Tibia II seta *pv*	**71.2**	4.9	**54.8**	2.3	**59**	**82.0**	4.0
Tarsus II seta *pl1*: length	**NA**		**51.8**	0.8	**45**	**NA**	
Tarsus II seta *pl1*: width	**NA**		**7.3**	0.4	**5**	**NA**	

NA= not applicable

TABLE 4. Comparative measurements (in µm) of newly described Heterozerconidae: males.

	Amyzozercon chocoensis average N=5	SD	*Ecuazercon cushuimensis* average N=5	SD	*Heterozercon calakmulensis* N=1	*Allozercon leytensis* average N=5	SD
Idiosoma length	**566.0**	35.1	**725.4**	17.9	**712**	**1311.3**	73.3
Idiosoma width	**504.6**	43.9	**703.6**	16.0	**598**	**1058.0**	31.8
Chelicera: length of base fixed digit	**74.2**	2.4	**82.8**	2.2	**71**	**117.0**	6.7
Movable digit: length	**120.2**	8.7	**194.2**	11.3	**95**	**293.8**	9.2
Movable digit: width	**5.8**	0.5	**8.6**	0.9	**8**	**17.2**	2.3
Spermatodactyl length	**119.8**	7.3	**184.8**	5.9	**134**	**315.2**	10.0
Palp: length	**174.8**	13.6	**203.0**	7.2	**201**	**371.2**	23.9
Palp: width at femur	**42.8**	1.5	**46.8**	1.3	**38**	**77.2**	6.3
Setae *j1*	**165.6**	8.0	**37.0**	5.4			
Elongate setae nr *j1*						**19.0**	3.9
Antero-lateral spines						**13.5**	1.0
Seta *Z2*	**185.8**	4.1	**137.6**	8.7		**6.0**	1.0
Seta *Z3*	**154.4**	7.9	**131.6**	8.8		**8.0**	1.4
Seta *Z4*	**117.6**	6.7	**89.8**	2.4			
Seta *Z5*	**64.6**	5.5	**40.8**	5.8	**25**	**269.7**	10.5
Seta *s6*	**95.8**	7.3	**11.4**	1.3			
Seta *S1*	**74.3**	6.7	**10.0**	1.4			
Seta *S2*	**80.0**	2.9	**11.0**	1.0			
Seta *S5*	**83.3**	6.3	**23.6**	2.4	**21**	**32.8**	3.8
Seta *R5*	**77.0**	3.6	**36.8**	3.6	**21**	**26.0**	2.3
Seta *st1*	**59.2**	5.4	**40.6**	2.3	**30**	**65.8**	15.0
Seta *st2*	**53.6**	5.0	**32.4**	1.7	**38**	**51.3**	14.5
Seta *st3*	**50.0**	6.7	**33.4**	4.3	**41**		
Seta *st4*	**46.4**	2.9	**NA**			**NA**	
Seta *st5*	**39.6**	2.1	**16.8**	1.7	**28**		
Seta *pa*	**46.6**	3.4	**45.6**	4.7	**51**	**90.3**	11.5
Seta *po*	**43.2**	3.3	**34.8**	3.3	**36**	**51.3**	2.1
Sucker cavity, maximum width	**NA**		**136.4**	5.9	**102**	**199.2**	21.9
Sucker, maximum width	**NA**		**112.4**	5.1	**79**	**146.0**	11.3
Leg I: length	**912.4**	43.3	**923.6**	27.6	**1060**	**2141.0**	103.4
Leg II: length	**595.4**	45.6	**609.8**	32.0	**700**	**1273.0**	69.8
Leg III: length	**607.8**	41.3	**626.6**	28.0	**670**	**1276.0**	63.2
Leg IV: length	**591.8**	66.3	**682.6**	49.2	**696**	**1398.0**	34.4
Femur I seta *al1*	**101.2**	2.6	**6.8**	1.5	**107**	**244.2**	28.5
Femur I seta *al2*	**67.6**	3.6	**9.4**	2.8	**77**	**180.8**	17.1
Femur I seta *v1*	**105.0**	7.0	**95.6**	4.9	**161**	**223.8**	16.8
Femur I seta *v2*	**46.6**	2.3	**85.6**	5.5	**149**	**134.0**	13.4
Genu I seta *av*	**93.4**	5.1	**99.0**	4.9	**157**	**186.5**	12.1
Genu I seta *pv*	**41.8**	3.3	**23.6**	1.9	**64**		
Femur II seta *al*	**31.0**	3.7	**30.4**	2.1	**42**	**71.2**	8.9
Femur II seta *pl*	**37.0**	5.6	**24.2**	2.8	**43**	**59.8**	7.8
Femur II seta *av1*	**58.0**	4.6	**44.2**	2.9	**90**	**73.4**	7.3
Femur II seta *pv1*: length	**63.6**	6.7	**50.4**	3.0	**55**	**125.6**	7.8
Femur II seta *pv1*: width	**2.9**	0.2	**3.6**	0.3	**12**	**29.8**	3.1
Genu II seta *av1*	**60.4**	4.8	**47.4**	2.7	**45**	**57.0**	7.9
Genu II seta *pv1*: length	**57.6**	6.0	**47.2**	1.3	**27**	**34.4**	4.0
Genu II seta *pv1*: width	**2.0**	0.0			**11**	**21.8**	2.2
Tibia II seta *pv*: length	**67.8**	2.8	**55.8**	2.0	**34**	**73.8**	6.8
Tibia II seta *pv*: width	**3.0**	0.0			**10**	**23.0**	0.8
Tarsus II seta *pl1*: length	**NA**		**44.6**	1.8	**43**	**NA**	
Tarsus II seta *pl1*: width	**NA**		**6.5**	1.0	**10**	**NA**	

NA= not applicable

Support for relationships among and within genera was substantially weaker, although there was moderate (<50–63% JK) support for the grouping of *Discozercon* and *Discomegistus*, as well as for the grouping of all Heterozerconidae except *Amyzozercon* + *Ecuazercon*.

The status of *Allozercon s.l.* was confirmed in a third set of analyses including the Vitzthum species, *Al. fecundissimus* (the type species of *Allozercon*) and *H. elapsus* (possible synonym of *H. audax* Berlese, the type species of *Asioheterozercon* Fain). It resulted in trees of length 300 (CI= 0.42; RI= 0.75), all of which showed *Al. fecundissimus* and *H elapsus* within a monophyletic *Allozercon*. This result confirms the assignment of all Heterozerconidae from the Oriental faunal region to the genus *Allozercon*.

Taxonomic section

In the following section all genera (previously described and new) are diagnosed based on the results of the phylogenetic analysis, focusing on unambiguous changes in the consensus tree (Fig. 97). The numbers in brackets refer to the character numbers as listed in Table 1. Where appropriate, a brief discussion of updates / modifications of previous diagnoses is added.

Heterozerconoidea

Diagnosis: Movable digit in adults with thin, strap-like dorsal extension (2); gnathotectum without prominent points (15); median dorsal setae minute (31); genitiventral and anal shields not fused (66, reversed within some Heterozerconidae); some marginal opisthosomal setae flattened (77.2); acrotarsus on legs I present (82); setae *av4* and *pv4* on tarsi IV absent (101).

Remarks: As noted in the character discussion, possession of opisthogastral suckers (63) is not assumed to be an apomorphy for this grouping, as homology of the discozerconid and the heterozerconid suckers is uncertain.

Berzercon Seeman & Baker 2013

Berzercon Seeman & Baker 2013: 131 [type species: *Berzercon ferdinandi* Seeman & Baker 2013, by monotypy].

Diagnosis: Anterior dorsal setae *j1* minute (<5µm) (28); sclerotized areas around sternal setae *st1* in female fused to each other (forming a sternal shield) (34); sclerotized areas near sternal setae *st2* in female fused to the genitiventral and endopodal shields (38); sternal lyrifissures *iv3* in female absent (45); sclerotized areas near sternal setae *st1* in male fused to both sternitiventral and endopodal shields (48); opisthogastral suckers in adults present, anterior to ventral shield, discozerconid type (63.2); insertion paranal setae (*pa*) anterior to the anus (72); postanal (*po*) seta less than 1/3 the length of paranal (*pa*) setae (73); equally spaced long marginal setae present (76).

Remarks: Seeman & Baker (2013) listed several presumed unique characters for this genus: 1) long marginal setae (76; somewhat similar, but shorter, marginal setae are present in *Discomegistus*), 2) a tripartite gnathotectum, 3) fusion of palp tibia and tarsus, 4) arrangement of ventral shields, 5) highly modified setae *hyp 1* in male. Characters 2, 3, and 5 were not included in this study, but appear apomorphic. Character 4 is not very specific, but the ventral shield arrangement is clearly distinct from that in *Discozercon* and *Discomegistus* (or Heterozerconidae), lacking the medial posterior extension of the genital / genitiventral shield.

Included species –

Berzercon ferdinandi Seeman & Baker 2013

Berzercon ferdinandi Seeman & Baker 2013: 132.

Type depository. Landcare Research, Auckland, New Zealand.

Material examined. Two female and two male paratypes (**OSAL 104613–104614, 114590, 114748**)

Remarks: All specimens were recovered from Carabidae, *Megadromus* sp., *Mecodema* sp. , and *Plocamostethus* sp. from New Zealand (Seeman & Baker 2013).

The grouping of all remaining Heterozerconoidea, that is Discozerconidae *s.s*. plus Heterozerconidae, is characterized by the following character states: inside movable digit female with brush-like structure (4); cornicula membranous (23); setae *Zv3* in adults absent (62, reversed in *Amyzozercon*); tibiae I setae *ad3*, *pd3* ((88), tibiae II–IV setae *ad2*, *pd3*, *pl2* (95–97), genua I setae *ad3*, *pd3* (86), genua IV seta *ad3* (99), femora II seta *pv2* (91), and femora III seta *v3* all absent (98). Although the number of characters listed is impressive, it is worthwhile noting that nearly all of them concern leg chaetotaxy, which is quite similar in *Berzercon* and Sejidae. Use of alternative outgroups renders most of these characters as apomorphies of *Berzercon*, reducing support for the lineage of Discozerconidae *s.s*. plus Heterozerconidae.

Discozerconidae *s.s.* Berlese 1910

Discozerconidae Berlese 1910a: 374 [type genus: *Discozercon* Berlese 1910, by monotypy].

Diagnosis: Sclerotized areas near setae *st5* in male not fused to sternitiventral shield. (53); opisthogastral suckers in adults present, anterior to ventral shield, discozerconid type (63.2); setae *Sv2* and *Sv3* not inserted on on the genitiventral (female) or sternitiventral (male) shields (67–70); genua III–IV seta *pd3* absent (100).

Discozercon Berlese 1910

Discozercon Berlese 1910a: 374 [type species: *Discozercon mirabilis* Berlese 1910, by monotypy].
Discozercon.—Trägårdh 1911: 2; Domrow 1956: 193; Lekveishvili & Klompen 2004: 6; Seeman & Baker 2013: 131.
(Figs 1, 23–24, 44, 53–54, 78, 87).

Diagnosis: Anterior dorsal setae *j1* minute (<5 μm) (28); sclerotized areas near sternal setae *st3* in female separate platelets (40); sclerotized areas near sternal setae *st5* in female separate from genitiventral shield (43); sclerotized areas near sternal setae *st2* in male separate platelets or area not sclerotized (50); sclerotized areas near sternal setae *st3* area in male separate platelets or no shield (52); paranal setae inserted anterior to anus (72); setae *S5* in male elongate (75); elongate, equally spaced marginal setae absent (76).

Included species –

Discozercon mirabilis Berlese 1910

Discozercon mirabilis Berlese 1910a: 374.
Discozercon mirabilis.—Berlese 1914: 146; Vitzthum 1925: 44.

Type depository. Holotype in ISZA, accession no. **130/1–3**.

Material examined. None.

Remarks. On *Scolopendra subspinipes* Leach (Scolopendridae) (Berlese 1910a) and *Scolopendra* sp. (Vitzthum 1925) from Java island, Indonesia.

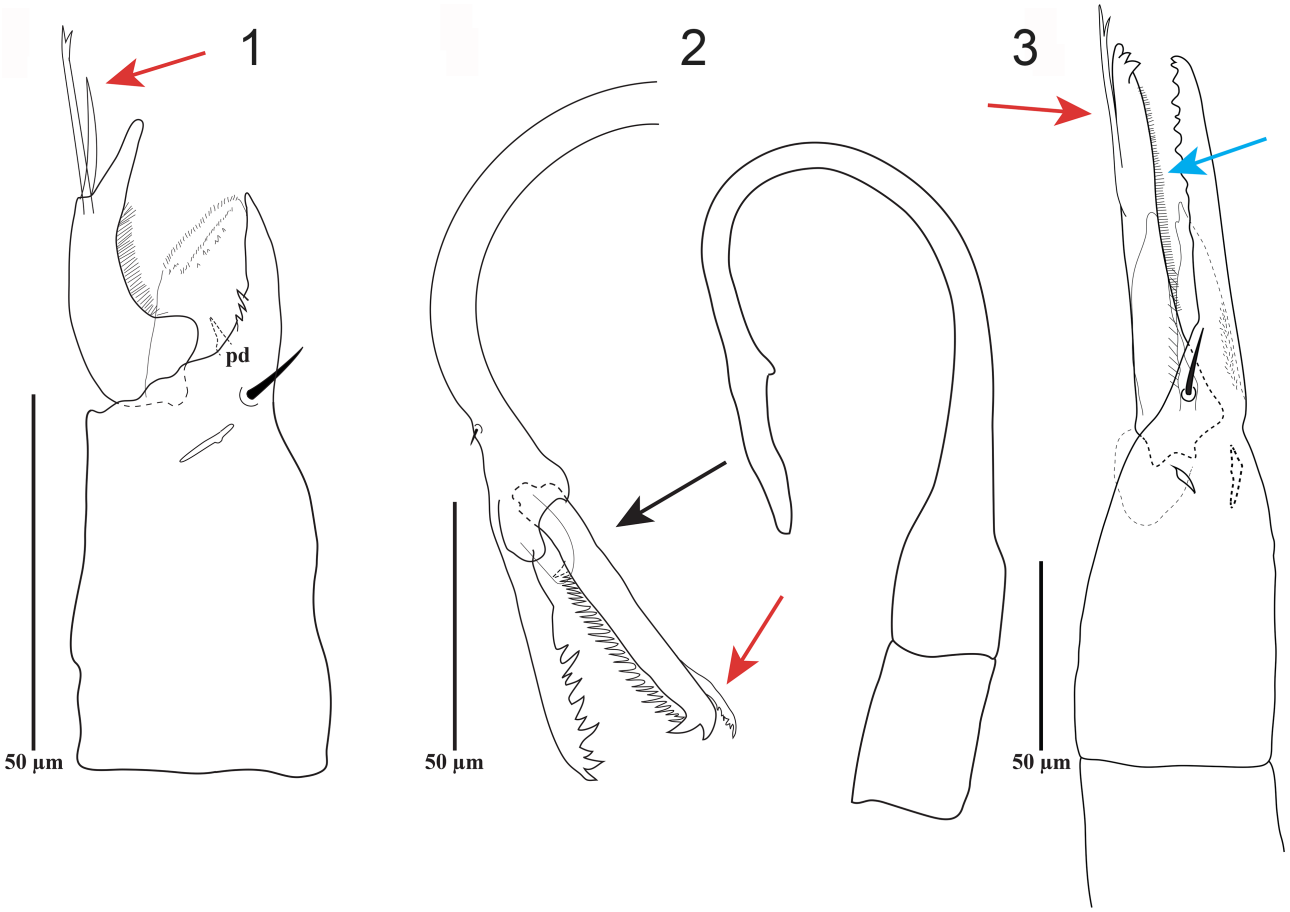
*Discozercon derric*ki Domrow 1956

Discozercon derricki Domrow 1956: 193.

Type depository. Queensland Museum, Brisbane, Australia.

Material examined. Two females and six males (**OSAL 004889–004891, 052735–052738**)

Remarks. On *Scolopendra* sp. (Scolopendridae) from Queensland, Australia (Domrow 1956), on scolopendrid centipedes from two localities in Queensland, Australia (OSAL).



FIGURES 1–3. Chelicera females: 1, Discozerconidae, *Discozercon derricki*., female (OSAL 052739); 2, Heterozerconidae, *Amyzozercon chocoensis*, female (OSAL 106741); 3, *Al.* (*Philippinozercon*) *makilingensis*, female (OSAL 053222; blue arrow: brush like structure on inside movable digit). Abbreviations: pd: pilus dentilus. Red arrows: thin, strap-like extensions on the movable digit.

Discomegistus Trägårdh 1911

Discomegistus Trägårdh 1911: 2 [type species: *Discomegistus pectinatus* Trägårdh 1911, by monotypy].
Discomegistus.—Vitzthum 1925: 44; Domrow 1956: 194; Seeman & Baker 2013: 131.
(Figs 20, 43, 88).

Diagnosis: Sclerotized areas around sternal setae *st1* in female fused to each other (34); sclerotized areas near sternal setae *st2* in female fused to genitiventral shield (38); equally spaced long marginal setae present (76).

Material examined. One male with no data (FMNH).

Remarks: In the single available male specimen metasternal setae *st4* appear absent (41; this designation is tentative, based on a single available specimen; it should be checked with additional material). Second, basitarsi II–IV show an added mid-dorsal sensillum (Fig. 88, red arrow) that has not been reported previously. This structure is not present in *Discozercon*, *Berzercon*, or in any other Heterozerconoidea examined. In fact, we are not aware of such a structure in any other Mesostigmata.

Included species –

Discomegistus pectinatus Trägårdh 1911

Discomegistus pectinatus Trägårdh 1911: 3.

Type depository. Unclear, possibly BMNH.

Material examined. None.

Remarks. On *Rhombocephalus gigantea* (now *Scolopendra gigantea* Linnaeus) (Scolopendridae) from Trinidad (Trägårdh 1911).

Heterozerconidae Berlese 1892

Heterozerconidae Berlese 1892: 97 [type genus: *Heterozercon* Berlese 1892 by monotypy].

Diagnosis. Movable digit of the chelicera in the female elongate (length > 6x basal width) (3); spermatodactyl present on fixed digit of the male (6); axial outgrowth of palp trochanter in female distinct and membranous (8); palp femur seta *pd1* added (10); lateral lips enlarged to form a trough (19); distance from setae *hyp3* to *sc* distinctly larger than distance from *hyp3* to *hyp2* (21.2, reversed in *Narceoheterozercon*, *Maracazercon*, many *Heterozercon*, and some *Afroheterozercon*); setal base-like structure on hypostome present (25); opisthogastral suckers in adults present, posterior to ventral shield (63.1, reversed in *Amyzozercon*); marginal opisthosomal setae all setiform (77.0); femora I seta *av* in male spine-like (104).

Remarks. The family is well characterized by a broad set of modifications of the female and male chelicera and hypostome and, possibly, by the presence of a pair of large ventral suckers posterior to the ventral shield (63 but see *Amyzozercon*).

The grouping of *Amyzozercon* and *Ecuazercon* is supported by a few unusual characters: basal part of fixed digit in female elongate, length width ratio 4–6 (Fig. 2) (1); posterior dorsal setae *Z2–Z4* elongate (32); sternal setae *st1* and lyrifissures *iv1* in female and males on separate shields or inserted in soft cuticle (36, 49); postero-marginal shields in female small, not extending lateral to opisthogastral suckers (80); femora I seta *av* in male large curved spine (104). This grouping is poorly supported in jackknife analyses with an arrangement of *Amyzozercon* as sistergroup to the remaining Heterozerconidae as the most common alternative option.

Amyzozercon new genus

Diagnosis: Hypostomal setae *hyp2* at least twice as long as *hyp3* (22); sclerotized areas near sternal setae *st3* in female separate platelets (40); metasternal setae *st4* and opisthogastral setae *Zv3* present (41, 62); sternal lyrifissures *iv3* in female absent (45); sclerotized areas near sternal setae *st2* in male fused to sternitiventral shield (50.0); sclerotized areas near sternal setae *st2* and *st3* in male completely fused (51.0); male genital opening positioned anterior sternal, between coxae II (55.1); opisthogastral suckers absent (63.0); opisthogastral setae *Sv2* and *Sv3* not inserted on the genitiventral or sternitiventral shields (67–70); setae *S5* in male elongate (>40 μm) (75); all setae on legs II of male setiform.

Type species: *Amyzozercon chocoensis* n. sp.

Etymology. The generic name combines “a”, Greek for not, without, with “myzo”, Greek for suck, and “zercon”, a common ending for generic names in Heterozerconidae. It refers to the primary character of this genus (within Heterozerconidae).

Remarks. “Undescribed Heterozerconidae without suckers” Lindquist *et al*. (2009b): 137; Seeman & Baker (2013): 130 probably refer to this genus.

Within Heterozerconidae, *Amyzozercon* is easily recognizable by the absence of opisthogastral suckers (62), the presence of multiple very long opisthonotal setae (32), and the retention of setae *st4* (41) and *Zv3* (62).

An examination of multiple females using light microscopy did not reveal any indication of secondary genital openings (solenostomes).

Included species –

***Amyzozercon chocoensis* new species**
(Figs 2, 4–5, 21, 25–26, 45, 55–56, 73–77).

Diagnosis. As for the genus.

Description. Female idiosoma length 652 (43), width 560 (57) (N=5); male idiosoma length 566 (35), width 505 (44) (N=5). Complete measurements in Tables 3–4.

Chelicera (Figs 2, 4–5). Basal part of fixed digit in female elongate, length width ratio 4–6. Movable digit in adults with thin, straplike dorsal extensions. Movable digit in female elongate, digit length >6 times basal width. Inside movable digit female with brush-like structure. Excrescences on male chelicera present, interdigital. Spermatodactyl on fixed digit of male chelicera present, of straight type.

Palp (Fig. 21). Axial outgrowth of palp trochanter in female distinct and membranous. Axial outgrowth of palp trochanter in male absent. Seta *pd1* on femur present. Setae on femur long, relatively thin, setiform. Setae *al2* and *pl* on genu present. Number of sensilla on tarsus 10–11. Formula: 2–6–6–14–10/11.

Gnathosoma (Figs 25–26). Gnathotectum of female without prominent points. Anterior margin gnathotectum serrate. Overall shape of gnathotectum intermediate between curved and blunt. Lateral lips enlarged to form a trough; posterior extension of the trough short, not extending beyond insertions of setae *hyp2*. Distance between setae *hyp3* and *sc* subequal to that between *hyp3* and *hyp2*. Setae *hyp2* at least twice as long as *hyp3*. Cornicula membranous without a distal notch. Additional setal base-like structure on hypostome present.

Dorsum (Fig. 45). Holodorsal shield in female covering most of the dorsum but leaving a wide strip of unsclerotized cuticle laterally and posteriorly, less so anteriorly. Holodorsal shield in male covering nearly entire dorsum. Peritrematal shield adjacent to dorsal shield but not fused to it. Anterior dorsal margin in adults with a single pair of elongate setae (*j1*) inserted on the anterior margin of the holodorsal shield. Antero-marginal area of dorsal shield in males without distinct spines. Median dorsal setae minute. Some posterior dorsal (*Z2–Z4*) and marginal (*s6*, *S1–S3*) setae elongate in both sexes. Of these, setae *Z2–Z3* in the females, and *s6*, *Z2–Z4* in the males on the shield.

Sternal area female (Fig. 55). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sclerites of sternal setae *st1* and *st2* not fused. Sternal setae *st1* and lyrifissures *iv1* not on the same shield. Areas near insertion sternal setae *st2* and *st3* sclerotized, forming isolated platelets. Metasternal setae *st4* present. Areas near insertion sternal setae *st5* sclerotized, fused to genitiventral shield. Sternal lyrifissures *iv1* in adults present. Sternal lyrifissures *iv3* in female absent. Distinct curved, sclerotized ridge on anterior margin of female genital shield absent. Structures suggesting secondary genital openings not observed.

Sternal area male (Fig. 56). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sternal setae *st1* and lyrifissures *iv1* not on the same shield. Sclerotized areas near insertions of sternal setae *st2*, *st3* and *st5* fused to sternitiventral shield. Sclerotized areas of sternal setae *st2* and *st3* completely fused. Sternal lyrifissures *iv3* absent. Male genital opening anterior sternal, between coxae II. Genital shields not overlapping base of the tritosternum. Sternitiventral area in male smooth.

Opisthogaster (Figs 55–56). Metapodal and sternitiventral shields in male not fused. Posterolateral margin of metapodal shields in adults rounded. Setae *Zv3* present. Opisthogastral suckers absent. Ventral shield area in male with a single shield. Sternitiventral and anal shields in male not fused. Setae *Sv2* and *Sv3* not inserted on genitiventral (female) or sternitiventral (male) shields. Setae *Sv2* and *Sv3* in female inserted in soft cuticle, in male inserted on margin metapodal shields. Setae *Jv5* inserted anterior to ventrianal line. Insertion of paranal setae (*pa*) at level of anus. Postanal (*po*) seta of similar length as paranal (*pa*) setae. Setae *Z5*, *S5*, *R5* and *R4* in both adults elongate. Marginal opisthosomal setae (other than elongate *S*-series setae) elongate. Postero-marginal shield in females small, not extending lateral to insertion setae *R5*.

