



Why does the Tricommatinae position bounce so much within Laniatores? A cladistic analysis, with description of a new family of Gonyleptoidea (Opiliones, Laniatores)

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The first cladistic analysis of the Tricommatinae is presented here based on a matrix with 88 terminals and 117 characters. The subfamily, hitherto with 28 genera and 53 species, is not recovered as a clade, instead it is composed of two nonsister clades, corresponding to the two main physiognomies of Tricommatinae *sensu lato*: (1) most of the diversity of the Tricommatinae, including the emblematic genera *Cryptogeobius* Mello-Leitão, 1935, and *Pseudopachylus* Roewer, 1912, and (2) the less familiar species, including the type genus *Tricommatulus* Roewer, 1912, plus a few relatives, totalling three genera with five species. The Tricommatinae *sensu stricto* are here reduced to their bare core, nested within Gonyleptidae, whereas **Cryptogeobiidae fam. nov.** is more basally placed within the Gonyleptoidea. The holotype and sole available material of *Tricommatulus brasiliensis* Roewer, 1912, type species of *Tricommatulus*, is restudied and is here redescribed and illustrated. *Pherania* Strand, 1942, is herein considered a junior subjective synonym of *Tricommatulus* and a key is given to the species of *Tricommatulus*. **Vorixax gen. nov.** of Tricommatinae is described along with the type species **Vorixax popeye sp. nov.**, an unusual species from Bahia, showing strange sexual dimorphism. Some changes have been introduced in the taxonomy of Cryptogeobiidae: (1) 13 genera are synonymized (two of them, *Berlesecaptus* Mello-Leitão, 1940, and *Simonoleptes*, originally in Phalangodidae); (2) 18 new combinations are made; (3) a neotype is designated for the type species *Berlesecaptus convexus* Mello-Leitão, 1940; (4) a new miniature species, **Paratricommatulus lockei sp. nov.**, is described from an area of conservation, Reserva Ecológica de Guapi-Açu, in Rio de Janeiro state, south-eastern Brazil.

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INTRODUCTION

The Tricommatinae are an elusive group of leaf-litter-dwelling Laniatores of consistently ambiguous systematic placement. They include 28 genera and 53 species of harvestmen distributed mainly in the Atlantic Forest of eastern Brazil, and which have long been considered to be a part of the artificial assemblage Phalangodidae – a gathering that represents

nothing in phylogenetic terms. The relationship of the Tricommatinae to the rest of the Phalangodidae was based only on symplesiomorphies, and phylogenetic work on Laniatores (Kury, 1991, 1993) led to a hypothesis of the Tricommatidae as a separate family, closest to the gonyleptid-like families, although not in the immediate vicinity of Gonyleptidae (Kury, 1992). Continued research on the matter led to a hypothesis of the Tricommatinae as highly derived Gonyleptidae, whose regressive characters were at first interpreted as plesiomorphic conditions (Kury, 1994, 2003a; Vogt

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& Kury, 1996). Recent molecular work (Pinto-da-Rocha *et al.*, 2014) suggested that the Tricommatinae should be placed back outside Gonyleptidae. The present work reveals that the Tricommatinae of Roewer actually belong to two unrelated groups, which finally explains why this subfamily has been bouncing back and forth between different groups of Gonyleptoidea over the years.

The Tricommatinae has a most convoluted taxonomic history. Created in 1912 by Roewer as Phalangodidae without scopula and with trimerous distitarsus I, lacking regard for other characters, it came to include assorted genera of Europe, South-East Asia, and Andean South America. A high number of 'tricommatines' has since been removed from this subfamily to Agoristenidae, Cladonychiidae, Cranaidae, Epedanidae, and other gonyleptid subfamilies (Avram, 1968; Martens, 1978; Kury, 1992, 1997) and vice versa (Kury, 1994, 1995a, 2003a; H. Soares, 1979). Besides, the subfamily itself has been transferred to the Gonyleptidae (Kury, 2003a) and found to be firmly nested in this family in Caetano & Machado (2013). After all those exclusions, the remaining nucleus of Tricommatinae still contains around 50 nominal species, distributed in the Brazilian Atlantic Forest, extending marginally into mixed forest of Argentina and Paraguay (Kury, 2003a).

The taxonomic study of the subfamily is further hindered by the existence of diverse monotypic genera, mostly based on females and very poorly characterized, and, especially until now by our ignorance about the male genitalia of the type species of the monotypic type genus. When the present author received on loan the male holotype of *Tricommatus brasiliensis*, the genitalia was already dissected and not associated to this material. Only many years later was it discovered that the penis had been removed and mounted on a slide in the context of a project on the nominal subfamilies of Phalangodidae, which resulted in an unpublished thesis. Fortunately, Michael Weber, the author of the thesis, made available an electronic version on the internet, which made the crucial knowledge of the genital structures available to a wider audience. Furthermore, Dr Weber graciously allowed the use of his illustrations here.

During the present study, it became clear that the systematic restlessness of Tricommatinae's placement was caused by it containing two unrelated lineages, which threw a great deal of noise into the system. The two conflicting physiognomies of what was hitherto known as Gonyleptidae Tricommatinae are: (1) the bulk of (false) 'tricommatines', including *Cryptogeobius* Mello-Leitão, 1935, and *Pseudopachylus* Roewer, 1912, and many other genera and (2) the *Pherania*-like species, including the type genus *Tricommatus* Roewer, 1912, plus a few relatives. Most of the diversity of the Tricommatinae belongs to this *Cryptogeobius*/

Pseudopachylus-like group. As they are not sister groups, this pattern is taxonomically addressed by recognizing and characterizing Cryptogeobiidae fam. nov. in Gonyleptoidea, including the *Cryptogeobius*/*Pseudopachylus*-like genera and reducing Tricommatinae to their bare core.

