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Ghilarovus robisoni n. sp., first record of Zetomotrichidae (Acari, Oribatida) from North America

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Original research

ABSTRACT

The oribatid mite family Zetomotrichidae is represented in warm regions of world, including Australia, South Africa, Mexico, South America and across the Palaearctic from southern Europe to Asia, but has been unreported from the USA and Canada. We describe a new zetomotrichid species, *Ghilarovus robisoni* n. sp., on the basis of adults, the first record of the genus and family from temperate North America. Specimens were collected from dry, usually rocky, vertical microhabitats in forests in southern USA. We provide a revised and expanded diagnosis for adults of *Ghilarovus*, discuss characters in Zetomotrichidae unique to the family, and provide a key to world *Ghilarovus* species.

Keywords oribatid mite; Arkansas; New Mexico; Texas; first record; North America; saxicole; alpha taxonomy

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Introduction

Representatives of the Zetomotrichidae are unknown from North America, north of Mexico (Marshall *et al.* 1987). They have been found in warm regions across the Palaearctic from southern Europe to India, China, Japan and Vietnam (Krivolutsky 1966, Krivolutsky & Karppinen 2006, Krivolutsky & Smelyansky 1996; Bayartogtokh & Smelyansky 2007), and are also known from Australia (Lee & Pajak 1987), Mexico (Mahunka 1983) and South America (Hammer 1958). First described from North Africa (Grandjean 1934), a diverse fauna is known in South Africa (Coetzee 1993, 1995). We describe a new zetomotrichid species, *Ghilarovus robisoni* n. sp., on the basis of adults collected from dry, usually rocky, vertical microhabitats in forests of Arkansas, New Mexico and Texas, USA. It represents the first record of this genus and family from temperate North America.

Species of *Ghilarovus* Krivolutsky, 1966 are found in southern Mexico, Spain, across central Asia, in China and Japan. The original short diagnosis of Krivolutsky (1966) was slightly modified by Bayartogtokh and Smelyansky (2007), who also described 3 new species, provided a key to world species and summarized distributions (their Fig. 9). Our objectives are to build on this latter work by describing the North American species, providing an expanded diagnosis for *Ghilarovus* adults, and revising their key to include *G. robisoni* n. sp. Then, we discuss the family classification and characters that are unique to Zetomotrichidae.

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Materials and Methods

Terminology and Conventions

Morphological terminology used in this study follows that developed by Grandjean (see Travé & Vachon 1975 for references, and Norton & Behan-Pelletier 2009 for overview).

The following conventions of measurement and description are used: measurements are in micrometers; *prodorsal setae* measured on dissected, slide-mounted specimens (*ro*, rostral seta; *le*, lamellar seta; *in*, interlamellar seta; *ex*, exobothridial seta; *bs*, bothridial seta (sensillus)); *total length*, measured from tip of rostrum to posterior edge of notogaster on specimens in cavity slides, except when noted; *notogastral width*, measured at widest part of notogaster on specimens in cavity slides; *leg setal formula*, given as setal count per segment, with famulus included in tarsus I count, and solenidial counts given in parentheses. The inclusion of a single leg setal notation in parentheses denotes a pseudosymmetrical pair. The unideficiency nomenclature for notogastral setae is used herein; probable synonymies of this nomenclature with the holotrichous nomenclature of Grandjean were outlined by R. A. Norton in Balogh and Balogh (1988).

Material Examined

Specimens examined are housed in various collections (see below).

Abbreviations for Collections

- CNC – Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.
- RNC – Personal collection of Roy A. Norton, Syracuse, New York, USA.
- USNM – National Museum of Natural History, Washington, D.C., USA.

Imagery

Specimens for scanning electron microscopy (SEM Quanta 600 FEI Company TM, Brno, Czech Republic) were removed from alcohol and cleaned by soaking in Terg-a-zyme® solution for 6–12 h, followed by brief (1–2 s) submersion in an ultrasonic bath. Specimens were critical-point dried using the EM CPD300 (Leica Microsystems, Vienna, Austria), mounted on Al-stubs with double sided sticky tape, and gold-coated in a Hummer sputter apparatus.

Differential interference contrast images were obtained using a Nikon DS-Fi1 camera and any image stacks were merged with the aid of the Helicon Focus Pro (v. 5.3) suite.

Taxonomy

Ghilarovus Krivolutsky, 1966

Type species: *Ghilarovus humeridens* Krivolutsky, 1966

Expanded diagnosis. *Adult*. Small to medium sized mites, 312–540. *Integument*. Surface of notogaster smooth. Cerotegument granular, present laterally on podosoma (Figs 5C, 5E). *Prodorsum*. Rostral margin denticulate (Figs 1A, 4A, 5D). Rostrum and region lateral to seta *le* with macropores (Fig. 4A). Lamella absent. Carina extending from seta *in* posteriorly to bothridium (Fig. 1A). Tutorium absent. Genal tooth absent. Pedotectum I uniformly curved; pedotectum II small, scaliform (Fig. 5D). Laterorostral carina extending dorsal to pedotectum I, following contour of pedotectum I, reaching anteriorly, midway to rostral margin (Fig. 5D). Bothridial seta filiform, barbed (Figs 1A, 5C). Bothridium cup-shaped (Fig. 6D). Dorsophragma absent; cheliceral retractor muscles inserting directly on prodorsal and notogastral cuticle (Figs 1A, 3D). *Notogaster*. Dorsosejugal scissure interrupted medially in region of insertions of cheliceral retractor muscles. Lenticulus absent. Octotaxic system expressed as macropores (Figs 1A, 6C). Posterior notogastral tectum divided or undivided; when divided, edges rounded, overlapping or not. 10 pairs of notogastral setae. Humeral region of notogaster with prominent process bearing seta *c2* (Figs 1A, 3A, 6C, 6D); seta *c2* longer, thicker and more barbed than other notogastral setae. Lyrifissure *ia* usually modified as humeral sac; lyriissure *im* usually

unmodified, occasionally modified as pyriform organ. *Lateral podosomal and epimeral region.* Apodemes III and IV absent (Fig. 1B). Epimeral setal formula 3-1-3-3 or 3-1-3-2. Custodium present (Figs 4B, 5C). Discidium absent. Circumpedal carina absent. Porose areas *Al*, *Am*, *Ah* absent. Acetabula I-IV in longitudinal alignment (Fig. 5C). *Anogenital region.* Four pairs of genital setae; one pair aggenital setae; one or two pairs of anal setae; two or three pairs of adanal setae (Figs 1B, 5B). Postanal porose area absent. Lyrifissure *ian* absent; lyrifissure *iad* oblique, positioned lateral to anterior margin of anal plate (Fig. 1B). *Gnathosoma.* Axillary saccule of subcapitulum absent. Palp setal formula 0-1-2-3-9(1), solenidion baculiform, appressed to palp surface, not forming double horn with eupathidium *acm* (Figs 1C, 6A). Chelicera chelate-dentate; setae of different forms: *chb* flattened, leaf-like (Figs 1D, 6A). Subcapitulum with seta *h* strongly directed anteriorly, setae *m* and *a* directed medially; adoral setae setose (Fig. 6B). Postpalpal seta *ep* spiniform. Trägårdh's organ present. *Legs.* Tridactylous. Leg IV not modified for jumping. Trochanters III and IV with dorsal ridge (Fig. 5C); trochanter III with outwardly curved ventral edge (Figs 5C, 5D). Femora III and IV with narrow ventral carina (Fig. 5C). Porose areas adaxially on femora I-IV and trochanters III and IV and ventrally on tibia and tarsi I-IV (Figs 2A-E). Solenidion *ω1* most proximal setiform structure on tarsus II, well separated from *ω2* (Figs 2C, 4D).