Legs (Figs 73–77). Tibiae and tarsi of legs I of similar width as the rest of the leg. Acrotarsus on legs I present. Femora I seta *ad3* present. Femora I setae *v3*, *v4* and *pl2* absent. Genua I setae *ad3* and *pd3* absent. Tibiae I seta *ad2* present, setae *ad3*, *av2* and *pv2* absent. Femora II setae *av2* and *pv2* absent. Genua II–IV setae *ad3* and *pl2* absent. Genua II seta *pd3* absent, genua III–IV seta *pd3* present. Tibiae II–IV setae *ad2*, *pd3* and *pl2* absent. Femora III seta *v3* absent. Tarsi IV setae *av4*, *pv4* absent. Complete chaetotaxy in Table 2. Coxae I setae in male setiform. Femora I setae *al1* and *al2* setiform, in anterolateral position. Femora I seta *av* in male a large, curved spine; seta *av* in females a much shorter, straight spine (Fig. 74). Femora II setae *al*, *pl*, *av* and *pv* in male setiform. Genua II seta

pv and tibiae II seta *pv* in male setiform. Tarsi II seta *pl1* setiform in both sexes. Trochanters III setae *al*, *av* and *pl* in male setiform.

Type depository: Holotype male at UNC Bogotá, accession number OSAL 106788. Paratypes at ICN, OSAL, FMNH.

Material examined. Colombia, Chocó, Tutunendo, field station, 48m, 5.7494 N 76.5217 W, 30–Mar-2010, Jimeno, E., Correa, J. & Klompen, H., ex 2 male and 1 female *Psammodesmus atratus* in rotting log, host accession number ICN-MD-1525–7, UNC Bogotá, 1 male, OSAL 106788 (holotype). Same data, 1 female, OSAL 102659; 1 female, OSAL 102660; 1 male, OSAL 106721; 1 female, OSAL 106741; 1 male, OSAL 106781; 1 female, OSAL 106782; 1 female, OSAL 106783; 1 female, OSAL 106784; 1 female, OSAL 106785; 1 female, OSAL 106786; 1 female, OSAL 106787; 1 male, OSAL 106789; same locality, 25–Mar-2010, Mosquera, J. & Mosquera, M. E., ex male *Psammodesmus atratus* (Chamberlin) (Polydesmida: Platyrhacidae) in rotting log, host accession number ICN-MD-1525–2, UNC Bogotá, 1 female, OSAL 103952; 26–Mar-2010, Jimeno, E., Correa, J. & Klompen, H., ex mix of 1 female *Psammodesmus atratus* and 1 female *P.* sp. in rotting log, 1 male, OSAL 106736. Colombia, Chocó, Quebrada Taparral, 20km N of Palestina on Rio San Juan, 4.1500 N 77.0667 W, 26–Jan-1969, Malkin, B., ex *Psammodesmus atratus*, field code FMJK 71–1005 (host at FMNH), 1 female 2 males (FMNH). Colombia, Chocó, Caño Decordo, between Cucurrupi & Noanama on Rio San Juan, 4.5333 N 76.8667 W, 1–5–Jan-1969, Malkin, B., ex polydesmid millipede, field code FMJK 71–1006 (host at FMNH), 2 females 3 males (FMNH). Colombia, no further data, field code CM-14 (host at FMNH), 1 female 1 male (FMNH).

Etymology. This specific designation is a combination of Choco, the faunal region (and province) from which the species is described, and "ensis" Latin for "place, locality".

Remarks. *Amyzozercon chocoensis* is somewhat unusual within Heterozerconidae by its association with polydesmid, rather than juliform, millipedes. We have a few single specimen records of *Allozercon* and *Narceoheterozercon* specimens from polydesmids, but these may be accidental. In contrast, *Amyzozercon*, *Ecuazercon*, and a few undescribed populations of *Heterozercon* (Jocelyn Martinez, pers. comm.) appear to be true polydesmid associates, recorded only from Polydesmida. At the Tutunendo site *Amyzozercon chocoensis* may be host specific, recorded only from *Psammodesmus atratus* (Chamberlin) (Platyrhacidae). Examination of multiple specimens of Batodesmini sp.1 (Polydesmida: Chelodesmidae) (accession numbers ICN-MD-1527–1, -1527–2, -1527–3), a species that was equally common in the same rotting logs, never yielded *Amyzozercon*.

We have specimens of other species of this new genus (from Brazil, Ecuador, and (possibly) Honduras), but numbers are low and/or host and locality data for these collections are incomplete, limiting the value of added descriptions.

Ecuazercon new genus

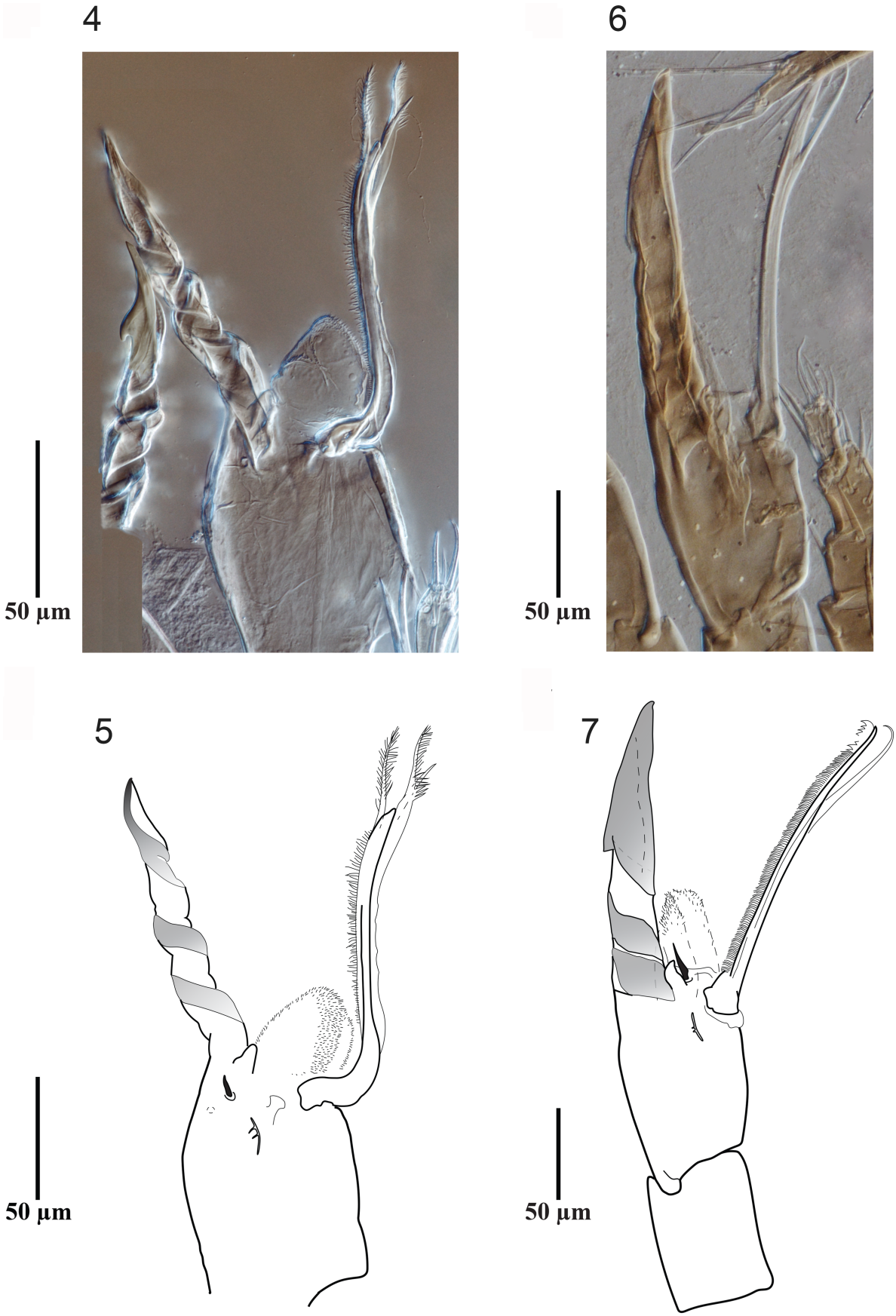
Diagnosis. Distance between setae *hyp3* and *sc* distinctly smaller than that between *hyp3* and *hyp2* (21); sclerotized areas near insertion sternal setae *st1* in male fused to sternitiventral shield (48); sternal lyrifissures *iv3* in male present (54); male genital shields overlaying tritosternum (56); some marginal opisthosomal setae in male peg-like spines (77, 78, shared with *Amheterozercon*); tibiae II–IV with seta *pl2* present (97); setae *pl1* on tarsi II spine-like (111, shared with *Amheterozercon*, *Heterozercon*, *Maracazercon*); all remaining setae on legs II of male setiform.

Type species: *Ecuazercon cushuimensis* n. sp.

Etymology. The generic name is a combination of Ecuador, the source of the specimens described, and "zercon", a common ending for generic names in Heterozerconidae.

Remarks. The main difference between this genus and *Amyzozercon* is the presence of well-developed ventral suckers. In many other characteristics, e.g., the shape of the female chelicera and elongate dorsal setae, it closely resembles that genus.

An examination of multiple females using light microscopy did not reveal any indication of secondary genital openings (solenostomes).



FIGURES 4–7. Heterozerconidae, chelicera males, photograph (top) and composite drawing (bottom): 4–5, *Amyzozercon chocoensis* (OSAL 106788); 6–7, *Ecuazercon cushuimensis* (FMNH-INS 4449621).

Included species –

***Ecuazercon cushuimensis* new species**
(Figs 6–7, 27–28, 46, 57–58, 79, 89)

Diagnosis. As for the genus.

Description. Female idiosoma length 819 (52), width 808 (62) (N=5); male idiosoma length 725 (18), width 704 (16) (N=5). Complete measurements in Tables 3–4.

Chelicera (Figs 6–7). Basal part of fixed digit in female elongate, length width ratio 4–6. Movable digit in adults with thin, straplike dorsal extensions. Movable digit in female elongate, digit length >6 times basal width. Inside movable digit female with brush-like structure. Excrescences on male chelicera present, interdigital. Spermatodactyl on fixed digit of male chelicera present, of the straight type.

Palp. Axial outgrowth of palp trochanter in female distinct and membranous. Axial outgrowth of palp trochanter in male absent. Seta *pd1* on femur present. Setae on femur long, thick spines. Setae *al2* and *pl* on genu present. Number of sensilla on palp tarsus 11–12. Formula: 2–6–5–13–11/12.

Gnathosoma (Figs 27–28). Gnathotectum of female without prominent points. Anterior margin gnathotectum serrate. Overall shape of gnathotectum blunt. Lateral lips enlarged to form a trough; posterior extension of the trough short, not extending beyond insertions of setae *hyp2*. Distance between setae *hyp3* and *sc* distinctly smaller than that between *hyp3* and *hyp2*. Setae *hyp2* subequal in length or slightly longer than *hyp3*. Cornicula membranous without a distal notch. Additional setal base-like structure on hypostome present.

Dorsum (Fig. 46). Holodorsal shield in female covering most of the dorsum but leaving a wide strip of unsclerotized cuticle laterally and posteriorly, less so anteriorly. Holodorsal shield in male covering entire dorsum. Anterior dorsal margin in female with a single, elongate pair of setae (*j1*) inserted on the anterior margin of the dorsal shield. Antero-marginal area of dorsal shield in males without distinct spines. Median dorsal setae minute. Posterior dorsal setae *Z2–Z4* elongate in both sexes, inserted on the dorsal shield; marginal setae *s6* and *S1–S3* elongate in females, but not in males. Small peg-like spinose setae in the marginal opisthosomal region of males may be homologous to elongate setae *s6* and *S1–S3* in females.

Sternal area female (Fig. 57). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sclerites of sternal setae *st1* and *st2* not fused. Sternal setae *st1* and lyrifissures *iv1* not on the same shield. Areas near insertion sternal setae *st2* sclerotized, forming isolated platelets. Areas near insertion sternal setae *st3* sclerotized, fused to genitiventral shield. Metasternal setae *st4* absent. Areas near insertion sternal setae *st5* sclerotized, fused to genitiventral shield. Sternal lyrifissures *iv1* and *iv3* in adults present. Distinct curved, sclerotized anterior margin of female genital shield absent. Structures suggesting secondary genital openings not observed.

Sternal area male (Fig. 58). Areas near insertion sternal setae *st1* sclerotized, fused to sternitiventral shield. Sternal setae *st1* and lyrifissures *iv1* not on the same shield. Sclerotized areas near insertion sternal setae *st2* fused to endopodal shield. Sclerotized areas of sternal setae *st2* and *st3* not fused. Sclerotized areas near sternal setae *st3* and *st5* fused with sternitiventral shield. Sternal lyrifissures *iv3* present. Male genital opening presternal. Genital shields overlaying base of the tritosternum. Sternitiventral area in male smooth.

Opisthogaster (Figs 57–58). Metapodal and sternitiventral shields in male not fused. Posterolateral margin of metapodal shields in adults rounded. Setae *Zv3* in adults absent. Opisthogastral suckers in adults present, posterior to ventral shield, of the heterozerconid type. Apodemes extending from opisthogastral suckers absent. Ventral shield area with a single shield. Sternitiventral and anal shields in male not fused. Setae *Sv2* and *Sv3* inserted on genitiventral (female) or sternitiventral (male) shields. Setae *Jv5* positioned anterior to ventrianal line. Insertion of paranal setae (*pa*) at level of anus. Postanal (*po*) seta of similar length as paranal (*pa*) setae. Setae *Z5* and *S5* in male medium in length, distinct. Lyrifissures *iv5* inserted near anterior margin of sucker. Postero-marginal shields in female small, not extending lateral beyond opisthogastral suckers.

Legs (Figs 79, 89). Tibiae and tarsi of legs I of similar width as the rest of the leg. Acrotarsus on legs I present. Femora I seta *ad3* present. Femora I setae *v3*, *v4* and *pl2* absent. Genua I setae *ad3* and *pd3* absent. Tibiae I seta *ad2* present, setae *ad3*, *av2*, *pv2* absent. Femora II seta *av2* and *pv2* absent. Genua II–IV setae *ad3* and *pl2* absent. Genua II seta *pd3* absent, genua III–IV seta *pd3* present. Tibiae II–IV seta *pl2* present. Tibiae II–IV setae *ad2* and *pd3* absent. Femora III seta *v3* absent. Tarsi IV setae *av4* and *pv4* absent. Complete chaetotaxy in Table 2. Coxae I setae in male somewhat spine-like. Femora I setae *al1* and *al2* setiform, in anterolateral position. Femora I seta

av in male a large, curved spine; seta *av* in female a short, straight spine. Femora II setae *al*, *pl*, *av* and *pv* in male setiform. Genua II seta *pv* and tibiae seta *pv* in male setiform. Tarsi II seta *pl1* spine in both sexes. Trochanters III in male with seta *al* thick seta, seta *pv2* spinose, setae *av* and *pl* setiform.

Type depository: Holotype male at FMNH, accession number FMNHINS 4449621. Paratypes at FMNH, OSAL.

Material examined. Ecuador, Morona-Santiago, Cushuimi, Rio Cushuime, ca. 150km SE of Puyo, 320m, 2.5208 S 77.7294 W, 4–Jun-1971, Malkin, B., ex male *Barydesmus* sp. (Polydesmida: Platyrhacidae), field code FMJK 71–1114, host accession number FMNHINS 1320, 1 male (holotype) 1 female (paratype). Same locality, 15–28–May-1971, Malkin, B., ex seven *Camptomorpha dorsalis* Silvestri (Polydesmida: Chelodesmidae)), field code FMJK 71–1118, host accession number FMNHINS 33998, 5 females 3 males; May-1971, Malkin, B., ex *Pycnotropis* sp. (Polydesmida: Aphelidesmidae), field code FMJK 71–1120, 1 male.

Etymology. This specific designation is a combination of Cushuimi, the type locality and "ensis" Latin for "place, locality".

Remarks. Comparing records for *Amyzozercon chocoensis* with those of *Ecuazercon cushuimensis* shows that both localities and hosts clearly differ. Our records of *Ecuazercon* are limited to the Cushuimi area in Ecuador (east of the Andes), while those of *A*. *chocoensis* are limited to the Choco region of Colombia (west of the Andes). Notably, while *A*. *chocoensis* showed local host specificity in Choco, *E*. *cushuimensis* was found on three different host species in three different families. The current records therefore do not support either local host specificity of *E*. *cushuimensis*, or genus level specificity for *Amyzozercon*. The latter conclusion is supported by the observation that the *Barydesmus* and *Camptomorpha* millipedes carrying *Ecuazercon* also carried a few specimens of *Amyzozercon* sp. Of course, a more adequate analysis of host specificity will require substantially more collections from different localities and with well identified hosts.

The grouping of the remaining Heterozerconidae is characterized by the reduction of dorsal setae *Z2–Z4* to minute (32.1); some marginal opisthosomal setae spine-like (77); the expansion of the postero-marginal shields in the female to well beyond the opisthogastral suckers (80); the presence of seta *pl2* on femora I (85; reversed in *Narceoheterozercon*); the transformation of setae *al1* and *al2* on femora I to a spinose shape and to an anteroventral position (103); and the transformation of femora I seta *av* in the male into large straight spines (104). Notably, most of these characters (except 32, 103) are sensitive to optimization.

Amheterozercon Fain 1989

Amheterozercon Fain 1989: 147 [type species: *Heterozercon oudemansi* Finnegan 1931, by original designation].
Zeterohercon Flechtmann & Johnston 1990: 143 (type species *Heterozercon oudemansi* Finnegan 1931, by original designation) [objective synonym of *Amheterozercon* Fain 1989 by Lindquist *et al*. 2009b].

Diagnosis. Spermatodactyl of male of flaccid type (7); axial outgrowth of palp trochanter in female distinct and sclerotized (8); apodemes extending from opisthosomal suckers in adults with distinct knobs (64); genitiventral and anal shields in male fused, line of fusion invisible (66); setae *S5* in the male very long (75); marginal opisthosomal setae peg-like spines (78, shared with male *Ecuazercon*); setae *pl1* on tarsi II spine-like (111, shared with *Ecuazercon*, *Heterozercon*, *Maracazercon*); all remaining setae on legs II of male setiform.

Remarks. Of the characters listed in Fain's (1989) diagnosis, only the transformation of 19–26 unidentified supernumerary setae on the margin of the opisthosoma to medium-long peg-like setae may be derived for this genus (character 78 in the current analysis). Both *Amheterozercon* Fain and *Zeterohercon* Flechtmann & Johnston were described with *Heterozercon oudemansi* as their type species, making *Zeterohercon* an objective synonym of *Amheterozercon*.

Flechtmann & Johnston (1990) noted the presence of a spermatheca inside some females. Based on that observation they assumed the presence of secondary genital openings even though they could not find such openings. In the current study we have not been able to find secondary genital openings in the females either.

In terms of host associations, species of *Amheterozercon* are unique among Heterozerconoidea by their association with snakes and amphisbaenids. A similar transition from millipedes (elongate heavily sclerotized organisms) to snakes and lizards (similar body shape) has been proposed in Paramegistidae (Klompen & Austin 2007).

Included species –

Amheterozercon oudemansi (Finnegan 1931)

Heterozercon oudemansi Finnegan 1931: 1349.
Heterozercon elegans Lizaso 1979: 140 [junior synonym of *A. oudemansi* Fain 1989: 155, Flechtmann & Johnston 1990: 143].
Amheterozercon oudemansi.—Fain 1989: 148.
Zeterohercon oudemansi.—Flechtmann & Johnston 1990: 143.

Type depositories. Holotype *H. oudemansi* deposited at BMNH; holotype *H. elegans* deposited at IBSP.

Material examined. None.

Remarks. Based on females and males on *Epicrates cenchria* (Linnaeus) (Boidae) from upper Amazon (*H. oudemansi*) (Finnegan 1931); on *Waglerophis* (now *Xenodon*) *merremii* (Wagler), *Mastigodryas* (now *Palusophis*) *bifossatus* (Raddi), and *Erythrolamprus aesculapii* (Linnaeus) (all Colubridae), from various sites in Brazil (*H. elegans*) (Lizaso 1979).

Amheterozercon amphisbaenae (Flechtmann & Johnston 1990)

Zeterohercon amphisbaenae Flechtmann & Johnston 1990: 145.
Amheterozercon amphisbaenae.—Lindquist *et al*. 2009b: 137.
(Figs 8–9, 29–30, 59–60, 80, 90).

Type depository. Holotype deposited at OSAL, accession no. OSAL 106933.

Material examined. Brazil: São Paulo, São Jose do Rio Preto, 20.8083 S 49.3811 W, 29–Mar-1990, Rizzo, A., ex *Amphisbaena alba*, AL 007865, 1 female, OSAL 052750; same collection data, 1 female OSAL 052751, 1 female OSAL 052752, 1 female F OSAL 052753, 1 female OSAL 052754, 1 male OSAL 052755, 1 male OSAL 052756, 1 male OSAL 052757, 1 male OSAL 052758, 1 male OSAL 052759, 1 male OSAL 052760, 1 male OSAL 052761, 1 male OSAL 052763, 1 male OSAL 106933

Remarks. Based on females and males ex *Amphisbaena alba* (Linnaeus) (Amphisbaenidae), from São Paulo state, Brazil (Flechtmann & Johnston 1990).

Resolution of relationships among the remaining five genera could not be resolved with any confidence, effectively leaving a polytomy of *Narceoheterozercon*, *Afroheterozercon*, *Maracazercon*, *Heterozercon*, and *Allozercon*. The grouping is characterized by the following state changes: anterior margin gnathotectum not serrate (16, reversed in some *Heterozercon*); posterior extension of lateral lips long, extending distinctly past *hyp 2* (20, exception *Heterozercon*); sternal lyrifissures *iv3* in male present (54.0, reversed in a few *Allozercon*); insertion paranal setae (*pa*) posterior to the anus (72, exception some *Heterozercon*); femora II seta *pv* in male spine (108, reversed in *Narceoheterozercon*); trochanters III seta *al* in male distinct spine (112, reversed in *Narceoheterozercon* ex Auburn C, *Afroheterozercon pachybolus*, and a few *Heterozercon*).

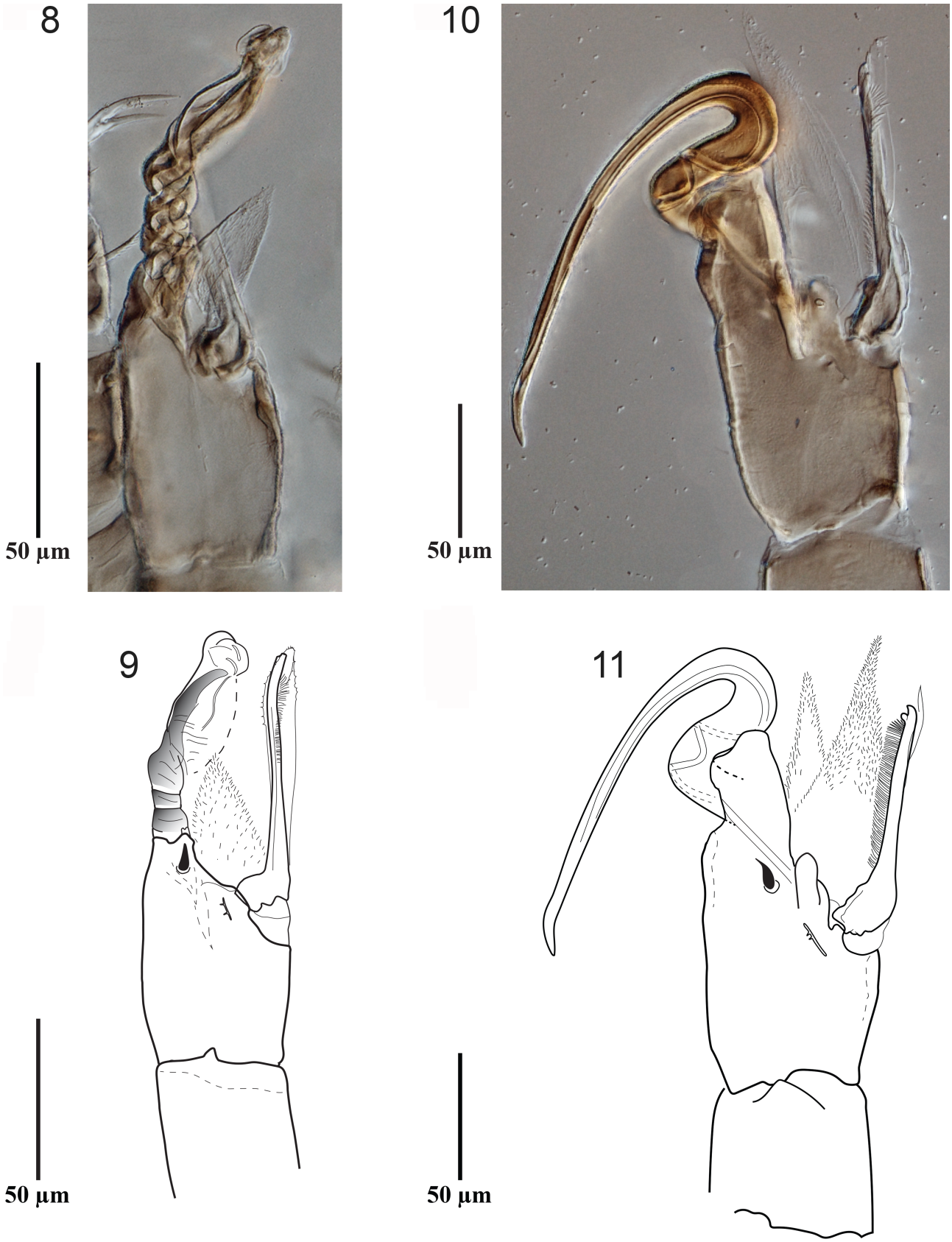
In general, the genera in this group can be distinguished by a set of characters involving the shape of setae, including the marginal opisthosomal setae (77, 78), the lateral and ventral setae on femora II of the male (105–107), ventral seta *pv* on genua and tibiae II of the male (109–110), and tarsi II seta *pl1* (111).

