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Ozark Highland Cunaxidae (Acari: Prostigmata): Descriptions and keys to genera found to occur in the region and a new phylogenetic hypothesis for the family

Michael Joseph Skvarla
University of Arkansas, Fayetteville

OZARK HIGHLAND CUNAXIDAE (ACARI: PROSTIGMATA): DESCRIPTIONS AND KEYS TO GENERA FOUND TO OCCUR IN THE REGION AND A NEW PHYLOGENETIC HYPOTHESIS FOR THE FAMILY

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Master of Science in Entomology

By

Michael Joseph Skvarla
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ABSTRACT

Fourteen genera of Cunaxidae (Acari: Prostigmata) are reported from the Ozark Highlands for the first time. Descriptions, diagnoses, and illustrated keys to genera and world species are given. Five new species are described and illustrated and an additional 6 known species are recorded from the region. The first rigorous phylogenetic hypothesis for Cunaxidae is presented. Based on morphology, it suggests the current subfamilial classification scheme does not reflect the evolutionary history of the family. Unfortunately, bootstrap values and resolution are low, suggesting the need for further indepth molecular analyses.

This thesis is approved for recommendation to the Graduate Council

Thesis Director:

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(Dr. Ashley Dowling)

Thesis Committee:

_____
(Dr. Don Steinkraus)

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(Dr. Tim Kring)

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DEDICATION. To my wife, Sarah, who has always supported me, especially while writing this thesis; and my parents, grandparents and brother for always believing I could accomplish anything.

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INTRODUCTION

Among the most successful, but least understood invertebrates are the mites. While they may not be as speciose as insects, they encompass nearly 5% of all described species (Wilson & Peter 1988). Mites have invaded a huge range of habitats untouched by other chelicerates including deep soil (Coineau *et al.* 1978; Walter & Proctor 1999; Ducarme *et al.* 2004), vertebrate and invertebrate hosts (DeVaney 1979; Gary & Page 1987; Gabryś 1991; Martin 1992; Mullen & O'Connor 2002; Ritter & Jong 2009), coral reefs (Otto 1999; Otto 2000), deep sea trenches (Bartsch 1989; Bartsch 1994), the polar regions (Convey 1994; Hawes *et al.* 2007), and freshwater (Cook 1967; Young 1969; Pieczynski 1976; Cook 1986; Biesiadka, Cichocka, & Zawal 1989; Di Sabatino, Gerecke, & Martin 2000). Most mites are predaceous, but many have exploited food sources unique to Chelicerata including plants (Jeppson, Kiefer, & Baker 1975; Annecke & Moran 1982), fungi (Mitchell & Parkinson 1976; Valenti, Ferrel, & Berryman 1997; Schneider, Renker, & Maraun 2005), bacteria (Krantz & Walter 2009), and like harvestmen, decaying plant and animal matter (Walter & Proctor 1999; Hubert, Kubátová, & Šárová 2000; Franklin *et al.* 2004; Pinto-da-Rocha, Machado, & Giribet 2007). In addition to holding pivotal ecological roles like nutrient cycling (Krantz & Walter 2009; Wickings & Grandy 2011), mites are also economically important as agricultural (Moutia 1958; Bugg & Waddington 1994; Meyer [Smith] & Craemer 1999; Childers 1994; Elwan 2000) and veterinary pests (Unsworth 1946; Baker & Nutting 1950; Estes, Richter, & Franklin 1971; Axtell & Arends 1990; Birrenkott *et al.* 2000), human and animal disease vectors (Camin 1948; Burgdorfer *et al.* 1985; Bell & Whelan 1993; Qiu *et al.* 2002; Rosen, Yeruham, & Braverman 2002; Takahashi *et al.* 2004;

Masters, Grigery, & Masters 2008), and biocontrol agents (Wright & Chambers 1994; McMurtry & Croft 1997; García-Marí & González-Zamora 1999; Walzer, Schausberger, & Schausberger 1999; Gerson, Smiley, & Ochoa 2007; Copping 2009).

Nevertheless, mites remain a relatively poorly known group largely overlooked by modern science. In fact, while 48,200 mite species are currently described (Halliday, O'Connor, & Baker 2000), it is estimated the true diversity is closer to 1,000,000 (Erwin 1991; Gaston 1991). While there are likely several reasons for this, the most significant is an underdeveloped taxonomic scheme. Few keys are available that are accessible to non-specialists, regional species diversity is generally very poorly known, and phylogenetic hypotheses have been tested for only a select few groups. This is especially true in acariform mites (1 of 2 major braches of the mite tree, the other being the parasitiforms, which includes ticks and Mesostigmata), which are the most diverse both in terms of species and life histories (Walter & Proctor 1999).

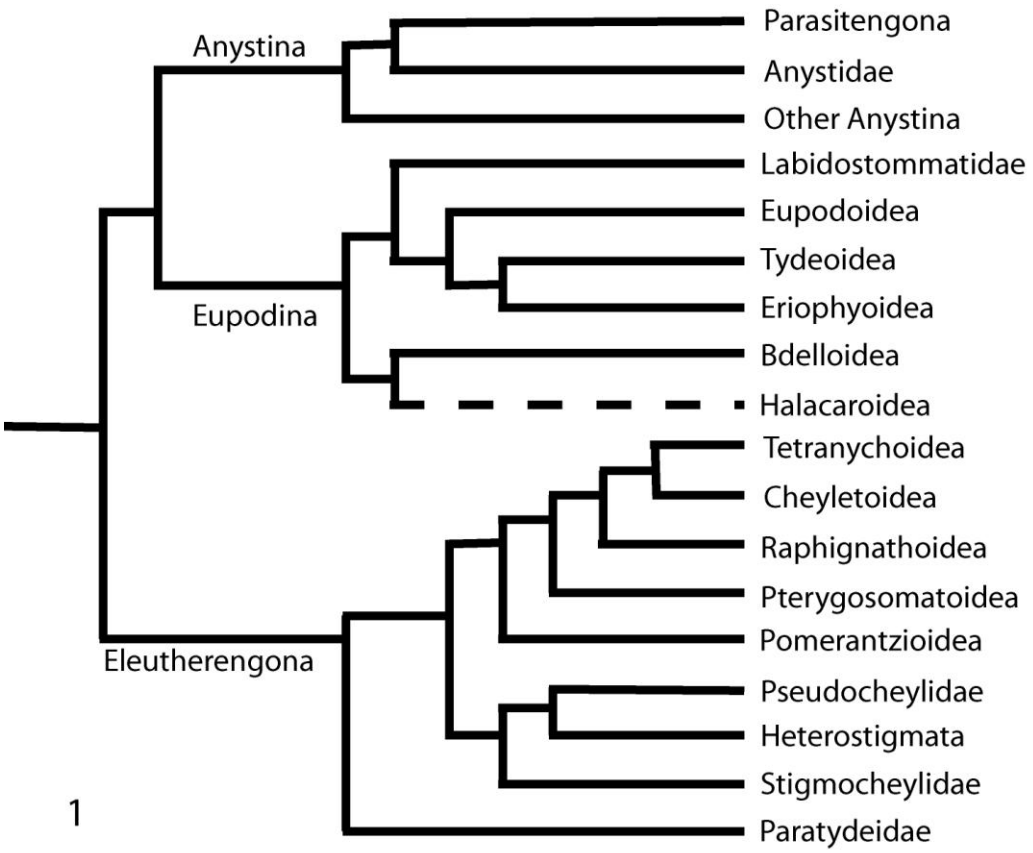
Depending on the classification system, acariform mites are divided into 2 or 3 major groups: Sarcoptaformes, Trombidiformes, and Endeostigmata. Endeostigmata is presently considered a "paraphyletic trashbin" containing basal taxa belonging to Sarcoptaformes and possibly Trombidiformes (O'Connor 1984; Walter & Proctor 1999), but is sometimes used for convenience. Sarcoptaformes includes Oribatida + Astigmata, which are major drivers of nutrient cycling in forest systems (Walter & Proctor 1999) and important in human and animal health (Fabiyi 1980; Peat *et al.* 1996). Trombidiformes is divided into two groups: Sphaerolichida (which consists of two uncommon families, Sphaerolichidae and Lordalychidae) and Prostigmata, which includes all of the major

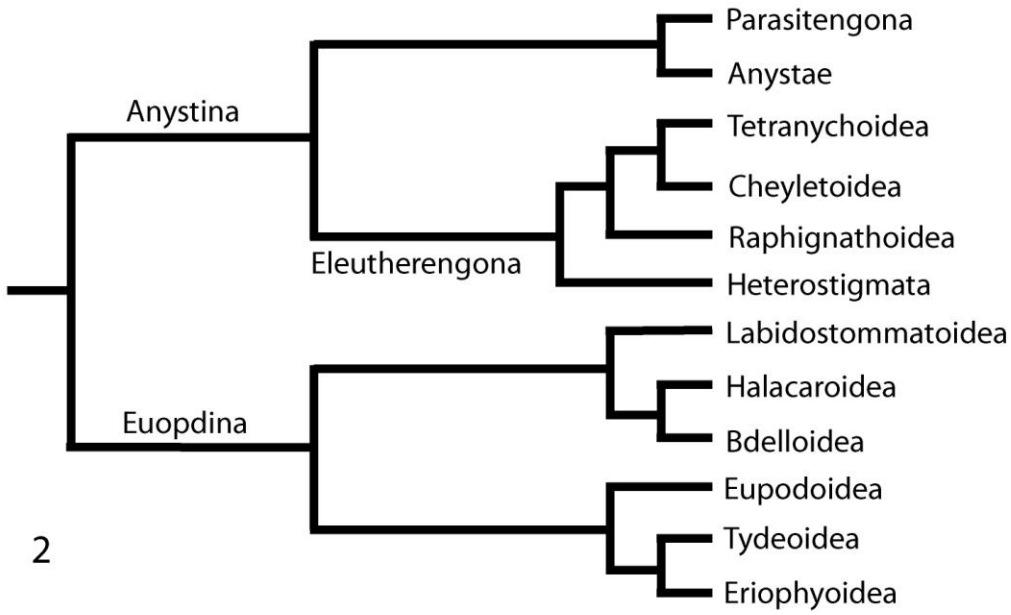
plant pests, important forest litter predators, the major aquatic (both salt and fresh water) lineages, and chiggers and relatives.

Multiple molecular phylogenetic studies have recovered a monophyletic Prostigmata (Dabert *et al.* 2010; Pepato, Rocha, & Dunlop 2010) when investigating relationships between higher taxa, but none have focused on taxa contained within the group, leaving current hypotheses within Prostigmata unreliable. Norton *et al.* (1993) and Lindquist (1996) provide cladograms of taxa within Prostigmata (Figs. 1 & 2), but the relationships are based on unpublished analyses (Proctor 1998). Both suggest a monophyletic Eupodina, which includes the economically important, phytophagous Eriophyoidea; Eupodoidea, which are generally fungivorous or predatory but include some species that can be pestiferous, such as *Penthaleus major*; Halacaroidea, the only lineage of fully aquatic marine mites; and Bdelloidea, which is comprised of two families of predatory mites.

Bdelloidea is probably a monophyletic lineage. A number of synapomorphies unite Bdellidae and Cunaxidae, such as the presence of leg trichobothria, leg segmentation, solenidia present on the palp tibiotarsi, and highly modified pedipalps. However, the relationship between these families remains unclear. Like Prostigmata, no rigorous phylogenetic work has been preformed within Bdelloidea. Most authors believe the two families sister groups (Norton *et al*. 1993; Lindquist 1996); though it is possible either Cunaxidae or Bdellidae is paraphyletic with respect to the other.

Cunaxidae are small (300 – 1000 µm), fast-moving mites that are often red, orange, or yellow. Worldwide there are 6 subfamilies and 27 genera containing approximately 330 described species. They are often present in forest systems in large





Figures 1 &2. Prostigmata cladograms. 1) From Norton *et al*., 1993. Dashed line represents uncertain affiliation. 2) From Lindquist, 1996.

numbers but can also be found in grasslands, agricultural fields, and anthropogenically disturbed areas. How cunaxids affect these systems through predation is unknown for a number of reasons: few comprehensive regional surveys have been carried out anywhere in the world and when they are included, cunaxids are often only reported at the genus level; keys to species are either regional or out of date and inaccurate, thus forcing non-specialists to accumulate primary species descriptions scattered throughout the literature if they wish to accurately identify specimens; and many species are undescribed. This work is intended to at least partially correct some of these deficiencies by providing updated diagnoses, historical reviews, and keys to subfamilies, genera and species; describing new species from the Ozark Highlands and Pennsylvania; and attempting to create the first rigorous phylogenetic hypothesis of Cunaxidae so classification can be based on evolutionary history.

Biology

All cunaxids are thought to be predaceous (Walter & Proctor 1999). They have been reported to feed on scales (Ewing & Webster 1912; Gerson 1971), Collembola (Sellnick 1926; Heryford 1965), nematodes (Walter & Kaplan 1991), phytophagous mites (Zaher *et al.* 1975a; Smiley, 1992; Sathiamma 1995; Arababi & Singh 2000; Ferla 2001; Lahiri *et al.* 2004; Castro & Moraes 2010) Psocoptera (Zaher *et al.* 1975a), and thrips (Milne 1977) and fail to survive when offered only plant material (Zaher *et al.* 1975a). Both ambush and active hunting have evolved within the family, sometimes within the same subfamily. In Cunaxinae, for instance, *Armascirus* and *Dactyloscirus*

wait, sometimes for hours, to ambush prey (Walter & Proctor 1999), whereas *Allocunaxa* actively searches for prey (Castro & Moraes 2010).

Cunaxids occur in most terrestrial habitats, including soil and leaf litter (Den Heyer 1977a; Luxton 1982); moss and lichen (Sepasgosarian 1978; Tseng 1980); on vegetation (Nesbitt 1946; Swift & Goff 2001; Ferla & Moraes 2002) including ornamental (Tagore & Putatunda 2003) and medicinal plants (Lahiri *et al.* 2004) and invasive weeds (Walter 1999); agricultural settings such as citrus trees (Muma 1960; Oliver 1968; Ramsey *et al.* 1972a; Soliman & Mahfood 1978; Quilici *et al.* 1997; Grout & Ueckermann 1999; Ferla & Moraes 2002; Fadamiro *et al.* 2009), cotton (Kuznetzov 1978), deciduous fruit trees (Lord 1949; Nesbitt 1964; Ramsey *et al.* 1972b; Quilici *et al.* 1997; Ferla & Moraes 1998; Ferla & Moraes 2002), grape vineyards (Jubb *et al.* 1985; Molnar 1997), guava trees (Mallikarjunappa & Nageshchandra 1990; Ferla & Moraes 2002;) and strawberries (Ferla *et al.* 2007); vertebrate nests (Garman 1948; Gupta & Chattopadhyay 1978; Gupta & Paul 1985; Estebanes-Gonzales 1997); caves (Cooreman 1954; Turk 1972; Zacharda 1978); duck pen litter (Copruz-Raros *et al.* 1988); tree holes (Atyeo 1958; Lin & Zhang 2002); house dust (Oliveria & Daemon 2003); and stored food products (Huges 1976; Tseng 1980; Fan 1992). Species, however, may specialize within a particular habitat: Muma (1965) reported *Armascirus taurus* to be most prevalent on the leaves of citrus trees while *Coleoscirus simplex* and *C. curtipalpus* were more common in the leaf litter and *Parabonzia bdelliformis* appears to be restricted almost exclusively to tree holes (Smiley 1992).

Cunaxids seem to prefer moist or damp habitats, but have also been collected from very dry or very wet areas (Den Heyer 1979a; Den Heyer 1980a). They are also

active year round. Den Heyer (1980a) collected all life stages of *Neocunaxoides* in the Transvaal Highveld during the summer (30°C+) and winter (minimum 0°C). Zaher *et al.* (1975b) collected cunaxids throughout the year and demonstrated a positive correlation between abundance and temperature; surprisingly, they also found a slight negative correlation between abundance and relative humidity.

Both sexual reproduction and thelytoky have been reported in Cunaxids (Walter & Proctor 1999; Castro & Moraes 2010). Castro and Moraes (2010) suggest that parthenogenesis may not be obligatory in *Cunaxatricha tarsospinosa* (males were described from a site approximately 450 km from the population they studied) but instead cyclic or facultative and possibly brought on by cellular endosymbionts.

A few species spin silk, which is used to protect eggs and quiescent, molting mites (Alberti & Ehrnsberger 1977); Castro and Moraes (2010) suggest that destruction of webbing surrounding eggs may reduce the viability of the eggs. It has also been proposed that some species may be venomous, though this has not been shown conclusively (Den Heyer 1980a; Smiley 1992; Walter & Proctor 1999).

Biogeography

Cunaxids have been found on every continent except Antarctica. Their true diversity is probably underrepresented in taxonomic literature as most areas have not been systematically sampled. Australia, for example, has only two reports of Cunaxidae: Womersley (1933) reported *Armascirus taurus* from Perth and *Cunaxa setirostris* from Perth and South Australia and Walter (1999) reported 5 undescribed species in 4 genera

from Queensland. With so little done, there are certainly numerous undescribed species and probably undescribed genera waiting to be found.

South Africa and the Philippines have the most well-documented cunaxid diversity thanks to the efforts of Den Heyer and Copruz-Raros. Even so, reports are still coming from those areas as new species and genera are discovered. South America was little studied until Castro and Den Heyer described 8 genera and 10 species from Brazil between 2008 and 2009.

The cunaxid fauna of Europe and North America north of Mexico fall between these two extremes. Most reports have been sporadic, though span more than a century (starting with Banks 1894 in the United States and Berlese 1887 in Europe). Robert L. Smiley , a well-known North American worker, never collected material. He instead worked on samples that were sent to him, often intercepted by the USDA at ports of entry, so rather than focusing on North American fauna he more generally worked on world species. This has led to a broad understanding of the species and genera that occur in North America that lacks depth.

Objectives

There are three objectives in this study. The first is to provide updated keys and other tools for researches interested in Cunaxidae. Previous studies of mites from natural ecosystems (Walter, 1999; Castro & Moraes, 2007) and agricultural plants (Muma, 1960; Jubb *et al.*, 1985; Ferla & Moraes, 1998;Feres, 2000; Feres *et al.*, 2002; Barbosa *et al.*, 2005) have often only reported cunaxids to the generic level. By making cunaxids more

accessible, researchers should be more willing to identify them to species in survey and other studies, thereby providing valuable data about species ranges, times of occurrence, and species composition in different habitats. I also hope that by gathering disparate information into one work, students and researchers who might otherwise have passed cunaxids by will be enticed to work on them.

The second objective is to describe new species and catalogue known species of Cunaxidae from the Ozark Highlands. There are two reasons for this: 1) The current extinction rate is estimated to be up to 1,000 times higher than the background extinction rate (Wilson, 1993); that is, species are currently going extinct 1,000 times faster than they they have historically. Combined with the fact that only 1.7 million of an estimated 10-100 million species ("WCU") have been described, there are many species that will slip into extinction before ever being discovered. This creates an environment that can be likened to a librarian in a burning library trying to catalogue and save the books before they are consumed by the flames. 2) This study is the first in-depth examination of cunaxid fauna to the species level in any region of North America north of Mexico. This will provide a baseline of comparison for biogeograhic studies in other areas.

The third objective is to provide a phylogenetic hypothesis for Cunaxidae using modern methods. In order to name species based on its evolutionary history a proper phylogeny must be elucidated. The only family-wide dendrograms (Den Heyer, 1980; Smiley, 1992) have been structured off of keys and not phylogenetic analysis of morphological or molecular characters. Bashir, Afzal, and Khan (2008) provide a dendrogram for 8 species of *Armascirus* using 24 characters; this study is based on multi-

variate analyses and percentage likeness between species instead of cladistic analyses and uses only Pakistani *Armascirus*, so it is of little use.

HISTORICAL REVIEWS, DIAGNOSES and KEYS TO SUBFAMILIES, GENERA, AND SPECIES

Introduction

Previous studies of mites from natural ecosystems (Castro & Moraes, 2007; Walter, 1999) and agricultural plants (Barbosa *et al.*, 2005; Feres, 2000; Feres *et al.*, 2002; Ferla & Moraes, 1998; Jubb *et al.*, 1985; Muma, 1960) have often only reported cunaxids to the generic level. This is problematic because so little is known about where cunaxid species occur, both regionally and in what habitats, and unfortunate because such reports are potentially very useful collectively if they were to identify the species found.

Part of the reason behind the lack of specific identification is the difficulty of reliably identifying cunaxids without extensive knowledge of the primary literature. Keys to cunaxid species are often regional keys, therefore useless to researchers outside of that specific region, and scattered across countless journals. The last comprehensive attempt (excluding Kalúz [2009], who gave a key to *Armascirus*) to present keys to world species was by Smiley (1992). The number of described species since Smiley published his monograph has doubled (166 to 330) and, perhaps most frustrating, his work is fraught with error (see Appendix 1). Updated keys reflecting known diversity and current taxonomic opinion are therefore imperative if non-cunaxid workers are to identify individuals to the specific rather than generic level.

Materials and Methods

During this study, 430 samples (413 deciduous leaf litter, 10 moss/lichen, 7 tree holes) were collected at sites across the Ozark Highlands in Arkansas and Missouri between 21 August 2009 and 9 May 2011 during all seasons (Fig. 3). In addition, 19

samples were collected in Pennsylvania, 5 in Ohio, 1 in West Virginia, and 8 in Texas (Fig. 4). Some samples were concentrated with a litter reducer (Martin 1977) in order to decrease the amount of material taken from the sites and increase the number of specimens per sample. Samples were processed using modified Berlese-Tullgren funnels for 3 to 7 days. Approximately half of all specimens collected are mounted on slides; the remaining specimens are stored in ethanol at -20°C. All slide mounted specimens are mounted in Hoyer's medium (see Krantz & Walter, 2009 for recipe). Illustrations were produced by the methods outlined by Fisher and Dowling (2010). Large stippling denotes arthrodial membrane. Because some illustrations are redrawn from previous works, a complete list of illustration citations are given in Appendix II.

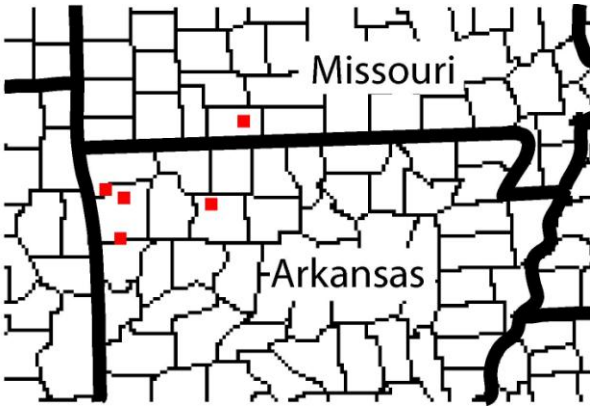


Figure 3. Ozark Highland collection site localities.

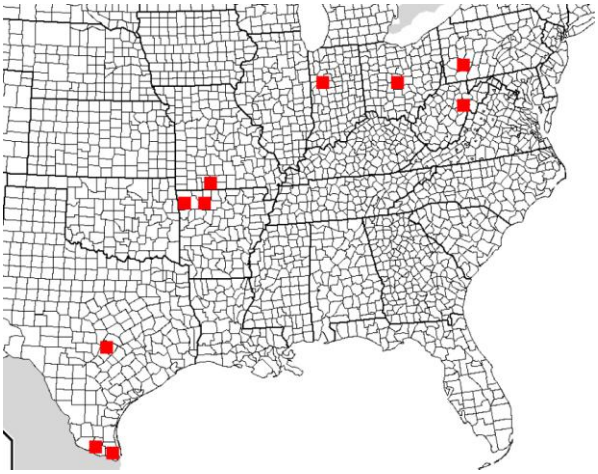


Figure 4. All collection site localities.

All measurements, including illustration scale bars, are in micrometers (µm). Setal notation follows Kethley (1990) as applied by Swift (1996) and Den Heyer and Castro (2008a). The term subcapitulum is used in place of hypognathum, which has been preferred by cunaxid workers in the past, as they are synonymous and subcapitulum is more widely accepted (Krantz & Walter 2009). The following abbreviations are used and

illustrated by Mejía-Recamier and Palacios-Vargas (2007): attenuate solenidion (asl), blunt rod-like solenidion (bsl), dorsodistal solenidion (dtsl), famulus (fam)(= peg organ), microseta (mst), paracoxal simple tactile setae (pcs), spine-like seta (spls), simple tactile seta (sts), terminal solenidion (tsl), trichobothria (T).

The diagnoses and keys presented here are based on the published literature. Unfortunately - through lack of resources, time, and perhaps foresight – most species included in the keys were not examined first hand. The accuracy of the keys is therefore dependent upon the accuracy of the published descriptions. Illustrations used in keys are intended to be diagrammatic: in many cases setae, solenidia, and other structures are not included in figures in order to increase clarity of the structure highlighted in the text. Always refer to the original description if descrepencies arise.

Relying on published descriptions had an influence on which characters were chosen for couplets. Often a character that is potentially useful and informative (such as the presence or absence of a cheliceral seta) is not reported. Sometimes the character in question was illustrated, but I tried to avoid relying on drawings too much as this requires my interpretation of the authors artistic skills and interpretation of the character. Thus, unlike previous keys, I often relied on characters such as setal counts of femoral segments. This may prove to be problematic as extra setae are sometimes reported on leg segments, though it may also be useful because it does not rely on ambiguous or hard to see characters.

Results and Discussion

698 specimens were slide mounted and identified to genus. 14 of 29 genera in 5 of 6 subfamilies were collected; Table 1 indicates the number of specimens slide mounted per genus and the distribution of world genera. Keys to genera and species include all described taxa unless otherwise noted. Many keys were produced *de novo*; those that were not include the base key's citation.

Subfamily	Genus	Number of Slide Specimens	Number of Species Collected	Number of Described Species	Distribution
Bonziinae	Bonzia	3	1	4	Europe, New Zealand, N. America, S. America,
	Parabonzia	15	1	7	Africa, Australia, N. America
Cunaxoidinae	Paracunaxoides	-	-	1	New Zealand
	Denhernaxoides	-	-	2	Italy, New Zealand
	Scutopalpus	-	-	12	China, Greece, Pakistan, Philippines, S. Africa, Ukraine
	Cunaxoides	24	3	15	Australia, Greece, Pakistan, N. America, Ukraine
	Dunaxeus	-	-	3	Brazil, S. Africa
	Funaxopsis	-	-	3	S. Africa
	Qunaxella	-	-	1	Brazil
	Bunaxella	-	-	3	S. Africa
	Neocunaxoides	22	3	14	Australia, China, N. America, Pakistan, Philippines, S. Africa
	Pulaeus	190	?	22	Cosmopolitan
	Lupaeus	18	?	15	Brazil, N. America, Philippines, S. Africa
Scirulinae	Scirula	2	1	2	China, Europe, N. America
Cunaxinae	Cunaxa	192	?	47	Cosmopolitan
	Rubroscirus	-	-	24	Africa, Australia, Mexico, Ukraine
	Cunaxatricha	-	-	1	Brazil
	Riscus	-	-	1	Thailand
	Allocunaxa	-	-	1	Brazil
	Armascirus	85	5	33	Cosmopolitan
	Dactyloscirus	35	2	24	Cosmopolitan
Coleoscirinae	Scutascirus	-	-	7	Brazil, Malaysia, Pakistan, S. Africa
	Coleoscirus	5	3	29	Cosmopolitan
	Neoscirula	16	1	28	Cosmopolitan
	Pseudobonzia	16	1	5	Japan, N. America, S. Africa, Thailand
	Neobonzia	38	4	22	China, N. America, Pakistan, Philippines, S. Africa, Ukraine
Orangescirulinae	Orangescirula	-	-	3	Costa Rica, China, Philippines

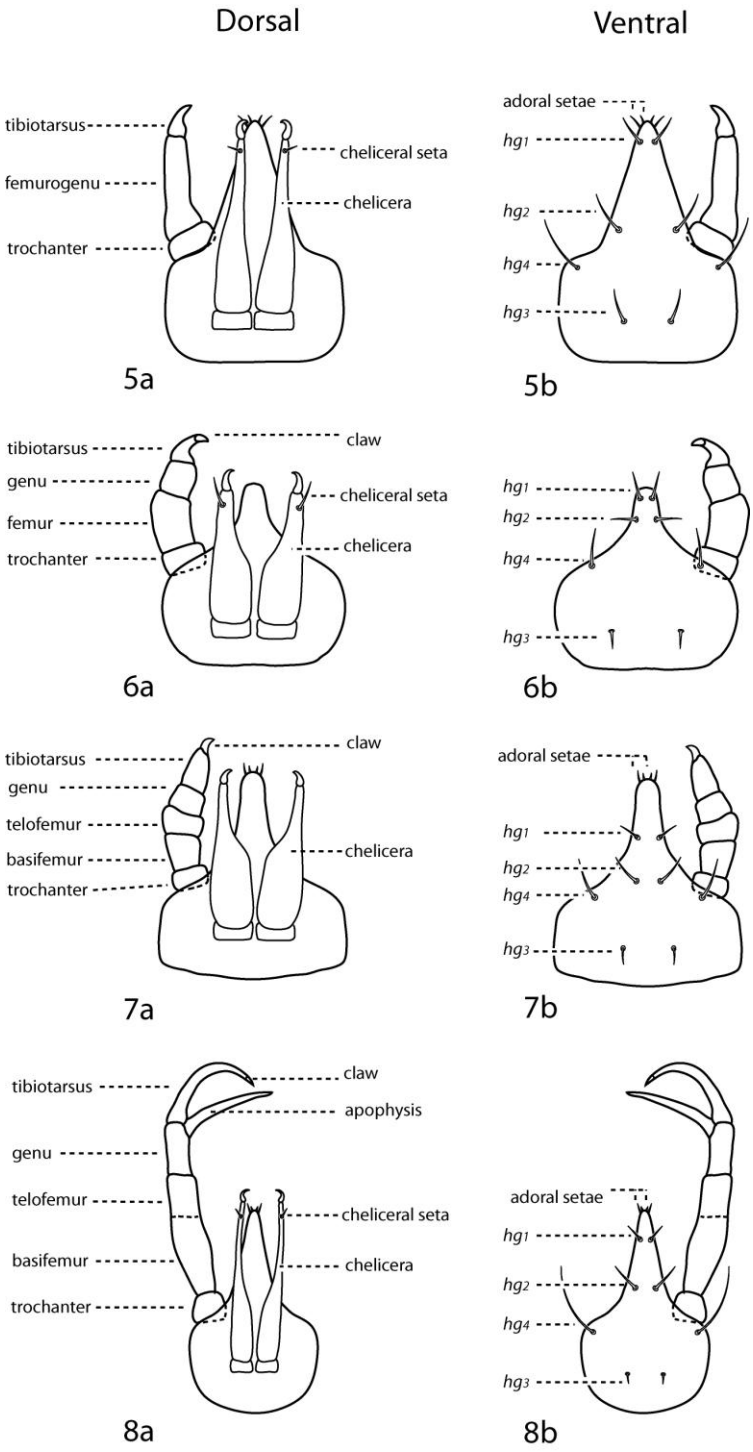
Table 1. Number of specimens slide moutned and species collected per genus during this study, number of described species per genus, and world distribution of genera. Genera labeled as cosmopolitan have been collected on every continent except Antarctica.

Cunaxidae

Historical review. Hermann separated three mites with elongated gnathosomas (=Bdelloidea) from *Acarus* into *Scirus*. However, Hermann died in 1794 and his papers were not published until after his death by his brother-in-law F. L. Hammer in 1804. Latrielle (1795) had by then separated the same mites into *Bdella*. Von Heyden (1826), recognizing that *Bdella* had priority over *Scirus*, synonomised *Scirus* with *Bdella* and erected *Cyta* and *Cunaxa*. Many authors, especially Berlese, continued to describe new mites as *Scirus*, even up through 1918. Dugés (1834a) erected Bdellidae (=Bdelloidea). Trouessart (1892) moved *Cunaxa* from Bdellidae to Trombidiidae and erected the subfamily Scirinae for it. Oudemans (1902) used Cunaxinae in the same sense that Trouessart (1892) used Scirinae, that is for those mites in the family Bdellidae (sensu Koch) that have palps with a curved terminal segment and movable chela only (= Cunaxidae *sensu* Thor). Thor (1902) erected Cunaxidae as a family separate from Bdellidae. Oudemans (1906) substituted Cunaxinae for Cunaxidae. Van der Hammen (1972) erected the superfamily Cunaxoidea over Bdelloidea, disregarding the priority of *Bdella* Latrielle (1795) over *Cunaxa* Von Heyden (1826). Den Heyer (1977b) erected Bonzinae for *Bonzia* and *Parabonzia.* Den Heyer (1978a) erected Coleoscirinae. Den Heyer (1978b) preserved the name Cunaxinae, but limited its concept to those cunaxids possessing 5-segmented palps that extend past the subcapitulum by at least the distal two segments. Den Heyer (1980c) erected the monobasic Scirulinae and recoginized the priority of Bdelloidea of Cunaxoidea. Bu and Li (1987a) erected Orangescirulinae. Smiley (1992) erected Denheyernaxoidinae, Neobonzinae, and Paracunaxoidinae as monotypic subfamilies; he also misspelled Bonzinae as Bonziinae. Den Heyer and Castro (2008b) noted that the original spelling of Bonzinae was with a single i. Den

Heyer and Castro (2009) moved *Denheyernaxoides* and *Paracunaxoides* to Cunaxoidinae, thus disregarding Denheyernaxoidinae and Paracunaxoidinae as valid subfamilies. Lin and Zhang (2010) provided a detailed historical review of Cunaxidae in China as well of a checklist of species found in that country. Den Heyer (2011) moved *Neobonzia* to Coleoscirinae, effectively disregarding Neobonzinae, and synonymized *Coleobonzia* with *Neobonzia*.

Diagnosis. *Gnathasoma* (Figs. 5–8) The palps are 3-, 4-, or 5-segmented and usually end in a strong claw (except most notably in *Pseudobonzia*). They may be shorter, equal to, or extend beyond the distal end of the subcapitulum. The femora may be divided into basi- and telofemora; sometimes they are secondarily fused, though a dark line often indicates the previous articulation (Figs. 7a,b illustrate a fully divided femur and figs. 8a,b illustrate a secondarily fused femur with a dark line. This is for illustration purposes only(i.e., cunaxids with long and short 5-segmented palps may have either fully divided or secondarily fused femora). One genus (*Allocunaxa*) is unique in that the telofemora and genua are fused, though the basifemoral/ telofemoral articulation is present. Apophyses may be present on the telofemora, adjoining the genua and tibiotarsi, or on the tibiotarsi. The subcapitulum is generally wedge-shaped. It may be patterned with random dots or papillae, dots or papillae forming lines, a single row of cells on the caudal edge, or reticulations forming polygonal cells. Up to 6 pairs of setae are present on the subcapitulum: $hg_{1–4}$ and 2 pairs of adoral setae. Hg_1 is usually straight, but is geniculate in Bonzinae and may be curved in *Neoscirula*; hg_4 are often the longest pair of subcapitular setae. A seta may be present or absent near the cheliceral digit.



Figures 5-8. Adoral and cheliceral setae may be present or absent, but have been included in some illustrations for clairity. 5) 3-segmented pedipalp (Cunaxoidinae). 6) 4-segmented pedipalp (Scirulinae). 7) 5-segmented pedipalp that does not extend beyond the subcapitulum by more than the distal half of the genua (Bonzinae, Coleoscirinae, and Orangescirulinae). 8) 5-segmented pedipalp that reaches beyond the subcapitulum by at least the distal half of the genua (Cunaxinae).

Dorsum (Fig. 9a). The idiosoma is diamond-shaped. The dorsal propodosoma is covered with a sclerotized shield that usually bears 2 pairs of setae (*ve* and *sci*) and 2 pairs of setose sensilla (*vi* and *sce*); rarely one pair of setae or sensillae are absent. The dorsal hysterosoma may be complemented with 1–5 plates and platelets. These plates and platelets may capture one or more pairs of setae. Up to 8 pairs of dorsal hysterosomal setae may be present (c_1–h_1, c_2, f_2, and h_2); h_2 may also occur ventrally. The setae may occur on small platelets that are barely larger than the setal socket. The integument that is not covered in shields, plates, or platelets is striated. Cupule *im* is present, usually laterad and slightly caudal to e_1. The dorsal idiosomal shields and plates may be plain or patterned with random dots or papillae, dots or papillae forming lines, or reticulations forming polygonal cells; the propodosomal shield and large hysterosomal shields may also have a pair of cells which form rows.

Venter (Fig. 9b) The ventral idiosoma may be complemented with 1 or a few small platelets in addition to the coxal plates. Coxal plates I–II are often fused in adults and may coalesce medially to form a sternal shield. Coxal plates III–IV are often fused in adults and may extend caudally beyond the genital plates. Each coxal plate may be complemented with 1–4 setae; extensive coxal plates or sternal shields may capture setae normally on the integument and therefore have more. The coxal plates may be plain or patterned with random dots or papillae, dots or papillae forming lines, or reticulations forming polygonal cells. Genital plates (sometimes called anal valves) are present in adults and bear 3 (rarely) or 4 (usually) setae, except in *Parabonzia* which may have up to 9 pairs of setae; 2 pairs of genital papillae are visible underneath the plates. Anal

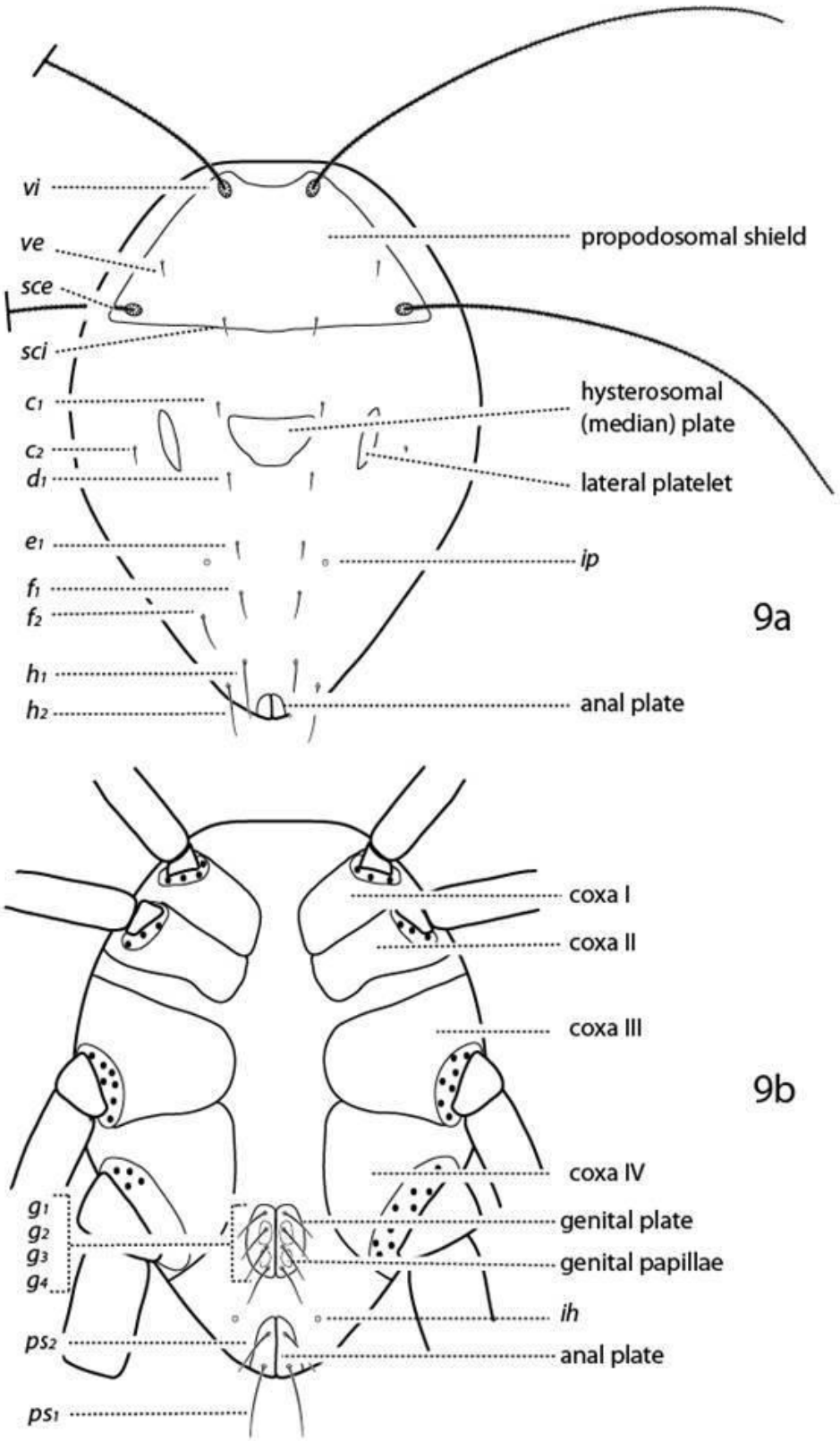


Figure 9. Generalized schematic of cunaxid morphology. 9a) Idiosoma, dorsal. 9b) Idiosoma, ventral.

plates (sometimes called anal valves) bear 1–2 setae (ps_{1-2}). Setae ps_2 may occur off the anal plates. The integument that is not covered in shields or plates is striated.

Key to Subfamilies of Cunaxidae

1 Telofemoral multi-branched seta present (except *Parabonzia mindanensis*) (Fig. 10) ..... Bonzinae

- Telofemoral multi-branched seta absent 2

2 (1) Palps 3 segmented (Figs. 5a,b) ..... Cunaxoidinae

- Palps 4 segmented (Figs. 6a,b) ..... Scirulinae

- Palps 5 segmented (the basifemora and telofemora may be partially fused) (Figs. 7a,b; 8a,b) 3

3 (2) Palps extend beyond the subcapitulum by at most the distal half of the tibiae (Fig. 7a,b) 4

- Palps extend beyond the subcapitulum by at least the distal half of the tibiae (Fig. 8a,b) ..... Cunaxinae

4 (3) Trichobothrium on tibiae IV present; setae hg_1 not geniculate; cheliceral seta usually present ..... Coleoscirinae

- Trichobothrium on tibiae IV absent; setae hg_1 geniculate; cheliceral seta absent ..... Orangescirulinae

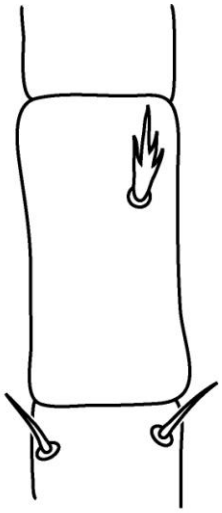


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Figure 10. Telofemoral branched seta present in Bonzinae

Bonzinae

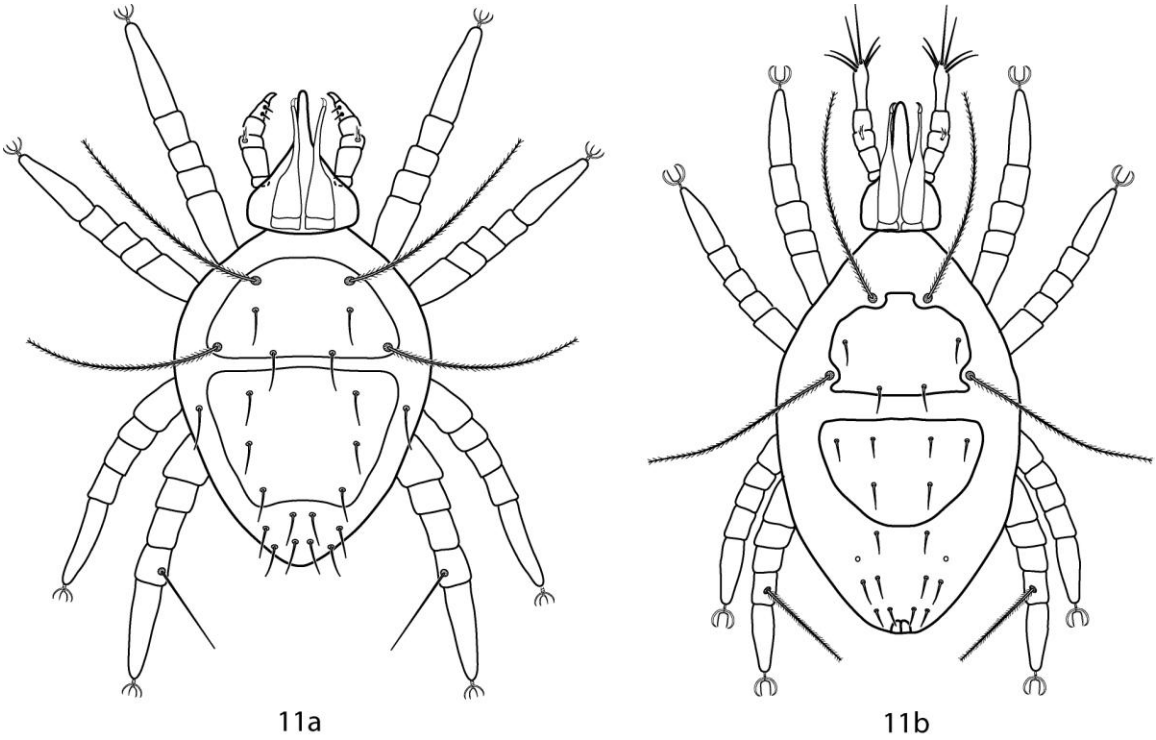


Figure11. Generalized Bonzinae, dorsal. 11a) *Bonzia*. 11b) *Parabonzia*

Historical Review. Oudemans (1927) erected *Bonzia* within Cunaxidae for *B. halacaroides*. Smiley (1975) erected *Parabonzia* for *Bonzia bdelliformis*. Den Heyer (1975) erected *Cunabdella* for *C. marthae*. Den Heyer (1977b) erected Bonzinae for the two genera. Kuznetzov and Livshitz (1979) synonymized *Cunabdella* with *Parabonzia*.

Diagnosis. Palps are 5 segmented and reach beyond the subcapitulum by at most the distal half of the tibiae. Apophyses are absent. A multi-branched seta is present dorsally on the telofemora. The tibiotarsi terminate in a stout claw or two strong setae. 2 pairs of adoral setae present or absent. 4 pairs of subcapitular setae (hg_{1-4}) present in *Bonzia*; up to 6 pairs of subcapitular setae (hg_{1-4} + additional setae) present in *Parabonzia*.

The dorsal propodosoma bears a shield complemented with 2 pairs of setae (*vi* and *sce*) and 2 pairs of setose sensillae (*ve* and *sci*). The dorsal hysterosoma may bear a shield; if a shield is present it may be complemented with a variable number of setae depending on the extent of the shield. Setae c_1–h_1, c_2, f_2 and h_2 present. The setae may be smooth or spiculate. Cupule *im* is present laterad and caudally of e_1. Unsclerotized integument is striated.

Coxae I–II may be fused or not and coxae III–IV may be fused or not. The genital plates bear 4–9 setae; 2 pairs of genital papillae are visible underneath the plates. Up to 4 pairs of setae present on the anal plates. Up to 9 pairs of setae on the integument between coxae II and the anal plates.

A trichobothria is present on leg tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female Bonzinae (modified from Smiley, 1992)

1 Palp tibiotarsal claw present; 2 palp tibiotarsal spine-like tubercles present (Fig. 11a); genital plates with 4 pairs of setae; internal genital setae absent ..... *Bonzia*

\- Palp tibiotarsal claw absent; 2 palp tibiotarsal spine-like tubercles absent (11b); genital plates with 5–9 pairs of setae; internal genital setae present ..... *Parabonzia*

Bonzia

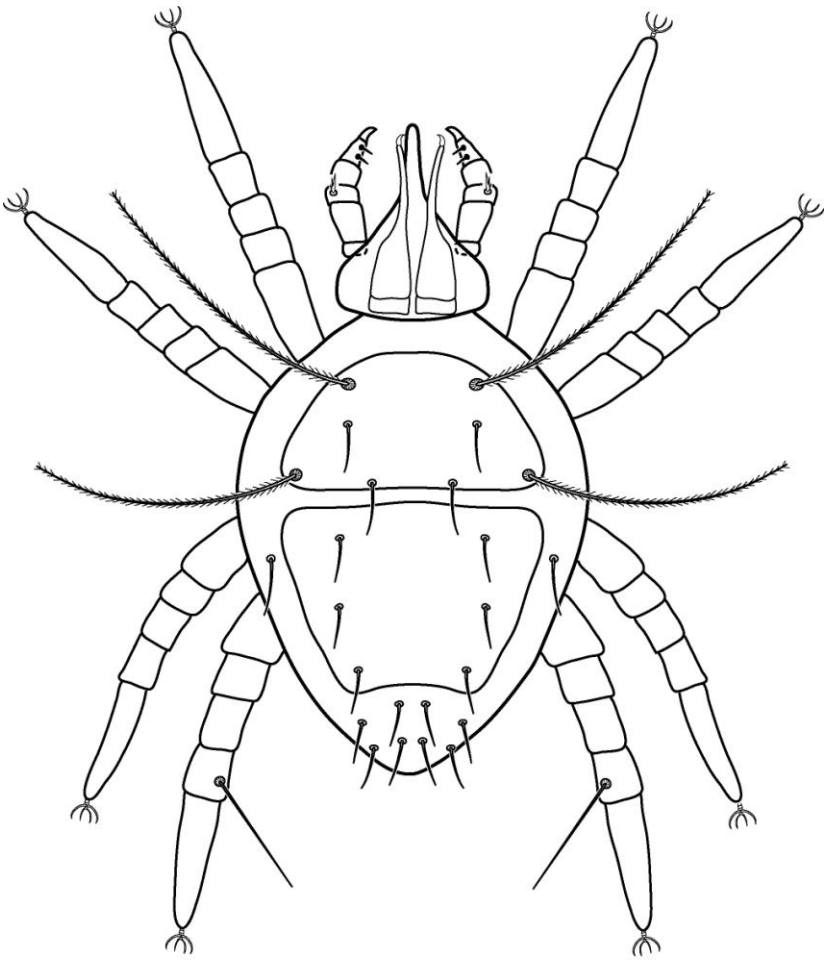


Figure 12. Generalized *Bonzia*, dorsal.

Historical Review. Oudemans (1927) erected *Bonzia* for *B. halacaroides*. Willmann (1939) described *B. sphagnicola* from Germany. Willmann (1950) described *B. rufofusca*. *Bonzia brownei* was described by Turk (1972). Kuznetzov and Livshitz (1979) reported *Bonzia* from Russia. Michocka (1987) reported *B. halacaroides* from Poland. Smiley (1992) described *B. woodi* and *B. yunkeri* and synonymized *B. rufofusca* and *B. brownei* with *B. halacaroides.*

Diagnosis. Palps are 5 segmented and reach beyond the subcapitulum by at most the distal half of the tibiae. Apophyses are absent. A dorsal multi-branched seta is present on the telofemora. The tibiotarsi terminate in a stout claw. 2 pairs of adoral setae are present or absent. 4 pairs of subcapitular setae ($hg_{1–4}$) are present. Setae hg_1 are geniculate.

The dorsal propodosoma bears a shield complemented with 2 pairs of setae (*vi* and *sce*) and 2 pairs of setose sensillae (*ve* and *sci*). The dorsal hysterosoma bears a shield that may be complemented with a variable number of setae depending on the extent of the shield. Setae c_1–h_1, c_2, f_2 and h_2 present. The setae may be smooth or spiculate. Cupule *im* is present laterad and caudally of e_1. The integument that does not bear shields or plates is striated.

Coxae I–II fused and coxae III–IV fused. The genital plates bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. 4 pairs of setae present on the anal plates. A trichobothria is present on leg tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female *Bonzia* (modified from Smiley 1992)

1 Tibiae IV trichobothria setose (Fig. 13a) 2

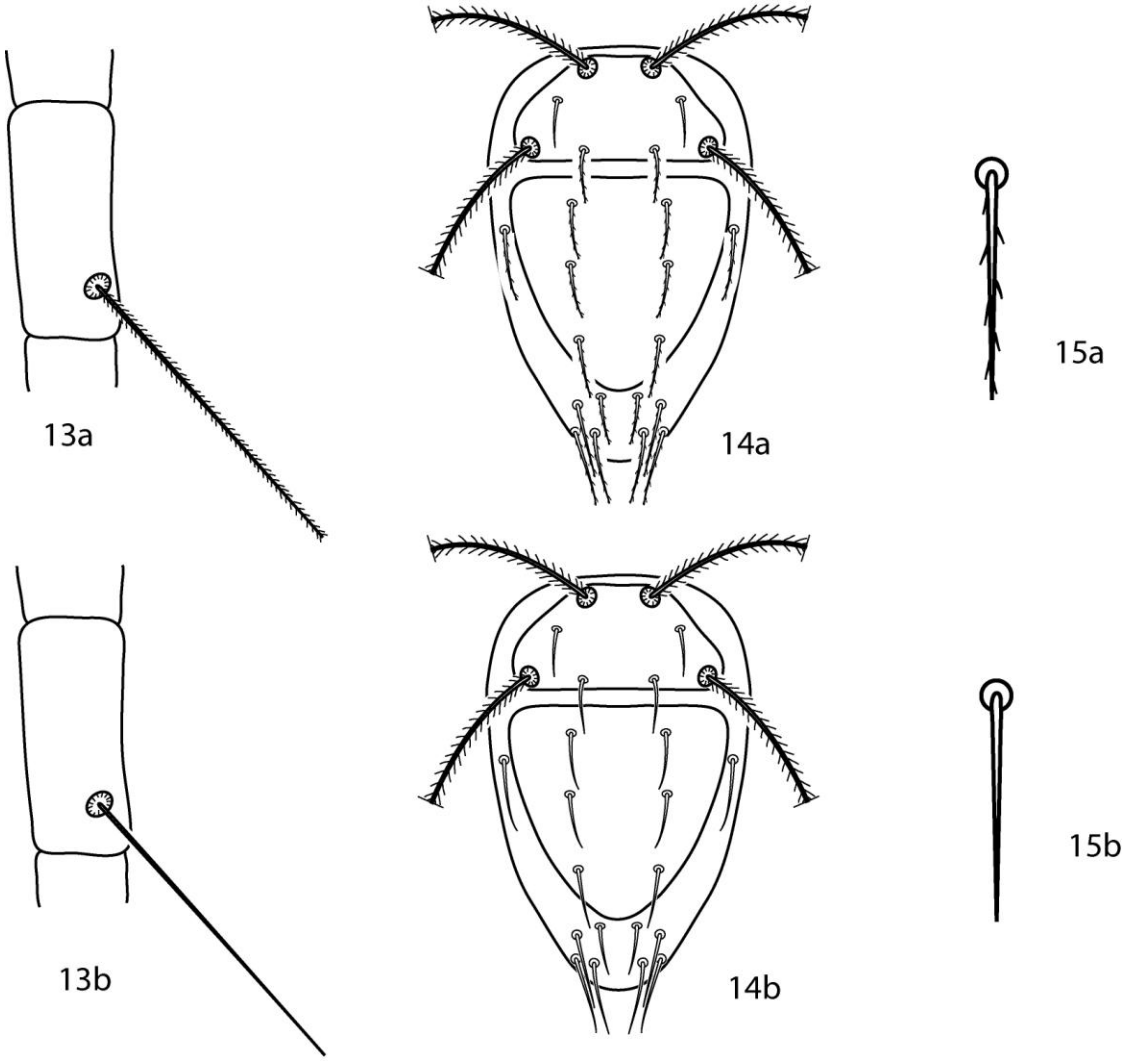
\- Tibiae IV trichobothria smooth (Fig. 13b) 3

2 (1) Hysterosomal shield with 2 pairs of setae; Germany ..... *B. sphagnicola*

- Hysterosomal shield with 3 pairs of setae; N. America, S. America, Europe (possibly cosmopolitan) ..... *B. halacaroides*

3 (1) Dorsal setae spiculate (Fig 14a, 15a); New Zealand ..... *B. woodi*

- Dorsal setae smooth (Fig 14b, 15b); USA: Virginia, Ozark Highlands .. *B. yunkeri*



Figures 13-15. *Bonzia* key illustrations. 13a) Setose tibial trichobothrium. 13b) Smooth tibial trichobothrium. 14a) Spiculate dorsal setae. 14b) Smooth dorsal setae. 15a) Close up of a spiculate seta. 15b) Close up of a smooth seta.

