



Article

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First report of the male of *Zamora granulata* Roewer, 1928, with implications on the higher taxonomy of the Zamorinae Kury, 1997 (Opiliones, Laniatores, Cranidae)

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Abstract

Males of *Zamora granulata* Roewer, 1928—a species known from Zamora, Ecuador—are reported for the first time. The study of this species, especially the male genitalia, along with all species of Zamorinae Kury, 1997, allowed to reach the following conclusions: 1) *Zamora vulcana* Kury, 1997, from Cotopaxi, Ecuador, does not belong to *Zamora* and is transferred to *Rivetinus* Roewer, 1914; 2) *Zamora granulata*, the name-bearer of Zamorinae, is not an Agoristenidae and therefore Zamorinae is placed in Cranidae; 3) Zamorinae is redefined based on previously unavailable information from male genitalia; (4) some genera hitherto placed in Zamorinae which present a combination of a generalized gonyleptoid habitus plus an agoristenid genitalia (which includes *Globibunus* Roewer, 1912 and *Rivetinus*), are placed in Globibuninae **subfam. nov.** Based on the examination of the holotype of *Prostygnus vestitus* Roewer, 1913 (from Ecuador, not Colombia, nor Venezuela), and new material of *Cutervolus albopunctatus* Roewer, 1957, the Prostyginae are restricted to *Cutervolus* Roewer, 1957 and *Prostygnus* Roewer, 1913, with distribution accordingly restricted to southern Ecuador and northern Peru. Iconographic complements are made on the type species of these two genera, and their male genitalia are illustrated for the first time. All other Prostyginae are considered Gonyleptoidea *incertae sedis*. Emended diagnoses are provided for Globibuninae, Prostyginae and Zamorinae.

Key words: Arachnida, harvestmen, Grassatores, Neotropics, Ecuador, Agoristenidae

Introduction

A recent expedition by members of the Arachnology section of the Museu Nacional (UFRJ, Rio de Janeiro) to Ecuador collected hitherto unreported males of *Zamora granulata* Roewer, 1928. This is an elusive species, which has been insistently classified among the Agoristenidae Šilhavý, 1973, but now is surprisingly shown to belong elsewhere. The unexpected combination of generalized gonyleptoid habitus (*i.e.*, scutum outline subrectangular to trapezoid, carapace and ocularium sexually dimorphic, greatly developed in male, chelicerae sexually dimorphic, swollen in male, pedipalpal femur with row of ventral spines, legs short) plus agoristenid genitalia (*i.e.*, ventral plate not defined as a single piece, distal lamina parva bilobed, with 4 ventral setae forming a square, distal truncus swollen with prostrate long trifid setae, stylus with dorsal hyaline keel), occurs in a second species of *Zamora* Roewer, 1928 and other Ecuadorian species. Kury (1997) detected this pattern and called this group Zamorinae Kury, 1997, but it will have to be renamed, because the name-bearer does not exhibit these traits.

Zamora granulata is redescribed below, based on the female holotype and newly collected males. Also, based on the examination of the holotype of the name-bearer of Prostyginae, *Prostygnus vestitus* Roewer, 1913, some complements are made to the description of this species which help define the Prostyginae.

Historical background of *Zamora*-Zamorinae

Roewer (1928) described the genus *Zamora* and its type species *Zamora granulata* based on a single female

(mistakenly reported as “male”) from Valle del Zamora, Ecuador, and classified the genus among the Phalangodidae Tricommatinae. It took almost 70 years for someone to tackle the taxonomy of this genus when Kury (1994), very cursorily, and without examination of material, transferred the monotypic genera *Zamora* Roewer, 1928, *Globibunus* Roewer, 1912 and *Ramonus* Roewer, 1956 along with some other Tricommatinae to Cranidae Prostygnae. A little later, Kury (1997) performed the first cladistic analysis of the Agoristenidae, described a second species of *Zamora* from the slope of Mount Cotopaxi, Ecuador, and in the process created the subfamily Zamorinae, which remarkably combined a generalized gonyleptoid habitus (which Kury related to prostygnines) with typical agoristenid genitalia. Kury’s Zamorinae included three species, *Zamora granulata*, *Zamora vulcana* Kury, 1997 and *Ramonus conifrons* Roewer, 1956. Apart from the species he was describing at that moment, Kury had not seen type material of any of his zamorines. The unity of Zamorinae was then supported by external features, notably the very elevated and coarsely granulated ocularium.

Kury (2003), still without examining material, removed another genus, *Rivetinus* Roewer, 1914 from the Tricommatinae, regarding it as “Grassatores incertae sedis”. Pinto-da-Rocha & Hara (2009) revisited agoristenid phylogeny, expanded Kury’s character matrix and examined crucial type material of some of Roewer’s species. Their results included augmenting the Zamorinae by the inclusion of *Globibunus* and *Rivetinus* and moving *Ramonus* back to the Prostygnae. In their analysis, *Zamora granulata* was also kept along with the other zamorines, but the female holotype could not provide much useful information.

Finally, in 2011, Kury and collaborators organized an expedition to Ecuador where they were able to secure males and females of *Zamora granulata*, allowing to access important characters of male genitalia for the first time. This discovery completely overturns the current hypothesis and leads to the dismantlement of the Zamorinae as will be shown below.

Methods

Descriptions of colors used the standard names of the 267 Color Centroids of the NBS/IBCC Color System (<http://www.dodomagnifico.com/Colors/Cent.html>) as described in Kury & Orrico (2006). Scanning Electron Microscopy was carried out with a JEOL JSM-6390LV at the Center for Scanning Electron Microscopy of the Museu Nacional/UFRJ. All measurements are in mm. All coordinates are given in decimal degrees.

Abbreviations of the repositories cited are: AMNH (American Museum of Natural History, New York, USA), MNRJ (Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil), MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru), QCAZ (Museo de Zoologia, Pontificia Universidad Católica de Quito) and SMF (Senckenberg Naturmuseum und Forschungsinstitut, Frankfurt, Germany). Other abbreviations used: CL = carapace maximum length, CW = carapace maximum width, AL = abdominal scutum length, AW = abdominal scutum maximum width, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus.

The subrectangular outline of dorsal scutum widest at middle with narrower parallel-sided carapace and coda (part of dorsal scutum, recognizable as the part with parallel straight sides, posterior to the main slope-change caused by the widened convex laterals—as in Kury 2012) and that occurs in many Gonyleptoidea is here called “type alpha” as in Kury et al (2007). Unarticulated cylindrical acuminate cuticular projections of body (usually referred to in literature as “spines”) are here called “spiniform processes”; the same on legs are called “apophyses”. The same kind of process, when short and tipped by a conspicuous seta, is called “setiferous tubercle”. Articulated spines of penis ventral plate are called macrosetae.

Tarsal formula: numbers of tarsomeres in tarsus I to IV, when an individual count is given, order is from left to right side (figures in parentheses denote number of tarsomeres only in the distitarsi I–II).