Cryptogeobiidae are medium/small to very small Gonyleptoidea that typically occur in leaf litter and may be found by sifting. There are two reported troglomorphic cave-dwelling species (H. Soares, 1972; Kury & Pérez-González, 2008). The Cryptogeobiidae show an astonishing variety of habitus (e.g. Fig. 1), shapes of dorsal scutum, ocularium, and build of legs (especially leg IV). The dorsal scutum is mostly unarmed, and almost all species lack a tarsal process (also called 'pseudonychium') on legs III–IV. The incredible plasticity of the Cryptogeobiidae appears to be the result of an ancient adaptive radiation that caused the appearance of miniature versions of Mitobatinae-like (e.g. Fig. 1A), *Pachylus*-like (e.g. Fig. 2D), and *Prostygnum*-like species. Most typical Cryptogeobiidae present the scutal area I entire, not divided into two halves, varied apophyses and lobes on basal segments of leg IV, and a penis with the ventral plate not yet individualized as in most gonyleptoids, but consisting of a swollen piece, herein named malleus (from Latin = hammer) and a distal roughly trapezoid blade called lamina parva (Kury, 1992, also e.g. Fig. 3). The latest descriptions (containing species with typical hammer-bearing penis) include one *Pseudopachylus* (Kury, 2006) and two *Spinopilar* (Kury, 1992; Kury & Pérez-González, 2008).

Recent expeditions of the Arachnology section of the Museu Nacional (UFRJ, Rio de Janeiro) collected tricommatines/cryptogeobiids from sifting leaf litter, including the long-lost/misplaced *Berlesecapitus convexus* (now allocated to *Zalanodius*) and two new species, one of which is described below as the type of the new genus *Voriox*.

SYSTEMATIC BACKGROUND

The Tricommatinae were conceived as a subfamily of the Phalangodidae (non-pseudonychiata Laniatores) by Roewer (1912), in its original concept including the species with distitarsus I three-jointed to contrast the two-jointed Phalangodinae. This poor, partly absence-based, definition led to the forceful inclusion in Tricommatinae of many unrelated taxa that were later proven to be members of many different families. This unfortunate subfamily included many European genera (all today considered junior synonyms of *Holoscotolemon* Roewer, 1915, in the Cladonychiidae), the Indonesian *Padangcola* Roewer, 1963 (transferred to the Epedanidae by Kury, 1992), many Andean taxa variously placed in the Agoristenidae, Cranaidae, and Gonyleptidae

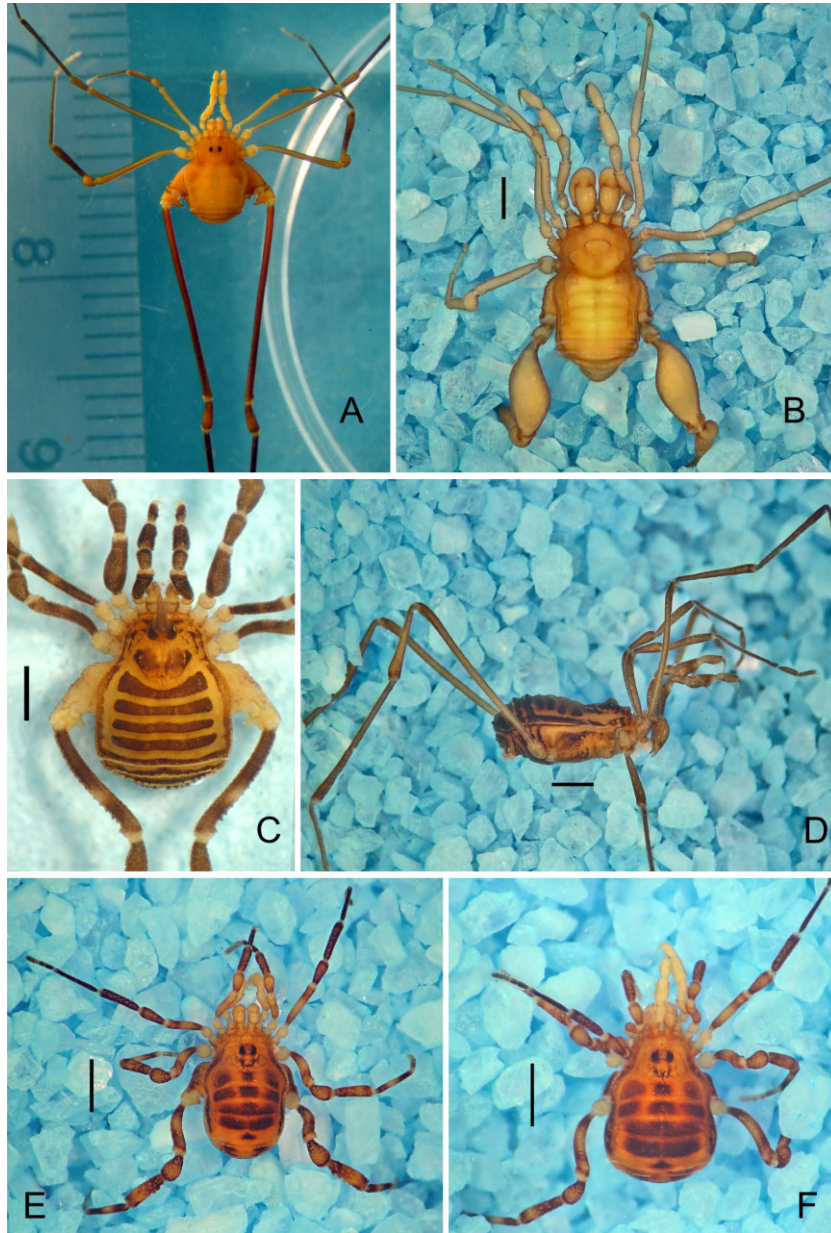


Figure 1. Cryptogeobiidae. Habitus of several species. A, Gen. sp. S, male (MNRJ 4558), dorsal view; B, *Pseudophalangodes unicolor*, male (MNRJ 7005), dorsal view; C, Gen. sp. T, male (MNRJ 18237), dorsal view; D, *Heteromeloleptes padbergi*, male (MNRJ 2243), lateral view; E, *Bunostigma singulare*, male (MNRJ 7679), dorsal view; F, Same, female. Scale bars = 1 mm.