Parabonzia

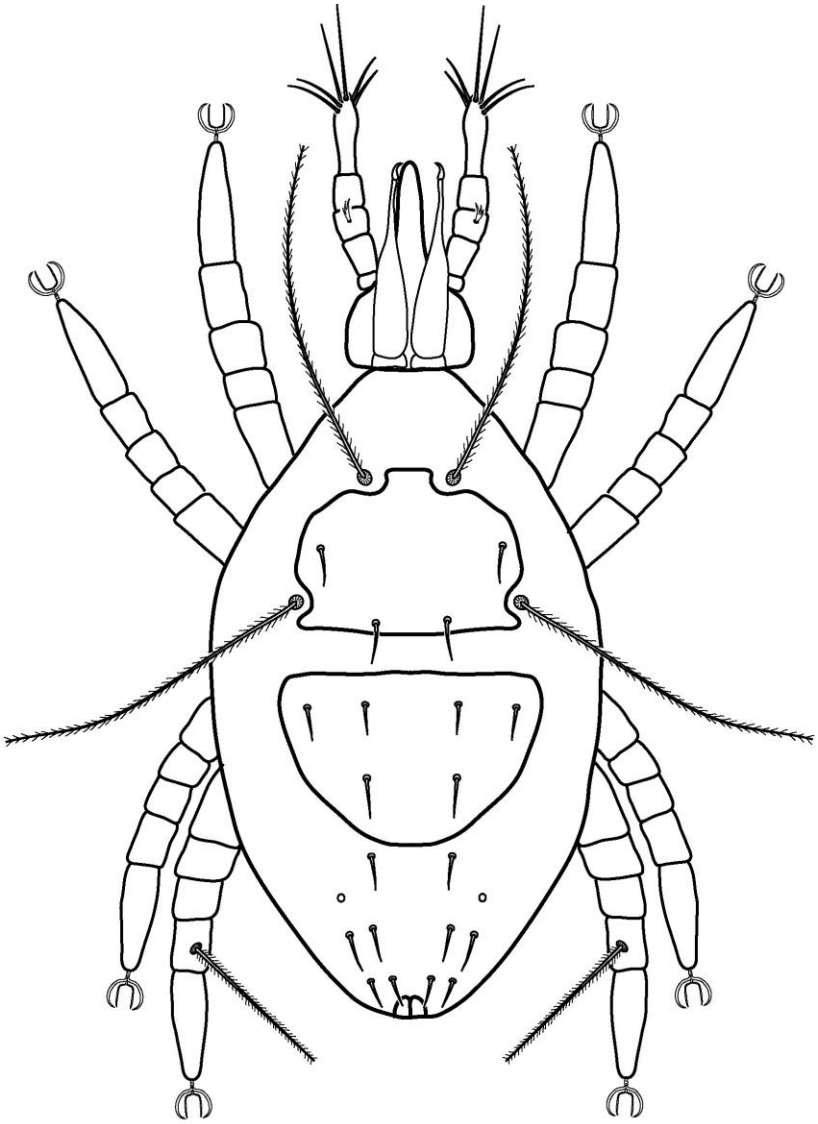


Figure 16. Generalized *Parabonzia*, dorsal.

Historical Review. Atyeo (1958) described *Bonzia bdelliformis* from a tree hole in Tennessee, USA. Smiley (1975) erected *Parabonzia* for *B. bdelliformis*. Den Heyer (1975) erected *Cunabdella* for *C. marthae*. Den Heyer (1977b) described *P. athiasae*. Kuznetzov and Livshitz (1979) synonymized *Cunabdella* with *Parabonzia* and reported *Parabonzia* from Russia. Smiley (1992) described *P. mumai* from Florida, USA and,

apparently unaware of Kuznetzov and Livshitz (1979), resynonymized *Cunabdella* with *Parabonzia* Corpuz-Raros (1996a) described *P. mindanensis* from the Philippines. Lin and Zhang (1998) described *P. trioxys.* Later they (Lin and Zhang, 2002) described *P. zhangi*.

Diagnosis. Palps are 5 segmented and reach beyond the subcapitulum by at most the distal half of the tibiae. Apophyses are absent. A multi-branched seta is present dorsally on the telofemora. The tibiotarsi terminate in two strong setae. 2 pairs of adoral setae are present or absent. Up to 6 pairs of subcapitular setae present.

The dorsal propodosoma bears a shield complemented with 2 pairs of setae (*vi* and *sce*) and 2 pairs of setose sensillae (*ve* and *sci*). The dorsal hysterosoma may bear a shield; if a shield is present it may be complemented with a variable number of setae depending on the extent of the shield. Setae c_1–h_1, c_2, f_2 and h_2 present. The setae are smooth. Cupule *im* is present laterad and caudally of e_1. The integument that does not bear shields or plates is striated.

Coxae I–II may be fused or not and coxae III–IV may be fused or not. The genital plates with up to 9 setae; 2 pairs of genital papillae are visible underneath the plates. Up to 4 pairs of setae present on the anal plates. Up to 9 pairs of setae on the integument between coxae II and the anal plates.

A trichobothrium is present on leg tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female *Parabonzia*

1 8–9 genital setae present 2

- 6–7 genital setae present 3

2 (1) Palpal telofemoral seta unbranched (Fig. 17a); Philippines, Mindanao Is. ..... *P. mindanensis*

- Palpal telofemoral seta branched, with 4–5 tines (Fig. 17b); China: Hubei Province ..... *P. zhangi*

3 (1) Hysterosomal shield with 3 setae 4

- Hysterosomal shield with 4 setae 6

4 (3) Palpal tibiotarsal sigmoid setae lightly barbed (Fig. 18); South Africa: West Transvaal ..... *P. marthae*

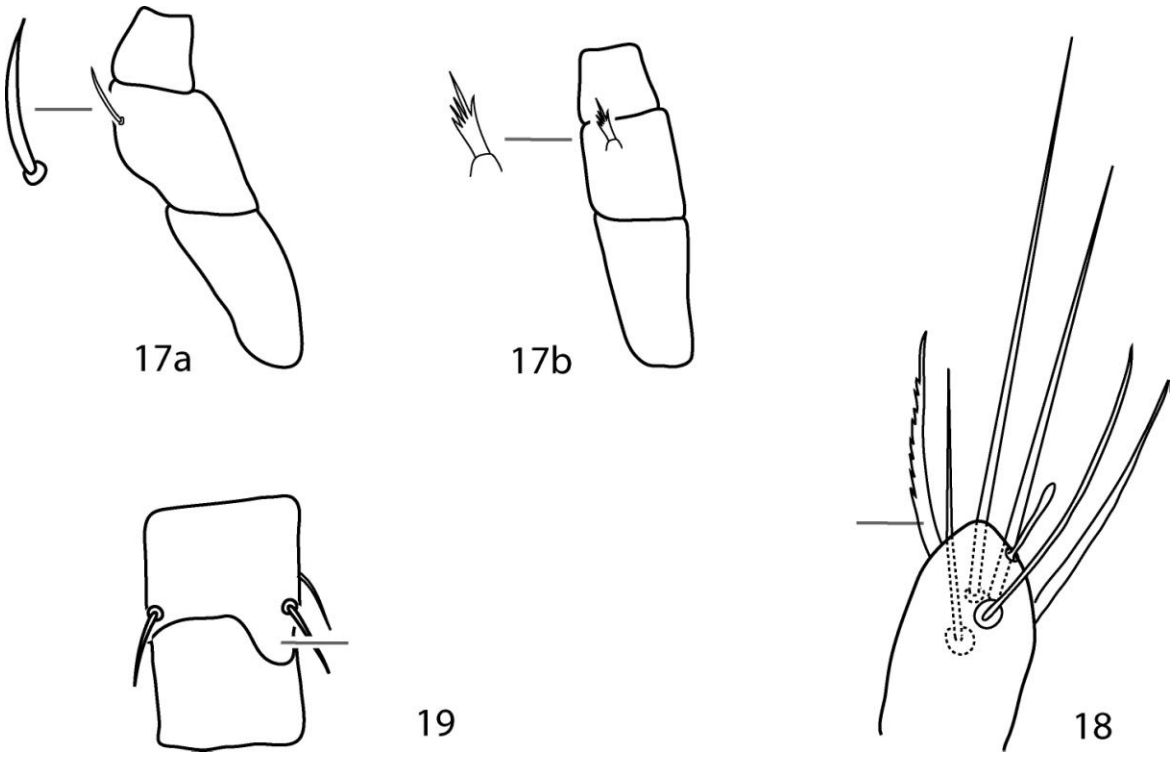
- Palpal tibiotarsal sigmoid setae smooth 5

5 (4) Large spur-like process present on femora III (Fig. 19); USA: Florida ..... *P. mumai*

- Large spur-like process absent on femora III; Ivory Coast ..... *P. athiasae*

6 (3) Coxae I–IV setal formula 7-5-6-7 sts; basifemora I–IV setal formula 4-7-3-2 sts; China: Fujian ..... *P. trioxys*

- Coxae I–IV setal formula 6-6 (sometimes 7)-7-7 sts; basifemora I–IV setal formula 5-8-3-2 sts; USA, Russia, S. Africa ..... *P. bdelliformis*



Figures 17-19. *Parabonzia* key illustrations. 17a) Unbranched palp telofemoral seta. 17b) Multi-branched palp telofemoral seta. 18) Lightly barbed palp tibiotarsal sigmoid seta. 19) Spur-like process on femora III.

Cunaxoidinae

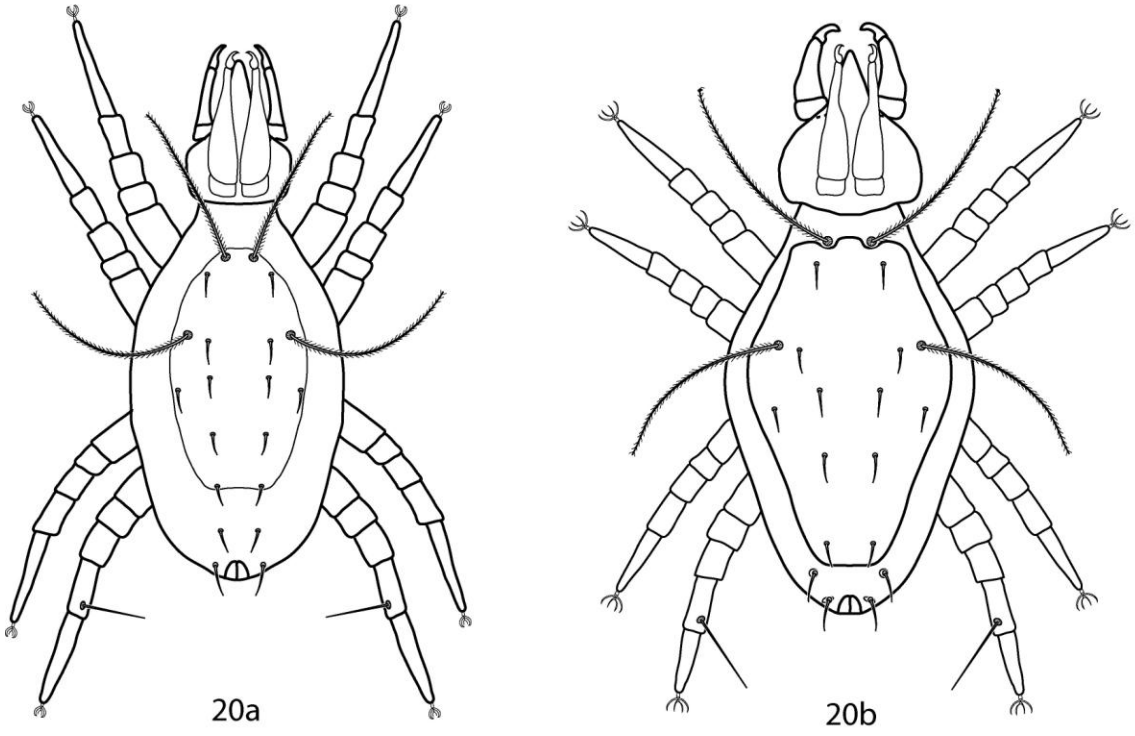


Figure 20. Generalized Cunaxoidinae , dorsal. 20a) *Cunaxoides*. 20b) Pulaeini (*Neocunaxoides*, *Pulaeus*, *Lupaeus*)

Historical Review. Koch (1838) established *Eupalus* and described the first mite belonging to Cunaxoidinae, *Eupalus croceus*. Baker and Hoffmann (1948) proposed *Cunaxoides* to replace *Eupalus* Koch as the name was pre-occupied (a fact that acarologists had missed for 100 years) by *Eupalus* Gistl; they also redescribed and reillustrated a number of known species. Radford (1950) proposed *Haleupalus* to replace *Eupalus*, though this name is invalid because it is predated by *Cunaxoides*. Smiley (1975) erected *Neocunaxoides* and reviewed *Cunaxoides*. Both genera were assigned to the newly established Cunaxoidinae by Den Heyer (1978c). *Pulaeus* was established by Den Heyer (1979b); the name is an anagram and nod to *Eupalus*. Den Heyer (1980d) erected *Scutopalpus* for those cunaxoidines with well-demarcated dorsal and ventral

plates. Smiley (1992) synonymized *Scutopalpus* with *Neocunaxoides* and *Haleupalus* with *Cunaxoides*; he also erected *Denheyernaxoides* and *Paracunaxoides* as monotypic genera in two new subfamilies, Denheyernaxoidinae and Paracunaxoidinae respectively. Castro and Den Heyer (2009) split a new genus, *Lupaeus*, from *Pulaeus* based on the number of setae on basifemora IV and pointed processes on the palp tibiotarsi and other harder to observe traits. Den Heyer and Castro (2009) split *Bunaxella, Dunaxeus, Funaxopsis*, and *Qunaxella* from *Neocunaxoides*; they also moved *Denheyernaxoides* and *Paracunaxoides* to Cunaxoidinae, thus disregarding Denheyernaxoidinae and Paracunaxoidinae as valid subfamilies.

Diagnosis. Palps are composed of 3 segments: a trochanter which lacks setae, fused femurogenu (femur + genu) which is complemented with 5 or 6 setae, and tibiotarsus (tibia + tarsus) which is complemented with 5 or 6 setae. The tibiotarsi may be complemented with a bladder- or bulb-like apophysis. The palps do not reach beyond the subcapitulum by more than the distal half of the tibiotarsi. The chelicerae may bear a seta near the cheliceral digit. 4 pairs of setae ($hg_{1–4}$) are present on the subcapitulum; setae hg_4 is often the longest. 2 pairs of adoral setae are present or absent.

The female dorsal idiosoma bears a propodosomal shield (absent in *Cunaxoides ulcerosus*) which is complemented with two pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and *sce*) and may bear a hysterosomal plate complemented with a varying number of setae; when present the dorsal hysterosomal plate may be fused with the propodosomal shield. The dorsal plates may or may not be well demarcated. Dorsal setae c_1–h_1 are present; c_2, f_2 and h_2 may also be present. If f_2 is present, f_1 and f_2 may be

located together on a small platelet. Setae not found on plates may be born on small platelets barely larger than the setal socket. Cupule *im* is present laterad and posterior of e_1. The integument that is not covered in shields or plates is striated

The female coxal plates vary in size, ranging between being restricted to the trochantral bases to being extensive and nearly forming a holoventral shield. The coxal plates may or may not be well demarcated. Coxal plates I–II are usually fused, as are coxal plates III–IV. Coxal plates I–II may coalesce medially to form a sternal shield. The genital plates each bear 4 setae ($g_{1–4}$); 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae (probably ps_1); one pair of setae is present ventrally on the integument near the anal plates (either ps_2 or *pa*). Cupule *ih* is present ventrally laterad the integumental setae associated with the anal plates. The integument that is not covered in shields or plates is striated.

The tarsi are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female Cunaxoidinae (modified from Den Heyer & Castro 2009)

1 Palpal tibiotarsi with 3 sts, 1 spls; New Zealand ..... *Paracunaxoides*

\- Palpal tibiotarsi with 5 or 6 sts, 0 spls 2

2 (1) Palpal femurogenu with 5 setae; long setae ending in terminal bulb-like knob (very small) on tarsi III and IV present; telofemoral setal formula not 5-5-4-3; usually 6 setae on palp tibiotarsus ..... Cunaxoidini 3

- Palpal femurogenu with 6 setae; long setae ending in terminal bulb-like knob (very small) on tarsi III and IV absent; telofemoral setal formula 5-5-4-3; usually 5 setae on palp tibiotarsus ..... Pulaeini 9

3 (2) Femora I and II divided; setae f_2 absent; trichobothrium on tibiae IV present or absent 4

- Femora I and II not divided; setae f_2 present; trichobothrium on tibiae IV absent ..... *Denheyernaxoides*

4 (3) Dorsum with ill-defined weakly sclerotized dorsal plates (Fig. 21a); subterminal pointed process on palp tibiotarsal claw present (Fig. 22a); small teeth (=serrated edge) on palp tibiotarsal claw present (Fig. 22a); cheliceral setae absent 5

- Dorsum with well-defined and sclerotized dorsal plates (Fig. 21b); subterminal pointed process on palp tibiotarsal claw absent (Fig.22b); small teeth on palp tibiotarsal claw absent (Fig. 22b); cheliceral setae present ..... *Scutopalpus*

5 (4) Trichobothrium on tibiae IV present; famulus present, on distal portion of tarsus I ..... *Cunaxoides*

- Trichobothrium on tibiae IV absent; famulus present or absent 6

6 (5) Tibiae III with 1 bsl, 3–5 sts; tibiae IV with 2 or 4 sts 7

- Tibiae III with 1 lts, 4 sts; tibiae IV with 1 lsts, 4 sts ..... *Dunaxeus*

7 (6) Tibiae III with 1 bsl, 3–5 sts; tibiae IV with 1 lts, 2 sts ..... *Funaxopsis*

- Tibiae III with 1 bsl, 5 sts; tibiae IV setal formula not as above 8

8 (7) Tibiae IV with 1 lsts, 4 sts; famulus present ..... *Qunaxella*

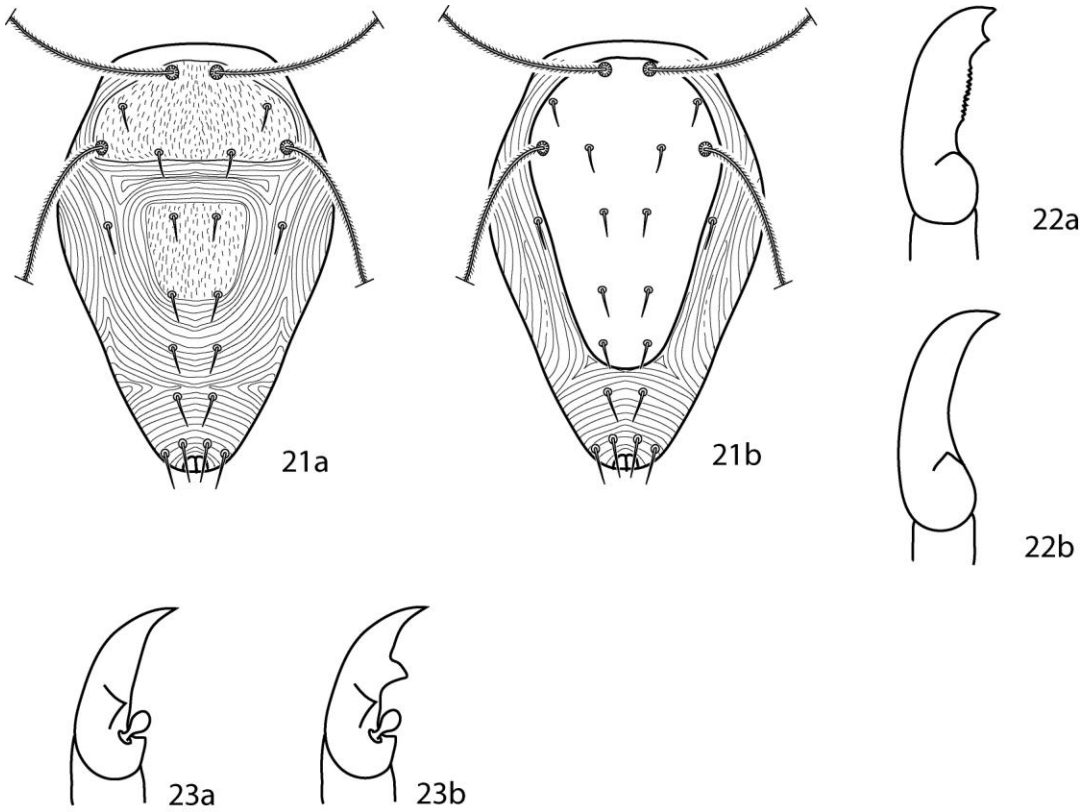
- Tibiae IV with 4 sts; famulus absent ..... *Bunaxella*

9 (2) Setae f_2 present; basifemora I–IV setal formula 4-6-3-1 or 4-6-3-2 10

- Setae f_2 absent; basifemora I–IV setal formula 3-5-2-0 (rarely with 3-5-2-1) ..... *Neocunaxoides*

10 (9) Basifemora I–IV setal formula 4-6-3-2; palp tibiotarsus with one pointed process (ventral) (Fig. 23a); famulus on proximal half of tarsus I; tibiae I–II with non-striated blunt solenidia ..... *Pulaeus*

- Basifemora I–IV setal formula 4-6-3-1; palp tibiotarsus with two pointed processes (1 ventral, 1 median) (Fig. 23b); famulus on distal half (subapical) of tarsus I; tibiae I–II with transversely striated blunt solenidia ..... *Lupaeus*



Figures 21–23. Cunaxoidinae key illustrations. Setae are removed from figures 22–23 for clairity. 21a) Idiosoma with poorly demarcated dorsal plates. 21b) Idiosoma with well demarcated dorsal plates. 22a) Palp tibiotarsus with subapical process and small teeth present. 22b) Palp tibiotarsus with subapical process and small teeth absent. 23a) Palp tibiotarsus with a single pointed process. 23b) Palp tibiotarsus with two pointed processes.

Cunaxoides

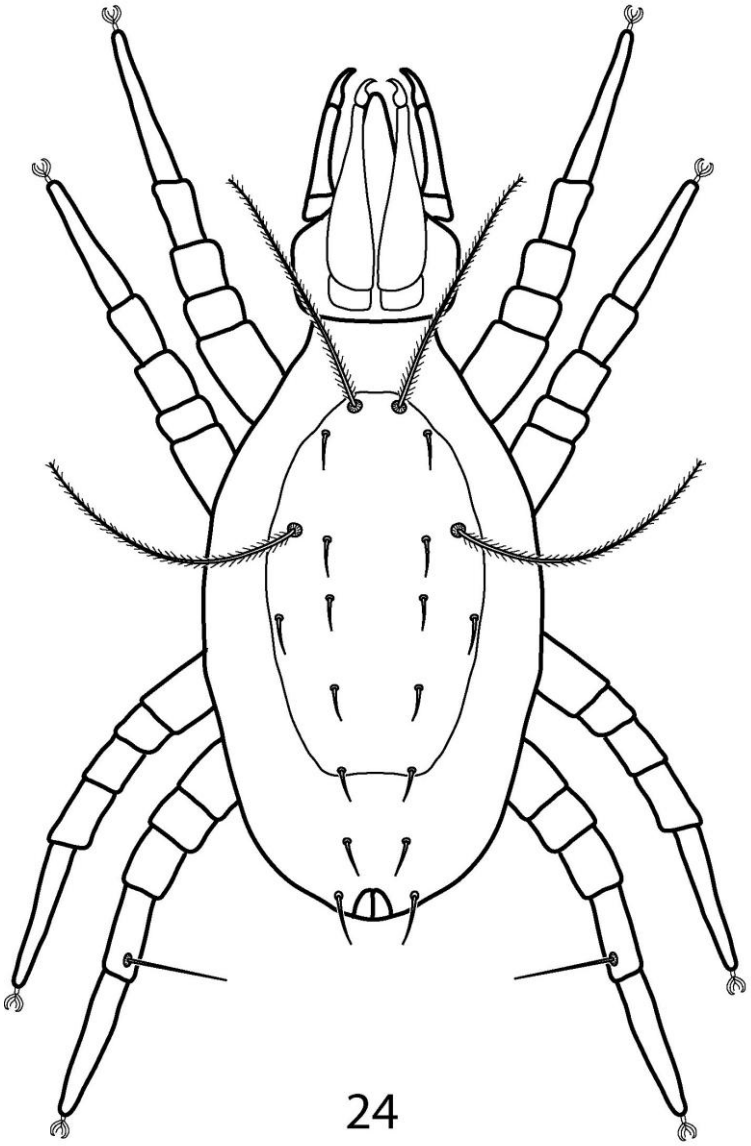


Figure 24. Generalized *Cunaxoides* , dorsal.

Historical Review. Koch (1938) described the first two *Cunaxoides* as *Eupalus croceus* and *E. minutissimus.* Koch (1841) described *E. vitellinus.* Trägårdh (1910) described *E. minima*. Ewing (1917) described *E. parvus* and its feeding on oyster-shell scale in the USA. Thor and Willmann (1941) redescribed and figured *E. croceus, E. minutissimus,* and *E. vitellinus*. Nesbitt (1946) described *E. biscutum*. Baker and

Hoffmann (1948) recognized that the name *Eupalus* was preoccupied and erected *Cunaxoides* to replace it; they transferred all known *Eupalus* to the new genus and figured each species. *Haleupalus oliveri* was described by Schruft (1971). Smiley (1975) synonymized *C. vitellinus* with *C. croceus* and provided a translation of Thor and Willmann's (1941) description of *C. croceus*. Den Heyer (1978c) placed *Cunaxoides* as the type genus in the newly erected Cunaxoidinae; he also redescribed the genus and redescribed and designated a neotype for *C. croceus*. Kuznetzov and Livshitz (1979) described *C. ulcerosus, C. longistriatus, C. fidus* and *C. desertus* and reported and figured *C. biscutum*, and *C. parvus* from Russia. Gupta and Ghosh (1980) described *C. nicobarensis*. *C. kielczewskii* was described by Michocka (1982). Smiley (1992) synonymized *Haleupalus oliveri* with *C. biscutum*, effectively synonymizing *Haleupalus* with *Cunaxoides*; he also moved *C. neopectinatus* to *Neocunaxoides*. Hu (1997) reported *C. croceus* and *C. ulcerosus* from China. Sionti and Papadoulis (2003) described *C. paracroceus* from Greece.

Diagnosis. Palps are 3 segmented. The femurogenua are at least twice as long as wide and is complemented with 5 setae. The tibiotarsi are at least twice as long as wide and usually complemented with 6 setae. A small apophysis occurs basally and a pointed process occurs near the terminal tip; a ridge runs between the apophysis and pointed process. 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral setae) are present on the subcapitulum; setae hg_4 is often the longest. A cheliceral seta is absent.

The dorsal propodosoma bears an ill-defined and weakly sclerotized shield that is complemented with 2 pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and

sce). The dorsal hysterosoma may or may not bear a plate; if a plate is present it is ill-defined and weakly sclerotized, may be complemented with a variable number of setae, and may or may not be fused with the propodosomal shield. Setae c_1–h_1, c_2, and h_2 are present. Cupule *im* is present laterad and posterior of e_1. The integument that is not covered in shields or plates is striated.

The coxal plates are weakly sclerotized and ill-defined; they can be recognized by possessing somewhat denser striations than the surrounding integument. Coxae I–II may be fused and may coalesce medially to form a sternal shield. Coxae III–IV may be fused. Each coxal plate is complemented with 2-4 setae. The genital plates each bear 4 setae ($g_{1–4}$); 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae; one pair of setae is present ventrally on the integument near the anal plates. Up to 7 pairs of setae present on the integument between the coxal and genital plates. Cupule *ih* is present ventrally laterad the integumental setae associated with the anal plates. The integument that is not covered in shields or plates is striated.

The tarsi are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Cunaxoides*

Cunaxoides neopectinatus and *C. clavatus* are returned to *Cunaxoides* from *Neocunaxoides* as they have5 setae on palp femurogenu, femora I and II are divided, and a trichobothrium present on tibia IV.

The following species have not been included because the original descriptions and subsequent papers describing them (Thor & Willmann 1941; Baker & Hoffmann, 1948) are not in English; known illustrations do not contain enough detail; and the types were not examined: *C. minima* (Trägårdh, 1910), *C. minutissimus* (Koch, 1938), *C. vitellinus* (Koch, 1941).

1 Dorsal hysterosomal median plate present (may be fused with propodosomal shield or only suggested by cuticular pattern) (Figs. 25a–c, 26a–d, 27) 2

\- Dorsal hysterosomal median plate absent (Figs. 28a, b, 29) 9

2 (1) Hysterosomal median plate obvious, sclerotized (Figs. 25a–d, 26a–c) 3

\- Hysterosomal median plate may not be obvious or sclerotized, may only be suggested by cuticular pattern (Fig. 27) ..... *C. kielczewskii*

3 (2) Hysterosomal median plate not complemented with setae ..... *C. parvus*

\- Hysterosomal median plate complemented with setae 4

4 (3) Hysterosomal median plate and propodosomal shield separate (Fig. 25a–c) 5

\- Hysterosomal median plate and propodosomal shield fused (Fig. 26a–d) 6

5 (4) Hysterosomal median plate complemented with c_1, d_1 (Fig. 25a) ..... *C. biscutum*

\- Hysterosomal median plate complemented with c_1, d_1, c_2 (Fig. 25b) ..... *C. fidus*

- Hysterosomal median plate complemented with c_1–e_1, c_2 (Figs. 25c) ..... *C. longistriatus*

6 (4) Hysterosomal shield complemented with setae c_1, d_1, c_2; dorsal shield complemented with dots forming broken striae (Figs. 26a, b) 7

- Hysterosomal shield complemented with setae c_1- e_1, c_2; dorsal shield complemented with dots not forming broken striae (Figs. 26c, d) 8

7 (6) Genua IV with 2 asl, 5 sts; striae between *sci* and c_1 parallel; setae *ve* and *sci* of equal length (Fig. 26a) ..... *C. croceus*

- Genua IV with 1 asl, 5 sts; striae between *sci* and c_1 U-shaped; setae *ve* ¾ the length of *sci* (Fig. 26b) ..... *C. paracroceus*

8 (6) Dorsal setae clavate (Fig. 26c); tibiotarsi with bifurcate seta absent ..... *C. clavatus*

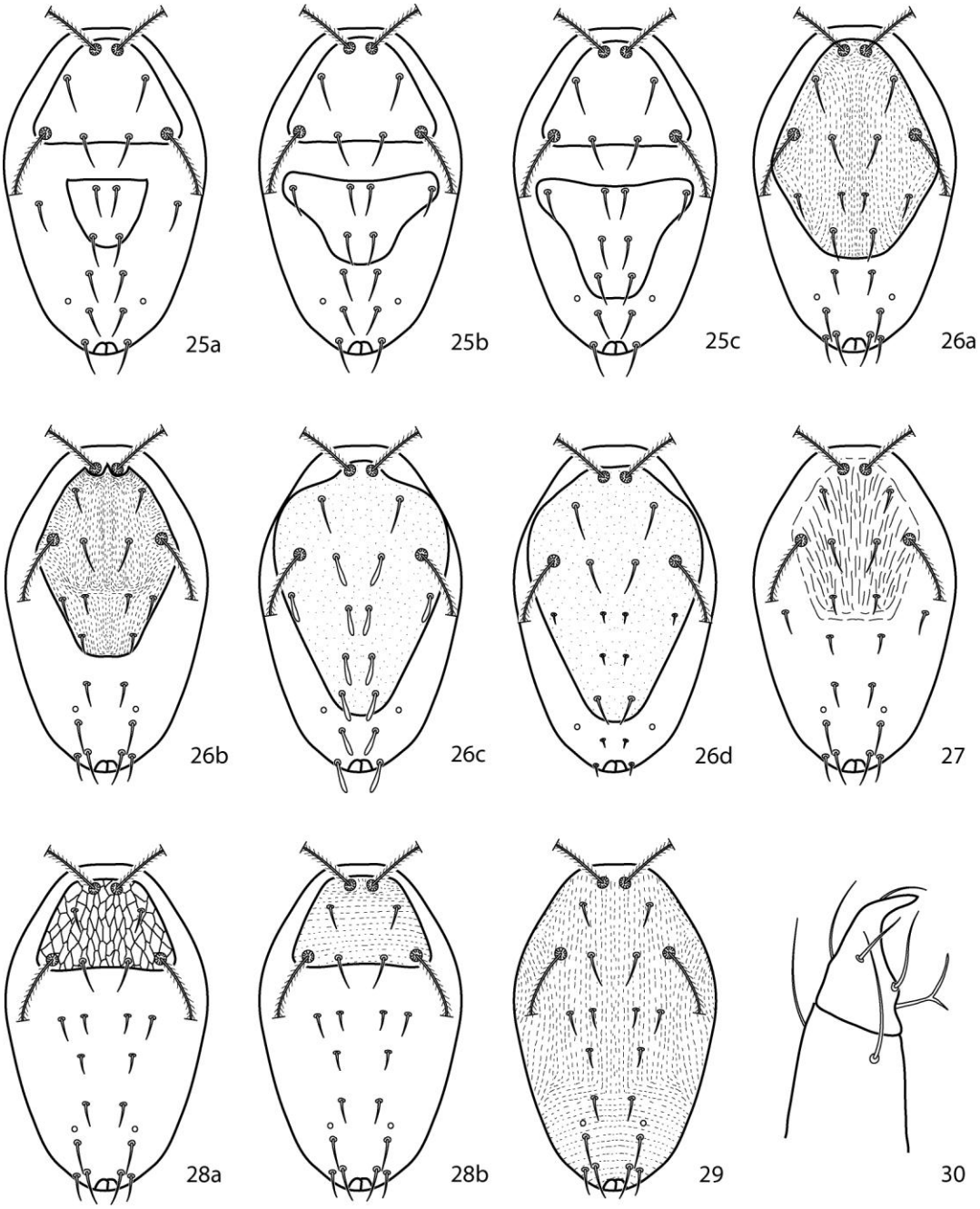
- Dorsal setae not clavate (Fig. 26d); tibiotarsi with bifurcate seta present (Fig. 30) ..... *C. neopectinatus*

9 (1) Propodosomal shield present (Figs. 28a, b) 10

- Propodosomal shield absent (Fig. 29) ..... *C. ulcerosus*

10 (9) Dorsal shield reticulated (Fig. 28a) ..... *C. desertus*

- Dorsal shield striated (Fig. 28b) ..... *C. nicobarensis*



Figures 25-30. *Cunaxoides* key illustrations. See key for explanations.

Neocunaxoides

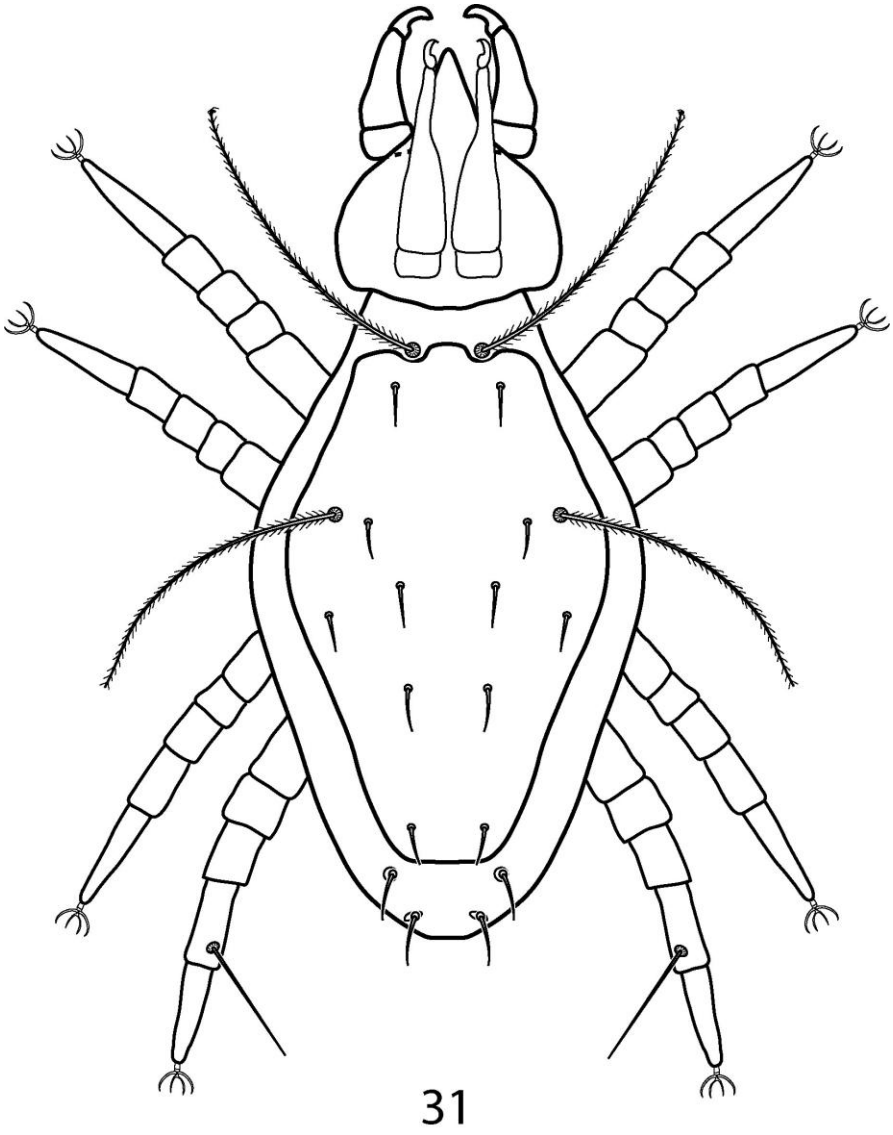


Figure 31. Generalized *Neocunaxoides*, dorsal.

Historical Review. Baker and Hoffmann (1948) described *Cunaxoides andrei*. Smiley (1975) erected *Neocunaxoides* and moved *N. andrei* to the genus. Gupta and Chattopadhyay (1978) described *N. biswasi* from bird nests in Bengal, India. Shiba (1978) described *Cunaxoides clathratus.* Den Heyer (1978c) placed *Neocunaxoides* in the subfamily Cunaxoidinae. Kuznetzov and Livshitz (1979) reported *C. andrei* from Russia, having either disagreed with or been unaware of Smiley's 1975 publication.

Chaudhri (1980) described *N. cinctus*. Den Heyer (1980a) described *N. lajumensis, N. rykei,* and *N. zuluensis* from South Africa. Tseng (1980) described *N. unguianalis* and reported and figured *N. andrei, N. whartoni* , and *N. osseus* from Taiwan. Michocka (1987) reported *N. andrei* from Poland. Inayatullah and Shahid (1989) described *N. dilato* and *N. kalamiensis*. *N. cerasoides* was described by Gupta (1991). Smiley (1992) synonymized *Scutopalpus* with *Neocunaxoides* and moved *Cunaxoides neopectinatus, C. clathratus,* and *C. trepidus* to *Neocunaxoides*. Corpuz-Raros (1996b) described *N. grandis* and *N. mahabaeus*. Hu (1997) reported *N. andrei* from China. Lin & Zhang (2000) reporded *Neocunaxoides neopectinatus* from fallen bamboo leaves, moss, and tree bark and *N. clavatus* from tea in China. Lin, Zhang, and Ji (2001) described *N. boltoides* and *N. fani*. They later (Lin, Zhang, & Ji 2003) described *N. ovatus*. Corpuz-Raros and Gruèzo (2007) described *N. ornatus*. Castro and Den Heyer (2009) moved *Pulaeus trepidus* (=*Neocunaxoides trepidus*) to *Scutopalpus*.

Diagnosis. Palps are 3 segmented. The femurogenua are at least twice as long as wide and is complemented with 6 setae. The tibiotarsi are at least twice as long as wide and usually complemented with 6 setae. The tibiotarsi possess two or three knob-like apophyses, a single spur, or sometimes a flange-like seta. 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral setae) are present on the subcapitulum; setae hg_4 is often the longest. A cheliceral seta is present.

The dorsal propodosoma bears a well-sclerotized shield which is complemented with 2 pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and *sce*). The dorsal hysterosoma bears a sclerotized plate that is variable in size and is fused with the

propodosomal shield; it may be complemented with a variable number of setae depending on the size of the plate. Setae c_1–h_1, c_2, and h_2 are present. Setae f_2 are absent. Cupule *im* is present laterad and posterior of e_1. The integument that is not covered in shields or plates is striated.

The coxal plates are sclerotized and well-defined. Coxae I–II may be fused and may coalesce medially for form a sternal shield. Coxae III–IV may be fused. Each coxal plate is complemented with 2-4 setae. The genital plates each bear 4 setae ($g_{1–4}$) that are usually in a straight now; 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae; one pair of setae is present ventrally on the integument near the anal plates. Cupule *ih* is present ventrally laterad the integumental setae associated with the anal plates. The integument that is not covered in shields or plates is striated.

The tarsi are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. The basifemora setal formula is 3-5-2-0. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Neocunaxoides*

Cunaxoides philippinensis (Corpuz-Raros, 2007) is regarded as belonging to *Neocunaxoides* because it has 6 seatae on the femurogenu and lacks setae f_2. *Neocunaxoides makapalus*, *N. philippinensis* (Corpuz-Raros, 1996b), *N. unguianalis*, and *N. rugosus* are regarded as belonging to *Scutopalpus* as they possess 5 sts on palp femurogenu and extensive dorsal shields. They have therefore not been included in the following key. *Neocunaxoides krama* is not regarded here as belonging to

Neocunaxoides because it does not possesses more than 5 setae on the femurogenu and 2 setae on basifemora IV; unfortunately, the original description is not detailed enough to provide proper generic placement at this time. *Neocunaxoides neopectinatus* is considered to belong to *Cunaxoides* as it has 5 setae on palp femurogenu, femora I and II divided, and a trichobothrium present on tibia IV.

Neocunaxoides biramus is not included in the key because it is only known from the male. It can be distinguished from all other *Neocunaxoides*, and indeed all described cunaxids, by the presence of a branched *sci* and 4 teeth on the lateral lips of the hypostome.

I agree with and follow Castro and Den Heyer (2009) and Den Heyer and Castro (2009) in regarding *Scutopalpus* as a valid and separate genus.

1 Coxae I–II fused medially to form sternal shield (Figs. 32a–d) 2

\- Coxae I–II not fused medially (may be connected anteromedially) (Fig. 33a–d) 6

2 (1) Posterior edge of coxae IV extending beyond anterior edge of genital plates (Figs. 32a,b) 3

\- Posterior edge of coxae IV not extending beyond anterior edge of genital plates (Fig. 32c, d) 5

3 (2) Small platelet anteriomedially of genital plates present (Fig. 32a) ..... *N. fani*

\- Small platelet anteriomedially of genital plates absent (Fig. 32b) 4

4 (3) Solid or broken band of papillae on ventral subcapitulum present (Fig. 34a); subcapitulum longer, length: width 1.75:1 ..... *N. zuluensis*

- Solid or broken band of papillae on ventral subcapitulum absent (Fig. 34b); subcapitulum shorter, length: width 1.25:1 ..... *N. lajumensis*

5 (2) Hysterosomal plate present, fused with propodosomal shield, and bearing c_1–e_1, c_2; small platelet anteriomedially of genital plates present (Fig. 32c) ..... *N. boltoides*

- Hysterosomal plate absent; small platelet anteriomedially of genital plates absent (Fig.32d) ..... *N. philippinensis* (=*Cunaxoides philippinensis*)

6 (1) Median platelet between coxae II present (Figs. 33a–c) 7

- Median platelet between coxae II absent (Fig. 33d) 13

7 (6) Basifemora V with 1 sts 8

- Basifemora V with 0 sts 11

8 (7) Basifemora I with 2 sts ..... *N. biswasi*

- Basifemora I with 3 sts 9

9 (8) All setae on palp of normal length, none extremely long 10

- 2 setae on palp femurogenu extremely long, nearly as long as segment; 1 distal palp tibiotarsal seta long, longer than segment (Fig. 35) ..... *N. mahabaeus*

10 (9) Basal subcapitular polygonal pattern elongate (Fig. 36a); foveolae on dorsal shield present (Fig. 37a) ..... *N. ornatus*

- Basal subcapitular polygonal pattern not elongate (Fig. 36b); foveolae on dorsal shield absent (Fig. 37b) ..... *N. grandis*

11 (7) Small platelet anteriomedially of genital plates present (Fig. 33a) ..... *N. ovatus*

- Small platelet anteriomedially of genital plates absent (Figs. 33b,c) 12

12 (11) Coxae I connected anteromedially (Fig. 33b); mushroom-shaped seta on palp tibiotarsi absent ..... *N. rykei*

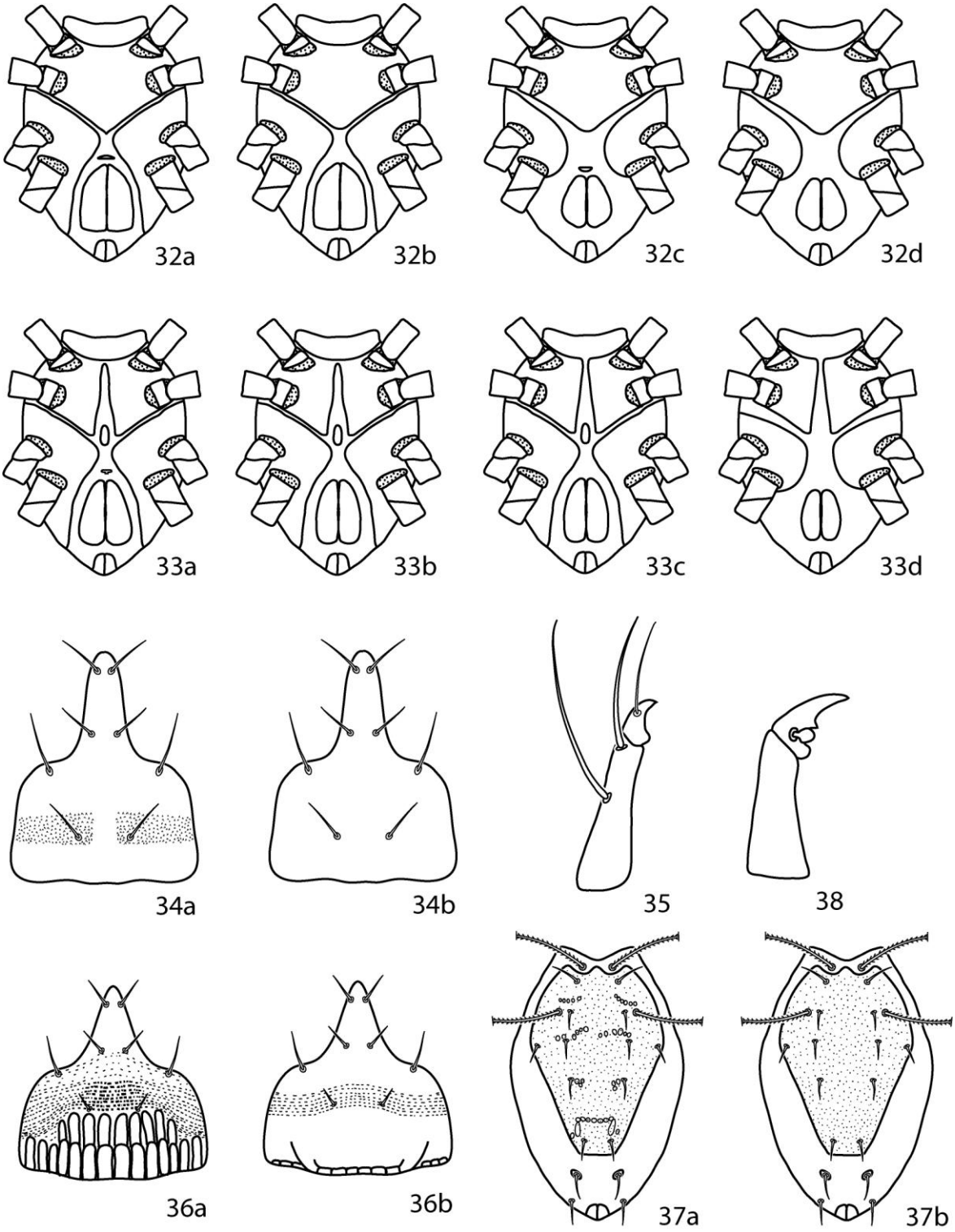
- Coxae I not connected anteromedially (Fig. 33c); mushroom-shaped seta on palp tibiotarsi present (Fig. 38) ..... *N. andrei*

13 (6) Femora I (basifemora I + telofemora I) with 6 setae ..... *N. cerasoides*

- Femora I (basifemora I + telofemora I) with 9 setae 15

14 (13) Coxae I-IV setal formula 2-3-3-1; combined femora (basifemora + telofemora) II-IV setal formula 11-7-5 ..... *N. dilato*

- Coxae I-IV setal formula 2-2-3-2; combined femora (basifemora + telofemora) II-IV setal formula 10-7-4 ..... *N. kalamiensis*



Figures 32-38. *Neocunaxoides* key illustrations. See key for explanations of figures.

Pulaeus

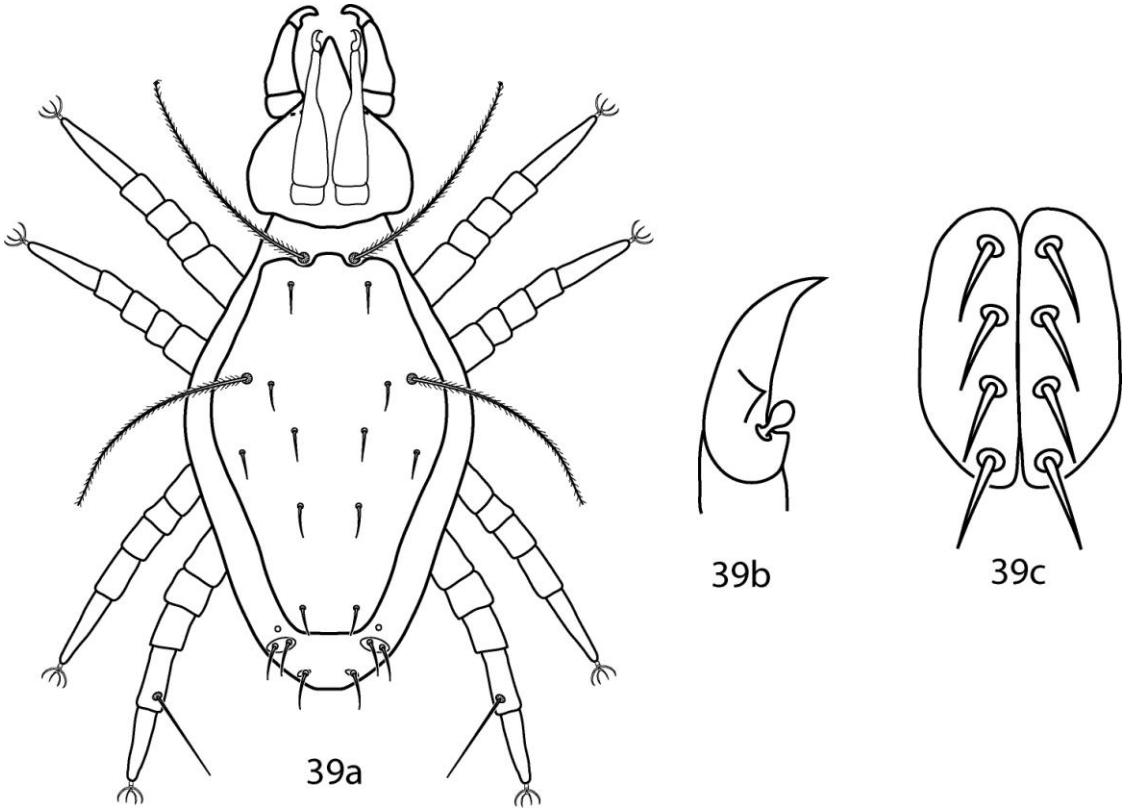


Figure 39. Generalized *Pulaeus*. 39a) Dorsum. 39b) Palp tibiotarsus, showing single pointed process and bladder-like apophysis. 39c) Genital plate.

Historical Review. Ewing (1909) described the first species of *Pulaeus* as *Eupalus pectinatus*. Berlese (1916) described *Eupalus sternalis*. Baker and Hoffmann (1948) proposed *Cunaxoides* to replace *Eupalus* as the name was preoccupied; described *Cunaxoides patzcuarensis, C. whartoni,* and *C. americanus*; and synonymized *C. sternalis* with *C. pectinatus*. They also redescribed and illustrated *C. pectinatus*. Muma (1960) described *C. pectinellus*. Shiba (1978) described *C. parapatzuarensis,* and *C. pseudominutus*. Kuznetzov and Livshitz (1979) reported *C. pectinatus* from Russia. Den Heyer (1979b) erected *Pulaeus* and moved the previously mentioned species into the new genus; he also redescribed *P. pectinatus* and described *P. glebulentus*. *Neocunaxoides cinctus* was described by Chaudhri (1980). Den Heyer (1981) confirmed the synonymy

of *P. sternalis* with *P. pectinatus*, and synonymized *C. pectinellus* with *P. pectinatus*; he also described *P. franciscae* and placed *Pulaeus* within Cunaxoidinae. El-Bishlawy and Rakha (1983) described *P. zaherii* from Egypt. Liang (1983) reported *P. pseudominutus* from China. *Pulaeus musci* was described by Liang (1985). Zaher and El-Bishlawy (1986) described *P. niloticus*. Bu and Li (1987b) described *P. longignathos* and *P. chongqingensis*. *Pulaeus ardeola* was described by Barilo (1991). Smiley (1992) synonymized *P. niloticus* with *P. subterraneus* and provided a key to known world species. Li *et al.* (1992) recorded *P. glebulentus* from Chongqing, China. Corpuz-Raros (1996c) described two species, *P. payatopalpus* and *P. rimandoi*, from the Philippines. Lin and Zhang (2000) reported *P. longignathos*, *P. musci*, and *P. pseudominutus* from China. Lin *et al.* (2003) reported *P. minutus* from China. Corpuz-Raros (2007) also described *P. cebuensis*, *P. palawanensis*, and *P. samarensis*. Castro and Den Heyer (2009) split *Lupaeus* from *Pulaeus* and described two new species: *P. mytraceus* and *P. quadrisolenidius*. Lin and Zhang (2010) argue that the "original species name *longignathos* [as in *Pulaeus longignathos*]…is the correct form in Greek. Some authors emended it to the Latinized from *longignathus* (e.g. Castro & Den Heyer, 2009: 2)." The spelling *longignathos* is followed here.

Diagnosis. Palps are 3 segmented. The femurogenua are at least twice as long as wide and are complemented with 6 setae. The tibiotarsi are at least twice as long as wide, are usually complemented with 6 setae, possess 1 pointed process, and may possess a bladder- or knob-like apophysis (Fig. 39b). 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral

setae) are present on the subcapitulum and setae hg_4 is often the longest. A cheliceral seta is present.

The dorsal propodosoma bears a well-sclerotized shield that is complemented with 2 pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and *sce*). The dorsal hysterosoma bears a sclerotized plate that is variable in size and is fused with the propodosomal shield; it may be complemented with a variable number of setae depending on the size of the plate. Setae c_1–h_1, c_2, f_2, and h_2 are present. Cupule *im* is present laterad and posterior of e_1. The integument that is not covered in shields or plates is striated.

The coxal plates are sclerotized and well-defined. Coxae I–II may be fused and may coalesce medially to form a sternal shield. Coxae III–IV may be fused. Each coxal plate is complemented with 2–4 setae. The genital plates each bear 4 setae ($g_{1–4}$) that are usually in a straight row (Fig. 39c); 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae; one pair of setae is present ventrally on the integument near the anal plates. Cupule *ih* is present ventrally laterad the integumental setae associated with the anal plates. The integument that is not covered in shields or plates is striated.

The tarsi are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. The basifemora setal formula is 4-6-3-2. The depression of the famulus occurs on proximal half of tarsus I. Tibiae I–II possess non-striated blunt solenidia. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Pulaeus* (heavily modified from Smiley 1992)**.**

P. ardeola was not included in the key because the original text is in Cyrillic script and the illustrations do not provide enough characters to differentiate it from other species. *P. cinctus* is moved from *Neocunaxoides* to *Pulaeus* based on features given in the original description, namely that f_2 is present and basifemora IV are complemented with 2 sts.

The following were species assigned to *Pulaeus* before *Lupaeus* was erected. The characters that divide the two genera are not given in the original descriptions and types have not been viewed. These indeterminable species are therefore not included in either generic key, but instead characters are given for each species that will serve to identify them.

P. parapatzuarensis – This species has a divided sternal plate, lacks a sclerotized area anterior to the genital plates, and does not have $f_{1,2}$ located on platelets. In addition it has 6 pairs of setae on the integument between coxal and genital plates.

P. patzcuarensis – This species can be recognized by the sternal plates being connected anteriorly and divided in a v-shape posteriorly.

P. pseudominutus – Setae e_1 being 3 times the length of c_1 and d_1 distinguishes this species.

P. payatopalpus - The hypostome is 2/3 the length of the gnathosoma and the pedipalps are extremely long and slender, at least 8 times longer than wide. In addition the tibiotarsus is complemented with a seta that is longer than the segment.

P. zaherii – This species can be recognized by the divided sternal plates, f_1 being 4/5 the length of e_1, and f_1 being ½ the length of f_2.