Systematic accounts

Gonyleptoidea incertae sedis

Included genera (current subfamily assignment). *Binamballeus* Roewer, 1952 (Prostygninae), *Chiriboga*

Roewer, 1959 (Prostygninae, formerly Cranainae), *Globitarsus* Roewer, 1913 (Prostygninae), *Lisarea* Roewer, 1943 (Prostygninae), *Meridanatus* Roewer, 1943 (Prostygninae), *Micropachylus* Roewer, 1913 (Prostygninae), *Palcabius* Roewer, 1956 (Agoristenidae Zamorinae, formerly Phalangodidae Phalangodinae), *Peladoius* Roewer, 1914 (Prostygninae), *Prostygnellus* Roewer, 1914 (Prostygninae), *Prostygnidius* Roewer, 1915 (Prostygninae), *Ramonus* Roewer, 1956 (complex story: Phalangodidae Tricommatinae to Cranidae Prostygninae to Agoristenidae Zamorinae to Cranidae Prostygninae), *Sclerostygnellus* Roewer, 1943 (Prostygninae), *Troya* Roewer, 1914 (Prostygninae) and *Yania* Roewer, 1914 (Cranidae Prostygninae, formerly Phalangodidae [currently Gonyleptidae] Tricommatinae).

Comments. Most of these generalized Gonyleptoidea from either Colombia, Ecuador, Peru or Venezuela, were at a given point in the Prostygninae. They are typically known from no more than external morphology and some only by females, therefore it is not possible for now to confirm their position within Prostygninae or to assign any of them to one of the relevant groups studied here or elsewhere, for example in the Manaosbiidae or Cranidae. *Palcabius* has been transferred to Zamorinae by Kury (2003) based on the greatly elevated and coarsely granular frontal hump, which is known to occur also in *Ramonus*. Male genitalia are unknown for this species. Therefore there is not as yet solid evidence to assign *Palcabius palpalis* Roewer, 1956 to any of these groups.

Assignment of *Ramonus*. This monotypic genus has been recently transferred to Prostygninae, once the male genitalia were described (Pinto-da-Rocha & Hara 2009). However, the perception of Prostygninae used then was broader than the more restricted one provided here. Under the present restriction of Prostygninae (see below), allocation of *Ramonus* to a given group is difficult. It is definitely not an Agoristenidae. It has a rectangular erect ventral plate, like Prostygninae, but this is widespread in Gonyleptoidea. It also has a stylar ventral process, which is known only in Gonyleptidae; the straight/truncate stylus is much different from that C-shaped of Prostygninae, visible in lateral view (Fig. 9, 11). The set ocularium + large single-spined frontal hump is unique. The shape of the scutum resembles *Rivetinus* or *Zamora*. All four legs are comparably thick and legs III–IV are unarmed (compare to those in Prostygninae, Figs. 6, 8). The scutal areas are straight (compare to the strongly arched areas in Prostygninae, Figs. 6, 8).

Agoristenidae Šilhavý, 1973

Globibuninae new subfam.

(Figs 1–5)

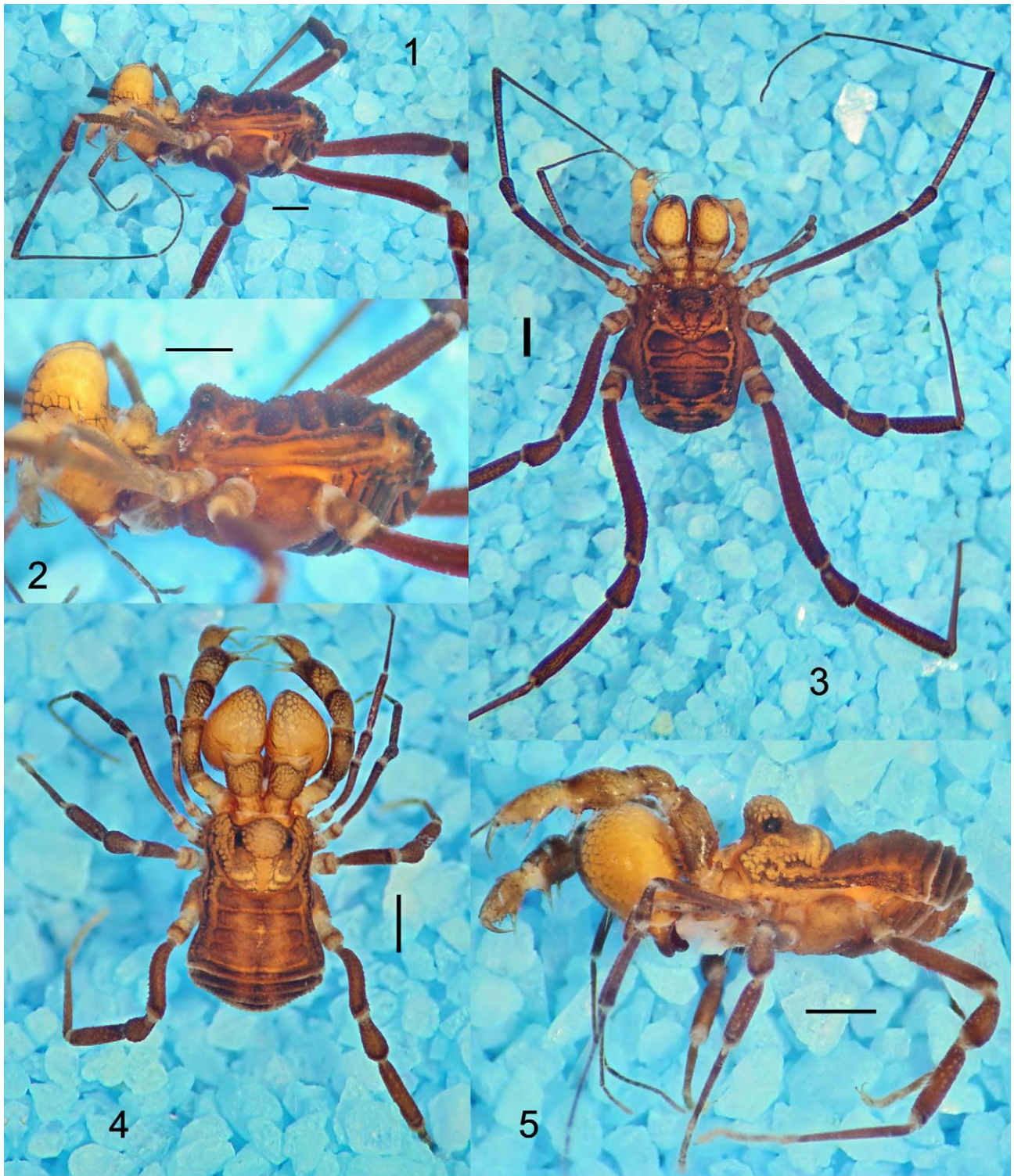
Diagnosis. Body (Figs 1–5): dorsal scutum shape variable, either trapezoid sinuous (*Rivetinus*) or subrectangular, widest at middle (*Globibunus*). Ocularium elevated, unarmed, densely granulate. Carapace well developed, its posterior border parabolic, and a little (*Rivetinus*) or considerably (*Globibunus*) shorter than abdominal scutum. All scutal areas and free tergites finely granular and unarmed. Mesotergum divided into 4 areas; area I either entire or divided longitudinally; areas II–IV straight rectangular (invading area I in *Globibunus*). Basichelicerite well-developed, but without widened bulla. Cheliceral hand swollen in male. Pedipalpal femur somewhat convex dorsally with ventral row of small setiferous tubercles, basal ones enlarged, patella and tibia dorsally smooth. Legs I–IV without conspicuous armature, legs III–IV thicker than the others, femora III–IV especially thickened (*Globibunus*). Penis: distal portion of penis truncus thickened, provided with paired elongate trifid macrosetae; ventral plate undefined, distal bilobed lamina parva, armed with short macrosetae. Glans sac columnar, unfolded, stylus straight, with conspicuous dorsal rounded keel (much reduced in *Rivetinus*), without any dorsal or ventral processes. Body and appendages uniform brown color, trochanters I–IV, chelicerae and pedipalps mottled, cheliceral hand and mesotergal grooves much lighter, sharply contrasting.