Narceoheterozercon Gerdeman & Klompen 2003

Narceoheterozercon Gerdeman & Klompen 2003: 352 [type species: *Narceoheterozercon ohioensis* Gerdeman & Klompen 2003, by original designation].

Diagnosis. Spermatodactyl long, recurved, and largely smooth (7, except in *Narceoheterozercon* ex Alabama-C); anterior dorsal setae *j1* minute (<5 μm) (28.2); sternal lyrifissures *iv1* in adults absent (44); sclerotized areas near sternal setae *st2* and *st3* in male completely fused (51.0); females with prominent, well sclerotized, solenostomes arching anteriorly from the antero-median corner of the ventral opisthosomal suckers (64, except in *Narceohet-*

erozercon ex Alabama-C); setae *S5* in adults minute (75), all marginal opisthosomal setae setiform (77, reversal); femora I seta *pl2* absent (85), femora II seta *pv* in males setiform (108, reversal); remaining setae on legs II of male all setiform.



FIGURES 8–11. Heterozerconidae, chelicera males, photograph (top) and composite drawing (bottom): 8–9, *Amheterozercon amphisbaenae* (OSAL 052760); 10–11, *Narceoheterozercon ohioensis* (OSAL 001221).

Remarks. The diagnosis of the genus by Gerdeman & Klompen (2003) included four characters: 1) female with prominent, well sclerotized, solenostomes arching anteriorly from the antero- median corner of the ventral opisthosomal suckers (64.2); 2) male with long, recurved, and largely smooth spermatodactyl (7.2); 3) male lacking prominent spines on legs II (107–110); 4) adults lacking spine-like marginal opisthosomal setae (77). Of these, characters 1and 2, while unique, are not shared by some taxa included in the genus in this study (e.g., population Alabama-C). As a result, the diagnosis (and support) for this genus is not strong. Data on additional species may help clarify the concept of this genus.

Most *Narceoheterozercon* species have secondary genital openings (solenostomes) in the female (Gerdeman 2002). These are located at the antero-internal corners of the opisthogastral suckers and continue internally in the form of sclerotized tubes (Fig. 61, arrow). Evidence that these tubes serve as secondary genital openings includes the observation that these structures are limited to the females, and the observation of a broken-off spermatodactyl in one of the tubes (Fig. 52).

Included species –

Narceoheterozercon ohioensis Gerdeman & Klompen, 2003

Narceoheterozercon ohioensis Gerdeman & Klompen 2003: 353.
Narceoheterozercon ohioensis.—Alberti *et al*. 2007: 557; Gerdeman *et al*. 2010: 93; Di Palma *et al*. 2008: 359; Di Palma *et al*. 2015: 640.
(Figs 10–11, 31–32, 52, 61–62, 81, 91).

Diagnosis. As for the genus.

Type depository. Holotype deposited at OSAL, accession no. OSAL 001259.

Material examined. As listed in Gerdeman & Klompen (2003).

Remarks. Description based on all instars. Associated with *Narceus annularis* (Rafinesque) (Spirobolida: Spirobolidae) from Ohio, U.S.A. (host vouchers at OSAL) (Gerdeman & Klompen 2003).

The anatomy of this species has been studied in some detail: structure spermatodactyl (Di Palma *et al*. 2008), ultrastructure of sperm (Alberti *et al*., 2007), and structure of the female genital system (Di Palma *et al*. 2015). Aspects of its ecology and phenology were studied by Gerdeman *et al*. (2000, 2010).

Afroheterozercon Fain 1989

Afroheterozercon Fain 1989: 147 [type species. *Heterozercon spirostreptus* Fain 1988, by original designation].
Afroheterozercon.—Evans 1992: 426; Klompen *et al*. 2013: 302.

Diagnosis. Spermatodactyl of male of compressed type (7, except in *Af. spirostreptus*); cornicula with a distal notch (24; Fig. 34, arrow); sclerotized areas near insertion sternal setae *st2* in female fused to endopodal shields (38); sclerotized areas near sternal setae *st2* and *st3* in male completely fused (51.0); endopodal and sternitiventral shield in male fused (58, shared with *Maracazercon*); metapodal and sternitiventral shields in male fused (59); sternitiventral and anal shields in male fused, but line of fusion still visible (66.1, shared with several species in other genera); marginal opisthosomal setae anchor-like (78.2); lyrifissures *iv5* in male absent (79).

Remarks. Of the 12 characters that can be distinguished in Fain's (1989) diagnosis of the genus, two (marginal opisthosomal region with numerous anchor-like spines (78), metapodal and sternitiventral shields fused (59)) are unique derived characters, the remainder are either primitive at this level, or are subject to multiple optimizations.

Distinct structures directly posterior to coxae IV of the females (Fig. 67, arrow) are assumed to be secondary genital openings (solenostomes). They are present in females of most species of *Afroheterozercon* examined (see Klompen *et al*. 2013) and absent in all males. The exception is *Af. spirostreptus* where females lack the structures posterior to coxae IV. This is also the only species where the male has a spermatodactyl that resembles the "straight", rather than the "compressed", type (Klompen *et al*. 2013).

Included species –

Afroheterozercon cautus (Berlese 1924)

Heterozercon cautus Berlese 1924: 251.
Afroheterozercon cautus.—Fain 1989: 147; Klompen, Amin & Gerdeman 2013: 321.

Type depository. Holotype deposited at ISZA, accession no. 221/40.

Material examined. Holotype male (ISZA).

Remarks. Based on single male from East Africa (Berlese 1924).

Afroheterozercon ancoratus Fain 1989

Afroheterozercon ancoratus Fain 1989: 153.
Afroheterozercon ancoratus.—Klompen, Amin & Gerdeman 2013: 317.

Type depository. Holotype deposited at RMCA.

Material examined. Holotype male, paratype female (RMCA).

Remarks. Based on females and males ex termite nest (*Cubitermes* sp.), Luki River, Mayumbe forest, Bas Zaire, Dem. Rep. Congo (Fain 1989).

Afroheterozercon pachybolus (Fain 1988)

Heterozercon pachybolus Fain 1988: 241.
Afroheterozercon pachybolus.—Fain 1989: 147; Klompen, Amin & Gerdeman 2013: 308.

Type depository. Holotype deposited at RMCA.

Material examined. Holotype male (RMCA) and specimens as listed in Klompen *et al*. (2013).

Remarks. Based on one male ex *Pachybolus macrosternus* Cook (Spirobolida: Pachybolidae) from Kwango river forest, Dem. Rep. Congo (Fain 1988). Additional material ex unidentified large millipede from Central African Republic (hosts at CASEnt) (Klompen *et al*. 2013).

Afroheterozercon spirostreptus (Fain 1988)

Heterozercon spirostreptus Fain 1988: 237.
Afroheterozercon spirostreptus.—Fain 1989: 147; Klompen, Amin & Gerdeman 2013: 313.

Type depository. Holotype deposited at RMCA.

Material examined. Two paratype females, two paratype males (RMCA) and specimens as listed in Klompen *et al*. (2013).

Remarks. Based on females and males from *Spirostreptus cornutus* Attems (Spirostreptida: Spirostreptidae) from Mayumbe forest, Bas Zaire, Dem. Rep. Congo (Fain 1988). Additional records ex unidentified large millipede (Spirostreptida) from Gabon (host at FMNH, accession no. FMNH-INS-5479 and 5486) (Klompen *et al*. 2013).

Afroheterozercon gabonensis Klompen, Amin & Gerdeman 2013

Afroheterozercon gabonensis Klompen, Amin & Gerdeman 2013: 314.

Type depository. Holotype deposited at FMNH, accession no. OSAL 053942.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex unidentified large millipedes (Spirostreptida) from Gabon (hosts at FMNH, accession no. FMNH-INS-5477 and 5478) (Klompen *et al*. 2013).

Afroheterozercon goodmani Klompen, Amin & Gerdeman 2013

Afroheterozercon goodmani Klompen, Amin & Gerdeman 2013: 316.

Type depository. Holotype deposited at FMNH, accession no. OSAL 102682.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex unidentified large millipedes (Spirostreptida) from Gabon (hosts at FMNH, accession no. FMNH-INS-5479 and 5486) (Klompen *et al*. 2013).

Afroheterozercon madagascariensis Klompen, Amin & Gerdeman 2013

Afroheterozercon madagascariensis Klompen, Amin & Gerdeman 2013: 319.

Type depository. Holotype deposited at FMNH, accession no. OSAL 053960.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex pitfall trap with multiple millipedes from Madagascar (host at FMNH, accession no. FMNH-INS-3957 (Spirostreptida), FMNH-INS-5443 and 3960 (Spirobolida)) (Klompen *et al*. 2013).

Afroheterozercon mahsbergi Klompen, Amin & Gerdeman 2013

Afroheterozercon mahsbergi Klompen, Amin & Gerdeman 2013: 305.
(Figs 12–13, 33–34, 47, 63–64, 82, 92).

Type depository. Holotype deposited at OSAL, accession no**.** OSAL 003042.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex *Pelmatojulus tigrinus* Hoffman & Mahsberg (Spirobolida: Pachybolidae), *Peridontopyge togoensis* Demange, *Peridontopyge maliensis* Pierrard, and *Lacinogonus* sp. (all Spirostreptida: Odontopygidae) (hosts at BUW) from Côte d'Ivoire (Klompen *et al*. 2013).

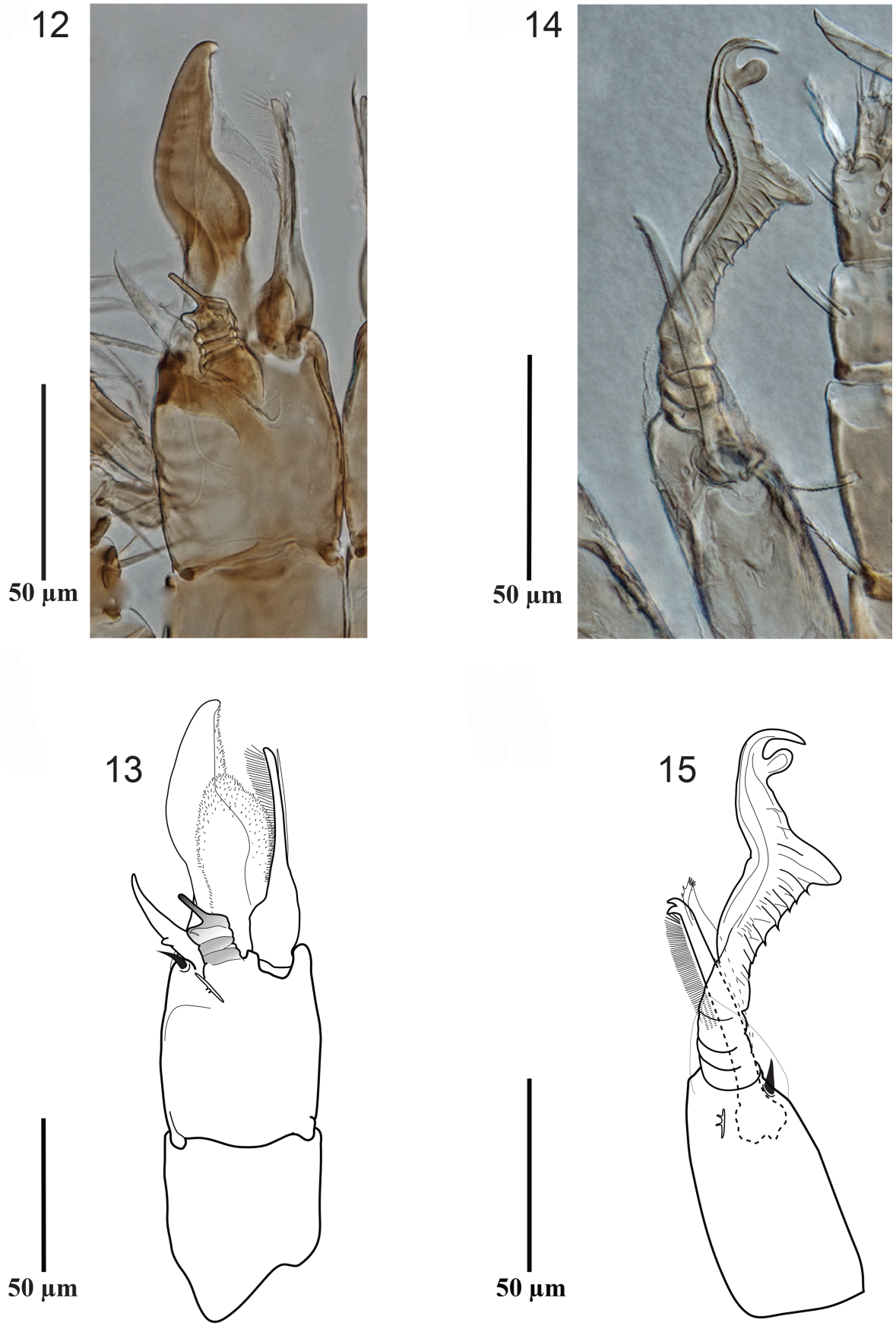
Afroheterozercon sanghae Klompen, Amin & Gerdeman 2013

Afroheterozercon sanghae Klompen, Amin & Gerdeman 2013: 312.

Type depository. Holotype deposited at CASEnt, accession no. CASEnt 9039945.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex unidentified large millipede from Central African Republic (hosts at CASEnt) (Klompen *et al*. 2013).



FIGURES 12–15. Heterozerconidae, chelicera males, photograph (top) and composite drawing (bottom): 12–13, *Afroheterozercon mahsbergi* (OSAL 003045); 14–15, *Heterozercon calakmulensis* (CNAC 012443).

Afroheterozercon tanzaniensis Klompen, Amin & Gerdeman 2013

Afroheterozercon tanzaniensis Klompen, Amin & Gerdeman 2013: 318.

Type depository. Holotype deposited at OSAL, accession no. OSAL 053955.

Material examined. As listed in Klompen *et al*. (2013).

Remarks. Based on females and males ex "common spirostreptid" from Tanzania (no data on host depository) (Klompen *et al*. 2013).

Maracazercon Fain 1989

Maracazeron Fain 1989: 148 [type species: *Maracazeron joliveti* Fain 1989, by original designation].

Diagnosis. Distance from setae *hyp3* to *sc* distinctly smaller than distance from *hyp3* to *hyp2* (21.0); platelets of sternal setae *st2* and *st3* in male completely fused (51); endopodal and sternitiventral shield in male fused (58, shared with *Afroheterozercon*); postanal seta less than 1/3 the length of paranal setae (73); marginal opisthosomal setae hook-like spines (78, shared with *Heterozercon*); femora II setae *al*, *pl*, and *av* in male spines (105–107, shared with *Heterozercon* and *Allozercon*); setae *pl1* on tarsi II spine-like (111; shared with *Ecuazercon*, *Amheterozercon*, *Heterozercon*).

Remarks. The above diagnosis adds some characteristics of the leg setation to Fain's (1989) diagnosis. This genus shares with *Afroheterozercon* the fusion of the endopodal and sternitiventral shields in the male, but differs from that genus by the lack of fusion between the metapodal and sternitiventral shields (58, 59). The resulting pattern of the male ventral shields is unique among Heterozerconidae.

Included species –

Maracazeron joliveti Fain 1989

Maracazercon joliveti Fain 1989: 154.

Type depository. Holotype deposited at IRSNB.

Material examined. Two paratype females, two paratype males (IRSBN).

Remarks. Based on females and males ex *Spirostreptus* sp.(Spirostreptida: Spirostreptidae), from Ilha de Maracá, Brazil (Fain 1989).

Heterozercon Berlese 1892

Heterozercon Berlese 1888: 206 [type species: *Heterozercon degeneratus* Berlese 1888, by monotypy].
Heterozercon.—Fain 1989, 148; Krantz & de Moraes 2011, 26; Di Palma *et al*. 2015, 640.

Diagnosis. Spermatodactyl shape flaccid (7); distance from setae *hyp3* to *sc* distinctly smaller than distance from *hyp3* to *hyp2* (21.0, reversed in some species); anterior dorsal setae *j1* minute (<5 μm) (28.2, few exceptions); female with a distinct curved, sclerotized ridge on anterior margin of female genitiventral shield (46; shared with *Al*. (*Philippinozercon*)); sclerotized areas near sternal setae *st2* in male forming isolated platelets (50); marginal opisthosomal setae hook-like spines (78, shared with *Maracazercon*); coxae I setae in male distinct spines (102, shared with *Narceoheterozercon* ex Alabama-C and a few *Afroheterozercon* species); femora II setae *al*, *pl*, and *av* in male spines (105–107, shared with *Maracazercon* and *Allozercon*); setae *pl1* on tarsi II spine-like (111, shared with *Ecuazercon*, *Amheterozercon*, *Maracazercon*).

Remarks. Available descriptions for the three described species are incomplete, a situation that is problematic especially given that *Heterozercon* is the type genus of the family. It suggests a need for a more complete descrip-

tion. We have examined specimens of undescribed populations that belong to the genus *Heterozercon* from Cuba, Venezuela, Brazil, Costa Rica, Nicaragua, Belize, and Mexico. The specimens from Cuba and Venezuela stand apart because of the heavy cuticular patterning on the venter (Fig. 51) and population Costa Rica 2 is unusual because of the extremely small opisthogastral suckers (much smaller than in *H. microsuctus* Fain). For this reason, we selected specimens from Campeche state in Mexico for description. This population is considered more representative for the genus. A more extensive revision of the *Heterozercon* species of Mexico is in progress (Martinez *et al*., in prep.).

The female genital system of an undescribed *Heterozercon* species from Brazil was described by Di Palma *et al*. (2015). These authors noted the presence of secondary genital openings (solenostomes) in females on the axial side of the opisthogastral suckers. This observation was confirmed in four different species examined in this study (*H. calakmulensis* n. sp., unidentified populations from Brazil, Costa Rica, Cuba). The openings are not very distinct and may be associated with small, sclerotized patches (Fig. 61, arrow).

Nymphs that probably belong to this genus have been described by Krantz & de Moraes (2011) from Brazil, although definitive associations with adults could not be made.

Included species –

Heterozercon degeneratus Berlese 1888.

Heterozercon degeneratus Berlese 1888: 207.
Heterozercon degeneratus.—Berlese 1892: 97; Fain 1989: 145.

Type depository. Holotype at ISZA, accession no. 57/43.

Material examined. None.

Remarks. Based on a single female collected under tree bark in Mato Grosso state, Brazil (Berlese 1888).

Heterozercon latus Berlese 1902

Heterozercon latus Berlese in Berlese & Leonardi 1902: 14.
Heterozercon latus.—Silvestri 1903: 172; Fain 1989: 145.

Type depository. Holotype at ISZA, accession no. 7 Myrm/16.

Material examined. None.

Remarks. Based on a single female from a termite nest (*Anoplotermes pacificus* Müller), Tacuri Pucu, Paraguay (Berlese 1892). Redescribed by Silvestri (1903)

Heterozercon microsuctus Fain 1989

Heterozercon microsuctus Fain 1989: 155.

Type depository. Holotype at IRSNB.

Material examined. Holotype male (IRSNB).

Remarks. Based on a single male on *Spirostreptus* sp. (Spirostreptida: Spirostreptidae), Ilha de Maracá, Brazil (Fain 1989).

Heterozercon calakmulensis new species
(Figs 14–15, 37–38, 67–68, 84, 94)

Diagnosis. Spermatodactyl complex, with a rounded protrusion just below the pointed tip; distance between setae *hyp3* and *sc* subequal to that between *hyp3* and *hyp*2; sternitiventral shield without distinct ridges; setae *Z5* minute, much smaller than *S5*; ventral and anal shields in male not fused.

Description. Female idiosoma length 834, width 698 (N=1); male idiosoma length 712, width 598 (N=1). All measurements in Tables 3–4.

Chelicera (Figs 14–15). Basal part of fixed digit in female stout, length width ratio 1–2. Movable digit in adults with thin, straplike dorsal extensions. Movable digit in female elongate, digit length >6 times basal width. Inside movable digit female with brush-like structure. Excrescences on male chelicera present, interdigital. Spermatodactyl on fixed digit of male chelicera, of the flaccid type.

Palp. Axial outgrowth of palp trochanter in female and male distinct and membranous. Seta *pd1* on femur present. Setae on femur long, thick spines. Seta *al2* and *pl* on genu present. Number of sensilla on palp tarsus 10–11. Formula: 2–6–5–14–10/11.

Gnathosoma (Figs 37–38). Gnathotectum of female without prominent points. Anterior margin gnathotectum not serrate. Overall shape of gnathotectum curved. Sexual differentiation in gnathotectum absent. Lateral lips enlarged to form a trough; posterior extension of the trough long, extending distinctly beyond insertions of setae *hyp2*. Distance between setae *hyp3* and *sc* subequal to that between *hyp3* and *hyp2*. Setae *hyp2* at least twice as long as *hyp3*. Cornicula membranous without distal notch. Additional setal base-like structure on hypostome present.

Dorsum. Dorsal shield in adults covering most of the dorsum; shield with distinct reticulation. Anterior dorsal margin in adults without elongate setae; setae *j1* absent or not distinct (e.g., minute). Antero-marginal area of dorsal shield in males without distinct spines. Median dorsal setae minute. Posterior dorsal setae (*Z2–Z4*) minute.

Sternal area female (Fig. 67). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sclerites of sternal setae *st1* and *st2* not fused. Sternal setae *st1* and lyrifissures *iv1* inserted on the same shield. Areas near insertion sternal setae *st2* sclerotized, forming isolated platelets. Areas near insertion sternal setae *st3* sclerotized, fused to genitiventral shield. Metasternal setae *st4* absent. Areas near insertion sternal setae *st5* sclerotized, fused to genitiventral shield. Sternal lyrifissures *iv1*, *iv2*, and *iv3* present. Distinct curved, sclerotized ridge on anterior margin of female genitiventral shield present.

Sternal area male (Fig. 68). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sternal setae *st1* and lyrifissures *iv1* inserted on the same shield. Sclerotized areas near insertion sternal setae *st2* forming isolated platelets. Sclerotized areas of sternal setae *st2* and *st3* not fused. Sclerotized areas near insertions sternal setae *st3* and *st5* fused with sternitiventral shield. Sternal lyrifissures *iv1*, *iv2*, and *iv3* present. Male genital opening presternal. Genital shields not overlapping base of the tritosternum. Sternitiventral area in male relatively smooth, with a few cuticular bumps, otherwise surface faintly reticulate.

Opisthogaster (Figs 67–68). Metapodal and sternitiventral shields in adults not fused. Posterolateral margin of metapodal shields rounded. Setae *Zv3* absent. Opisthogastral suckers present, posterior to ventral shield, of heterozerconid type. Secondary genital openings of female on axial side of opisthogastral suckers, associated with a few small sclerites (Fig. 67, arrow). Apodemes extending from opisthogastral suckers absent. Ventral shield area with a single shield. Sternitiventral and anal shields in male partly fused, not fused in female. Setae *Sv2* not inserted on genitiventral (female) or sternitiventral (male) shield. Setae *Sv3* inserted on genitiventral (female) or sternitiventral (male) shield. Setae *Jv5* inserted anterior to ventrianal line. Insertion paranal setae (*pa*) at level of anus. Postanal (*po*) seta similar in length to paranal (*pa*) setae. Setae *Z5* minute; setae *S5*, *R5* and *R4* of medium length. Number of marginal opisthosomal setae small, modified into hook-like spines. Lyrifissures *iv5* inserted near anterior margin of suckers. Postero-marginal shield in both sexes wide, extending lateral well beyond opisthogastral suckers.

Legs (Figs 84, 94). Tibiae and tarsi of legs I of similar width as rest of the leg. Acrotarsus on legs I present. Femora I setae *ad3* and *pl2* present, setae *v3* and *v4* absent. Genua I setae *ad3* and *pd3* absent. Tibiae I seta *ad2* present, setae *ad3*, *av2* and *pv2* absent. Femora II setae *av2* and *pv2* absent. Genua II–IV setae *ad3* and *pl2* absent. Genua II seta *pd3* absent, genua III–IV seta *pd3* present. Tibiae II–IV setae *ad2*, *pd3* and *pl2* absent. Femora III seta *v3* absent. Tarsi IV setae *av4* and *pv4* absent. Complete chaetotaxy in Table 2. Both coxae I setae in male distinct spines with rounded tips. Femora I setae *al1* and *al2* in male spine-like, in anteroventral position; setae *al1* and *al2* in female sturdy setae, not spines. Femora I seta *av* and *pv* in male large straight spines; setae *av* and *pv* in female spines, but much shorter than in male. Femora II seta *al* in male spine-like and ventral in position, setae *av* and *pv* in male spines; setae *av* and *pv* in female much thinner. Genua II seta *pv* and tibiae II seta *pv* in male spines, barely half as long as seta *av*; setae *pv* in female setiform and as long as *av*. Tarsi II seta *pl1* a spine in both sexes, thinner in female. Trochanters III in male with seta *al* spine-like, setae *av* and *pl* setiform.