Metasarcinae (e.g. Kury, 2003a), and finally some Brazilian Gonyleptidae Pachylinae (e.g. Kury, 2003a). By contrast, a large fraction of the species that are today considered to be Tricommatinae were formerly included in either the Pachylinae or Bourguyiinae (Kury, 2003a). Others were previously classified as Phalangodinae or as Stygnopsidae because of the two-segmented distitarsus I (e.g. H. Soares, 1979; Kury, 1995a; this paper). A curious effect of all this misplacing can be seen in de Mello-Leitão & Feio (1949: 318)

in the description of the new genus *Tingomaria*, which they duly compared with *Bacigalupo* Mello-Leitão, 1933, *Vima* Hirst, 1912, *Pseudopucroliia* Roewer, 1912, and *Pseudophalangodes* Roewer, 1912, only the last one of which still remains in the Tricommatinae, the others currently being in three subfamilies in two different families.

Kury (1992), working on *Spinopilar*, recognized a greater affinity of the Tricommatinae with the Gonyleptidae-like families instead of the Phalangodidae,

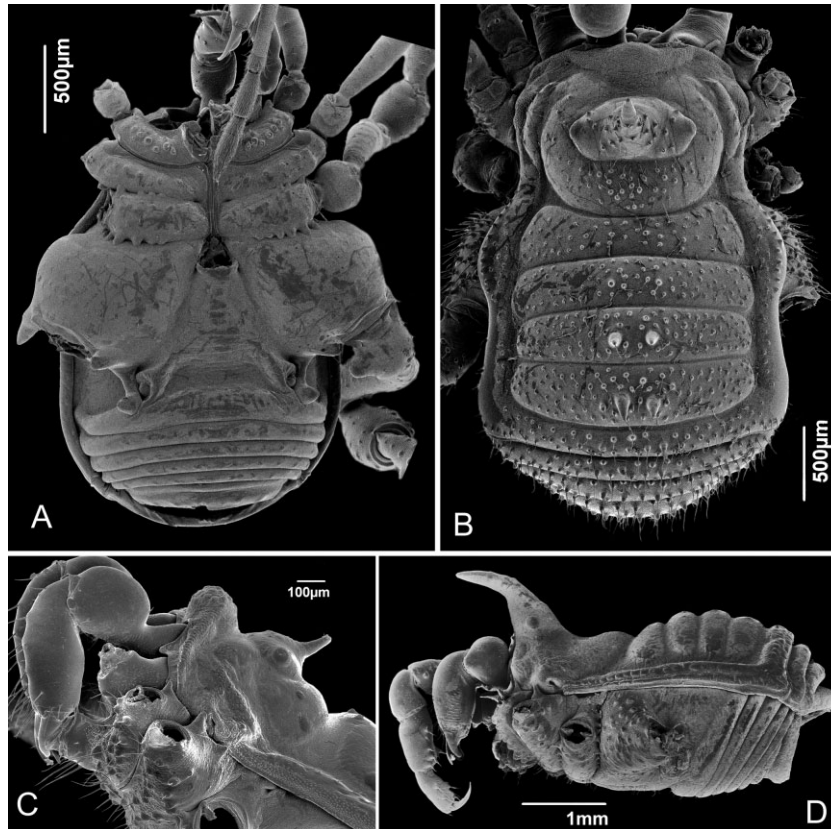


Figure 2. Cryptogeobiidae. A, *Bunostigma singulare*, male (MNRJ 7679), coxae, stigmatic area and sternites, ventral view; B, Gen. sp. P, male (MNRJ 16192) dorsal scutum, dorsal view; C, *Spinopilar armatus*, male (MNRJ 2251) carapace, coxae I–III, chelicerae, lateral view; D, *Bissulla paradoxa*, male (MZSP 432) body with chelicera/pedipalp, lateral view.

but could not at that time relate it to any of the families and raised it to familial rank amongst the Gonyleptoidea. Kury (2003a) went further and proposed that the Tricommatinae should be ranked within the Gonyleptidae. Caetano & Machado (2013) used one *Camarana* and one *Cryptogeobius* as terminals in their analysis of Gonyleptidae. Pinto-da-Rocha *et al.* (2014), after a molecular cladistic analysis using three terminals of Cryptogeobiidae, proposed that 'Tricommatinae' should be removed from Gonyleptidae.

CONVENTIONS

Descriptions of countless new genera and species would needlessly burden this work; therefore, undescribed species are treated by using 'Gen. sp., A, B, C', etc. These are listed along with the official species in the Material examined section with museum voucher numbers for reference. Some necessary alpha taxonomy will be presented elsewhere to formalize their existence to science.

Most terminology is explained directly in the list of characters and states. 'Fasciolate hyaline apophyses'

(Figs 4A, 5A, B) is a newly introduced term that refers to apophyses of basal segments of male leg IV, which are not hardened conical processes, but made of many lesser sclerotized units that give an impression of a bundle of transparent fibres.

Terminology introduced here for description of genital morphology of Cryptogeobiidae is:

Malleus (= hammer): proximal part of ventral plate, not forming the lamina parva. It typically bears the macrosetae A and B. The hammer may be immensely swollen and may bear a ventral haematodocha, here called hyaline button (Fig. 3D).

Podium: apical part of the ventral truncus, not forming the ventral plate, providing a flat surface on which the glans is incumbent. This formation is present in most Gonyleptoidea and occurs in many shapes.

Pre-podium: region of hammer adjacent to podium, and which in Cryptogeobiidae may be greatly enlarged, defining the shape of the pars distalis of the penis.