1 Sternal plate divided medially (Fig. 40a,b) 2

- Sternal plate not divided medially (Fig. 41a, b) 11

2 (1) Median platelet between coxae II– III present (Fig. 40a) 3

- Median platelet between coxae II– III absent (Fig. 40b) 4

3 (2) Palp tibiotarsus with elongate apophysis (Fig. 42a); median seta anterior to genital opening present ..... *P. chongqingensis*

- Palp tibiotarsus with flat apophysis (Fig. 42b); median seta anterior to genital opening absent ..... *P. glebulentus*

4 (2) Setae f_1 and f_2 located on sclerotized platelets or shields 5

- Setae f_1 and f_2 not located on sclerotized platelets or shields 9

5 (4) Palp femurogenu at least 6 times as long as wide ..... *P. rimandoi*

- Palp femurogenu at most 4 times as long as wide 6

6 (5) Genua II with 2 solenidia ..... *P. samarensis*

- Genua II with 3 solenidia 7

- Genua II with 4 solenidia 8

7 (6) Setae f_1 and h_1 approximately equal in length ..... *P. myrtaceus*

- Setae f_1 approximately half the length as h_1 ..... *P. musci*

8 (6) Dorsal shield with punctuations (Fig. 43a) ..... *P. quadrisolenidius*

- Dorsal shield with flat broken striae (Fig. 43b) ..... *P. whartoni*

9 (4) 4 pairs of setae on integument between coxal and genital plates *P. cintus*

- 5 pairs of setae on integument between coxal and genital plates *P. palawanensis*
- 6 pairs of setae on integument between coxal and genital plates 10

10 (9) Sensillum *vi* approximately as long as *sce*; setae f_1 approximately equal in length to h_1 ..... *P. cebuensis*

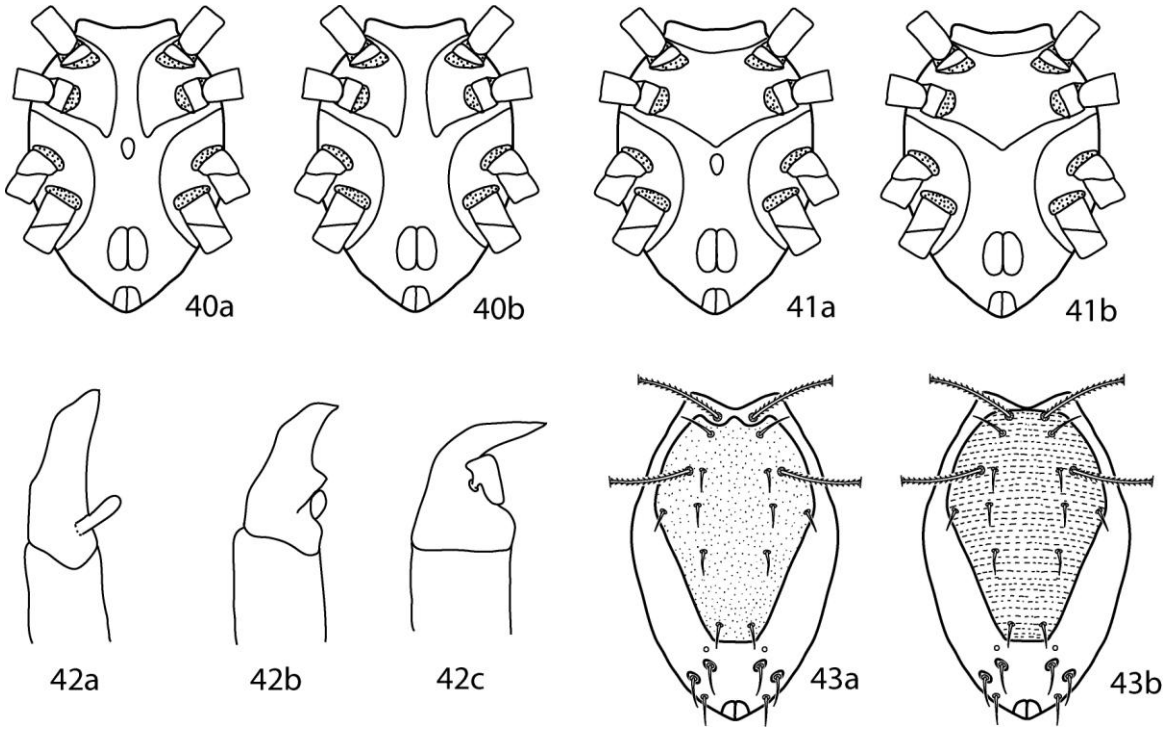
- Sensillum *vi* longer than *sce*; setae f_1 approximately 1.25 the length of h_1 ..... P. *franciscae*

11 (1) Dorsum punctuate (Fig. 43a); ventral medial platelet present (Fig. 41a); palpal tibiotarsus with truncate, flange-like apophysis (Fig. 42c) ..... *P. pectinatus*

- Dorsum striated (Fig. 43b); ventral medial platelet absent (Fig. 41b); palpal tibiotarsus with elongate apophysis (Fig. 42a) 12

12 (11) Palp femurogenua at most 4 times as long as wide; setae f_1 and f_2 approximately equal in length ..... *P. americanus*

- Palp femurogenua at least 6 times as long as wide; setae f_1 ¼ longer than f_2 ..... *P. longignathos*



Figures 40-43. *Pulaeus* key illustrations. Setae removed for clairity. 40-41) Venter. 40a) Coxae I-II not coalesced medially, median platelet present. 40b) Coxae I-II not coalesced medially, median platelet absent. 41a) Coxae I-II coalesced medially, median platelet present. 41b) Coxae I-II coalesced medially, median platelet absent. 42a-c) Palp tibiotarsus. 42a) Tibiotarsus with elongate apophysis. 42b) Tibiotarsus with flat apophysis. 42c) Tibiotarsus with flange-like apophysis. 43a, b) Dorsum. 43a) Dorsal shield with punctures. 43b) Dorsal shield with broken striae.

Lupaeus

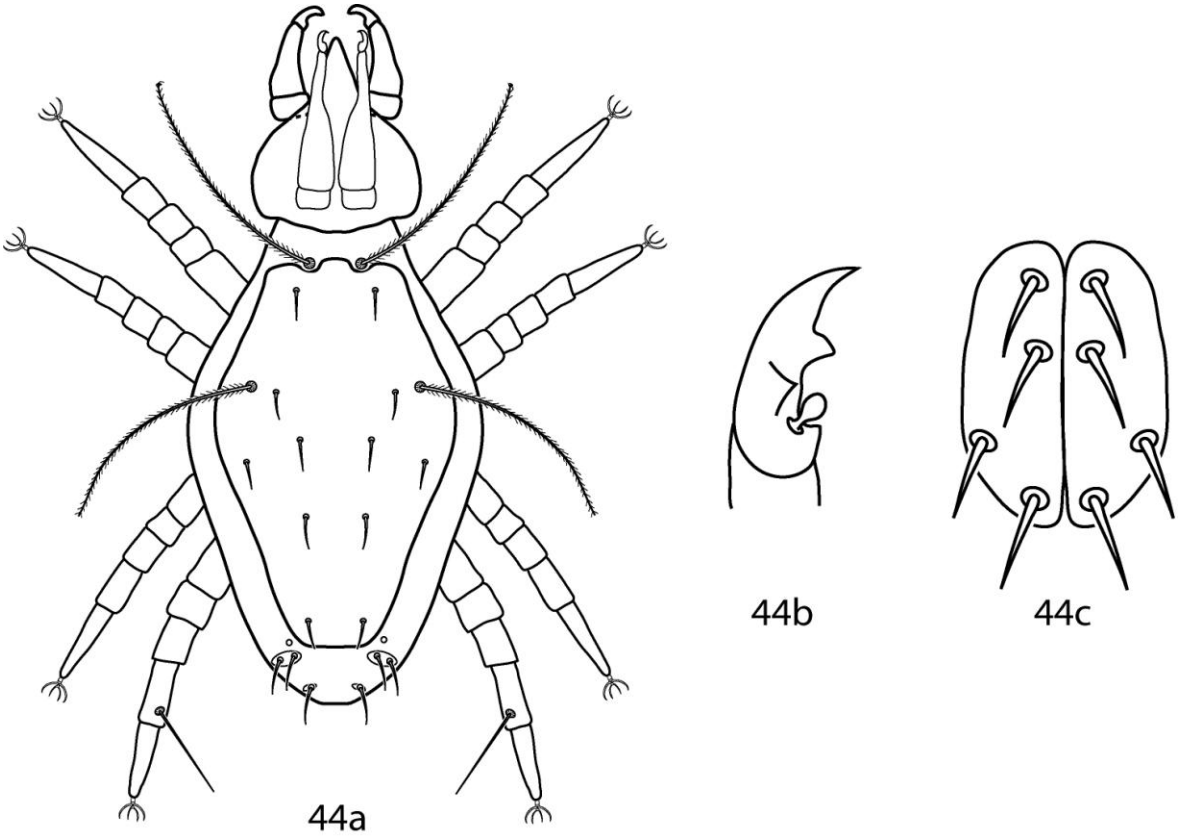


Figure 44. Generalized *Lupaeus*. 44a) Dorsum. 44b) Palp tibiotarsus, showing two pointed processes and bladder-like apophysis. 44c) Genital plate.

Historical Review. Berlese (1916) described *Eupalus subterraneus*. Thor and Willmann (1941) redescribed *E. subterraneus*. Baker and Hoffmann (1948) erected *Cunaxoides* in place of *Eupalus* as *Eupalus* was pre-occupied; they also described *Cunaxoides americanus* and *C. minutus* and redescribed and illustrated *C. subterraneus*. Kuznetzov and Livshitz (1979) reported *C. americanus* from Russia. Den Heyer (1979b) erected *Pulaeus*, moving those species with f_2 present and setae present on basifemora IV to the new genus from *Cunaxoides*; he also described *P. martini* and *P. clarae* and placed *Pulaeus* into the subfamily Cunaxoidinae. *Pulaeus platygnathus* was described by Bu and Li (1991). Corpuz-Raros (1996c) described *P. dentatus, P. lenis, P. longisetus, P.*

villacarlosae, and *P. filipinus* from the Philippines. Hu (1997) reported *P. platygnathus* from China. Lin and Zhang (2000) reported *P. platygnathus* from China. Lin and Zhang (2003) reported *P. minutus* from China. Corpuz-Raros (2007) described *P. polilloensis* and *P. philippinensis* from the Philippines. Castro and Den Heyer (2009) erected *Lupaeus* and moved into it those species of *Pulaeus* that possess two pointed processes on the palp tibiotarsus and 1 simple seta on basifemora IV; they also described *Lupaeus lectus* and *L. lobidorsalis* and provided a key to the Brazilian and South African species.

Diagnosis. Palps are 3 segmented. The femurogenua are at least twice as long as wide and is complemented with 6 setae. The tibiotarsi are at least twice as long as wide, are usually complemented with 6 setae; they possess 2 or 3 pointed processes and may possess a bladder- or knob-like apophysis (Fig. 44b). 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral setae) are present on the subcapitulum; setae hg_4 is often the longest. A seta is present near the cheliceral digit.

The dorsal propodosoma bears a well-sclerotized shield that is complemented with 2 pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and *sce*). The dorsal hysterosoma bears a sclerotized plate that is variable in size and is fused with the propodosomal shield; it may be complemented with a variable number of setae depending on the size of the plate. Setae c_1–h_1, c_2, f_2, and h_2 are present. Cupule *im* is present laterad and posterior of e_1. The integument that is not covered in shields or plates is striated.

The coxal plates are sclerotized and well-defined. Coxae I–II may be fused and may coalesce medially to form a sternal shield. Coxae III–IV may be fused. Each coxal

plate is complemented with 2–4 setae. The genital plates each bear 4 setae ($g_{1–4}$). Setae $g_{1,2,4}$ usually occur in a straight line near the midline and setae g_3 occur near the edge of the genital plates (Fig. 44c). 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae; one pair of setae is present ventrally on the integument near the anal plates. Cupule *ih* is present ventrally laterad the integumental setae associated with the anal plates. The integument that is not covered in shields or plates is striated.

The tarsi are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. The basifemora setal formula is 4-6-3-1. The depression of the famulus occurs on distal half of tarsus I. Tibiae I–II possess striated blunt solenidia. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Lupaeus*

Lupaeus longisetus is known only from the male and is not included in the key. It can be recognized by the following characters: small platelet between the edges of a divided sternal shield absent, basifemora I with 3 sts, and setae e_1 elongate and barbed (Fig. 45a).

Lupaeus polilloensis is only known from the male and is not included in the key. It can be recoginized by the following characters: small platelet between the edges of a divided sternal shield absent; basifemora I–II setal formula 4-6; platelets complemented with setae f_1, f_2 with fused medially into one plate; and the dorsal shield densely granulate (Fig. 45b).

The following species are moved to *Lupaeus* from *Pulaeus* based on the account reported by Smiley 1992: *L. minutus* (Baker & Hoffmann) and *L. subterraneus* (Berlese)

1 Small platelet ventromedially between edges of divided sternal plate present (Fig. 46A) ..... *L. martini*

- Small platelet ventromedially between edges of divided sternal plate absent (Fig. 46b) 2

2 (1) Basifemora I with 4 sts 3

- Basifemora I with 5 sts ..... *L. filipinus*

3 (2) Basifemora II with 4 sts ..... *L. minutes*

- Basifemora II with 5 sts 4

- Basifemora II with 6 sts 7

4 (3) Setae f_1 shorter than c_1 ..... *L. lenis*

- Setae f_1 the same length as c_1 ..... *L. lectus*

- Setae f_1 longer than c_1, usually by at least 1.5 times 5

5 (4) Genua I with 9 total simple setae and solenidia ..... *L. dentatus*

- Genua I with 7 total simple setae and solenidia 6

6 (5) Setae c_1–e_1 equal in length ..... *L. lobidorsalis*

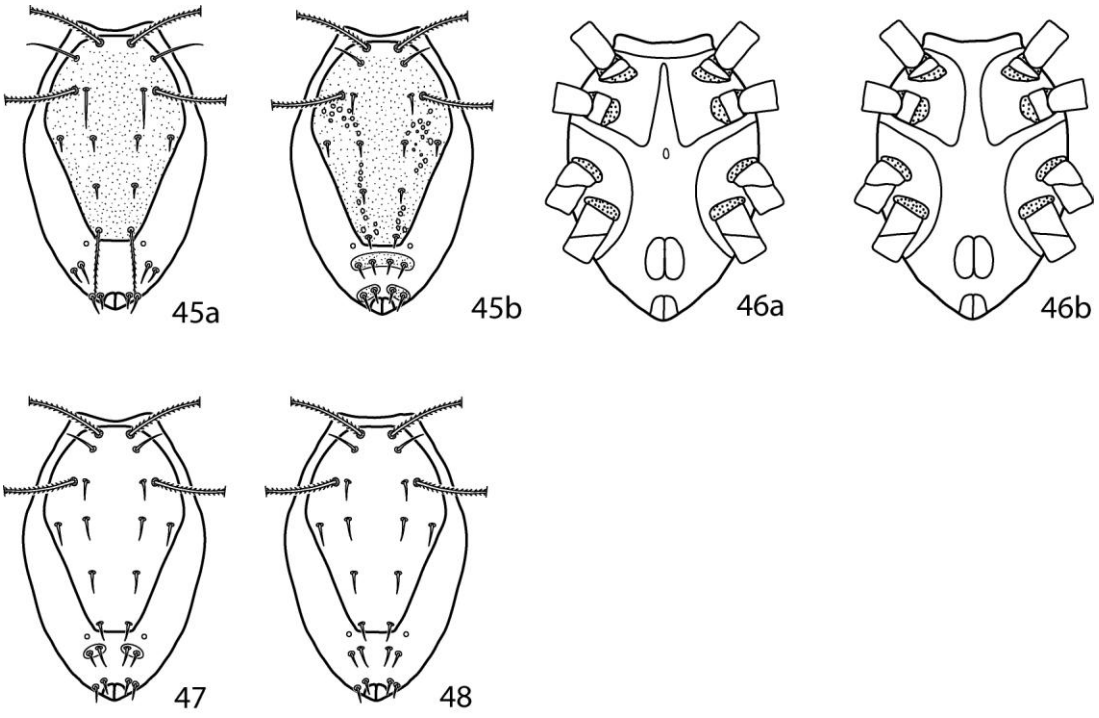
- Setae e_1 one-fourth longer than c_1,d_1 ..... *L. subterraneus*

7 (3) Platelets complemented with f_1,f_2 present, separate or fused medially (Figs 47) ..... *L. villacarlosae*

- Platelets complemented with f_1,f_2 absent (Fig. 48) 8

8 (7) Cheliceral seta not as long as width of cheliceral digit ..... *L. platygnathus*

- Cheliceral seta longer than width of cheliceral digit ..... *L. clarae*



Figures 45–49. *Lupaeus* key illustrations. Setae and cupules removed from figures 46a, b to increase clairity. 45a) *L. longisetus*, dorsal. 45b) *L. polilloensis*, dorsal. 46a) Ventral, small platelet present. 46b) Ventral, small platelet absent. 47) Setae f_1,f_2 born on small platelets. 48) Setae f_1,f_2 born on integument.

Scirulinae, ***Scirula***

This is a monobasic subfamily, with the single genus containing two described and one undescribed species. The subfamily and genus are therefore treated together.

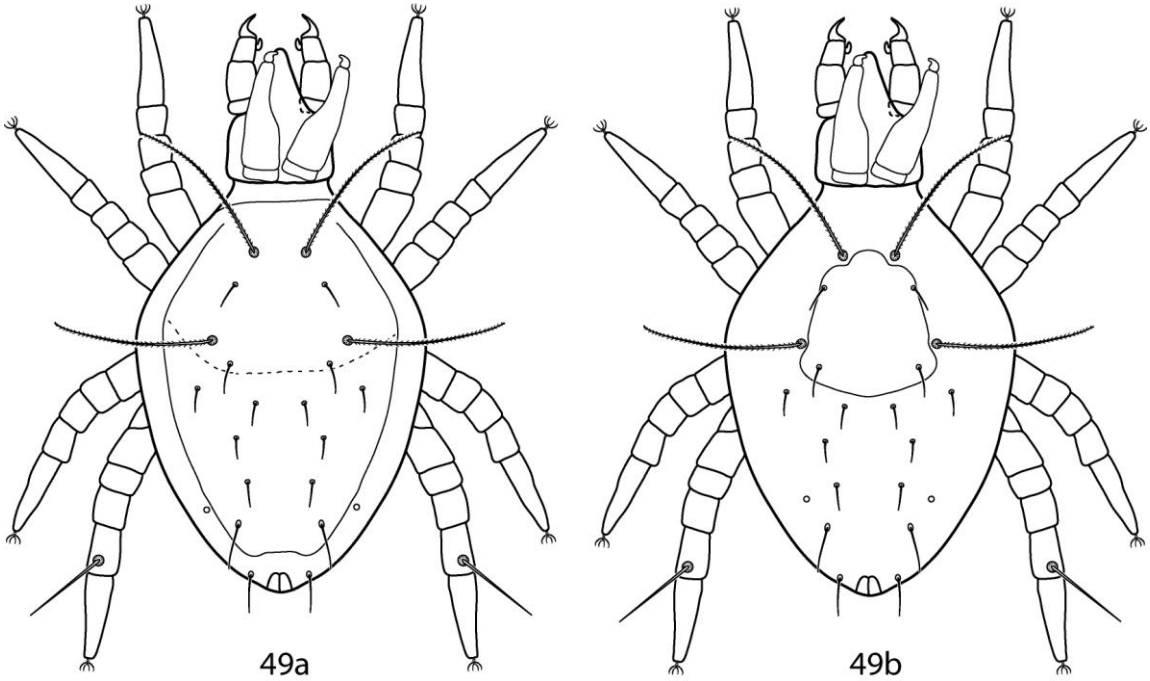


Figure 49a. *Scirula impressa* Berlese. 49b. *Scirula* sp.

Historical Review. Berlese (1887) erected *Scirula* for *S. impressa*. Thor and Willmann (1941) and Baker and Hoffmann (1948) redescribed and illustrated *S. impressa.* Den Heyer (1980c) erected Scirulinae for the then monotypic genus. Michocka (1987) reported *S. impressa* from Poland. Smiley (1992) redescribed and illustrated *S. impressa*. Lin (1997) described *S. pappilata* from China.

Diagnosis. The palps are four-segmented and do not reach beyond the subcapitulum. A flange-like apophysis is present on either the genua or tibiotarsi. The palps end in a stout claw. 4 pairs of subcapitular setae (hg_{1-4}) are present.

The dorsal propodosoma is covered in a plate that bears 4 pairs of setae: 2 pairs of simple setae (*ve* and *sci*) and 2 pairs of setose sensilla (*vi* and *sce*). The dorsal hysterosoma may or may not be complemented with a plate. 6 dorsal setae, c_1–h_1, c_2 are present. Cupule *im* is present.

The ventral idiosoma is covered by a complete shield resulting from the fusion of coxae I-IV. The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. Cupule *ih* is present. The anal plates bear 2 pairs of setae (ps_1 & ps_2); 1 pair of setae is born on integument next to anal plates.

Key to adult female *Scirula*

1 Hysterosomal shield present (Fig. 49a); Japan, USA, Denmark, Italy ..... *S. impressa*

\- Hysterosomal shield absent (Fig. 49b) 2

2 (1) Flange-like apophysis present on palpal tibiotarsi; USA: Pennsylvania, Ozark Highlands (Fig. 49b) ..... *Scirula* **sp. nov.**

\- Flange-like apophysis present on palpal genu; China: Fujian ..... *S. pappilata*

Cunaxinae

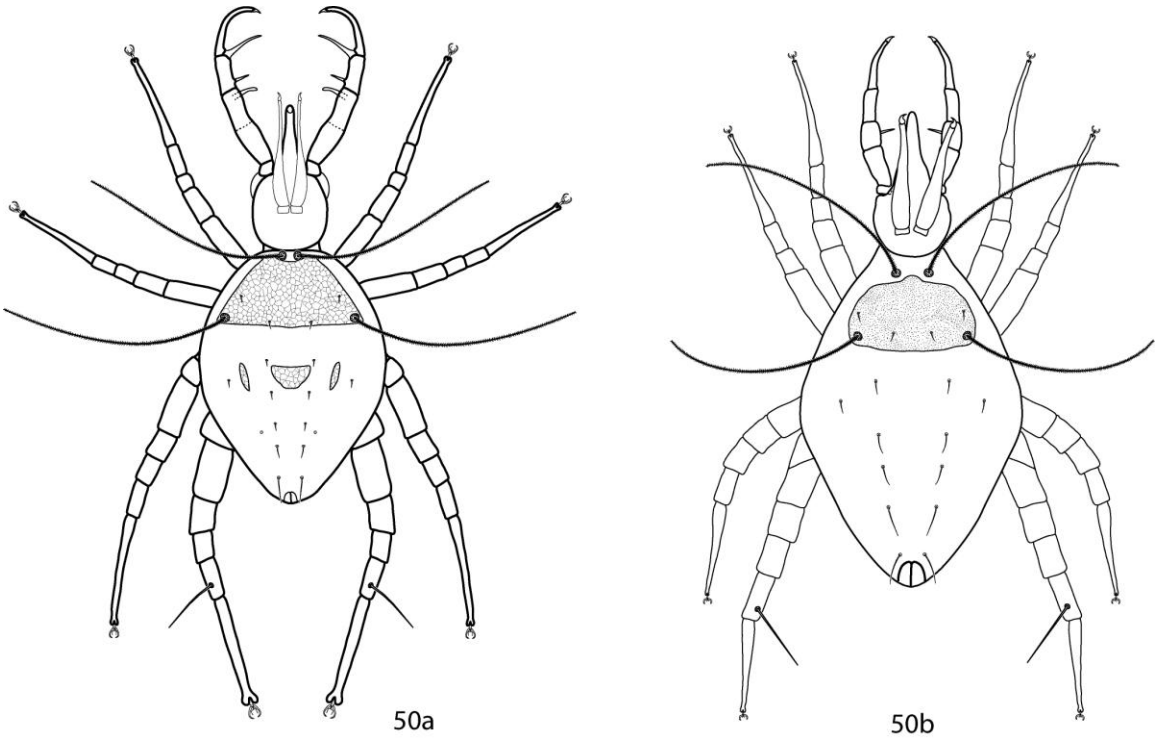


Figure 50. Generalized Cunaxinae. 50a) *Armascirus*. 50b) *Cunaxa*.

Historical Review. Von Heyden (1826) erected *Cunaxa* for *Scirus setirostris.* Oudemans (1902) used Cunaxinae in the same sense that Trouessart (1892) used Scirinae, that is for those mites in the family Bdellidae (*sensu* Koch) that have palps with a curved terminal segment and movable chela only (= Cunaxidae *sensu* Thor). Oudemans (1906) substituted Cunaxinae for Cunaxidae. Berlese (1916) erected *Dactyloscirus* as a subgenus of *Scirus* to accommodate *Scirus* (*Dactyloscirus*) *eupaloides*. Oudemans (1922) erected *Rosenhofia* to accommodate *R. machairodus*. Vitzthum (1931) raised *Dactyloscirus* to full generic status but later (1940-43) treated it as a subgenus. Thor & Willmann (1941) again elevated *Dactyloscirus* to generic status and designated *Dactyloscirus eupaloides* as the type specimen. Baker & Hoffmann (1948) regarded *Dactyloscirus* as a senior synonym of *Cunaxa*. Smiley (1975)

synonymized *Rosenhofia* with *Dactyloscirus.* Den Heyer (1978b) preserved the name Cunaxinae, but limited its concept to those cunaxids possessing 5-segmented palps that extend past the subcapitulum by at least the distal two segments; he also erected *Armascirus*. Den Heyer (1979c) erected *Rubroscirus* for *R. africanus*. Gupta and Ghosh (1980) erected *Indocunaxa*. Smiley (1992) synomised *Rubroscirus* with *Cunaxa* but failed to give his reasoning for doing so. Den Heyer (2006) erected *Riscus* for a species known only from Thailand. Castro and Den Heyer (2008) erected *Cunaxatricha* and provided a key to the genera of Cunaxinae. Den Heyer and Castro (2008c) erected *Allocunaxa* for a Neotropical species, synonymized *Indocunaxa* with *Armascirus*, and provided the most up-to-date key to world genera of Cunaxinae.

Diagnosis. The palps are 5 segmented and extend beyond the subcapitulum by at least the distal half of the tibiae. The basifemora and telofemora are fused but often dark line remains to indicate the division between the segments; the telofemora and genua are also fused in this manner in *Allocunaxa*. Apophyses may be present on the telofemora and between the genua and tibiotarsi. The tibiotarsi end in a strong claw. A seta may be present near the cheliceral digit. Up to 6 pairs of setae are present on the subcapitulum; setae $hg_{1–4}$ always present, 2 pairs of adoral setae may be present or absent. Setae hg_4 is the longest. In species with apophyses the apophyses of the males are shorter.

The female dorsal propodosoma bears a shield that is complemented with 2 pairs of setae (*ve* and *sci*) and two pairs of setose sensillae (*vi* and *sce*). The dorsal hysterosoma may bear any combination of a median plate and lateral platelets (i.e., plate and platelets absent, only the plate present, only the lateral platelets present, or both the

plate and lateral platelets present). The median plate, if present, may be complemented with 0-6 pairs of dorsal setae; the lateral platelets, if present, may bear setae c_2. Setae not born on plates or platelets may be born on tiny platelets barely larger than the setal socket. The integument that does not bear plates or platelets is striated. Males differ in that the dorsal shields are often more extensive and may be holodorsal.

Coxae I–II may be fused or divided and may coalesce medially to form a sternal shield; coxae III–IV may be fused or divided and may extend caudally past the genital plates. The coxae may be complemented with up to 3 setae each. The genital plates each bear 4 setae ($g_{1–4}$); 2 pairs of genital papillae are visible underneath the plates. Anal plates complemented with at least one pair of setae, ps_1. Setae ps_2 may be present or absent, either on the anal plates or on the integument adjacent to the anal plates. Setae h_2 present ventrally on the integument adjacent to the anal plates. Cupule *ih* present laterad of h_2. The integument that does not bear plates is striated.

The tarsi are constricted apically so as to end in lobes. A trichobothria on tibia IV is present or absent.

Key to adult female Cunaxinae (modified from Den Heyer & Castro 2008c)

1 Anal seta ps_2 absent; palp telofemora with dorsal simple seta (Fig. 51a–e); tarsal lobes small to medium size (Fig. 53a); dorsal plates reticulated or not (Fig. 54a–c) ..... Cunaxini 2

- Anal seta ps_2 present; palp telofemora with dorsal spine-like seta (Fig. 52a, b); tarsal lobes medium to large size (Fig. 53b); dorsal plates always reticulated (Fig. 54c) ..... Armascirini 6

2 (1) Dorsal plates never reticulated (Fig. 54a, b); integumental striae smooth or lobed; coxae II–IV setal formula usually 1-3-2 (rarely 2-3-1) ..... *Cunaxa*

- Dorsal plates usually reticulated (Fig. 54c); integumental striae usually papillated; coxae II–IV setal formula usually 1-3-1 3

3 (2) Palpal telofemora with one or more apophyses (Fig. 51a); sensillae *vi* and *sce* not densely pilose ..... *Rubroscirus*

- Palpal telofemora without apophyses (Fig. 51b–e); sensillae *vi* and *sce* densely pilose 4

4 (3) Tibiae IV trichobothrium present 5

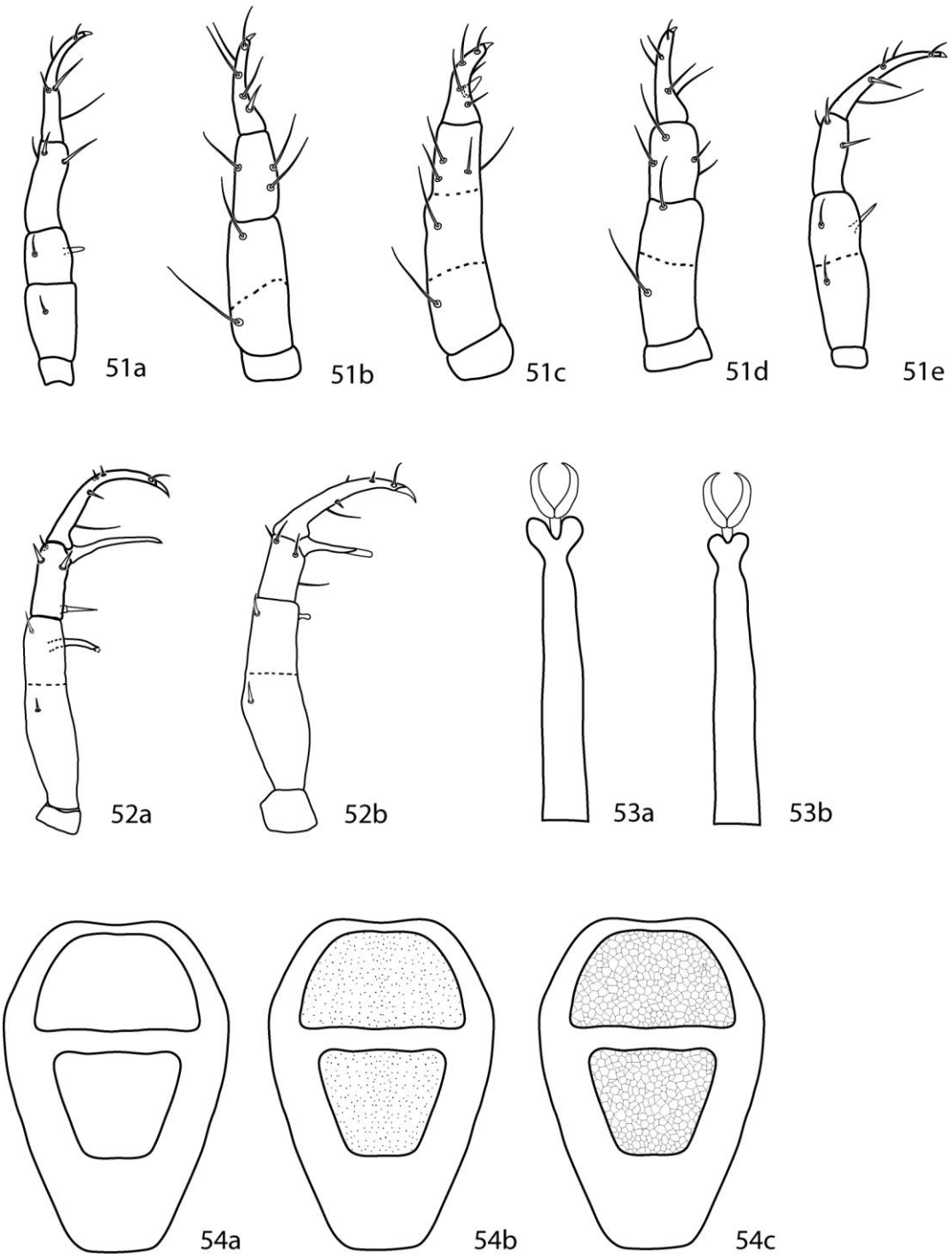
- Tibiae IV trichobothrium absent ..... *Cunaxatricha*

5 Articulation joint between palpal telofemora and genua functional (Fig. 51b) ..... *Riscus*

- Articulation joint between palpal telofemora and genua fused/non-functional (Fig. 51c) ..... *Allocunaxa*

6 (1) Palpal basifemora with simple seta(Fig. 52a); coxae II–IV setal formula 1-3-3 (male) or 2-3-3 (female); famulus normal; palpal apophyses usually long in females and short in males, and with pointed apices (Fig. 52a)..... *Armascirus*

- Palpal basifemora with spine-like seta(Fig. 52b); coxae II–IV setal formula 3-3-3; famulus large, broad based with tri-pronged tip; palpal apophyses usually equal length in females and males, and with bulbous apices (Fig. 52b)..... *Dactyloscirus*



Figures 51–54. 51-52) Pedipalps, dorsal. 51a) *Rubroscirus*. 51b) *Riscus*. 51c) *Allocunaxa*. 51d) *Cunaxatricha*. 51e) *Cunaxa*. 52a) *Armascirus*. 52b) *Dactyloscirus*. 53a, b) Distal end of tarsus. 53a) *Armascirini*, showing large tarsal lobes. 53b) *Cunaxini*, showing small to medium tarsal lobes. 54a–c) Idiosoma, dorsal. Setae and cupules have been removed for clairity. Shape of propodosomal plate and presence or absence , shape, and extent of hysterosomal plate(s) will differ between species. 54a) Plates smooth. 54b) Plates with dot-like pattern. 54c) Plates with reticulated pattern.

Armascirus

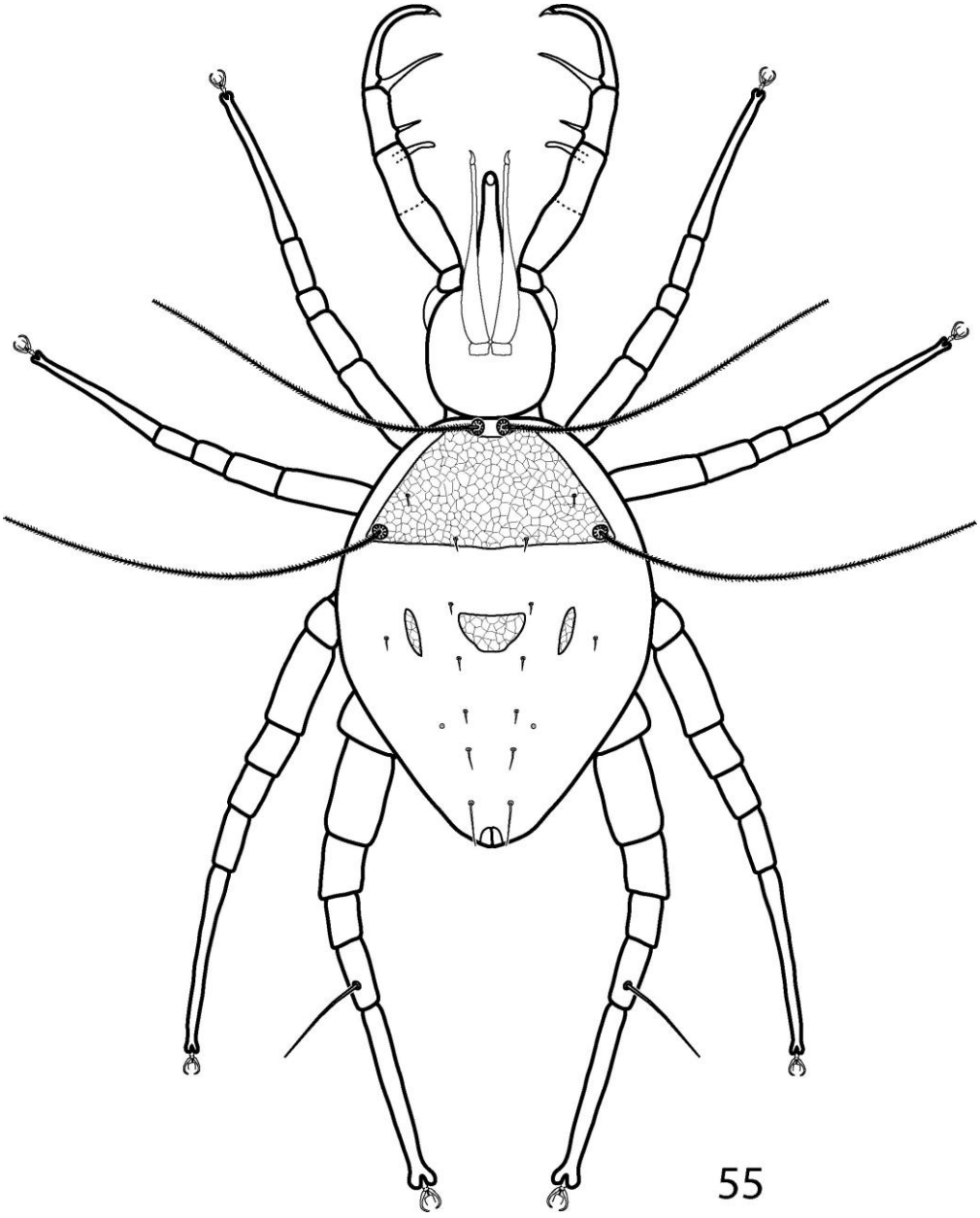


Figure 55. Generalized *Armascirus*. Presence or absence, shape, and extent of hysterosomal plates varies between species.

Historical Review. The first *Armascirus* was described by Kramer (1881) as *Scirus taurus*. Berlese (1888) described *S. taurus* var. *bison.* Banks (1894) described *S. quadripilus.* Thor (1902) transferred *S. taurus* to *Cunaxa*. Banks (1914) described *C. armata*. Womersley (1933) reported *C. taurus* from Australia. Thor and Willmann

(1941) transferred *S. taurus* var. *bison* to *Cunaxa* and raised it to full species status, viz. *C. bison* and transferred *S. quadripilus* to *Cunaxa*; they also redescribed and figured *C. armata, C. bison, C. quadripilus,* and C. *taurus*. Baker and Hoffmann (1948) synonymized *S. quadripilus* and *C. armata* with *C. taurus*; they followed Thor and Willmann (1941) in placing *C. taurus* var. *bison* in *Cunaxa* but declined to recognize it as a species and instead kept it as a variety or subspecies of *C. taurus*. Zaher *et al.* (1975b) collected *C. taurus* in Egypt. Chaudhri (1977) described *Dactyloscirus ebrius* and *D. fuscus* from Pakistan. Den Heyer (1978b) split *Armascirus* from *Dactyloscirus* and *Cunaxa* and raised the subfamily Cunaxinae to accommodate them, thus refining the definitions of all three genera; he transferred *C. taurus and C. bison* to the new; and described *A. huyssteeni, A. lebowensis, A. limpopoensis,* and *A. albiziae*. Kuznetzov and Livshitz (1979) redescribed and figured *C. taurus* and *C. bison* from Russia, either disagreeing with or being unaware of Den Heyer's 1978 publication. Tseng (1980) reported *A. taurus* from Taiwan. Chaudhri (1980) described *D. fixus* from Pakistan. Den Heyer (1980c) erected the tribe *Armascirini* and made *Dactyloscirus* and *Armascirus* the sole representatives. Gupta and Ghosh (1980) erected *Indocunaxa,* a monotypic genus with *I. smileyi* as the type species. Liang (1983) reported *A. taurus* from China. Michocka (1987) described *D. rafalskii* from Poland. *A. mactator* and *A. pluri* were described by Muhammad and Chaudhri (1991). Smiley (1992) described *A. gimplei, A. anastosi, A. harrisoni, A. heryfordi, A. virginiensis, D. bakeri,* and *D. campbelli*; he also transferred *A. bison* to *Dactyloscirus.* Corpuz-Raros (1995) described *A. garciai* and *A. makilingensis* from the Philippines. Hu (1997) reported *A. bison* and *A. taurus* from China. *Armascirus satianaensis* and *A. asghari* were described by Bashir and Afzal

(2005). Corpuz-Raros and Gruèzo described *A. javanus*. Corpuz-Raros (2008) described *A. bifidus*. Bashir, Afzal, and Khan described four species from Pakistan, *A. akhtari*, *A. jasmina*, *A. sabrii*, and *A. gojraensis*. Den Heyer and Castro (2008c) synonymized *Indocunaxa* with *Armascirus*. Kalúz (2009) described *A. cyaneus* and *A. cerris* from Central Europe and transferred *D. bison*, *D. campbelli*, *D. ebrius*, *D. fixus*, *D. fuscus*, and *D. rafalskii* to *Armascirus*.

Diagnosis. The palps are 5-segmented and end in a strong claw. They extend beyond the subcapitulum by at least the last segment and are often adorned with an apophysis between the genua and tibiotarsi, which tapers to a point; this apophysis is shorter in males than in females. The basifemora are complemented with a simple seta and the telofemora with a spine-like seta; these two segments are fused, although a line remains visible and they can thus be differentiated.

The subcapitulum is complemented with 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral setae). It can be covered by integumental papillae which are either randomly distributed or form a polygonal, reticulated pattern.

The female dorsal idiosoma has at least one sclerotized plate that bears 2 pairs of setose sensillae (*vi* and *sce*) and 2 pairs of simple setae (*ve* and *sci*). 0–4 other major plates and platelets may also be present. All plates, if present, are covered by integumental papillae that form a reticulated pattern. The integument between the plates is striated. 7 pairs of setae, $c_{1–2}$, d_1–h_1, are present. Each seta, when not on a major plate or platelet, is surrounded by a minute platelet that is only slightly larger than the setal socket. Cupule *im* is present, usually laterad or in the proximity of e_1. The dorsal

idiosoma of males is similar except a single large plate complemented with c_{1-2}, d_1–e_1 is present.

The female ventral idiosoma is complemented by the coxal, genital, and anal plates. The coxal plates are reticulated in the same manner as the dorsal plates. Coxae I and II are often fused as are coxae III and IV. The setal formula for coxae I–IV is males 3-1-3-3 (including the paracoxal seta) or females 3-2-3-3 (including the paracoxal seta). The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae (ps_1). 2 pairs of setae (ps_2 and h_2) are associated with but do not occur on the anal plates. Cupule *ih* is present in close proximity to h_2. The integument between plates is striated and bears 5–7 pairs of additional setae. The ventral idiosoma of males is similar except the coxal plates are much more extensive. A sclerotized aedeagus is often visible in association with the genital plates.

The legs are comparatively long, at least ¾ the length, and often longer than the body. The famulus on tarsi I is normally shaped. The tarsi are constricted apically, resulting in large tarsal lobes. A trichobothria is present on leg tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female *Armascirus*. The following key, based on one presented by Kalúz (2009), has been modified and illustrated to reduce ambiguous characters and language. The following species, in addition to those newly described in this work, have been included: *Armascirus javanus, A. garciai, A. makilingensis* and *A. apoensis*. In addition, *A. bakeri* (Smiley, 1992), which possesses a palpal basifemoral simple seta and

has a leg I–IV telofemoral chaetotaxy of 4-4-4-4 sts, is moved from *Dactyloscirus* to *Armascirus* based on the generic diagnosis given in this work and by Den Heyer and Castro (2008c).

1 Hysterosomal median shield present (Figs. 56a–i, 57a–d) 2

\- Hysterosomal median shield absent (Figs. 58a–c) 28

2 (1) Median shield complemented with setae, small or large (Figs. 56a–i) 3

\- Median shield not complemented with setae, small (Figs. 57a–d) 22

3 (2) One pair of setae (d_1) on hysterosomal median shield (Figs. 56a–f) 4

\- Two or more pairs of setae on hysterosomal median shield (Figs. 56g–i) 18

4 (3) Lateral hysterosomal platelets present (Figs. 56a–d) 5

\- Lateral hysterosomal platelets absent (Figs. 56e,f) 15

5 (4) Setae c_1 very short, the distance between the bases of c_1–c_1 20 times the length of c_1; venter caudally from coxae II with 5 pairs of simple setae (excluding genital, coxal, and anal setae) ..... *A. rafalskii*

\- Setae c_1 longer, the distance between the bases of c_1–c_1 less than 10 times the length of c_1; venter caudally from coxae II with 6 or more pairs of simple setae (excluding genital, coxal, and anal setae) 6

6 (5) The distance between caudal parts of hysterosomal lateral platelets wider than the distance between their frontal parts (Figs. 56a,b) 7

- The distance between caudal parts of hysterosomal lateral platelets shorter than the distance between their frontal parts (Figs. 56c,d) 9

7 (6) Lateral hysterosomal platelets equal to or longer than hysterosomal median shield (Fig 56a); venter caudally from coxae II with 6 pairs of simple setae (excluding genital, coxal, and anal setae) ..... *A. jasmina*

- Lateral hysterosomal platelets shorter than hysterosomal median shield (Fig 56b); venter caudally from coxae II with 7 pairs of simple setae (excluding genital, coxal, and anal setae) 8

8 (7) Palpal genua with 3 spls, 1 sts; important leg I–IV sts chaetotaxy: coxae 3-1-3-2, basifemora 4-5-3-1, genua 8-8-6-5, tibiae 5-6-6-6, tarsi 15-12-8-9 ..... *A. akhtari*

- Palpal genua with 3 spls; important leg I–IV sts chaetotaxy: coxae 3-2-3-3, basifemora 4-4-3-3, genua 8-4-6-7, tibiae 6-5-6-5, tarsi 11-10-9-7 ..... *A. satianaensis*

9 (6) Venter caudally from coxae II with 7–8 pairs of simple setae (excluding genital, coxal, and anal setae) 10

- Venter caudally from coxae II with 6 pairs of simple setae (excluding genital, coxal, and anal setae) 11

10 (9) Apophyses adjoining palpal genua longer than genu; median shield pointed caudally (Fig. 56c); venter caudally from coxae II with 7 pairs of setae (excluding genital, coxal, and anal setae); tarsal sts chaetotaxy I–IV 18-15-13-1 ..... *A. asghari*

- Apophyses adjoining palpal genua shorter than genu; median shield truncated caudally (Fig. 56d); venter caudally from coxae II with 8 pairs of setae (excluding genital, coxal, and anal setae); tarsal sts chaetotaxy I–IV 2 ..... *A. albiziae*

11 (9) Tarsus I with more than 27 setae; tarsus II with at least 24 setae 12

- Tarsus I with less than 25 setae; tarsus II with less than 23 setae 13

12 (11) Leg genua I with 4 bsl, 4 sts; genital valve with random dot-like lobes; tarsal sts chaetotaxy I–IV 29-25-23-22 ..... *A. pluri*

- Leg genua I with 2 asl, 4 bsl, 3 sts; genital valve longitudinal rows of dot-like lobes; tarsal sts chaetotaxy I–IV 29-24-22-21 ..... *A. mactator*

13 (11) Palpal telofemora with 1 apophysis, 2 spls; palpal genua with 1 ap, 2 spls, 2 sts ..... *A. huyssteeni*

- Palpal telofemora with 1 apophysis, 1 spls; palpal genua with 1 ap, 3 spls, 1 sts 14

14(13) Genua II with 1 asl, 5 sts; genua IV with 2 asl, 5 sts ..... *A. taurus*

- Genua II with 1 asl, 6 sts; genua IV with 2 asl, 4 sts ..... *A. primigenius* **sp. nov.**

15 (4) Hysterosomal median shield with a straight or concave frontal margin and with very acute anterior lateral corners (angle less than 45°) (Fig. 56e) 16

- Hysterosomal median shield with convex frontal margin and with rounded anterior lateral corners (Fig. 56f) 17

16 (15) Palpal genua with 1 ap, 2 spls, 1 sts; legs I–IV sts formulae (excluding solenidia): basifemora 1-2-1-0; telofemora 4-4-4-4; genua 6-7-5-6; h_1 4 times the length of c_1; hysterosomal shield width: length = 2.2:1 ..... *A. sabrii*

- Palpal genua with 1 ap, 3 spls, 1 sts; legs I–IV sts formulae (excluding solenidia): basifemora 2-2-1-1; telofemora 4-4-4-3; genua 8-6-6-6; h_1 3 times the length of c_1; hysterosomal shield width: length 1.5:1 ..... *A. gojraensis*

17 (15) Apophysis adjoining genu and tibiotarsus shorter than palpal tibiotarsus; palpal telofemoral apophyses three times longer than spine-like seta; distance between the bases of *sci–sci* 9 times the length of *sci* ..... *A. bison*

- Apophysis adjoining genu and tibiotarsus longer than palpal tibiotarsus; palpal telofemoral apophyses three times longer than spine-like seta; distance between the bases of *sci–sci* 5 times the length of *sci* ..... *A. fixus*

18 (3) Hysterosomal median shield with 2 pairs of setae (c_1, d_1) (Fig. 56g) 19

- Hysterosomal median shield with more than 2 pairs of setae (Figs. 56h, i) 20

19 (18) Palpal telofemora with 2 ap, 1 spls; palpal genua with 2 spls, 2 sts; venter caudally from coxae II with 6 pairs of simple setae (excluding genital, coxal, and anal setae); tarsi I–IV with 21-20-15-13 sts (excluding solenidia); the distance between bases of c_1–c_1 4 times the distance of h_1–h_1; distance between c_1–c_1 5 times the length of c_1 ..... *A. anastosi*

- Palpal telofemora with 1 ap, 1 spls; palpal genua with 3 spls, 1 sts; venter caudally from coxae II with 5 pairs of simple setae (excluding genital, coxal, and anal setae); tarsi I–IV with 19-13-13-13 sts (excluding solenidia); the distance between c_1–c_1 2 times the distance between h_1–h_1; the distance between c_1–c_1 4 times the length of c_1 ..... *A. heryfordi*

20 (18) Hysterosomal shield bearing 3 pairs of setae (c_1, d_1, e_1) (Fig. 56h); apophysis adjacent to palpal genua and tibiotarsi absent 21

- Hysterosomal shield bearing 5 pairs of setae (c_1, c_2, d_1–f_1) (Fig. 56i); apophysis adjacent to palpal genua and tibiotarsi present ..... *A. ebrius*

21(20) 5 pairs of genital setae; palp claw bifid (Fig. 59a); hysterosomal setae not serrate ..... *A. apoensis*

- 4 pairs of genital setae; palp claw entire, not bifid (Fig. 59b); hysterosomal setae serrate ..... *A. fuscus*

22 (2) Lateral hysterosomal platelets present (Figs. 57a–c) 23

- Lateral hysterosomal platelets absent (Fig. 57d) 25

23 (22) Hysterosomal platelets large, as long as median shield (Fig. 57a); width: length of hysterosomal median shield 1:1; venter caudally from coxae II with 7 pairs of sts (excluding genital and anal setae); genital setae g_1–g_4 equal in length ..... *A. cerris*

- Hysterosomal platelets large or small (Figs. 57b,c); width: length of hysterosomal median shield 2:1; venter caudally from coxae II with 6 pairs of sts (excluding genital and anal setae); genital setae g_3 & g_4 ca 1.3 times longer than g_1 & g_2 24

24 (23) Hysterosomal platelets as long as median shield (Fig. 57b) ..... *A. ozarkensis* **sp. nov.**

- Hysterosomal platelets ½ as long as median shield (Fig. 57c) ..... *A. gimplei*

25 (22) Apophysis on palp telofemur extends to distal margin of segment; 2 pairs of ventral pregenital setae thickened and spiculate; f_1 1/3 length of h_1 ..... *A. makilingensis*

- Apophysis on palp telofemur extends well beyond distal margin of segment; ventral pregenital setae not thickened and spiculate; f_1 subequal to h_1 26

26 (25) Palpal telofemora with 2 ap, 1 spls; the distance between the bases of c_1–c_1 two times the distance of d_1–d_1 ..... *A. limpopoensis*

- Palp telofemora with 1 ap, 1 spls; the distances between the bases of c_1–c_1 = d_1–d_1 27

27 (26) Palp tibiotarsus with 1 spls, 4 sts ..... *A. harrisoni*

- Palp tibiotarsus with 1 spls, 3 sts ..... *A. bakeri*

28 (1) Palpal telofemoral apophyses long, reaching apical apophysis on palpal genu; lateral platelets present 29

- Palpal telofemoral apophyses short, not reaching apical apophysis on palpal genu; lateral platelets present or absent 30

29 (28) Palpal basifemora with 1 subrectangular apophysis; palp tibiotarsal spls 3 times the length of terminal claw; hysterosomal platelets small, equal in length to c_2 (Fig. 58a); coxal chaetotaxy I–IV 3-2-3-3 ..... *A. lebowensis*

- Palpal basifemora without subrectangular apophysis; palp tibiotarsal spls equal in length to terminal claw; hysterosomal platelets long, 2–3 times the length of c_2 (Fig. 58b); coxal chaetotaxy I–V 3-1-3-1 ..... *A. campbelli*

30 (28) Coxal chaetotaxy I–IV 3-2-3-3 31

- Coxal chaetotaxy I–IV 3-2-3-2 33

31 (30) Palpal telofemora with 1 apophysis, 2 spls, 1 sts; the distance between d_1–d_1 9 times the length of d_1; palpal genua with 2 spls, 1 sts ..... *A. cyaneus*

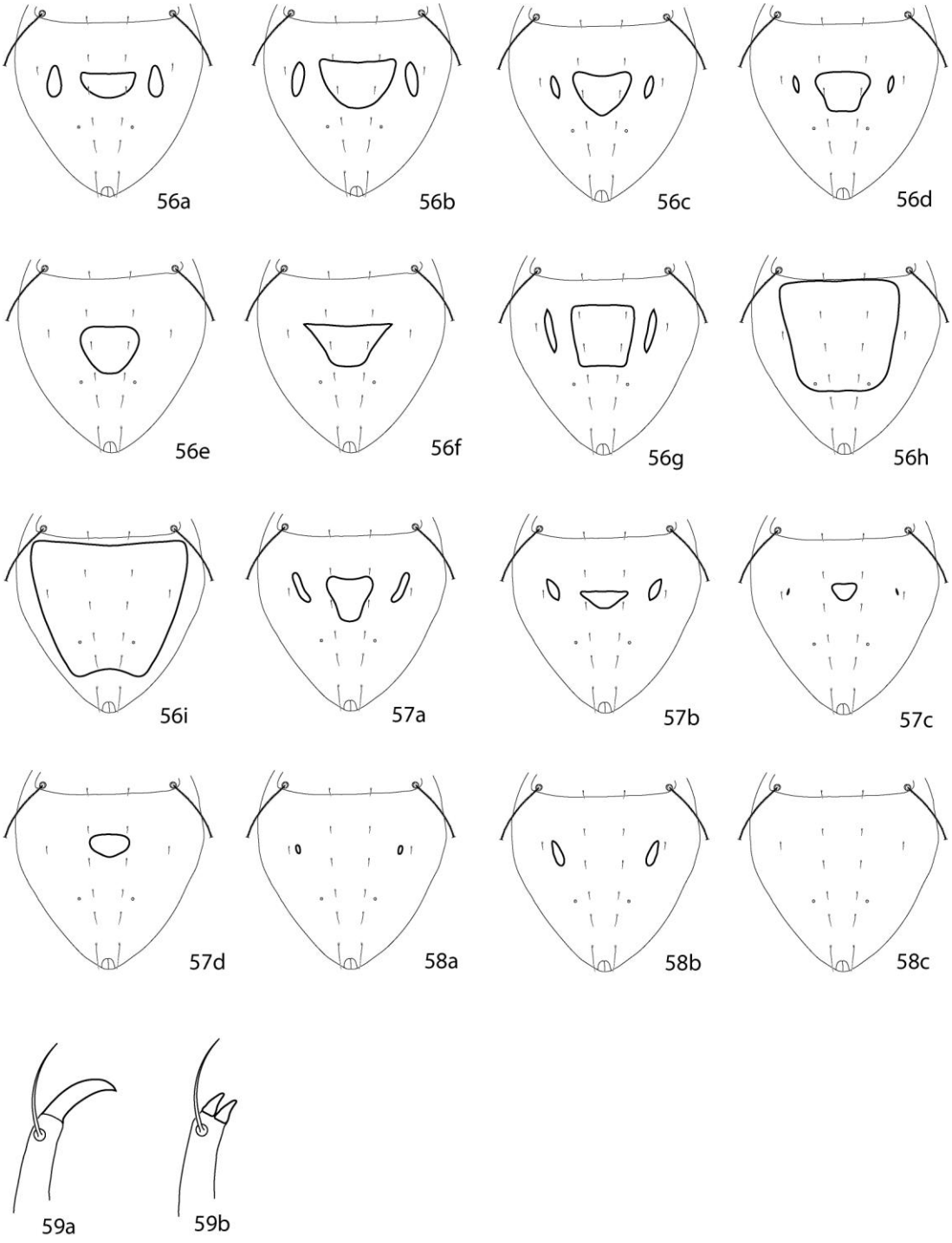
- Palpal telofemora with 1 apophysis, 2 spls; the distance between d_1–d_1 4 times the length of d_1; palpal genua chaetotaxy not as above 32

32 (31) Hysterosomal platelets present (Fig 58b); palpal genua with 2 spls, 2 sts; basifemora with 5-5-4-2 sts ..... *A. virginiensis*

- Hysterosomal platelets absent (Fig. 58c); palpal genua with 1 spls, 1 sts; basifemora with 6-6-4-2 sts ..... *A. javanus*

33 (30) Palpal telofemoral apophyses as long as width of telofemora; palpal genu with 1 apophysis, 2 spls, 2 sts ..... *A. pennsylvanicus* **sp. nov.**

- Palpal telofemoral apophyses only 1/3 width of telofemora; palpal genu with 1 apophysis, 3 spls, 1 sts ..... *A. garciai*



Figures 56–59. *Armascirus* key illustrations. 56–58) Dorsal idiosoma. 56a–e) Hysterosomal shield large, complemented with setae. 57a–d) Hysterosomal shield small, not complemented with setae. 58a–c) Hysterosomal shield absent. 59a, b) Pedipalp tibiotarsal claw. 59a) Single claw. 59b) Bifid claw. See key for further explaination.