Juveniles: Unknown.

Included extant species (in alphabetical order after type):

Type species: *Ghilarovus humeridens* Krivolutsky, 1966; Central Asia, Iran

Ghilarovus armenicus Khanbekyan, 1990; Armenia

Ghilarovus changulicensis Wen, 1990; China

Ghilarovus daliensis Yamamoto and Aoki, 2000; Japan

Ghilarovus elegans Mahunka, 1983; southern Mexico

Ghilarovus hispanicus guadarramicus Subías, 1977; Spain

Ghilarovus hispanicus hispanicus Subías and Pérez-Íñigo, 1977; Spain

Ghilarovus khentiicus Bayartogtokh and Smelyansky, 2007; Mongolia

Ghilarovus krivolutskyi Bayartogtokh and Smelyansky, 2007; Mongolia

Ghilarovus kvavadzei Murvanidze, 2014; Caucasus

Ghilarovus mongolicus Bayartogtokh and Smelyansky, 2007; Mongolia

Ghilarovus robisoni n. sp.; USA

Ghilarovus sanukiensis Fujikawa, 2005; Japan

Ghilarovus saxicola Aoki and Hirauchi, 2000; Japan

Ghilarovus stipatus Krivolutsky and Smelyansky, 1997; Central Asia

Ghilarovus turcmenicus Krivolutsky, 1974; Turkmenistan

Remarks

1. Coetzee (1993) included *Ghilarovus* in the subfamily Zetomotrichinae Grandjean, 1954 (see below). *Ghilarovus* is distinct from other genera in the subfamily by the combination of: leg IV not modified for jumping, notogastral seta *c2* expressed as long, thick seta, 4 pairs of genital setae, notogastral surface smooth (Coetzee 1993).
2. In Zetomotrichidae lyrifissures *ia* and *im* can be modified as either a large or small sac-like structure. Grandjean (1934, 1954b) named the sac in the position of lyriisse *ia* a 'humeral sac' because of its shape and position in *Zetomotrichus lacrimans* Grandjean, 1934, the type species; and the structure in the position of lyriisse *im* a 'pyriform organ' because of its pear-like shape. However, in the zetomotrichid genus *Mikizetes*, lyriisse *ia* is modified as a pyriform shaped structure, which Covarrubias (1969) named 'humeral pyriform organ', 'pyriform organ' and 'humeral organ' in the same publication. In *Ghilarovus* lyriisse *ia* is modified as a humeral sac (*hs*), but this modification appears variable among *Ghilarovus* species, as indicated by Murvanidze (2014). The humeral sac is present in *G. elegans*, *G. khentiicus*, *G. krivolutskyi*, *G. mongolicus*, *G. sanukensis*, *G.*

saxicola and *G. robisoni n. sp.* It is not mentioned or illustrated in the descriptions of *G. armenicus*, *G. humeridens*, *G. stipatus* and *G. turcmenicus* but may have been overlooked, especially as it could collapse in older specimens. In the descriptions of *G. changliensis*, *G. daliensis*, *G. kvavadzei*, *G. hispanicus hispanicus* and *G. hispanicus guadarramicus* it is noted as not visible.

3. There has been confusion in descriptions of *Ghilarovus* species on the presence or absence of the pyriform organ found in the position of lyrifissure *im*. The pyriform organ is illustrated as present in *G. elegans* (Mahunka 1983, his Fig. 58), but lyrifissure *im* is also illustrated. Yamamoto and Aoki (2000) described both *im* and the presence of the pyriform organ “near *im*, inside the body” in *G. daliensis*. Similarly, Bayartogtokh and Smelyansky (2007) described both *im* and the pyriform organ as present in *G. krivolutskyi*, as did Murvanidze (2014) in *G. kvavadzei*. We consider these as possible misinterpretations, with the illustrated structure possibly the darkened contents of the opisthonotal gland rather than the pyriform organ described by Grandjean (1954b). In Figs 1A and 3A of *G. robisoni n. sp.*, *im* is shown as anterior to the opisthonotal gland, which has a dark, vase-like shape, which could be misinterpreted (Figs 3A, 3F). Hypertrophy of lyrifissures is not unique to Zetomotrichidae. Grandjean (1957) noted a similar hypertrophy or transformation of either lyrifissure *ih* or *ips* in the galumnid *Cryptogalumna cryptodonta* Grandjean, 1957, where the hypertrophy is in the form of an interal mass positioned lateral to the opening of the opisthonotal gland. A modification of lyrifissure *im* as a tubercle-like structure was described in *Scapheremaeus argentinensis* Travé and Fernandez (1986). However, in all examples of lyrifissure hypertrophication the function of each modification and the contents of the humeral sac and pyriform organ are unknown.
4. The notogaster of some *Ghilarovus* species has a complete posterior tectum (*G. armenicus*, *G. changlingensis*, *G. elegans*, *G. hispanicus hispanicus*, *G. hispanicus guadarramicus*, *G. humeridens*, *G. kvavadzei*, *G. sanukiensis*, *G. stipatus*), while in others it is medially divided, with lobes either overlapping (*G. krivolutskyi*, *G. mongolicus*, *G. robisoni n. sp.*, *G. saxicola*) or separate (*G. khentiicus*). The medial division can be difficult to detect and could have been overlooked in some species, e.g., *G. daliensis* and *G. turcmenicus*, where it is neither illustrated nor described.

Description

Ghilarovus robisoni n. sp.

Zoobank: [8C2690BD-DDFB-4C9F-8A49-9548F60CF136](https://zoobank.org/8C2690BD-DDFB-4C9F-8A49-9548F60CF136)

Figures 1–6

Material Examined

Holotype: adult female (CNC1097998), Arkansas, Montgomery Co., Ouachita National Park, Crystal Vista Train, 34°5.06' N 93°6.00' W, 18.x.2009 (V. Behan-Pelletier) from lichens on rocks.

Paratypes: 10 with same data as holotype; Texas, Uvalde Co., Garner State Park, Big Cedar Trail, 29°34.090' N 99°44.876' W, 27-ii-2007 (V. Behan-Pelletier) 6 from cedar, oak, madrone litter; Guadeloupe State Park, 29°52.443'N 98°29.139'W, 3.iii.2007 (V. Behan-Pelletier) 7 from moss, maidenhair fern on ledge in floodplain; Bandera Co., Lost Maples State Natural Area, Can Creek Trail, 29°48.984' N 99°34.599' W, 28.ii.2007 (V. Behan-Pelletier) 2 males from moss and lichens on overhanging N-facing rockwall; Madera Canyon Camp, 20 mi NW Fort Davis, 6000', 21.vii.1973, (E. E. Lindquist) 1 male from high water litter by stream edge; New Mexico, Eddy Co., 17.vi.1992 (J. Cokendolpher) 2 females from entrance of Hidden cave. Paratypes deposited in the CNC (CNC1097999–1098005), USNM, and RNC.

Other material examined: Additional individuals from the type locality were studied with scanning electron microscopy.