Type depository. Holotype male, accession number CNAC 012443, and female paratype, CNAC 012444, at CNAC.

Material examined. Mexico: Campeche, Calakmul Biosphere Reserve, Bel-Ha, ~150m, 18.9473 N 89.3155 W, 5–Jul-2005, Vázquez, M. M., 1 male, CNAC 012443, holotype; same data, 1 female, CNAC 012444, paratype.

Etymology. The species name is derived from the collecting locality, near the ruins of the ancient Mayan city of Calakmul.

Remarks. *Heterozercon calakmulensis* differs from *H. microsuctus* in the shape of the spermatodactyl (with a rounded protrusion near the tip which is absent in *H. microsuctus*) and in the size of the opisthogastral suckers (of "standard" size vs. distinctly smaller than average in *H. microsuctus*). Distinguishing this species from the Berlese species, *H. degeneratus* and *H. latus*, is more problematical given the lack of detail in these older descriptions. It appears that *H. degeneratus* shares the relatively small opisthogastral suckers with *H. microsuctus* (as already noted by Fain (1989)) but neither Berlese (1902) or Silvestri (1903) provide sufficient information to distinguish *H. calakmulensis* from *H. latum*.

The designation of the medium pair of longer setae on the posterior margin sclerite as *S5* is based on comparative observations for other *Heterozercon* species. Some of these show the same arrangement as *H. calakmulensis*, in others an added pair of distinctly longer setae is visible internal of, but very close to, the setae here designated as *S5*. We consider that pair of setae *Z5*. Because no such setae can be observed in *H. calakmulensis* we hypothesize that *Z5* in *H. calakmulensis* are absent or, more likely, reduced to the size of the accessory setae on the sclerite.

Heterozercon sp. (published records of unidentified species).

Unidentified specimens of Heterozerconidae were recorded from *Rhinocricus duvernoyi* (Karsch) (Spirobolida: Rhinocricidae) in La Habana province, Cuba (Prieto Trueba & Tcherva 2005). These specimens most likely belong to the genus *Heterozercon* given that we have studied specimens of that genus from Cuba.

Allozercon Vitzthum 1926

Allozercon Vitzthum 1926: 104 [type species. *Allozercon fecundissimus* Vitzthum 1926, by original designation].

Allozercon.—Womersley 1958: 129; Flechtmann & Johnston 1990: 147; Gerdeman & Garcia 2010: 93; Di Palma *et al*. 2015: 640; Gerdeman *et al*. 2018: 9.

Asioheterozercon Fain 1989: 146 (type species *Heterozercon audax* Berlese 1910 by original designation); Evans 1992: 426 [junior synonym of *Allozercon* Vitzthum 1926 by Gerdeman *et al*. 2018: 9].

Alloheterozercon.—Gerdeman & Klompen 2003: 353 [incorrect subsequent spelling].

Diagnosis. Axial outgrowth of palp trochanter in male distinct and sclerotized, solid (9); setae *hyp2* at least twice as long as setae *hyp3* (22); insertion sternal setae *st2* and *st3* in female and *st3* in male on isolated platelets (38, 40, 52); insertion sternal setae *st1* in male on isolated platelets (48); opisthogastral setae *Jv5* inserted posterior to ventrianal fusion line (71); all marginal opisthosomal setae setiform (77, reversal); femora II setae *al*, *pl*, and *av* in male spines (105–107, shared with *Maracazercon* and *Heterozercon*); genual and tibial setae *pv* on legs II in male spine-like (109, 110).

Remarks. A re-evaluation of the 11 characters listed by Fain (1989) for the genus *Asioheterozercon*, shows that two are included in the updated diagnosis of *Allozercon* listed above: palpal trochanter with its apico-internal angle strongly produced and bearing 2 setae (our character 9) and anal shield with five setae (71). Three of the remaining characters are variable among the S.E. Asian populations: tarsus and tibia of legs I much narrower than the other segments of that leg (81.2); anterior region of the dorsum with 20–40 long and stiff setae (29.1); antero-lateral margin of dorsal shield in male with numerous small spines (30.1). One is incorrect: palp trochanter in female bears only one seta. Seta *v2* is in fact present and is inserted on the membranous axial outgrowth of the trochanter. However, it is highly reduced (Fig. 39). The remaining characters are imprecise or refer to primitive character states at this taxonomic level. To further clarify the status of *Allozercon* a complete description is provided for one of the nine geographically separate populations for which we have specimens available. These nine populations originate in the Philippines (Bohol, Leyte, Mindoro, Samar, and Siquijor islands), Thailand (Saraburi and Bangkok), Laos, and India. The remaining taxa will be described in an upcoming revision of the genus.

Di Palma *et al*. (2015), in a study of the anatomy of the female genital system, found no indication of second-

ary genital openings (solenostomes) in females of an unidentified *Allozercon* species from Cebu island, Philippines. Examination of all available slide mounted *Allozercon* females also failed to find any indication of secondary genital openings either near the opisthogastral suckers (as in *Heterozercon* or *Narceoheterozercon*) or posterior to coxae IV (as in *Afroheterozercon*). In the absence of evidence to the contrary, we assume that *Allozercon* species do not have a secondary genital system in the females.

Immatures of an *Allozercon* species from Bangkok, Thailand were partially described in Gerdeman *et al*. (2018), but a complete description of *Allozercon* immatures is not yet available.

Allozercon Błaszak 1984 (Zerconidae) is a junior homonym of *Allozercon* Vitzthum 1926 (Kemal & Koçak 2009; Koçak & Kemal 2008). The zerconid genus name was replaced by *Blaszakzercon* Kemal & Koçak (Gerdeman *et al*. 2018).

Included species –

Allozercon fecundissimus Vitzthum 1926

Allozercon fecundissimus Vitzthum 1926: 107.
Allozercon fecundissimus.—Womersley 1958: 129; Fain 1989: 145.

Type depository. Holotype was deposited in the Vitzthum collection. It is lost.

Material examined. None.

Remarks. The description was based on a single specimen collected from litter at Bogor (as Buitenzorg), Java, Indonesia (Vitzthum 1926). While the specimen figured by Womersley (1958) almost certainly belongs to the genus *Allozercon*, the species level identification is uncertain given that Vitzthum's specimen came from Java, and Womersley's from continental Malaysia.

Allozercon audax (Berlese 1910) n. comb.

Heterozercon audax Berlese 1910b: 247.
Heterozercon audax.—Vitzthum 1925: 37; Fain 1989: 145.
Heterozercon elapsus Vitzthum 1926: 106 [junior synonym of *Heterozercon audax* Berlese 1910 by Vitzthum 1925: 37].

Type depository. Holotype of *H. audax* at ISZA, accession number 87/4. The holotype and unique specimen of *H. elapsus* was lost before completion of the description and the description was prepared entirely from memory (Vitzthum 1926).

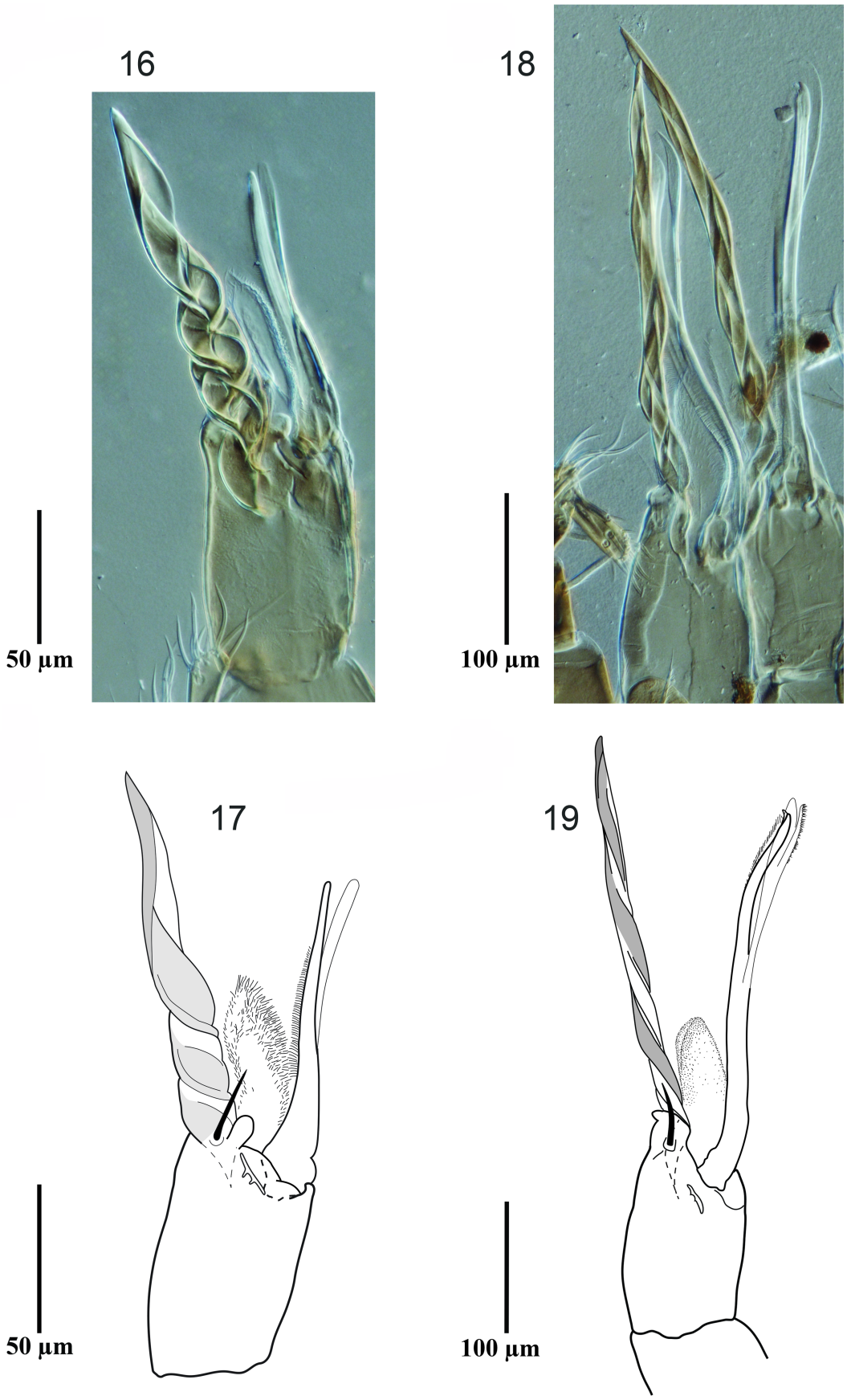
Remarks. Based on females and males from "*Scolopendra*" spp. and "*Spirostreptus depak*" spp. from at least three different localities on Java, Indonesia (Berlese 1910b); *H. elapsus* on *Thyropygus* sp. (Spirostreptida: Spirostreptidae) collected on Sumatra, Indonesia (Vitzthum 1926). Fain (1989) noted that *H. elapsus* may be a valid species.

Allozercon leytensis new species
(Figs 18–19, 39–40, 69–70, 85, 95)

Diagnosis. Anterior dorsal body margin in both adults with multiple medium to long setae; antero-marginal area of dorsal shield in males with small, hook-like spines; sternal lyrifissures *iv3* in male absent.

Description. Female idiosoma length 1530 (152), width 1287 (186) (N=5); male idiosoma length 1311 (73), width 1058 (32) (N= 5). Complete measurements in Tables 3–4.

Chelicera (Figs 18–19). Basal part of fixed digit in female stout, length width ratio 1–2. Movable digit in adults with thin, straplike dorsal extensions. Movable digit in female elongate, digit length >6 times basal width. Inside movable digit female with brush-like structure. Excrescences on male chelicera interdigital. Spermatodactyl on fixed digit of male chelicera, of the straight type.



FIGURES 16–19. Heterozerconidae, chelicera males, photograph (top) and composite drawing (bottom): 16–17, *Allozercon* ex Mindoro (OSAL 053284); 18–19, *Allozercon leytensis* n. sp. (OSAL 053250).

Palp. Axial outgrowth of palp trochanter in female distinct and membranous. Seta *v2* in female poorly developed, setal base barely visible. Axial outgrowth of palp trochanter in male distinct and sclerotized, solid. Seta *pd1* on femur present. Setae on femur long, thick spines. Seta *al2* on genu absent, seta *pl* present. Number of sensilla on palp tarsus 12. Formula: 2–6–5–14–12.

Gnathosoma (Figs 39–40). Gnathotectum of female without prominent points. Anterior margin gnathotectum not serrate. Overall shape of gnathotectum curved. Lateral lips enlarged to form a trough; posterior extension of the trough long, extending distinctly past insertions of setae *hyp2*. Distance between setae *hyp3* and *sc* subequal to that between *hyp3* and *hyp2*. Setae *hyp2* at least twice as long as *hyp3*. Cornicula membranous, without distal notch. Additional setal base-like structure on hypostome present.

Dorsum (Figs 48–50). Dorsal shield in older females not fully covering the dorsum, shield in recently molted females and in males covering entire dorsum. Peritrematal shield may be adjacent to dorsal shield but never fused to it. Anterior dorsal margin of idiosoma in both sexes with multiple medium to long setae, inserted anterior to the dorsal shield in females, on the shield in males (average number female 8 (1); male 7 (3)). Antero-marginal area of dorsal shield in males with small, hook-like spines (average number 31 (2)). Median dorsal setae minute. Posterior dorsal setae *Z2–Z4* minute.

Sternal area female (Fig. 69). Areas near insertion sternal setae *st1* sclerotized, forming isolated platelets. Sclerites of sternal setae *st1* and *st2* not fused. Sternal setae *st1* and lyrifissures *iv1* inserted on the same shield. Areas near insertion sternal setae *st2* sclerotized, forming isolated platelets. Areas near insertion sternal setae *st3* sclerotized, fused to genitiventral shield or on isolated platelets close to genitiventral shield. Metasternal setae *st4* absent. Areas near insertion sternal setae *st5* sclerotized, fused to genitiventral shield. Sternal lyrifissures *iv1* in adults present. Sternal lyrifissures *iv3* absent. Distinct curved, sclerotized ridge on anterior margin of genital shield absent.

Sternal area male (Fig. 70). Areas near insertion sternal setae *st1* sclerotized, fused to endopodal shield. Sternal setae *st1* and lyrifissures *iv1* inserted on same shield. Sclerotized areas near insertion sternal setae *st2* fused to endopodal shield. Sclerotized areas of sternal setae *st2* and *st3* not fused. Areas near insertion sternal setae *st3* sclerotized, fused to sternitiventral shield or on isolated platelets adjacent to sternitiventral shield. Sclerotized areas near insertion sternal setae *st5* fused with sternitiventral shield. Sternal lyrifissures *iv3* absent. Genital opening presternal. Genital shield overlaying base of the tritosternum. Sternitiventral area smooth.

Opisthogaster (Figs 69–70). Metapodal and sternitiventral shields in male not fused. Posterolateral margin of metapodal shields in adults rounded. Setae *Zv3* in adults absent. Opisthogastral suckers in adults present, posterior to ventral shield, heterozerconid type. Apodemes extending from opisthogastral suckers present, small but distinct knobs in posterior position (both sexes). Ventral shield area with a single shield. Sternitiventral and anal shields in male fused, but line of fusion still visible. Setae *Sv2* and *Sv3* inserted on the genitiventral (female) or sternitiventral (male) shields. Additional seta(e) present in unsclerotized area between metapodal and ventrigenital shields. Setae *Jv5* inserted posterior to ventrianal fusion line. Insertion paranal setae (*pa*) posterior to the anus. Postanal (*po*) seta of similar length as paranal (*pa*) setae. Setae *Z5* in male elongate, setae *S5* medium in length. Marginal opisthosomal setae small, setiform. Lyrifissures *iv5* inserted near anterior margin of the suckers. Postero-marginal shields in both sexes wide, extending lateral well beyond opisthogastral suckers.

Legs (Figs 85, 95). Tibiae and tarsi of legs I somewhat narrowed relative to the rest of the leg. Acrotarsus on legs I present. Femora I setae *ad3* and *pl2* present, setae *v3* and *v4* absent. Genua I setae *ad3* and *pd3* absent. Tibiae I seta *ad2* present, setae *ad3*, *av2* and *pv2* absent. Femora II setae *av2* and *pv2* absent. Genua II–IV setae *ad3* and *pl2* absent. Genua II setae *pd3* absent, genua III–IV seta *pd3* present. Tibiae II–IV setae *ad2*, *pd3* and *pl2* absent. Femora III seta *v3* absent. Tarsi IV setae *av4* and *pv4* absent. Complete chaetotaxy in Table 2. Coxae I setae in male setiform. Femora I setae *al1* and *al2* in male spinose, in anteroventral position. Femora I seta *av* in male large, straight spine. Femora II seta *al* in male setiform. Femora II seta *pl* in male spine and ventral in position. Femora II setae *av* and *pv* in male spines. Genua II seta *pv* and tibiae II seta *pv* in male spines, barely half as long as setae *av*; in female setiform and as long as *av*. Tarsi II seta *pl1* in both sexes setiform. Trochanters III in male: seta *al* spine-like, setae *av* and *pl* setiform.

Type depositories: Holotype male at UPLB, accession number UPLB MNH ACA-01335. Paratypes at UPLB and OSAL

Material examined. Philippines, Leyte Prov., Leyte Is., VISCA, Hubasan Creek, 10.7731 N 124.8109 E, 7–Jun-2000, Gerdeman, Beverly S. & Garcia, Rufino C., ex millipede, BSG 00–0607–45, 1 male, holotype, UPLB MNH ACA-01335. Same data, 1 female, OSAL 053240; 1F, OSAL 053241; same locality, date and collectors, ex big black millipede, BSG 00–0607–13,14,15,16, 1 female, OSAL 0053242; same data, 1 female, OSAL 053243; 1

male, OSAL 053244; ex big black female millipede, BSG 00–0607–19–21, 1 female, OSAL 053245; 1 female, OSAL 053246; 1 female, OSAL 053247; 1 male, OSAL 053248; ex big brown male millipede, BSG 00–0607–41, 1 female, OSAL 053249; ex litter, 1 male, OSAL053250; 1 female, OSAL 053251; Philippines, Southern Leyte Prov., Leyte Is., Silago, 10.5333 N 125.1178 E, 16–Jun-2000, Gerdeman, Beverly S., Garcia, Rufino C., ex litter, BSG 00–0616–1, 1 female, OSAL 053184; same locality, date and collectors, ex black female millipede, BSG 00–0616–12, 1 male, OSAL 053185; 1 male, OSAL 106780.

Etymology. Named after the island on which the specimens were recovered.

Remarks. *Allozercon leytensis* differs from both *Al. audax* and *Al. fecundissimus* by the presence of a set of distinct setae on the anterior margin of the body and from *Al. elapsus* (= *audax*) by much shorter setae *Z5*.

Specimens of *Al. leytensis* occasionally co-occurred with specimens of *Al.* (*Philippinozercon*) sp. on the same millipede hosts. Co-occurrence of multiple species of Heterozerconidae on a single host individual was previously reported for *Afroheterozercon* species in Central African Republic and Gabon (Klompen *et al*. 2013) and, as noted earlier, for *Amyzozercon* and *Ecuazercon* on polydesmids in Ecuador.

Allozercon (*Philippinozercon*) (Gerdeman, Garcia, Herczak & Klompen 2018) n. comb.

Philippinozercon Gerdeman, Garcia, Herczak & Klompen (2018): 10 [type species: *Philippinozercon makilingensis* Gerdeman, Garcia, Herczak & Klompen 2018, by original designation].

Diagnosis. Axial outgrowth of palp trochanter in male distinct and membranous (9, reversal?); palp genu seta *pl* absent in adults (13); anterior dorsal setae *j1* minute (<5 μm) (28.2, with few reversals); distinct curved, sclerotized ridge on anterior margin of female genitiventral shield present (46; shared with *Heterozercon*); postero-lateral margin of metapodal shields appears cut off, with sharp angle (61), setae *S5* in male minute (75).

Remarks. In terms of the number of unique characters, *Philippinozercon* has more apomorphies than the majority of heterozerconid genera. Even so, it consistently appears as nested within *Allozercon*, and is therefore reclassified as a subgenus of *Allozercon*.

Allozercon (*P.*) *makilingensis* is one of only two species of Heterozerconidae for which all immature instars have been described (Gerdeman *et al*. 2018). Basic phenology of this species was described in Gerdeman & Garcia (2009(2010)).

Included species –

Allozercon (*Philippinozercon*) *makilingensis* (Gerdeman, Garcia, Herczak & Klompen 2018) n. comb.

Philippinozercon makilingensis Gerdeman, Garcia, Herczak & Klompen 2018: 11.
(Figs 3, 22, 41–42, 70–71, 85, 95)

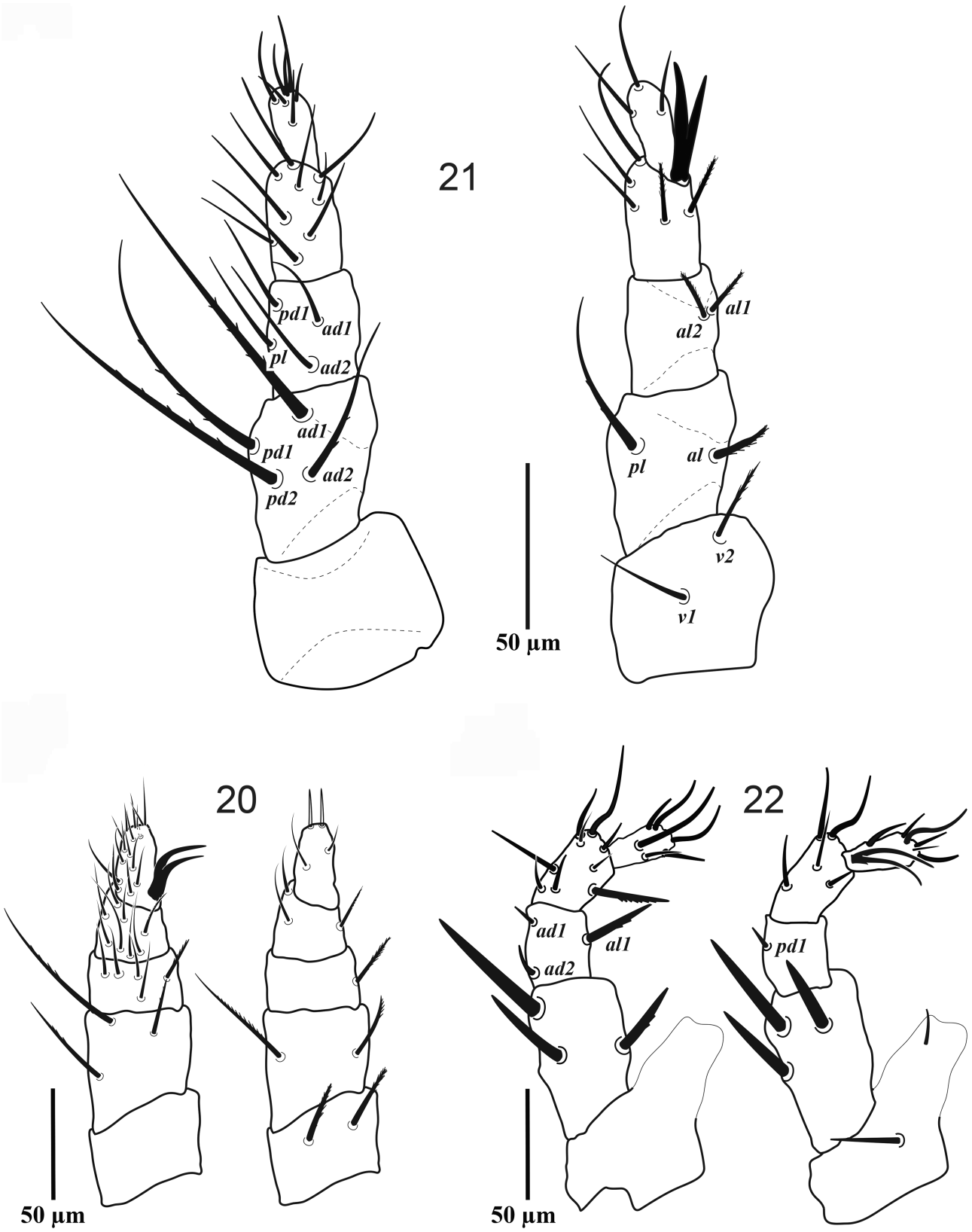
Type depository. Holotype at UPLB, accession no. OSAL 053267.

Material examined. As in Gerdeman *et al*. (2018).