Dactyloscirus

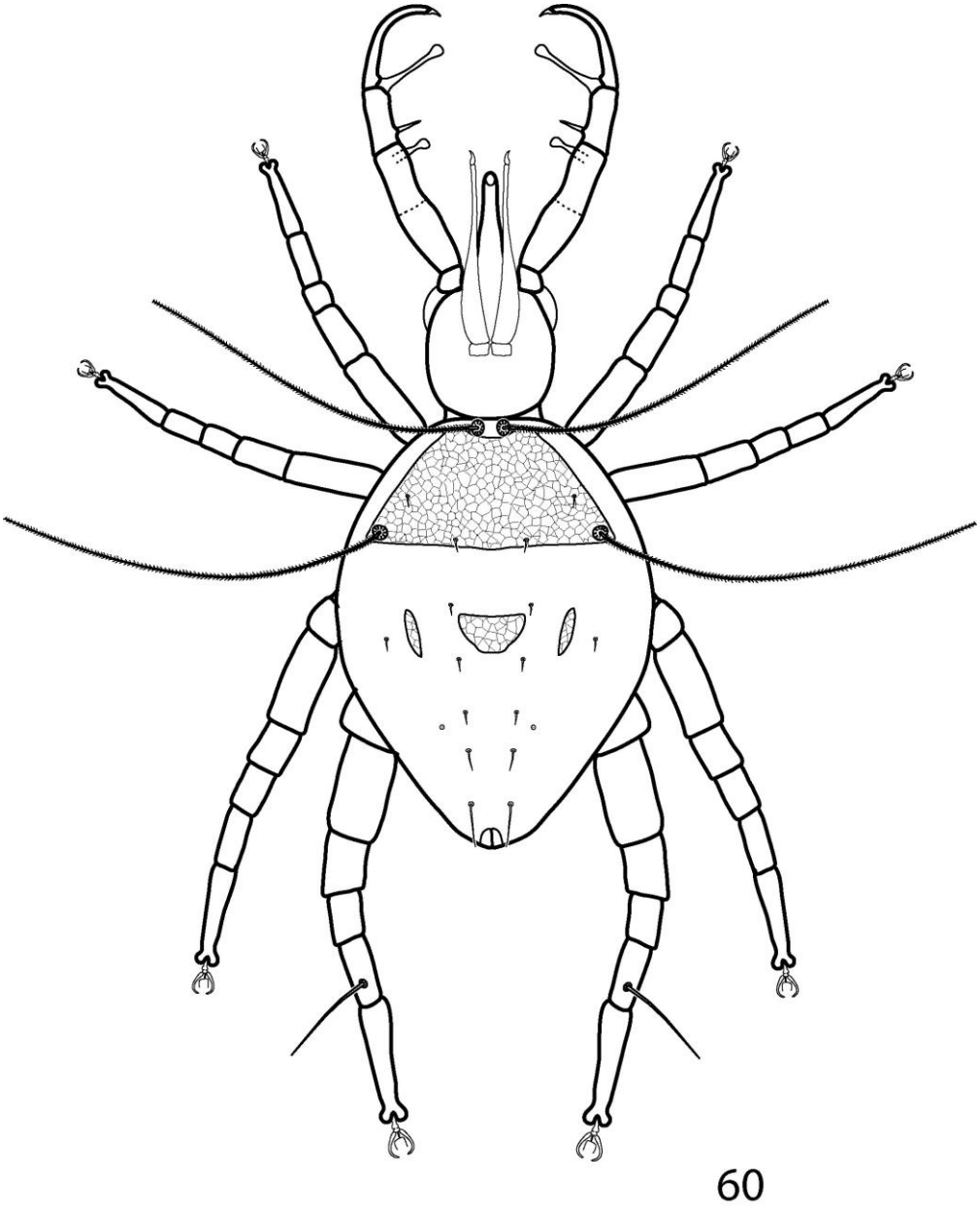


Figure 60. Generalized *Dactyloscirus*. Presence or absence, shape, and extent of hysterosomal plates varies between species.

Historical Review. Trägårdh (1905) described *Scirus inermis*. Berlese (1916) erected *Dactyloscirus* as a subgenus of *Scirus* to accommodate *Scirus* (*Dactyloscirus*) *eupaloides*. He also described *Scirus dorcas* but failed to recognize that they were

congeneric. Oudemans (1922) described *Rosenhofia machairodus*. Halbert (1923) redescribed and figured *S. inermis* from Ireland. Sellnick (1926) transferred *S. inermis* to *Cunaxa*. Vitzthum (1931) raised *Dactyloscirus* to full generic status but later (1940-43) treated it as a subgenus. Thor & Willmann (1941) again elevated *Dactyloscirus* to generic status and designated *Dactyloscirus eupaloides* as the type specimen; they also transferred *C. inermis* and *S. dorcas* to *Dactyloscirus*. Baker & Hoffmann (1948) regarded *Dactyloscirus* as a senior synonym of *Cunaxa*. Smiley (1975) synonymized *Rosenhofia* with *Dactyloscirus*. Zaher *et al.* (1975b) reported *D. inermis* from Egypt (though they called it *Cunaxa inermis*). Chaudhri (1977) described *D. fuscus*. Den Heyer (1978b) split *Armascirus* from *Dactyloscirus* and *Cunaxa* and raised the subfamily Cunaxinae to accommodate them, thus refining the definitions of all three genera. Den Heyer (1979a) described *D. condylus* and *D. dolichosetosus*. Den Heyer (1980c) erected the tribe *Armascirini* and made *Dactyloscirus* and *Armascirus* the sole representatives. Gupta and Ghosh (1980) described *Cunaxoides nicobarensis*. *Dactyloscirus pataliputraensis* was described by Gupta (1981). Liang (1986) described *D. humuli* from China. Michocka (1987) reported *D. inermis* from Poland. Smiley (1992) transferred *Cunaxoides nicobarensis* to *Dactyloscirus* and described *D. mansoni*, *D. johnstoni*, and *D. poppi*. Corpuz-Raros (1995) described *D. philippinensis, D. rosarioae,* and *D. agricolus*. Inayatullah and Shahid (1996) described *D. illutus, D. minys,* and *D. orsi*. Swift (1996) described *D. hoffmannae* and *D. smileyi* from the Hawaiian Islands. Hu (1997) reported *D. inermis* and *D. humuli* from China. Corpuz-Raros (2008) described *D. apoensis, D. discocondylus,* and *D. trifidus.*

Diagnosis. The palps are 5 segmented and extend beyond the subcapitulum by at least the last segment. They end in a strong claw and are often adorned with an apophysis between the genua and tibiotarsi. This apophysis can be long or short and generally ends in a bulbous, hyaline tip; it can however end in a tapering point as in *Armascirus*. This apophysis can be approximately equal between males and females or can be shorter in males. The basifemora and telofemora are complemented with spine-like setae; these two segments are fused, although a line remains visible and they can thus be differentiated.

The subcapitulum is complemented with 6 pairs of setae ($hg_{1–4}$ and 2 pairs of adoral setae). It can be covered by integumental papillae that are either randomly distributed or form a polygonal, reticulated pattern.

The female dorsal idiosoma has at least one sclerotized plate that bears 2 pairs of setose sensillae (*vi* and *sce*) and 2 pairs of simple setae (*ve* and *sci*). 0–4 other major plates and platelets may also be present. All plates, if present, are covered by integumental papillae that form a reticulated pattern. The integument between the plates is striated. 7 pairs of setae ($c_{1–2}$, d_1–h_1) are present. Each seta, when not on a major plate or platelet, is surrounded by a minute platelet that is only slightly larger than the setal socket. Cupule *im* is present, usually laterad or in the proximity of e_1. The dorsal idiosoma of males is similar except a single large plate complemented with $c_{1–2}$, d_1–e_1 is present.

The female ventral idiosoma is complemented by the coxal, genital and anal plates. The coxal plates are reticulated in the same manner as the dorsal plates. Coxae I and II are often fused, as are coxae III and IV. The setal formula for coxae I–IV is 3-3-3-

3 (including paracoxal seta). The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae (ps_1). 2 pairs of setae (ps_2 and h_2) are associated with, but do not occur on, the anal plates. Cupule *ih* is present in close proximity to h_2. The integument between plates is striated and bears 5–7 pairs of additional setae. The ventral idiosoma of males is similar except the coxal plates are much more extensive. A sclerotized aedeagus is often visible in association with the genital plates.

The legs are comparatively short, generally not exceeding ¾ the length of the body. The famulus on tarsi I is enlarged and ends in a tri-tipped prong. The tarsi are constricted apically, resulting in large tarsal lobes. A trichobothria is present on leg tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female Dactyloscirus. The following key, based on one presented by Smiley (1992), has been modified and illustrated to reduce ambiguous characters. The following species, in addition to those newly described in this work, have been included for completeness: *Dactyloscirus philippinensis, D. trifidus, D. orsi, D. minys, D. dicondylus, D. agricolus, D. rosarioae, D. bifidus, D. illutus, D. smileyi* and *D. hoffmannae*.

1 Palpal tibiotarsi and genua with adjoining apophyses (Fig 61a–i) 2

\- Palpal tibiotarsi and genua without adjoining apophyses (Fig 62a–d) 19

2 (1) Dorsal hysterosomal lateral platelets present (Fig. 63a–d) 3

- Dorsal hysterosomal lateral platelets absent (Figs. 64a–f) 11

3 (2) Palp telofemora with one or two apophyses (Fig. 65a–c) 4

- Palp telofemora without an apophysis; distribution unknown ..... *D. poppi*

4 (3) Palpal telofemora with 1 apophysis (Figs. 65a, b) 5

- Palpal telofemora with 2 apophyses: 1 basal, flattened and disc-shaped, 1 apical, short, thick and bulbous (Fig. 65c); South Africa ..... *D. condylus*

5 (4) Lateral platelets inconspicuous, length less than 2 times the length of c_1 or c_2; cosmopolitan (Fig. 63a) ..... *D. inermis*

- Lateral platelets large, length greater than 2 times the length of c_1 or c_2 (Fig. 63b–d) 6

6 (5) Dorsal setae f_1 and h_1 equal in length; median shield present (Figs. 63b,c) or absent (Fig. 63d) 7

- Dorsal setae f_1 shorter than h_1; median shield absent (Figs. 63d) 9

7 (6) Apophysis adjoining palpal genua and telofemora as long or longer than length of genu, blunt or pointed distally (Fig 61, c); median shield present (Figs. 63b, c) 8

- Apophysis adjoining palpal genua and telofemora shorter than length of genu, blunt distally (Fig. 61a); median shield absent (Fig. 63d); South Africa .....

D. dolichosetosus

8 (7) Apophysis adjoining palpal genua and telofemora pointed distally (Fig 61b); palp tibiotarsi with 4 sts; median shield complimented with setae c_1, d_1; e_1 on small platelets (Fig. 63b); leg basifemora with 5-5-3-1 sts; Luzon I., Philippines D. *philippinensis*

- Apophysis adjoining palpal genua and telofemora blunted distally (Fig. 61c); setae c_1–e_1 on median shield (Fig. 63c); palp tibiotarsi with 5 sts; leg basifemora with 5-5-3-2 sts; Ozark Mountains, USA *D. pseudophilippinensis* **sp. nov**

9 (6) Apophysis adjoining palpal genua and telofemora inconspicuous: circular, minute and hyaline (Fig. 61d); Oahu I., Hawaiian Islands *D. hoffmannae*

- Apophysis adjoining palpal genua and telofemora conspicuous: short, blunt apically (Fig. 61e) 10

10 (9) Genital setae g_3 longest, 1.5–1.7 times the length of g_2 and g_4, more than 2 times the length of g_1; Kauai I., Hawaiian Islands *D. smileyi*

- Genital setae g_4 longest, 2 times the length of $g_{1–3}$; Shanghai, China *D. humuli*

11 (2) Dorsal hysterosomal median shield present (Figs. 64a–e) 12

- Dorsal hysterosomal median shield absent (Fig. 64f) 15

12 (11) Median shield complemented with d_1 only (Fig. 64a); Punjab, Pakistan…*D. fixus*

- Median shield complemented with 2 or more pairs of setae (Figs. 64b–e) 13

13 (12) Median shield complemented with c_1,d_1 (Fig. 64b); apophysis adjacent to palpal genua and tibiotarsi blunt distally (Fig. 61c); Mexico, Philippines ..... *D. mansoni*

- Median shield complemented with c_1–e_1 (Figs. 64c,d); apophysis adjacent to palpal genua and tibiotarsi blunt or pointed distally 14
- Median shield complemented with c_1–e_1, c_2 (Fig. 64e); apophysis adjacent to palpal genua and tibiotarsi pointed distally ..... *D. illutus*

14 (13) Apophysis adjacent to palpal genua and tibiotarsi blunt distally (Fig. 61e); median shield triangular and nearly as wide as propodosomal shield (Fig. 64c); Bihar, India ..... *D. pataliputraensis*

- Apophysis adjacent to palpal genua and tibiotarsi tapering and pointed distally (Fig. 61f); median shield subrectangular and not as wide as propodosomal shield (Fig. 64d); Mexico ..... *D. johnstoni*

15 (11) Palp tibiotarsal claw entire, not branched (Figs. 61a–g) 16

- Palp tibiotarsal claw bifid (Figs. 61h, i); Polillo I., Philippines ..... *D. bifidus*

16 (15) Palpal telofemora without apophysis (Fig. 61g); apophysis adjoining palpal genua and telofemora longer than telofemora and tapering to a point; Sumatra, Indonesia ..... *D. machairodus*

- Palpal telofemora with 1 or 2 apophyses (Figs. 65a–d); apophysis adjoining palpal genu and telofemur shorter than telofemora and with a bulbus tip (Figs. 61a, d) 17

17 (16) Palpal telofemora with 1 apical apophysis (Figs. 65a,b); apophysis adjoining genua and tibiotarsi larger (Fig. 61a) 18

- Palpal telofemora inner surface with 2 apophyses: 1 basal, flattened and disc-shaped, 1 apical, short, thick and bulbous (Fig. 65d); apophysis adjoining genua and tibiotarsi small, inconspicuous (Fig. 61d); Luzon I., Philippines ..... *D. discocondylus*

18 (17) Basal pair of adoral setae very long, more than 4 times the distal pair; palp telofemoral apophysis about as long as width of segment (Fig. 65a); genital setae g_4 twice as long as g_1–g_3; Luzon I., Philippines ..... *D. rosarioae*

- Basal pair of adoral setae not unusually long, subequal to distal pair; palp telofemoral apophysis short, less than width of segment (Fig. 65b); genital setae g_4 only slightly longer than g_1–g_3; Luzon I., Philippines ..... *D. agricolus*

19 (1) Median shield present (Figs. 64d,e) 20

- Median shield absent (Fig. 64f) 21

20 (19) Median shield complimented with c_1–e_1 (Fig. 64d) ; Europe, North and South America ..... *D. eupaloides*

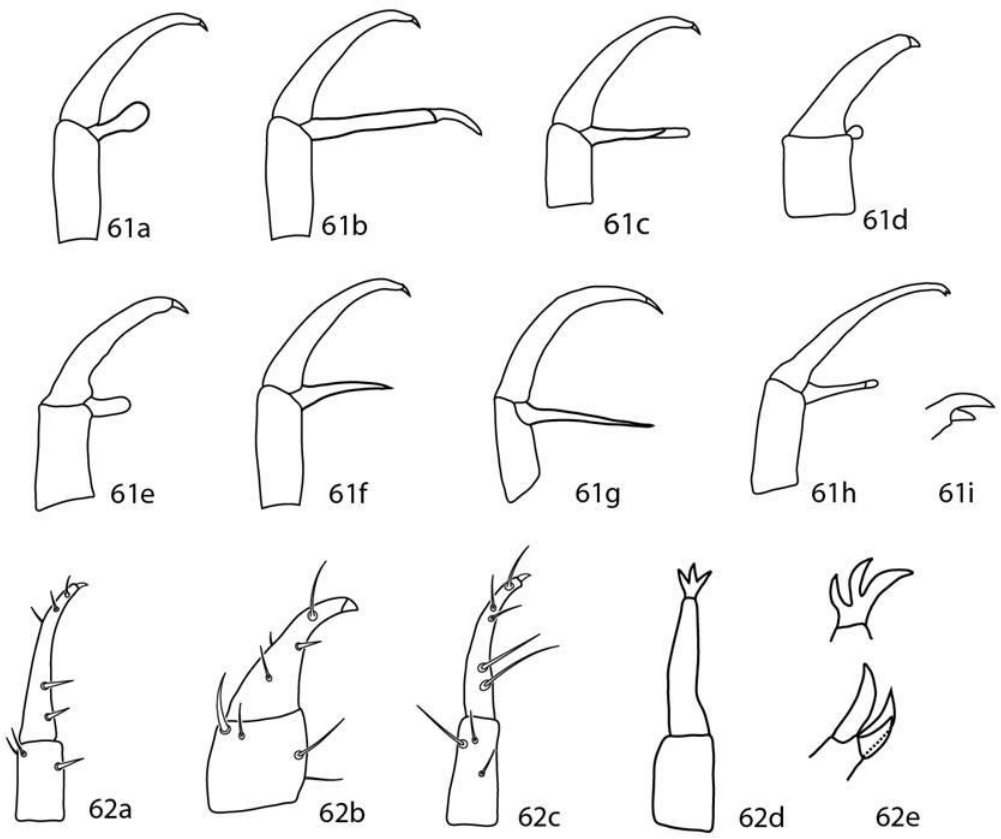
- Median shield complimented with c_1–e_1, c_2 (Fig. 64e); Peshawar, Pakistan ..... *D. minys*

21 (19) Palp tibiotarsal claw entire, unbranched (Figs. 62a, b); coxal setal formula not as different 21

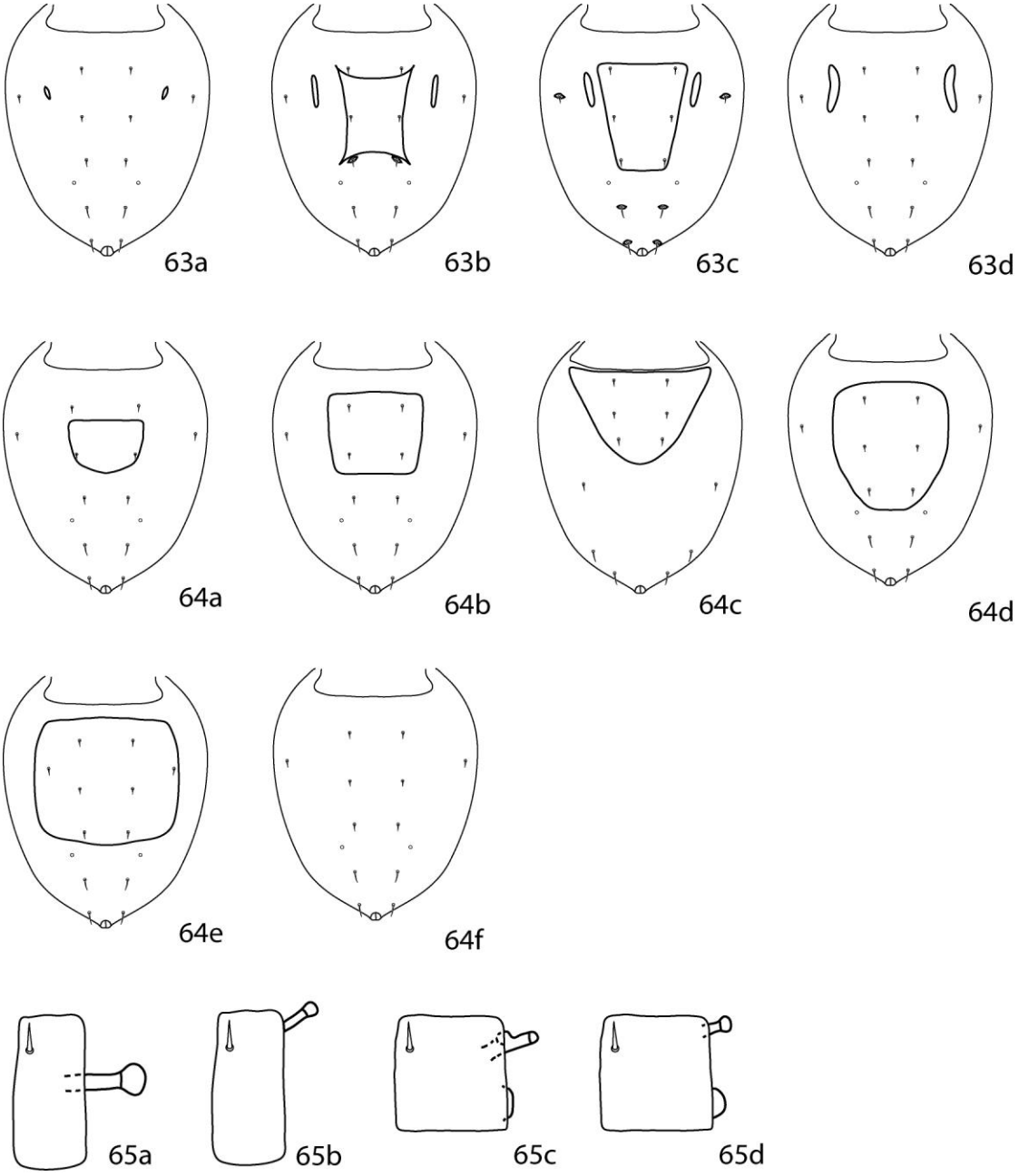
- Palp tibiotarsal claw trifid (Figs. 62c,d); coxal setal formula 3-3-3-3 sts; Luzon I., Philippines ..... *D. trifidus*

22 (21) Palp setal formulae: genua, 1 spls, 2 sts; tibiotarsi, 1 spls, 1 spur-like setae, 1 dtsl, 3 sts (Fig. 62a); coxal setal formula 3-1-3-2 sts; Peshawar, Pakistan .. *D. orsi*

- Palp setal formulae: genua, 3 sts; tibiotarsi, 1 dtsl, 4 sts (Fig. 62b); coxal setal formula 3-2-2-1; Nicobar I., India ..... *D. nicobarensis*



Figures 61–62. 61a–h & 62a–d) Pedipalpal genu and tibiotarsus. 61i) Close up of bifid claw. 62e) Close up of trifid claw. See key for further explaination.



Figures 63–65. 63–64) Idiosoma, dorsal. 63a–d) Lateral platelets present. 64a–f) Lateral platelets absent. 65a–d) Dorsal telofemora, illustrating various kinds of apophyses. See key for further explaination.

Cunaxa

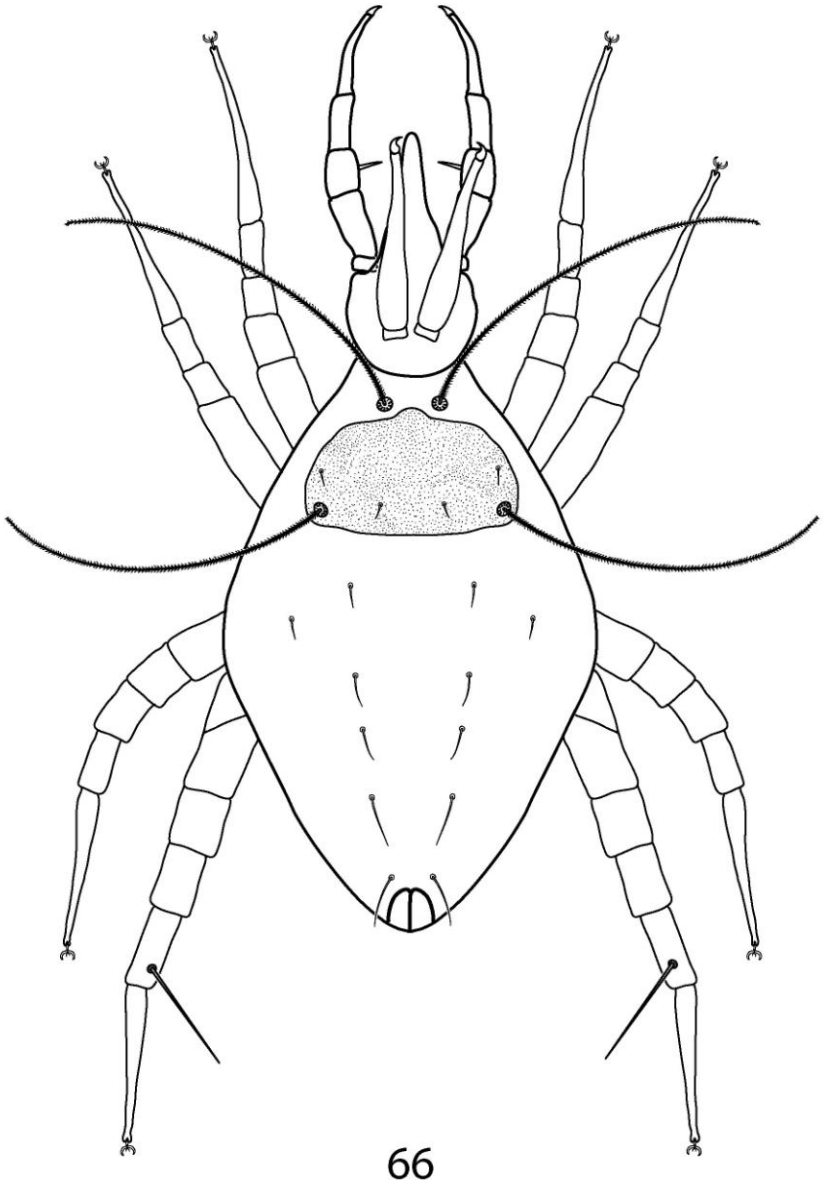


Figure 66. Generalized *Cunaxa*, dorsal.

Historical Review. Herman (1804) erected *Scirus* for *S. setirostris* and placed it with two mites that are now considered to belong to the family Bdellidae. Von Heyden (1826) erected *Cunaxa* for *Scirus setirostris.* Dugés (1834a) described *S. elaphus*. Dugés (1834b) described *S. tenuirostris*. Koch (1836) described *S. stabulicola* and *S. sagax* and

later (1838) *S. paludicola*. Gervais (1841) described *S. obisium.* Berlese (1888) synonymized *S. elaphus, S. stabulicola, S. sagax,* and *S. paludicola* with *S. setirostris.* Berlese (1887) described *S. capreolus*. Thor (1902) erected Cunaxidae and split *Cunaxa* from Bdellidae. Ewing (1913) described *S. laricis*. *S. setirostris* var. *gazella* was described by Berlese (1916). Thor and Willmann (1941) redescribed and figured *S. laricis* after transferring it to *Cunaxa*; they also transferred *S. setirostris* var. *gazella* to *Cunaxa*, though kept it as a subspecies of *C. setirostris* and synonymized *S. tenuirostris* and *S. obisium* with *C. setirostris*. Baker and Hoffmann (1948) redescribed and figured *C. setirostris* var. *gazella* and *C. capreolus* and described *C. womersleyi* and *C. veracruzana*. Zaher *et al.* (1975b) reported *C. setirostris* and *C. capreolus* from Egypt. Den Heyer (1978b) erected Cunaxinae and assigned *Cunaxa* to the subfamily. Den Heyer (1979d) elevated *C. setirostris* var. *gazella* to full species status; described *C. carina, C. terrula, C. lamberti, C. meiringi*, and *C. grobleri* and redescribed; and figured *C. capreola* and *C. gazella*. He then (Den Heyer 1979e) described five more species from South Africa: *C. hermanni, C. sordwanaensis, C. potchensis, C. brevicrura,* and *C. magoebaensis*. Kuznetzov and Livshitz (1979) redescribed and figured *C. capreolus* and *C. setirostris* from Russia. Chaudhri (1980) described *C. doxa*. Gupta and Paul (1985) described *C. curassavica, C. prinia,* and *C. crista*. Tseng (1980) reported *C. womersleyi* and *C. setirostris* from Taiwan. Bu and Li (1987c) reported *C. capreola* from China. Michocka (1987) reported *C. setirostris* from Poland. Muhammad *et al.* described *Rubroscirus valentis* from Pakistan. Smiley (1992) described *C. mageei, C. thailandicus, C. evansi*, and *C. neogazella*; he also synonymized *Rubroscirus* with *Cunaxa*, though failed to include his evidence for doing so. Muhammad and Chaudhri (1993) described

Rubroscirus vasile and *R. otiosus* from Pakistan. Corpuz-Raros and Garcia (1995) described five species from the Philippines: *C. luzonica*, *C. romblonensis*, *C. pantabanganensis*, *C. cogonae*, and *C. mercedesae*. Hu (1997) reported 28 species of Cunaxidae from China. Khaustov and Kuznetzov (1998) described *C. heterostriata*, *C. anomala*, *C. sudakensis* and *C. bochkovi*. Chinniah and Mohanasundaram (2001) described *C. eupatoriae*. Sergeyenko (2003) described *C. dentata*. Sionti and Papadoulis (2003) described *C. thessalica* from Greece. Bei *et al.* recorded *C. mageei* from China. Bashir, Afzal, and Ali (2005) described *C. reticulatus* and moved *Rubroscirus valentis*, *R. vasile*, and *R. otiosus* to *Cunaxa*. Bashir and Afzal (2006) described *C. jaoiensis*. Sergeyenko (2009) described *C. gordeevae*, *C. guanotoleranta*, *C. maculata*, *C. papuliphora*, *C. violaphila* and *C. yaylensis*. Den Heyer (2009) designated a neotype of *C. setirostris* while redescribing and illustrating the species.

Diagnosis. The palps are 5 segmented and reach beyond the subcapitulum by at most the distal half of the tibiae. An apophysis on the telofemora may be present or absent. The dorsolateral setae on the basi- and telofemora are simple. Stout spine-like setae may be present or absent on the genua and tibiotarsi. The tibiotarsi end in a strong claw. 6 pairs of setae occur on the subcapitulum: 2 pairs of adoral setae and 4 pairs of subcapitular setae (hg_{1-4}). The subcapitulum may be smooth or patterned with random dots but is never reticulated.

The dorsal propodosoma bears a shield that is complemented with 2 pairs of setae (*vi* and *sce*) and 2 pairs of setose sensillae (*ve* and *sci*). The dorsal hysterosoma may bear a shield; if a shield is present it may bear up to 4 pairs of setae. The dorsal shields may

be smooth or patterned with random dots but are never reticulated. Lateral platelets (as in *Armascirus* and *Dactyloscirus*) are absent. Setae c_1–h_1, and c_2 are present. If they are not born on the median plate, setae may be born on small platelets that are barely larger than the setal socket. Cupule *im* is present laterad and caudally of e_1. The integument not bearing the propodosomal shield and median plate (if present) is striated. The striations are smooth or lobed but never papillated.

Coxae I–II may be fused and coxae III–IV may be fused. Coxae II–IV setal formula is 1-3-2. The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. The anal plates bear one pair of setae (ps_1). 1 pair of setae (h_2) is associated with, but do not occur on, the anal plates. Cupule *ih* is present in close proximity to h_2. The integument between plates is striated and bears up to 7 pairs of additional setae.

The tarsi are long and slender; they are constricted distally but the tarsal lobes are small and not conspicuous as in *Armascirus* and *Dactyloscirus*. A trichobothria is present on tibia IV. The ambulacral claws occur on either side of a 4-rayed empodium.

Key to adult female *Cunaxa* (part after Sergeyenko 2009)

Cunaxa bochkovi is not included in the key because the original description is in Cyrillic and the illustration does not contain enough detail or diagnostic characteristics.

Cunaxa reticulatus is moved to *Rubroscirus* and *C. valentis*, *C. vasile*, and *C. otiosus* returned to *Rubroscirus* as they posess dorsal plates that are reticulated instead of smooth as in *Cunaxa*.

1 Setae *ve* present (Fig. 67a–d) 2

Setae *ve* absent (Fig. 67e) ..... *C. anomala*

2 (1) Basifemora I with 1 sts ..... *C. prinia*

- Basifemora I with 3 sts 3

- Basifemora I with 4 sts 10

- Basifemora I with 5 sts 32

3 (2) Genua I with 3 solenidia 4

- Genua I with 4 solenidia 5

4 (3) Genua II with 1 solenidion; setae f_1, h_1 smooth (Fig. 68a) ..... *C. setirostris*

- Genua II with 2 solenidia; setae f_1, h_1 spiculate (Fig. 68b) ..... *C. magoebaensis*

5 (3) Coxae I–IV with 3-1-3-2 sts 6

- Coxae I–IV with 3-2-3-1 sts ..... *C. eupatoriae*

6 (5) Dorsal setae short (c_1–f_1, c_2: 7-10, h_1: 17) ..... *C. mercedesae*

- Dorsal setae longer (19-40) 7

7 (6) Oval area formed by broken striae around setae *sci* present (Fig. 67a) ..... *C. maculata*

- Oval area formed by broken striae around setae *sci* absent (Fig. 67b) 8

8 (7) Genua II proximal solenidion extremely short, its length subequal to the diameter of its alveolus; ventral surface of the coxal region of hypognathum smooth ..... *C. guanotoleranta*

- Genua II proximal solenidion long, its length several times longer than the diameter of its alveolus; ventral surface of the coxal region of the hypognathum with numerous papillae 9

9 (8) Length of setae *sci* longer than half the distance between their bases; dorsal hysterosomal striae distinctly lobed (= with festoons) (Fig. 69a) ..... *C. papuliphora*

- Length of setae *sci* shorter or equal to half the distance between their bases; dorsal hysterosomal striae smooth (Fig. 69b) ..... *C. gordeevae*

10 (2) Basifemora III with 2 sts 11

- Basifemora III with 3 sts 12

- Basifemora III with 4 sts 30

11 (10) Basifemora IV with 1 sts; cheliceral longitudinal striations present (Fig. 70a) ..... C. *heterostriata*

- Basifemora IV with 0 sts; cheliceral longitudinal striations absent (Fig. 70b) ..... *C. yaylensis*

12 (10) Basifemora IV with 0 sts ..... *C. violaphila*

- Basifemora IV with 1 sts 13
- Basifemora IV with 2 sts ..... *C. brevicrura*
- Basifemora IV with 5 sts ..... *C. meiringi*

13 (12) Median plate present (may be indistinctly defined) (Fig. 71a–e) 14
- Median plate absent (Fig. 71f) 26

14 (13) Telofemoral apophysis uncinated (Fig. 72a) ..... *C. capreolus*
- Telofemoral apophysis present or absent; if present, not uncinated (Fig. 72b, c) 15

15 (14) Telofemoral apophysis truncated (Fig. 72b) ..... *C. carina*
- Telofemoral apophysis not truncated (Fig. 72c–e) 16

16 (15) Line of small sharp spines on palp tibiotarsi present (Fig. 73a) ..... *C. dentata*
- Line of small sharp spines on palp tibiotarsi absent (Fig. 73b) 17

17 (16) Median plate complemented with c_2 (Fig. 71a–d) 18
- Median plate not complemented with c_2 (Fig. 71e) ..... *C. terrula*

18 (17) Median plate indistinctly defined (Fig. 71a) 19
- Median plate distinctly defined (Fig. 71b–d) 20

19 (18) Setae f_1, h_1 smooth ..... *C. romblonensis*

- Setae f_1, h_1 finely setose ..... *C. sordwanaensis*

20 (18) Median shield complemented with c_1, d_1, c_2 (Fig. 71b) ..... *C. sudakensis*

- Median shield complemented with c_1–e_1, c_2 (Fig. 71c, d) 21

21 (20) Coxae IV with 1 sts 22

- Coxae IV with 2 sts 23

22 (21) Broken striae that form cell-like structures on median shield present (Fig. 71c) ..... *C. thailandicus*

- Broken striae that form cell-like structures on median shield absent (Fig. 71d) ..... C. *veracruzana*

23 (21) Setae c_1 longer than all other dorsal setae ..... *C. womersleyi*

- Setae c_1 not longer than all other dorsal setae 24

24 (23) Genua I–IV with 4-2-1-1 solenidia ..... *C. lamberti*

- Genua I–IV with 3-1-1-1 solenidia 25

25 (24) Setae c_1–h_1 approximately equal in length ..... *C. hermanni*

- Setae c_1–e_1 half as long as f_1, h_1 ..... *C. thessalica*

26 (13) Telofemoral apophysis uncinated (Fig. 72a) ..... *C. pantabanganensis*

- Telofemoral apophysis not uncinated (Fig. 72b-e) 27

27 (26) Propodosomal shield striated (Fig. 67c) 28

- Propodosomal shield smooth (Fig. 67d) ..... *C. potchensis*

28 (27) Setae f_1, h_1 smooth (Fig. 68a) 29

- Setae f_1, h_1 spiculate (Fig. 68b) ..... *C. gazella*

29 (28) Palp telofemoral apophysis short and cone-like (Fig. 72c) ..... *C. mageei*

- Palp telofemoral apophysis short and finger-like (Fig. 72d) ..... *C. neogazella*

30 (10) Median plate present (Fig. 71d); basifemora IV with 1 sts ..... *C. luzonica*

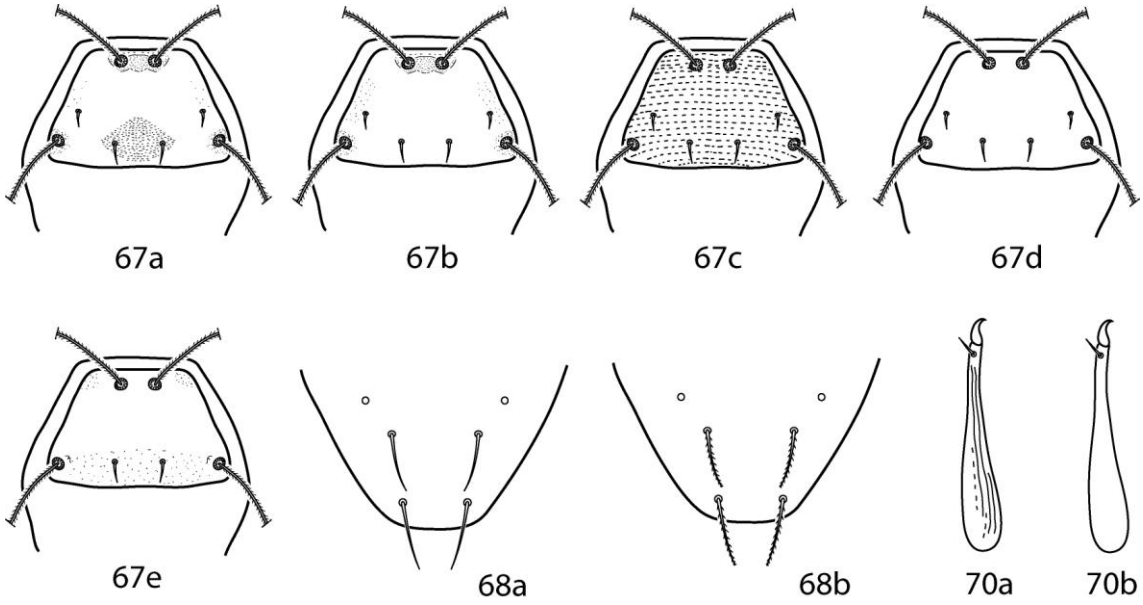
- Median plate absent (Fig. 71f); basifemora IV with 1 or 2 sts 31

31 (30) Basifemora IV with 1 sts ..... *C. cogonae*

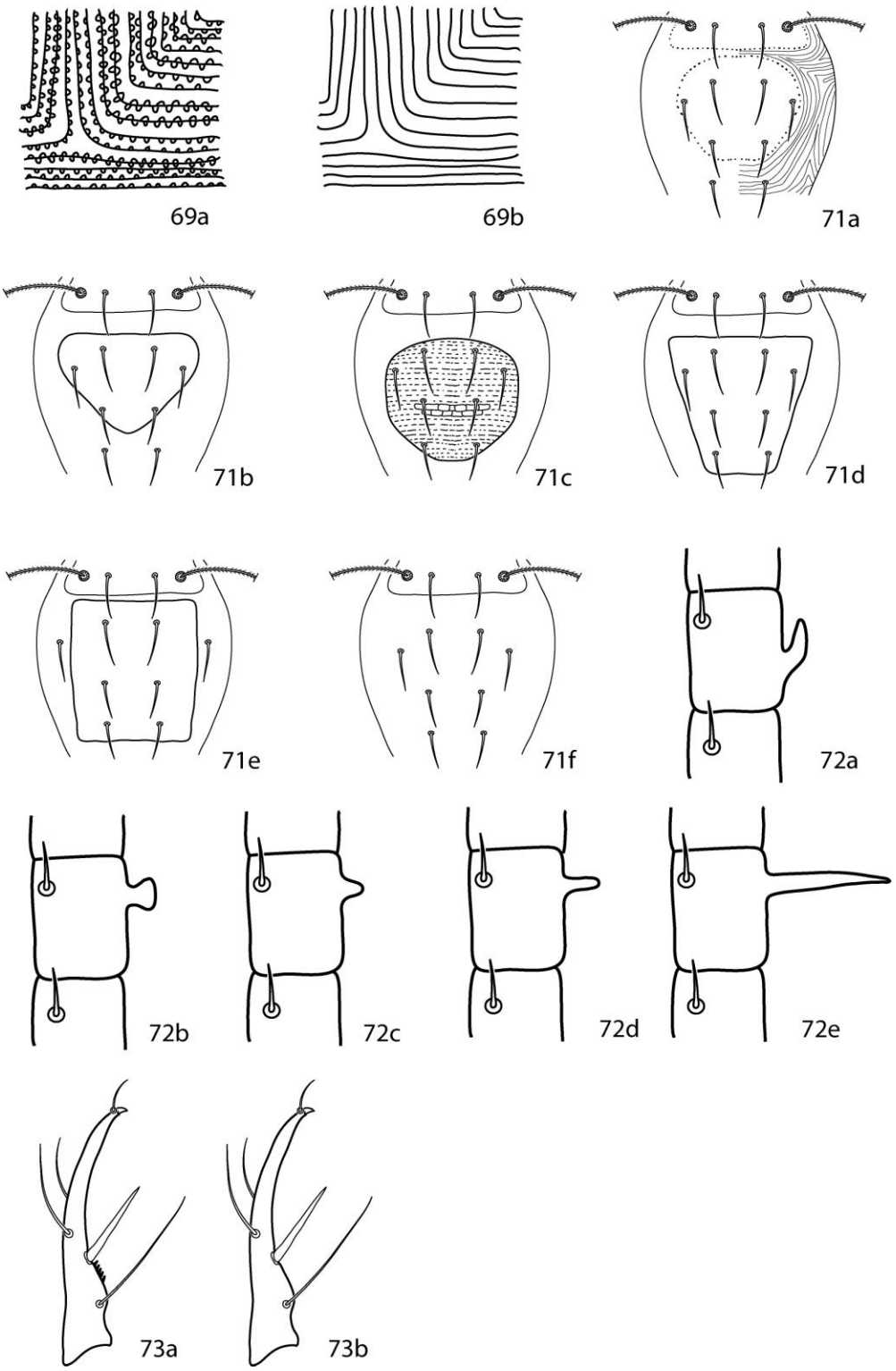
- Basifemora IV with 2 sts ..... *C. doxa*

32 (2) Basifemora III with 4 sts ..... *C. evansi*

- Basifemora III with 6 sts ..... *C. grobleri*

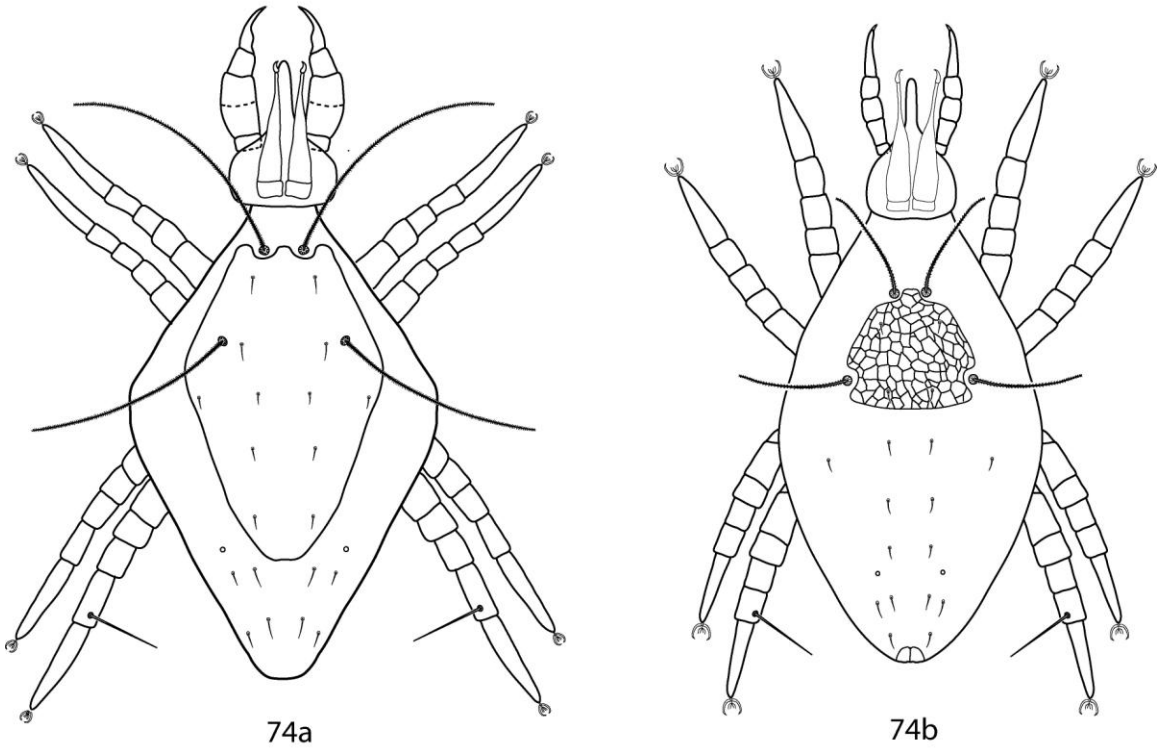


Figures 67, 68, 70. *Cunaxa* key illustrations. 67a–e) Propodosomal shield, dorsal. 68a) Smooth f_1, h_1. 68b.) Spiculate f_1, h_1. 70a, b) Chelicerae. See key for further explaination.



Figures 69, 71–73. *Cunaxa* key illustrations. 69a, b) Integumental striations. 71a–f) Examples of variation in the hysterosomal median plate. 72a–e) Examples of variation in the pedipalpal telofemoral apophysis. 73a, b) Pedipalp tibiotarsus. 73a) Tibiotarsus with small teeth present. 73b) Tibiotarsus with small teeth absent. See key for further explaination.

Coleoscirinae



Figures 74a, b . Examples of generalized Coleoscirines. 74a. *Coleoscirius.* 74b. *Pseudobonzia*.

Historical review. Berlese (1888) described the first Coleoscirinae, *Scirus curtipalpus*, from Argentina. Berlese (1916) then erected *Coleoscirus* for two new species, *C. halacaroides* and *C. corniculatus* (*C. corniculatus* was later synonomised with *C. curtipalpus* by Den Heyer 1979x). Smiley (1975) erected *Pseudocunaxa* and *Pseudobonzia*. *Scutascirus* was erected by Den Heyer (1976) for a South African species, *S. polyscutosus*. Den Heyer (1977a) erected *Neoscirula* for three South African cunaxids. Den Heyer (1978a) synomised *Pseudocunaxa* with *Coleoscirus* and erected Coleoscirinae for the known genera. Tseng (1980) erected *Lapicunaxa* for two species from Taiwan. Smiley (1992) moved *Neoscirula* from Coleoscirinae to Bonzinae, synomised *Lapicunaxa* with *Coleoscirus*, and erected *Neobonzia* in Neobonzinae. Den

Heyer and Castro (2008a) erected *Coleobonzia* for some species previously contained in *Pseudobonzia*. Den Heyer and Castro (2008b) moved *Neoscirula* back to Coleoscirinae. Den Heyer (2011) moved *Neobonzia* to Coleoscirinae, effectively disregarding Neobonzinae, and synomized *Coleobonzia* with *Neobonzia*.

Diagnosis. The palps are five-segmented and reach beyond the subcapitulum by at most the distal half of the tibiotarsi. The basifemora and telofemora are fused but retain a dark line. The tibiotarsi are usually complemented with a tubercle and a dorsodistal solenidion. The palps end in a stout claw. A cheliceral seta may be present or absent near the cheliceral digit. Subcapitulum bears 6 pairs of setae: 2 pairs of adoral setae and 4 pairs of subcapitular setae ($hg_{1–4}$). Setae hg_4 are often the longest.

The dorsal propodosoma is covered in a shield that bears 4 pairs of setae: 2 pairs of simple setae (*ve* and *sci*) and 2 pairs of setose sensilla (*vi* and *sce*). The dorsal hysterosoma may or may not have a median plate; if present this plate may be separate or fused to the propodosomal shield. Plates and shields may be smooth or variously covered with papillae that form reticulations. Up to 8 pairs of setae are present on the dorsal hysterosoma (c_1–f_1, c_2, f_2, h_2); if these setae do not occur on larger plates or shields they may be born on small platelets that are barely larger than the setal socket. Cupule *im* is present, usually laterad or in the proximity of e_1. The unsclerotized integument is striated.

Coxae I–II are fused and may coalesce medially to form a single sternal plate. Each pair of coxae is complemented with 3 pairs of setae; if they form an extensive sternal shield setae normally born on the unsclerotized integument may be located on the

shield. Coxae III–IV are fused; they may be restricted to the trochantral bases or extend posteriorly beyond the genital plates. Each pair of coxae is complemented with 3 pairs of setae; if the plates are extensive they may bear setae normally born on the unsclerotized integument. The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. 1–8 pairs of setae may be present on the integument between coxae III and the genital plates. The anal plates are complemented with 2 pairs of setae ($ps_{1\text{-}2}$). Two pairs of setae (h_2, *pa*) are located on the integument near the anal plates. Cupule *ih* is present in close proximity to h_2.

The legs are shorter than the idiosoma; they are never constricted apically so as to end in lobes. A trichobothria is present on leg tibia IV. Two claws occur on either side of a four-rayed empodium.

Key to adult female Coleoscirinae (modified from Den Heyer & Castro 2008a)

1 Idiosomal plates well-developed and defined; hysterosomal plate present and fused to propodosomal plate (Figs. 75a, b); females and most males with coxae I–II fused medially into a sternal shield (Fig. 76a); apices of some solenidia, especially on tarsi I, swollen 2

\- Idiosomal plates poorly developed and sometimes ill-defined; hysterosomal plate absent (Figs. 75c, d); coxae I–II usually not fused medially and restricted to trochantral bases (Figs. 76b, c); solenidia on tarsi I & II usually cylindrical 3

2 (1) Idiosoma with 15 to 19 plates, including 4 pairs of dorsolateral plates (Fig. 75a); 2 dorsal plates; palp tibiotarsal ventral tubercle bifurcate (Fig. 77a) ..... *Scutascirus*

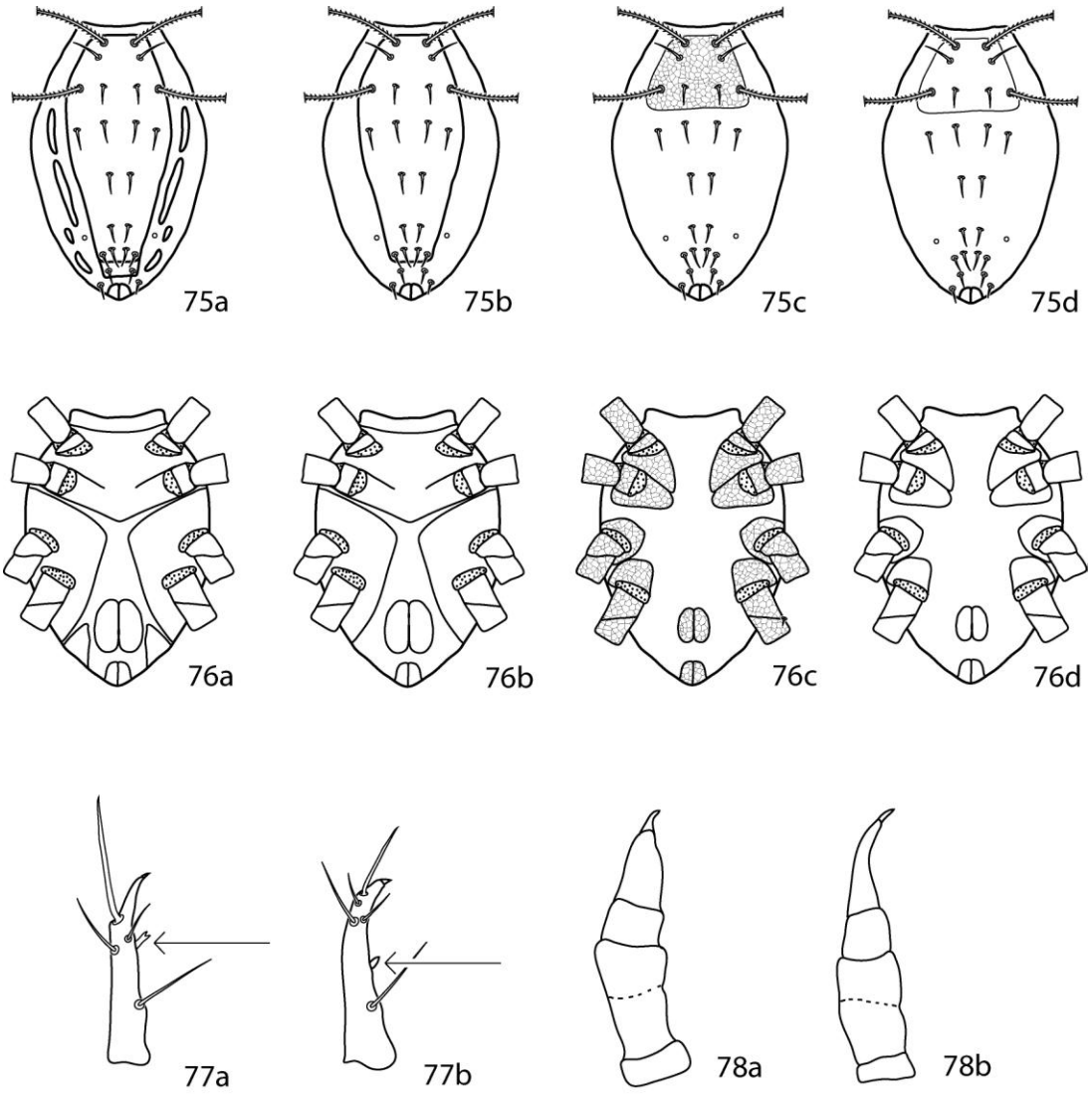
- Idiosomal with no more than 8 plates; dorsolateral plates absent (Fig. 75b); females with only one dorsal plate but males with up to 3 dorsal plates; palp tibiotarsal ventral tubercle not bifurcate, plain (Fig. 77b) ..... *Coleoscirus*

3 (1) Palp tibiotarsus short and nearly cone-like (Fig. 78a); cheliceral trochanters broad; ambulacral claws smooth ..... *Neoscirula*

- Palp tibiotarsus long and usually narrow and S-shaped (Fig. 78b); cheliceral trochanters narrow; ambulacral claws rippled 4

4 (3) Subcuticular reticulated pattern present on propodosomal, coxal, and genital plates: usually very conspicuous, even proximal leg segments may possess such pattern (Figs. 75c, 76b) ..... *Pseudobonzia*

- Subcuticular reticulated pattern absent or restricted to the edge of coxal plates (Figs. 75d, 76c) ..... *Neobonzia*



Figures 75–78. Cunaxoidinae key illustrations. 75a–d) Idiosoma, dorsal. Position of setae will vary between species. 76a–d) Idiosoma, ventral. 75a, 76a) Generalized *Scutascirus*. Presence, position, and extent of lateral plates will vary between species. 75b, 76b) Generalized *Coleoscirus*. 75c, 76c) Generalized *Pseudobonzia*. 75d, 76d) Generalized *Neobonzia*. 77a, b) Pedipalpal tibiotarsus. 77a) *Scutascirus*, arrow points to bifurcate tubercle. 77b) *Coleoscirus*, arrow points to plan tubercle. 78a, b) Pedipalps. 78a. *Neoscirula*, showing short, cone-like tibiotarsus. 78b) *Pseudobonzia* and *Neobonzia*, showing elongate, s-shaped palp.