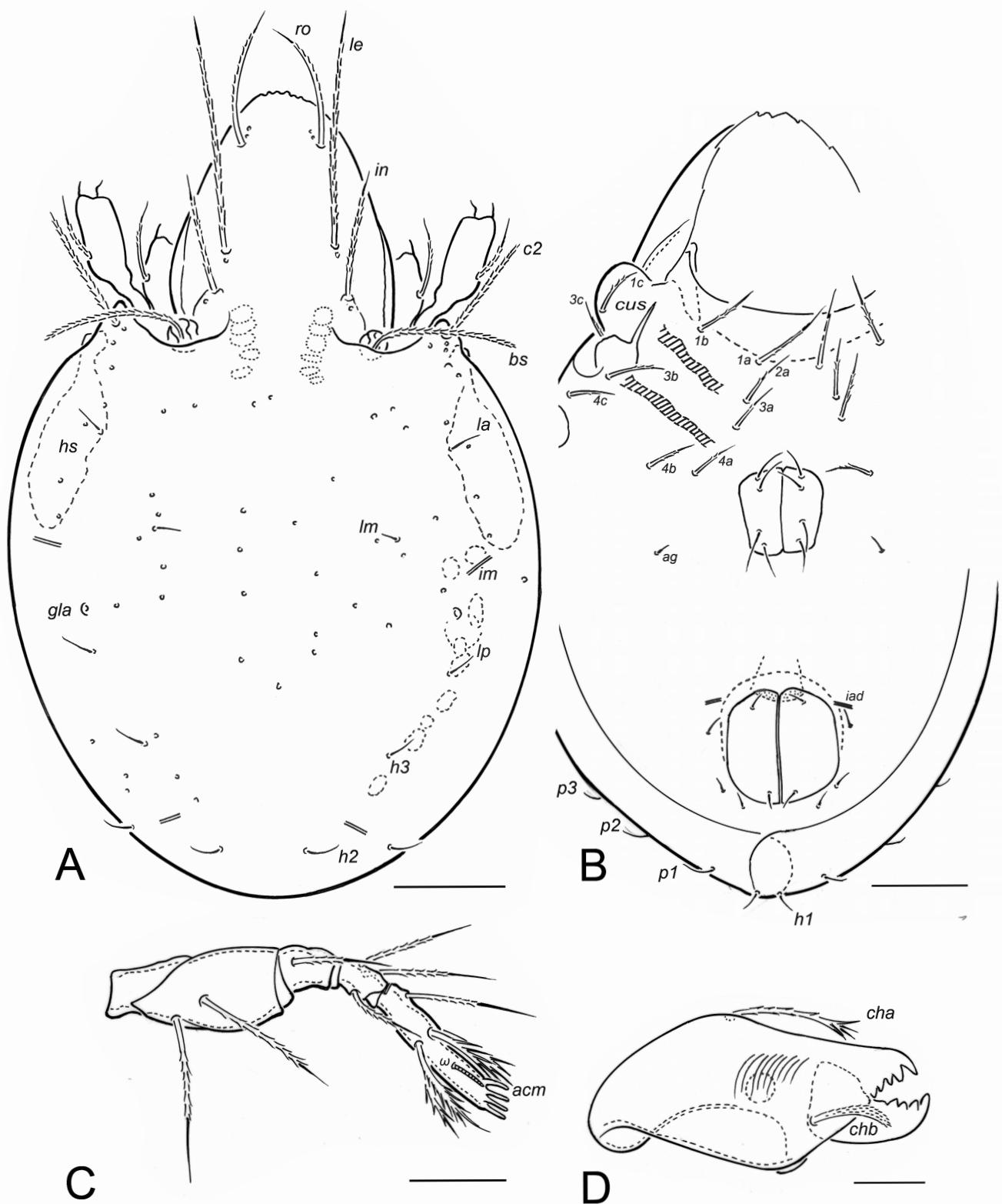


Figure 1 *Ghilarovus robisoni* n. sp., adult female: A – dorsal, only trochanters I and II illustrated; B – ventral, legs and subcapitulum not illustrated; C – palp; D – chelicera, antiaxial aspect, Trägårdh's organ not illustrated. Scale bars: A, B = 50 µm; C, D = 20 µm.