Included genera. *Globibunus* Roewer, 1912 (type genus) and *Rivetinus* Roewer, 1914.

Distribution. *Globibunus rubrofemoratus* Roewer, 1912, is known from the Eastern Cordillera realm montane forests (WWF NT0121, Fig. 27), altitude ca. 2200 m, while both species of *Rivetinus* are endemic to the Northern Andean Páramo (WWF NT1006, Fig. 27), altitude 3500–4150 m. See details in Table 1.

Material examined. *Globibunus rubrofemoratus* Roewer, 1912: 22 ♂ 21 ♀ (MNRJ 19308) from Ecuador, Loja, Zamora Huayco, Reserva Privada El Madrigal, S 04.03977°, W 079.17515°, 2200 m, 27.iii.2011, A Chagas, A Giupponi & A Kury leg.; 2 ♂ 2 ♀ (QCAZ 240), same data. *Rivetinus minutus* Roewer, 1914: 1 ♂ 1 ♀ (MNRJ

19221), from Ecuador, Pichincha, Reserva Cayambe-Coca, Laguna de San Marcos, N 00.10767°, W 077.99889°, 3573 m, 18.iii.2011, A Chagas, A Giupponi, A Kury & M Vega leg.



FIGURES 1–5. Globibuninae from Ecuador, habitus. *Globibunus rubrofemoratus* Roewer, 1912 ♂ (MNRJ 19308) from Loja, 1. Left lateral view; 2. Same, detail; 3. Dorsal view; *Rivetinus minutus* Roewer, 1914 ♂ (MNRJ 19221), from Pichincha, 4. Dorsal view; 5. Left lateral view. Scale bars = 1 mm.

TABLE 1. Geographical records of all species of Globibuninae and Zamorinae used in the map (Fig. 27). Places without original georeferencing with only 2 decimal places.

species	locality	WWF Eco	latitude	longitude	alt.	voucher
<i>G. rubrofemoratus</i>	Reserva Privada El Madrigal	NT0121	-4.0398	-79.1752	2200	MNRJ 19308
<i>G. rubrofemoratus</i>	Loja Valley	NT0121	-4.04	-79.20	2200	♂ holotype, SMF RI 245
<i>R. minutus</i>	Laguna de San Marcos	NT1006	0.1077	-77.9989	3573	MNRJ 19221
<i>R. minutus</i>	El Pelado	NT1006	0.71	-77.93	4151	♂ holotype, MNHN
<i>R. vulcanus</i>	northwestern slope of Mount Cotopaxi	NT1006	-0.66	-78.52	3500	♂ holotype, AMNH
<i>Z. granulata</i>	Rio Alpayacu	NT0121	-1.4672	-78.1031	1065	MNRJ 19266
<i>Z. granulata</i>	Morona-Santiago, near Macas	NT0121	-2.1908	-78.0829	1196	MNRJ 19283
<i>Z. granulata</i>	Morona-Santiago, road to Sucua	NT0121	-2.3485	-78.1587	929	MNRJ 19298
<i>Z. granulata</i>	Zamora Valley	NT0121	-3.76	-78.69	2000	♀ holotype, SMF RII 108

Rivetinus Roewer, 1914

(Figs 4–5)

Rivetinus Roewer 1914: 131; Kury 2003: 28 (catalogue with full citations) [type species: *Rivetinus minutus* Roewer, 1914, by monotypy].

Diagnosis. 1) dorsal scutum outline in dorsal view trapezoid, much wider at posterior margin, which is strongly convex (subrectangular, with constrictions much attenuated, widening gradually towards central part relative both to anterior and posterior parts in *Globibunus*); 2) ocularium (in lateral view) as high as 7 times the diameter of the cornea (3 times in *Globibunus*); 3) ocularium (in dorsal view) as long as 50% of the carapace (30% in *Globibunus*); 4) flattened apophyses (“teeth”) flanking cheliceral socket well developed (small in *Globibunus*); 5) valley between carapace and area I deep in lateral view (poorly marked in *Globibunus*); 6) area II anterior margin straight (area II advancing in its mid portion into area I in *Globibunus*); 7) pedipalpal patella unarmed; 8) legs I–IV short, with femur IV sinuous (legs elongate and femur IV substraight in *Globibunus*); 9) coxa IV of male poorly developed, in situ (in dorsal view) barely reaching middle area II (well developed, reaching area III in *Globibunus*); 10) lobes of ventral plate elongate (blunt and rounded in *Globibunus*); 11) dorsal keel of stylus much reduced (well developed in *Globibunus*).

Included species. *Rivetinus minutus* Roewer, 1914 and *Rivetinus vulcanus* (Kury, 1997) **new comb.**

Rivetinus vulcanus (Kury, 1997) **new comb.**

Zamora vulcana Kury 1997: 340, figs. 4–14; Kury 2003: 35.

Type data. ♂ holotype ♀ paratype, (AMNH, examined), from Ecuador, Cotopaxi, northwestern slope of Mount Cotopaxi, 3500 m, 26.vii–5.viii.1969, P & B Wygodzinsky leg.

Diagnosis. Ocularium armed with two paramedian spiniform processes; scutal area I divided into two halves; coxae II and III with apical spiniform apophyses; pedipalp and legs coarsely and densely granulate.

Remarks. It is interesting to note that in the cladistic analysis of Pinto-da-Rocha & Hara (2009), when *Zamora granulata* was very poorly known, *Zamora vulcana* appeared as sister group of *Globibunus rubrofemoratus*. The character uniting both terminals was “coxa II with strong apical posterior apophysis”, which must have been a lapse, since in the diagnosis of *Globibunus* they state: “coxae II–III without conspicuous armature”.