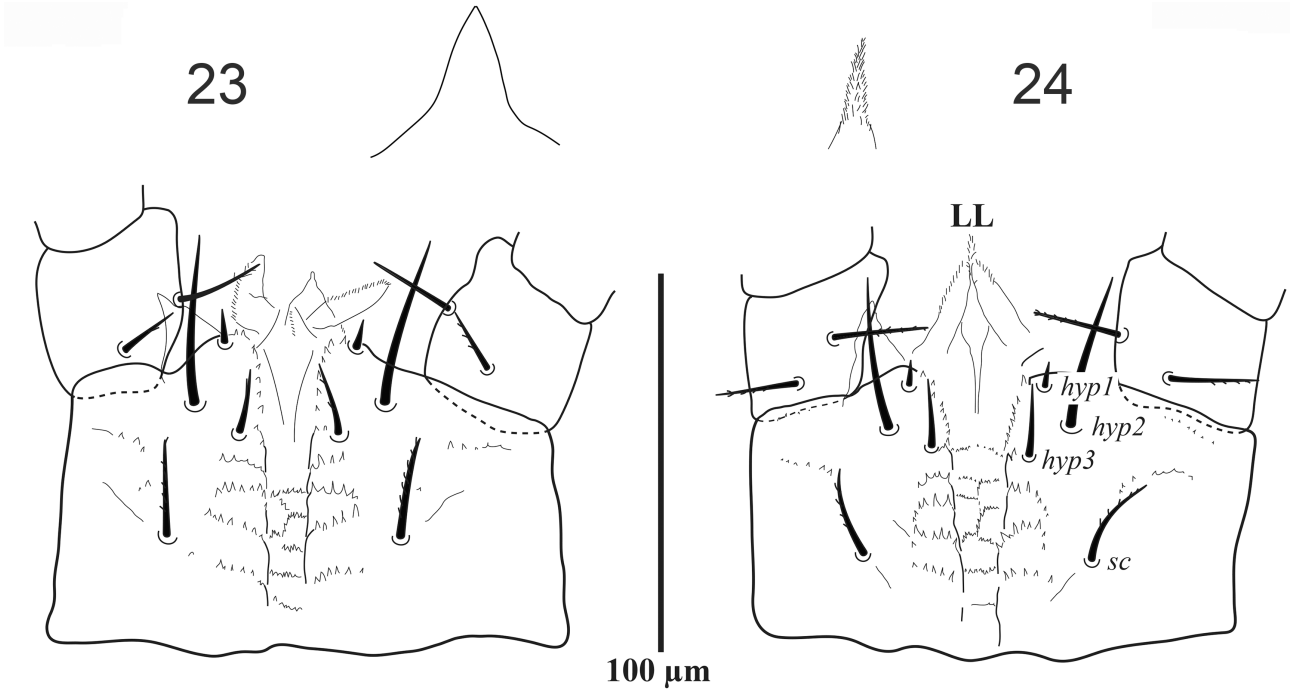
Remarks. Based on all instars, ex millipede frass and millipedes from the Philippines. Some millipede hosts identified as *Trigoniulus macropygus* Silvestri (Spirobolida: Trigoniulidae), others still unidentified (hosts at FMNH) (Gerdeman *et al*. 2018).

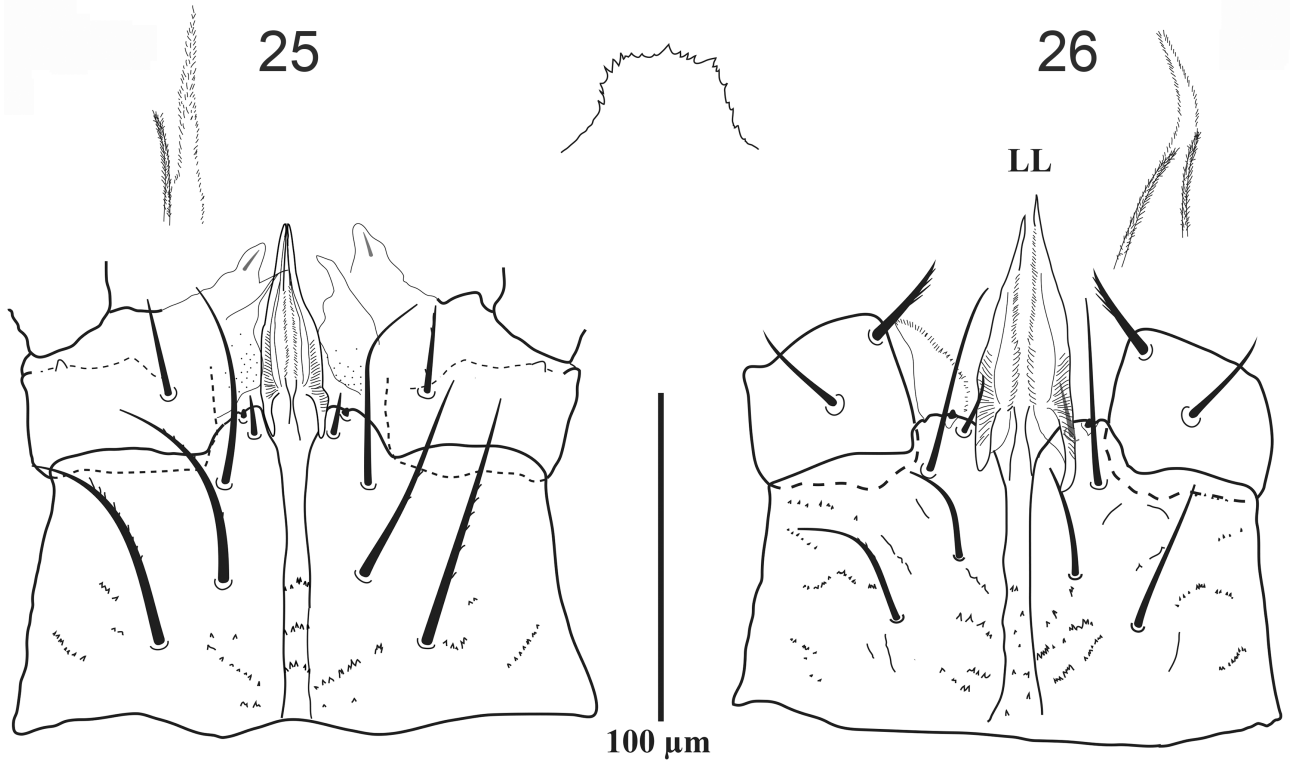
Allozercon sp. (published records of unidentified species).

Unidentified specimens of Heterozerconidae were recorded from *Phyllogonostreptus nigrolabiatu*s (Newport) (Spirostreptida, Harpagophoridae) from Dhawrwar, Mysore, India (Rangaswamy & Channa Basavanna 1973), from Paradoxosomatidae (Polydesmida) on Cebu island, Philippines (Di Palma *et al*. 2015), and from unidentified millipedes in Malaysia (Fain 1989), the Philippines (Gerdeman & Garcia 2010), and Laos (Di Palma *et al*. 2015). Given the collection localities, all of these specimens most likely belong to the genus *Allozercon*.

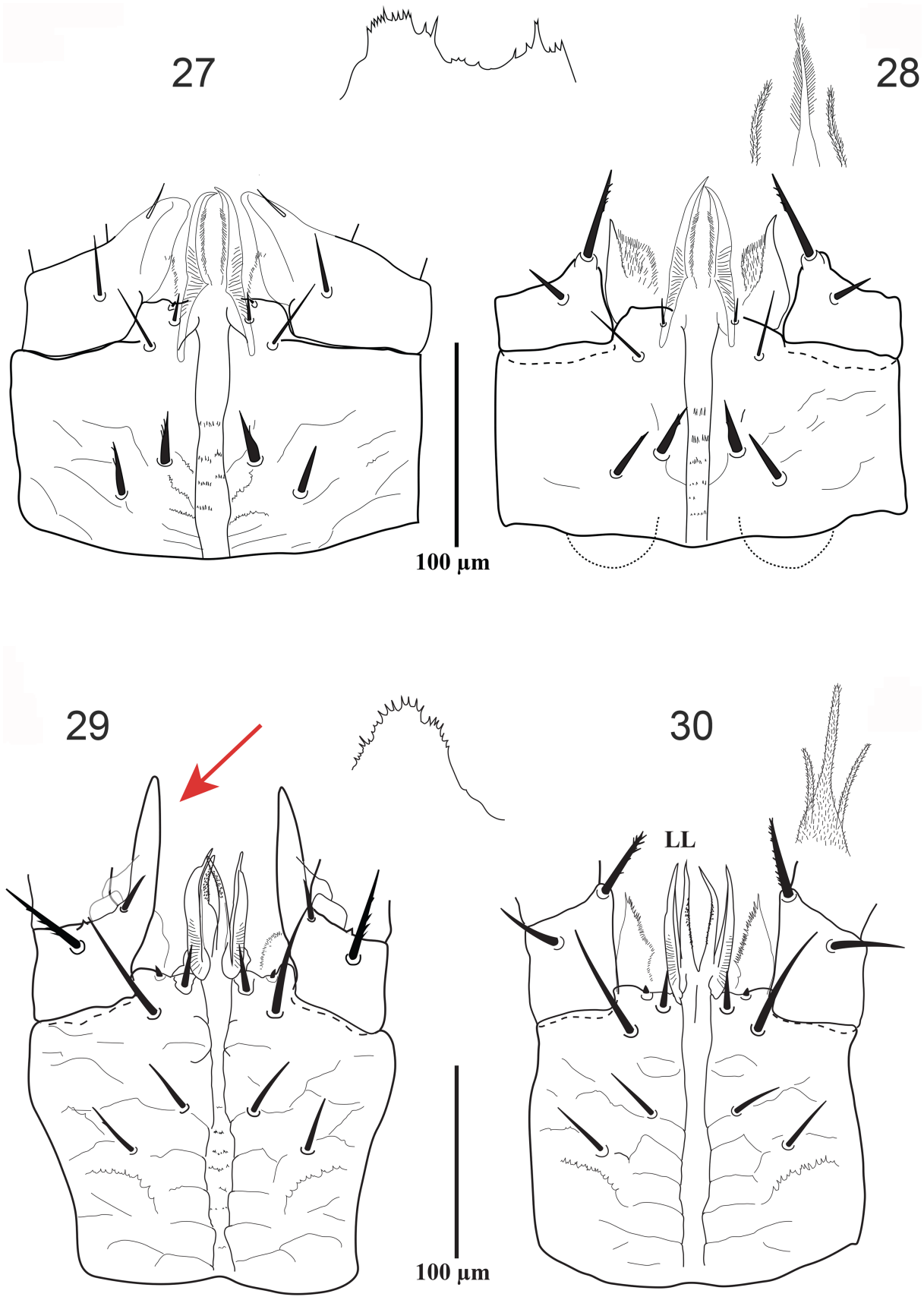


FIGURES 20–22. Left palp, adults: 20, Discozerconidae, *Discomegistus* sp., male (FMNH); 21; Heterozerconidae, *Amyzozercon chocoensis*, male (OSAL 106788); 22, *Al.* (*Philippinozercon*) *makilingensis*, male (OSAL 053267, redrawn from Gerdeman *et al*. (2018)).

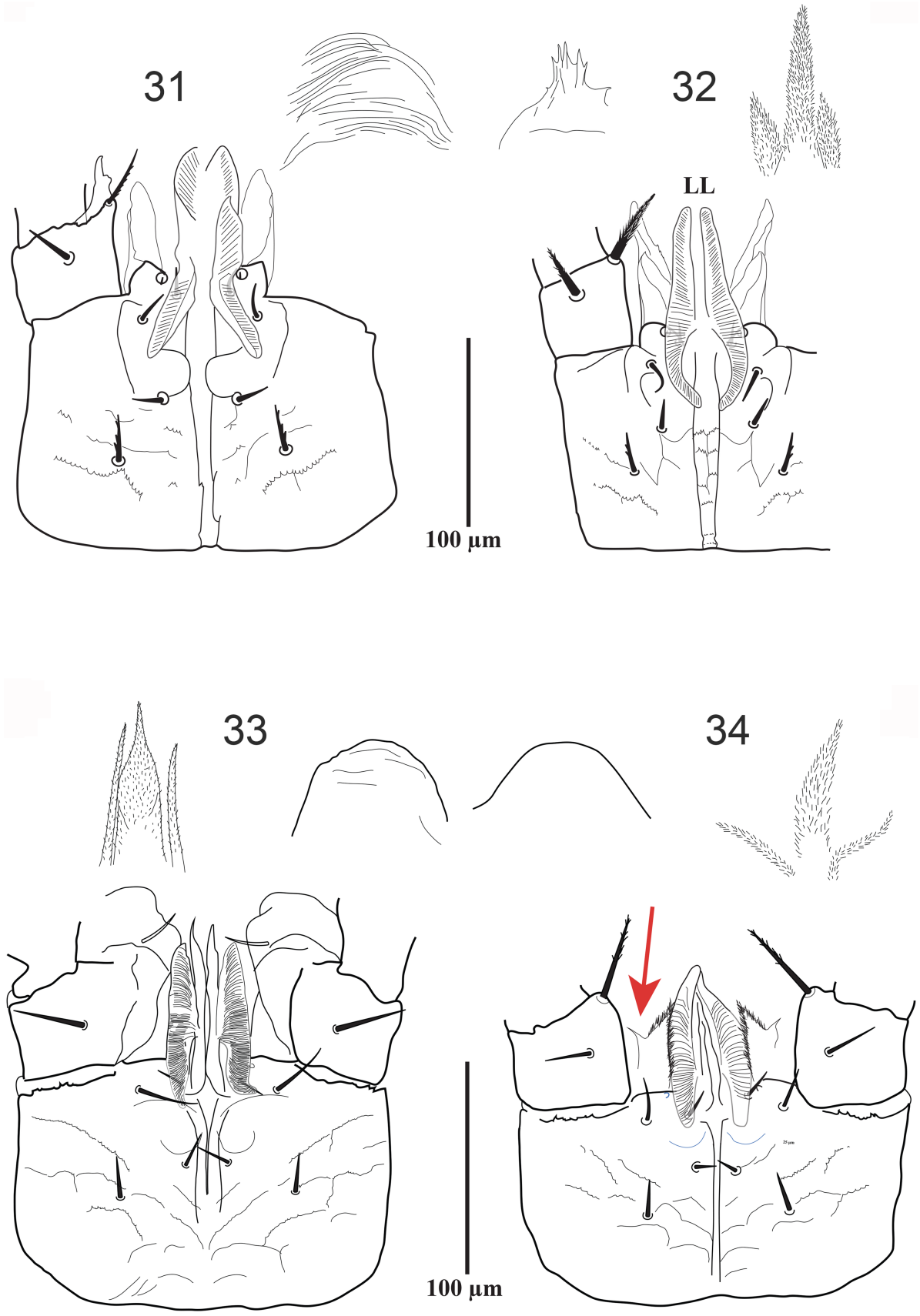




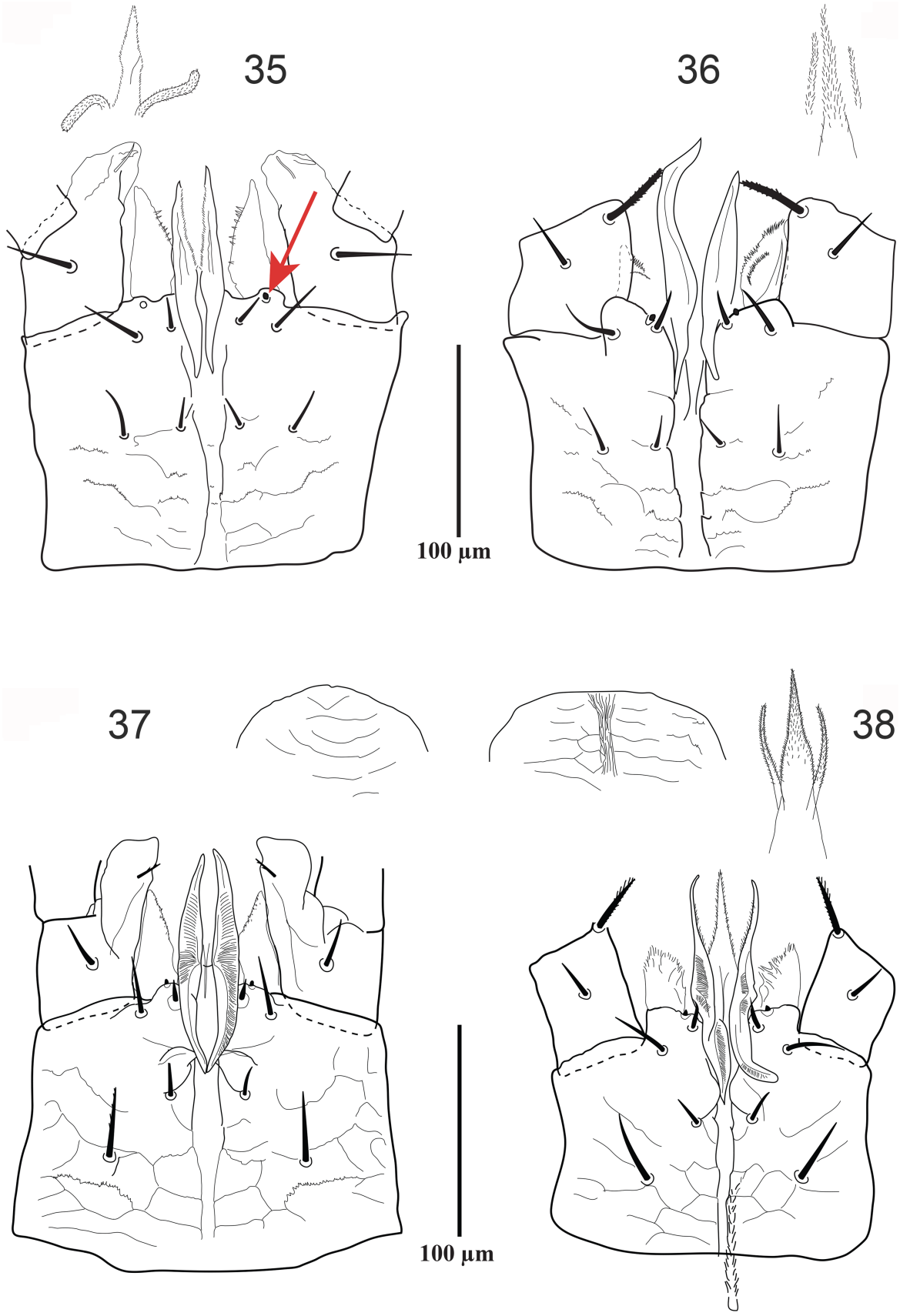
FIGURES 23–26. Gnathosoma, adults: 23, Discozerconidae, *Discozercon derricki*, female (OSAL 052739); 24, *Discozercon derricki*, male (OSAL 004889); 25, Heterozerconidae, *Amyzozercon chocoensis*, female (OSAL 106787); 26, *Amyzozercon chocoensis*, male (OSAL 106721). Insets gnathotectum and labrum + salivary stylets. Abbreviations: LL, lateral lips.



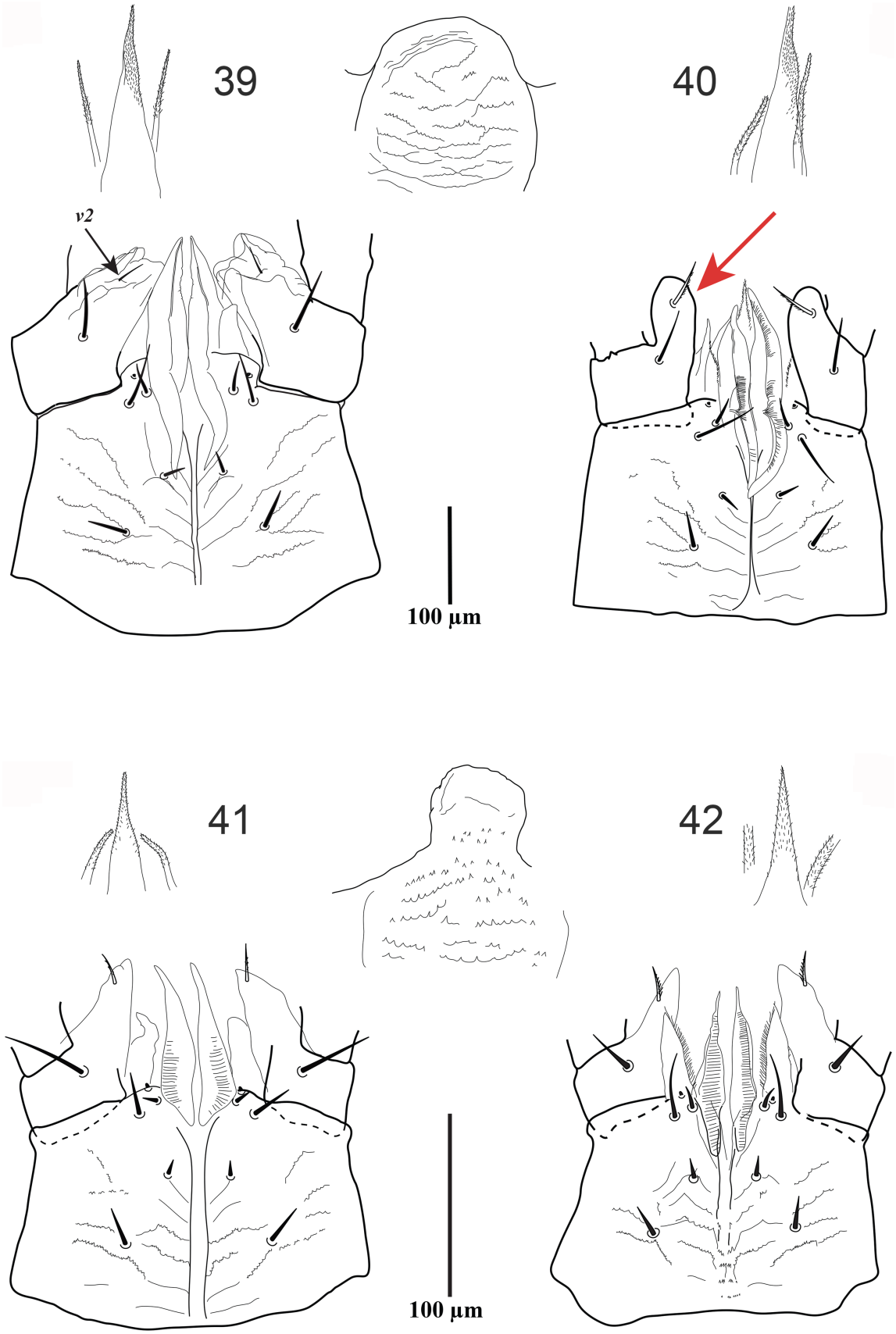
FIGURES 27–30. Heterozerconidae, gnathosoma, adults: 27, *Ecuazercon cushuimensis*, female (FMJK 71–1118); 28, *Ecuazercon cushuimensis*, male (FMJK 71–1114); 29, *Amheterozercon amphisbaenae*, female (OSAL 052751; red arrow: sclerotized axial extension of palp trochanter); 30, *Amheterozercon amphisbaenae*, male (OSAL 052761). Inset: gnathotectum and labrum + salivary stylets. Abbreviations: LL, lateral lips.



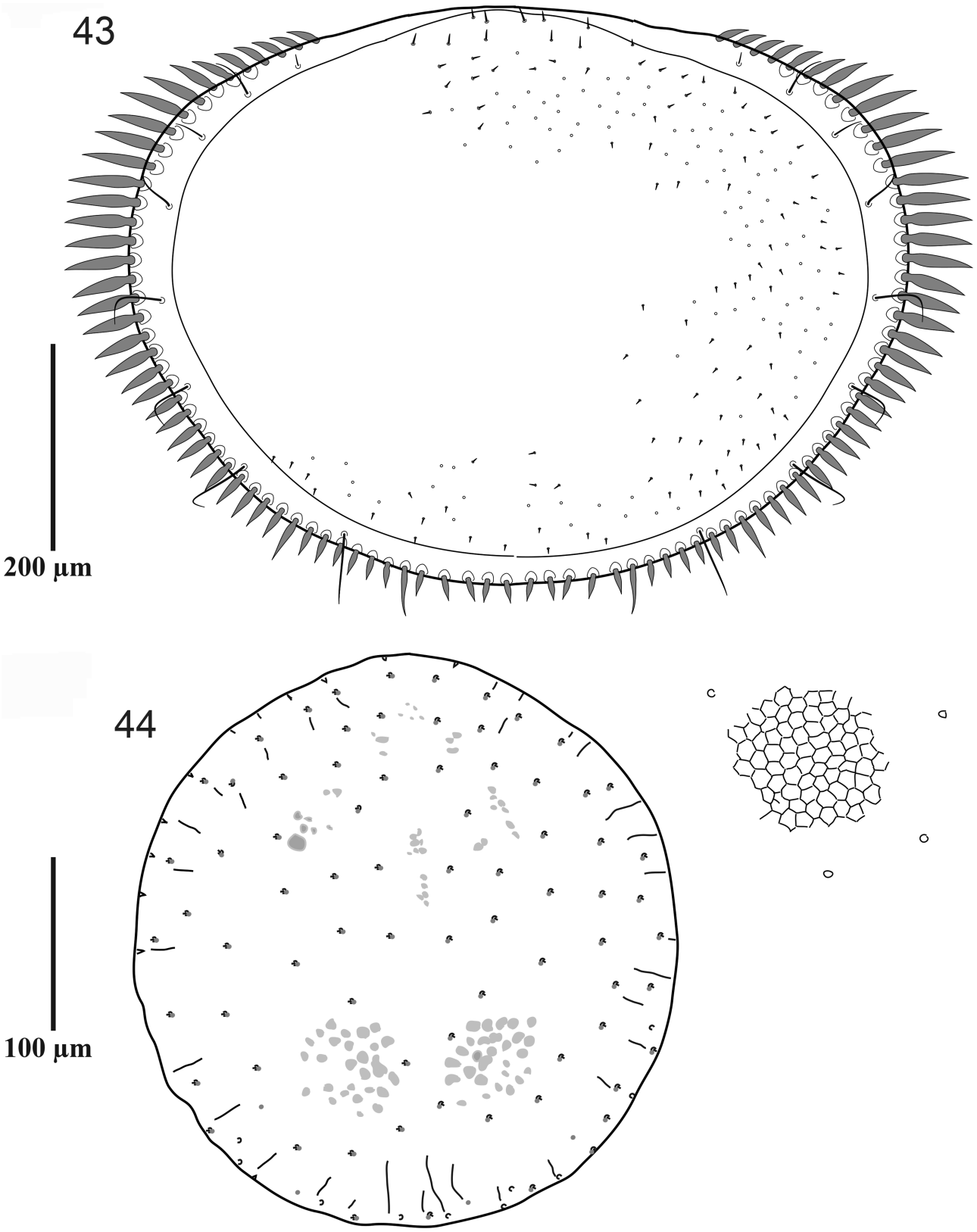
FIGURES 31–34. Heterozerconidae, gnathosoma, adults: 31, *Narceoheterozercon ohioensis*, female (OSAL 001054); 32, *Narceoheterozercon ohioensis*, male (redrawn from Gerdeman & Klompen (2003)); 33, *Afroheterozercon mahsbergi*, female (OSAL 003037); 34, *Afroheterozercon mahsbergi*, male (OSAL 003042; red arrow: notch in corniculus). Inset: gnathotectum (female and male) and labrum + salivary stylets. Abbreviations: LL, lateral lips.