Descriptions of colours use the standard names of the 267 Color Centroids of the NBS/IBCC Color System (<http://people.csail.mit.edu/jaffer/Color/Dictionaries>

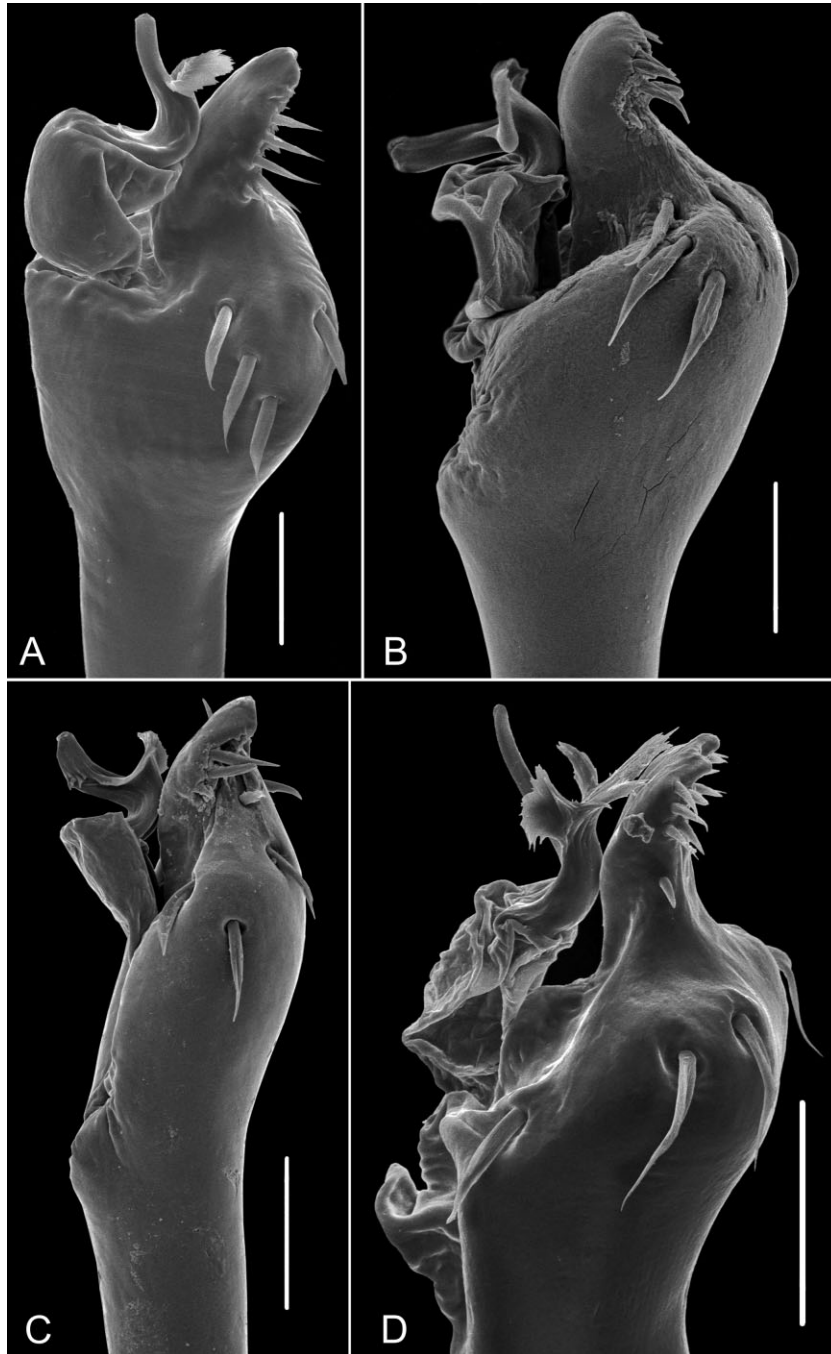


Figure 3. Cryptogeobiidae, distal part of penis, lateral view. A, *Taquara bicoloripes*, male (MNRJ 2218). B, Gen. sp. P, male (MNRJ 16192). C, *Bunostigma singulare*, male (MNRJ 7679). D, Gen. sp. AD, male (MNRJ 5592). Scale bars = 0.05 mm (A–C), 0.1 mm (D).

#nbs-iscc) as explained 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. Unless otherwise stated, all measurements are in mm.

Abbreviations of the repositories cited are: IBSP, Instituto Butantan, São Paulo; SMF, Senckenberg

Museum, Frankfurt; MNRJ, Museu Nacional, Rio de Janeiro; MZSP, Museu de Zoologia, São Paulo.

Abbreviations of the Brazilian states cited in the Material examined section are: BA, Bahia; ES, Espírito Santo; MG, Minas Gerais; PR, Paraná; RJ, Rio de Janeiro; SC, Santa Catarina; SP, São Paulo.