Coleoscirus

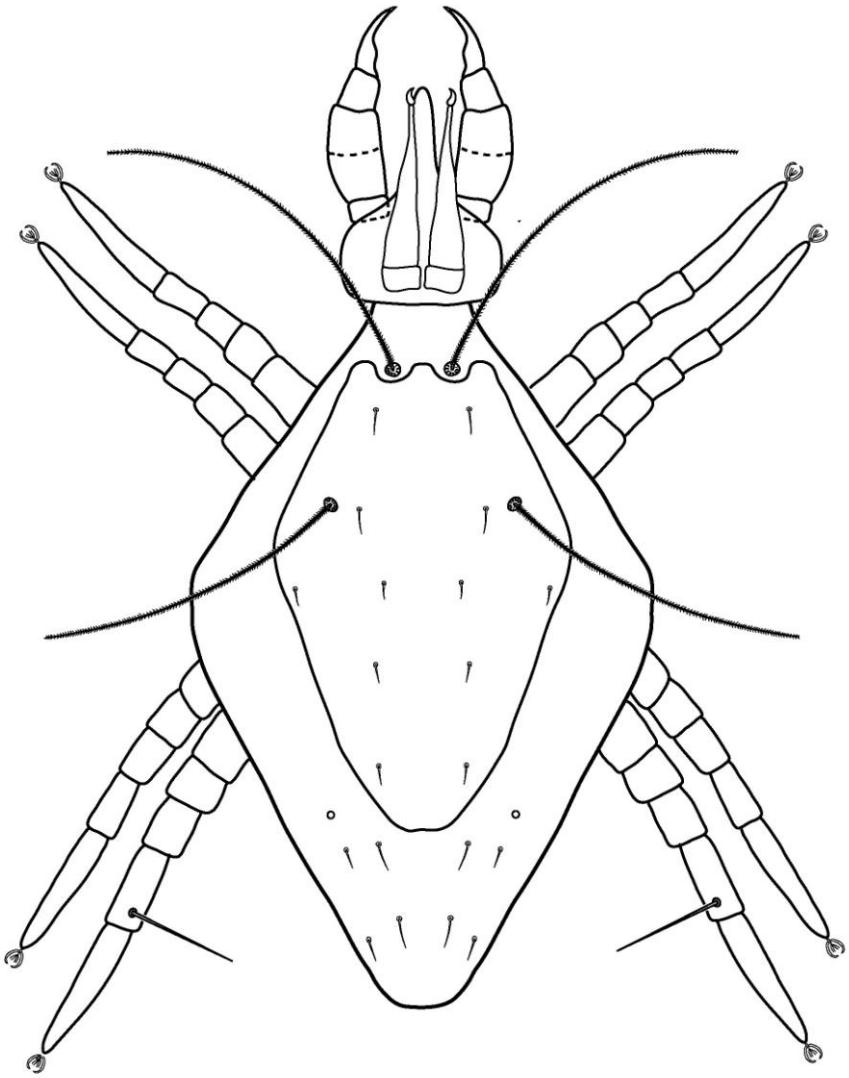


Figure 79. Generalized *Coleoscirus*.

Historical Review. Berlese (1916) erected *Coleoscirus* to accommodate two species, the type-species *C. halacaroides* and *C. corniculatus*. He had previously described two other species that would be assigned to the genus, *Scirus curtipalpus* (Berlese, 1888) and *Scirus brevicornis* (Berlese 1905), but failed to recognize they belonged to *Coleoscirus*. Ewing (1917) described *Scirus simplex* from refuse hog hair in

Illinois, USA. Thor and Willmann (1941) transferred *S. curtipalpus*, *S. brevicornis*, and *S. simplex* to *Cunaxa* and provided redescriptions and illustrations. Baker and Hoffmann (1948) described *Cunaxa mexicana*, as well as redescribing and illustrating *Cunaxa simplex*, *Coleoscirus curtipalpus*, and *Coleoscirus brevicornis*. Zaher *et al.* (1975b) reported *C. simplex* from Egypt. Smiley (1975) provided an English translation of Berlese's (1916) description of *Coleoscirus* but failed to include the genus in his key to genera; he also erected *Pseudocunaxa* for *Cunaxa simplex* and closely related species. Den Heyer (1978a) erected Coleoscirinae, designating *Coleoscirus* as the type genus and described *Coleoscirus magdalenae* and *C. tuberculatus*; he also synonymized *Pseudocunaxa* with *Coleoscirus* and *Coleoscirus corniculatus* with *C. curtipalpus*. Shiba (1978) described *Cunaxa mizunoi*. Tseng (1980) erected *Lapicunaxa horidula* and *L. monospinosus*. Chaudhri (1980) described *Pseudocunaxa baptus*. Den Heyer (1980b) described *Coleoscirus coatesi*, *C. breslauensis*, and *C. buartsus*, and synonymized *C magdalenae* with *C. simplex.* Sepasgosarian (1984) included *Coleoscirus* with *Scutascirus* in a newly erected tribe, Coleoscirini, within Coleoscirinae. Smiley (1992) synonymized *Lapicunaxa* with *Coleoscirus* and transferred *Cunaxa mizunoi* and *Pseudocunaxa baptus* to *Coleoscirus*; he also synonymized *Cunaxa mexicanus* with *Coleoscirus curtipalpus* and provided a key to known world species. *Coleoscirus carnus* and *C. disparis* were described by Muhammad and Chaudhri (1992a). Inayatullah and Shahid (1993) described *Pseudocunaxa carex, P. mardi,* and *P. kayfayati,* apparently unaware or ignoring that Den Heyer (1980) had synonymized *Pseudocunaxa* with *Coleoscirus* thirteen years earlier. Bu & Li (1987c) reported *C. buartsus* from China. Corpuz-Raros (1996d) described six species of *Coleoscirus*, *C. intermedius, C. barrioni,*

C. dayamilocus, *C. bakeri*, *C. leytensis*, and *C. philippinensis*. Hu (1997) reported *C. monospinosus*, *C. horidula*, and *C. buartsus* from China. Bashir, Afzal, and Khan (2006) reaffirmed Den Heyer's (1980) synonimization of *Pseudocunaxa* and *Coleoscirus* by treating *P. carex*, *P. maradi* and *P. kayfayati* as *Coleoscirus*; they also mention a second paper by Muhammad and Chaudhri (1992b) that described two additional species of *Coleoscirus* from Pakistan that I have been unable to obtain. Lin *et al.* (2003) reported *C. simplex* from China. *Coleoscirus raviensis* and *C. tobaensis* were described by Bashir, Afzal, and Khan (2008).

Diagnosis. The palps are 5-segmented; the basifemora and telofemora are fused but retain a dark line that indicates the presence of the joint. The palps extend beyond the subcapitulum by at most the apical half of the tibiotarsi. The palp tibiotarsal tubercle is plain, not bifurcate as in *Scutascirus*. Subcapitulum bears 6 pairs of setae: 2 pairs of adoral setae and 4 pairs of subcapitular setae ($hg_{1–4}$).

The female idiosoma is heavily sclerotized and the plates are well demarcated. A single dorsal shield is present; it may range in size from terminating anteriorly to cupule *im* to being holodorsal. No papillated line or other marking indicates the separation of the propodosomal and hysterosomal shields. Two pairs of setae and two pairs of setose sensillae are present on the propodosomal. Setae c_1–h_1, c_2, and f_2 and cupule *im* are present dorsally. Dorsolateral plates, which are present in *Scutascirus*, are absent.

Coxae I–II are fused and coalesce medially to form a sternal shield which often has a prominent apex caudally. The sternal plate is complemented with 5-7 pairs of setae. Coxae III–IV are fused and may extend laterally and caudally past the genital

plates. The genital plates each bear 4 setae; 2 pairs of genital papillae are visible underneath the plates. The anal plates bear two pairs of setae (ps_1 and ps_2). Seta h_2 are located ventrally near the anal plates. Cupule *ih* is present in close proximity to h_2.

The legs are shorter than the idiosoma; they are never constricted apically so as to end in lobes. The apices of solenidia, especially on tarsi I, may be swollen. A trichobothria is present on leg tibia IV. Two claws occur on either side of a four-rayed empodium.

Males are similar except up to three shields or plates may occur on the dorsal idiosoma (that is the propodosomal shield may not be fused to a hysterosomal plate and up to two hysterosomal plates may be present) and coxae I–IV may be fused into a holoventral shield.

Key to adult female *Coleoscirus*.

Coleoscirus brevicornis (Berlese) has been excluded from the key as the original publication (Berlese, 1905) and subsequent publication detailing the species (Thor & Willmann 1941) are in Italian and German and the accompanying illustrations provide too little detail. Den Heyer (1978a) is the last author to mention the species, but only indicates that it belongs to *Coleoscirus*.

Coleoscirus carex, C. kayfayati, and *C. mardi* have been excluded from the key as the authors did not provide enough information in the original descriptions to include them.

1 Basifemora I with 4 setae 2

- Basifemora I with 5 setae 4

2 (1) Basifemora II-IV setal formula 5-4-2 3

- Basifemora II-IV setal formula 6-4-2 ..... *C. trudus*

3 (2) Telofemora I-IV setal formula 4-4-4-3 ..... *C. baptus*

- Telofemora I-IV setal formula 4-5-4-3 ..... *C. raviensis*

4 (1) Basifemora II with 5 setae 5

- Basifemora II with 6 setae 12

5 (4) Basifemora III with 4 setae 6

- Basifemora III with 5 setae 8

6 (5) Basifemora IV with 2 setae 7

- Basifemora IV with 3 setae ..... *C. halacaroides*

7 (6) Horizontal reticulations on dorsal shield present (Fig. 80) ..... *C. horidula*

- Horizontal reticulations on dorsal shield absent ..... *C. monospinosus*

8 (5) Basifemora I-IV setal formula 4-5-3-3 ..... *C. curtipalpis*

- Basifemora I-IV setal formula 9

9 (8) Sternal shield bilobed posteriorly ..... *C. barrioni*

- Sternal shield not bilobed posteriorly 10

10 (9) Extensive reticulations on gnathasoma present (Fig. 81) ..... *C. bakeri*

- Extensive reticulations on gnathasoma absent 11

11 (10) Hysterosomal shield present, complemented with c_1-f_1, c_2, f_2 ..... *C. philippinensis*

- Hysterosomal shield absent ..... *C. intermedius*

12 (4) Basifemora III with 4 setae 13

- Basifemora III with 5 setae 17

- Basifemora III with 6 setae 20

13 (12) Telofemora I-IV setal formula 4-4-4-3 ..... *C. simplex*

- Telofemora I-IV setal formula 5-5-4-3 14

14 (13) Setae f_1, f_2 born on soft integument 15

- Setae f_1, f_2 born on dorsal shield ..... *C. tobaensis*

15 (14) Sternal plate rounded posteriomedially (Fig. 82a) ..... *C. tuberculatus*

- Sternal plate truncated posteriomedially (Fig. 82b) 16

16(15) Light reticulation on dorsal shield present; dorsal shield evenly sclerotized (Fig. 83a) ..... *C. buartsus*

- Light reticulation on dorsal shield absent; dorsal shield unevenly sclerotized (Fig. 83b) ..... *C. coatesi*

17(12) Sternal shield indented posteriomedially (Fig. 84a) ..... *C. mizunoi*

- Sternal shield not indented posteriomedially (Fig. 84b) 18

18 (17) Setae f_2 born on soft integument ..... *C. disparis*

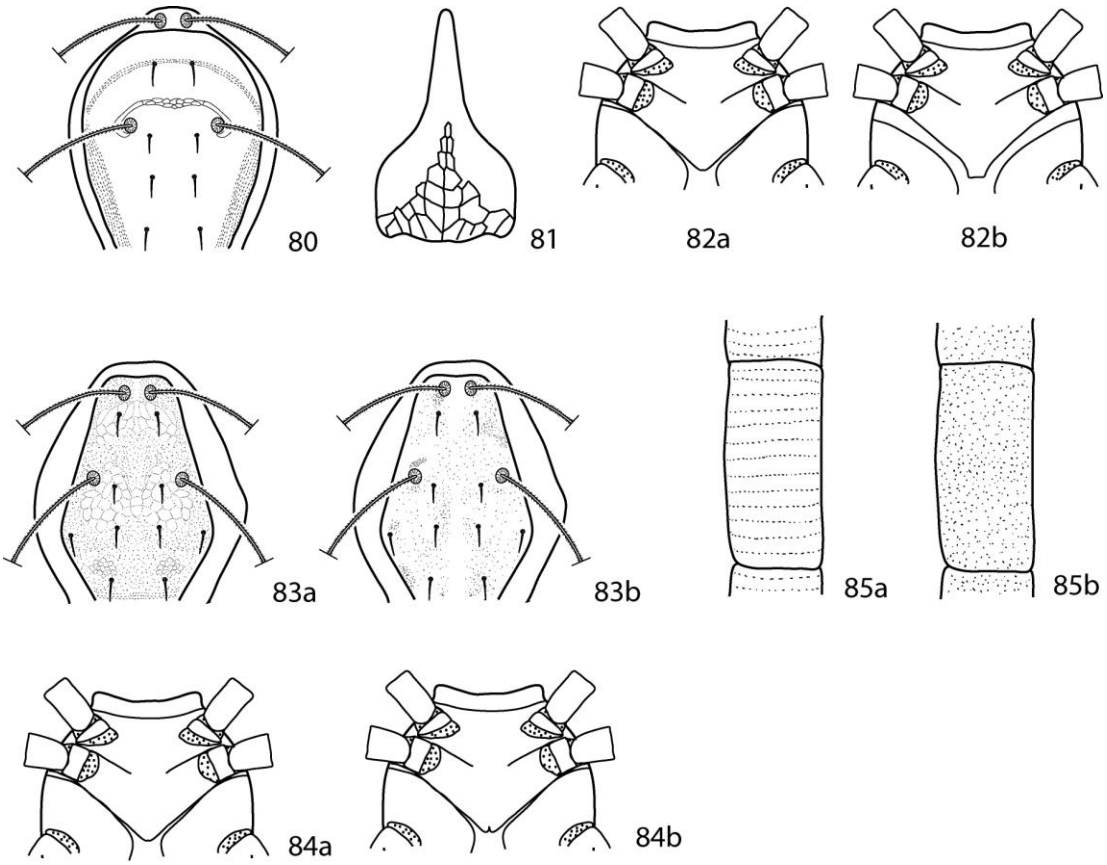
- Setae f_2 born on dorsal shield 19

19 (18) Integumental dots on legs I-IV forming rows (Fig. 85a) ..... *C. carnus*

- Integumental dots on legs I-IV forming random (Fig. 85b) ..... *C. breslauensis*

20 (12) Basifemora IV with 2 setae ..... *C. leytensis*

- Basifemora IV with 3 setae ..... *C. dayamilocus*



Figures 80–85. *Coleoscirus* key illustrations. 80, 83a, 83b, 84a, 84b) Idiosoma, dorsal. 81) Gnathasoma. 82a, 82b, 84a, 84b) Idiosoma, ventral. 85a, 85b) Leg segments. See key for further explainations.

Neoscirula

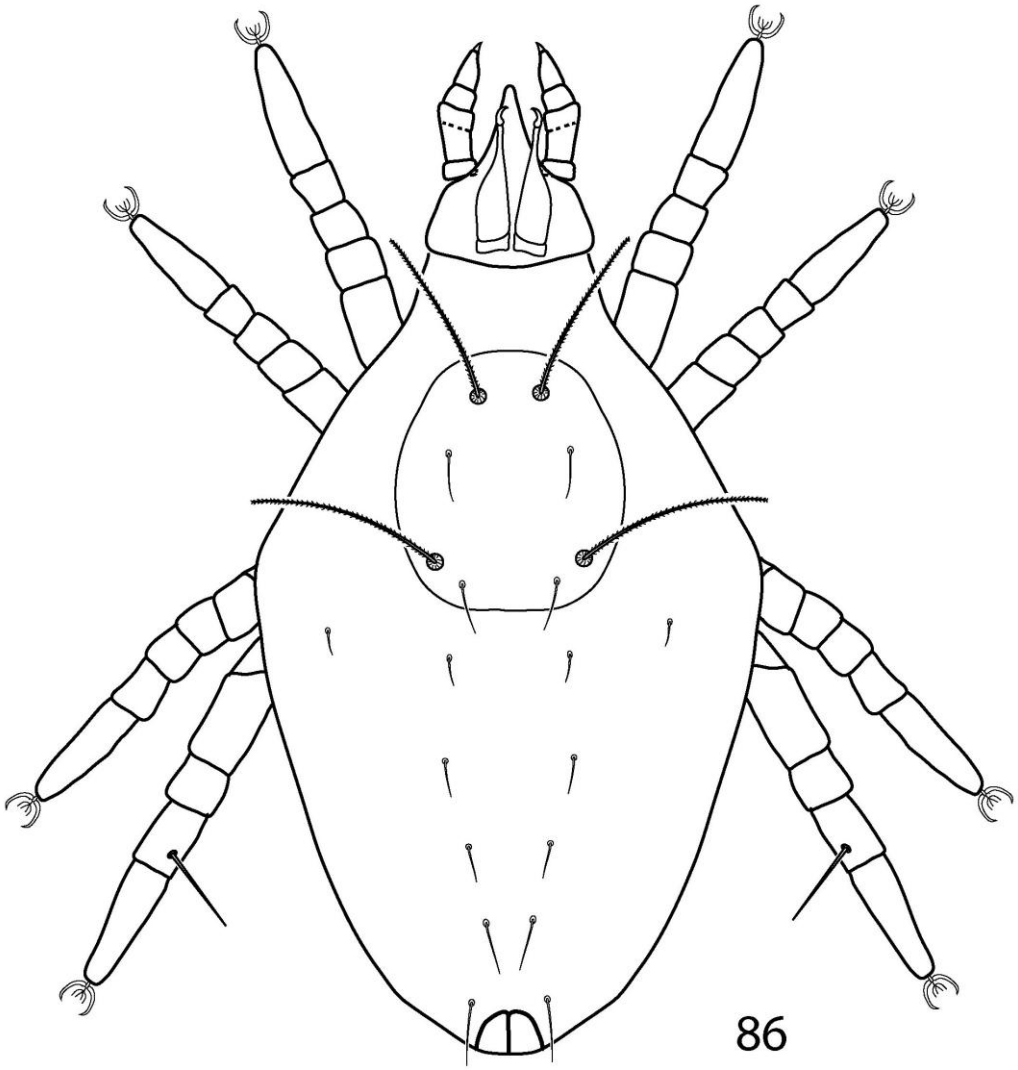


Figure 86. Generalized *Neoscirula*.

Historical Review. Den Heyer (1977a) erected *Neoscirula* for three African cunaxids, *N. theroni*, *N. natalensis*, and *N. sevidi*. Shiba (1978) described the first *Neoscirula* outside of Africa, *Coleoscirus ogawai*. Den Heyer (1978a) erected the subfamily Coleoscirinae and assigned *Neoscirula* to it. Den Heyer (1980b) described another African *Neoscirula*, *N. delareyi*. *N. vitulus* was described from Ukraine by Barilo (1991). Smiley (1992) transferred *Neoscirula* from Coleoscirinae to Bonzinae as he

thought setae g_1 were geniculate; he also described *N. luxtoni, N. proctorae, N. kenworthyi*, moved *N. ogawai* from *Coleoscirus*, and provided a key to known world species. *N. abraensis, N. aspirasi, N. imperata, N. makilingica, N. puntiglupa* were described by Corpuz-Raros (1996a) from the Philippines. Lin & Zhang (1998) described *N. miaofengensis*, and *N. bidens.* *N. saitoi* was described by Lin & Zhang (2002). Corpuz-Raros (2007) described two more Philippine *Neoscirula, N. laboensis, N. taclobanensis*. *N. aliciae, N. baloghi, N. hoffmannae* were described from Mexico by Mejía-Recamier & Palacios-Vargas (2007). Skvarla, Fisher, and Dowling (2011) described *N. reticulata*.

Diagnosis. The palps are five-segmented and end in a strong claw, which is complemented with a tooth in some species; they extend to the tip of the hypognathum or slightly beyond. The basifemur and telofemur are fused but retain the suture; each has a dorsolateral simple or spine-like seta. The palp tibiotarsus is short and cone-like. Four pairs of setae are present on the hypognathum ($hg_{1–4}$). Seta hg_1 is longest and in some species bent at 90 degrees, though it is not geniculate as in Bonzinae. Adoral setae present or absent. The chelicerae usually bear a seta near the digit, though it may be absent.

The propodosomal shield is weakly sclerotized and ill-defined. It is granulated or papillated; some species possess subcuticular reticulations. Coxal plates I–II may be separate or fused medially into a single sternal shield. Coxal plates III–IV contiguous on either side, restricted to area around trochantral bases. Dorsal cupules *im* present laterad to e_1; ventral cupules *ih* present near h_2, anal plates.

All legs are shorter than the body. The tarsi are never constricted apically so as to end in lobes. The apices of solenidia are cylindrical, not swollen as in *Coleoscirus* and *Scutascirus*. A trichobothria is present on leg tibia IV. Ambulacral claws are smooth and occur on either side of a 4-rayed empodium.

Key to adult female *Neoscirula.*

1 Coxal plates I–II fused to form a sternal shield 2

\- Coxal plates I–II widely separated 6

2 (1) Cheliceral seta present 3

\- Cheliceral seta absent 5

3 (2) Palp basifemoral dorsal seta spine-like (Fig. 87a); Luzon Is., Philippines ..... *N. makilingica*

\- Palp basifemoral dorsal seta simple (Fig. 87b) 4

4 (3) Propodosomal shield with polygonal subcuticular sculpturing (Fig. 88a); posteromedial portion of sternal shield V-shaped, without polygonal subcuticular sculpturing (Fig. 89a); 6 pairs of setae between coxae III–IV (excluding genital setae); Luzon Is., Philippines ..... *N. aspirasi*

\- Propodosomal shield without polygonal subcuticular sculpturing (Fig.88b); posteromedial portion of sternal shield rounded, with polygonal subcuticular

sculpturing (Fig. 89b.); 4 pairs of setae between coxae III–IV (excluding genital setae); Malaysia; Philippines ..... *N. ogawai*

5 (2) Chelicerae with dorsomedial reticulations (Fig. 90a); genua II with 5 setae and 2 solenidia; genua IV with 5 setae and 1 solenidion; Interior Highlands, USA ..... *N. reticulata*

- Chelicerae without dorsomedial reticulations (Fig. 90b); genua II with 4 setae and 2 solenidia; genua IV with 4 setae and 1 solenidion; Jalisco, Mexico ..... *N. baloghi*

6 (1) Palp genua with hook-like apophysis (Fig. 91a); South Africa ..... *N. natalensis*

- Palp genua without hook-like apophysis (Fig. 91b) 7

7 (6) Palp tibiotarsal claw with a tooth, giving bifid appearance (Fig. 92a) 8

- Palp tibiotarsal claw without a tooth (Fig. 92b) 13

8 (7) Cheliceral seta present; palpal tibiotarsi with tubercle (Fig. 93a) 9

- Cheliceral seta absent; palp tibiotarsi without tubercle (Fig. 93b); São Paulo, Brazil ..... *N. oliveirai*

9 (8) Basifemora II with 4 setae; telofemora I–II 4-4 setae; hypognathum with ventro-apical shield-like process (Fig. 94a); New Zealand; Philippines ..... *N. luxtoni*

- Basifemora II with 5 or 6 setae; telofemora I–II 5-5 setae; hypognathum without ventro-apical shield-like process (Fig. 94b) 10

10 (9) Basifemora II with 5 setae 11

- Basifemora II with 6 setae 12

11 (10) Basifemora I with 4 setae; telofemora III with 4 setae; 7 pairs of setae between coxae III–IV (excluding genital setae); Jalisco, Mexico ..... *N. aliciae*

- Basifemora I with 5 setae; telofemora III with 3 setae; 5 pairs of setae between coxae III–IV (excluding genital setae); Luzon Is., Philippines ..... *N. laboensis*

12 (10) Chelicerae tapering to digit gradually (Fig. 95a); Fujian, China ..... *N. bidens*

- Chelicerae tapering to digit suddenly (Fig. 95b); São Paulo, Brazil *N. flechtmanni*

13 (7) Palp basifemoral dorsal seta spine-like (Fig. 87a) 14

- Palp basifemoral dorsal seta simple (Fig. 87b) 18

14 (13) Telofemora I–II with 4-4 setae; New Zealand ..... *N. proctorae*

- Telofemora I–II with 5-5 setae 15

15 (14) Propodosomal shield with polygonal subcuticular sculpturing (Fig. 96a); Fujian, China ..... *N. saitoi*

- Propodosomal shield without polygonal subcuticular sculpturing (Fig. 96b) 16

16 (15) Cheliceral seta short, less than half the length of movable digit; South Africa ..... *N. sevidi*

- Cheliceral seta long, nearly as long or longer than movable digit 17

17 (16) Chelicerae basally narrow, 5–6 times longer than wide; Jalisco, Mexico ..... *N. hoffmannae*

- Chelicera basally broad, 2–3 times longer than wide; São Paulo, Brazil ..... *N. queirozi*

18 (13) Coxal plates I–II with polygonal subcuticular sculpturing (as in Fig. 89a) 19

- Coxal plates I–II without polygonal subcuticular sculpturing (as in Fig. 89b) ... 23

19 (18) Propodosomal shield with polygonal subcuticular sculpturing (Fig. 88a) 20

- Propodosomal shield without polygonal subcuticular sculpturing (Fig. 88b) 21

20 (19) Basifemora II with 4 setae; telofemora I–II 4-4 setae; Maryland, USA ..... *N. kenworthyi*

- Basifemora II with 5 setae; telofemora I–II with 5-5 setae; Leyte Is., Philippines ... *N. taclobanensis*

21 (19) Hypognathal setae hg_1 more than two times as long as setae $hg_{2–4}$; coxae II with 4 setae; Fujian, China ..... *N. miaofengensis*

- Hypognathal setae hg_1 no more than two times as long as setae $hg_{2–4}$; coxae II with 3 setae 22

22 (21) Chelicerae basally narrow, less than three times the width of the distal end; hypognathum narrow, nearly twice as long as wide; Uzbekistan ..... *N. vitulus*

- Chelicerae basally broad, four times the width of the distal end; hypognathum wide, nearly as wide as long; South Africa ..... *N. delareyi*

23 (18) Propodosomal shield with polygonal subcuticular sculpturing 24

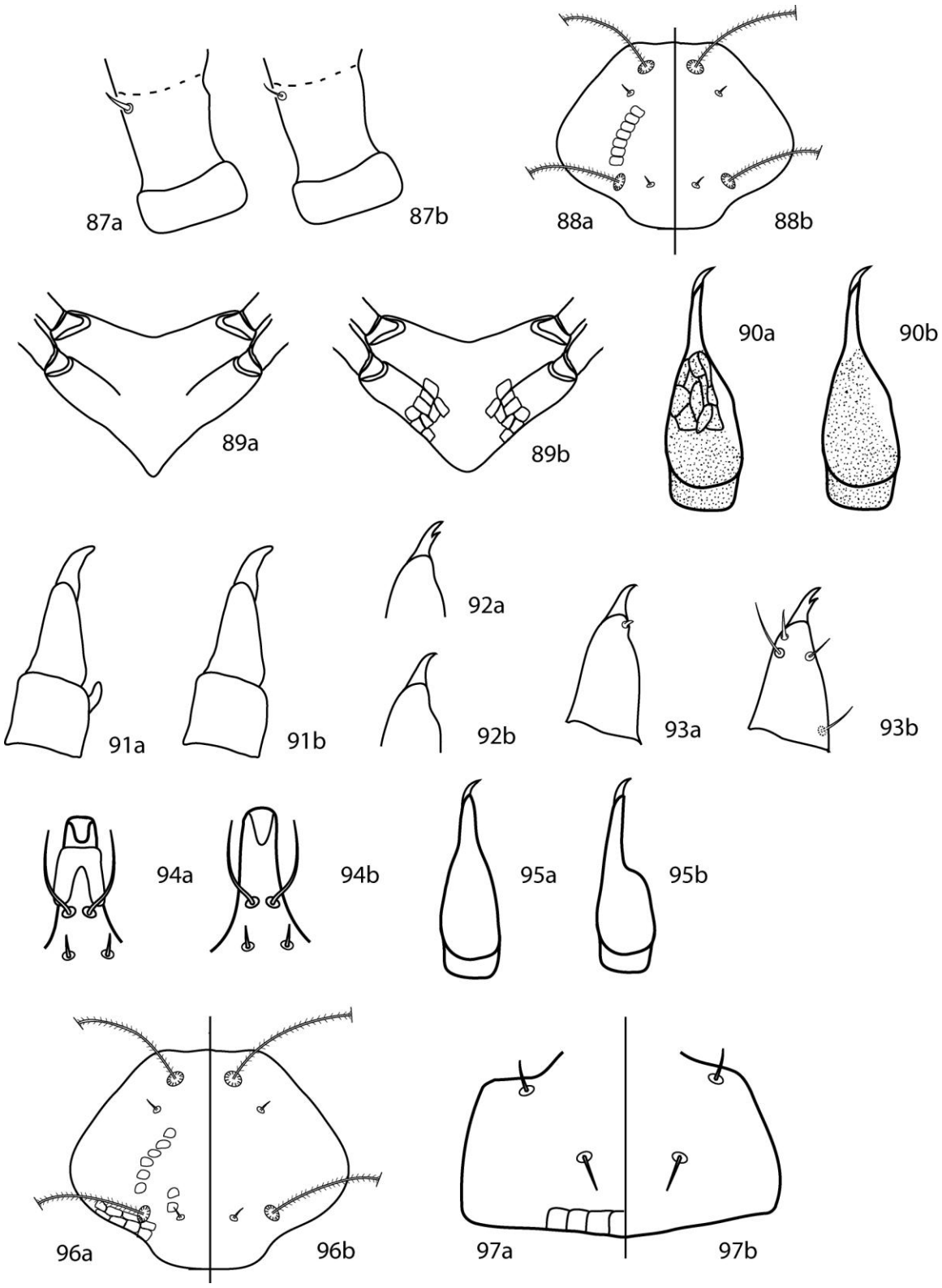
- Propodosomal shield without polygonal subcuticular sculpturing; Luzon Is., Philippines ..... *N. imperata*

24 (23) Subcapitulum with row of basal polygonal subcuticular sculpturing (Fig. 97a); ventrally with 7 pairs of simple setae between coxae III–IV 25

- Subcapitulum without row of basal polygonal subcuticular sculpturing (Fig. 97b); ventrally with 6 pairs of simple setae between coxae III–IV; Luzon Is., Philippines ..... *N. abraensis*

25 (24) Basifemora II with 4 setae; telofemora I–II with 4-4 setae; Western Transvaal, South Africa ..... *N. theroni*

- Basifemora II with 5 setae; telofemora I–II with 5-5 setae; Luzon Is., Philippines ..... *N. puntiglupa*



Figures 87–97. *Neoscirula* key illustrations. See key for explanations.

Pseudobonzia

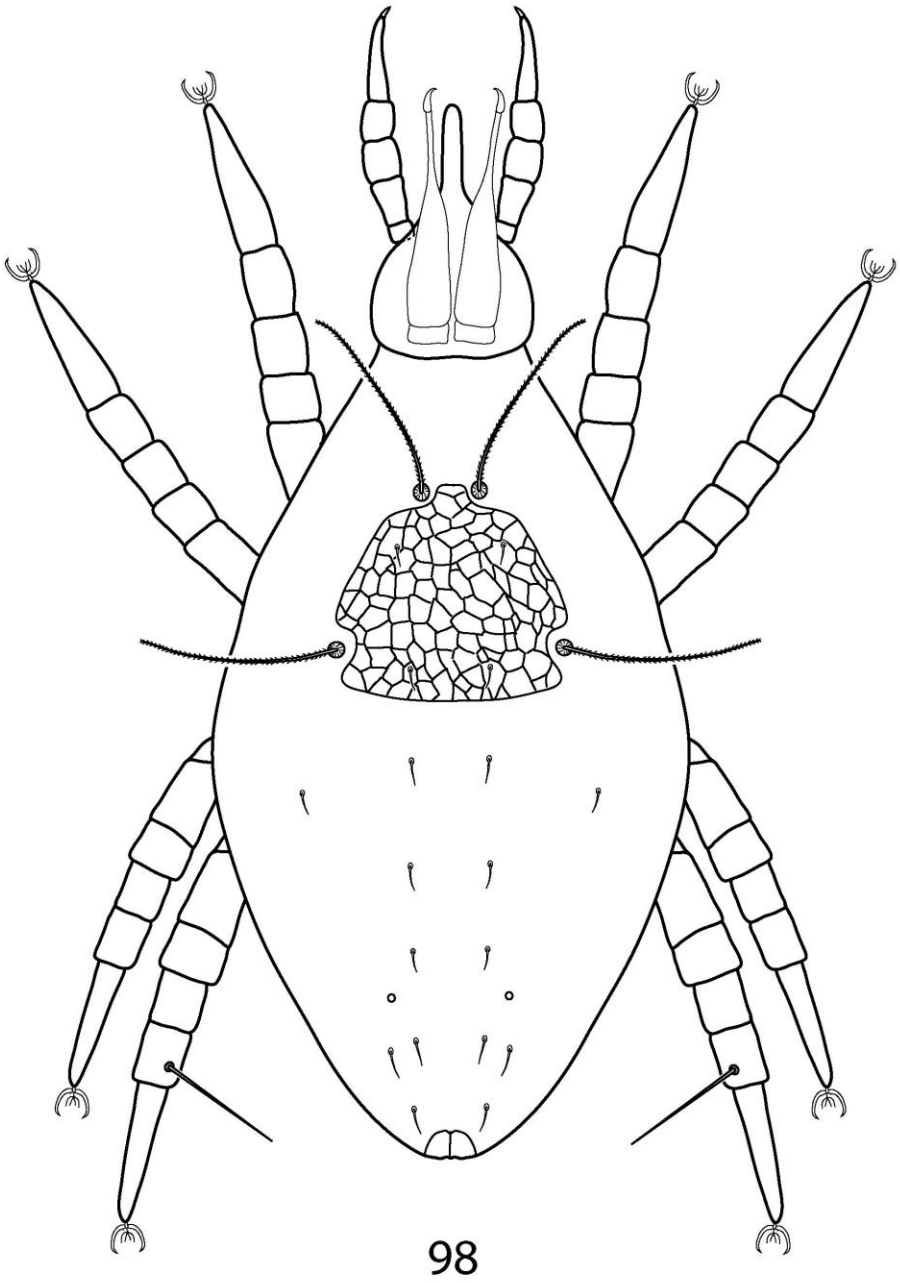


Figure 98. Generalized *Pseudobonzia*.

Historical Review. Heryford (1965) described the first *Pseudobonzia*, *Cunaxa reticulata*. Smiley (1975) erected the genus *Pseudobonzia*, with *C. reticulata* as the type species. Den Heyer (1977c) redescribed the genus and described *P. neoreticulata*.

Smiley (1992) described *P. delfinadobakerae, P. landwehri*, and *P yini;* he also provided a key to known world species. Fuangarown and Lekprayoon (2004) described *P. tangkansingae*. Den Heyer and Castro (2008a) split *Coleobonzia* from *Pseudobonzia*.

Diagnosis. The palps are 5-segmented and reach beyond the subcapitulum by at most the distal half of the last segment. Simple or spine-like setae are present on the basi- and telofemora. The palp tibiotarsi are long and S-shaped (as opposed to short and cylindrical as in *Neoscirula*). Four pairs of setae ($hg_{1–4}$) are present on the subcapitulum. 2 pairs of adoral setae are present. A cheliceral seta is usually present near the digit. An extensive reticulated pattern is present on the gnathosoma.

The female idiosomal plates are lightly sclerotized and may not be well defined or demarcated. The propodosomal plate bears 2 pairs of setae (*ve* and *sci*) and 2 pairs of setose sensillae (*vi* and *sce*). An extensive reticulated pattern is present. A hysterosomal plate is absent. Setae c_1–h_1 are present; setae c_2, f_2, and h_2 may be present or absent. Cupules *im* are present laterad and caudally of e_1. The integument is striated.

The female coxal plates are restricted to the trochantral bases. Coxae I–II are fused. Coxae III–IV are also fused. All coxae are lightly sclerotized and may be ill-defined. An extensive reticulated pattern is on the coxae. I–IV usually have the simple setal formula 3-3-3-3. The genital plates each bear 3–4 setae; 2 pairs of genital papillae are visible underneath the plates. 2 pairs of setae ($ps_{1–2}$) occur on the anal plates and 1 pair of setae (*pa*) occurs on the integument near the anal plates. Cupules *ih* are present ventrally near the anal plates.

The reticulated pattern present on the coxae may be present on the basal leg podomeres. The tarsi are never constricted apically so as to end in lobes. The apices of solenidia are cylindrical, not swollen as in *Coleoscirus* and *Scutascirus*. A trichobothria is present on leg tibia IV. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Pseudobonzia* (modified from Den Heyer and Castro 2008a)

1 Palp basifemora and telofemora with similar setae, either spine-like or simple (Fig. 99a, b); propodosomal shield conspicuously reticulated 2

\- Palp basifemora with simple seta, palp telofemora with spine-like seta (Fig. 99c); propodosomal shield not conspicuously reticulated ..... *P. delfinadobakerae*

2 (1) Palp basifemora and telofemora with simple setae (Fig. 99a); setae f_2 present or absent 3

\- Palp basifemora and telofemora with spine-like setae (Fig. 99b); setae f_2 present ..... *P. yini*

3 (2) Setae f_2 present 4

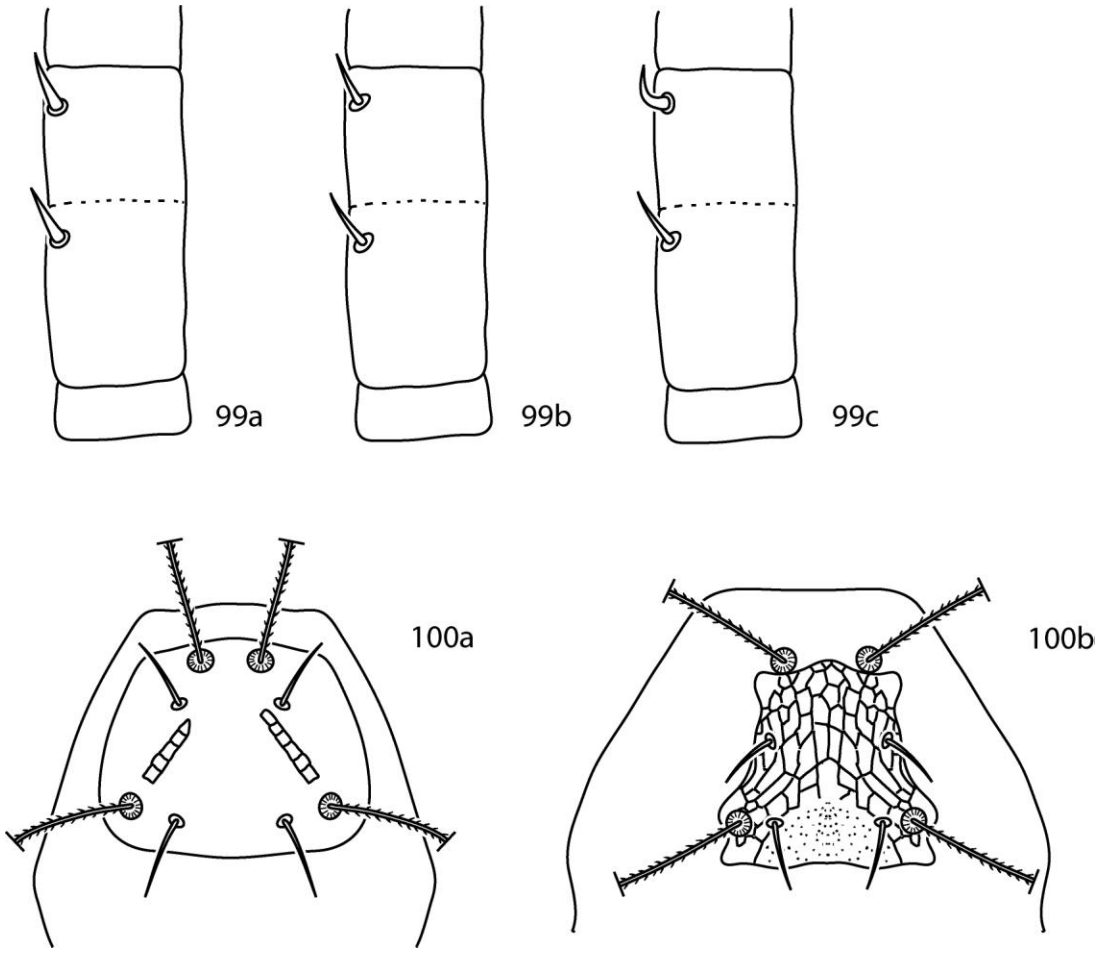
\- Setae f_2 absent 5

4 (3) Propodosomal shield convex posteromedially (Fig. 100a) ..... *P. neoreticulata*

\- Propodosomal shield not convex posteromedially (Fig. 100b) ..... *P. landwehri*

5 (3) Proximal leg podomeres reticulated ..... *P. clathratus*

\- Proximal leg podomeres not reticulated ..... *P. reticulata*



Figures 99–100. *Pseudobonzia* key illustrations. 99a–99c) Pedipalp basifemora and telofemora. 99a) Spine-like setae on both segments. 99b) Simple setae on both segments. 99c) Simple seta on basifemur, spine-like seta on telofemora. 100a, b) Idiosoma, dorsal. 100a) Propodosomal plate convex posteriomedially. 100b) Propodosomal plate not convex posteriomedially.

Neobonzia

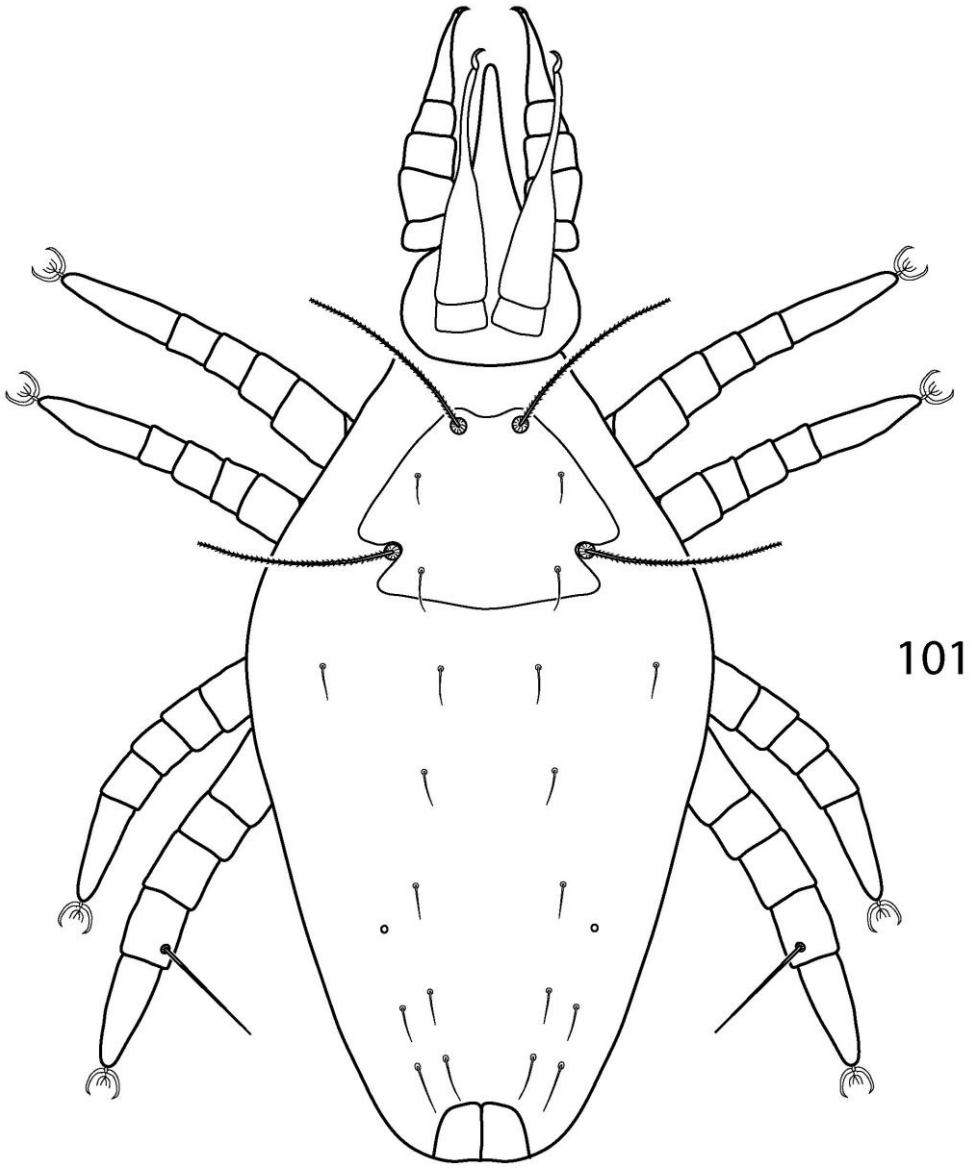


Figure 101. Generalized *Neobonzia*.

Historical Review. Berlese (1910) described the first species of *Neobonzia*, *Scirus parvirostris*. Thor and Willmann (1941) moved *S. parvirostris* to *Cunaxa*. Baker and Hoffmann (1948) described *Cunaxa snowi*. Heryford (1965) described *Cunaxa reticulata*. Smiley (1975) erected the genus *Pseudobonzia*, with *C. reticulata* as the type

species. Den Heyer (1977c) redescribed *Pseudobonzia*, moved *C. parvirostris* to *Pseudobonzia*, and described six new species from South Africa: *P. argillae, P. nona, P. lootsi, P. themedae, P. saaymani,* and *P. neoreticulata*. *Pseudobonzia parilis* was described by Chaudhri (1977). Den Heyer (1980b) described *P. smileyi* and transferred *C. snowi* to *Pseudobonzia*. Chaudhri (1980) described *P. numida*. Luxton (1982) described *P. breviscuta* from New Zealand peat moss. Liang (1983) reported *P. themedae* from China. *Pseudobonzia shanghaiensis* was described by Liang (1984). Smiley (1992) described *P. newzealandicus, P. yini, P. landwehri,* and *P. summersi*; reported *P. saaymani* from the USA and Canada; and erected a new monotypic subfamily, Neobonzinae, and genus, *Neobonzia*, for *N. moseri*. Corpuz-Raros and Garcia (1996) described two species from the Philippines, *P. gruezoi* and *P. longispina*. Hu (1997) reported *P. shanghaiensis* and *P. themedae* from China. Sergeyenko (2005) described *P. kuznetzovi*. *P. clavata* was described by Corpuz-Raros (2008). Den Heyer and Castro (2008a) split a new genus, *Coleobonzia*, from *Pseudobonzia*. They retained 6 species (*P. clathratus, P. delfinadobaakerae, P. landwehri, P. neoreticulata, P. reticulata,* and *P. yini*) in *Pseudobonzia* and transferred all other species to *Coleobonzia*. Den Heyer (2011) synonymized *Coleobonzia* with *Neobonzia* and moved *Neobonzia* to Coleoscirinae, effectively disregarding Neobonzinae.

Coleoscirinae.

Diagnosis. The palps are 5-segmented and reach beyond the subcapitulum by at most the distal half of the last segment. Simple setae are present on the basi- and telofemora. The palp tibiotarsi are long and S-shaped (as opposed to short and cylindrical as in *Neoscirula*). Four pairs of setae ($hg_{1–4}$) are present on the subcapitulum.

2 pairs of adoral setae are present. A cheliceral seta is usually present near the digit. An extensive reticulated pattern is absent from the gnathosoma, though a row of single cells may be present caudally.

The female idiosomal plates are lightly sclerotized and may not be well defined or demarcated. The propodosomal plate bears 2 pairs of setae (*ve* and *sci*) and 2 pairs of setose sensillae (*vi* and *sce*). An extensive reticulated pattern is absent, although a pair of rows of up to 6 cells may be present. The propodosomal plate may be covered with random dots or papillae. A hysterosomal plate is absent. Setae c_1–h_1, and usually c_2 and f_2 are present dorsally; h_2 may be present or absent. Cupules *im* are present laterad and sometimes caudally of e_1. The integument is striated.

The female coxal plates are usually restricted to the trochantral bases, though sometimes coxae I–II may nearly touch medially. Coxae I–II are fused. Coxae III–IV are also fused. All coxae are lightly sclerotized and may be ill-defined. An extensive reticulated pattern is absent from the coxae, though a row of cells or reticulated pattern may be present near the edges. The coxal plates may be covered with random dots or papillae. Coxae I–IV usually have the simple setal formula 3-3-3-3 (*N. parilis* is the exception with 2-2-3-2). The genital plates each bear 3–4 setae; 2 pairs of genital papillae are visible underneath the plates. 2 pairs of setae ($ps_{1–2}$) usually occur on the anal plates and 1 pair of setae (*pa*) occurs on the integument near the anal plates. However, at least one species (*N. clavata*) has 3 pairs of setae present on the anal plates and 0 pairs of setae on the integument. The third pair of setae is probably the para-anal setae that have migrated onto the anal plates, but without having seen the specimen this is purely speculation. Cupules *ih* are present ventrally near the anal plates.

The tarsi are never constricted apically so as to end in lobes. The apices of solenidia are cylindrical, not swollen as in *Coleoscirus* and *Scutascirus*. A trichobothria is present on leg tibia IV. The ambulacral claws are rippled and occur on either side of a 4-rayed empodium.

Key to adult female *Neobonzia*.

Neobonzia parvirostris (Berlese, 1910) is known only from the male and so is not included in the key. *N. breviscuta* (Luxton, 1982) is not included in the key as an insufficient number of characters are given in the original description.

1 Sensilla *vi* and *sce* clavate (Figs. 102a, b) 2

\- Sensilla *vi* and *sce* not clavate, normal (Fig. 102c) 3

2 (1) Sensilla *vi* and *sce* short, length less than width of propodosomal plate (Fig. 102a) ..... *N. clavata*

\- Sensilla *vi* and *sce* long, length greater than width of propodosomal plate (Fig. 102b) ..... *N. clava*

3 (1) Coxae I–IV with 2-2-3-2 sts ..... *N. parilis*

\- Coxae I–IV with 3-3-3-3 sts 4

4 (3) Basifemora I with 2 sts 5

\- Basifemora I with 3 sts ..... *N. longispina*

- Basifemora I with 4 sts 7
- Basifemora I with 5 sts 12

5 (4) Basifemora II–IV with 2-2-1 sts ..... *N. moseri*
- Basifemora II–IV with 3-3-1 sts 6

6 (5) Telofemora I–IV with 4-6-4-2 sts ..... *N. themedae*
- Telofemora I–IV with 5-5-4-3 sts ..... *N. lootsi*

7 (4) Basifemora II with 4 sts 8
- Basifemora II with 6 sts 10

8 (7) Basifemora III–IV with 4-2 sts 9
- Basifemora III–IV with 6-1 sts ..... *N. newzealandicus*

9 (8) Palp tibiotarsal tubercle present ..... *N. moraesi*
- Palp tibiotarsal tubercle absent ..... *N. saaymani*

10 (7) Basifemora III–IV with 3-0 sts ..... *N. nona*
- Basifemora III–IV with 3-1 sts ..... *N. argillae*
- Basifemora III–IV with 4-2 sts 11

11 (10) *Ve* and *sci* subequal ..... *N. smileyi*

- *Ve* about half as long as *sci* ..... *N. summersi*

12 (4) Basifemora II with 5 sts 13

- Basifemora II with 6 sts 14

13 (12) Coxae I–II nearly touching medially (Fig. 103a) ..... *N. snowi*

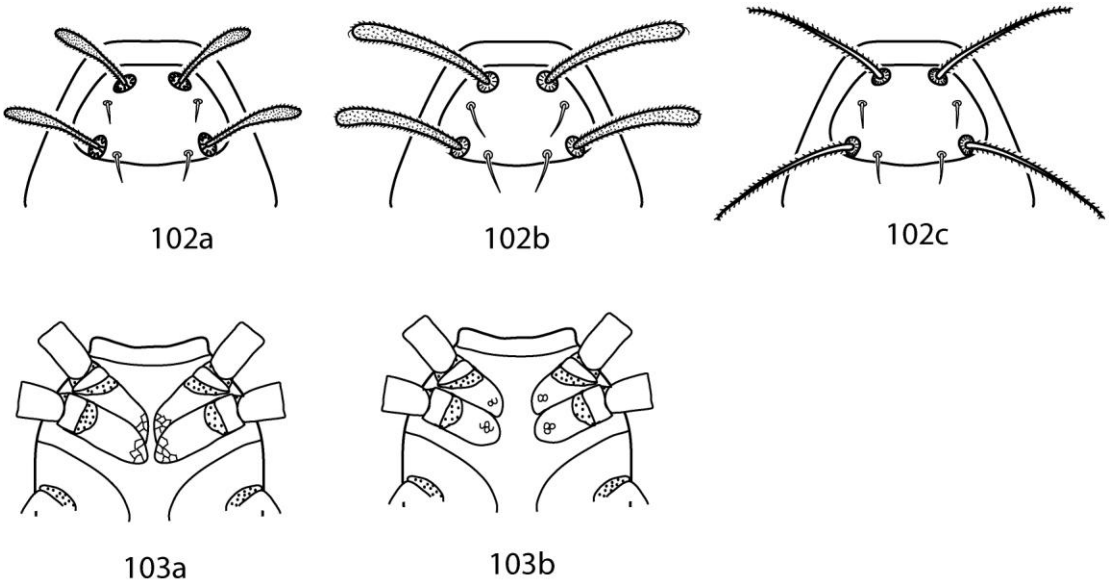
- Coxae I–II widely separated medially (Fig. 103b) ..... *N. gruezoi*

14 (12) Basifemora III–IV with 5-2 sts 15

- Basifemora III–IV with 6-2 sts ..... *N. numida*

15 (14) Setae g_4 longest; posterior corners of propodosomal shield angled ..... *N. shanghaiensis*

- Setae g_3 longest; posterior corners of propodosomal shield rounded ..... *N. kuznetzovi*



Figures 102–103. *Neobonzia* key illustrations. 102a–102c) Propodosoma, dorsal. 103a, b) Propodosoma, ventral.

III. **DESCRIPTIONS AND DIAGNOSES OF SPECIES FOUND IN THE OZARK HIGHLANDS AND OTHER AREAS**

Materials and Methods

See previous chapter for more in depth materials and methods.

Empodia and ambulacral claws have been omitted from leg illustrations. All measurements, including illustration scale bars, are in micrometers (μm). Setal notation follows Kethley (1990) as applied by Swift (1996) and Den Heyer and Castro (2008a). The term subcapitulum is used in place of hypognathum, which has been preferred by cunaxid workers in the past, as they are synonymous and subcapitulum is more widely accepted (Krantz & Walter 2009). The following abbreviations are used and illustrated by Mejía-Recamier and Palacios-Vargas (2007): attenuate solenidion (asl), blunt rod-like solenidion (bsl), dorsodistal solenidion (dtsl), famulus (fam)(= peg organ), microseta (mst), paracoxal simple tactile setae (pcs), spine-like seta (spls), simple tactile seta (sts), terminal solenidion (tsl), trichobothria (T).

Results

698 specimens were slide mounted and identified to genus. 14 of 29 genera in 5 of 6 subfamilies were collected. Because of time constraints not every specimen was identified to species; the following are those species recorded as occurring in the Ozark Highlands (with the exception of *Armascirus pennsylvanicus*, which is known only from the holotype collected in Pennsylvania).

Descriptions and Diagnoses

Bonzia yunkeri Smiley, 1992

Bonzia yunkeri Smiley 1992: 50;

Diagnosis. This species can be distinguished from other *Bonzia* by having smooth dorsal setae and a smooth trichobothrium on leg tibiae IV.

Remarks. *Bonzia yunkeri* has previously been reported from Virginia.