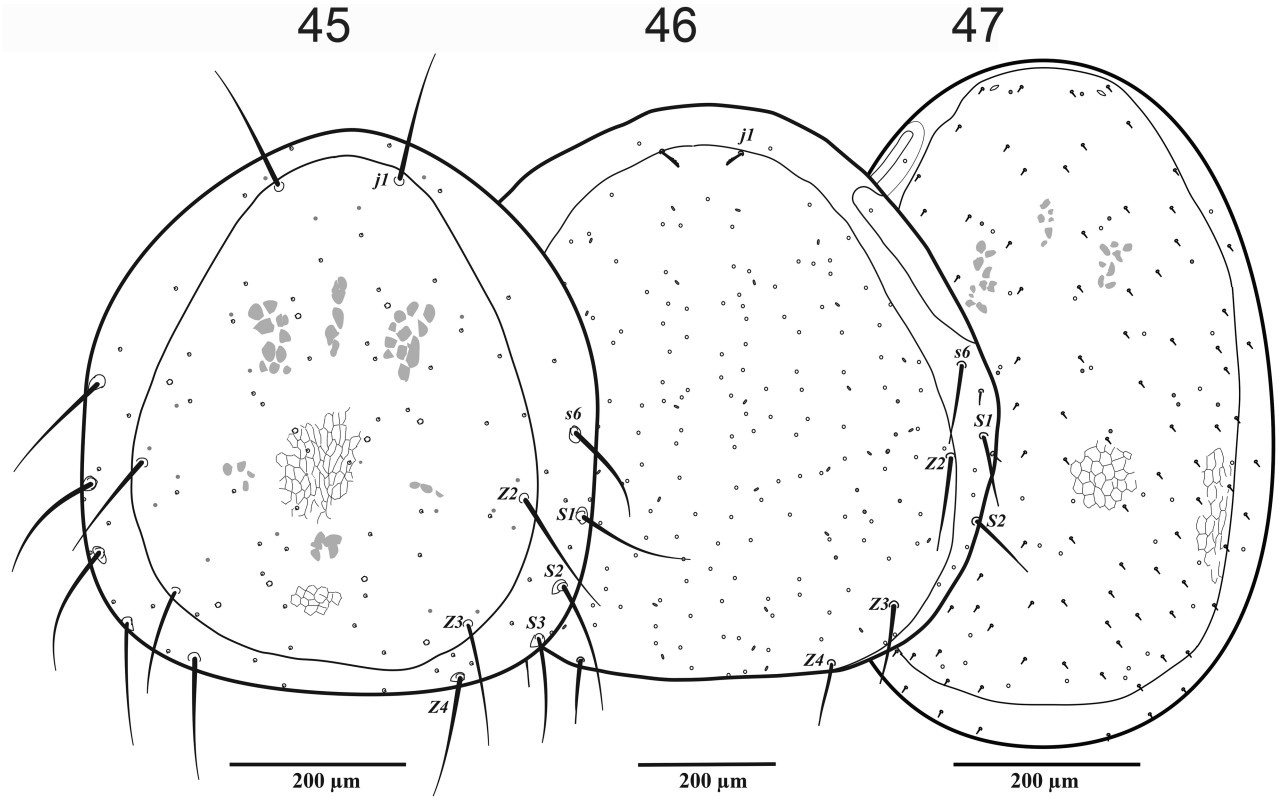
FIGURES 35–38. Heterozerconidae, gnathosoma, adults: 35, *Maracazercon joliveti*, female (paratype, #74–71; red arrow: setal base-like structure on hypostome); 36, *Maracazercon joliveti*, male (paratype; #74–75); 37, *Heterozercon calakmulensis*, female (CNAC 012444); 38, *Heterozercon calakmulensis*, male (CNAC 012443). Inset: gnathotectum (female and male) and labrum + salivary stylets.



FIGURES 39–42. Heterozerconidae, gnathosoma, adults: 39, *Allozercon leytensis* n. sp., female (OSAL 053243); 40, *Allozercon leytensis* n. sp., male (UPLB MNH ACA-01335; red arrow: sclerotized axial extension of palp trochanter); 41, *Al*. (*Philippinozercon*) *makilingensis*, female (OSAL 053271); 42, *Al*. (*Philippinozercon*) *makilingensis* male (OSAL 102161). Inset: gnathotectum and labrum + salivary stylets.

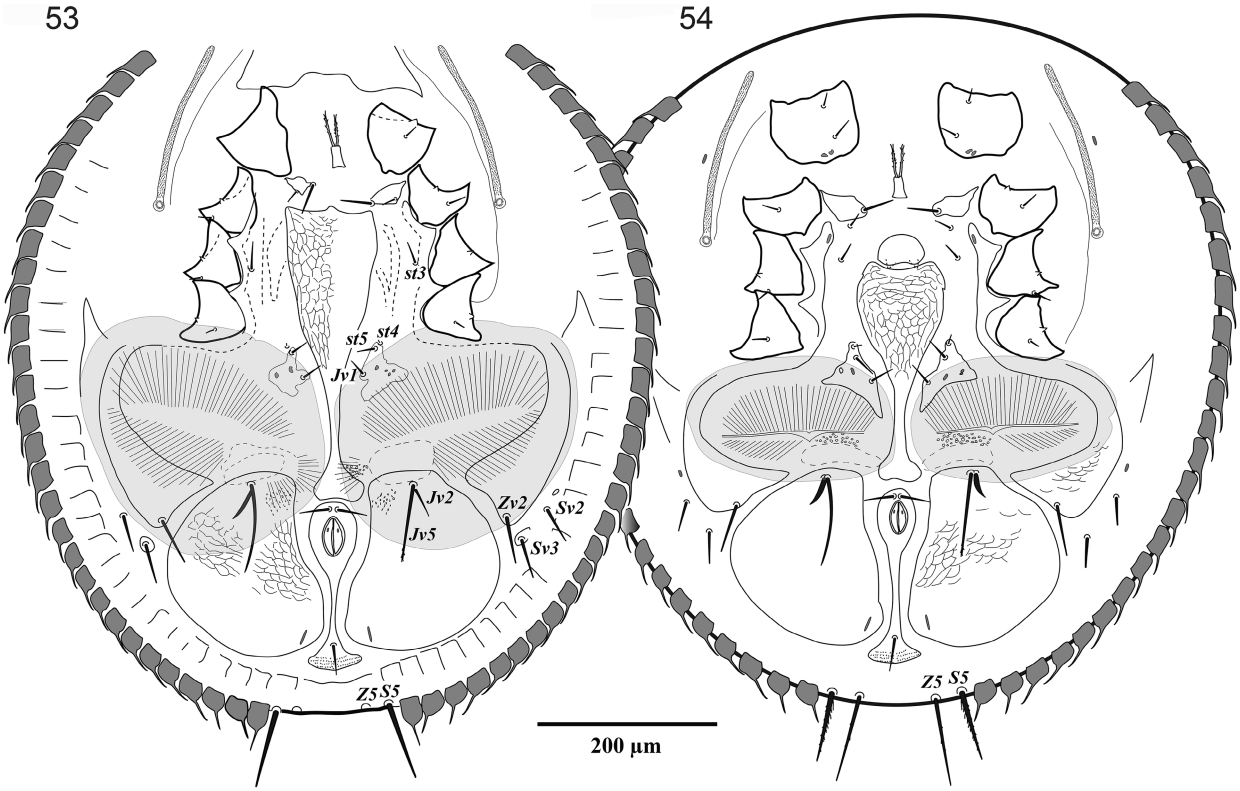


FIGURES 43–44. Discozerconidae, idiosoma dorsal: 43, *Discomegistus* sp., male (FMNH); 44, *Discozercon derricki*. Inset: patterning dorsal cuticle.

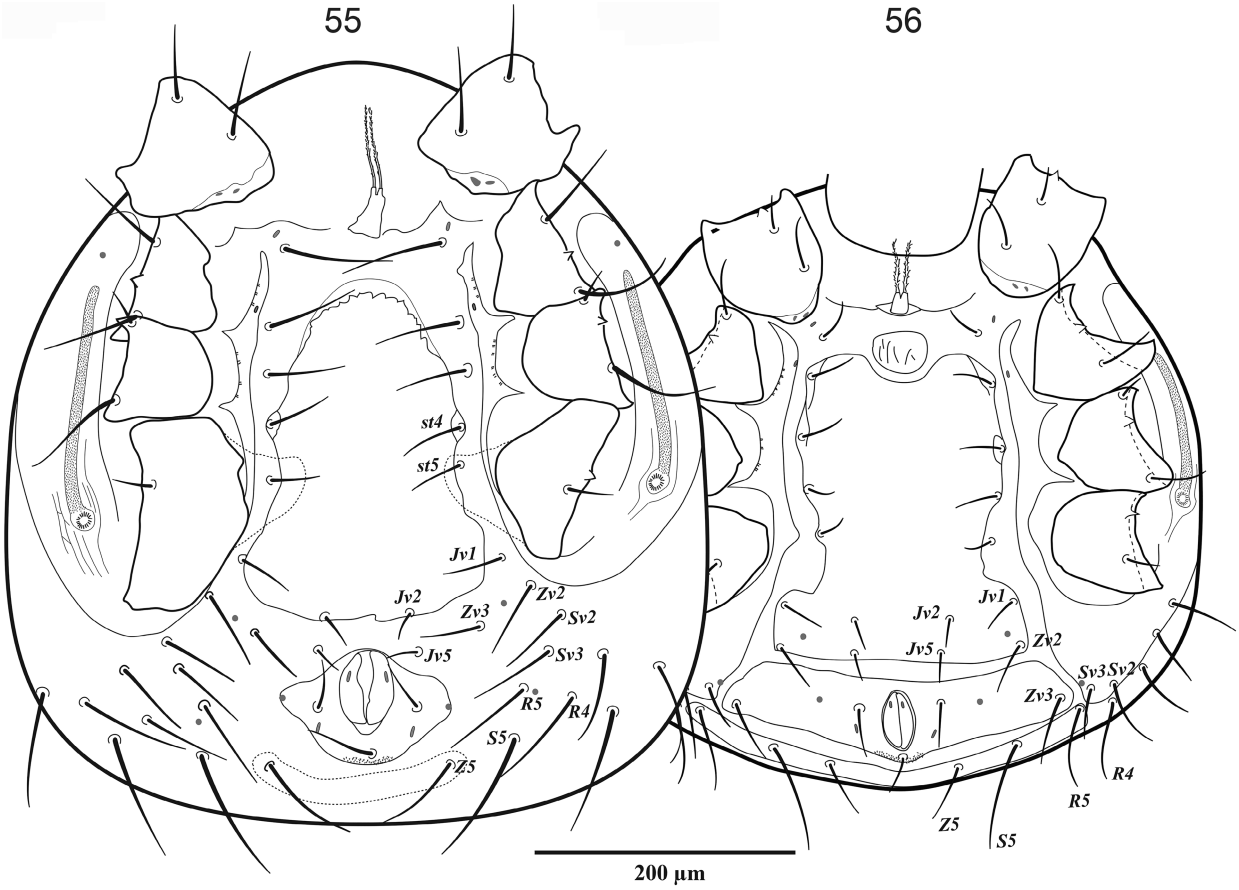


FIGURES 45–47. Heterozerconidae, idiosoma dorsal: 45, *Amyzozercon chocoensis*, female (OSAL 106741); 46, *Ecuazercon cushuimensis*, female (FMJK 71–1118); 47, *Afroheterozercon mahsbergi*, male (OSAL 003042)

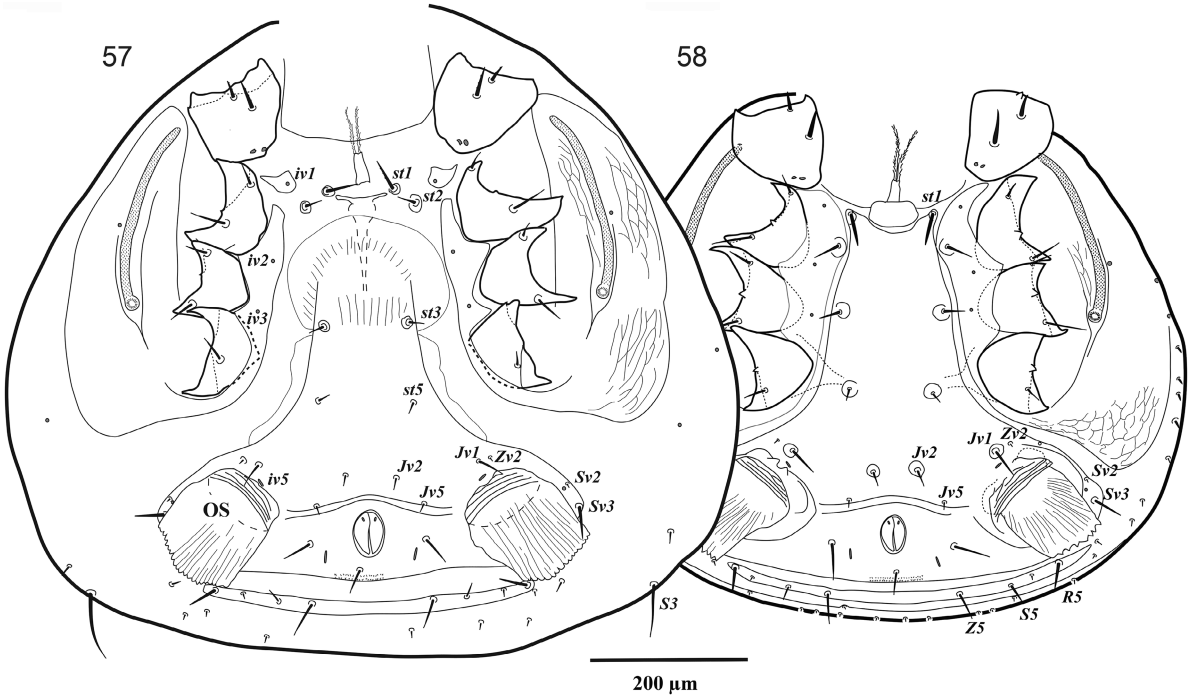
FIGURES 48–52. Heterozerconidae, details idiosoma: 48, *Allozercon leytensis* n. sp., female, hypertrichy of setae in *j1* position (OSAL 053251); 49, same for male (OSAL 106780); 50, *Allozercon leytensis* n. sp., male, anterolateral spines (OSAL 106780); 50a, detail antero-lateral spines; 51, *Heterozercon* ex Cuba, female, venter (OSAL 125446); 52, *Narceoheterozercon* sp., broken off spermatodactyl (red arrow) in female secondary genital opening / sclerotized tube (OSAL 159712).



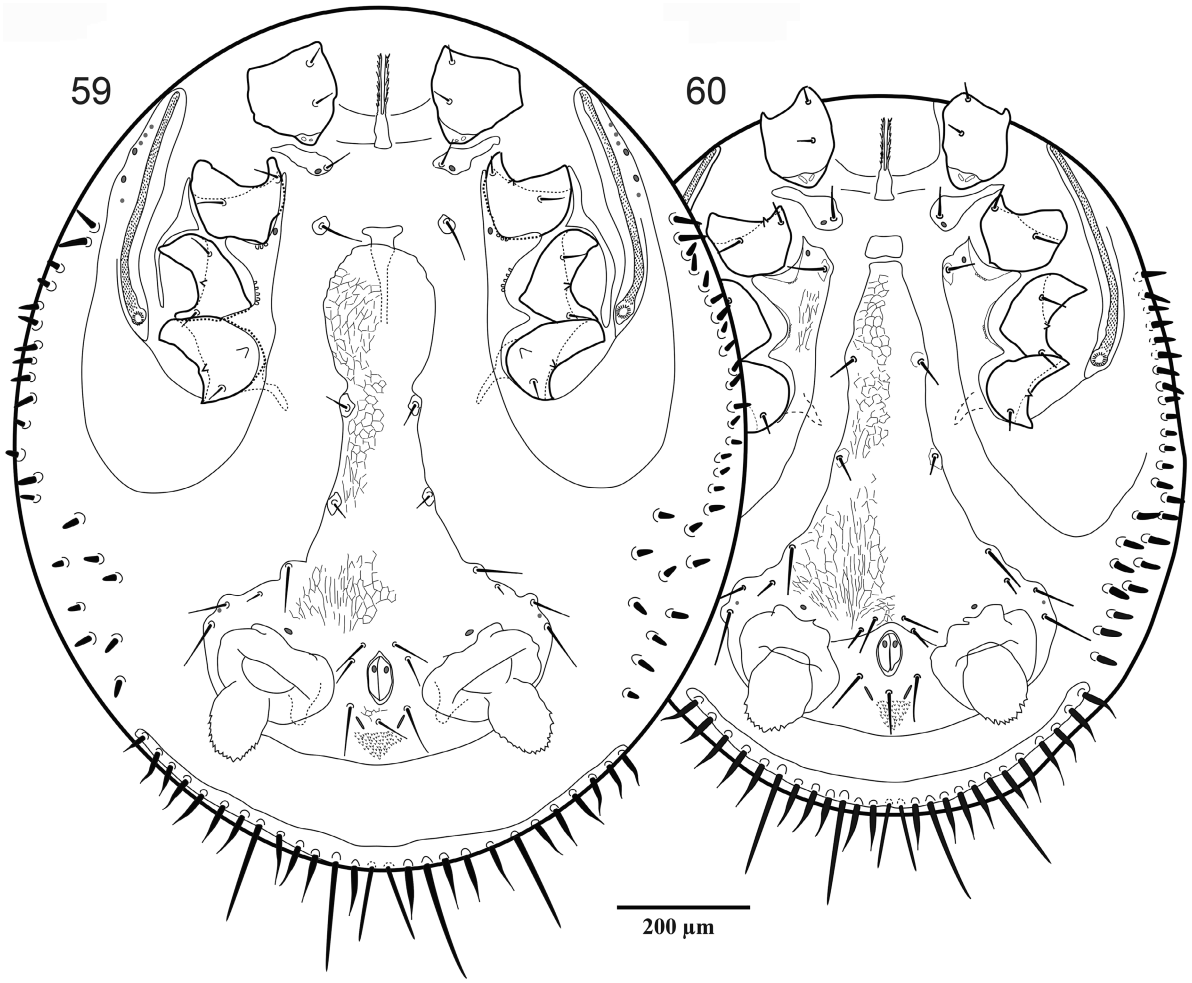
FIGURES 53–54. Discozerconidae, *Discozercon derricki*, idiosoma venter: 53, female (OSAL 052738); 54, male (OSAL 004891).



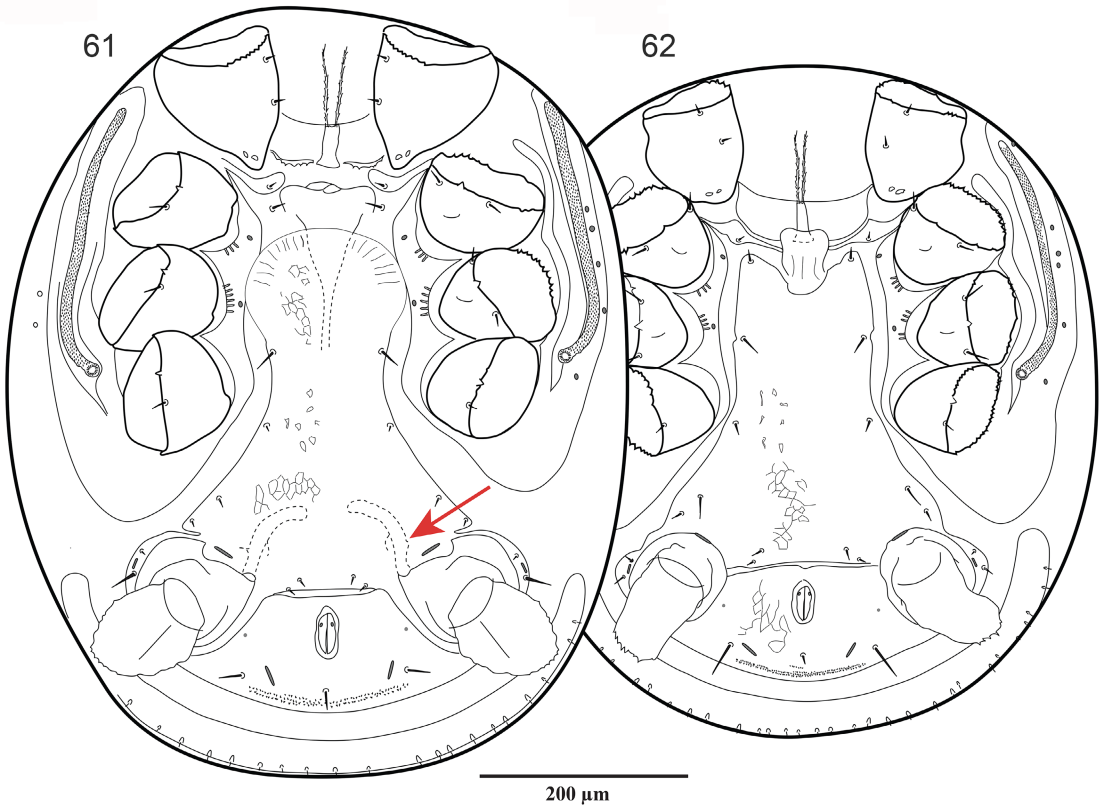
FIGURES 55–56. Heterozerconidae, *Amyzozercon chocoensis*, idiosoma venter: 55, female (OSAL 106741); 56, male (OSAL 102562).



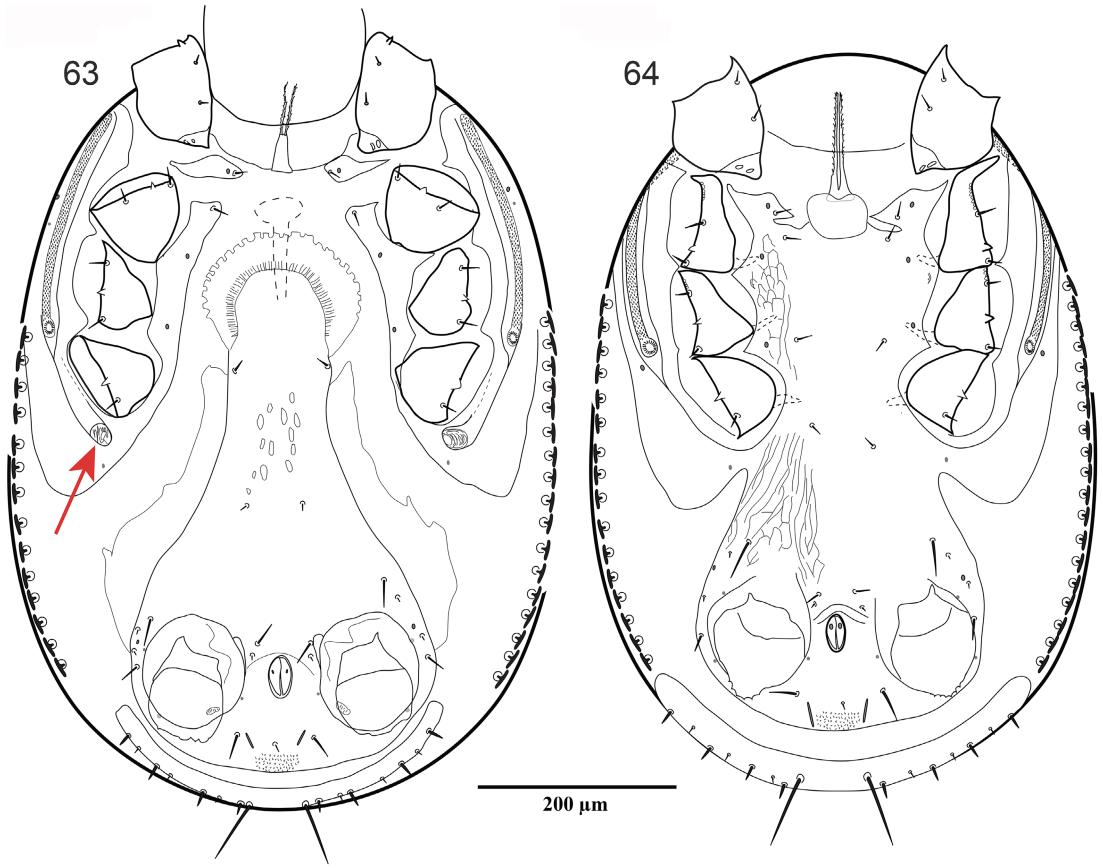
FIGURES 57–58. Heterozerconidae, *Ecuazercon cushuimensis*, idiosoma venter: 57, female (FMJK 71–1118); 58, male (FMJK 71–1118). Abbreviations: OS, opisthogastral suckers.