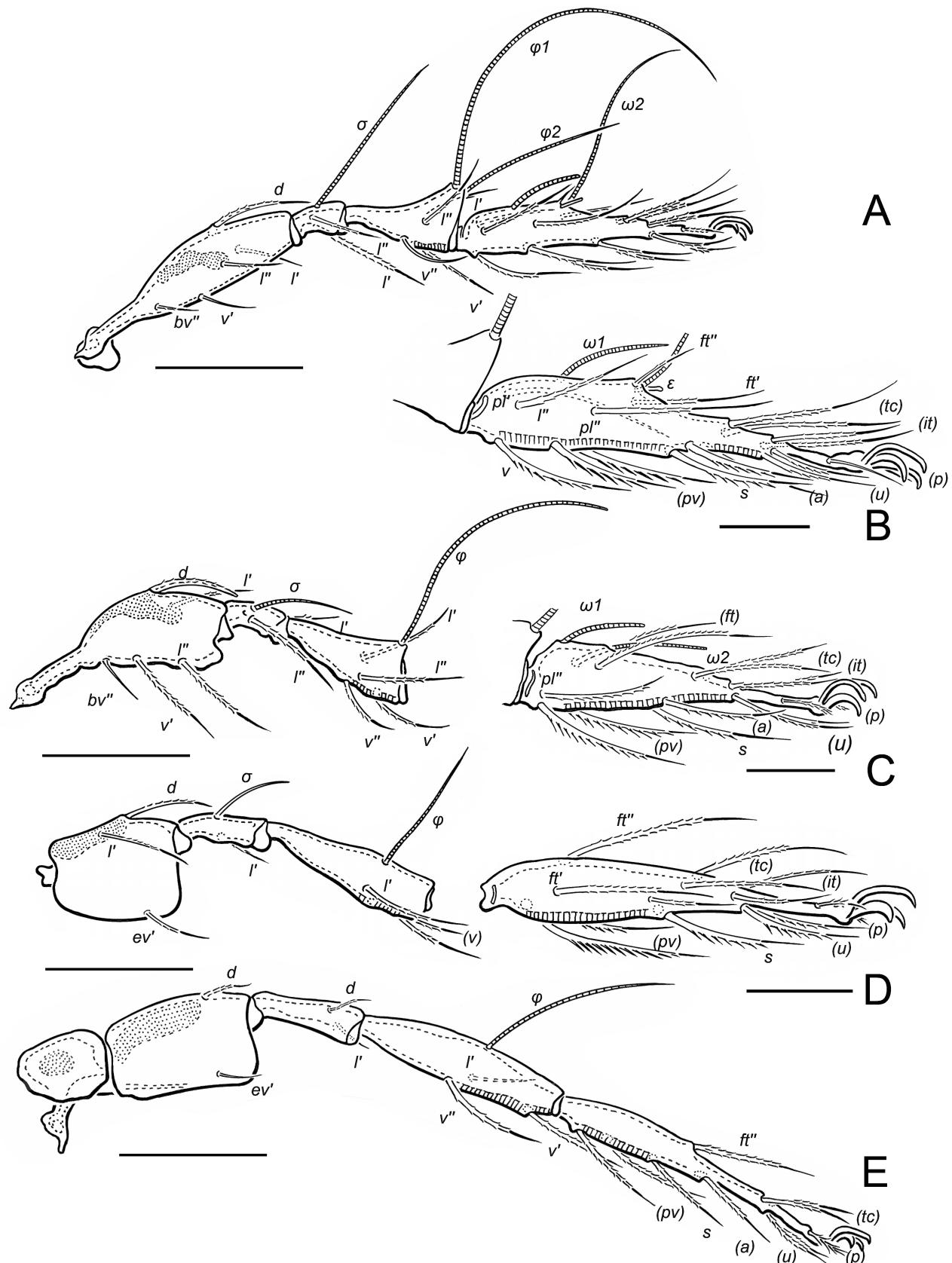


Figure 2 *Ghilarovus robisoni* n. sp., adult female: legs I–IV, all antiaxial aspect: A – leg I, trochanter not illustrated; B – tarsus I at higher magnification; C – leg II, trochanter not illustrated, tarsus II at higher magnification than femur, genu, tibia II; D – leg III, trochanter not illustrated, tarsus III at higher magnification than femur, genu, tibia III; E – leg IV. Scale bars: A, E; C (femur, genu tibia), D (femur, genu tibia) = 50 µm; B, C, D (tarsus) = 20 µm.

Diagnosis

Adult. Total length 288–365. Rostrum with 15–18 short dentes, subequal in size; medial dentes more closely positioned than lateral ones. Seta *ro* 60–65 long, barbed, acuminate. Lamellar seta 103–107 long, heavily barbed, tapered distally. Seta *in* 62–70 long, barbed (subequally to *le*). Bothridial seta filiform, 76–82 long. Five to 7 macropores present laterally between bothridium and seta *le*. Posterior notogastral tectum divided, with overlapping lobes. Humeral sac (*hs*) present, extending posteriorly almost to level of lyrifissure *im*. Notogastral setae smooth, acuminate, 13–17 long, except *c2* 52–55 long, strongly barbed, tapered. Pyriform organ absent. Prodorsum with 3 pores in longitudinal alignment lateral and posterior to seta *in*. Notogaster with 3 pores closely adjacent posterior to seta *c2*. Custodium 23–25 long, strongly tapered, extending to base of pedotectum I. Adanal setation 3 pairs.

Description

Adults

Dimensions — Total length: females (n = 7) 344 (322–365); males (n = 4) 300 (range 288–326). Notogastral width: females (n = 2) 228 (216, 240); males (n = 2) 211 (211, 211).

Integument — Cerotegument present laterally on podosoma, finely and densely granulate (Fig. 5E). Integument with dark spots laterally and posteriorly on notogaster (Figs. 3B, 3G). Longitudinal, fine ridges present laterally on epimeres, podosoma and anterior notogaster (Fig. 5E). System of macropores positioned on prodorsum and notogaster as indicated in Fig. 1A; pores often covered by small patch of cerotegument (Fig. 5D). On prodorsum 3 pores in longitudinal alignment lateral and posterior to seta *in* (Fig. 4A), others on rostral tectum. On notogaster 3 pores closely adjacent posterior to seta *c2* (Fig. 3C, arrow).

Prodorsum — Rostrum with 15–18 short dentes, subequal in size, about 2 in length; medially dentes more closely adjacent than lateral ones. Seta *ro* 60–65 long, barbed along length, acuminate, curved anteromedially; mutual distance about 38 (Fig. 1A). Seta *le* 103–107 long, heavily barbed, tapered distally; mutual distance about 47 (Fig. 5A). Seta *in* 62–70 long, barbed (subequally to *le*), tapered; mutual distance about 61 (Fig. 1A). Bothridial seta setiform, 76–82 long, directed posterolaterally (Figs 1A, 6C). Seta *ex* thin, weakly barbed, 11–14 (Fig. 6D). Three to 5 pairs of overlapping muscle sigilla in dorsosejugal region (Fig. 3D).

Lateral region of podosoma — Laterorostral ridge dorsal of pedotectum I 55–60 long (Fig. 4C). Custodium 23–25 long, strongly tapered, extending to base of pedotectum I (Figs 1B, 4B arrow).

Notogaster — Humeral region rounded dorsally, with cleft (Fig. 6D) and pointed to rounded lobe ventrally (Figs 3A, 3C, 6C, 6D). Setae smooth, acuminate, 13–17 long, except *c2* 52–55 long, strongly barbed, tapered, positioned dorsally on humeral tubercle (Figs 1A, 3E, 5A, 5E). Seta *lm* positioned medially, in longitudinal alignment with bothridial seta (Fig. 1A). Lyrifissure *ia* not evident (Fig. 1A). Humeral sac about 50 long (Fig. 3A), difficult to see in preserved specimens. Lyrifissure *im* positioned lateral of seta *lm* (Figs 1A, 3A). Opening of opisthonotal gland (*gla*) between *im* and seta *lp* (Figs 1A, 3A).

Ventral Region — Epimeral setae barbed, acuminate, with *1a* and *1b* strongly directed anteriorly (Fig. 5B); setae *1a*, *1b*, *1c* thicker than other epimeral setae; measurements: *1a*, 25–36; *1b*, 25–28; *1c*, 30–35; *2a*, 12–19; *3a*, 10–19; *3b*, 38; *3c*, 28–30; *4a*, 14, *4b*, 11; *4c*, 22–26. Genital, aggenital, anal and adanal setae smooth; genital setae 10–16, other setae about 9. Lyrifissure *iad* anterolateral of anal plate. Narrow band (about 2 wide) of continuously porose integument extending along edge of ventral plate; discrete marginoventral series of porose areas absent.

Gnathosoma — Cheliceral length 95–110; digits each with 5 teeth (Figs 1D, 6A). Cheliceral seta *cha* thick, setiform, acuminate, about 43, with distal barbs splayed and longer than proximal barbs; *chb* strongly barbed, penicillate, tapered, 23–25 (Figs 1D, 6A). Length of seta *h>m>a*; seta *h* strongly barbed, directed anteriorly, 39 long; *m* barbed, directed almost transversely, 36