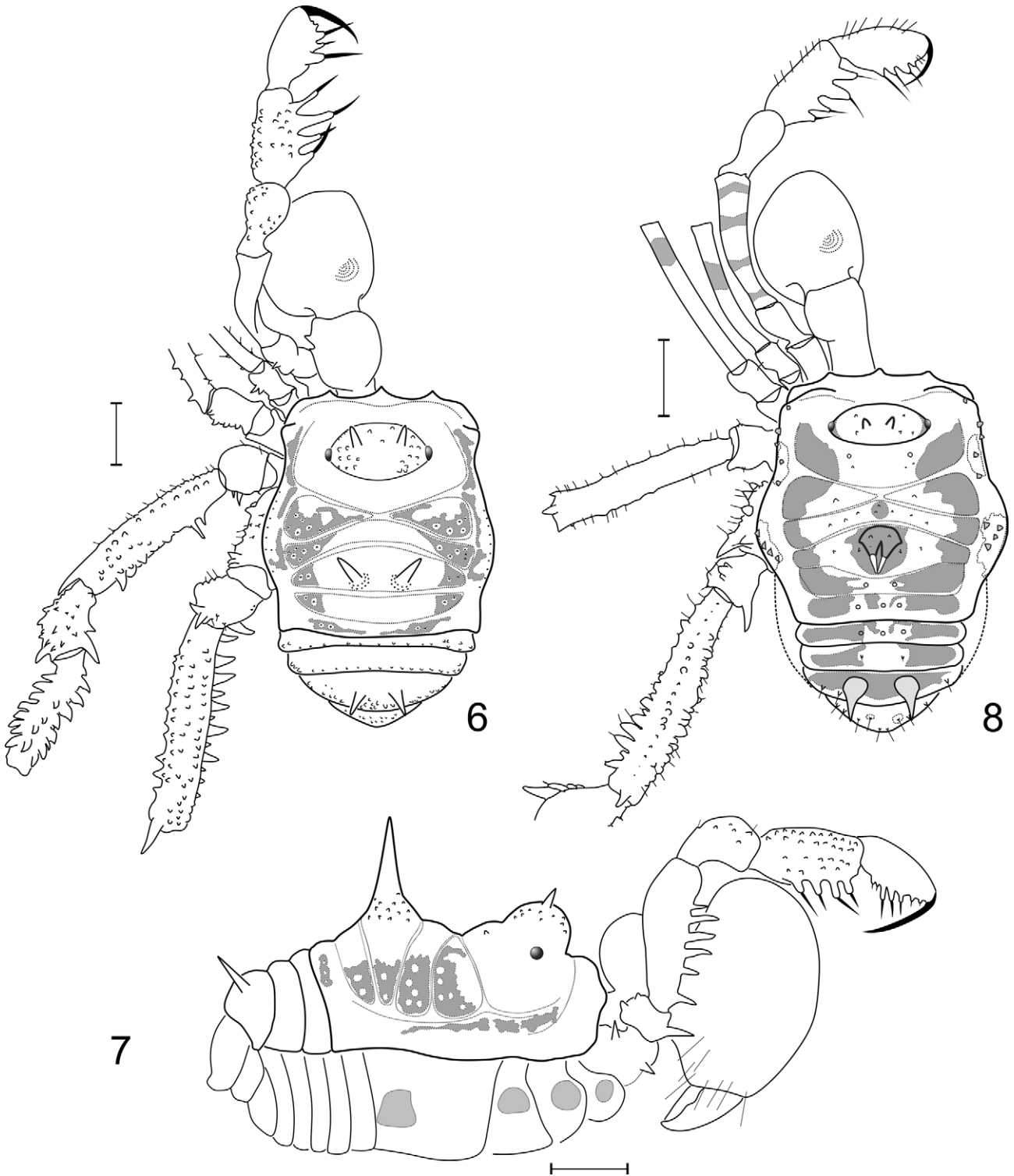
Cranaidae Roewer, 1913

Prostygninae Roewer, 1913

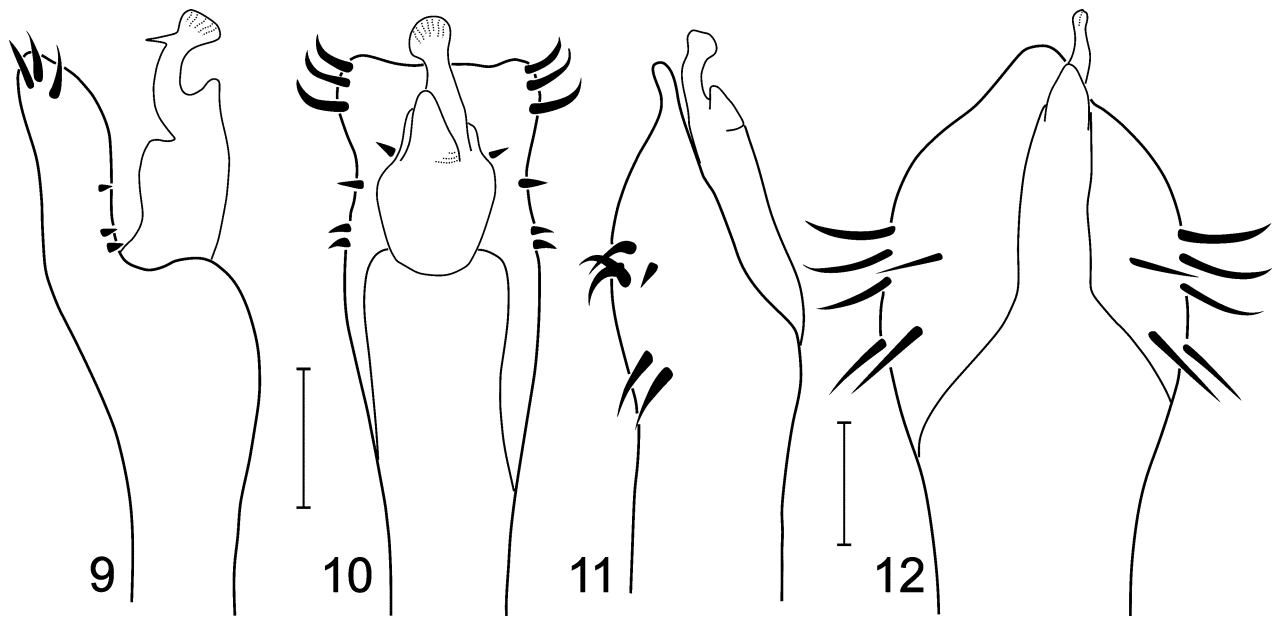
(Figs 6–12)

Gonyleptidae Prostygninae Roewer 1913: 140.

Cranaidae Prostygninae: Kury 1994: 140 (partim).



FIGURES 6–8. *Prostygus vestitus* Roewer, 1913, ♂ holotype (SMF RI 840/36), from Zamora-Chinchipe, southern Ecuador, habitus, 6. Dorsal view; 7. Right lateral view; *Cutervolus albopunctatus* Roewer, 1957, ♂ (MUSM 210), from Cajamarca, northern Peru, 8. Habitus dorsal view. Gray areas represent patches of white. Scale bars = 1 mm.



FIGURES 9–12. Distal part of penis: *Prostygnum vestitus* Roewer, 1913, ♂ holotype (SMF RI 840/36), from Zamora-Chinchipec, 8. Left lateral view; 9. Dorsal view. *Cutervolus albopunctatus* Roewer, 1957, ♂ (MUSM 210), from Cajamarca, 10. Left lateral view; 11. Dorsal view. Scale bars = 100 µm.