Materials examined. (3 individuals on slides). 2 females, *ex.* leaf litter, USA, Arkansas, Washington Co, Devil's Den State Park, "Trachymolgus Hill" (35°46.817 N, 094°14.750 W). 24 April 2010, by M.J. Skvarla. APGD 10-0424-007 ● 1 female, *ex.* leaf litter, USA, Arkansas, Newton Co, Buffalo National River, Boen Gulf (35°52.073 N, 093° 24.099 W)

Parabonzia bdelliformis (Atyeo, 1960)

Bonzia bdelliformis Atyeo 1958: 173; Den Heyer 1975: 665.

Cunabdella bdelliformis (Atyeo) Den Heyer 1975: 665; Kuznetzov & Livshitz 1979: 1233

Parabonzia bdelliformis (Atyeo) Smiley 1975: 228; Den Heyer 1977b: 601; Kuznetzov & Livshitz 1979: 1233

Diagnosis. This species can be distinguished from other *Parabonzia* by the relatively small spines of the multi-branched setae and setae c_1 being longer than the distance between c_1 and c_2.

Remarks. *Parabonzia bdelliformis*, in addition to South Africa and Russia, has been previously reported from Ohio, Tennessee, Georgia, Oklahoma, and Texas in the United States. It is therefore not surprising that it was also found in Arkansas. Smiley (1992) reported specimens being collected from duff at the base of trees, leaf litter on a log, and tree holes. All specimens collected during this study were found in tree holes; they were present in 3 of 7 tree holes sampled and when found were quite numerous. While this species may also be found outside of tree holes, none were collected in leaf litter despite collections made within a yard of a tree hole that produced specimens. It is suspected that tree holes may be the preferred habitat of *P. bdelliformis*.

Materials examined. (14 individuals on slides). 7 females, *ex.* wet organic material in tree hole at base of tree, USA, Arkansas, Newton Co, Buffalo National River, Boen Gulf (36°02.016 N, 093° 20.137 W). 19 September 2010, by M.J. Skvarla. APDG 10-0919-001 ● 7 females, *ex.* tree hole at base of tree, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.259 N, 093° 20.880 W). 8 October 2011, by M.J. Skvarla. APGD 10-1008-004.

***Armascirus ozarkensis* Skvarla & Dowling sp. nov**

Diagnosis. *Armascirus ozarkensis* most closely resembles *A. gimplei* and *A. cerris* in that it has a small hysterosomal shield that is not complemented with dorsal setae and has lateral platelets. It can be distinguished from *A. gimplei* by the comparatively long lateral platelets and from *A. cerris* by the 6 pairs of ventral setae after coxae II (not including coxal, genital and anal setae).

Female. Idiosoma 388–575 (471, n=6) long, 313–475 (371) wide.

Gnathosoma (Fig. 104). *Subcapitulum* (Fig. 104a) longer than ½ the length of the idiosoma, 270–330 (307). 6 pairs of setae present: 2 pairs of adoral setae and 4 pairs of subcapitular setae ($hg_{1–4}$). Setae $hg_{1,2,3}$ shorter than hg_4 (27, 37, 14, 75). *Palp* (Fig. 104b) 380–473 (410). Chaetotaxy: trochanter, 0; basifemur- 1 sts; telofemur- 1 spls, 1 apophysis; genu- 1 sts, 3 spls, 1 apophysis adjoining genu and tibiotarsus; tibiotarsus- 1 spls, 1 dtsl, 3 sts. The tibiotarsus ends in a claw. *Chelicera* (Fig. 104c) 228-295 (267), elongate, base 4 times width of ap*ex.*

Dorsum (Fig. 105a). Propodosomal shield present and reticulate. Two setose trichobothria (*vi* and *sce*) present on shield; 358–478 (414) and 488–623 (554), respectively. 2 setae (*ve* and *sci*) also present on shield; 11–15 (12) and 7–15 (11), respectively. Hysterosomal (median) shield present but small, lateral platelets present; all plates reticulate. Setae c_1, c_2, d_1–h_1 on minute sclerotized plates barely larger than setal socket; 11, 12, 14, 18, 33 and 38, respectively. Cupule *im* present, laterad to e_1. Integument striated.

Venter (Fig. 105b). Coxal plates I and II fused but retaining suture, with reticulate sculpturing and bearing 3 sts and 2 sts, respectively. Coxal plates III and IV also fused

but retaining suture, with reticulate sculpturing and bearing 3 sts and 1 pcs – 2 sts, respectively. 6 pairs of dorsal setae after coxae II (not including coxal, genital and anal setae). Genital plates weakly sclerotized with 4 pairs of setae ($g_{1–4}$) and 2 pairs of papillae. 3 pairs of setae on or adjacent to anal plates: 2 pseudanal setae ($ps_{1–2}$) and h_2. Cupule *ih* present laterad to ps_2.

Legs (Fig. 106a–d). Legs I, III and IV longer than body, leg II shorter. Leg I 400–563 (494), leg II 373–525 (453), leg III 455–593 (453), leg IV 480–650 (567). Chaetotaxy: trochanters I-IV, 1-1-2-1; basifemora I-IV, 5-5-4-2; telofemora I-IV, 4-4-4-4; genua I with 1 mst, 4 asl, 4 sts; genua II with 2 asl, 5 sts; genua III with 1 bsl, 5 sts; genua IV with 2 asl, 5 sts; tibiae I with 1 mst, 2 asl, 4 sts; tibiae II with 1 asl, 5 sts; tibiae III with 1 asl, 5 sts; tibiae IV with 1 T, 4 sts; tarsi I with 4 asl, 2 tsl, 1 mst, 21 sts; tarsi II with 1 bsl, 1 tsl, 21 sts; tarsi III with 1 tsl, 21 sts; tarsi IV with 20 sts.

Male and developmental stages. Unknown.

Etymology. This species is named after the Ozark Highlands, the area in which it was collected.

Materials examined (6 individuals on slides)**.** HOLOTYPE, 1 female, *ex.* wet cedar and oak litter in rock crevice, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°01.924 N, 093°20.040 W), 28 May 2010, J. R. Fisher and M. J. Skvarla, APGD 10-0528-008 ● PARATYPE, 1 female, ex cedar and oak litter drift against rocks, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°01.924 N, 093°20.040 W). 28 May 2010, by J. R. Fisher and M. J. Skvarla. APGD 10-0528-007 ●

PARATYPE, 1 female, *ex.* mixed cedar and deciduous litter, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°01.924 N, 093°20.040 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-005 ● PARATYPE, 1 female, *ex.* moist mixed deciduous litter drifted against slope in creek bottom, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.016 N, 093°20.137 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-006 ● PARATYPE, 1 female, ex cedar litter, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°01.924 N, 093°20.040 W). 29 Aug 2009, by J. R. Fisher. APGD 09-0829-002 ● PARATYPE, 1 female, ex mixed deciduous litter, USA, Arkansas, Washington Co, Devil's Den State Park (35°46.817 N, 094°14.750 W). 30 Aug 2009, by J. R. Fisher. APGD 09-0830-006

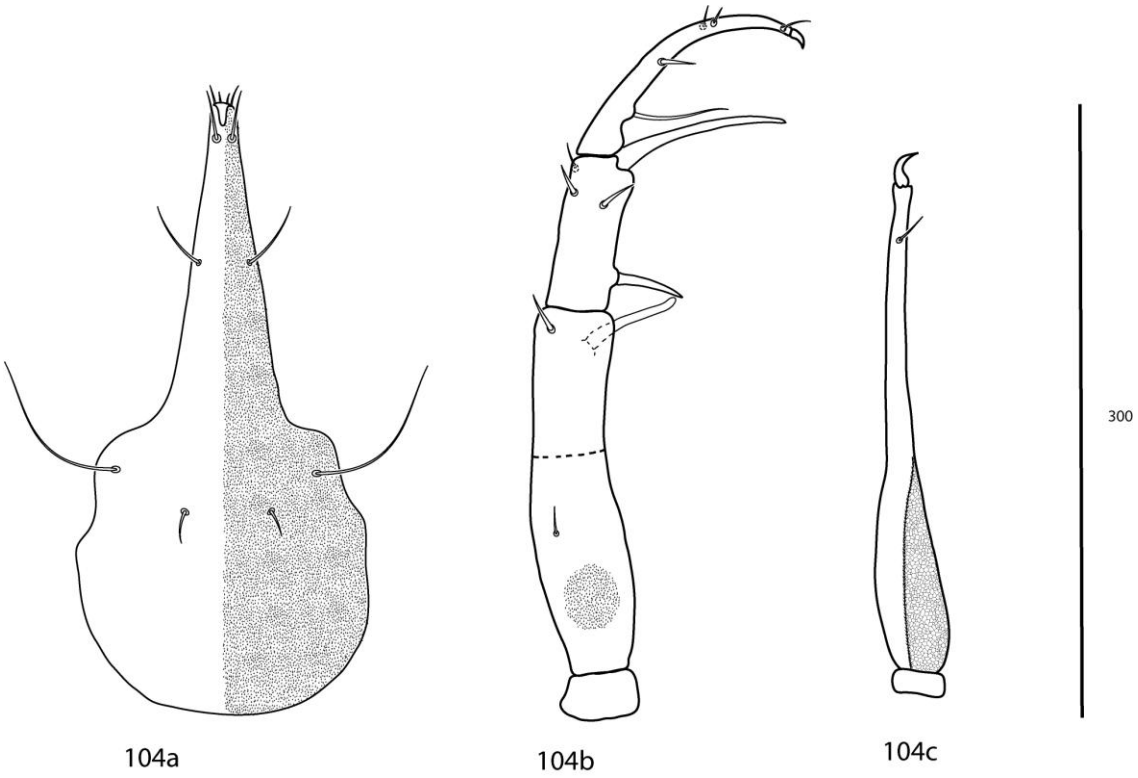


Figure 104. *Armascirus ozarkensis* **sp. nov.** – female, gnathosoma. 104a) Subcapitulum. 104b) Pedipalp. The dot-like pattern illustrated on the basifemur is present on all segments except the tibiotarsus. 104c) Chelicera

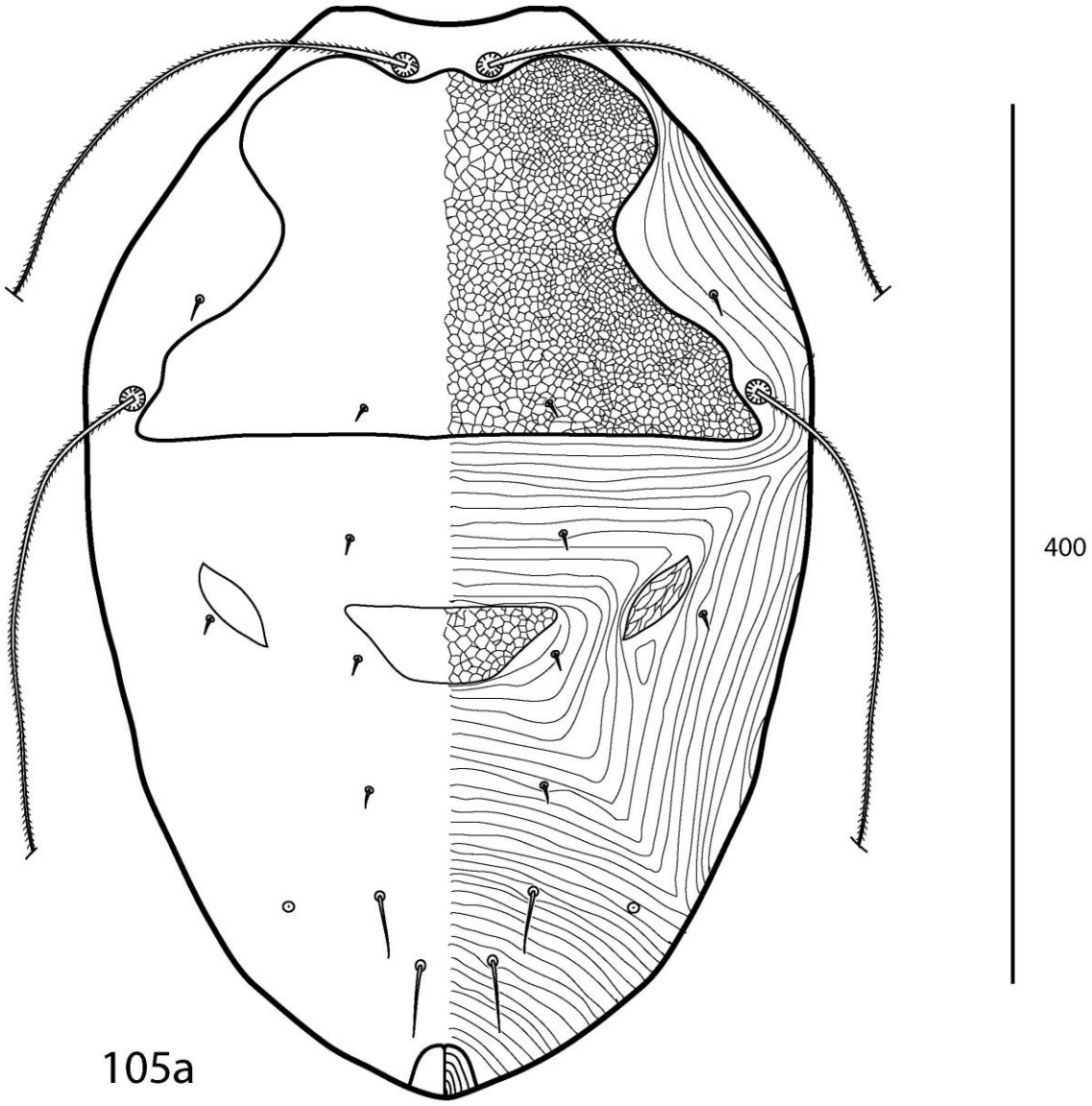


Figure 105a. *Armascirus ozarkensis* **sp. nov.** – female, idiosoma, dorsum

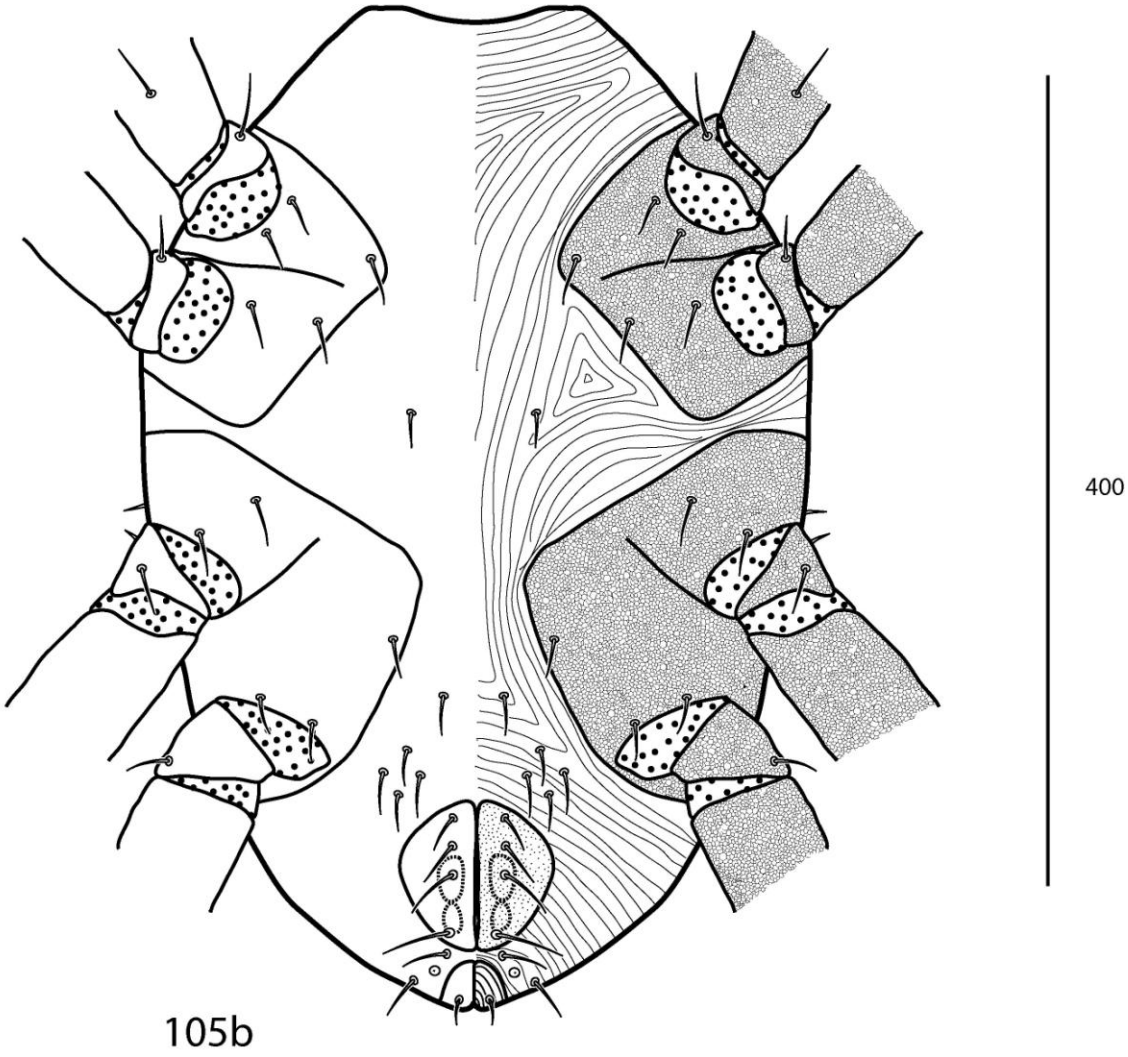


Figure 105b. *Armascirus ozarkensis* **sp. nov.** – female, idiosoma, venter

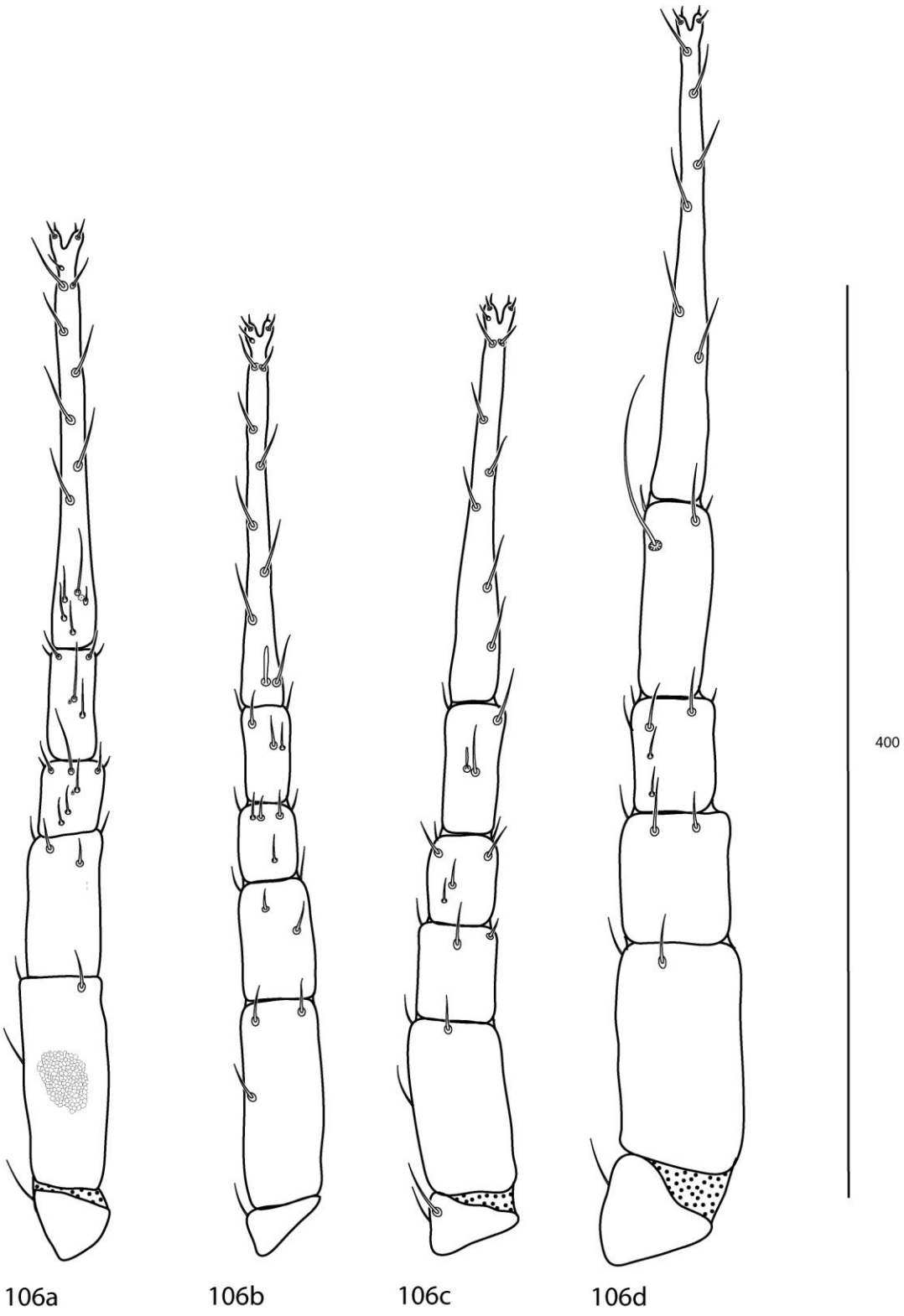


Figure 106. *Armascirus ozarkensis* **sp. nov.** – female, legs, dorsum. Reticulated pattern illustrated on basifemora I is present on all segments of all legs. 106a) Leg I. 106b) Leg II. 106c) Leg III. 106d) Leg IV.

***Armascirus pennsylvanicus* Skvarla & Dowling sp. nov.**

Diagnosis. *Armascirus pennsylvanicus* most closely resembles *A. virginiensis* Smiley, 1992 as it lacks a hysterosomal (median) shield and the apical apophysis on the palp telofemur does not reach the apical apophysis on the palp genu. It can be distinguished from *A. virginiensis* by the chaetotaxy of the palp tibiotarsi (1 spls + 4 sts instead of 1 spls + 3 sts), coxae IV bearing 3 setae instead of 2 and the distances between d_1–d_1 and *sci*–*sci*.

Female. Idiosoma 500 (n=1) long, 375 wide.

Gnathosoma (Fig. 8). *Subcapitulum* (Fig. 107a) nearly ½ the length of the idiosoma, 265. 2 pairs of adoral setae present. Four pairs of setae ($hg_{1–4}$); $hg_{1,2,4}$ subequal, hg_3 longer by more than 3 times (20, 26, 73, 20). *Palp* (Fig. 107b) 403. Chaetotaxy: trochanter - 0; basifemur - 1 sts; telofemur - 2 spls, 1 apophysis; genu - 2 spls, 2 sts, 1 apophysis adjoining genu and tibiotarsus; tibiotarsus - 1 spls, 1 dtsl, 3 sts. The tibiotarsus ends in a claw. *Chelicera* (Fig. 107c) 238, elongate, base 4 times width of ap*ex*.

Dorsum (Fig. 108a). Propodosomal shield present and weakly reticulate. Two setose trichobothria (*vi* and *sce*) present on shield; 335 and 488, respectively. Two setae (*ve* and *sci*) also present on shield; 11 and 10, respectively. Hysterosomal (median) shield absent, lateral platelets present and reticulate. Setae c_1, c_2 d_1–h_1 on minute sclerotized plates barely larger than the setal socket; 11, 10, 10, 15, 26 and 35, respectively. Cupule *im* present, laterad to e_1. Integument striated.

Venter (Fig. 108b). Coxal plates I and II fused but retaining suture, with weak reticulate sculpturing and bearing 3 sts - 2 sts, respectively. Coxal plates III and IV also fused, but retaining suture, with weak reticulate sculpturing and bearing 3 sts - 1 pcs, and 2 sts, respectively. Genital plates weakly sclerotized with 4 pairs of setae (g_1–g_4) and 2 pairs of papillae. Three pairs of setae on or adjacent to anal plates: 2 pseudanal setae ($ps_{1–2}$) and h_2. Cupule *ih* present laterad to ps_2.

Legs (Fig. 109a–d). Legs I and II shorter than body, 475 and 455; legs III and IV longer than body, 528 and 513. Chaetotaxy: trochanters I–IV, 1-1-2-1; basifemora I–IV, 5-5-4-2; telofemora I–IV, 4-4-4-4; genua I with 4 asl, 1 mst, 4 sts; genua II with 2 asl, 5 sts; genua III with 1 asl, 5 sts; genua IV with 2 asl, 5 sts; tibiae I with 1 asl, 1 mst, 4 sts; tibiae II with 1 asl, 5 sts; tibiae III with 1 bsl, 5 sts; tibiae IV with 1 T, 3 sts; tarsi I with 4 asl, 1 mst, 2 tsl, 19 sts; tarsi II with 1 bsl, 1 tsl, 19 sts; tarsi III with 1 tsl, 18 sts; tarsi IV- with 17 sts.

Male and developmental stages. Unknown.

Etymology. This species is named after the state in which it was collected.

Material examined (1 individual on a slide)**.** HOLOTYPE, 1 female, *ex.* maple and oak litter under mountain laurel along creek edge, USA, Pennsylvania, Somerset Co, Laurel Hill State Park, nr. Eberly Scout Reservation (40°01.182 N, 079°14.548 W). 26 Aug 2010, by M. J. Skvarla. APGD 10-0826-010

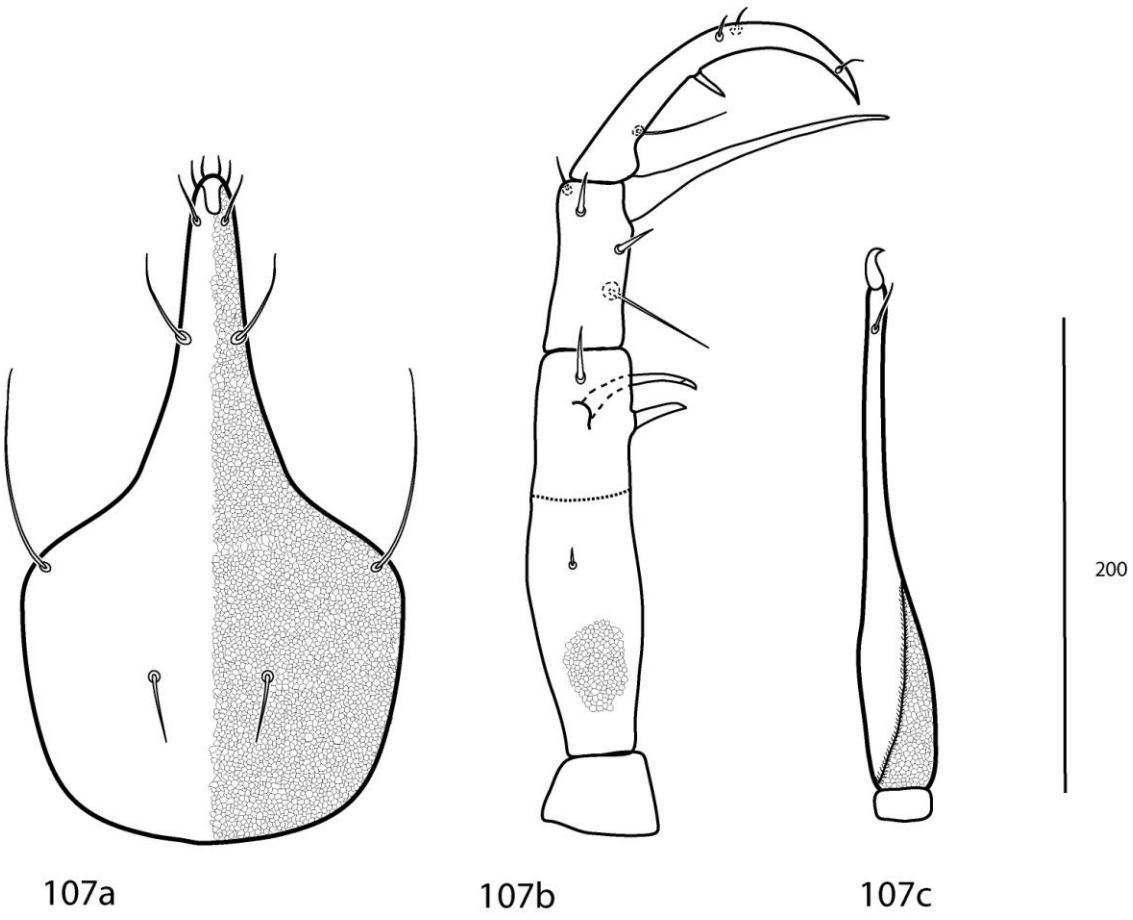


Figure 107. *Armascirus pennsylvanicus* **sp. nov.** – female, gnathosoma. 107a) Subcapitulum. 107b) Pedipalp. The dot-like pattern illustrated on the basifemur is present on all segments except the tibiotarsus. 107c) Chelicera

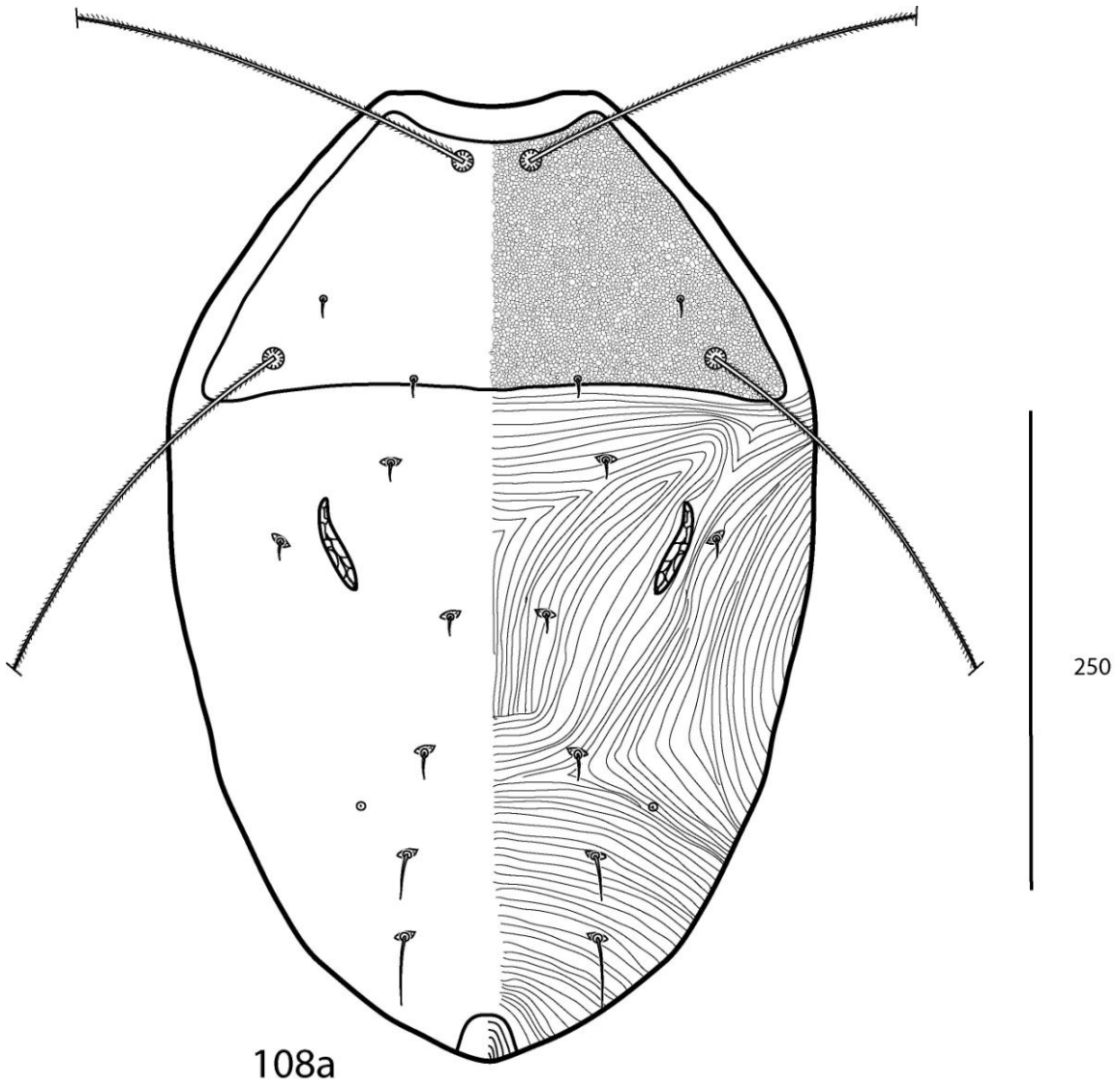


Figure 108a. *Armascirus pennsylvanicus* **sp. nov.** – female, idiosoma, dorsum.

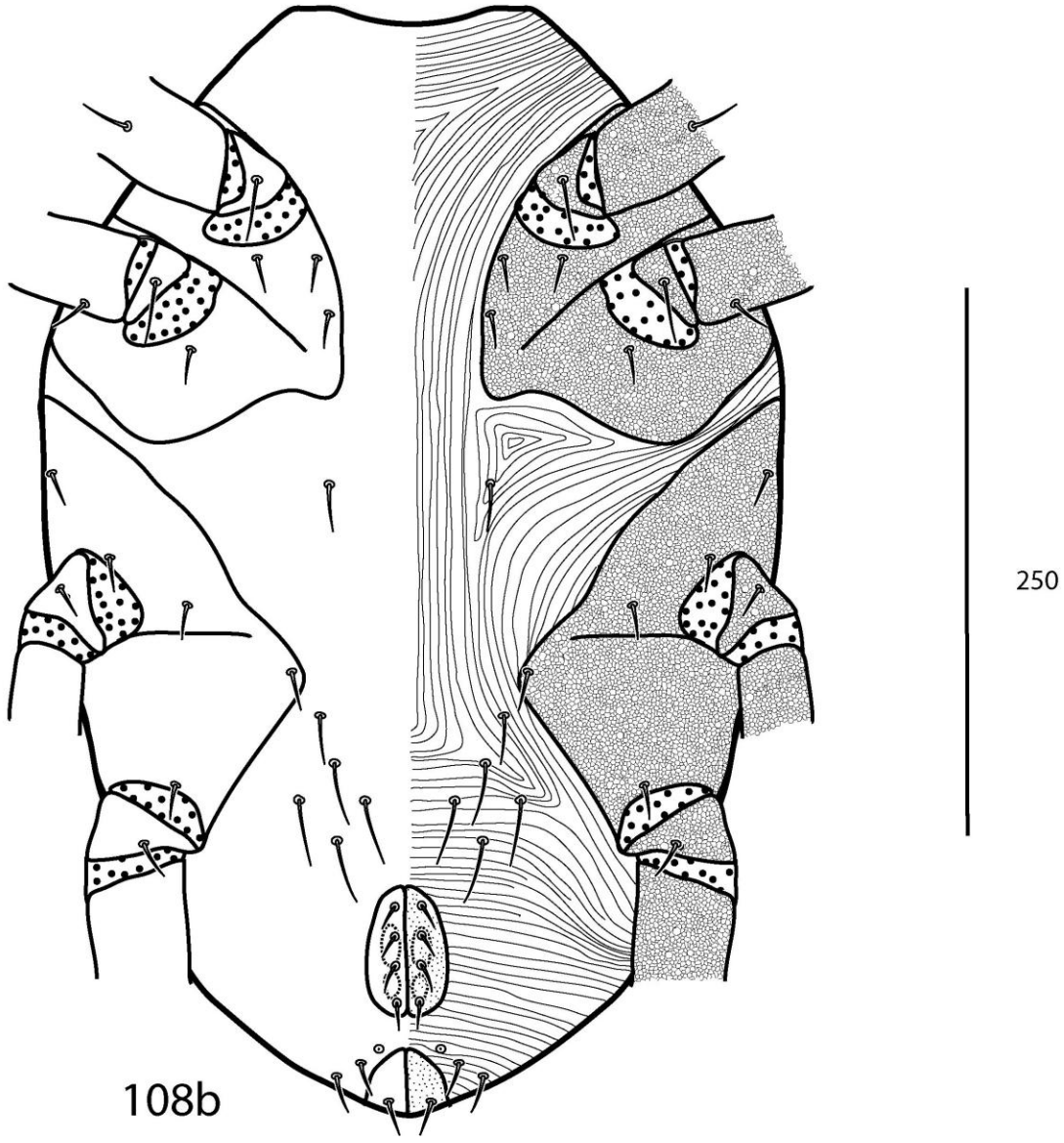


Figure 109b. *Armascirus pennsylvanicus* **sp. nov.** – female, idiosoma, venter.

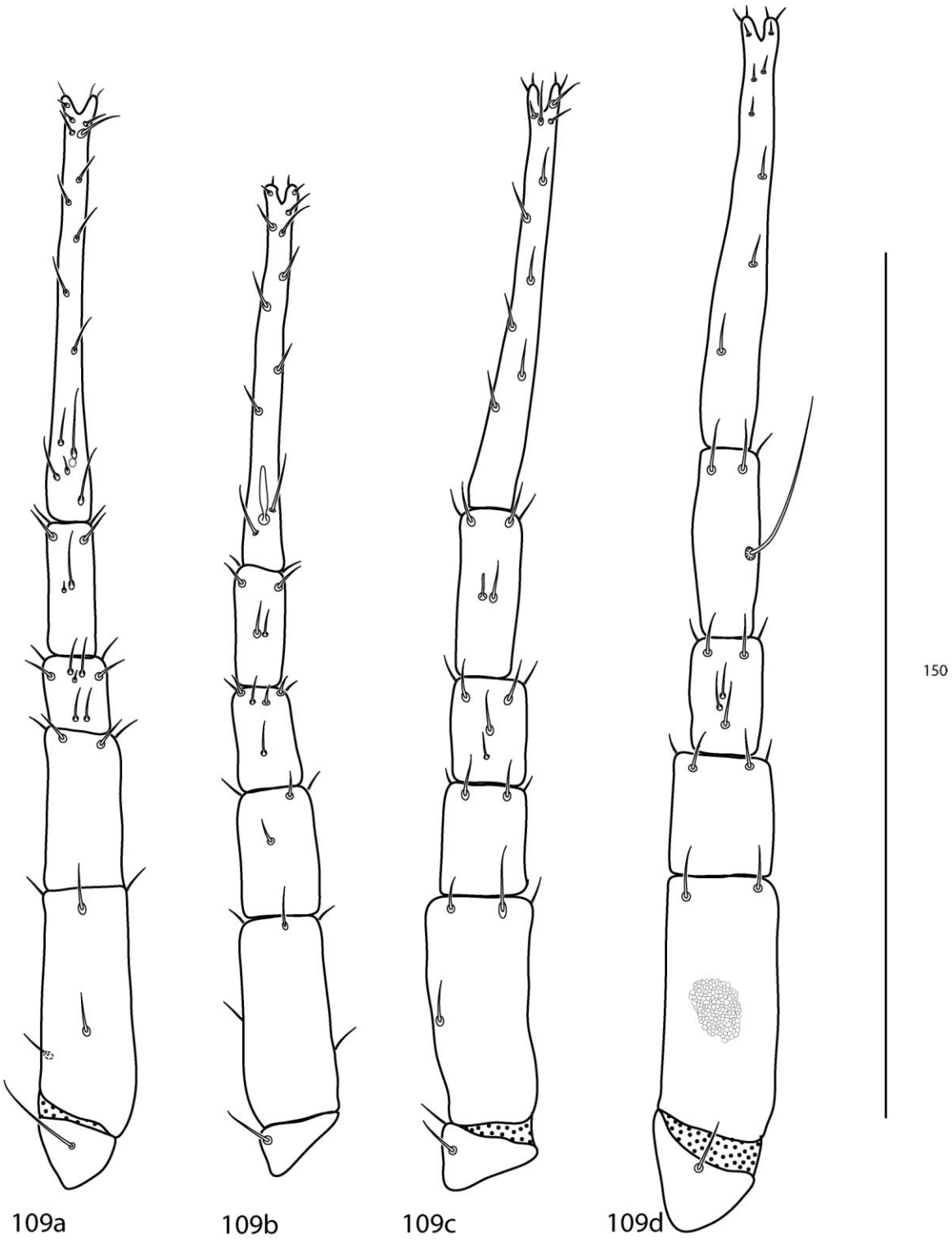


Figure 109. *Armascirus pennsylvanicus* **sp. nov.** – female, legs, dorsum. Reticulated pattern illustrated on basifemur IV is present on all segments of all legs. 109a) Leg I. 109b) Leg II. 109c) Leg III. 109d) Leg IV.

***Armascirus primigenius* Skvarla & Dowling sp. nov.**

Diagnosis. *Armascirus primigenius* most closely resembles *A. taurus* in that it has a small hysterosomal (median) shield that is complemented with a single pair of setae (d_1), has lateral platelets and 6 pairs of ventral setae caudally from coxae II (excluding coxal, genital and anal setae). It can be distinguished from *A. taurus* by differences in leg chaetotaxy, specifically genua II with 2 asl + 5 sts instead of 1 asl + 5 sts, and genua IV with 2 asl + 4 sts instead of 2 asl + 5 sts.

Female. Idiosoma 400–725 (556, n=15) long, 290–500 (394) wide.

Gnathosoma (Fig. 11). *Subcapitulum* (Fig. 110a) approximately ½ the length of the idiosoma, 250–295 (274). 2 pairs of adoral setae present. Four pairs of setae (hg_{1-4}); $hg_{1,2,3}$ longer than hg_4 and increasing in size (19, 28, 75, 12). *Palp* (Fig. 110b) 325–475 (381). Chaetotaxy: trochanter - 0; basifemur - 1 sts; telofemur - 1 spls, 1 apophysis; genu - 1 sts, 3 spls, 1 apophysis adjoining genu and tibiotarsus; tibiotarsus - 1 spls, 1 dtsl, 3 sts. The tibiotarsus ends in a claw. *Chelicera* (Fig. 110c) 210–255 (227), elongate and base 3 times width of ap*ex.*

Dorsum (Fig. 111a). Propodosomal shield present with reticulate sculpturing. Two setose trichobothria (*vi* and *sce*) present on shield; 310–425 (357) and 410–550 (486), respectively. Two setae (*ve* and *sci*) also present on shield; 10–20 (16) and 10–18 (15), respectively. Hysterosomal (median) shield present, with reticulate sculpturing. Lateral platelets present, also with reticulate sculpturing. Setae c_1,c_2 e_1–h_1 on minute sclerotized plates barely larger than the setal socket; seta d_1 present on the hysterosomal shield. Setae c_1, c_2, d_1–h_1 11, 12, 14, 18, 33 and 38, respectively. Cupule *im* present and laterad to e_1. Integument striated.

Venter (Fig. 111b). Coxal plates I and II fused but retaining suture, with reticulate sculpturing and bearing 3 sts – 2 sts, respectively. Coxal plates III and IV also fused but retaining suture, with reticulate sculpturing and bearing 3 sts – 1 pcs, 2 sts, respectively. 6 pairs of dorsal setae after coxae II (not including coxal, genital and anal setae). Genital plates weakly sclerotized, with 4 pairs of setae ($g_{1–4}$) and 2 pairs of papillae. Three pairs of setae on or adjacent to anal plates: 2 pseudanal setae ($ps_{1–2}$) and h_2. Cupule *ih* present laterad to ps_2.

Legs (Fig. 112a–d). Legs I, II and III shorter than body; leg IV subequal. Leg I 375–500 (448), leg II 365–515 (431), leg III 430–525 (495), leg IV 485–650 (559). Chaetotaxy: trochanters I–IV, 1-1-2-1; basifemora I–IV, 5-5-4-2; telofemora I–IV, 4-4-4-4; genua I with 1 mst, 4 asl, 4 sts; genua II with 2 asl, 5 sts; genua III with 1 asl, 5 sts; genua IV with 1 asl, 4 sts; tibiae I with 1 mst, 2 asl, 4 sts; tibiae II with 1 asl, 5 sts; tibiae III with 1 asl, 5 sts; tibiae IV with 1 T, 4 sts; tarsi I with 4 asl, 2 tsl, 1 mst, 17 sts; tarsi II with 1 bsl, 1 tsl, 17 sts; tarsi III with 1 tsl, 16 sts; tarsi IV with 18 sts.

Male and developmental stages. Unknown.

Etymology. Two *Armascirus*, *A. taurus* and *A. bison*, are named after bovines. As this new species appears closely related to *A. taurus* the authors thought it appropriate to borrow the name of another bovid, specifically the aurochs, *Bos primigenius*.

Materials examined (15 individuals on slides)**.** HOLOTYPE, 1 female, *ex.* cedar litter in rocky area, USA, Missouri, Taney Co, Mark Twain National Forest (36°41.199 N, 092° 58.274 W). 23 May 2010, by J. R. Fisher and D. M. Keeler. APGD 10-0523-010

● PARATYPE, 1 female, *ex.* leaf litter under chinquapin oak, USA, Missouri, Taney Co, Mark Twain National Forest (36°41.199 N, 092° 58.274 W). 23 May 2010, by J. R. Fisher and D. M. Keeler. APGD 10-0523-011 ● PARATYPE, 5 females, *ex.* old growth leaf litter, USA, Arkansas, Washington Co., Ozark National Forest, Weddington. 16 October 2009, by J. R. Fisher. APGD 09-1016-001 ● PARATYPE, 1 female, *ex.* leaf litter, USA, Arkansas, Washington Co., Devil's Den State Park (35°46.835 N, 094° 14.765W). 30 August 2009, by J. R. Fisher. APGD 09-0830-003 ● PARATYPE, 1 female, *ex.* leaf litter, USA, Arkansas, Washington Co., Devil's Den State Park (35°46.835 N, 094° 14.765W). 30 August 2009, by J. R. Fisher. APGD 09-0830-004 ● PARATYPE, 1 female, *ex.* mixed cedar and deciduous litter drifted against logs and rocks, USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf (36°02.381 N, 093° 20.394 W). 19 September 2010, by M. J. Skvarla. APGD 10-0919-010 ● PARATYPE, 1 female, *ex.* cedar litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 21 August 2009, by J. R. Fisher and M. J. Skvarla. APGD 09-0821-010 ● PARATYPE, 1 female, *ex.* dense litter drift by log, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 29 August 2009, by J. R. Fisher and M. J. Skvarla. APGD 09-0829-004 ● PARATYPE, 1 female, *ex.* mixed cedar and deciduous litter by log, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 18 September 2009, by J. R. Fisher and M. J. Skvarla. APGD 09-0918-004 ● PARATYPE, 1 female, *ex.* mixed cedar and deciduous litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-004 ● PARATYPE, 1 female, *ex.* low bush blueberry litter on

top of bluff, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek. 21 August 2009, by J. R. Fisher. APGD 09-0821-004

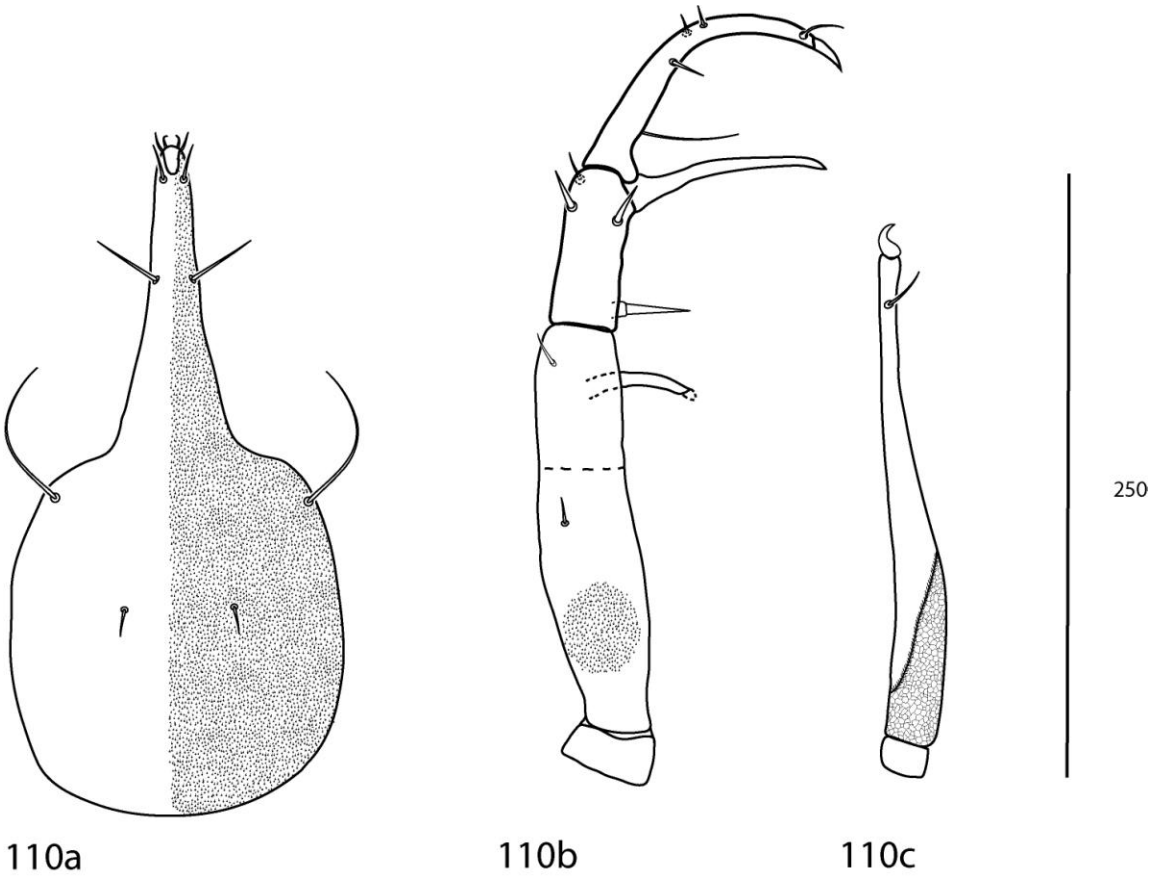


Figure 110. *Armascirus primigenius* **sp. nov.** – female, gnathosoma. 110a) Subcapitulum. 110b) Pedipalp. 110c) Chelicera.

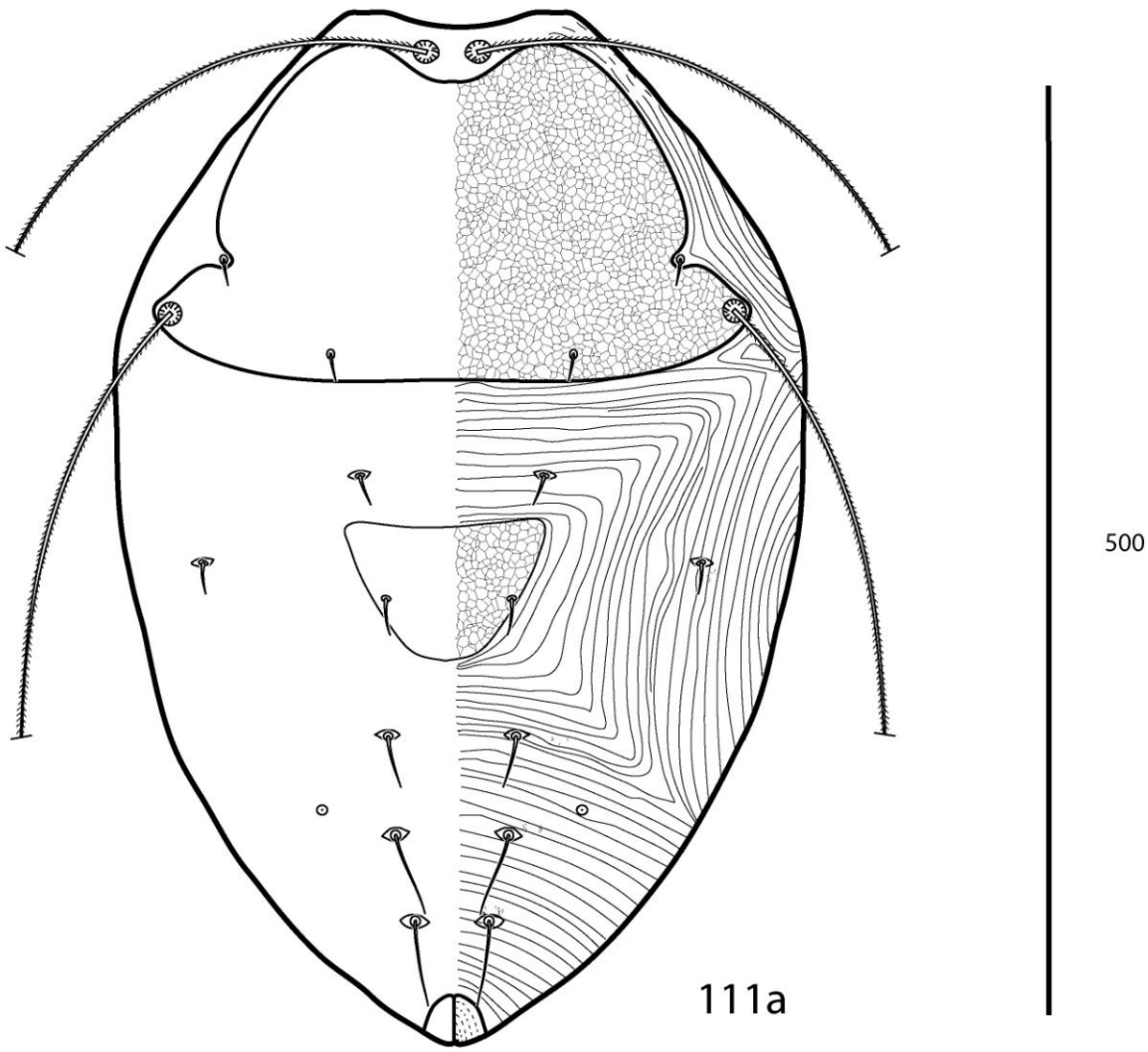


Figure 111a. *Armascirus primigenius* **sp. nov.** – female, idiosoma, dorsum.