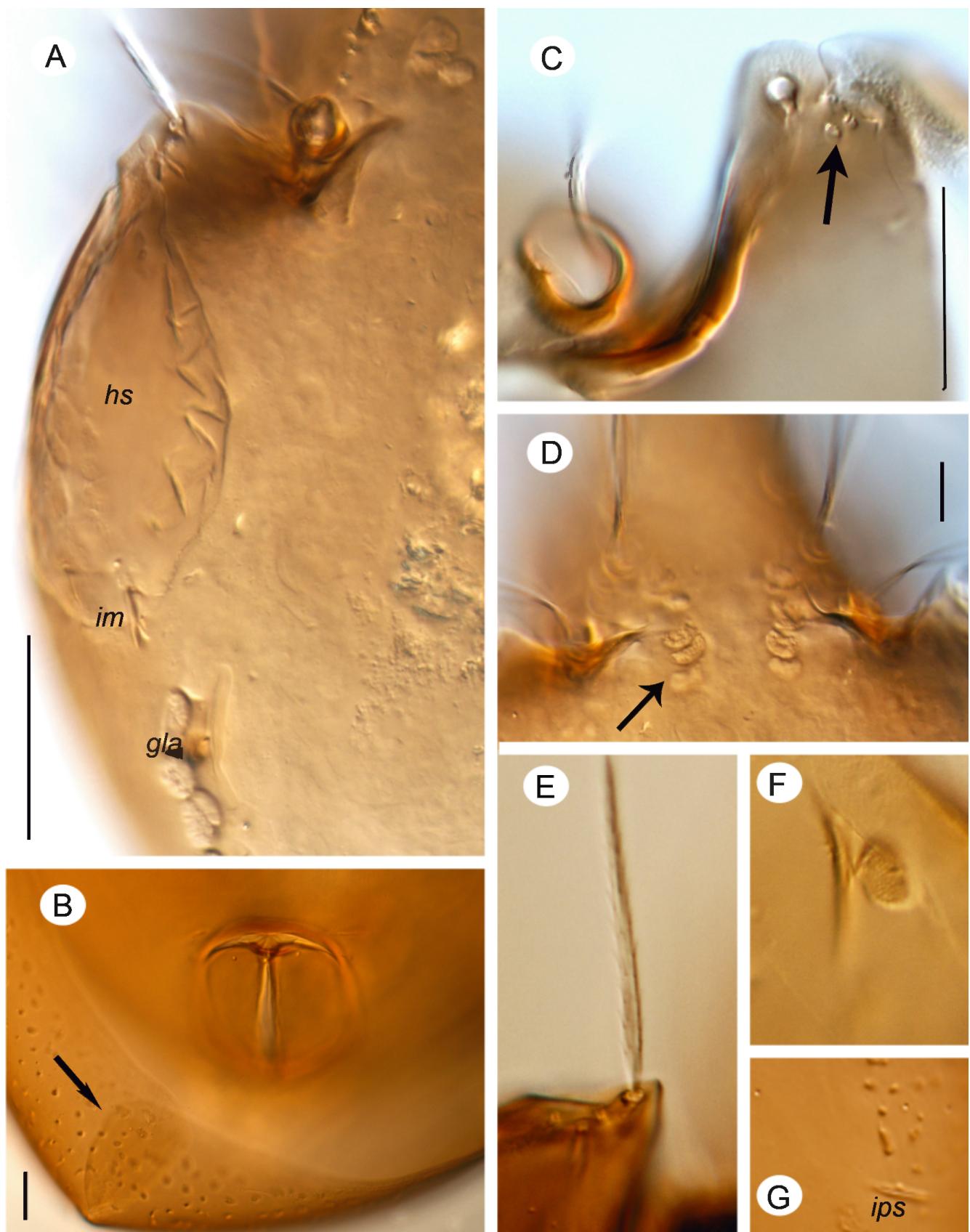


Figure 3 *Ghilarovus robisoni* n. sp., adult female: A – lateral of notogaster showing humeral sac (*hs*), lyrifissure *im*, opisthonotal gland opening (*gla*); B – posterior of notogaster showing overlapping lobes of posterior tectum (arrow); C – humeral region of notogaster, with insertion of seta *c* (seta *c* absent) and arrow to pores adjacent to seta *c*; D – dorsosejugal region, with arrow to muscle sigilla (attachments for cheliceral muscles); E – seta *c*; F – opisthonotal gland; G – detail of notogaster by lyrifissure *ips*. Scale bars: A = 50 µm; B-D = 20 µm.

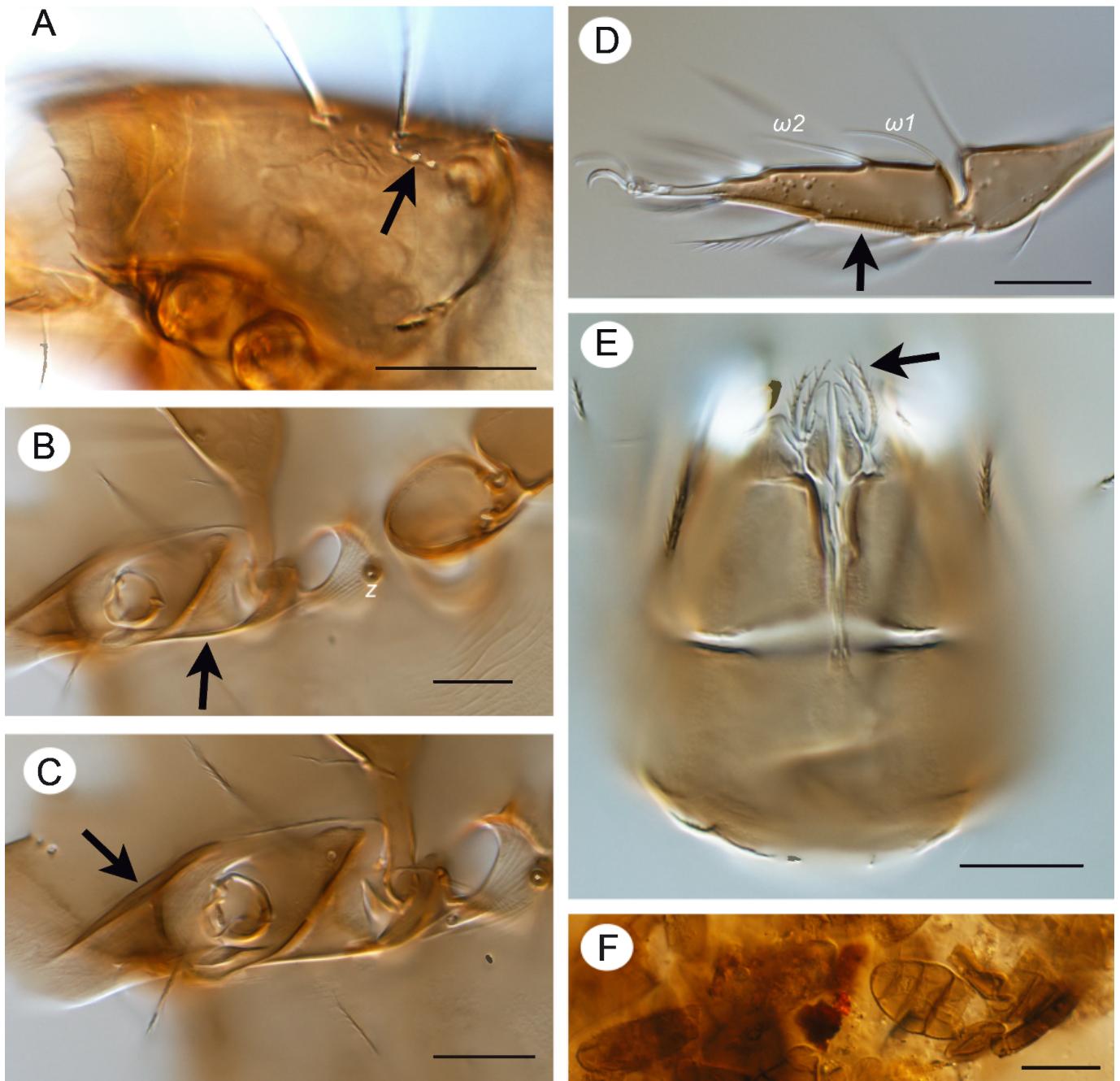


Figure 4 *Ghilarovus robisoni* n. sp., adult female: A – lateral of prodorsum showing dentate rostrum; arrow to pores lateral of seta *in*; B – lateral of podosoma in region of acetabula I-IV; trochanters I, II and IV visible; arrow to custodium; C – detail of lateral of podosoma in region of acetabula I-III; arrow to ridge dorsal of pedotectum I; D – tarsus II and distal part of tibia II; arrow to porose region ventrally on tarsus II; E – ventral of subcapitulum showing strongly barbed setae *or* (arrow); F – gut contents. Scale bars: A = 50 µm; B-F = 20 µm.

long; *a* strongly barbed, curving anteriorly, 12 long (Fig. 6A). Adoral setae strongly barbed, about 17 (Figs 6A, 6B). Solenidion on palptarsus about 6 long, tightly adpressed to segment; *acm*, (*ul*) and *su* about 4; other palptarsal setae setiform. Trägårdh's organ as illustrated by Grandjean (1934).