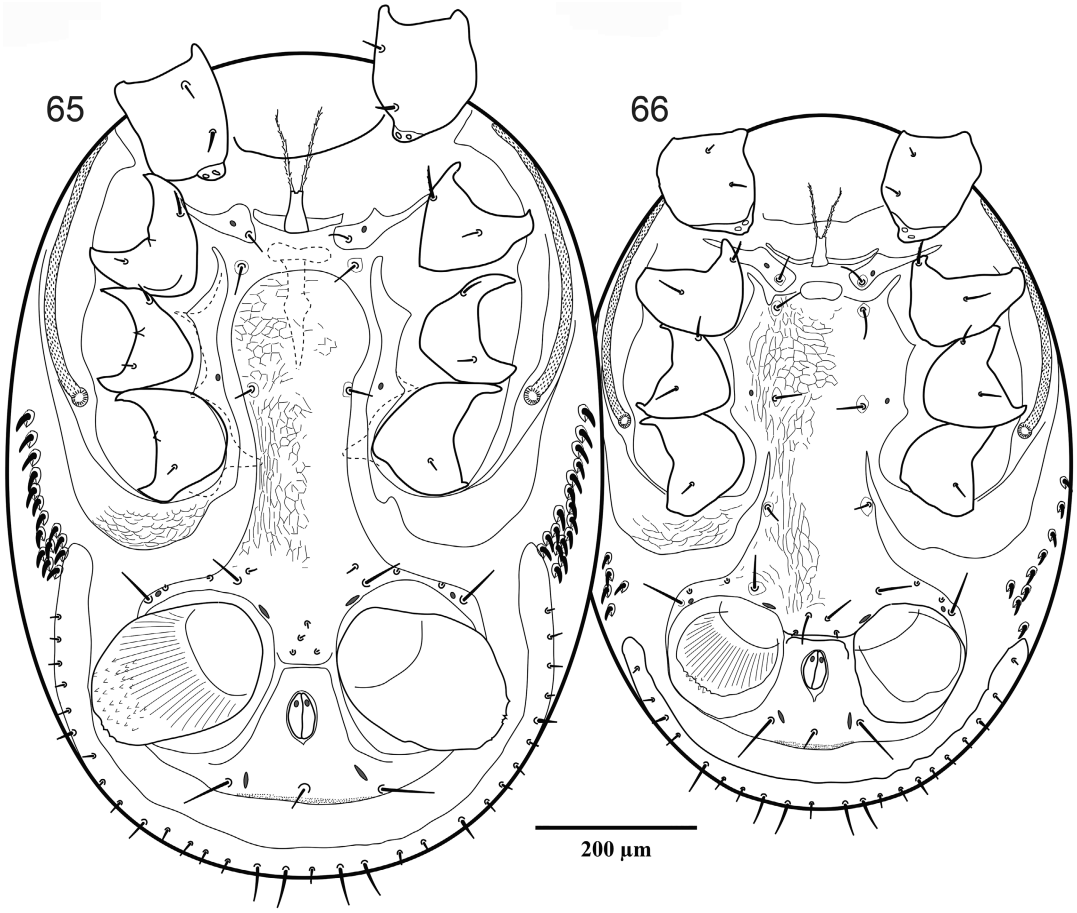
FIGURES 59–60. Heterozerconidae, *Amheterozercon amphisbaenae*, idiosoma venter: 59, female (OSAL 052751); 60, male (OSAL 052761).



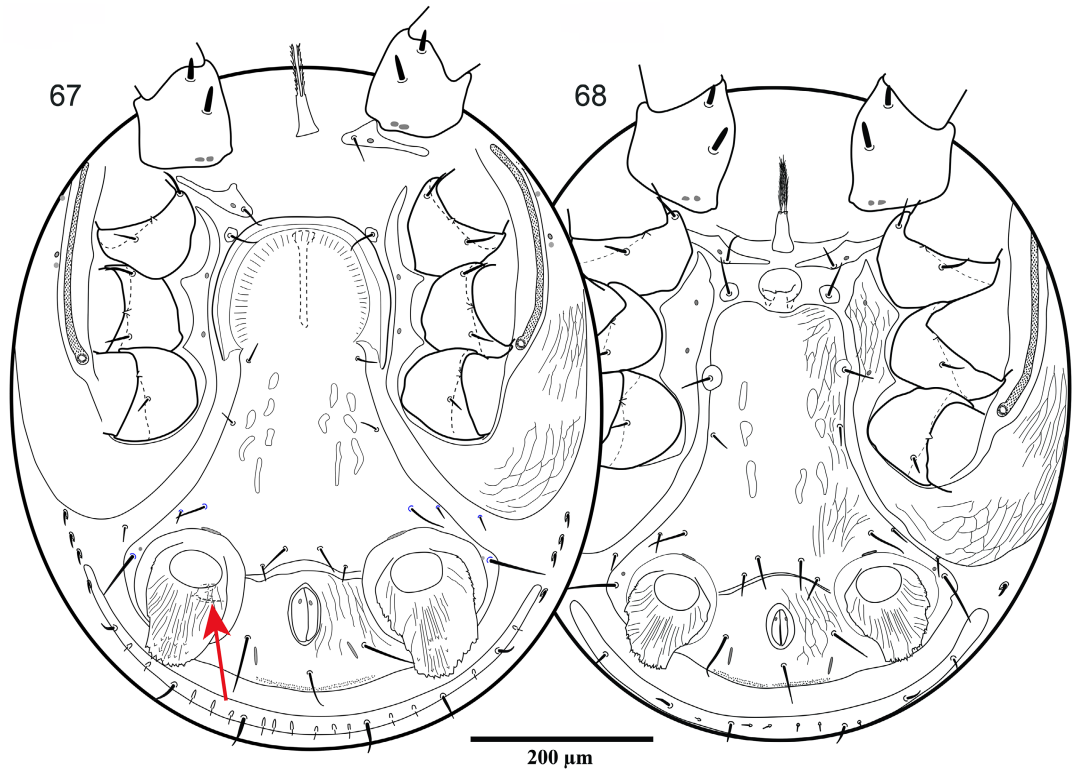
FIGURES 61–62. Heterozerconidae, *Narceoheterozercon ohioensis*, idiosoma venter: 61, female; 62, male. Male redrawn from Gerdeman & Klompen (2003).



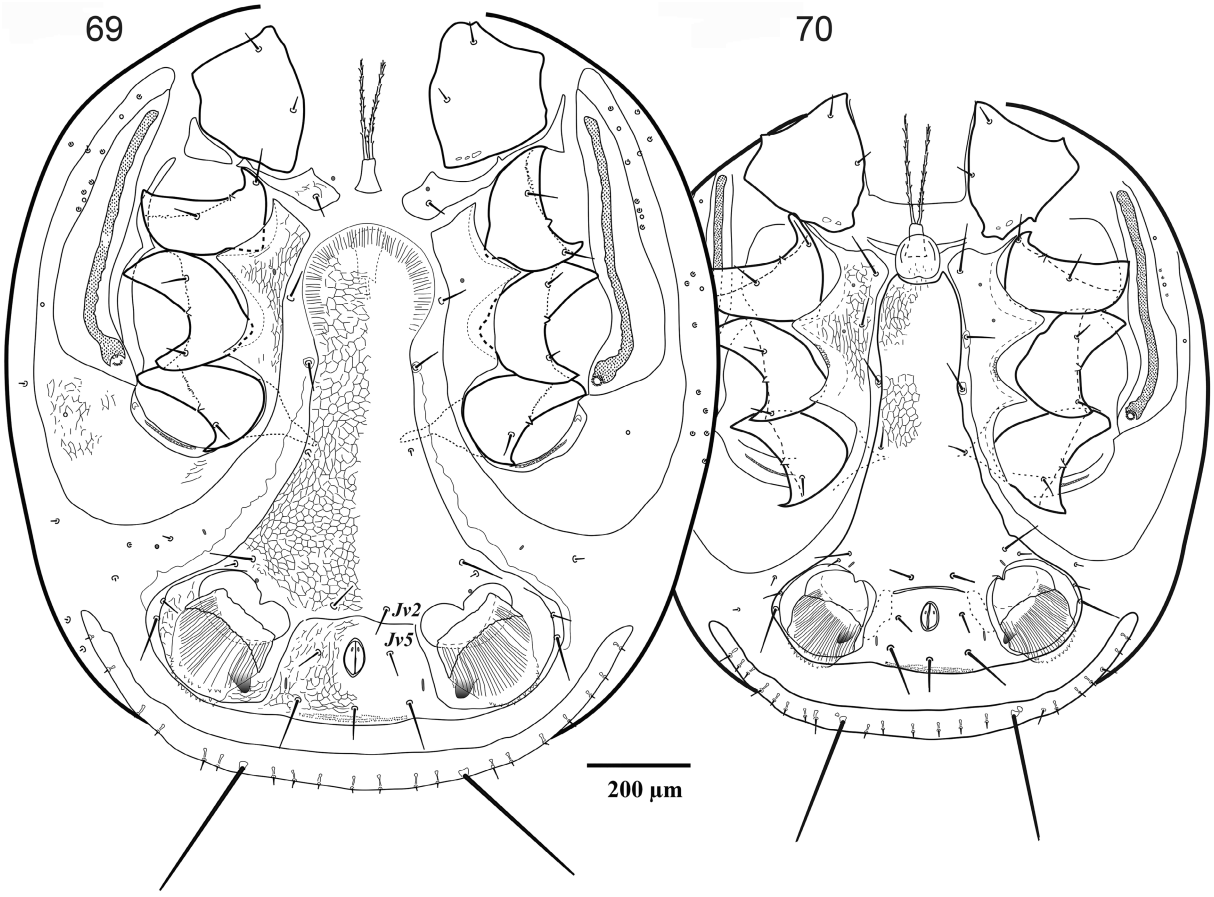
FIGURES 63–64. Heterozerconidae, *Afroheterozercon mahsbergi*, idiosoma venter: 63, female (OSAL 003040, published); 64, male (OSAL 003042, redrawn from Klompen *et al*. (2013)).



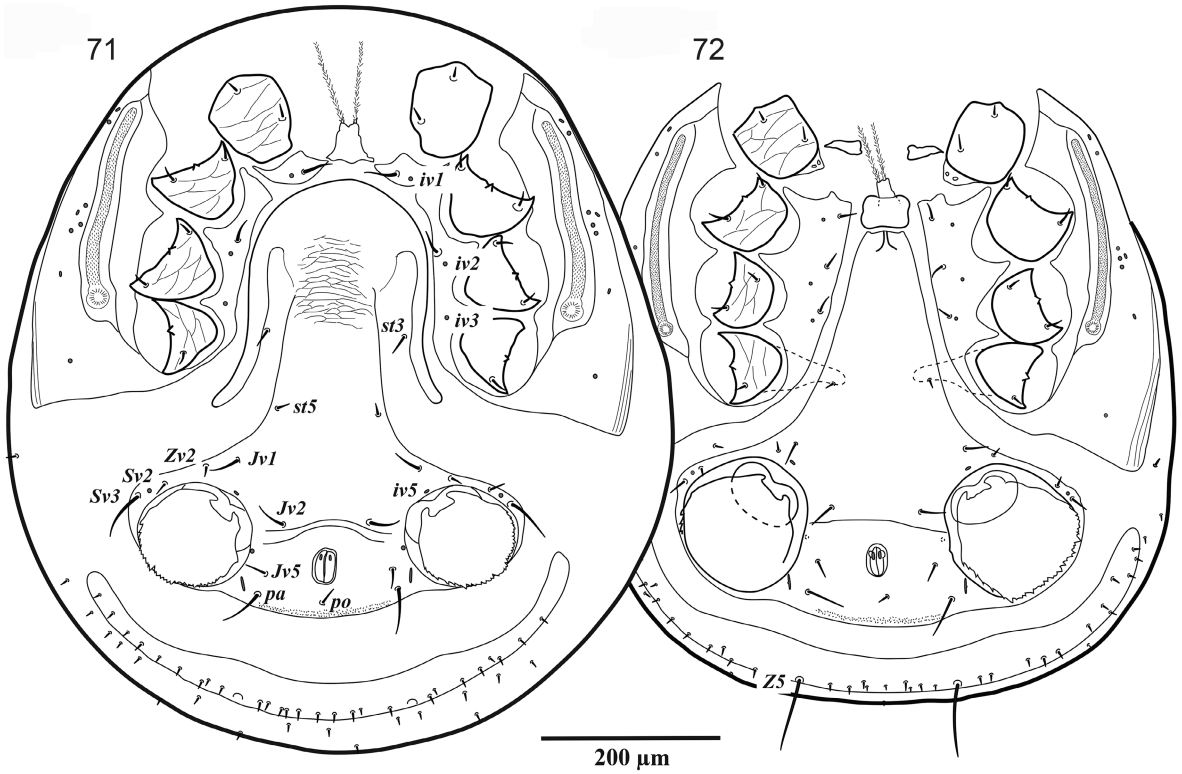
FIGURES 65–66. Heterozerconidae, *Maracazercon joliveti*, idiosoma venter: 65, female (paratype); 66, male (paratype).



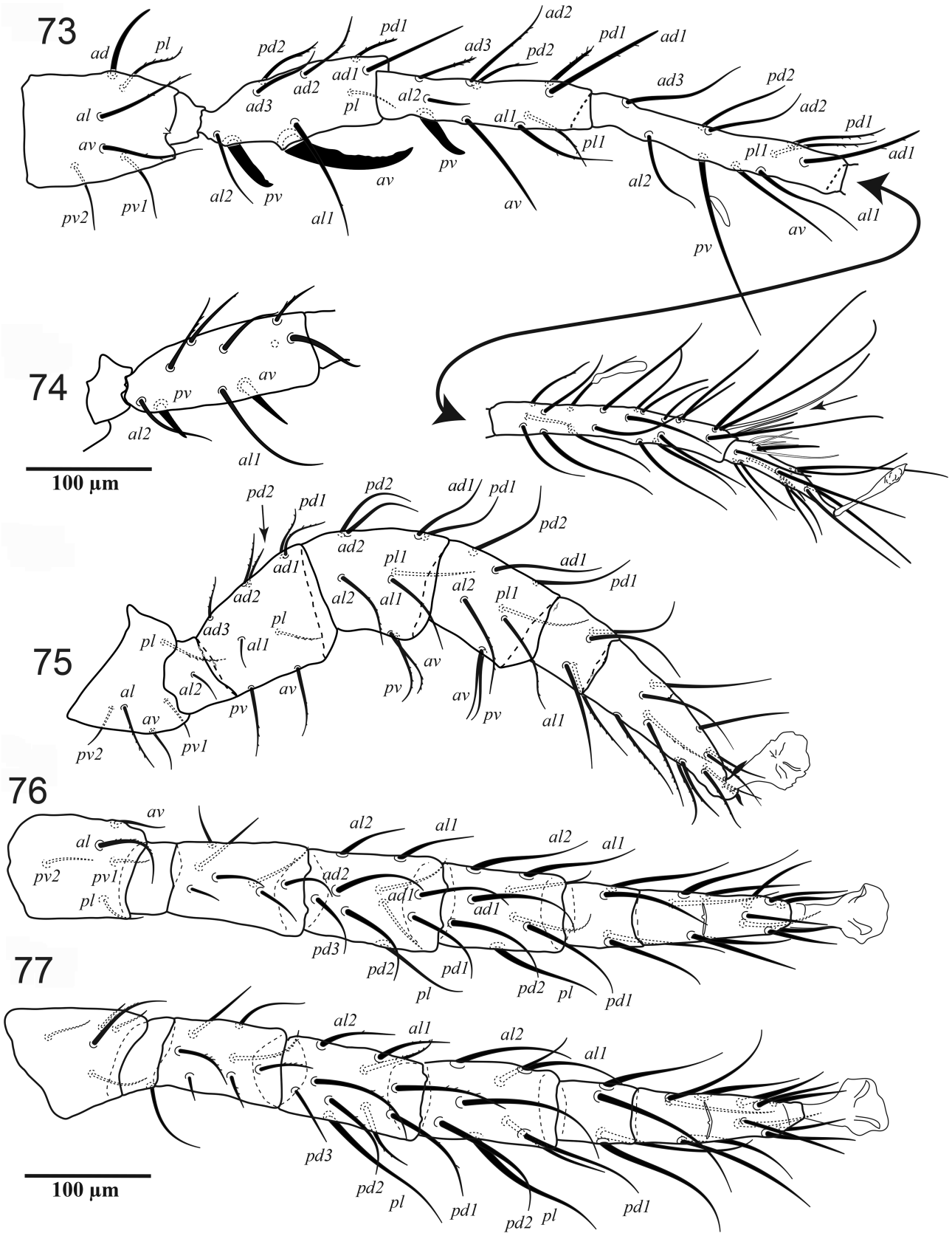
FIGURES 67–68. Heterozerconidae, *Heterozercon calakmulensis* n. sp., idiosoma venter: 67, female (CNAC 012444); 68, male (CNAC 012443).



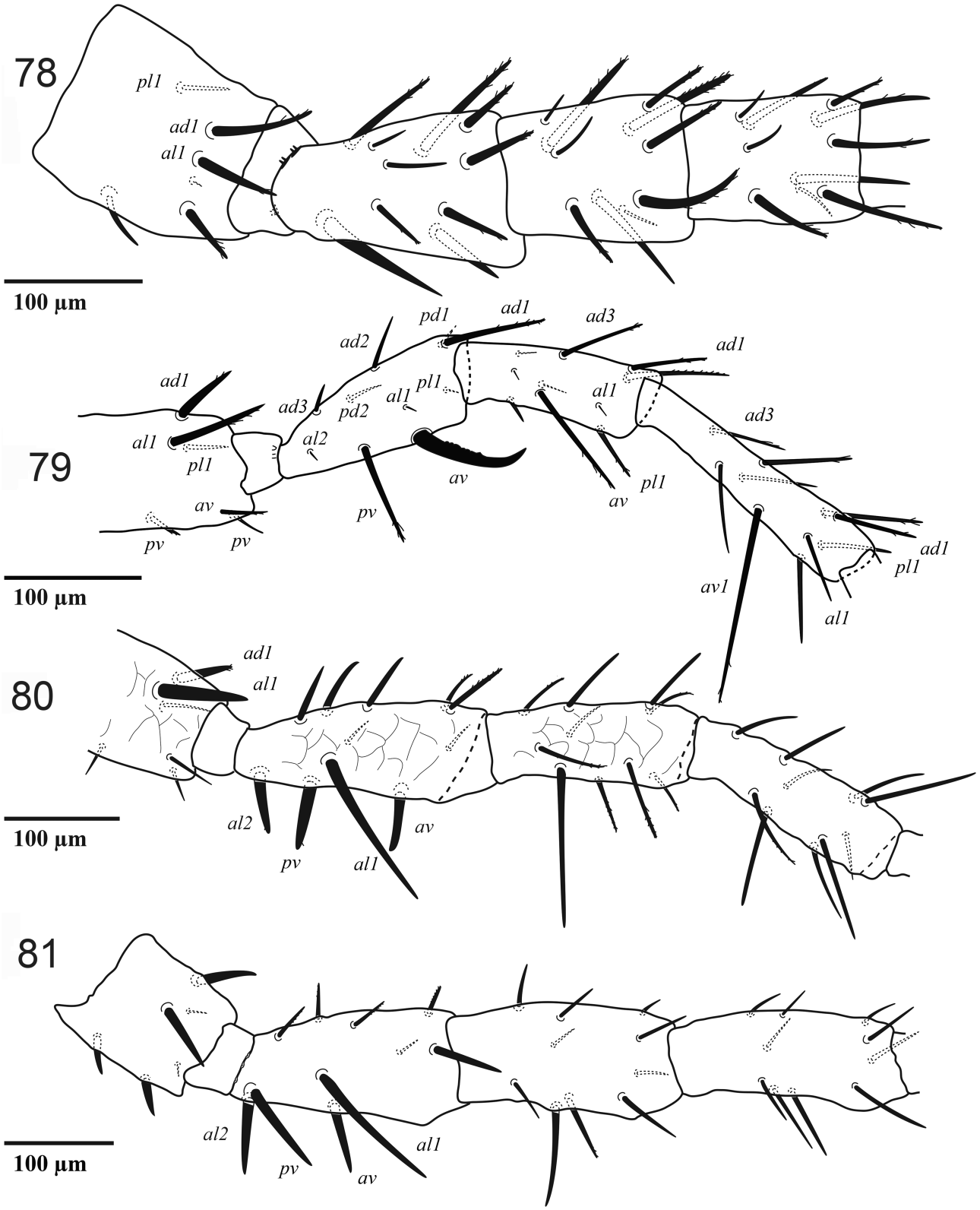
FIGURES 69–70. Heterozerconidae, *Allozercon leytensis* n. sp., idiosoma venter: 69, female (OSAL 053251); 70, male (UPLB MNH ACA-01335).



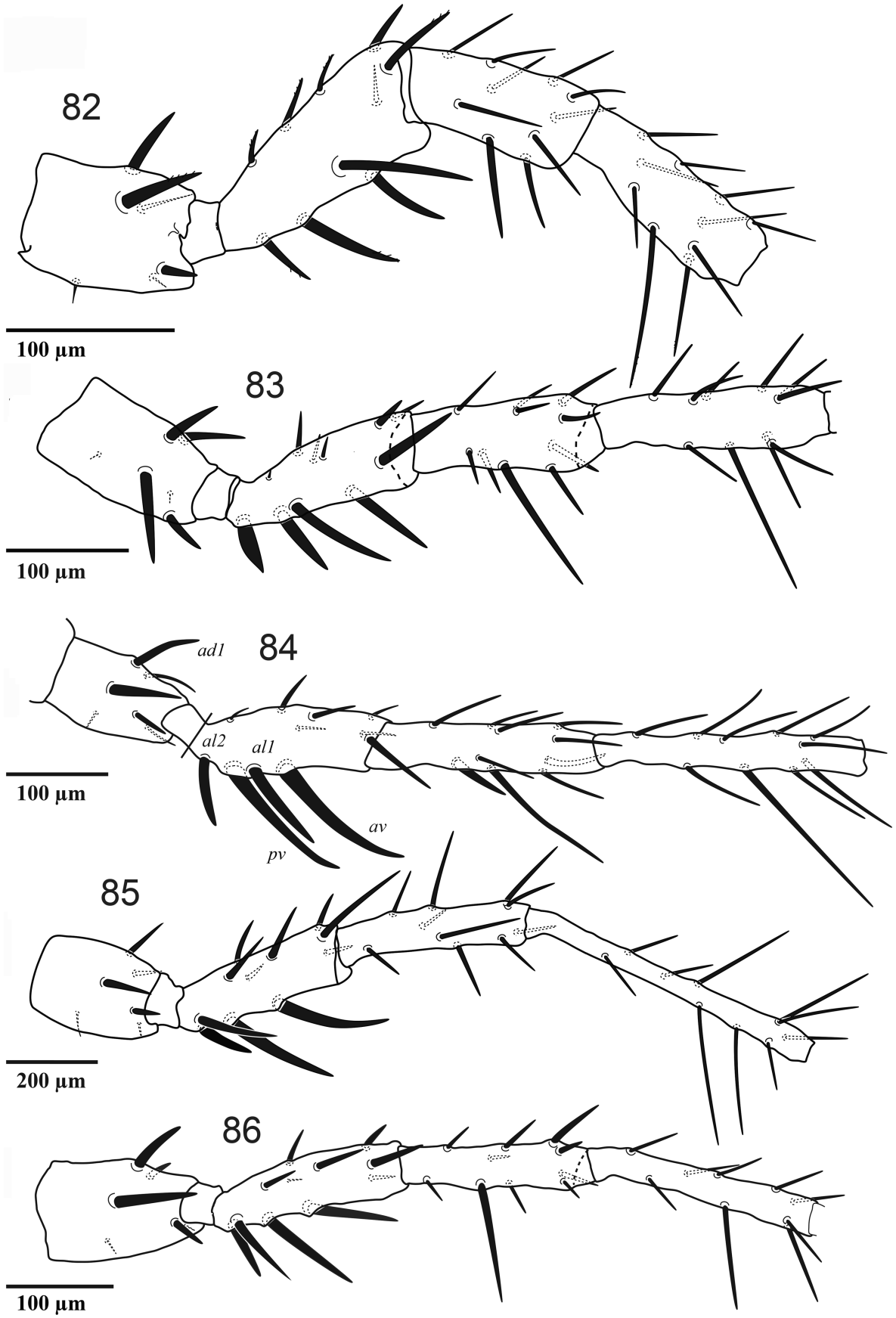
FIGURES 71–72. Heterozerconidae, *Al*. (*Philippinozercon*) *makilingensis*, idiosoma venter: 71, female (OSAL 053222); 72, male (OSAL 053267, both redrawn from Gerdeman *et al*. (2018)).