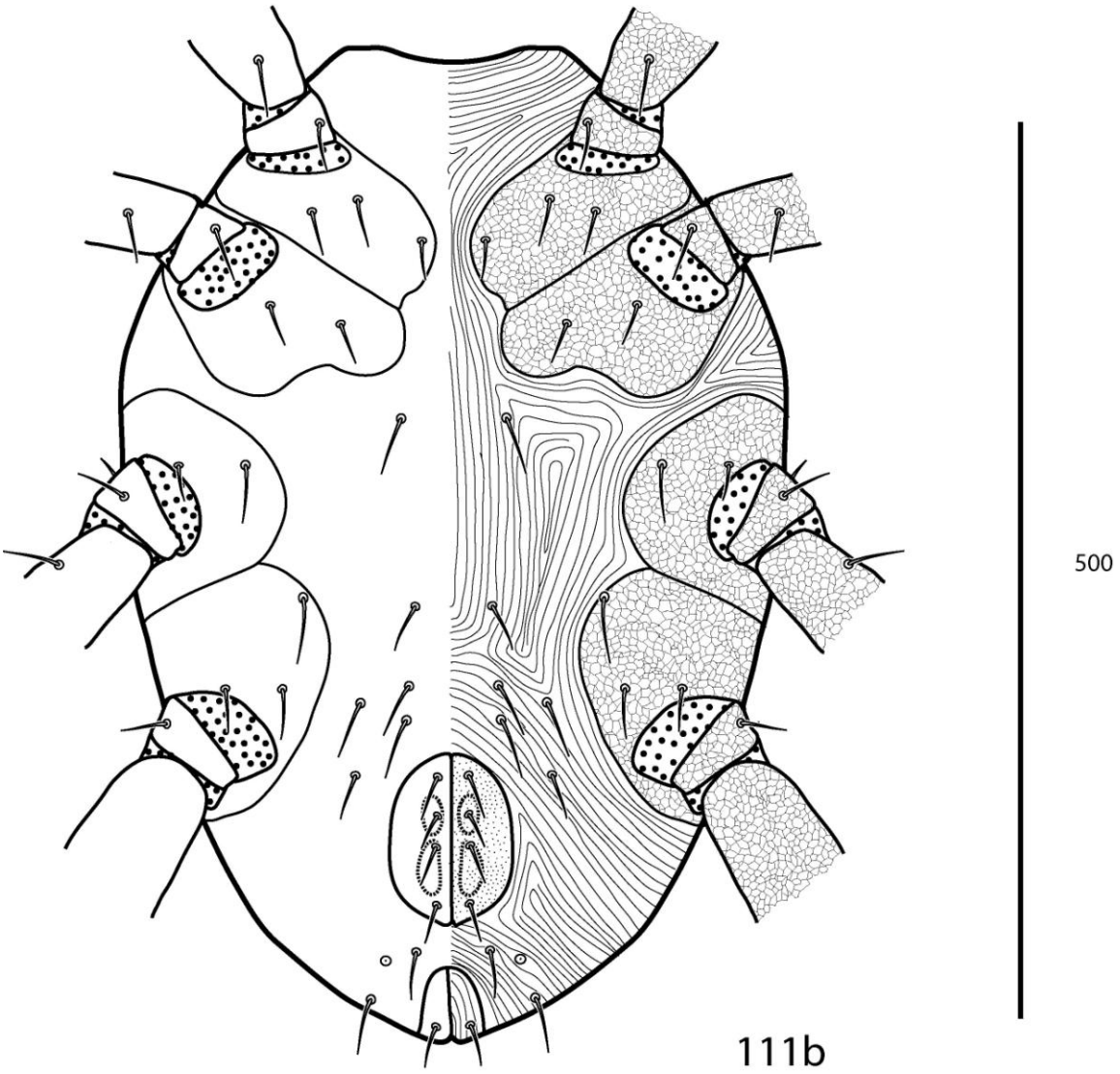


Figure 111b. *Armascirus primigenius* **sp. nov.** – female, idiosoma, venter

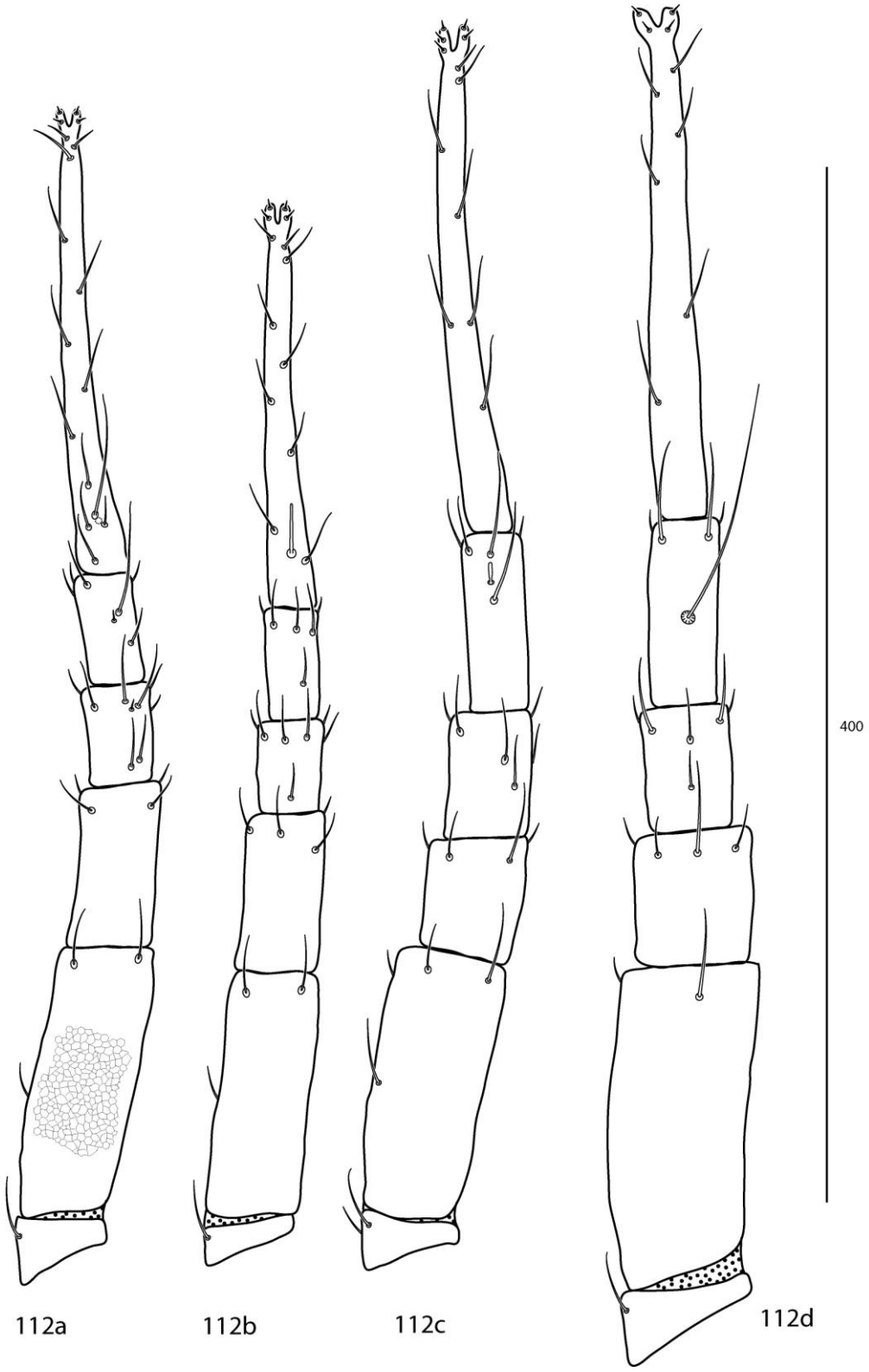


Figure 112. *Armascirus primigenius* **sp. nov.** – female, legs, dorsum. Reticulated pattern illustrated on basifemur I present on all segments of all legs. 112a) Leg I. 112b) Leg II. 112c) Leg III. 112d) Leg IV.

***Armascirus gimplei* Smiley, 1992**

Armascirus gimplei Smiley 1992: 139; Kalúz 2009: 37.

Diagnosis. *Armascirus gimplei* most closely resembles *A. ozarkensis* and *A. cerris* in that it has a small hysterosomal (median) shield that is not complemented with dorsal setae and has lateral platelets. It can be differentiated from *A. cerris* because it has 6 setae after coxae II (not including coxal, genital and anal setae) instead of 7. It can be differentiated from *A. ozarkensis* based on the lateral platelets, which are conspicuous and as long as the median shield in *A. ozarkensis* and inconspicuous and only as long as or slightly longer than c_2 in *A. gimplei*.

Remarks. After examining both the holotype and the newly collected specimen, differences between the original description and the specimens were found. Smiley (1992) states that the lateral hysterosomal platelets of *A. gimplei* are small and that c_2 is located on the platelets. In reality the platelets are small and inconspicuous, but occur on the integument between d_1 and c_2 much as they do in other *Armascirus*. The structures previously reported as the lateral platelets are the same tiny platelets that occur at the base of all dorsal setae that are situated in the integument away from larger plates and shields.

The integument around the setae laterad of coxae III appears to be more sclerotized than the surrounding cuticle. This area does not bear the reticulated pattern of the coxal or dorsal plates but the striations present on the integument are thicker and more pronounced.. The structure is not visible in the holotype so I were unable to determine if it is present across the species or an anomaly of the specimen examined.

In addition, differences between the new specimen and the published leg setal formulae were found as follows: tibiae I with 2 asl, 1 mst, 4 sts; tibiae III with 1 bsl, 5 sts (holotype tibiae I with 2 asl, 5 sts; tibiae III with sts). Unfortunately the holotype is in a poor condition that does not allow these leg segments to be viewed, and therefore these differences cannot be corroborated with the type. The subcapitulum (Fig. 113a), palp (Fig. 113b), chelicera (Fig. 113c), idiosoma (114a, b), and legs (Fig. 115a–d) have been illustrated based on the Ozark specimen to aid in identification.

Material Examined (2 individuals on slides)**.** HOLOTYPE, 1 female, collected from *Tillandsia* sp., Mexico, Vera Cruz. 6 April 1966, by J. T. Watt. ● 1 female, *ex.* mixed cedar and deciduous litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-005.

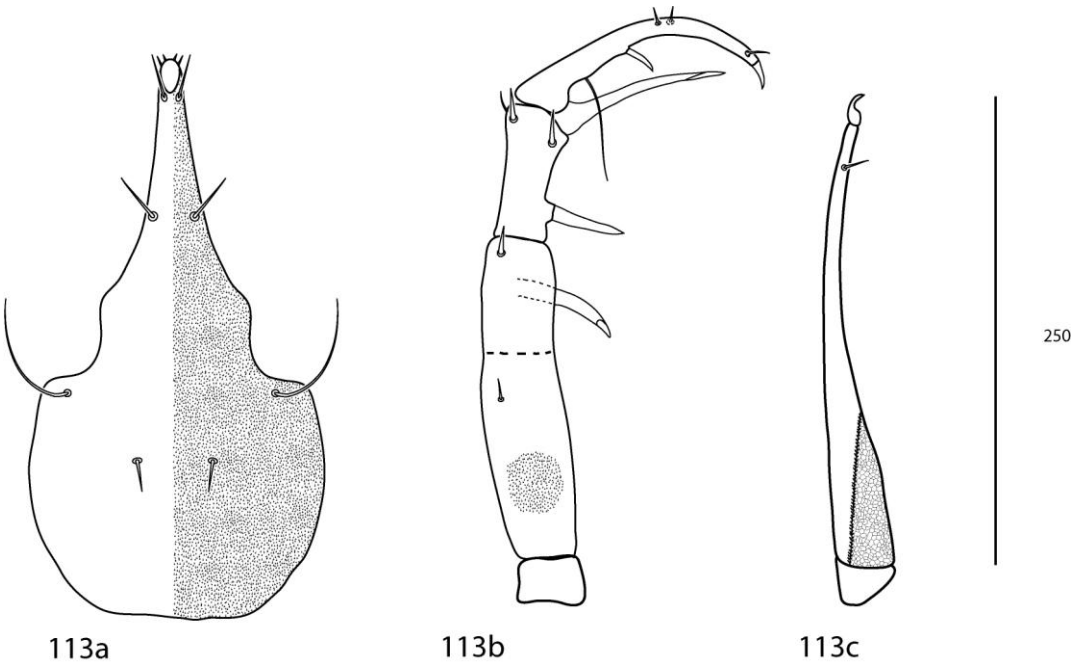


Figure 113. *Armascirus gimplei* Smiley – female, gnathosoma. 113a) Subcapitulum. 113b) Pedipalp. 113c) Chelicera.

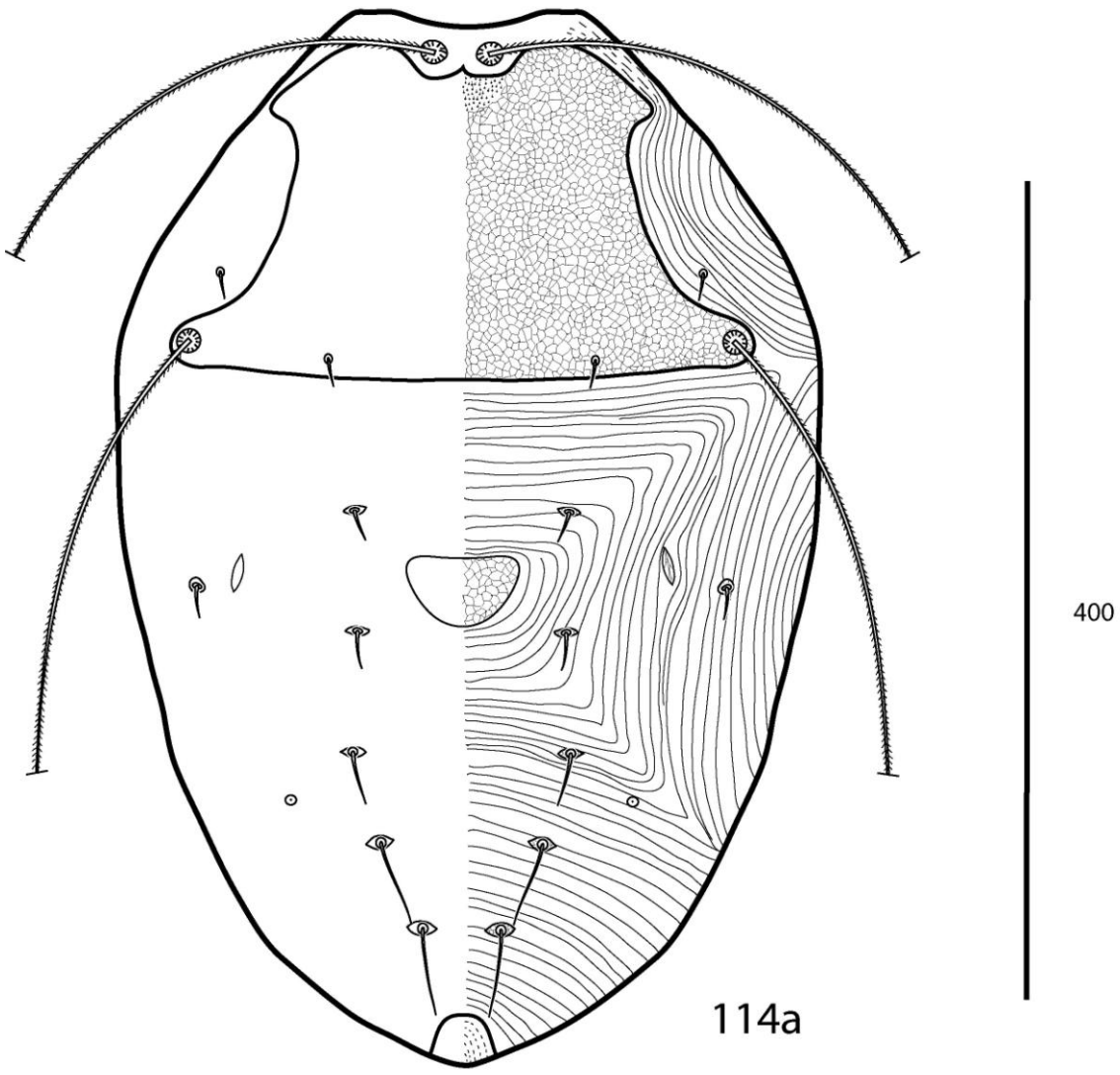


Figure 114a. *Armascirus gimplei* Smiley – female, idiosoma, dorsum.

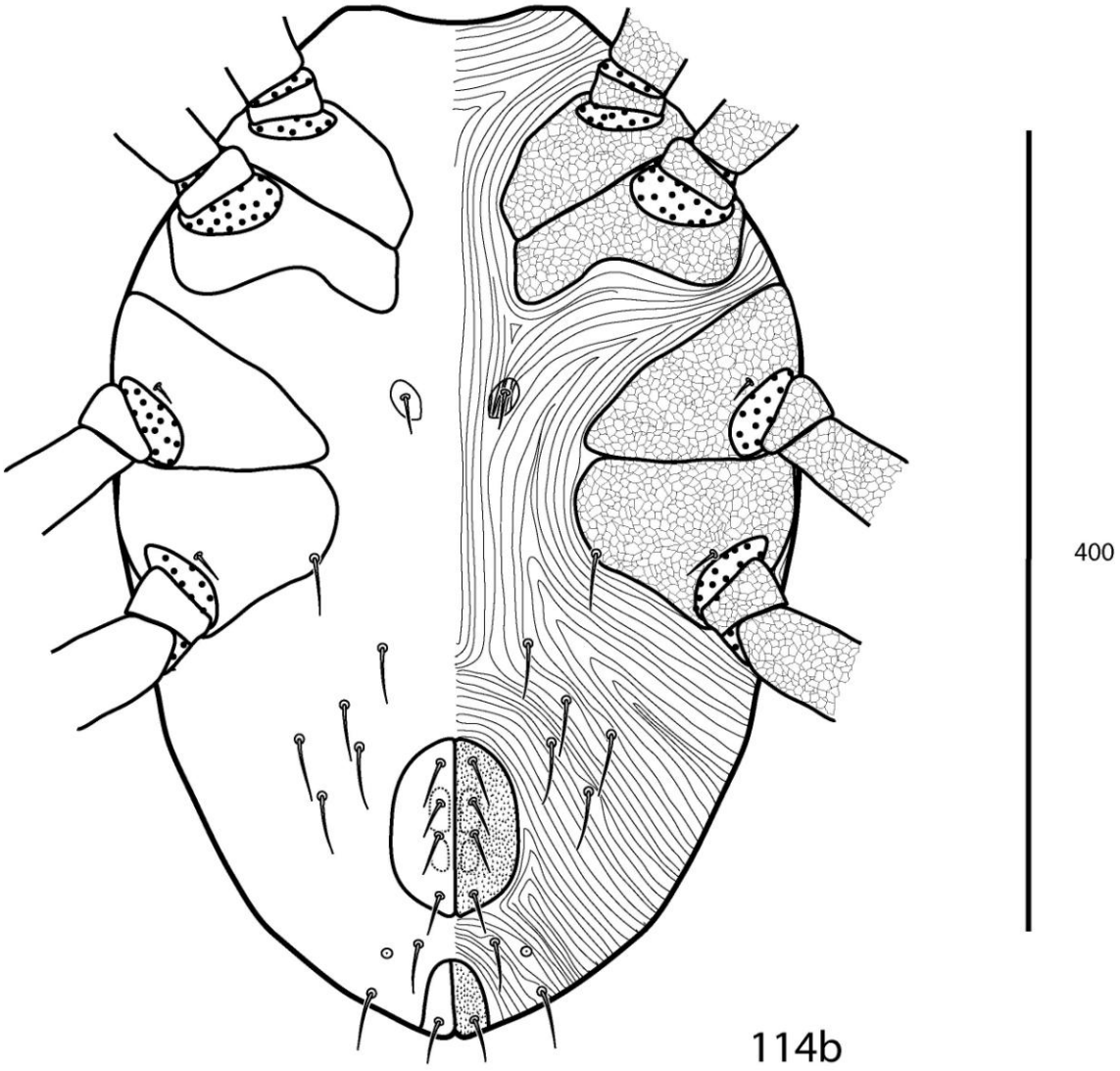


Figure 114b. *Armascirus gimplei* Smiley – female, idiosoma, venter

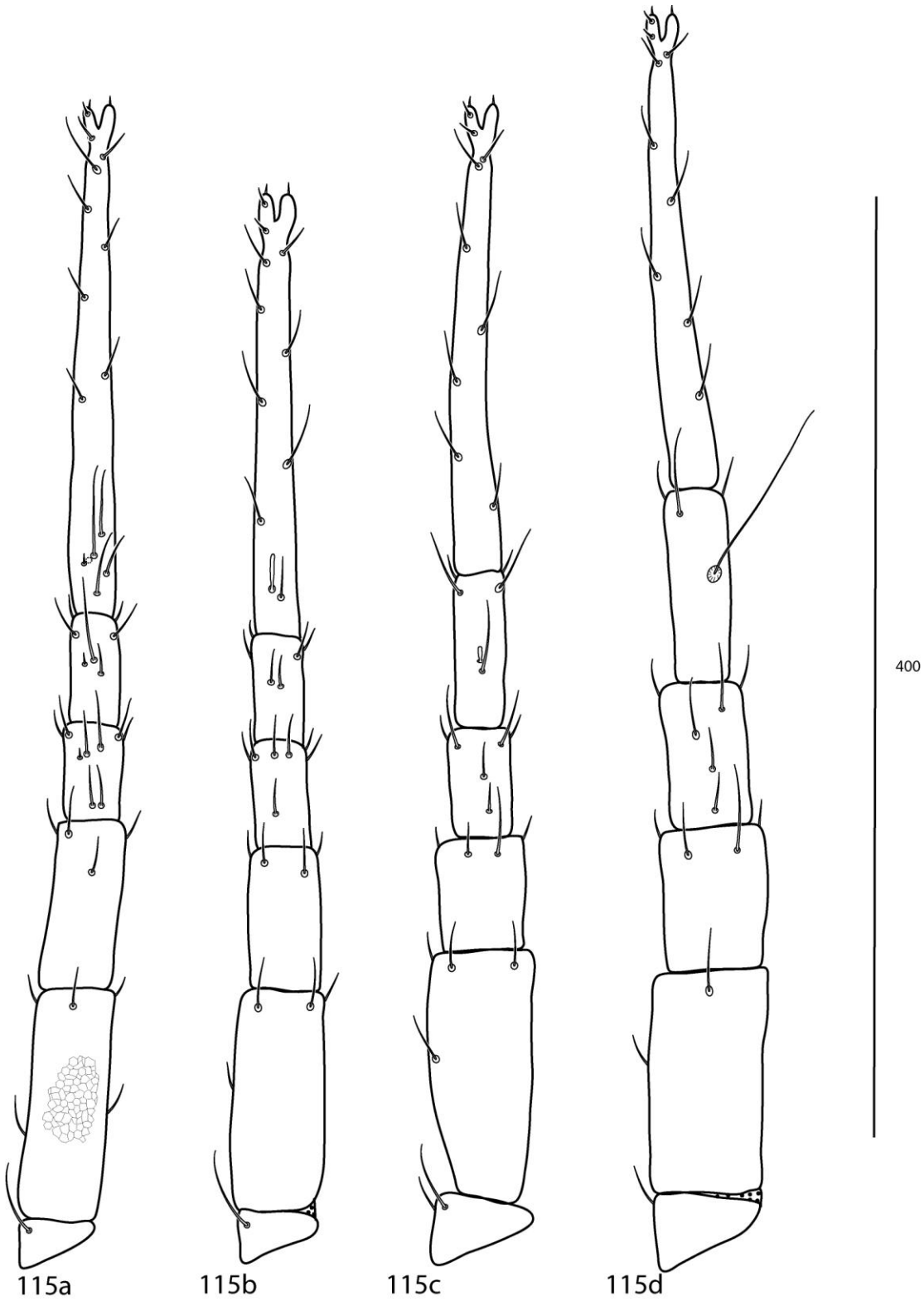


Figure 115. *Armascirus gimplei* Smiley – female, legs, dorsum. The reticulated pattern illustrated on basifemur I is present on all segments of all legs. 115a) Leg I. 115b) Leg II. 115c) Leg III. 115d) Leg IV.

***Armascirus harrisoni* Smiley, 1992**

Armascirus harrisoni Smiley 1992: 139; Kalúz 2009: 37.

Diagnosis. *Armascirus harrisoni* most closely resembles *A. bakeri* in that it has a small median shield that is not complemented with dorsal setae and lacks lateral platelets (Fig. 117a). It can be distinguished from *A. bakeri* based on the palp tibiotarsal formula, which is 1 spls and 4 sts instead of 1 spls and 3 sts. *Armascirus harrisoni* may also resemble *A. makilingensis*, but lacks thickened, spiculate ventral setae (Fig. 116b), or *A. limpopoensis*, but has 1 apophysis and 1 spls on the palpal telofemora instead of 2 apophyses and 1 spls (Fig. 116b).

Remarks. After examining the types (two individuals) and newly collected specimens (23 individuals), many discrepancies between the original description and the specimens were found. The following setal formula was observed in both the type specimens and specimens collected in the Ozark Highlands: trochanters I–IV, 1-1-2-1; basifemora I–IV, 5-5-4-2; telofemora I–IV, 4-4-4-4; genua I with 4 asl, 1 mst, 4 sts; genua IV with 2 asl, 5 sts; tibiae I with 2 asl, 1 mst, 4 sts; tibiae III with 1 bsl, 5 sts; tarsi I with 4 asl, 1 fam, 2 tsl, 16 sts; tarsi II with 1 bsl, 1 tsl, 18 sts; tarsi III with 1 tsl, 18 sts; tarsi IV with 19 sts. The subcapitulum (Fig. 116a), palp (Fig. 116b), chelicera (Fig. 116c), idiosoma (Fig. 117a, b), and legs (Fig. 118a–d) have been illustrated to aid in identification.

Material Examined (25 individuals on slides)**.** HOLOTYPE, 1 female, collected from outer bark of Loblolly Pine, USA, Louisiana, Livingston Parish, Maurepas. 19 September 1963, by J. C. Moser. ● PARATYPE, 1 female, collected from outer bark of

Loblolly Pine, USA, Louisiana, Livingston Parish, Maurepas. 19 September 1963, by J. C. Moser. ● 1 female, *ex.* low bush blueberry litter on top of bluff, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek. 21 August 2009, by J. R. Fisher. APGD 09-0821-004. ● 2 females, ex cedar litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 21 August 2009, by J. R. Fisher. APGD 09-0821-010. ● 1 female, ex cedar litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 29 August 2009, by J. R. Fisher. APGD 09-0829-002. ● 1 female, ex leaf litter around boulders, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 07 September 2009, by J. R. Fisher. APGD 09-0907-005. ● 1 female, ex litter in rock crevice, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 18 September 2009, by J. R. Fisher and M. J. Skvarla. APGD 09-0918-003. ● 1 female, ex wet mixed cedar and oak litter in rock crevice, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 28 May 2010, by J. R. Fisher and M. J. Skvarla. APGD 10-0528-008. ● 1 female, ex wet mixed cedar and oak litter in rock crevice, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 28 May 2010, by J. R. Fisher and M. J. Skvarla. APGD 10-0528-008. ● 1 female, ex mixed cedar and deciduous litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-004. ● 1 female, ex mixed cedar and deciduous litter, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°01.924 N, 093° 20.040 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-005. ● 1 female, ex deciduous litter in tall grass near pond,

USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°02.289 N, 093° 20.455 W). 09 October 2010, by M. J. Skvarla. APGD 10-1009-003. ● 1 female, ex deciduous litter drifted along bank of creek flood basin, USA, Arkansas, Newton Co., Buffalo National River, Steel Creek (36°02.016 N, 093° 20.137 W). 10 October 2010, by M. J. Skvarla. APGD 10-1010-003. ● 1 female, ex thin litter layer in secondary forest next to pull off, USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf. 26 April 2010, by M. J. Skvarla. APGD 10-0426-024. ● 1 female, ex thin litter layer in secondary forest next to pull off, USA, Arkansas, Newton Co., Buffalo National River, Boen Gulf. 19 September 2010, by M. J. Skvarla. APGD 10-0919-006. ● 1 female, caught in malaise trap, USA, Arkansas, Washington Co., Ozark National Forest, Weddington (36°06.477 N, 093° 23.446 W) ● 1 female, ex cedar litter in rocky area, USA, Missouri, Taney Co. (36°41.199 N, 092°58.274 W). 23 May 2010, by J. R. Fisher and D. M. Keeler. APGD 10-0523-009 ● 2 females, ex litter in rocky area, USA, Missouri, Taney Co. (36°41.199 N, 092°58.274 W). 23 May 2010, by J. R. Fisher and D. M. Keeler. APGD 10-0523-007 ● 5 females, collected in pitfalls in open rocky area with reindeer moss, USA, Missouri, Madison Co, Rockpile Mountain Wilderness. 1 July 2010, by J. R. Fisher and D. M. Keeler. APGD 10-0701-001.

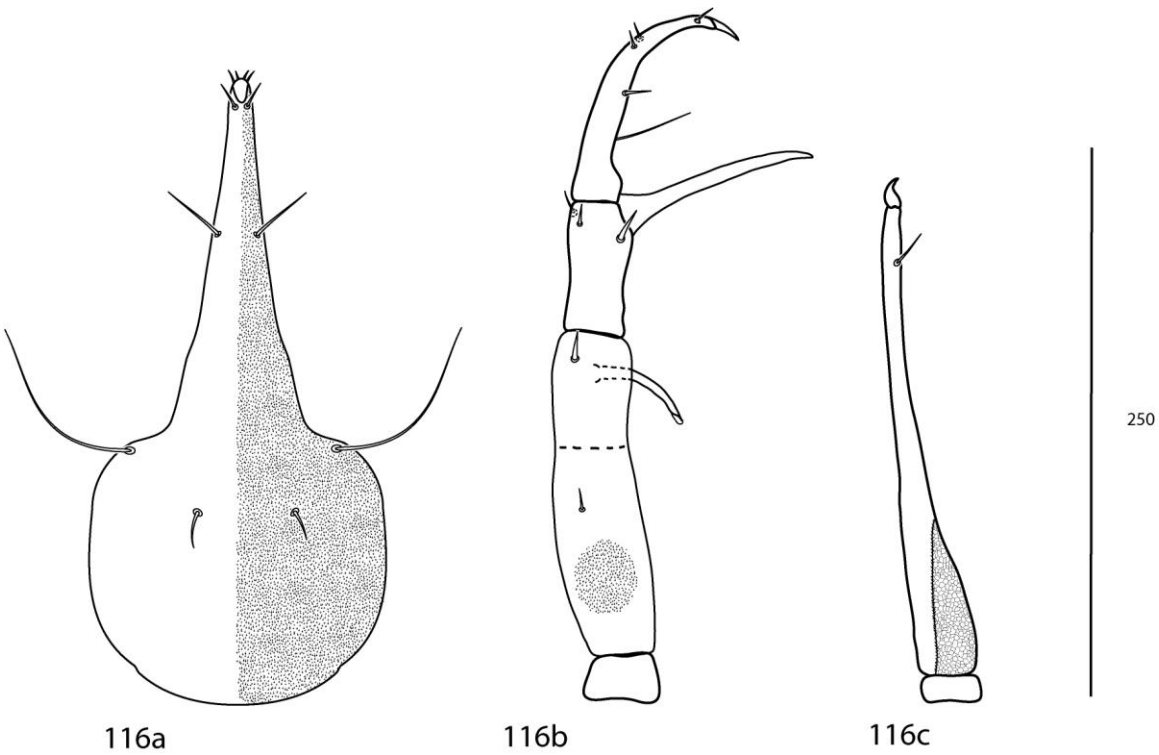


Figure 116. *Armascirus harrisoni* Smiley – female, gnathosoma. Dot-like pattern illustrated on palpal basifemur present on all segments except tibiotarsus. 116a) Subcapitulum. 116b) Pedipalp. 116c) Chelicera.

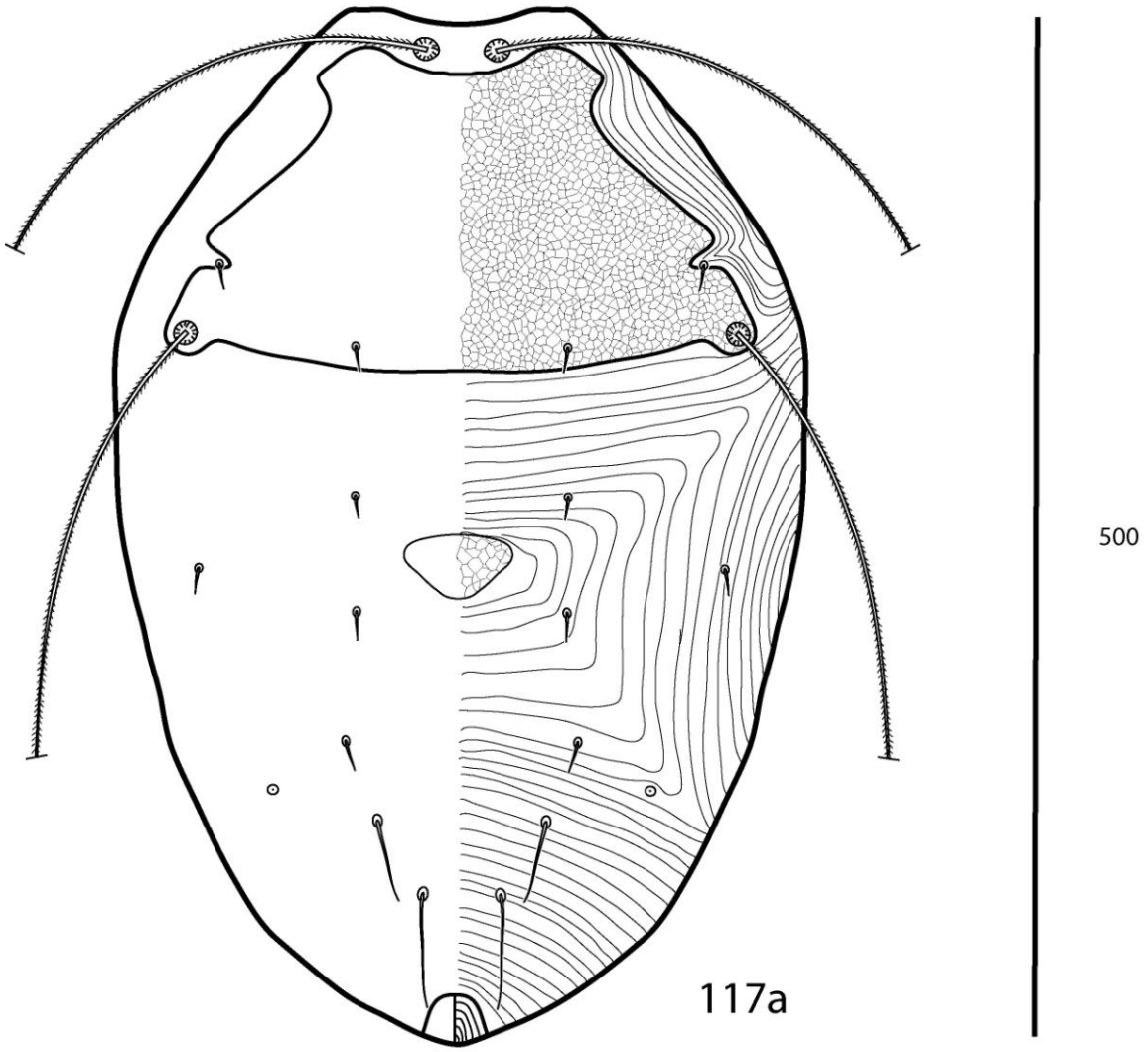


Figure 117a. *Armascirus harrisoni* Smiley – female, idiosoma, dorsum.

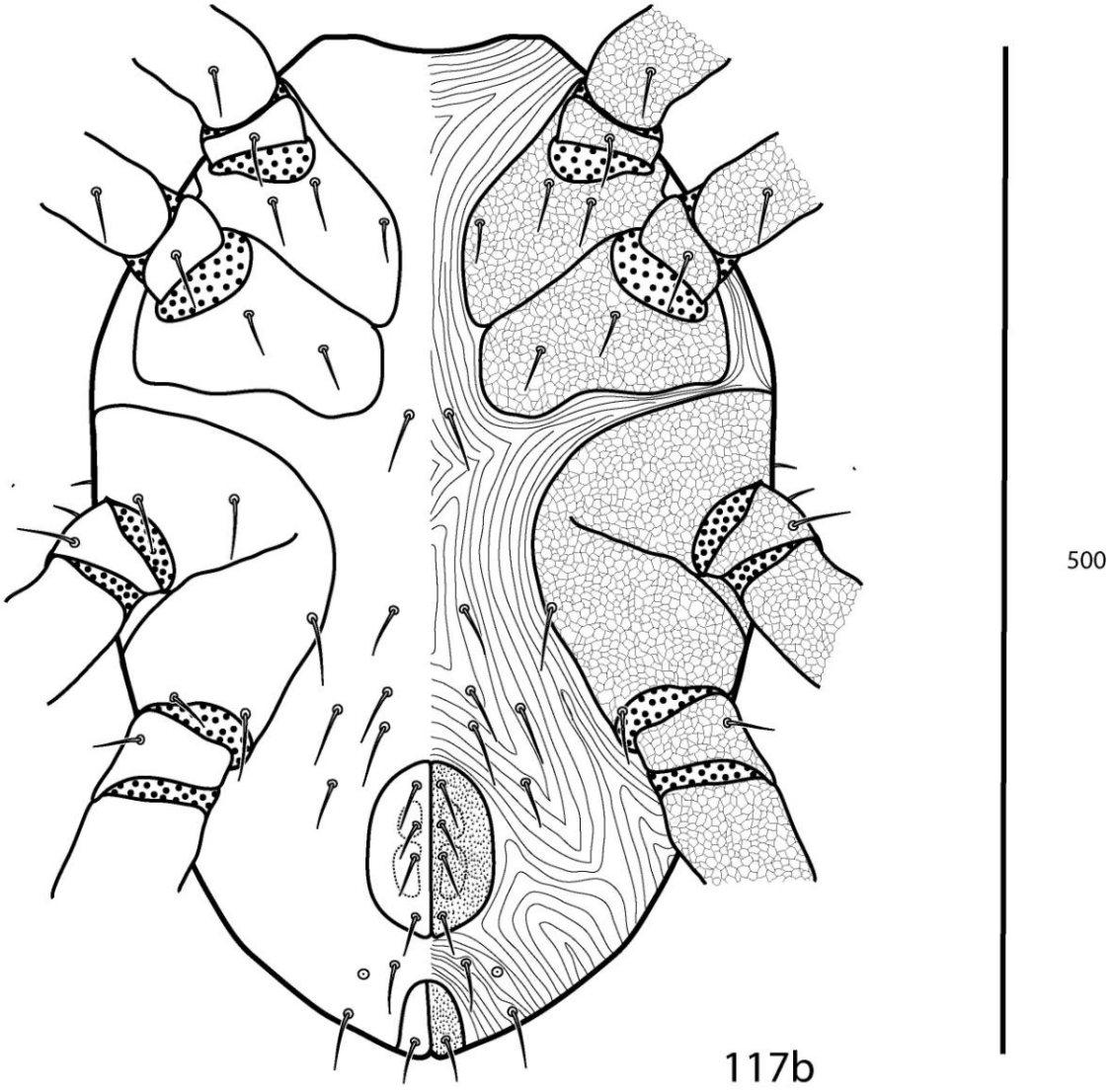


Figure 117b. *Armascirus harrisoni* Smiley – female, idiosoma, venter.

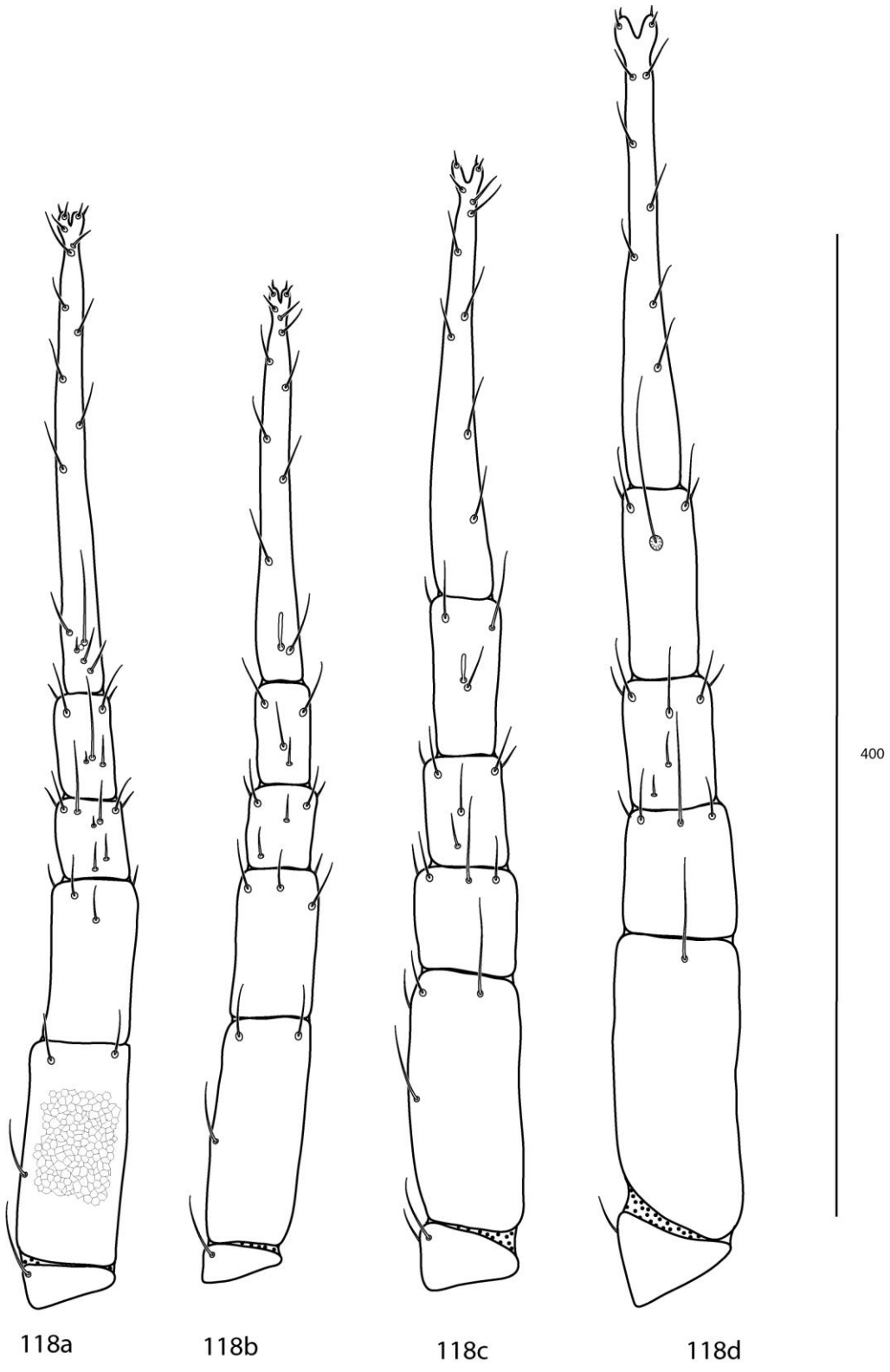


Figure 118. *Armascirus harrisoni* Smiley – female, legs, dorsum. Reticulated pattern illustrated on leg I basifemur present on all segments of all legs. 118a) Leg I. 118b) Leg II. 118c) Leg III. 118d) Leg IV.

***Dactyloscirus pseudophilippinensis* Skvarla & Dowling sp. nov.**

Diagnosis. *Dactyloscirus pseudophilippinensis* most closely resembles *D. philippinensis* in possessing a median shield and lateral platelets and having a single distally pointed apophysis adjoining the palpal genu and tibiotarsus. The apophysis on the palp basifemur is also very short and inconspicuous and blunted distally. *Dactyloscirus pseudophilippinensis* can be distinguished from *D. philippinensis* based on the following setal formulae: palp tibiotarsi with 5 sts instead of 4 sts; leg basifemora 5-5-3-2 sts instead of 5-5-3-1 sts.

Female. Idiosoma 388–513 (433, n=3) long, 273–375 (320) wide.

Gnathosoma (Fig. 119). *Subcapitulum* (Fig. 119a) longer than ½ the length of the idiosoma, 263–298 (278). 2 pairs of adoral setae present, the basal pair short and inconspicuous. Four pairs of setae (hg_{1-4}); hg_2 and hg_4 short, hg_1 2 times and hg_3 6 times as long as hg_2 and hg_4 (15, 7, 44, 8). *Palp* (Fig. 119b) 288–300 (293). Chaetotaxy: trochanter, absent; basifemur with 1 sts; telofemur with 1 spls and 1 apophysis, short and blunt distally; genu with 4 sts and apophysis adjoining genu and tibiotarsus long and blunted distally, apically hyaline; tibiotarsus with 1 spls (small and inconspicuous), 1 dtsl and 3 sts (1 long, basal; 2 short on apical half). The tibiotarsus ends in a claw. *Chelicera* (Fig. 119c) 205–225 (217), elongate, slightly curved and reticulate basally.

Dorsum (Fig. 120a). Propodosomal shield present and reticulate. Two setose trichobothria (*vi* and *sce*) present on shield; 215–263 (234) and 233 (n=1), respectively. Two setae (*ve* and *sci*) also present on shield; 6–10 (7) and 12–15 (14), respectively. Hysterosomal (median) shield and lateral platelets present, reticulate. Setae c_1– e_1 on median shield; 11, 13 and 16, respectively. C_2, f_1, h_1 on minute sclerotized plates barely

larger than setal socket; 11, 26 and 30, respectively. Cupule *im* present and laterad to e_1. Integument striated.

Venter (Fig. 120b). Coxal plates I and II fused but retaining suture, without polygonal pattern ventrally and bearing 3 sts and 3 sts, respectively. Coxal plates III and IV also fused but retaining suture, with reticulate pattern and bearing 3 sts - 1 pcs and 2 sts, respectively. 5 pairs of dorsal setae after coxae II (not including genital and anal setae). Genital plates weakly sclerotized and bearing 4 pairs of setae ($g_{1–4}$) and 2 pairs of papillae; $g_{1,2,3}$ arranged longitudinally, g_4 moved laterad of g_3 near the edge of the plate. Three pairs of setae on or adjacent to anal plates: 2 pseudanal setae ($ps_{1–2}$) and h_2. Cupule *ih* present and laterad to ps_2.

Legs (Fig. 121a–d). Legs I–IV shorter than body: 338–385 (363), 290–343 (316), 325–340 (333) and 338–388 (363), respectively. Chaetotaxy: trochanters I–IV, 1-1-2-1; basifemora I–IV, 5-5-3-2; telofemora I–IV, 5-5-4-4; genua I with 4 asl, 1 mst, 4 sts; genua II with 2 asl, 5 sts; genua III with 1 asl, 5 sts; genua IV with 2 asl, 5 sts; tibiae I with 2 asl, 1 mst, 4 sts; tibiae II with 1 asl, 5 sts; tibiae III with 1 bsl, 5 sts; tibiae IV with 1 T, 4 sts; tarsi I with 4 asl, 1 fam, 2 tsl, 15 sts; tarsi II with 1 asl, 1 tsl, 13 sts; tarsi III with 1 tsl, 17 sts; tarsi IV with 17 sts.

Male and developmental stages. Unknown

Etymology. This species is so named because it closely resembles *D. philippinensis*.

Materials examined (3 individuals on slides). HOLOTYPE, 1 female, *ex.* deciduous litter in grass on top of ridge, USA, Arkansas, Washington Co, Ozark National Forest, Weddington (36°06.322 N, 094°23.390 W). 26 July 2010, by M. J. Skvarla. APGD 10-0726-006 ● PARATYPE, 1 female, *ex.* moist deciduous litter drifted against slope in creek bottom, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.016 N, 093°20.137 W). 30 July 2010, by M. J. Skvarla. APGD 10-0730-006 ● PARATYPE, 1 female, *ex.* deciduous litter in grass on top of ridge, USA, Arkansas, Washington Co, Ozark National Forest, Weddington (36°06.322 N, 094°23.390 W). 15 Sept 2010, by M. J. Skvarla. APGD 10-0915-001

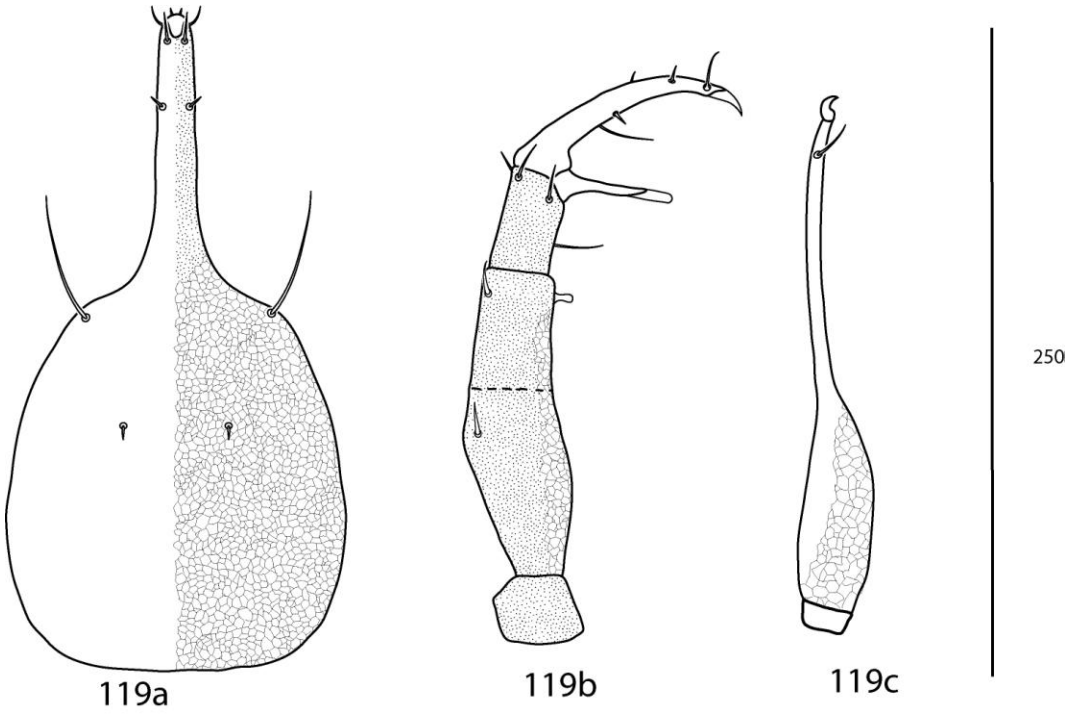


Figure 119. *Dactyloscirus pseudophilippinensis* **sp. nov.** – female, gnathasoma. 119a) Subcapitulum. 119b) Pedipalp. 119c) Chelicera.

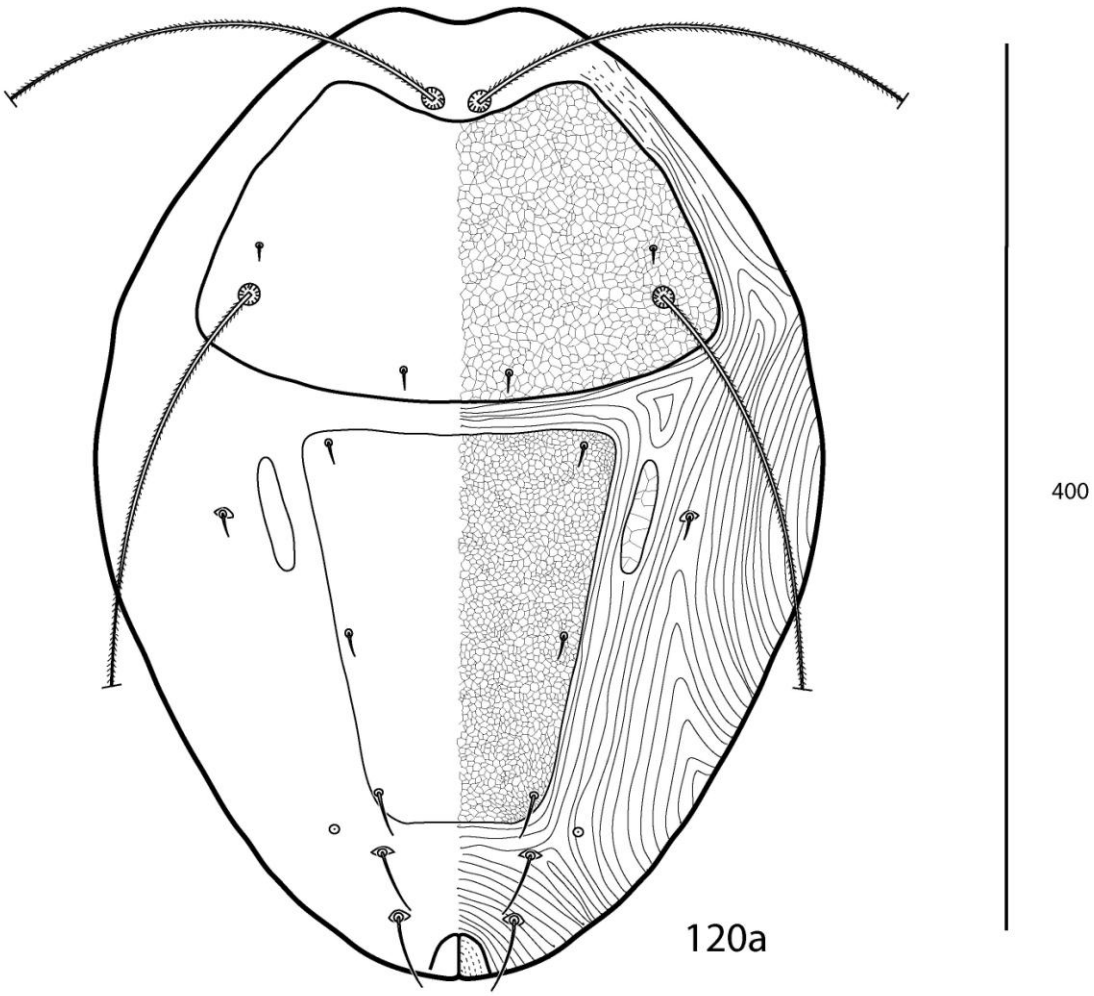


Figure 120a. *Dactyloscirus pseudophilippinensis* **sp. nov.** – female, idiosoma, dorsum.

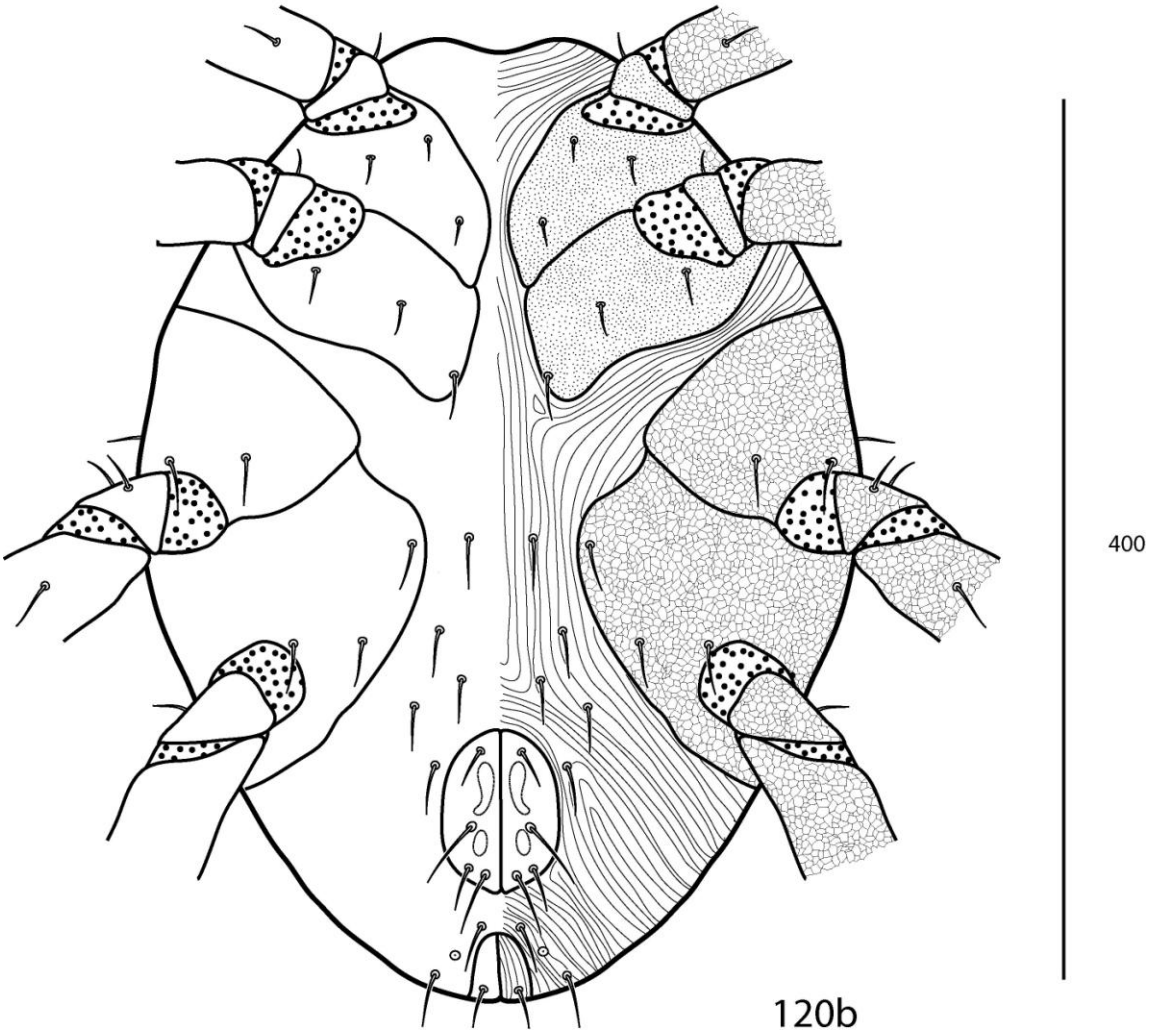


Figure 120b. *Dactyloscirus pseudophilippinensis* **sp. nov.** – female, idiosoma, venter.