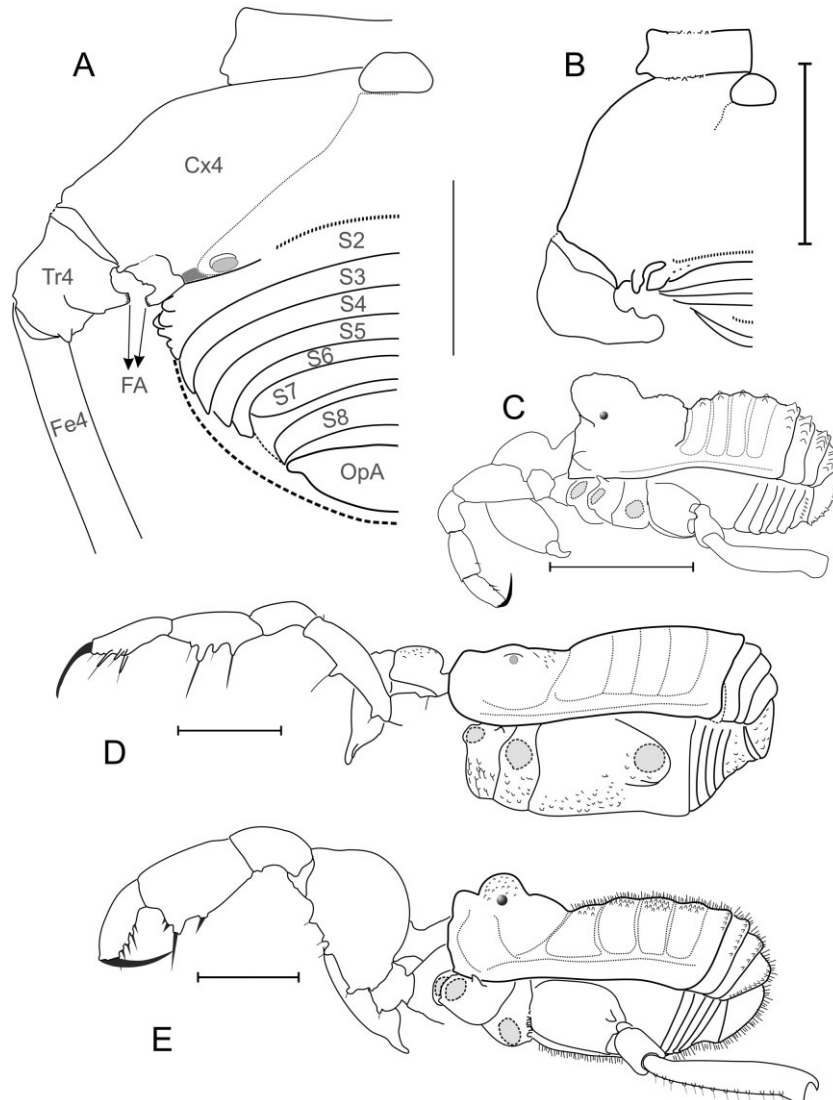


Figure 4. Cryptogeobiidae. A, *Tibangara nephelina*, male (MNRJ 1964). Opisthosoma, ventral view, schematic, lacking most tubercles and setae. B, *Spinopilar armatus*, male (MNRJ 4508). Opisthosoma, ventral view, schematic, lacking most tubercles and setae. C, Gen. sp. F (MZSP 10022). Habitus, lateral view. D, *Pararezendesius luridus* (MNRJ 9000). Same. E, Gen. sp. H (MZSP 15747). Same. Abbreviations: Cx, coxa; FA, interlocking fasciolate apophyses of coxa and trochanter; Fe, femur; OpA, operculum anale (tergite 9); S2–S8, sternites; Tr, trochanter. Scale bars = 1 mm.

Other abbreviations used are: AL, abdominal scutum length; alt., altitude; AW, abdominal scutum width; CL, carapace length; CW, carapace width; Fe, femur; leg., legit (i.e., collected); Mt, metatarsus; Pa, patella; Ta, tarsus; Ti, tibia; Tr, trochanter; VP, ventral plate of penis.

The A–E system of naming the macrosetae of ventral plate follows A. B. Kury & O. M. Villarreal (unpubl. data).

Two important molecular analyses involving Gonyleptoidea and that are profusely cited here are abbreviated for fluency as: SG11, Sharma & Giribet (2011); PA14, Pinto-da-Rocha *et al.* (2014).

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 distitarsus I–II).

MATERIAL EXAMINED

Non-exhaustive, representative material of the Tricommatinae and Cryptogeobiidae used in the analysis is listed here. The combinations used are the new ones, as proposed here after the cladistic analysis. Undescribed species are given as ‘Gen. sp. letter of alphabet’, and the generic allocation that the

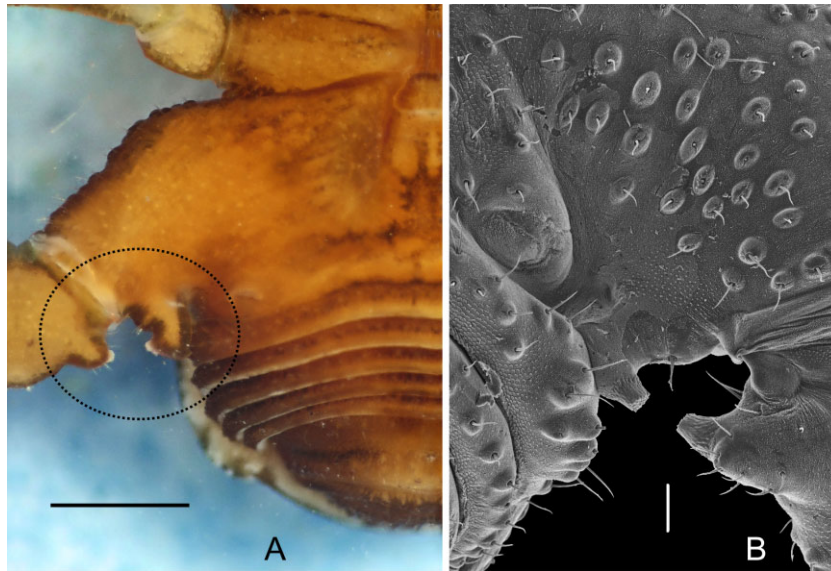


Figure 5. Cryptogeobiidae. Matching hyaline fasciolate apophyses (FAP), ‘alpha shark’s fin’ of trochanter IV and ‘horse’s head’ of coxa IV. A, *Pseudopachylus longipes*, male (MNRJ 17649), ventral view of stigmatic area and base of leg IV. B, *Tibangara nephelina*, male (MNRJ 1964). The same region as preceding illustration, showing ‘bundle’ structure of both FAP. Scale bars = 1 mm (A), 0.1 mm (B).

species will probably have, once described, is given in parentheses. As the very great majority of records are from Brazil, the name of this country is omitted and the Brazilian states are noted by their standard two-letter abbreviation as defined above.

OUTGROUPS

Paramitraceras sp. 4 ♂ 8 ♀ (AMNH) Mexico, Chiapas, 8 km north-east of Chiapa, 26.viii.1966, J. & W. Ivie leg. In spite of belonging to a remotely placed family, the use of this genus in the prime outgroup is appropriate because in the past no fewer than three species of ‘Tricommatinae s.l.’ (today each placed in a different genus) have been described as *Paramitraceras*.

Eutimesius sp. 1 ♂ (IAvH 3000120) Colombia, Norte de Santander, Toledo, Vereda El Diamante, Finca La Primavera. Parque Nacional Natural Tama, Santa Naria, Alto de Herrera. 7°7’N, 72°13’ W, alt. 1000 m Bosque, Captura manual. 22.iv.1999 E. Gonzalez leg. This species is used here because the features of the male genitalia are not as heavily modified as in many Stygnidae, and thus are useful for establishing homologies.