Legs (Figs 2A–E, 4D, 5B, 5E) — Setal and solenidial formula (I to IV): trochanters: 1-1-2-0; femora: 5-5-3-2; genua: 2(1)-2(1)-1(1)-2; tibiae: 4(2)-4(1)-3(1)-3(1); tarsi: 20(2)-16(2)-15-12; leg setation given in Table 1. Only setae (*p*) on tarsus I eupathidial. Tarsal lyrifissure positioned

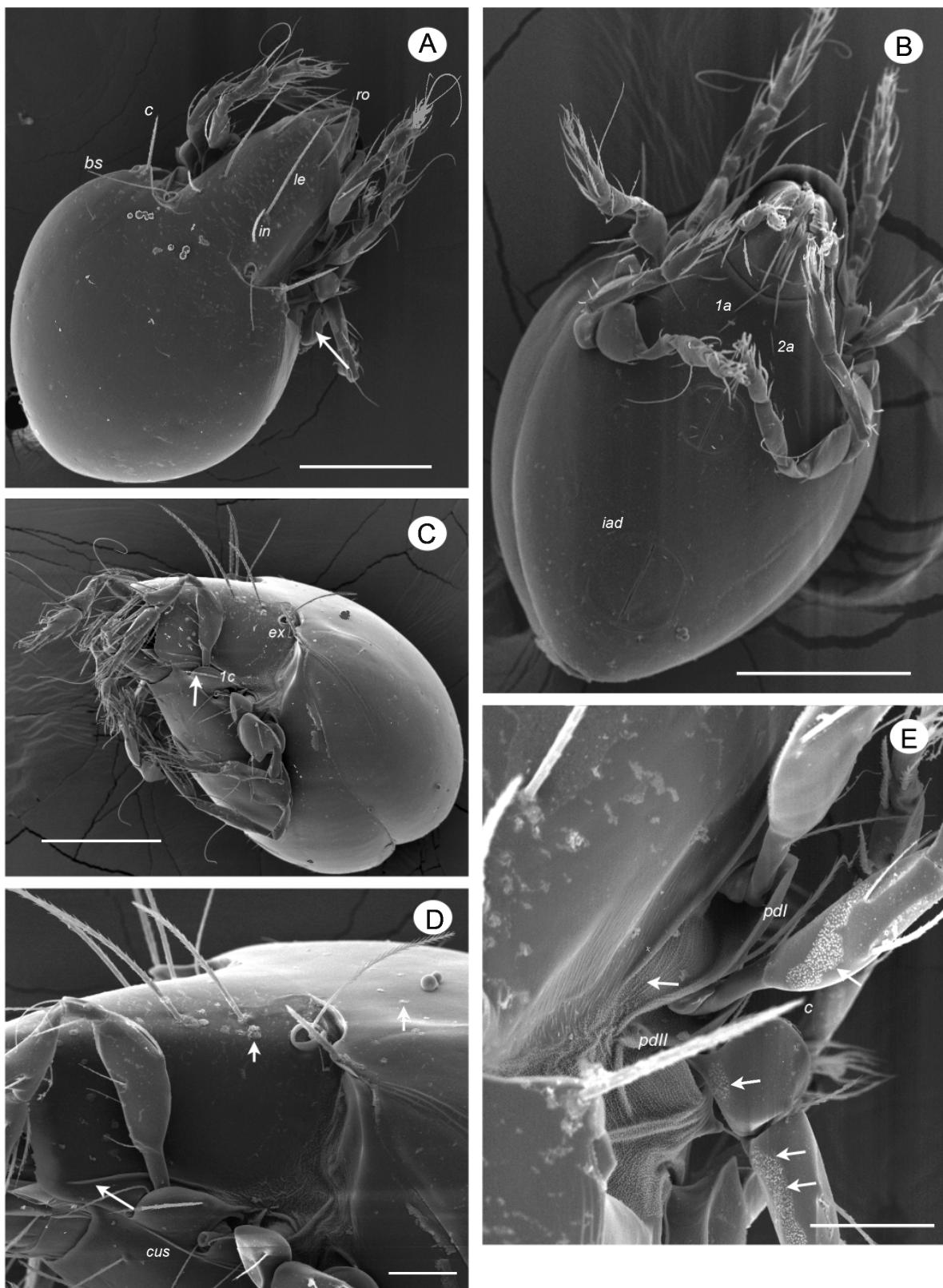


Figure 5 *Ghilarovus robisoni* n. sp., scanning electron micrographs of adult female: A – dorsal habitus, with arrow to dorsal carina on trochanter IV; B – ventral habitus; C – lateral habitus, with arrow to pedotectum I; (leg II broken off); D – lateral of propodosoma, showing small cerotegument patch above prodorsal and notogastral macropores (short arrows); long arrow to carina dorsal of pedotectum I; (leg II broken off); E – detail of humeral region and lateral of prodorsum, showing fine ridges on lateral of prodorsum (arrow); cerotegument on porose areas of trochanters and femora (arrows); pedotectum I and II in dorsal view. Scale bars: A–C = 100 µm; D, E = 25 µm.