Diagnosis. Body (Figs 6–8): dorsal scutum subrectangular, widest at middle and well-marked constrictions (“type alpha”), anterior and posterior borders straight. Ocularium elevated, armed with a pair of acuminate spiniform processes and covered with coarse granulation. Carapace well developed, almost as long as abdominal scutum, posterior border wide V-shaped (*Prostygnum*) or slightly arched posteriorly (*Cutervolus*). Dorsal scutum finely granular, lateral margin with patches of yellow contrasting granules. Mesotergum divided into 4 scutal areas; area I divided into 2 triangular halves by expansion of both area II and carapace; areas II–III strongly arched; area III armed with very high, erect paramedian spiniform processes, which may be placed on a common mound (*Cutervolus*). Free tergite III (= tergite VIII) with paramedian pair of enlarged spines. Basichelicerite well-developed, and with greatly swollen bulla. Cheliceral hand swollen in male. Pedipalpal femur poorly developed, with ventral row of setiferous tubercles, pedipalpal patella and tibia dorsally coated with coarse granulation. Legs III–IV much thicker than I–II, trochanter to tibia armed with enlarged spiniform apophyses, mostly arranged in longitudinal rows; legs I–II without conspicuous armature. Penis (Figs 9–12): ventral plate in the same plane as the truncus, rectangular (*Prostygnum*) or pentagonal (*Cutervolus*) with 2 groups of cylindrical macrosetae, basal set shortest (*Prostygnum*) or not (*Cutervolus*). Glans sac columnar, smooth, stylus C-curved (in lateral view), with short dorsal process. Body and appendages more or less uniformly brown; some granules on dorsal scutum in contrasting pale yellow; legs III–IV much darker than the rest; scutal grooves not contrasting.

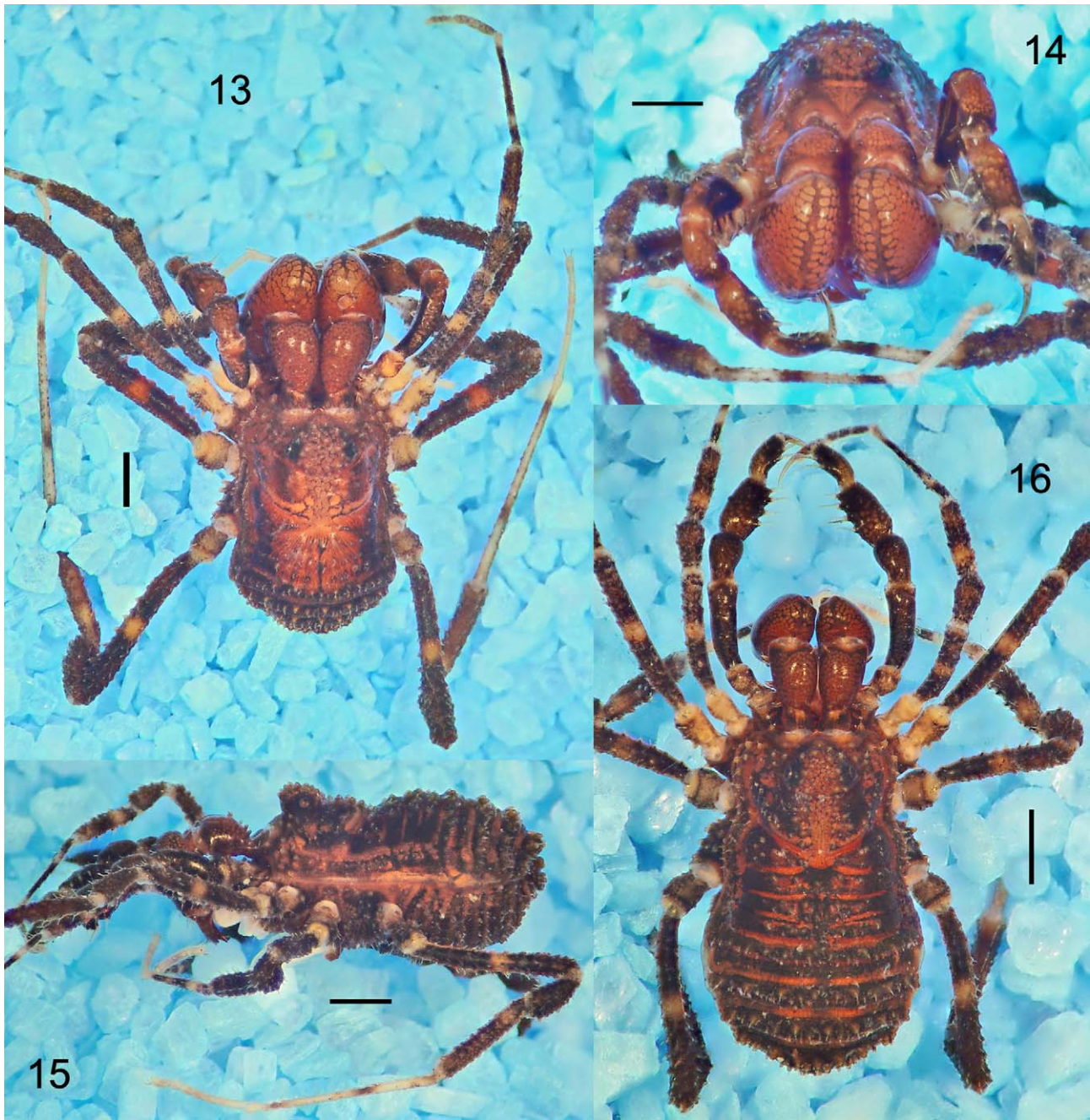
Included genera. *Cutervolus* Roewer, 1957 and *Prostygnum* Roewer, 1913.

Material examined. *Prostygnum vestitus* Roewer, 1913: ♂ holotype (SMF RI 840/36), from “Columbien: Maracaibo” in the original description, but labels reads “Columbien: Sabanilla”. This has been interpreted as Venezuela by Kury (2003), but most likely it refers to Sabanilla, between Loja and Zamora [Ecuador, Zamora-Chinchipec]. *Cutervolus albopunctatus* Roewer, 1957: 1 ♂ (MUSM 210) from Peru, Cajamarca, San Andrés de Cutervo, 2430 m, cloud forest, 14.iii.1989, Diana Silva leg.

Distribution. Southern Ecuador and northern Peru.

Zamorinae Kury, 1997, new familial assignment (Figs 13–26)

Zamorinae Kury 1997: 339; Kury 2003: 34; Pinto-da-Rocha & Hara 2009: 36.



FIGURES 13–16. *Zamora granulata* Roewer, 1928, ♂ (MNRJ 19266), from Pastaza, habitus, 13. Dorsal view; 14. Frontal view; ♀ (MNRJ 19298), from Morona-Santiago, habitus, 15. Left lateral view; 16. Dorsal view. Scale bars = 1 mm.

Diagnosis. Body (Figs 13, 15–16): dorsal scutum rectangular with sides slightly sinuous, anterior border straight, posterior border strongly convex. Ocularium elevated, unarmed, covered with coarse acuminate setiferous tubercles (Fig 14). Carapace well developed, slightly longer than abdominal scutum, posterior border somewhat squared U-shaped. Posterior margin of dorsal scutum, free tergites and sternites each with a transverse row of gross granules, otherwise unarmed. Mesotergum divided into 4 unarmed scutal areas; area I divided into 2 triangular halves by expansion of both area II and carapace. Basichelicerite well developed, elongate and with retrolateral apophyses. Cheliceral hand swollen in male. Pedipalpal femur convex with a dorsal (short and small) and a ventral (enlarged) row of setiferous tubercles, patella and tibia dorsally smooth. Legs I–IV without conspicuous armature, femur III of male thicker than the others. Penis (Figs 22–26): ventral plate leaned dorsally, short, with 2 groups of macrosetae, basal ones short and thin, distal ones large and spatulate. Glans sac columnar, smooth, stylus short, without any dorsal or ventral processes. Body and appendages uniformly brown; trochanters I–III mottled and

much lighter; mesotergum yellow in the middle with dark brown radiating pattern; mesotergal grooves not contrasting.