Globibunus rubrofemoratus Roewer, 1912–22 ♂ 21 ♀ (MNRJ 19308) Ecuador, Loja, Zamora huayco, Reserva Privada El Madrigal, 4° 2’23.17’’S, 79°10’30.53’’W, alt. 2200 m, 27.iii.2011 A. Chagas, A. Giupponi & A. Kury leg.

Incasarcus diana Kury & Maury, 1998: ♂ holotype, 2 ♀ paratypes (MUSM 414); Peru, Cuzco, Parque Nacional Manu, road Paucartambo–Pilcopata,

c. 13°01’40’’S, 71°16’40’’W, 2900 m, 19.ii.1990 A. Cano & D. Silva leg./1 ♂ 2 ♀ paratypes (MNRJ 5315) same location (loc.), 14.ii.1990 D. Silva leg.

Ampycus telifer (Butler, 1873): 1 ♂ 1 ♀ (AMNH AK 021) Peru, Amazonas, Upper Marañon river, between Río Cenipa and Río Nieva, 10.ix.1924 Kluge leg./2 ♂ 1 ♀ (FMNH AK 121b) Ecuador, Pastaza, Cusuimi on Rio Cusuimi, 150 km south-east of Puyo, 300 m, 18–23.vii.1971, B. Malkin leg.

Camposicola altifrons Mello-Leitão, 1924: 1 ♂ 1 ♀ (MNRJ 11370), RJ, Cambuci, forest near Balneário de Santa Inês, 19–20.vi.2011, A. P. L. Giupponi, G. G. Enne & A. Pérez leg.

Discocyrtoides nigricans (Mello-Leitão, 1922): 12 ♂ 17 ♀ (MNRJ 18884), MG, Poços de Caldas, Morro do Ferro, xii.1964, J. Becker leg.

Prostygnum vestitus Roewer, 1913: ♂ holotype (SMF RI 840/36), Ecuador, Zamora-Chinchi, Sabanilla.

Pseudopucroliia mutica (Perty, 1833): 14 ♂ 8 ♀ (MNRJ 02168), BA, Porto Seguro, Praia de Itaperapuã, 26–28.v.2004, A. Chagas Jr. leg.

Soaresia uncina H. Soares, 1945: 6 ♂ 3 ♀ (MNRJ 05465), RJ, Rezende: Serrinha do Alambari, 850 m, leaf litter, 29–31.xii.1992, A. B. Kury leg.

Triglochynura curvispina Mello-Leitão, 1924: 2 ♂ 1 ♀ (MNRJ 01968), RJ, Angra dos Reis, Ilha Grande, Araçatiba, i.2007, A. P. L. Giupponi leg.

Gen. sp. C (undescribed genus, superficially similar to *Vorriax*): 2 ♂ 2 ♀ (MNRJ 18214), ES, Santa Teresa, Reserva Biológica (REBIO) Augusto Ruschi, 12.viii.2006, T. Bernabé, D. Mota, T. Souza & E. Soeiro leg./4 ♂ 2 ♀ (MNRJ 18748), same loc., 26.x.2006, T. Bernabé leg.

TRICOMMATINAE

Caramaschia singularis Kury, 2002: ♂ holotype (MNRJ 4409) BA, Itagibá, Fazenda Pedra Branca, 23.i.1975, U. Caramaschi, J. Jim, C. M. Carvalho & S. A. Mioni leg.

Gen. sp. A (*Caramaschia*): 2 ♂ 3 ♀ (MNRJ 5758) RJ, Rio de Janeiro: Parque Estadual da Pedra Branca, Floresta do Engenho de Dentro, in leaf litter, 06.v.1999, A. B. Kury & A. P. L. Giupponi leg./1 ♂ 2 ♀ 1 pullus (MNRJ 6912) RJ, Rio de Janeiro: Parque Estadual da Pedra Branca, Floresta do Engenho de Dentro, in leaf litter, 27.v.1995, A. B. Kury, M. S. Baptista & M. G. Vogt leg./1 ♀ (MNRJ 5823) RJ, Rio de Janeiro: Morro da Urca, 15.xi.1990, R. & A. Baptista leg.

Gen. sp. B (*Caramaschia*): 2 ♂ 5 ♀ (MNRJ 17553) RJ, Casimiro de Abreu, Barra de São João slope of Morro de São João, 21–24.iii.2003 A. B. Kury *et al.* leg.

Tricommatus brasiliensis Roewer, 1912: ♂ holotype (SMF RI 220), SC, without further locality data.

Tricommatus giupponii (Kury, 2003) [hitherto in *Pherania*]: ♂ holotype, 2 ♂ 3 ♀ paratypes (MNRJ 4494) SC, Florianópolis, Ilha de Santa Catarina, forest on hill behind buildings of APAE, ÚNICA and SESI, 15–17.xii.1999 A. P. L. Giupponi & D. Pedroso leg.

Tricommatus pygmaeus (Sørensen, 1932) [hitherto in *Pherania*]: ♂ holotype (BMNH), SC, Blumenau, E. Keyserling leg.

Voriax popeye gen. et sp. nov.: 16 ♂ 49 ♀ types (MNRJ 17722), BA, Porto Seguro, Arraial d'Ajuda, Fazenda do Sr. Valter, 24–27.ii.2005, A. B. Kury *et al.* leg.

CRYPTOGEOBIIIDAE

Bissulla paradoxa Roewer, 1929: 1 ♂ (MNRJ-HS 336) SP, Cananéia, Morro São João, 17.xi.1952, O. Schubart leg./3 ♂ 3 ♀ (MZSP 432) SP, São Paulo, 23.iii.1943, F. Lane & B. A. M. Soares leg./1 ♂ (MZSP 9348) SP, Tapiraí, 15.xi.1952, O. Schubart leg.

Bissulla singularis (Soares & Soares, 1949) [hitherto in *Machairosceles*]: 1 ♂ paratype (MNRJ-HS 0152) PR, Morretes, Marumbi, viii.1946, C. N. Gofferjé leg.