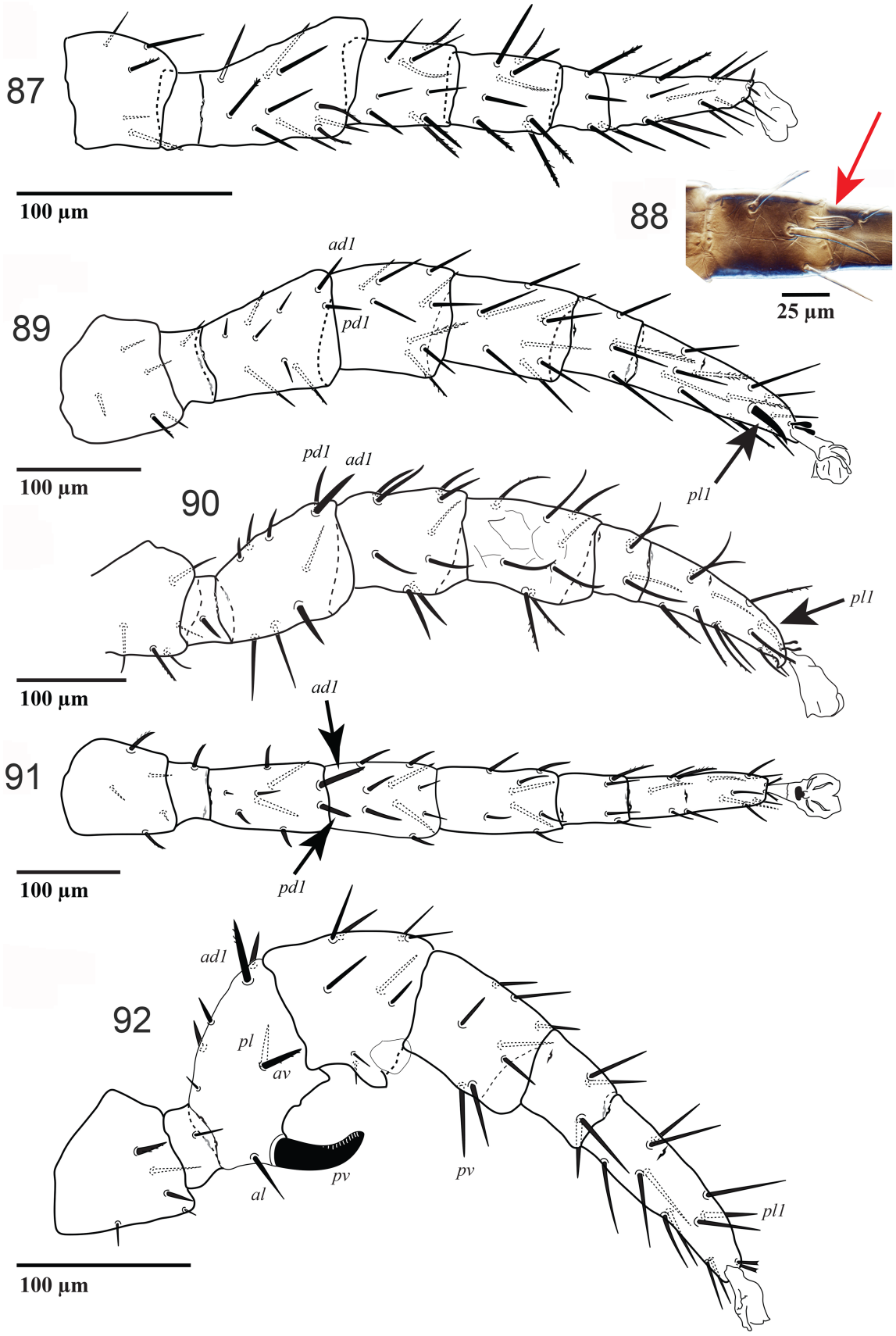
FIGURES 73–77. Heterozerconidae, *Amyzozercon chocoensis*, legs: 73, leg I, male (OSAL 106736); 74, femur I, female (OSAL 106783), 75, leg II, male (OSAL 106736); 76, leg III, male (OSAL 106789); 77, leg IV, male (OSAL 106789).



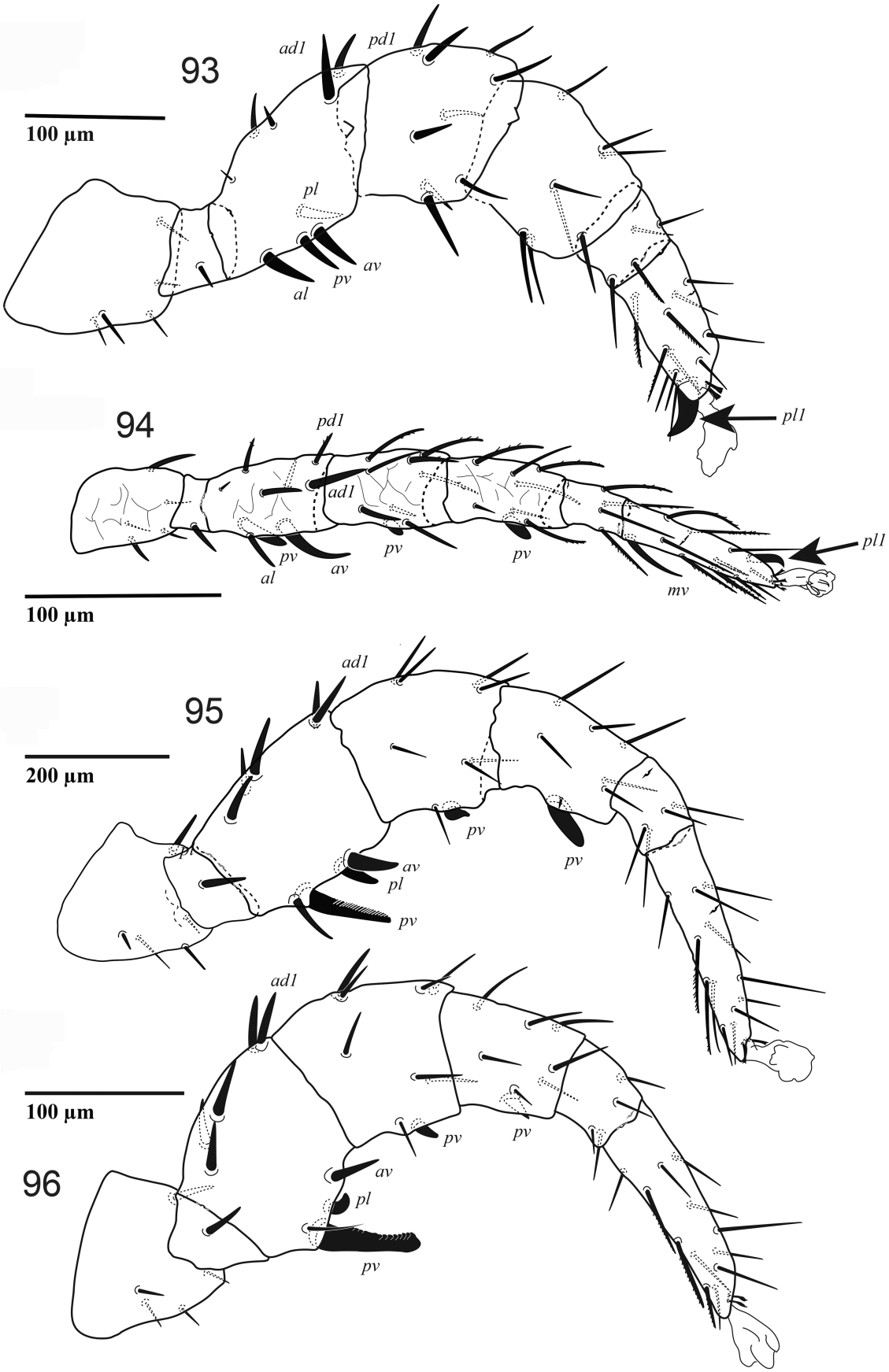
FIGURES 78–81. Leg I, male: 78, Discozerconidae, *Discozercon derricki* (OSAL 004889); 79, Heterozerconidae, *Ecuazercon cushuimensis*, (FMNH-INS 4449621); 80, *Amheterozercon amphisbaenae* (OSAL 052763); 81, *Narceoheterozercon ohioensis*, redrawn from Gerdeman & Klompen (2003).



FIGURES 82–86. Heterozerconidae, leg I, male. 82, *Afroheterozercon mahsbergi* (OSAL 003042, published); 83, *Maracazercon joliveti* (paratype); 84, *Heterozercon calakmulensis* n. sp. (CNAC 012443); 85, *Allozercon leytensis* n. sp. (OSAL 053185); 86, *Al*. (*Philippinozercon*) *makilingensis* (OSAL 0053267, redrawn from Gerdeman *et al*. (2018)).



FIGURES 87–92. Leg II, male, antero-dorsal view: 87, Discozerconidae, *Discozercon derricki* (OSAL 004889); 88, *Discomegistus* sp., male, basitarsus IV (FMNH; red arrow: mid-dorsal sensillum); 89, Heterozerconidae, *Ecuazercon cushuimensis*, (FMJK 71–1118); 90, *Amheterozercon amphisbaenae* (OSAL 052763); 91 *Narceoheterozercon ohioensis*, redrawn from Gerdeman & Klompen (2003); 92, *Afroheterozercon mahsbergi* (OSAL 003042, published).



FIGURES 93–96. Heterozerconidae, leg II, male: 93, *Maracazercon joliveti* (paratype); 94, *Heterozercon calakmulensis* n. sp. (CNAC 012443); 95, *Allozercon leytensis* n. sp. (OSAL 053185); 96, *Al*. (*Philippinozercon*) *makilingensis* (OSAL 053267, redrawn from Gerdeman *et al*. (2018)).

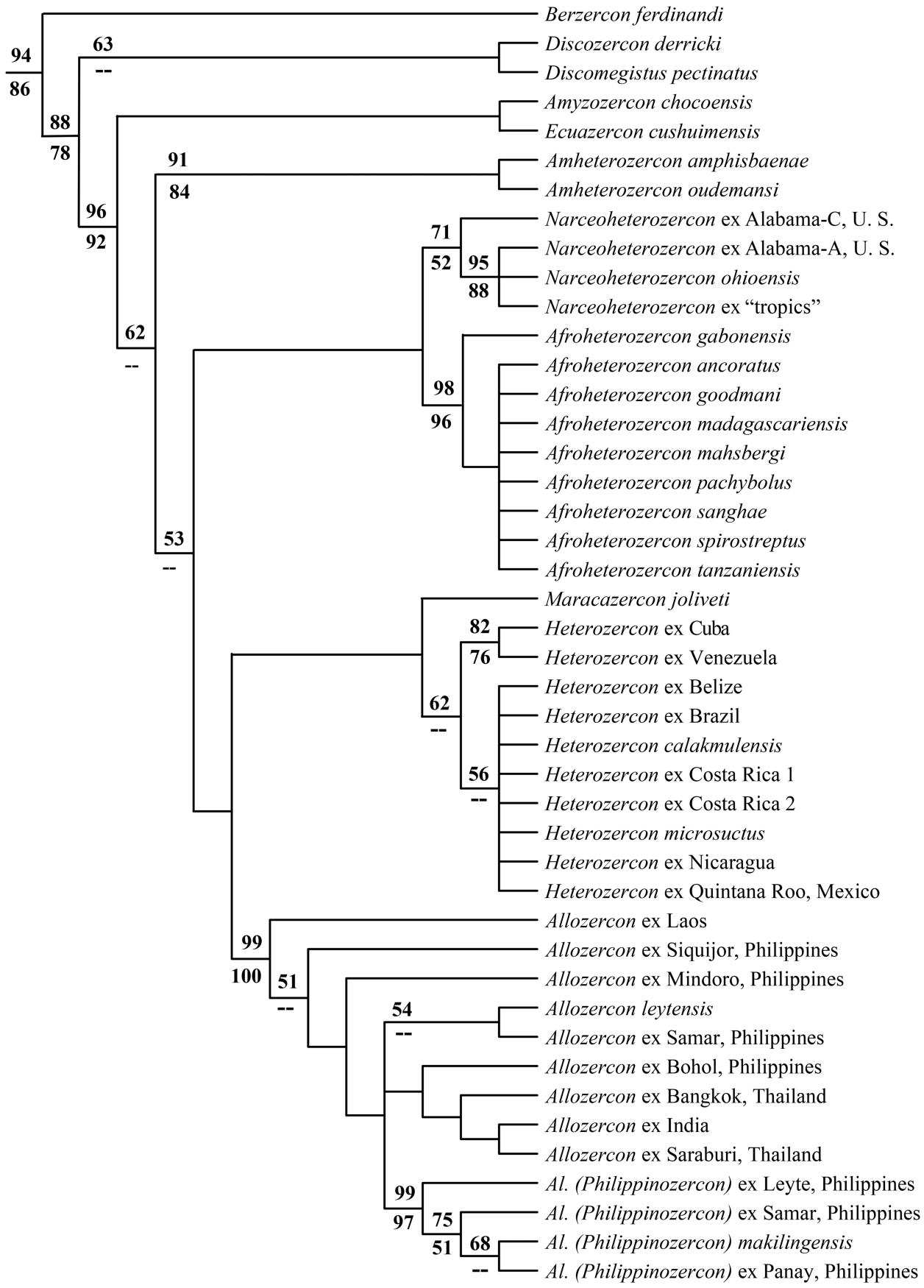


FIGURE 97. Strict consensus tree of relationships in the Heterozerconoidea using Sejina as sole outgroups. Numbers indicate jackknife support as calculated in PAUP (above line) and TNT (below). -- = support below 50%.

Key to the genera of Heterozerconoidea

The following key allows separation of adults of the genera recognized in this study.

1. With a pair of large opisthogastral suckers, inserted anterior to ventral shield and somewhat translucent; males without spermatodactyl; movable digit of female chelicera stout (length ~3x width) … Discozerconidae *s.l.* 2
– With a pair of opisthogastral suckers of varying size, inserted posterior to the ventral shield, more or less solid OR opisthogastral suckers absent; spermatodactyl on fixed digit of male chelicera; movable digit of female chelicera elongate (length >6x basal width) … Heterozerconidae 4
2 (1) Flattened marginal setae limited to posterior margin; with 9 pairs of opisthogastral setae (in addition to paranal and postanal setae); peritremes short (not extending beyond coxae II); New Zealand . . . . . *Berzercon*
– Flattened marginal setae extending along posterior and lateral margin; with 8 pairs of opisthogastral setae (in addition to paranal and postanal setae); peritremes relatively long (extending to coxae I) … Discozerconidae *s.s.* 3
3 (2) Endopodal and sternitiventral shields in male not fused; marginal setae flag-like (Figs 53–54); S.E. Asia to Australia . . . . . *Discozercon*
– Endopodal and sternitiventral shields in male fused; flattened marginal setae dagger-shaped (Fig. 43); South and Central America . . . . . *Discomegistus*
4 (1) Opisthogastral suckers absent; South America . . . . . *Amyzozercon*
– Opisthogastral suckers present 5
5 (4) With several elongate posterior dorsal setae (Fig. 46); South America . . . . . *Ecuazercon*
– All posterior dorsal setae minute 6
6 (5) Marginal opisthosomal setae spine-like, often hypertrichous 7
– Marginal opisthosomal setae setiform 9
7 (6) Spines straight, peg-like (Fig. 59); parasitic on vertebrates; South America . . . . . *Amheterozercon*
– Spines anchor-like (Fig. 63); spermatodactyl in male usually of compact type (Figs 14–15); Africa . . . . . *Afroheterozercon*
– Spines bent, hook-like (Figs 65, 67); associated with millipedes; Neotropics 8
8 (7) Anterior margin of female genital shield membranous; endopodal and sternitiventral shields in males fused . . *Maracazercon*
– Anterior margin of female genital shield sclerotized (Fig. 67); endopodal and sternitiventral shields in males not fused . . . . . *Heterozercon*
9 (6) Setae *Jv5* inserted anterior to ventrianal fusion line; spermatodactyl often recurved (Figs 10–11); genua II seta *pv* in male setiform; North America . . . . . *Narceoheterozercon*
– Setae *Jv5* inserted posterior to ventrianal fusion line; spermatodactyl always of straight type; genua II seta *pv* in male spinose (Fig. 95); South Asia . . . . . *Allozercon* 10
10 (9) Posterolateral corner of metapodal shield rounded; anterior margin of female genital shield membranous . . . . *Al.* (*Allozercon*)
– Postero-lateral corner of metapodal shields with a sharp angle (“cut-off”; Figs 71–72); anterior margin of female genital shield sclerotized . . . . . *Al.* (*Philippinozercon*)

Removed from Heterozerconidae

Atacoseius Berlese 1905

Atacoseius Berlese 1905: 162 [type species: *Atacoseius pellucens* Berlese 1905, by monotypy].
Atacoseius.—Baker & Wharton 1952: 56; Domrow 1956: 195; Hallan 2017.

Locality: Bogor (as Buitenzorg), Java, Indonesia.

Remarks. The description of this monotypic genus is based entirely on the dorsum and the pattern of long setae on the legs, as the venter in both available specimens was not visible (Berlese 1905). Berlese (1905) noted some resemblance with Heterozerconidae, and this species has occasionally been grouped in Heterozerconidae. However, the combination of relatively short cheliceral digits, presence of an added pair of long setae on the prodorsum (in addition to the setae referred to as *j1* in this study), six pairs of long postero-lateral and posterior setae, the insertion pattern of the long filiform setae on legs I (multiple long setae on the genua, tibiae, and tarsi; shorter ones on the femora), and the absence of any indication of long spine-like setae on femora I, make it unlikely that this species belongs in Heterozerconidae. A more likely option would be in Trigynaspida, possibly Paramegistidae.

Discussion

Biogeography

All genera of Heterozerconidae have geographical distributions restricted to a single biogeographic area (*Afroheterozercon* Afrotropical; *Allozercon*, Oriental; *Narceoheterozercon*, Nearctic; *Amheterozercon*, *Amyzozercon*, *Ecuazercon*, *Heterozercon*, *Maracazercon*, all Neotropical). This geographic distribution pattern raises questions on how this pattern was established: where did the family originate, and can we reconstruct how the current distributions were established? The systematic analysis allows some preliminary hypotheses on the geographic origin of the family. The observation that the first two lineages in Heterozerconidae (*Amyzozercon* + *Ecuazercon*, *Amheterozercon*) are from South America is consistent with an origin in that region. This would require secondary expansions into North America (*Narceoheterozercon*), Africa (*Afroheterozercon*) and Southeast Asia (*Allozercon*). What is less clear is how and when this dispersal from South America might have happened. Dispersal from the Neotropics to the Nearctic along the Panamanian landbridge seems relatively straightforward, hypotheses for the other two genera are less obvious. The simplest hypothesis for the origin of *Afroheterozercon* would be separation at the time Africa drifted apart from South America around 90 mya (mid-Cretaceous), which would make this a very old genus. This leaves the issue of *Allozercon*. Dispersal from South America to India and migration from India to Southeast Asia is possible, but such a hypothesis is problematic. For starters, such a hypothesis requires either dispersal through Africa to India (while leaving no descendants of this lineage in Africa) or travel from Antarctica from the south (possible vicariance and once again requiring great age). A third alternative might be direct dispersal from South America to Southeast Asia. This option puts less constraints on the age of the genus, but it is unclear how these non-vagile mites on non-vagile hosts could traverse the Pacific Ocean.

Representatives of the Discozerconidae *s.l.* have been recorded from Southeast Asia, Australia, and South America, but available data are too sparse to allow anything other than the assumption that this lineage, like Heterozerconidae, has a southern (Gondwanan) origin.

In summary, despite the distinct pattern of geographic distribution of the genera of Heterozerconidae, it is still largely unclear how this pattern was established.

Host associations

Berzercon and most members of the putative sistergroup to Heterozerconoidea, Sejoidea, are associated with Coleoptera. Nearly all other Heterozerconoidea are associated with Myriapoda. Given the current phylogeny, this suggests an early transition in Heterozerconoidea from associations with Coleoptera (*Berzercon*) to associations with Myriapoda (all remaining taxa). Within the myriapod associated taxa, the first split is between those taxa associated with Chilopoda (Discozerconidae *s. s.*) and those largely associated with Diplopoda (Heterozerconidae) which might suggest some level of co-speciation. The initial split in Heterozerconidae between associates of polydesmid millipedes (*Amyzozercon*, *Ecuazercon*) and those associated with spirobolids / spirostreptids might suggests a continuation of this co-speciation pattern but with low confidence. The sister lineage of *Amyzozercon* + *Ecuazercon* includes a variety of host associations. Even excluding the obvious host switch to vertebrate associations in *Amheterozercon*, the remaining taxa still have variable host associations, the majority with spirobolids / spirostreptids, but occasionally also with polydesmids (e.g., in *Heterozercon*). In summary, host associations in Heterozerconoidea appear to be shaped by 1–2 large host shifts (to myriapods and to vertebrates), some co-speciation (Discozerconidae *s. s.* vs. Heterozerconidae), and a mix of moderate host specificity at the generic level and (possibly) higher specificity at the species level (e.g., *Amyzozercon chocoensis*, *Al.* (*Ph*) *makilingensis*). Confirming host specificity at the generic or species level is currently difficult given the small number of records, and the lack of adequate host identification for most records.

Spermatodactyl shape

The shape of the spermatodactyl varies considerably within the family, but far less within genera. Many genera are

characterized by their "own" spermatodactyl shape. The "straight" type, sclerotized and extending into a pointed, sclerotized tip (Figs 4–7, 16–19), seems to be the basal type. Again, assuming the proposed phylogeny is valid, all modified shapes appear to be independently derived from this basal shape. Among the populations/species of *Narceoheterozercon* with recurved spermatodactyls, the length of the spermatodactyl may be correlated with the length of the sclerotized tube in the females. For example, in *N. ohioensis*, the female tubes averaged 136 μm (129–142; N=3) and the male spermatodactyls 254 μm (249–259; N=3), in a female and male from population Alabama-A those numbers were 139 and 270 μm (N=1), and in specimens from a "culture from tropics" (no further locality data) female tubes averaged 377 μm (372–387; N=3) and male spermatodactyls 719 μm (705, 733; N=2) (the spermatodactyl of a single male from Florida was of similar size, 663 μm). Despite the substantial difference in absolute sizes, the ratios of male structure length / female structure length in each population / species are very similar, ranging from 1.87 to 1.94, in the three measured populations. Clearly larger sample sizes are required, but if these observations hold, they suggest parallel evolution of genital systems in males and females of *Narceoheterozercon*. Similar patterns have not been observed for the other genera.

Mating systems

As noted in the introduction, mating mechanisms in Heterozerconidae show significant variability, including in female genital structures (Di Palma *et al*. 2015). Careful examination of females in a wide range of taxa did not reveal any evidence of a secondary genital system in females of *Amyzozercon*, *Ecuazercon*, *Maracazercon*, and *Allozercon*. In contrast, most females of *Heterozercon* and *Narceoheterozercon* have a secondary genital system with openings near the opisthogastral suckers. Females in most species of *Afroheterozercon* (not *Af. spirostreptus*) have well sclerotized structures immediately posterior to coxae IV which we assume are openings of a secondary genital system in that genus (see above). Finally, Flechtmann & Johnston (1990) noted part of a spermatheca in *Amheterozercon amphisbaenae* suggesting that genus may also have female secondary genital structures. We stress that light microscopy of slide-mounted specimens does not allow the more definitive conclusions provided by TEM studies of internal structures (e.g. Di Palma *et al*. 2015) and our conclusion on absence of secondary genital systems therefore have to be tentative. With these caveats and within the context of the proposed phylogeny, the above observations suggest that secondary genital systems in females of Heterozerconidae developed after the evolution of male spermatodactyls and may have evolved independently in various lineages. One more oddity: in all taxa without confirmed secondary genital systems in females, including *Narceoheterozercon* ex Alabama-C and *Af. spirostreptus*, the males have a similar type of spermatodactyl, the type defined as "straight". In contrast, males in taxa where a secondary genital system in females has been observed have modified (not straight) spermatodactyls. In light of the Walter & Proctor (2013) hypothesis, is the "straight" shape more suited for piercing e.g. the vaginal walls, with all alternative shapes modified to fit the available female secondary genital openings? As usual, more data is needed, in this case on mating behavior in heterozerconid species that lack secondary genital openings in females.

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