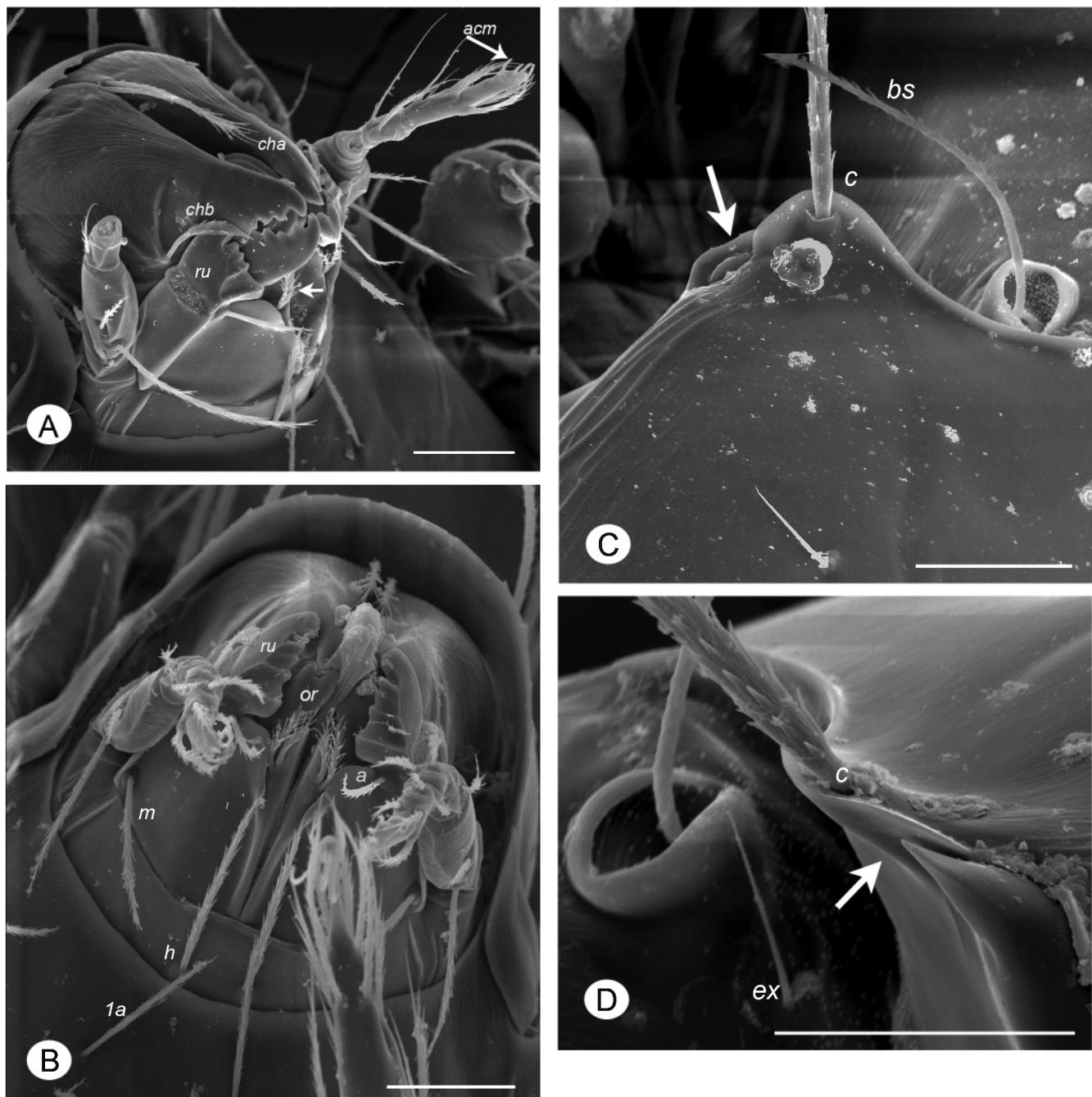


Figure 6 *Ghilarovus robisoni* n. sp., scanning electron micrographs of adult female: A – lateral of subcapitulum; with small arrow to adoral seta *or*, and showing rutellum (*ru*) and difference in morphology between cheliceral setae *cha* and *chb*; B – subcapitulum in ventral view; C – detail of humeral region, dorsal aspect, with detail of proximal part of notogastral seta *c* and bothridial seta (*bs*); arrow to area viewed from lateral aspect in Fig. D (arrow); D – detail of humeral region, laterofrontal aspect; arrow to area viewed from dorsal aspect in Fig. C (arrow). Scale bars = 20 μ m.

antiaxially. Dorsolateral porose areas present on femora I–IV and trochanters III, IV (Fig. 5E); with anteroventral porose area on tibiae I–IV and posteroventral porose area on tarsi I–IV (Figs 2A–E). On tarsi I and II, ventral porose area extending to base of seta *s* (Figs 2B, 2C). Solenidion $\varphi 1$ of tibia I borne on anterodorsal tubercle. Solenidion $\omega 1$ of tarsus II proximal to seta *ft'* (Figs 2C, 4D).

Gender differences

No sexual dimorphism exists in external morphology, except for males being slightly smaller than females, their genital plates being slightly smaller proportionally than in females, and in the typical genitalic differences.

Etymology

This species is named for Henry W. Robison, Emeritus Professor at Southern Arkansas University, who in addition to a long history of distinguished research in ichthyology and herpetology has collected Acari for the CNC throughout Arkansas.

Ecology

This species is a saxicole, found associated with mosses and lichens among rocks and rock faces in forest and prairie habitats. This is generally similar to the habitat where Subías and Pérez-Íñigo (1977) found *G. hispanicus hispanicus* and Subías (1977) found *G. hispanicus guadarramicus*, species these authors also called saxicoles. Gut contents indicate that adults feed on fungi, and decomposed plant material (Fig. 4F).

Remarks

1. The expression of the palptarsal solenidion and eupathidium *acm* in *Ghilarovus robisoni n. sp.* is identical to that in *Zetomotrichus lacrimans*, in *Mikizetes* as described by Covarrubias (1969) and in *G. hispanicus hispanicus* as described by Subías and Pérez-Íñigo (1977). The solenidion is short and recumbent and is positioned half way between *acm* and setae (*lt*); *acm* is closely adjacent to the terminal eupathidia (*ul*) and *sul*. Such an expression of the solenidion with relationship to *acm* is unknown in poronotic Brachypylina (Grandjean 1954a) and is more similar to that found in some pycnonotic Brachypylinae, e.g., *Anderemaeus* (Norton & Ermilov 2019).
2. Solenidion *ω1* is positioned proximally on tarsus II and is proximal to seta *ft'*. The usual position in poronotic Brachypylina is distal to seta *ft'* and almost aligned transversely with *ft''* (Grandjean 1940). We found a scattered distribution of this trait in Ceratozetidae, Punctoribatidae and the tectoribatid *Tectoribates* (Behan-Pelletier & Walter 2013).
3. Grandjean (1954b) considered the prodorsal and notogastral macropores in Zetomotrichidae as possibly the result of fragmentation of the octotaxic system and porose areas *Al*, *Am*, *Ah*, and this hypothesis was supported by Covarrubias (1969) and tentatively for notogastral macropores by Norton and Alberti (1997). This hypothesis is supported by SEM studies of macropores in early derivative Brachypylina, *Hermannella punctulata* and *Poroliodes farinosus* where pores were associated with small saccules (Alberti *et al.* 1997). In *G. robisoni n. sp.* there are patches of either cerotegument or secretion visible on the surface of some macropores (Fig. 5D).

Table 1 Leg setation and solenidia of adult *Ghilarovus robisoni n. sp.*, single prime (') indicates setae on anterior and double prime (") setae on posterior, seta in parenthesis indicates the presence of both setae.