Included genera. *Zamora* Roewer, 1928.

Genus *Zamora* Roewer, 1928

Zamora Roewer 1928: 541; Kury 1994: 140; Kury 1997: 340; Kury 2003: 34; Kury & Alonso-Zarazaga 2011: 49 [type species: *Zamora granulata* Roewer, 1928, by monotypy].

Etymology. From place name Zamora, Ecuador. Gender feminine.

Diagnosis. Same as for the subfamily.

Zamora granulata Roewer, 1928

(Figs 13–26)

Zamora granulata Roewer 1928: 542, fig. 5; Kury 1997: 340; Kury 2003: 34; Kury & Alonso-Zarazaga 2011: 49.

Type data. ♀ holotype (SMF RII 108/6, examined), [wrongly reported as a ♂ in the original description] from “Ecuador, Tal des Zamora”, ca. 2000 m.

Distribution. *Zamora granulata* is known from the Eastern Cordillera realm montane forests (WWF NT0121), altitude 1050–2000 m. See details in Table 1.

Other material examined. 1 ♀ (MNRJ 19298) Ecuador, Morona-Santiago, just outside Macas, on the road to Sucua (S 02.34852°, W 078.15875°, 929 m); 1 ♂ (MNRJ 19283) Ecuador, Morona-Santiago, near Macas, “Eco-Park”, owner Mr. Alex, S 02.19075°, W 078.08288°, 1196 m, 24.iii.2011, A Chagas, A Giupponi & A Kury leg.; 1 ♂ 1 ♀ (MNRJ 19266) Ecuador, Pastaza, Rio Alpayacu, between Shell and Mera, along the river banks, S 01.46715°, W 078.10314°, 1065 m, 22.iii.2011, A Chagas, A Giupponi, A Kury & M Vega leg. These three localities as well as the type locality all lie in the range 900–2000m and in the WWF Eco-Region NT0121 (Eastern Cordillera real montane forests, Fig. 27).

Description. male (MNRJ 19266). Measurements. CL = 1.9, CW = 2.8, AL = 1.5, AW = 3.0.

Dorsum (Figs 13, 17–18). Dorsal scutum subrectangular, with anterior border straight and posterior border convex. Laterals of dorsal scutum softly divergent, with two well-marked constrictions. Carapace well developed, slightly longer than abdominal scutum, posterior border somewhat squared U-shaped, anterior corners with enlarged teeth. Ocularium elevated, unarmed, but densely covered with coarse acuminate setiferous tubercles. Mesotergum divided into 4 unarmed scutal areas; area I divided into 2 triangular halves by expansion of both area II and carapace, areas II–IV parallel to one another and arched posteriorly and provided each with a median transverse row of setiferous tubercles. Area IV divided by a longitudinal groove. Posterior margin of dorsal scutum, free tergites and sternites each with a transverse row of coarse setiferous tubercles, otherwise unarmed.

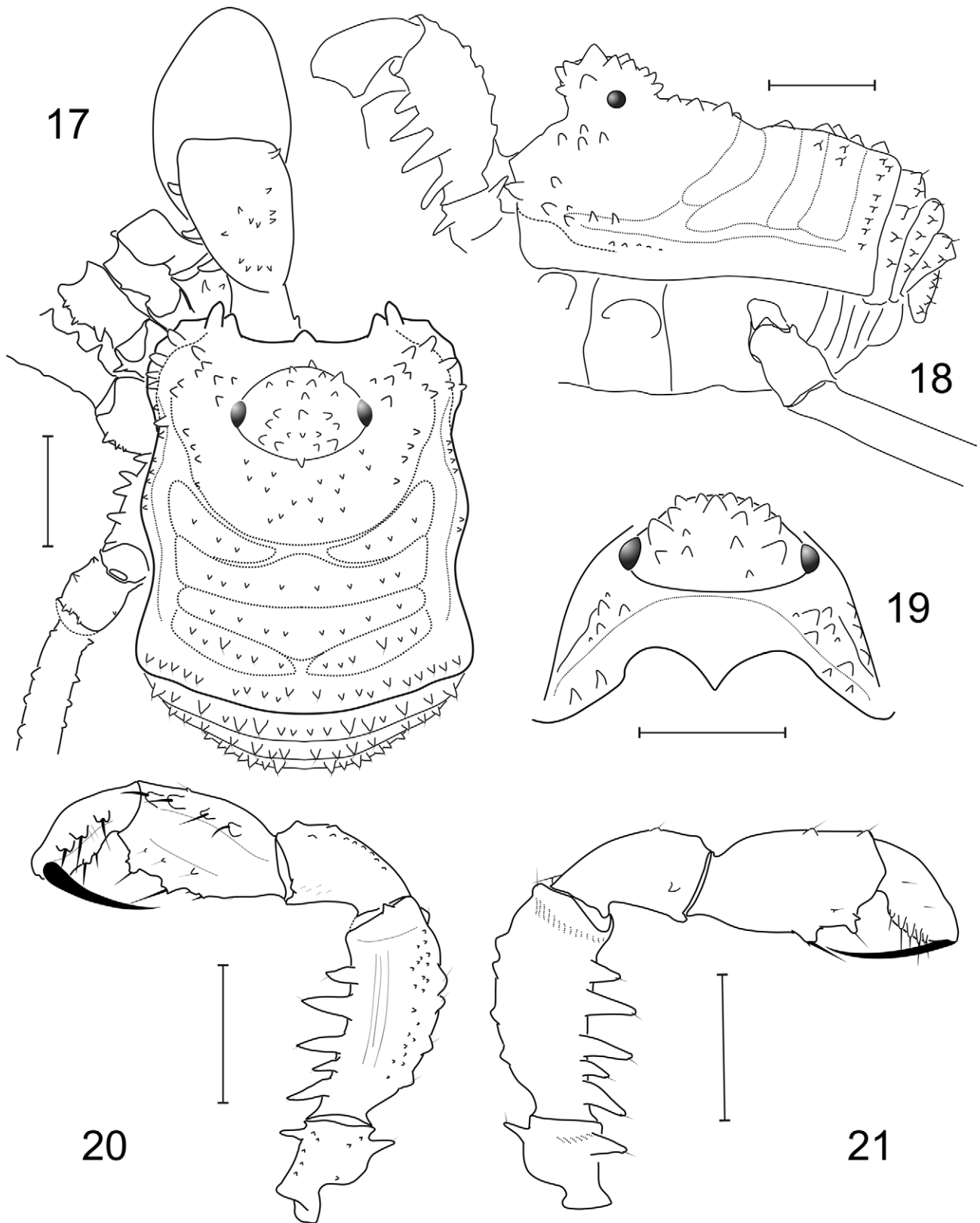
Chelicera (Figs 13–14, 17). Basichelicerite well developed, robust, with ectal and dorsal apophyses, and another dorsomeso apical. Cheliceral hand kidney-shaped swollen, unarmed.