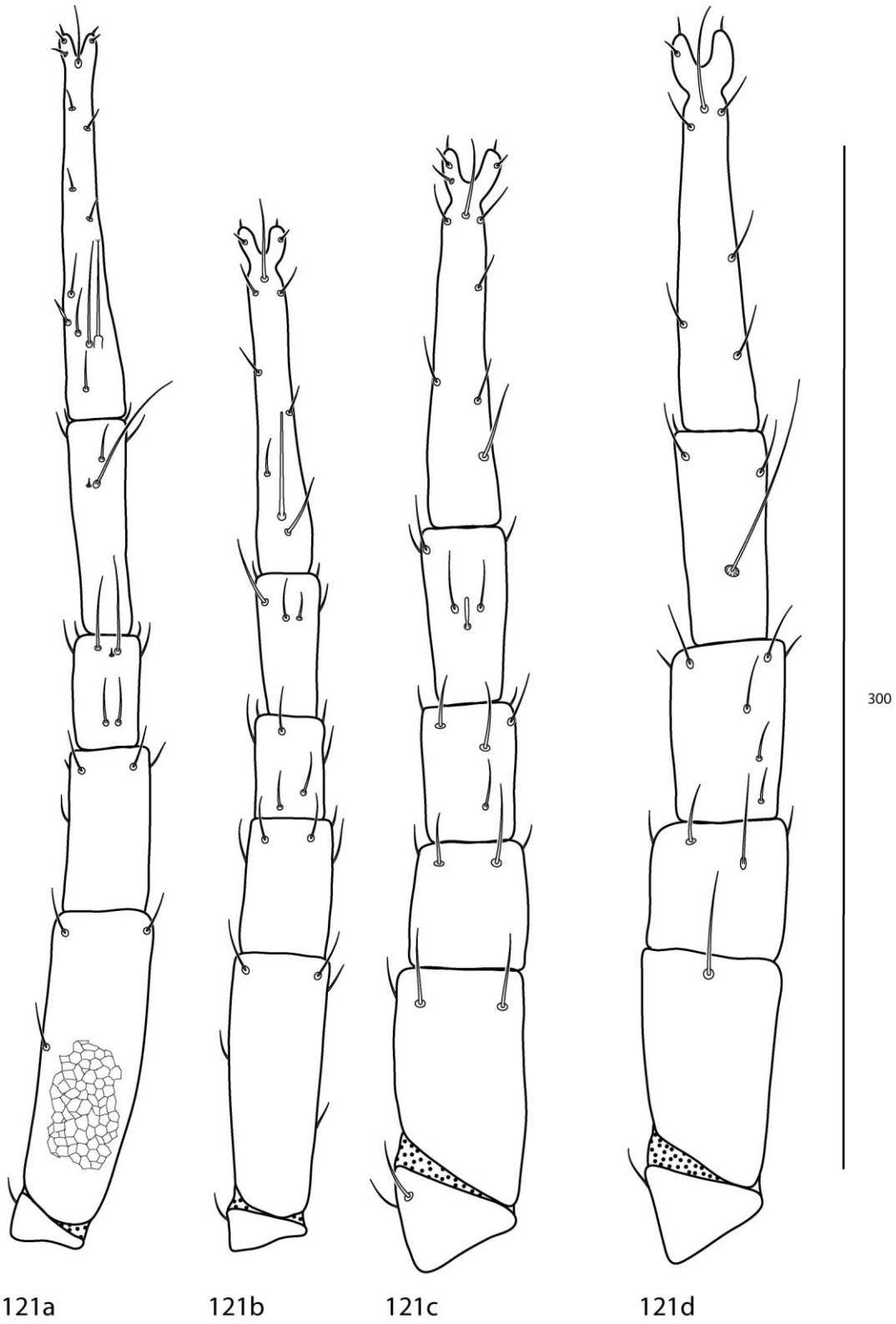


Figure 121. *Dactyloscirus pseudophilippinensis* **sp. nov.** – female, legs, dorsum. Reticulated pattern illustrated on leg I basifemur present on all segments of all legs. 121a) Leg I. 121b) Leg II. 121c) Leg III. 121d) Leg IV.

***Dactyloscirus dolichosetosus* Den Heyer, 1979.**

Dactyloscirus dolichosetosus Den Heyer 1979a: 96; Sepasgosarian 1984: 141; Smiley 1992: 223. Castro 2008: 91.

Diagnosis. *Dactyloscirus dolichosetosus* resembles *D. humuli*, *D. smileyi* and *D. condylus* in that it possesses long lateral platelets but lacks a median shield. It can be distinguished from *D. humuli* and *D. smileyi* by the length of setae f_1 and h_1: f_1 is shorter than h_1 in *D. humuli* and *D. smileyi* but equal in length in *D. dolichosetosus*. *Dactyloscirus dolichosetosus* possesses one telofemoral apophysis whereas *D.* condylus possesses a second flattened apophysis basally.

Remarks. Until recently this species was reported only from South Africa by Den Heyer (1979). The range expansion presented here, combined with Castro (2008) which reported it from Brazil, suggest it may have a much wider, possibly cosmopolitan, range. Den Heyer (1979) provides an abundance of illustrations and SEM images.

Material examined (17 individuals on slides)**.** 2 females, ex litter, USA, Mississippi, Lee Co, Natchez Trace mi 260 (34°08.083 N, 068°50.250 W). 16 June 2009, by J. G. Hill. APGD 10-0119-001 ● 1 females, ex litter, USA, Mississippi, Lee Co, Natchez Trace mi 260 (34°07.800 N, 068°50.300 W). 16 June 2009, by J. G. Hill. APGD 10-0205-002 ● 1 females, ex litter, USA, Mississippi, Lee Co, Natchez Trace mi 260 (34°16.40 N, 088°44.883 W). 16 June 2009, by J. G. Hill. Chickasaw ViII B ● 3 females, ex sycamore (*Platanus occidentalis*) litter on stable island in creek, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.259 N, 093°20.880

W). 8 October 2010, by M. J. Skvarla. APGD 10-1008-001 ● 1 female, ex saturated moss along creek bank, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.259 N, 093°20.880 W). 8 October 2010, by M. J. Skvarla. APGD 10-1008-005 ●1 female, ex moss along creek bank, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°02.016 N, 093°20.137 W). 10 October 2010, by M. J. Skvarla. APGD 10-1010-001 ●5 females, ex maple (*Acer* sp.) litter drift against small log in secondary forest, USA, Pennsylvania, Westmoreland Co, Irwin, Paintertown (40°22.183 N, 079°41.917 W). 19 July 2010, by M. J. Skvarla. APGD 10-0725-003 ● 1 female, ex maple (*Acer* sp.) and oak (*Quercus*) litter, USA, Pennsylvania, Westmoreland Co, Irwin, Paintertown (40°22.183 N, 079°41.917 W). 2 October 2010, by M. J. Skvarla. APGD 10-1002-003 ●1 female, USA, Pennsylvania, Somerset Co, Laurel Hill State Park, nr. Eberly Scout Reservation (40°00.963 N, 079°14.233 W). 26 August 2010, by M. J. Skvarla. APGD 10-0826-003 ● 1 tritonymph, pitfall in oak and juniper scrub, Missouri, Taney Co, Mark Twain National Forest, Hercules Glades (36°41.196 N, 092°58.263). 09 June 2010, by J. R. Fisher and M. J. Skvarla. APGD 10-0609-004.

***Neoscirula reticulata* Skvarla (in press)**

Diagnosis: *Neoscirula reticulata* Skvarla (in press) and *N. baloghi* Mejía-Recamier & Palacios-Vargas, 2007 can be distinguished from other *Neoscirula* by a lack of a cheliceral seta and medially fused coxal plates I and II. *N. reticulata* can be distinguished from *N. baloghi* by the presence of reticulations on the chelicerae, as well as differences in leg chaetotaxy as follows: genua II, 2 ats-5 sts; genua IV, 1 ats-5 sts.

Female. Idiosoma 265-338 (307, n=6) long, 195-238 wide (213).

Gnathosoma (Fig. 122). *Hypognathum* (Fig. 122a) small, less than ¼ length of idiosoma, 69-73 (71). Adoral setae absent. Four pairs of setae (hg_{1-4}): hg_1 is bent and nearly twice as long (20) as the other three (11, 9, 10). Single row of posterior polygonal ornamentation present. *Palp* (Fig. 122b) 44-53 (49). Chaetotaxy: trochanter, absent; basifemur, 1 sts; telofemur, 1 spls; genu, 4 sts; tibiotarsus, 4 sts, 1 spls, 1 dtsl. The tibiotarsus ends in a stout claw which lacks a tooth. *Chelicera* (Fig. 122c) 68-75 (71), thin distally with broad base; integument granulated dorsally, dorsomedially reticulate, and smooth ventrally.

Dorsum (Fig. 123a). Single oval propodosomal shield; finely granulated, lacking subcuticular reticulation. Two setose sensillae, *vi* and *sce*, on shield; 95 and 82, respectively. Two setae, *ve* and *sci*, also on shield; 21 and 9, respectively. Seven pairs of hysterosomal setae present; all occur on sclerotized, granulated plates. Setae c_1, c_2, d_1, e_1, and h_2 approximately equal in length (15, 12, 14, 16, 17); f_1 and h_1 longer (21, 24). f_2 absent. Cupule *im* present, laterad to e_1. Integument between setae striated.

Venter (Fig. 123b). Coxal plates I and II well sclerotized, fine subcuticular granulation forming striations. Plates fused medially into a sternal shield with narrowly rounded posterior tip. Complimented with 7 pairs of sts, sometimes capturing an extra pair of setae between coxae III. Coxal plates III and IV also well sclerotized and finely granulated. Coxae III with 3 sts, one of which may appear dorsal; coxae IV with 2 sts and 1 pcs. 3 pairs of setae on integument between coxae III and IV (not including pair sometimes captured by sternal shield). Granulae on integument form striations around coxae. Genital plates weakly sclerotized with 4 pairs of setae and 2 pairs of papillae.

Anal plates bearing 2 pairs of pseudanal setae (ps_1 & ps_2). Cupule *ih* present laterad to para-anal setae (*pa*).

Legs (Fig. 124a-d). All shorter than idiosoma. Length: I, 125-155 (143); II, 118-138 (127); III, 135-155 (146); IV, 153-190 (165). Setal formulae: trochanters 1-1-2-1 sts; basifemora, 4-5-3-1 sts; telofemora, 5-5-4-3 sts; genua I, 3 ats, 1mst, 4 sts; genua II, 2 asl, 5 sts; genua III, 1 asl, 5h sts; genua IV, 1 asl, 5 sts; tibiae I, 2 bsl, 5 sts; tibiae II, 1 bsl, 5 sts; tibiae III, 1 bsl, 5 sts; tibiae IV, 1 T, 4 sts; tarsi I, 2 bbsl ,2 asl, 1 fam, 2 tsl, 20 sts; tarsi II, 1 bsl, 20 sts; tarsi III, 1 tsl, 19 sts; tarsi IV, 19 sts.

Male and immatures. Unknown.

Etymology: This species is named for the distinctive reticulations on the chelicerae.

Material examined (6 individuals on slides). HOLOTYPE, female, *ex.* mixed cedar and oak litter, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (36°01.942 N, 093°20.010 W), 28 May 2010, J. R. Fisher and M. J. Skvarla, APGD 10-0528-008,001 ● PARATYPE, 2 females, *ex.* mixed cedar and oak litter, USA, Arkansas, Newton Co, Buffalo National River, Steel Creek (N 36°01.942 , W 093°20.010), 28 May 2010, J. R. Fisher and M. J. Skvarla, APGD 10-0528-008,002-003 ● PARATYPE, 3 females, *ex.* litter, USA, Missouri, Taney Co., Mark Twain National Forest (N 36°40.017, W 92°53.367), 22 May 2010, J. R. Fisher and D. M. Keeler, APGD 10-0522-002, 001-003.

Remarks. From Skvarla, Fisher, and Dowling (2011):

Neoscirula reticulata Skvarla **sp. nov.**, from the North American Ozark Highlands, most resembles *N. baloghi* Mejía-Recamier & Palacios-Vargas, 2007, from Jalisco, Mexico. This biogeographic relationship between the temperate forests of eastern North America and Mexico is not unusual. Well-known cases displaying this affinity include mosses (Crum 1952; Redfearn 1986), higher plants (Braun 1955; Dressler 1954; Miranda & Sharp 1950; Watson 1891), fungi (Miranda & Sharp 1950, Sharp 1948), and snakes, flying squirrels and plethodontid salamanders (see Martin & Harrel 1957). To the authors' knowledge, the present study represents the first attempt to implicate a mite, and perhaps any arthropod, as a representative of the Mexican-East North American affinity. The presumed low-dispersal capabilities and hyperdiversity of soil/litter dwelling organisms, as well as their underrepresentation in biogeographic studies, make them perfect candidates to address such questions .

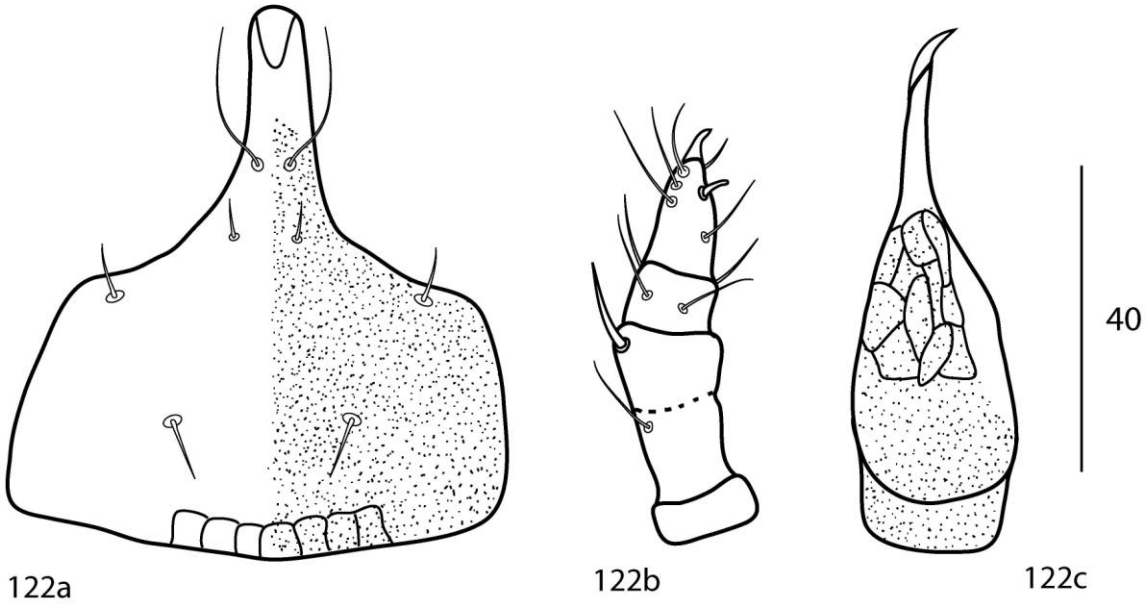


Figure 122. *Neoscirula reticulata* **sp. nov.** – female, gnathosoma. 122a. Subcapitulum. 122b. Pedipalp. 122c. Chelicera.

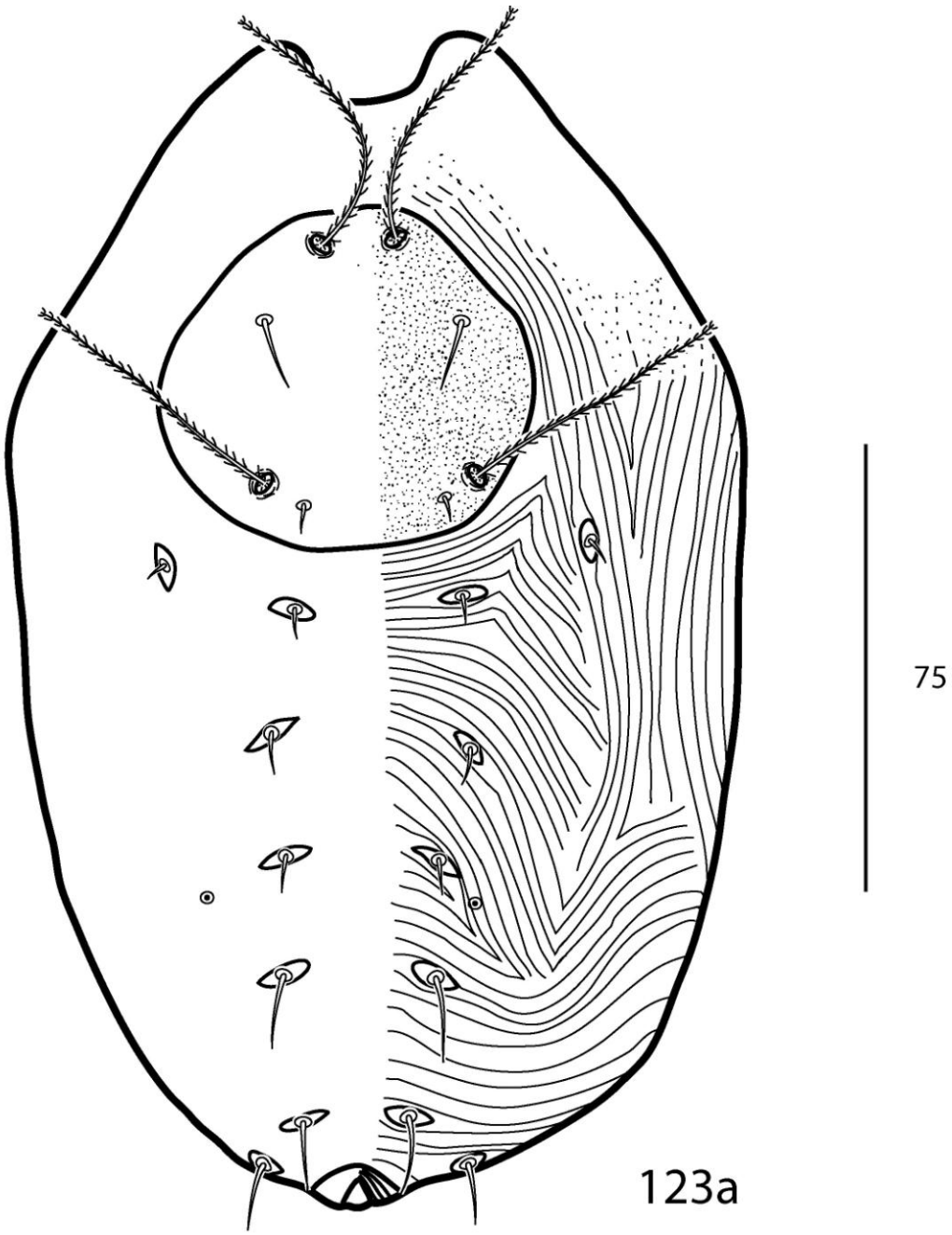


Figure 123a. *Neoscirula reticulata* **sp. nov.** – female, idiosoma, dorsum.

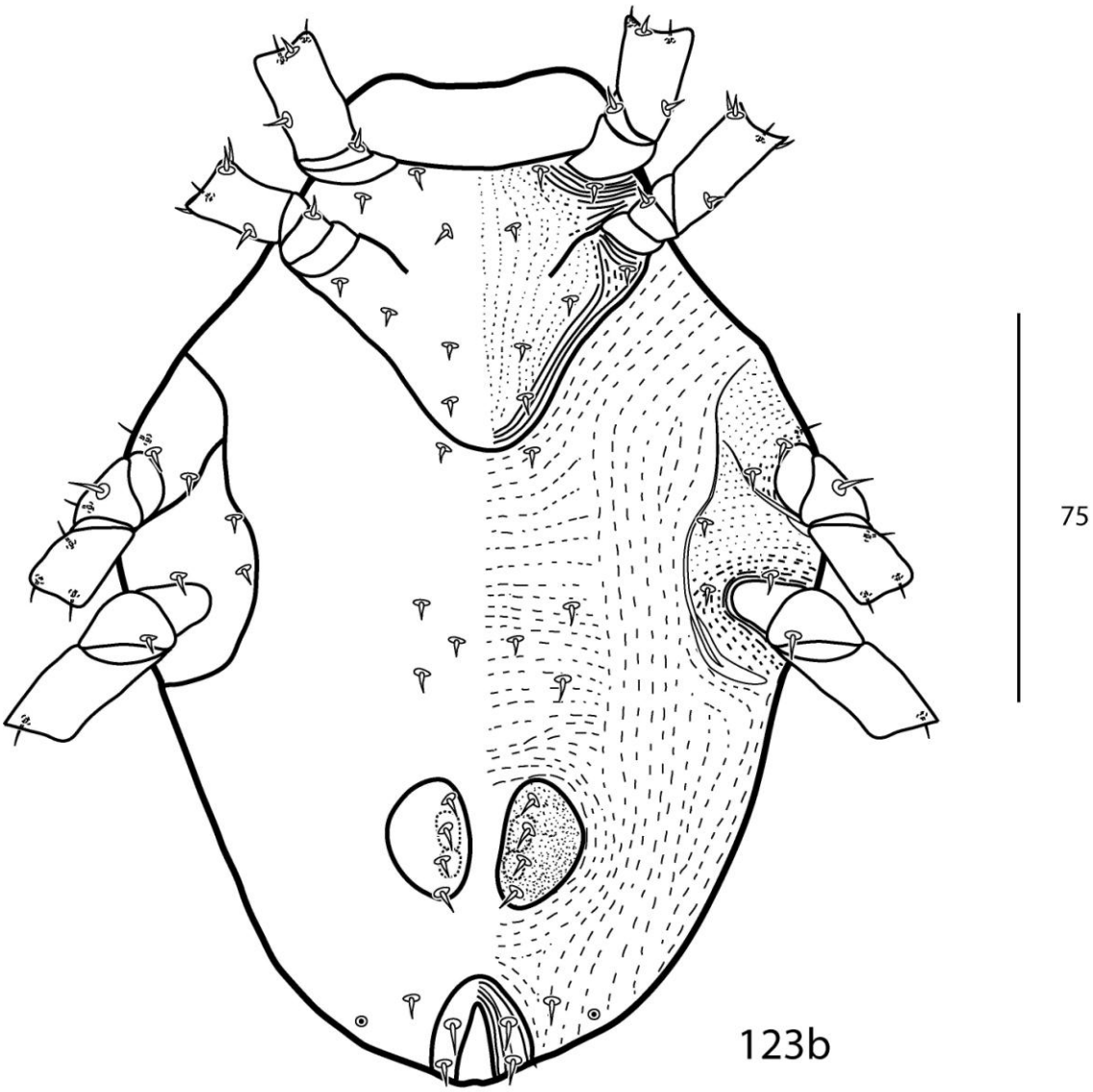


Figure 123b. *Neoscirula reticulata* **sp. nov.** – female, idiosoma, venter.

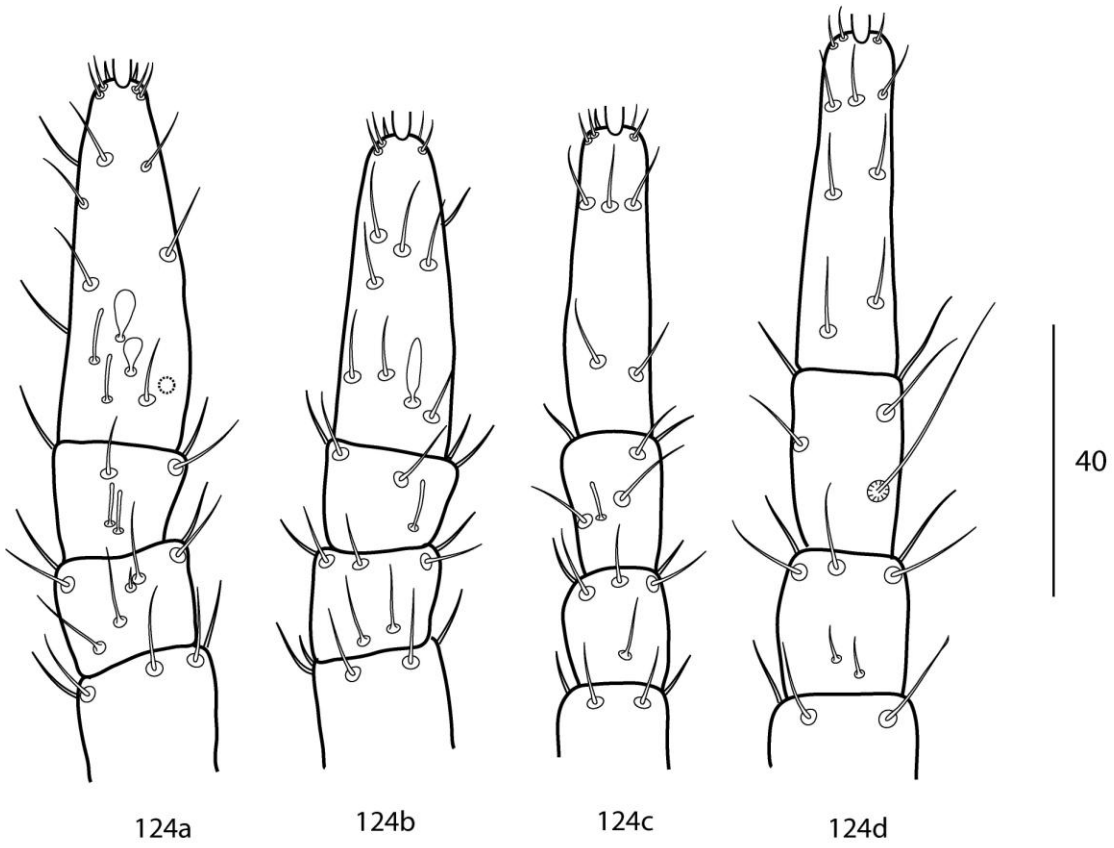


Figure 124. *Neoscirula reticulata* **sp. nov.** – female, legs: telofemora, genua, tibiae, and tarsi. 124a) Leg I. 124b) Leg II. 124c) Leg III. 124d) Leg IV.

***Pseudobonzia reticulata* (Heryford, 1965)**

Cunaxa reticulata Heryford 1965: 310.

Pseudobonzia reticulata Smiley 1975: 242; Den Heyer 1977c: 193; 1980b: 121; Sepasgosarian 1984: 143; Den Heyer & Castro 2008a: 44.

Diagnosis. *Pseudobonzia reticulata* can be differentiated from congeners by having simple setae on the basi- and telofemora, lacking setae f_2, and lacking the reticulated pattern on the leg podomeres.

Remarks. *P. reticulata* has previously only been reported from "humus litter from [an] abandoned grain silo" in Kansas. It is thus not surprising to find it in the Ozark Highlands; this is the first time, however, that it has been collected in a natural setting, specifically from leaf litter collected among tall, dead grass.

Materials examined (1 individual on a slide). 1 female, ex leaf litter among grass along ridge top, USA, Arkansas, Washington/Benton Co, Ozark National Forest, Weddington (36°06.322 N, 93°23.390 W). 15 September 2010, by M.J. Skvarla. APGD 10-0915-001.

IV. PHYLOGENETIC HYPOTHESES of CUNAXIDAE

Introduction

O'Connor (1984), Dabert *et al.* (2010) and Pepato, Rocha, & Dunlop (2010) recovered a monophyletic Prostigmata using morphological or molecular data when testing phylogenetic hypotheses about acariform mites. However, no rigorous phylogenetic hypothesis has been published focusing on Prostigmata. Norton et al. (1993) and Lindquist (1996) provided cladograms of taxa within Prostigmata (Figs. 1 & 2), but the relationships were based on unpublished analyses and data (Proctor 1998). Bdelloidea are often considered members of Eupodina, sister to the aquatic and mostly marine superfamily Halacaroidea. Vitzthum (1940-43) suggested Cunaxidae are closely related to Sperchontidae (Hydrachnida) based on the resemblance palpal shape and form and the claw-like tarsal empodium with rated tenent hairs, though this suggestion has been largely ignored.

Bdelloidea is probably a monophyletic lineage as both Bdellidae and Cunaxidae share a number of derived characters, such as the presence of trichobothria on leg segments, a solenidia present on the palp tibiotarsi, and unique leg segmentation consisting of a divided femur and fused tibiotarsus. How the two families are related is unclear. Most acarologists believe them to be sister to each other, though some think one family is paraphyletic with respect to the other or that they are wholly unrelated.

In order to test the current generic and subfamilial classification scheme of Cunaxidae the relationship between Cunaxidae and Bdellidae must be established. Subfamilies and genera have traditionally been proposed with little or no cladistic backing. This has two major problems. First, basal taxa may be grouped into genera or

subfamilies because they have fewer derived characters or share pleisomorphic characters lost derived taxa. Second, highly derived taxa that occur within established groupings may be classified separate from those groups, leading to paraphyly of the larger group. Both of these situations lead to classifications that do not reflect evolutionary history and are thus misleading.

In addition to testing the current classification scheme, evolutionary trends can be tracked across the phylogeny. Smiley (1992) considered *Parabonzia* the most basal cunaxid genus as they share a number of characteristics with Bdellidae, including 6–9 pairs of setae on the subcapitulum and "a five segmented palpus which resembles the palpi of the Bdellidae". He also considers cunaxids with 3–segmented palps the most derived, having "body sizes [that] are smaller and…adaptations to exploit different habitats and smaller prey." Without an established phylogeny these opinions cannot be corroborated and evolutionary trends within the family cannot be traced.

Materials and Methods

Cladistic Analysis. The analysis included every genus of Cunaxidae (26 genera) and Bdellidae (13 genera) as ingroup taxa and Anystidae, Eupodidae, Tydeidae, and Labidostommatidae as outgroup taxa. Halacarioidea, which has been suggested as the sister group of Bdelloidea, has been excluded from this analysis as their many adaptations to an aquatic lifestyle make determining homologies problematic. Forty seven characters were scored from adult females; males and non-adult stages were excluded as they are unknown from most species of Cunaxidae.

Characters states were obtained from literature and, when possible, confirmed with specimens. Characters present in at least two taxa, and thus potentially informative,

were included. Characters were equally weighted and unordered. Characters were coded as polymorphicwhen more than one character state existed within a single taxa. In some instances an apparently polymorphic character (for example, tarsal lobes absent; present and small; present and large) was divided into two characters (character 1: tarsal lobes absent or present; character 2: if present, tarsal lobes small or large) as an underlying relationship appeared to exist between the characters.

Character states that could not be determined were coded with a question mark. The uncertainty of a character was due to the complete absence of the character in the taxa in question (such as the number of setae on the palp femurogenu when the femora and genua of a particular taxa are not fused) or to uncertainty as to the homology of the character across taxa. A question mark was also scored when the state of a character could not be determined from the literature.

A heuristic search was carried out using Mesquite 2.74 (Maddison & Maddison 2010); this search was capped at 1000 trees. Trees were rearranged by subtree pruning and regrafting. A strict concensus tree was calculated using the resulting 1000 most parsimonious cladograms. Bootstap values, consistency index (C.I.) and retention index (R.I.) were calculated using WinClada 1.00.08 (Nixon 2002).

Characters and Character States.

Gnathasoma

I. *Shape of gnathasoma*: normal (0); elongated (1).

II. *Setae* hg_1: not geniculate (0); geniculate (1).

III. *Number of subcapitular setae*: 2 (0); 4 (1); 5 or more (2).

IV. *Pedipalps extend beyond distal end of subcapitulum by at least the last two segments*: no (0); yes (1).

V. *Pedipalp ends in a claw*: no (0); yes (1).

VI. *Pedipalp fixed digit*: absent (0); present (1).

VII. *Pedipalp femora divided*: no (0); yes (1).

VIII. *Pedipalp femora and genua fused*: no (0); yes (1).

IX. *Pedipalp tibiae and tarsi fused*: no (0); yes (1).

X. *Femoral apophysis*: absent (0); present (1).

XI. *Apophysis between genua and tibiae*: absent (0); present (1).

XII. *Number of setae on femurogenua*: 5 (5); 6 (6).

XIII. *Number of setae on basifemora*: 1 (0); more than 1 (1).

XIV. *Shape of basifemoral seta if only 1 seta present*: simple (0); spine-like (1).

XV. *Shape of telofemoral seta*: simple (0); spine-like (1); multi-branched (2).

XVI. *Cheliceral fixed digit*: absent (0); present (1).

XVII. *Number of cheliceral seta(e)*: 0 (0); 1(1), more than 1 (2).

XVIII. *Number of adoral setae*: 0 (0); 1 (1); 2 (2).

Dorsal idiosoma

XIX. *Eyes*: absent (0); present (1).

XX. *Naso*: absent (0); present (1).

XXI. *Number of dorsal trichobothria*. 0 (0); 1 (1); 2(2).

XXII. *Hysterosomal median plate*: absent (0); present (1).

XXIII. *Hysterosomal median plate fused to propodosomal shield if median plate present*: no (0); yes (1).

XXIV. *Idiosomal plates and shields patterned with reticulations*: no (0); yes (1).

XXV. *Cupule* ia: absent (0); present (1).

XXVI. *Cupule* im: absent (0); present (1).

XXVII. *Cupule* ip: absent (0); present (1).

XXVIII. *Setae* f_2: absent (0); present (1).

Ventral idiosoma

XXIX. *Coxae I-II fused into sternal shield*: no (0); yes (1).

XXX. *Number of setae on coxae I*: 3 or fewer (0); more than 3 (1).

XXXI. *Number of setae on coxae II*: 3 or fewer (0); more than 3 (1).

XXXII. *Number of setae on coxae III*: 3 or fewer (0); more than 3 (1).

XXXIII. *Number of setae on coxae IVI*: 3 or fewer (0); more than 3 (1)

XXXIV. *Internal genital setae*: absent (0); present (1).

XXXV. *Cupule* ih: absent (0); present (1).

XXXVI. *Number of setae on genital plates*: 4 (0); more than 4 (1).

Legs

XXXVII. *Tibiae I trichoborhtium*: absent (0); present (1).

XXXVIII. *Tibiae II trichoborhtium*: absent (0); present (1).

XXXIX. *Tarsus III trichoborhtium*: absent (0); present (1).

XL. *Tibiae IV trichoborhtium*: absent (0); present (1).

XLI. *Tarsus IV trichoborhtium*: absent (0); present (1).

XLII. *Tasri constricted distally, forming lobes*: no (0); yes (1).

XLIII. *Tarsal lobes, if present*: small (0); large (1).

XLIV. *Leg tibiae divided into basi- and telofemora*: no (0); yes (1).

XLV. *Shape of empodium*: pad-like (0); 4-rayed (1).

XLVI. *Ambulacral claw sculpturing*: smooth (0); rippled (1)

XLVII. *Number of setae complementing anal plates*: 1 (1); 2 (2); more than 2 (3)

The coded matrix run in this analysis is presented in Appendix III.

Results and Discussion

The heuristic search resulted in 1000 cladograms with a length of 131 (CI = 52; RI = 86). The strict concensus of these cladograms is given in Figure 125. Bootstrap values >50 are presented over each branch.

Monophyly of Bdelloidea and Cunaxidae. The strict concensus cladogram suggests that Bdelloidea is a monophyletic lingeage and that Cunaxidae and Bdellidae are sister clades, rather than a single clade in which one family grades into the other. The exclusion of Halacaroidea is problematic for both of these assumptions as some halacaroids seem to share a number of characters with Bdelloidea (e.g., elongated gnathasoma, elongated pedipalps) and Cunaxidae (claw-like empodium). I attempted to include Halacaridae in the analysis, but was unsure of the homology and state of more than half of the characters. Inclusion of Halacaroidea within a molecular phylogeny may change one or both of the conclusions suggested by the morphological cladogram.

Validity of subfamilies. *Parabonzia* is suggested by the strict concensus cladogram to be the most basal cunaxid genus and sister to the rest of the family. This is not surprising as *Parabonzia* shares many characteristics with Bdellidae. This conclusion is not in line with the current classification scheme, however, which places *Parabonzia* and *Bonzia* in a single subfamily, Bonzinae. This grouping is based mainly on the

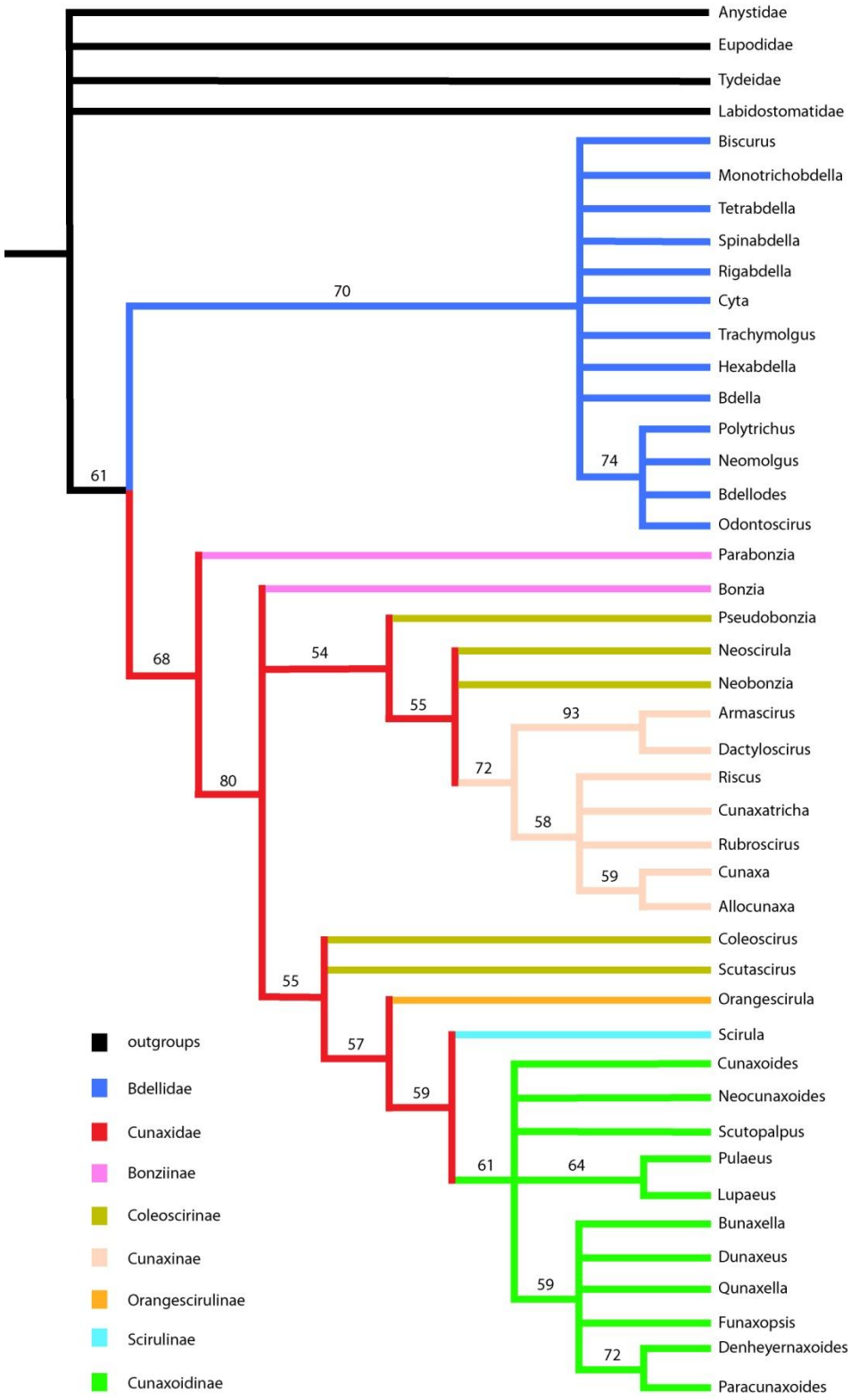


Figure 125. Strict concensus tree of 1000 most parsimonious trees (length = 131; CI = 52; RI = 86) obtained using 47 characters. Bootstrap values > 50 are presented over each branch. Subfamilies are color coded according to figure key.

presence of a multi-branced seta on the palp telofemora, which does not appear in any other cunaxid or bdellid genera.

The subfamily Cunaxinae is recovered as a monophyletic lineage within a larger clade formed by the addition of three genera (*Pseudobonzia*, *Neoscirula*, and *Neobonzia*) currently classified within Coleoscirinae. This suggests that Cunaxinae is a valid subfamily, but should be redefined to accomidate the two coleoscirine genera. The defining character of the clade is the absence of fusion between a hysterosomal plate (if it is present) with the propodosomal plate and presence of 5-segmented palps

There is second clade formed by a grade composed of a basal polytomy of *Coleoscirus* and *Scutascirus* followed bya grade of the monobasic Orangescirulinae and Scirulinae leading to a subclade comprising the Cunaxoidinae that is internally unresolved. The number of palpal segments is reduced through fusion of segments from 5 in the basal taxa to 4 in *Scirula* to 3 in the Cunaxoidinae; the only character defining this clade is the expansion of the hysterosomal plate and fusion with the propodosomal shield.

The lack of resolution and support in the cladogram is problematic in terms of possible taxonomic revisions. There are trends that suggest the need for changes in classification, but resolution and support are too weak to confidently make those changes. For example, as mentioned above *Bonzia* is not recovered with *Parabonzia*, thus prompting the disolusion of Bonzinae. However, *Bonzia*'s placement within Cunaxidae is uncertain. With more data it may be recovered with *Parabonzia*, or within the two major clades.

The classification of the clade containing *Coleoscirus*, *Scutascirus*, Scirulinae, Orangescirulinae, and Cunaxoidinae depends on having better resolution. If the basal polytomy is resolved and *Coleoscirus* and *Scutascirus* form a monophyletic lineage the clade could be broken into two subfamilies: *Coleoscirus* + *Scutascirus* and Orangescirulinae + Scirulinae + Cunaxoidinae. Alternately, it could be broken into four subfamilies, *Coleoscirus* + *Scutascirus*, Orangescirulinae, Scirulinae, Cunaxoidinae. If the basal polytomy is resolved and the coleoscirine genera are not monophyletic, that is they grade into the rest of the clade, five subfamilies could be proposed - viz. Coleoscirinae, Scutascirinae, Orangescirulinae, Scirulinae, and Cunaxoidinae - or one diverse subfamily could be redefined to include all of the taxa.

Evolutionary trends. While the strict concensus cladogram is not resolved enough to be a basis for classification changes, it does suggest directions in evolutionary trends. *Parabonzia* is the only genus of Cunaxidae that has long sensory setae on the palps and lacks a claw on the tibiotarsi. This suggests that the common ancestor of Cunaxidae and Bdellidae had more bdellid-like palps. It also suggests that the the tibiotarsal claw and addition of other spines and apophyses has been important in cunaxid evolution as very few taxa have lost them.

The most derived taxa (*Allocunaxa* in the *Pseudobonzia* + *Neoscirula* + *Neobonzia* + Cunaxinae clade and Cunaxoidinae in the *Coleoscirus* + *Scutascirus* + Scirulinae + Orangescirulinae + Cunaxoidinae clade) have palps in which the basifemora, telofemora, and genu have fused into a femurogenu, resulting in a functionally 3-segmented pedipalp. This fusion in *Allocunaxa* is complete, though the previous articulations are indicated by the presence of dark lines. The palp segmentation of Cunaxoidinae can be inferred

through muscle attachment and setal placement as there are no lines that indicate the fused segments. In addition there are many species across multiple genera that demonstrate this fusion in Cunaxoidinae as opposed to the single known species of *Allocunaxa*. This seems to indicate that the fusion is more recent evolutionarily in *Allocunaxa* than it is in Cunaxoidinae. It is interesting that unrelated, derived taxa seem to be convergently reducing the number of functional palp segments.

Conculsions. The morphological phylogenetic hypothesis presented here illustrates possible inconsistancies between current classification schemes and evolutionary history. A more resolved, better supported phylogeny must be elucidaded before such changes can be made with any kind of confidence. As the morphological characters presented in this study did not provide the needed reolusion and support genetic characters are the next logical step.

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Appendix I – Examples of Errors in Smiley (1992)

1. Bonzinae and Cunaxinae (spelled as proposed by the original authors) are consistently misspelled as Bonziinae and Cunaxiinae.

2. *Cunaxa meiringi* is spelled without an i, viz. *Cunaxa meiring*.

3. In a flow diagram (p. 36), the name Coleoscirulinae appears. Smiley apparently meant Coleoscirinae. However, in the key to subfamilies (p. 41) neither Coleoscirinae or Coleoscirulinae appear.

4. Smiley states about the legs that "[n]o efforts were made to designate or study the chaetotaxy" but then synonymised *Rubroscirus* and *Cunaxa* on the basis of leg chaetotaxy. He made no effort to explain why he ignored all other generic characteristics of *Rubroscirus* (viz., the dorsal plates of *Rubroscirus* being reticulated and the dorsal plates of *Cunaxa* totally lacking in reticulations).

5. The same illustrations are used to redescribe *Cunaxa setirostris* (in Smiley 1975, drawings 12A & B) and describe *Cunaxa metzi* (in Smiley 1992, drawings 98A & B) with absolutely no explaination.

Appendix II – Illustration citations

Some illustrations have been redrawn from published sources. Citations for the original publications are given below. Illustrations not included in this appendix are original works by the author.

Figure 1	Norton *et al.*, 1993
Figure 2	Lindquist, 1996
Figure 17a	Corpuz-Raros, 1996c
Figure 17b	Lin & Zhang, 2002
Figure 18	Den Heyer, 1975
Figure 19	Smiley, 1992
Figures 23a, b	Castro & Den Heyer, 2009
Figure 25a	Nesbitt, 1946
Figures 25b, c	Kuznetzov & Livshitz, 1979
Figure 26a	Oudemans, 1931
Figure 26b	Sionti & Papadoulis, 2003
Figures 26c, d	Smiley, 1992
Figure 27	Michocka, 1982
Figure 28a	Kuznetzov & Livshitz, 1979
Figure 28b	Gupta & Ghosh, 1980
Figure 29	Kuznetzov & Livshitz, 1979
Figures 32a, c	Lin, Zhang & Ji, 2001
Figure 32d	Corpuz-Raros, 2007
Figure 33a	Lin, Zhang & Ji, 2003

Figure 33b	Den Heyer, 1980
Figure 33c	Baker & Hoffmann, 1948
Figures 34a, b	Den Heyer, 1980
Figure 35	Corpuz-Raros, 1996b
Figures 36a, 37a	Corpuz-Raros & Gruèzo, 2007
Figures 36b, 37b	Corpuz-Raros, 1996b
Figure 38	Baker & Hoffmann, 1948
Figure 39b	Castro & Den Heyer, 2009
Figures 41a, 42c, 43a	Smiley, 1992
Figure 44b.	Castro & Den Heyer, 2009
Figures 45a, b	Corpuz-Raros, 1996
Figure 46a	Den Heyer, 1981
Figure 47	Corpuz-Raros, 1996
Figure 49a	Smiley, 1992
Figure 51a	Den Heyer 1979c
Figure 51b	Den Heyer 2006
Figure 51c	Den Heyer and Castro 2008c
Figure 51d	Castro and Den Heyer 2008
Figure 56a	Bashir, Afzal & Khan, 2008
Figure 56c	Bashir & Afzal, 2005
Figure 56d	Den Heyer, 1978b
Figure 56i	Chaudhri, 1977
Figure 57a	Kalúz, 2009

Figure 58a	Den Heyer, 1978
Figure 58b	Smiley, 1992
Figure 59a	Corpuz-Raros, 2008
Figure 59b	Chaudhri, 1977
Figure 61a	Den Heyer, 1979a
Figure 61b	Corpuz-Raros, 1995
Figure 61d	Swift, 1996
Figure 61f	Smiley, 1992
Figures 61h, i	Corpuz-Raros, 2008
Figure 62a	Inayatullah & Shahid, 1996
Figure 62b	Gupta & Ghosh, 1980
Figures 62c, d	Corpuz-Raros, 2008
Figure 63a	Smiley, 1992
Figure 63b	Corpuz-Raros, 1995
Figure 64a	Chaudhri, 1980
Figure 64b	Smiley, 1992
Figure 64c	Gupta, 1981
Figure 64d	Smiley, 1992
Figure 64e	Inayatullah & Shahid, 1996
Figure 65a, b	Corpuz-Raros, 1995
Figure 65c	Den Heyer, 1979a
Figure 65d	Corpuz-Raros, 2008
Figure 67a	Sergeyenko, 2009

Figure 67d	Den Heyer, 1979e
Figure 67e	Khaustov & Kuznetzov, 1998
Figure 68a	Den Heyer 2009
Figure 68b	Den Heyer, 1979a
Figures 69a, b	Sergeyenko, 2009
Figure 70a	Khaustov & Kuznetzov ,1998
Figure 70b	Sergeyenko, 2009
Figure 71b	Khaustov & Kuznetzov, 1998
Figure 71c	Smiley, 1992
Figure 71d	Baker & Hoffmann, 1949
Figure 71e	Den Heyer, 1979d
Figure 72a	Smiley, 1992
Figure 72b	Den Heyer, 1979d
Figure 72c, d	Smiley, 1992
Figure 73a	Sergeyenko, 2003
Figure 80	Tseng, 1980
Figure 81	Corpuz-Raros, 1996
Figure 82a	Den Heyer, 1978c
Figure 83a, b	Den Heyer, 1980b
Figure 84a	Shiba, 1978
Figure 85a	Muhammad & Chaudhri, 1992
Figure 85b	Den Heyer, 1980b
Figure 87a	Corpuz-Raros, 1996

Figures 88a, 89a	Corpuz-Raros, 1996
Figure 88b, 89b	Shiba, 1978
Figure 90b	Mejía-Recamier & Palacios-Vargas, 2007
Figure 91b	Den Heyer, 1977a
Figure 93b	Den Heyer & Castro, 2008b
Figure 94a	Smiley, 1992
Figure 95a	Lin & Zhang, 1998
Figure 95b	Den Heyer & Castro, 2008b
Figure 96a	Lin & Zhang, 2002
Figure 97b	Corpuz-Raros, 1996
Figure 99b, c	Smiley, 1992
Figure 100a	Den Heyer, 1977
Figure 100b	Smiley, 1992
Figure 102a	Corpuz-Raros, 2008
Figure 102b	Den Heyer & Castro, 2008a
Figure 103a	Baker & Hoffmann,1948
Figure 103b	Corpuz-Raros & Garcia, 1996

Appendix III – Character Matrix used in Morphological Phylogenetic Analysis

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXV	XXVI	XXVII	XXVIII	XXIX	XXX
Anystidae	0	0	1&2	0&1	1	1	0	1	0&1	0	0	?	?	?	0	0	?	?	1	1	2	0	?	0	1	0&1	0&1	0&1	1	1
Eupodidae	0	0	1	0	0	0	0	0	1	0	0	?	?	?	0	1	1	1	0&1	1	2	0	?	0	0&1	0&1	0&1	0	0	0
Tydeidae	0	0	?	0	0	0	0	0	1	0	0	?	?	?	0	?	?	?	0	0	1	?	?	0	1	1	0	?	?	?
Labidostomatid	0	0	?	0	?	0	0	?	0	0	0	?	?	?	0	1	2	0	1	0	2	1	1	0	0	0	0	1	1	1
Parabonzia	1	0	2	0	0	0	0	1	0	1	0	?	1	0	2	0	1	2	0	0	2	1	0	0	0	1	0	1	1	1
Bonzia	1	1	1	0	1	0	0	1	0	1	0	?	1	0	2	0	0&1	2	0	0	2	1	0	0	0	1	0	1	0	0
Coleoscirus	1	0	1	0	1	0	0	1	0	1	0	?	1	0	0	0	1	2	0	0	2	1	1	0&1	0	1	0	1	0	0
Scutascirus	1	0	1	0	1	0	0	1	0	1	0	?	1	0	?	0	1	2	0	0	2	1	1	0&1	0	1	0	1	0	0
Neoscirula	1	0	1	0	1	0	0	1	0	1	0	?	1	0&1	?	0	0&1	2	0	0	2	0	?	0&1	0	1	0	0&1	0	0
Pseudobonzia	1	0	1	0	1	0	0	1	0	1	0	?	1	0	?	0	1	2	0	0	2	0	?	0	0	1	0	0	0	0
Neobonzia	1	0	1	0	1	0	0	1	0	1	0	?	1	0	0	0	1	2	0	0	2	0	?	1	0	1	0	0	0	0
Armascirus	1	0	1	1	1	0	1	1	0	1	1	?	1	0	1	0	1	2	0	0	2	0&1	0	1	0	1	0	0	0	0
Dactyloscirus	1	0	1	1	1	0	1	1	0	1	1	?	1	1	1	0	1	2	0	0	2	0&1	0	1	0	1	0	0	0	0
Cunaxa	1	0	1	1	1	0	1	1	0	1	0	?	1	0	0	0	1	2	0	0	2	0&1	0	0	0	1	0	0	0	0
Riscus	1	0	1	1	1	0	0	1	0	1	0	?	1	0	0	0	1	2	0	0	2	0	?	1	0	1	0	0	0	0
Allocunaxa	1	0	1	1	1	0	0	1	0	1	0	?	1	0	0	0	1	2	0	0	2	1	0	0	0	1	0	0	0	0
Cunaxatricha	1	0	1	1	1	0	0	1	0	1	0	?	1	0	0	0	1	2	0	0	2	0	?	1	0	1	0	0	0	0
Rubroscirus	?	?	?	?	?	?	?	?	0	1	0	?	1	0	0	0	1	2	0	0	2	0&1	0	1	0	1	0	0	0	0
Pulaeus	1	0	1	0	1	0	0	0	1	1	0	5	?	?	?	0	1	2	0	0	2	1	1	0	0	1	0	0&1	0	0
Lupaeus	1	0	1	0	1	0	0	0	1	1	0	5	?	?	?	0	1	2	0	0	2	1	1	0	0	1	0	0&1	0	0
Cunaxoides	1	0	1	0	1	0	0	0	1	1	0	5	?	?	?	0	0	2	0	0	2	1	0&1	0	0	1	0	0&1	0	0
Neocunaxoides	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	1	2	0	0	2	1	1	0	0	1	0	0&1	0	0
Denheyernaxoides	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	?	0	0	0	2	0	?	0	0	1	0	0	0	0
Scutopalpus	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	?	2	0	0	2	1	1	0	0	1	0	0&1	0	0
Bunaxella	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	0	2	0	0	2	0	?	0	0	1	0	0	0	0
Dunaxeus	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	0	2	0	0	2	0	?	0	0	1	0	0	0	0
Qunaxella	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	0	2	0	0	2	0	?	0	0	1	0	0	0	0
Funaxopsis	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	0	2	0	0	2	0	?	0	0	1	0	1	0	0
Paracunaxoides	1	0	1	0	1	0	0	0	1	1	0	6	?	?	?	0	?	0	0	0	2	0	?	0	0	1	0	0	0	0
Orangescirula	1	1	1	0	1	0	0	1	0	1	0	?	1	1	1	0	0	2	0	0	2	1	1	1	0	1	0	?	0	0
Scirula	1	0	1	0	1	0	0	0	0	1	0	?	1	1	1	0	1	2	0	0	2	1	1	0	0	1	0	1	0	0
Polytrichus	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	0	0
Biscirus	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	0	1	1
Monotrichobdella	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	0	1	1
Tertabdella	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	0	1	1
Spinabdella	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	0	1	1
Rigibdella	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	1	0	0	?	?	?	?	1	1
Cyta	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	1	1	1	?	1	1
Trachymolgus	1	0	0	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	1	0	0	1	1	1	1	1	1
Hexabdella	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	1	1
Bdella	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	1	1
Neomolgus	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	1	1
Bdellodes	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	1	1
Odontoscirus	1	0	2	0	0	0	0	1	0	1	0	?	2	?	0	1	?	2	1	0	2	0	?	0	?	?	?	?	1	1

	XXXI	XXXII	XXXIII	XXXIV	XXXV	XXXVI	XXXVII	XXXVIII	XXXIX	XL	XLI	XLII	XLIII	XLIV	XLV	XLVI	XLVII
Anystidae	1	0&1	?	0&1	1	1	0	0	0	0	0	0	?	0	0	?	?
Eupodidae	0	0	1	0&1	1	1	0	0	0	0	0	0	?	0&1	0	?	?
Tydeidae	?	?	1	1	1	1	0	0	0	0	0	0	?	?	0	?	?
Labidostomatid	1	1	?	0	1	1	0	0	0	0	0	0	?	0	0	?	3
Parabonzia	1	1	1	1	1	1	0	0	0	1	0	0	?	1	1	?	3
Bonzia	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	2
Coleoscirus	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	2
Scutascirus	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	2
Neoscirula	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	0	2
Pseudobonzia	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	1	2
Neobonzia	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	1	2
Armascirus	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	?	2
Dactyloscirus	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	?	2
Cunaxa	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	?	1
Riscus	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	?	1
Allocunaxa	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	?	1
Cunaxatricha	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	?	1
Rubroscirus	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	?	1
Pulaeus	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	1
Lupaeus	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	1
Cunaxoides	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	?	1
Neocunaxoides	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	?	1
Denheyernaxoides	0	0	0	1	1	0	0	0	0	1	0	0	?	1	1	?	1
Scutopalpus	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	?	1
Bunaxella	0	0	0	1	0	0	0	0	0	0	0	0	?	1	1	?	1
Dunaxeus	0	0	0	1	0	0	0	0	0	0	0	0	?	1	1	?	1
Qunaxella	0	0	0	1	0	0	0	0	0	0	0	0	?	1	1	?	1
Funaxopsis	0	0	0	1	0	0	0	0	0	0	0	0	?	1	1	?	1
Paracunaxoides	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	?	1
Orangescirula	0	0	0	1	0	0	0	0	0	0	0	0	?	1	1	?	2
Scirula	0	0	0	1	0	0	0	0	0	1	0	0	?	1	1	?	?
Polytrichus	0	0	1	1	1	1	1	1	1	1	1	0	?	1	0	?	?
Biscirus	1	1	1	?	1	1	1	0	0	1	1	0	?	1	0	?	?
Monotrichobdella	1	1	1	?	1	1	1	0	1	1	1	0	?	1	0	?	?
Tertabdella	1	1	1	?	1	1	0	0	1	0	1	0	?	1	0	?	?
Spinabdella	1	1	1	?	1	1	1	0	1	1	1	0	?	1	0	?	?
Rigibdella	1	1	1	?	1	1	1	0	1	1	0	0	?	1	0	?	?
Cyta	1	1	1	0	1	1	1	0	1	1	0	0	?	1	0	?	?
Trachymolgus	1	1	1	0	1	1	1	0	1	1	0	0	?	1	0	?	?
Hexabdella	1	1	1	?	1	1	1	0	1	1	0	0	?	1	0	?	?
Bdella	1	1	1	?	1	1	1	0	1	1	1	0	?	1	0	?	?
Neomolgus	1	1	1	?	1	1	1	1	1	1	1	0	?	1	0	?	?
Bdellodes	1	1	1	?	1	1	1	1	1	1	1	0	?	1	0	?	?
Odontoscirus	1	1	1	?	1	1	1	1	1	1	1	0	?	1	0	?	?