Gen. sp. X (*Bissulla*): ♂ holotype (MZSP 17252), Miracatu, Serra de Itimirim (boundary with Iguape), 20.xii.1998, R. Pinto-da-Rocha & R. S. Bérnils leg.

Gen. sp. Y (*Bissulla*): 1 ♂ (ZMUC AK 042a) SP, Santos, xii.1893, H. Brauns leg.

Gen. sp. Z (*Bissulla*): 1 ♂ 1 juvenile (juv.) (MCZ) SP, São Paulo: Zoological Park Água Funda, on rotten wood. 9.viii.1962, W. L. Brown col.

Gen. sp. AA (*Bissulla*): ♂ holotype, 1 ♀ paratype (MZSP 18090) PR, São José dos Pinhais: Represa da Usina Hidroelétrica de Guaricana, 08.iii.1999, A. B. Kury, R. Pinto & A. P. L. Giupponi col.

Gen. sp. AB (*Bissulla*): ♂ holotype (MZSP 14779) SC, Ilhota: Parque Botânico do Morro do Baú, 04.ii.1996, A. B. Bonaldo, A. B. Kury & R. Pinto col.

Bresslavius debilis (Mello-Leitão, 1940): ♂ holotype (MNRJ 0403), RJ, Rio de Janeiro: Jacarepaguá, Santa Bárbara, Pau da Fome, 700 m, A. O. Martins leg. (collector name from the description, but may be wrong because it is associated with wrong locality data).

Bresslavius hirsutus Mello-Leitão, 1935: 4 ♀ syntypes (MNRJ 42327), RJ, Petrópolis, Independência, R. Arlé leg.

Gen. sp. M (*Bresslavius*): ♂ holotype (MNRJ 8923), MG, Rio Preto, between Rio Preto and Santa Bárbara do Monte Verde, primary forest 1100–1300 m, 14–20.v.2002, A. P. C. Giupponi *et al.* leg.

Gen. sp. N (*Bresslavius*): 2 ♂ 1 ♀ (MNRJ 17687) RJ, Mangaratiba, Reserva Ecológica Rio das Pedras near Club Mediterranée, 11–12.xi.2004 A. P. L. Giupponi leg.

Gen. sp. O (*Bresslavius*): 3 ♂ 2 ♀ (MNRJ 17461), RJ, Casimiro de Abreu, Barra de São João, Fazendas Reunidas, 21–24.iii.2003, A. B. Kury *et al.* leg.

Gen. sp. P (*Bresslavius*): 1 ♂ (MNRJ 16194) RJ, Teresópolis, Parque Nacional da Serra dos Órgãos, Rancho Frio Trail, 4–5.viii.2005, A. B. Kury, A. P. L. Giupponi, D. R. Pedroso & V. D. Orrico leg.

Bunostigma singulare Mello-Leitão, 1935: ♂ lectotype, 1 ♂ 3 ♀ paralectotypes (MNRJ 41788) and 2 ♀ paralectotypes (MNRJ 42677), RJ, Rio de Janeiro, P. N. Parque Nacional da Tijuca, Bico do Papagaio peak, R. Arlé leg./1 ♂ (MNRJ 4765) same loc., 3.iii.2001, A. P. L. Giupponi, D. R. Pedroso & D. F. Almeida leg./1 ♂ 1 ♀ (MNRJ 4950), same loc., Trilha da Caveira 8.ix.2001, A. Pérez & A. P. L. Giupponi leg./1 ♂ 1 ♀ (MNRJ 07679), same loc., close to Gruta do Belmiro, 15.vi.2012, A. B. Kury, C. M. Barros, D. R. Pedroso & G. S. Miranda leg.

Camarana flavipalpi B. Soares, 1945: 1 ♂ (MNRJ 05648) SP, Ubatuba, Morro do Corcovado, 17.i.1996, G. Machado leg./1 ♂ (MNRJ 06073) SP, Ubatuba, Picinguaba, Rodovia Rio-Santos Km 3, 13.x.1985, R. L. C. Baptista leg.

Camarana minor Mello-Leitão, 1935: ♂ holotype (MNRJ 42475) RJ, Rio de Janeiro, Jacarepaguá, C. Couceiro leg.; 6 ♂ 14 ♀ (MNRJ 02214) RJ, Mangaratiba, Reserva Ecológica do Rio das Pedras (RERP) 25–26.ix.2009, A. Giupponi & A. Kury leg.

Cryptogeobius clavitibialis (Roewer, 1949): ♂ holotype (SMF RII 1561/11), RJ, 'Pirahy' (= currently spelled Pirai).

Cryptogeobius crassipes Mello-Leitão, 1935: 2 ♀ syntypes (MNRJ 41758), RJ, Rio de Janeiro, Gávea R. Arlé leg./17 ♂ 24 ♀ (MNRJ 05918), RJ, Rio de Janeiro, Praia Vermelha, sifting litter, 20.xi.1990, A. B. Kury leg./10 ♂ 9 ♀ (MNRJ 05821), RJ, Rio de Janeiro, Morro da Urca, 15.xi.1990, R. L. C. Baptista & A. R. P. Baptista leg.

Gen. sp. D (genus uncertain): 1 ♂ (MZSP 14756), SC, road Concórdia-Joaçaba, 30.i.1996, A. B. Bonaldo, A. B. Kury & R. Pinto-da-Rocha leg.

Gen. sp. E (genus uncertain): 2 ♂ 2 ♀ (MNRJ 18753), ES, Santa Teresa, REBIO Augusto Ruschi, leaf litter, 25.x.2006, T. N. Bernabé leg.

Gen. sp. F (genus uncertain): 1 ♂ 1 ♀ (MZSP 10022) SP, Cananéia, 17.xi.1952, O. Schubart leg.

Gen. sp. G (genus uncertain): 4 ♂ 12 ♀ 1 juv. (MACN AK 002) RJ, Ilha Grande, Enseada das Palmas, 2–12.ii.1997, M. Ramirez leg.

Gen. sp. L (*Spinopilar*): 1 ♂ 1 ♀ (MNRJ 17480) SP, Monteiro Lobato, 1–8.iv.2002, E. G. Vasconcelos leg.