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
I	<i>v'</i>	<i>d</i> , (<i>l</i>), <i>v'</i> , <i>bv''</i>	(<i>l</i>), <i>σ</i>	(<i>l</i>), (<i>v</i>), <i>φ1</i> , <i>φ2</i>	(<i>ft</i>), (<i>pl</i>), (<i>tc</i>), (<i>it</i>), (<i>p</i>), (<i>u</i>), (<i>a</i>), <i>s</i> , (<i>pv</i>), (<i>v</i>), <i>ε</i> , <i>ω1</i> , <i>ω2</i>
II	<i>v'</i>	<i>d</i> , (<i>l</i>), <i>v''</i> , <i>bv''</i>	(<i>l</i>), <i>σ</i>	(<i>l</i>), (<i>v</i>), <i>φ</i>	(<i>ft</i>), (<i>tc</i>), (<i>it</i>), (<i>p</i>), (<i>u</i>), (<i>a</i>), <i>s</i> , (<i>pv</i>), <i>pl''</i> , <i>ω1</i> , <i>ω2</i>
III	<i>d</i> , <i>l'</i>	<i>d</i> , <i>l'</i> , <i>ev'</i>	<i>l'</i> , <i>σ</i>	<i>l'</i> , (<i>v</i>), <i>φ</i>	(<i>ft</i>), (<i>tc</i>), (<i>it</i>), (<i>p</i>), (<i>u</i>), (<i>a</i>), <i>s</i> , (<i>pv</i>)
IV	-	<i>d</i> , <i>ev'</i>	<i>d</i> , <i>l'</i>	<i>l'</i> , (<i>v</i>), <i>φ</i>	<i>ft''</i> , (<i>tc</i>), (<i>p</i>), (<i>u</i>), (<i>a</i>), <i>s</i> , (<i>pv</i>)

4. The dark spots on the lateral and posterior of the notogaster in *G. robisoni n. sp.* and also found in *Zetomothricus lacrimans*, are not tubercles or depressions; they are within the integument, as described by Grandjean (1954b); these have also been noted in *G. hispanicus hispanicus* by Subías and Pérez-Iñigo (1977).

World key to adults of *Ghilarovus*

1. Adanal setation 2 pairs	2
— Adanal setation 3 pairs	6
2. Posterior tectum of notogaster medially divided	3
— Posterior tectum of notogaster not divided	5
3. Borders of divided posterior tectum not overlapping	
..... <i>G. khentiicus</i> Bayartogtokh & Smelyansky, 2007	
— Borders of divided posterior tectum with overlapping lobes	4
4. Humeral sac absent	<i>G. daliensis</i> Yamamoto & Aoki, 2000
— Humeral sac present	<i>G. saxicola</i> Aoki & Hirauchi, 2000
5. Humeral sac absent	<i>G. kvaradzei</i> Murvanidze, 2014
— Humeral sac present	<i>G. sanukiensis</i> Fujikawa, 2005
6. Posterior tectum of notogaster medially divided	7
— Posterior tectum of notogaster undivided	9
7. Bothridial seta subequal in length to rostral seta and seta <i>c2</i>	
..... <i>G. mongolicus</i> Bayartogtokh & Smelyansky, 2007	
— Bothridial seta longer than rostral seta and seta <i>c2</i>	8
8. Seta <i>le</i> 103–107, 2x length of seta <i>c2</i> (52–55), >1.5x seta <i>ro</i>	<i>G. robisoni n. sp.</i>
— Seta <i>le</i> <2x seta <i>c2</i> and seta <i>ro</i>	<i>G. krivolutsyi</i> Bayartogtokh & Smelyansky, 2007
9. Both humeral sac and pyriform organ present	<i>G. elegans</i> Mahunka, 1983
— Humeral sac and pyriform organ absent	10
10. Rostral dentes regular in size, small to medium	11
— Rostral dentes irregular in size; medial six much longer than lateral dentes	
..... <i>G. turmenicus</i> Krivolutsky, 1974	
11. Rostral dentes medium in length	12
— Rostral dentes short	13
12. Rostrum with about 12 dentes of similar spacing; medially ones slightly longer than lateral ones; body length 430–434	<i>G. armenicus</i> Khanbekyan, 1990
— Anterior four dentes of rostrum slightly larger than lateral teeth, with deep incision posterior to fourth anterior tooth; prodorsal setae smooth; body length 482	
..... <i>G. humeridens</i> Krivolutsky, 1966	
13. Prodorsal and epimeral setae smooth	<i>G. stipatus</i> Krivolutsky & Smelyansky, 1997
— Prodorsal setae and epimeral setae '3a, 1b, 1c, 3c and 4c conspicuously barbed	14

14. One pair of anal setae present *G. hispanicus guadarramicus* Subías, 1977
— Two pairs of anal setae present
.. *G. hispanicus hispanicus* Subías & Perez-Iñigo, 1977 and *G. changlingensis* Wen, 1990 (we are unable to separate these species based on their descriptions)

Discussion

Without known immatures, Grandjean (1954a, b) was unable to place Zetomotrichidae in a superfamily, but Covarrubias (1969) described the protonymph and deutonymph of *Mikizetes diamantensis* Hammer, 1958, and placed Zetomotrichidae in the unranked taxon Excentrosclerosae, based on the presence of excentrosclerites at the base of gastronotal setae *la*, *lp* and *h2*. The deutonymph of the zetomotrichid *Desertozetes metsamoricus* Khanbekyan, 1990 was also illustrated, although as noted by Norton and Ermilov (2014) (Appendix, 2017), the association with the adult is doubtful. Zetomotrichidae were formally placed in Oripodoidea (as the junior synonym Oribatuloidea) by Balogh (1961). Subsequently, Subías (2004) recognized the monobasic superfamily Zetomotrichoidea, but his classification generally has not been followed, e.g., Norton and Behan-Pelletier (2009), Schatz *et al.* (2011).

There is a suite of character states that contribute to the uniqueness of Zetomotrichidae (Grandjean 1954a, b). Species of *Zetomotrichus* (and subsequently described *Keralotrichus* Mahunka, 1985, *Demisalto* Coetzee, 1993, *Saltatrichus*, Coetzee 1993) can possibly jump in a manner thought to be similar to that found in Zetorchestidae, using modified legs IV which are displaced dorsally and have robust spine-like genu seta *l'* and tarsal setae *ft*" and *tc*", though jumping has not been observed for any species. Other genera in the family, *Mikizetes* Hammer, 1958, *Ghilarovus* Krivolutsky, 1966, *Pallidacarus* Krivolutsky, 1975, *Rohria* Balogh and Mahunka, 1977, *Oglasascarus* Bernini, 1978, *Anoplozetes* Lee and Pajak, 1987, *Desertozetes* Khanbekyan, 1990, *Mabulatrichus* Coetzee, 1993, *Floritrichus* Coetzee, 2003, *Turkmenitrichus* Krivolutsky and Karppinen, 2006, lack these modifications of leg IV. The notogaster has a posterior tectum with or without medially overlapping lobes; a character state found in Licheremaeoidea (Adhaesozetidae) and Ceratozetoidea (Chamobatidae, Humerobatidae, Maudheimiidae, Puncitorbatidae, Ramsayellidae, Zetomimidae), but unknown elsewhere in Oripodoidea (Behan-Pelletier 2001). The usual octotaxic system is absent but the notogaster carries macropores which are possible fragments of this system. On the palptarsus the solenidion is independent, not associated with eupathidium *acm* to form the “double horn”, unknown elsewhere in Oripodoidea. Members of Zetomotrichidae also lack the circumpedal carina.

Presently, 2 subfamilies are recognized (Coetzee 2003), Zetomotrichinae Grandjean, 1954, including *Zetomotrichus*, *Keralotrichus*, *Demisalto*, *Saltatrichus*, *Mikizetes*, *Desertozetes*, *Ghilarovus*, *Oglasascarus*, *Anoplozetes*, *Mabulatrichus*, *Turkmenitrichus*, and *Rohriinae* Balogh and Balogh, 1984, including *Rohria*, *Pallidacarus*, *Floritrichus*. Subías (2004) considered *Saltatrichus* a subgenus of *Demisalto*, *Oglasascarus* a subgenus of *Mikizetes* and *Keralotrichus* a subgenus of *Zetomotrichus*. Clearly, a family revision is needed.

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