Pedipalpus (Figs 20–21). Trochanter short, with one ventral and one dorsal large setiferous tubercles. Femur a little convex and with a dorsal row of low tubercles, ventrally armed with five robust spiniform apophyses. Patella short and unarmed, except for two very small mediodorso apical setiferous tubercles. Patella–tarsus dorsally smooth. Tibia (ventro-mesal iiIi) (ventro-ectal IiIi) and tarsus (ventro-mesal iiiiii) (ventro-ectal iii) each with a ventro-mesal and a ventro-ectal row of a few delicate and short spines.

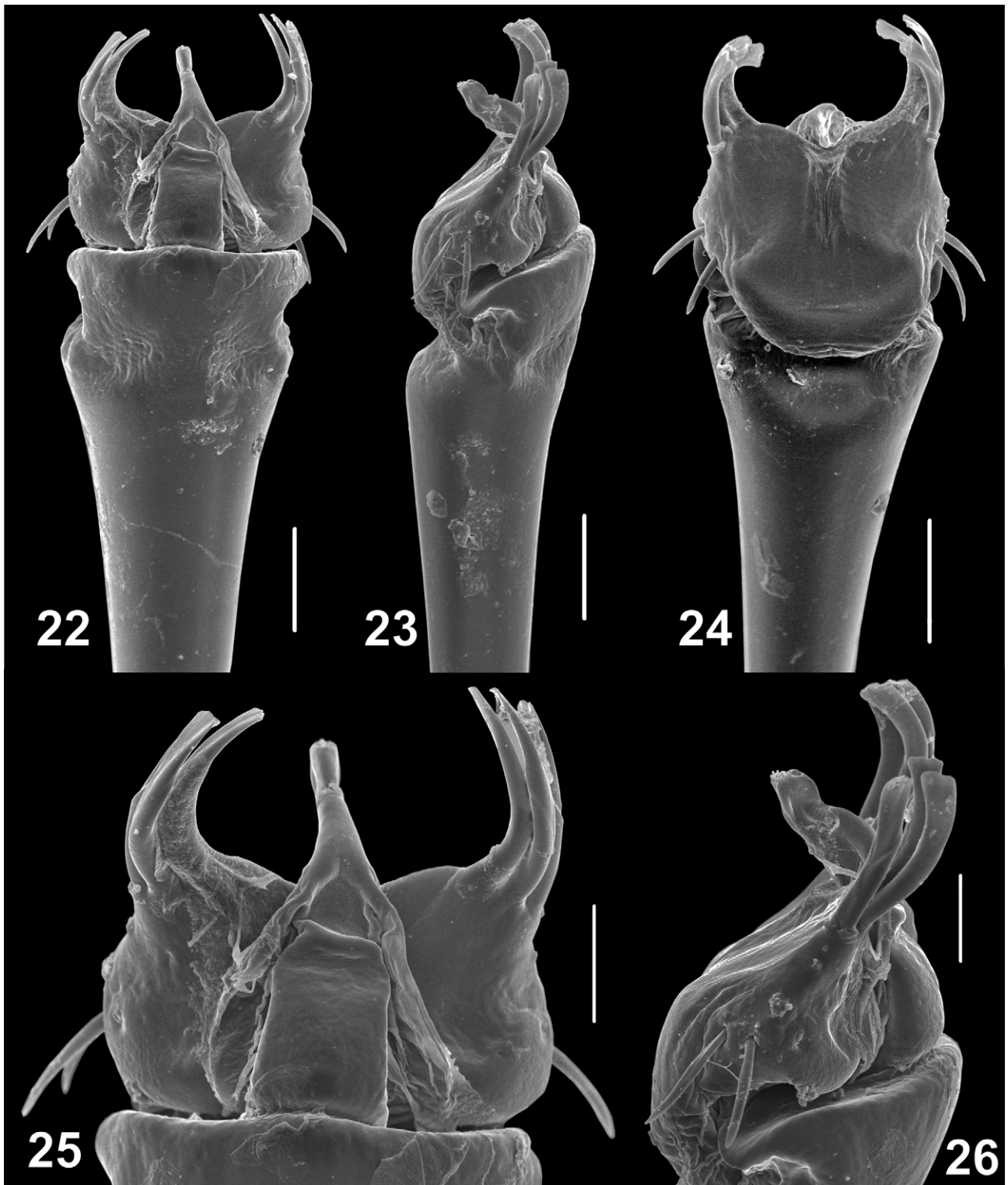
Legs (Figs 13, 17). Legs I–IV short and without prominent spiniform apophyses, but densely covered with acuminate tubercles. Metatarsus I not swollen. Femur–Tibia III covered by rows of robust setiferous tubercles with enlarged prodorsal spiniform apophyses. All femora substraight. Femur III clearly thicker than the others. Femur IV with a ventro-ectal and a ventro-mesal row of acuminate setiferous tubercles. Tarsal counts: 6(3)/10(3)/6/8.

Color. Background of body and appendages Strong Reddish Brown (40). Dorsal scutum densely mottled in Very Dark Red (17), especially the laterals of mesotergum, and middle of mesotergum with a pattern of thin lines radiating from mid scutal groove. Posterior margin of dorsal scutum and free tergites entirely Very Dark Red (17),

with lighter granules. Chelicerae and pedipalps Strong Reddish Brown (40), loosely honeycombed in Very Dark Red (17). Legs I–IV predominantly Very Dark Red (17), except for one lighter ring on each femur; trochanters I–IV and metatarsi–tarsi I–IV which are Dark Orange Yellow (72).



FIGURES 17–21. *Zamora granulata* Roewer, 1928, ♂ (MNRJ 19266), from Pastaza: 17. Habitus, dorsal view; 18. Same, left lateral view; 19. Ocularium, frontal view; 20. Right pedipalpus, ectal; 21. Left pedipalpus, mesal. Scale bars = 1 mm.



FIGURES 22–26. *Zamora granulata* Roewer, 1928, ♂ (MNRJ 19266), from Pastaza. Distal part of penis: 22. Dorsal view; 23. Same, right lateral view; 24. Same, ventral view; 25. Glans complex and ventral plate, dorsal view; 26. Same, lateral view. Scale bars = 100 μ m (Figs. 22–24), 50 μ m (Figs. 25–26).

Male genitalia (Figs 22–26). Truncus swollen towards the apex, this substraight with a pair of paramedian dorsal rounded concavities, reaching about half-length of ventral plate. Ventral plate leaned dorsally, rectangular very short (wider than long), distal border with shallow cleft, with 3 pairs of distal macrosetae, these large, spatulate, directed anteriorly and 2 pairs of basal macrosetae, these short, thin, directed oblique- and posteriorly. Glans sac columnar, smooth, stylus Y-shaped, without any dorsal or ventral processes and leaned against the ventral plate. Apex of stylus dorsally with many villi.

Female (Figs 15–16). Similar to male, except for the smaller ocularium (and consequently carapace), cheliceral hand not swollen, pedipalpal femur less robust and more weakly armed, femora III-IV weaker than those of male, and femur III as thick as the others. Color pattern identical to the male, excepted for the radiating pattern on mesotergum.

Variation. Tarsal counts of male and female specimens in Table 2.

TABLE 2. Tarsal counts of males and females of *Zamora granulata* Roewer, 1928.

specimen	sex	Ta1	Ta2	Ta3	Ta4
MNRJ 19266	♂	6-6	?-10	6-6	7-7
MNRJ 19266	♀	6-6	?-9	6-6	7-7
MNRJ 19283	♂	6-6	10-10	6-6	7-7
MNRJ 19298	♀	6-6	9-10	6-6	7-7

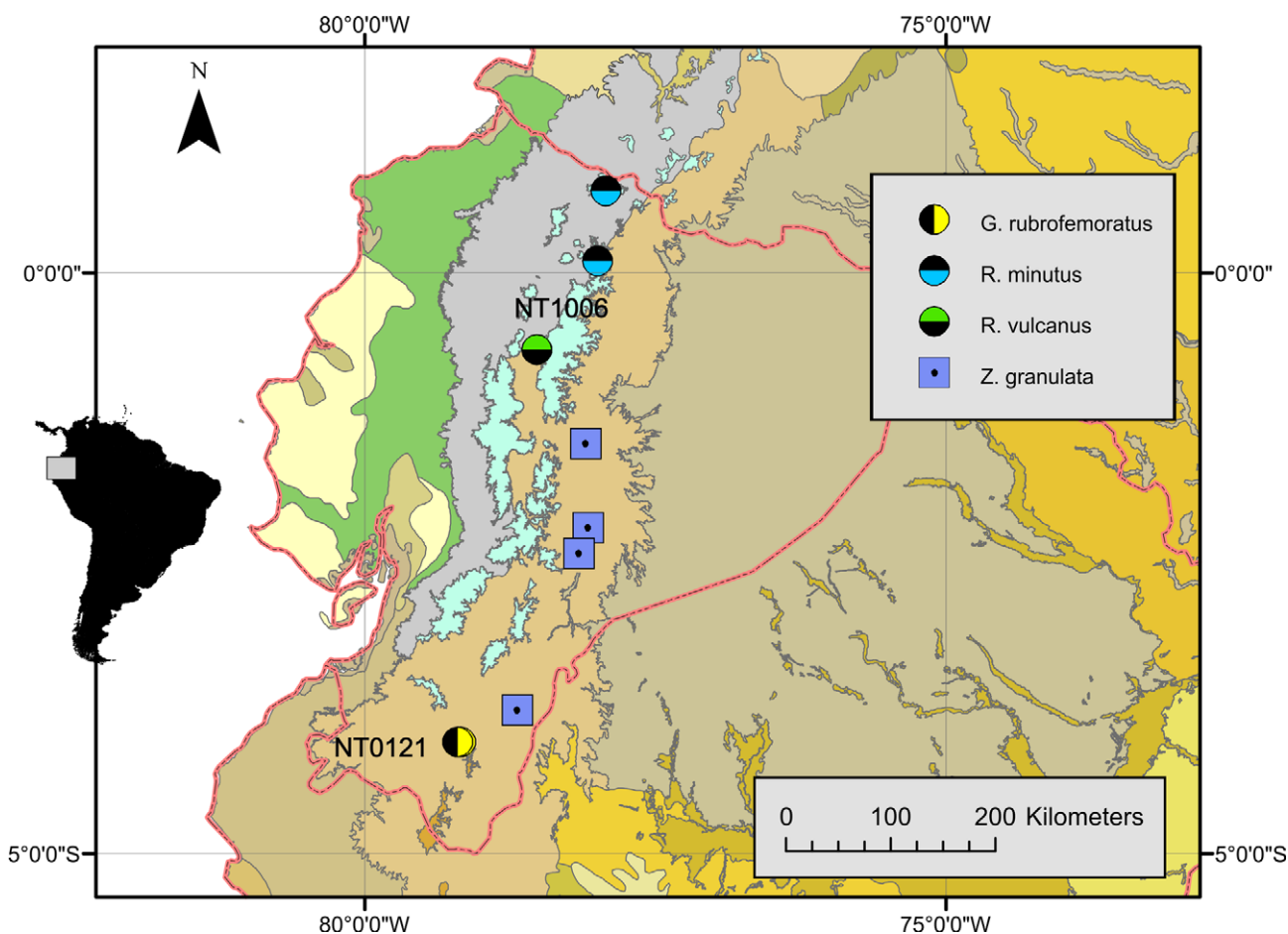


FIGURE 27. Ecuador, showing distribution of the Globibuninae and Zamorinae in WWF Ecoregions. Coordinates in Table 1. The two points for *G. rubrofemoratus* are almost collapsed at this scale due to their proximity. Color patches represent the WWF Ecoregions, of which the two relevant are marked.

Discussion and conclusions

***Zamora* as a Cranaiidae.** Placement of *Zamora granulata* in Cranaiidae is firmly supported by a putative synapomorphy of the family (at least for Heterocranainae, Cranainae and Stygnicranainae): ventral plate inclined dorsally, forming an acute angle with the truncus (Orrico & Kury 2009). In the groundplan of Gonyleptoidea, the ventral plate and the truncus are in parallel planes, state present in basal Gonyleptidae, Stygnidae, Cosmetidae and also in Prostyginae. External morphology is very similar in Prostyginae, Zamorinae and Globibuninae (*e.g.*,

pedipalpal femur with ventral row of setiferous tubercles; ocularium elevated and roughly granular; carapace sexually dimorphic), and without information on genital morphology it is not possible in the present state of knowledge to reliably assign any species, as Pinto-da-Rocha & Hara (2009) already suggested. The allocation of Prostyginae in Cranidae is only weakly supported (Orrico & Kury 2009), but it is so far the best hypothesis of phylogeny for the group.

Why to keep Zamorinae as a monotypic subfamily? The diversity of Cranidae is surely underestimated, as a great number of undescribed species from Colombia and Ecuador has been detected in collections (pers. obs.). Descriptions of new species are becoming common in the last decades while illustrations of male genitalia are being more and more provided for old species (e.g., González-Sponga 2003; Kury 1994; Kury 1995; Kury 2012; Pinto-da-Rocha & Bonaldo 2011; Pinto-da-Rocha & Kury 2003; Pinto-da-Rocha & Kury 2007). This increase in the corpus of described genital structures is leading to frequent reassessments of the relationships in the family. The five recognized subfamilies of Cranidae each represent different morphological plans of penis construction, and their composition is shifting and likely to increase in the next decades. An alternative to keeping the name Zamorinae would be to simply leave *Zamora* without any subfamilial assignment. Another option would be to assign *Zamora* to any of the four existing subfamilies, in spite of the striking differences described above. In the same way as old species were recently proven to belong in Globibuninae, Zamorinae should grow in described diversity as study on Cranidae progresses.

Insufficiency of external morphology for the familial assignment. The penial morphology of Agoristenidae is strikingly different from that of the other Gonyleptoidea. Upon dissection there is no doubt as to whether a given species belongs to Agoristenidae. The Globibuninae is a remarkable group in that it combines a generalized cranid facies with clearly agoristenid genitalia. This similarity in body features is so outstanding that it led species to be wrongly placed in one or another group prior to examination of penial morphology (Kury 1994; 1997). In this case, educated guesses, which worked well for other groups of Laniatores, failed to ascertain the correct taxonomic position of species known only by external morphological features. There is a number of species of Gonyleptoidea from Ecuador which resemble either Zamorinae or Globibuninae, but it is a better strategy to wait until they are more thoroughly examined—there have been enough of hasty familial assignments in these groups.

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