Gen. sp. S (probably undescribed genus): 1 ♂ 1 ♀ (MNRJ 4558) RJ, Rio de Janeiro, Parque Nacional da Tijuca, Bico do Pagagaio trail, 15.vi.2001, R. L. C. Baptista & L. E. Goes e Silva leg.

Heteromeloleptes fasciatus (Mello-Leitão, 1932): 2 ♂ 1 ♀ (MNRJ 05562), RJ, Itatiaia, PN Itatiaia, Vêu da Noiva, Córrego Maromba, 1100 m, 02–03.ii.1997, A. B. Kury, R. Pinto-da-Rocha & L. Mestre leg.

Heteromeloleptes hirsutus (Soares & Soares, 1970): 2 ♂ 9 ♀ (MNRJ 05581), MG, Itamonte, PN Itatiaia, Entrada para o Vale dos Lírios, 2400 m, 04.ii.1997, A. B. Kury, R. Pinto-da-Rocha & L. Mestre leg.

Heteromeloleptes padbergi Mello-Leitão, 1931: 1 ♂ (MNRJ 04430), MG, Itamonte, Brejo da Lapa, 15.xii.1991, R. L. C. Baptista & A. R. P. Baptista leg./2 ♂ (MNRJ 02243), MG, Bom Jardim de Minas, Vale do Taboão, 12–14.ix.2008, I. S. Oliveira leg.

Gen. sp. AC (*Heteromeloleptes*): 1 ♂ (MNRJ 07031), Santa Rita do Ibitipoca, PARES do Ibitipoca, 18–21.vi.2009, I. S. Oliveira leg.

Gen. sp. AD (*Heteromeloleptes*): 3 ♂ 3 ♀ (MNRJ 05584), MG, Itamonte, PN Itatiaia, Entrada para o Vale dos Lírios, 2400 m, 04.ii.1997, A. B. Kury, R. Pinto-da-Rocha & L. Mestre leg./2 ♂ 1 ♀ (MNRJ 05592), MG, Itamonte, Brejo da Lapa, 2200 m, 05–06.ii.1997, A. B. Kury, R. Pinto-da-Rocha & L. Mestre leg.

Lanesoares inermis (B. Soares, 1944): ♂ ♀ syntypes (MZSP 449) SP, Alto da Serra/1 ♀ (MZSP 28690c) SP, Salesópolis, Estação Biológica de Boracéia, ix.1997, C. Rheims leg./1 ♂ (MZSP 17616) SP, Salesópolis, Estação Biológica Boracéia, 26–28.i.1999, 900 m, R. Pinto, S. Casari, E. Ramirez & R. S. Bernils leg.; 1 ♂ 1 ♀ (MZSP 17733) same loc., 21–22.i.1997, R. Pinto leg.; 2 ♂ (IBSP 7790) v.2001, Curso I Graduação Universidade de São Paulo (USP) leg./1 ♀ (MZSP 17663) SP, Alto da Serra, 25–26.i.1997, R. Pinto & S. Casari leg./1 ♂ (IBSP 4884) SP, Mogi das Cruzes, Fazenda São Simão, 10–14.xi.2003, A. V. da Costa leg./1 ♂ (MZSP 9989) SP, Mogi das Cruzes, Rancho Carmelita Cyllo Torres, 1.x.1976, Kayagima leg.

Pararezendesius luridus H. Soares, 1972: ♀ holotype (MZSP 9360) SP, Iporanga: Minas de São Francisco/1 ♂ (MNRJ 9000) Iporanga: Caverna Água Suja, 6.iii.1984, E. Trajano leg.; 1 ♂ (MNRJ 6884) Gruta Harpa do Xá, 16.iv.1989, R. L. C. Baptista leg.; 1 ♂

(MNRJ 4951) Gruta Jane Mansfield, ground, darkness zone, 1990, R. L. C. Baptista leg.

Paratricommatus colatinae (Soares & Soares, 1946) [hitherto in *Neoarminda*]: 1 ♂ 3 ♀ (MNRJ 16245) ES, Cariacica: Reserva Biológica de Duas Bocas. Alto do Alegre. 20°17'29.72"S, 40°31'10.16"W alt. 596 m, 13.x.2005, A. Giupponi, A. Kury, V. Orrico, M. Milleri, R. Rodrigues & T. Souza leg.

Paratricommatus hexabunus (Mello-Leitão, 1940): ♀ holotype (MNRJ 156), RJ, Mangaratiba.

Paratricommatus inermis (Soares & Soares, 1954): ♀ holotype (MZSP 1179), RJ, Rio de Janeiro, Corcovado, 30.vi.1946, P. Wygodzinsky leg.

Paratricommatus lockei sp. nov.: ♂ holotype (MNRJ 07582), 11 ♂ 18 ♀ paratypes (MNRJ, details listed below in the description) RJ, Cachoeiras de Macacu, Reserva Ecológica de Guapi-Açu (REGUA), various dates A. P. L. Giupponi & J. S. Silva leg.

Paratricommatus mahnerti (Soares & Soares, 1985): ♂ holotype 1 ♂ paratype (MHNG, not examined)/1 ♂ paratype (MNRJ-HS 825), Paraguay, Puerto Stroessner.

Paratricommatus modestus Piza, 1943: 1 ♂ (MZSP 22360) SP, Mairiporã, Cantareira (P. E. da Pedra Grande), Winckler, 14.viii.2000, C. L. Firmo *et al.* leg.

Gen. sp. H (*Paratricommatus*): ♂ holotype 1 ♀ 4 juv. paratypes (MZSP 15747), Campos do Jordão, Parque Estadual Campos do Jordão, 04–07.iv.1997, R. Pinto-da-Rocha & S. Casari leg.

Pseudopachylus eximius (Mello-Leitão, 1936): ♀ holotype of *Caporiacoius eximius* (MNRJ 42277 – wrongly stated as 42280 in the original description), PR, Antonina, Frederico Lange de Morretes col., examined, both legs I lost, all legs II–III present in the vial, but detached from body/1 ♂ ‘allotype’ 4 ♀ (MNRJ-HS 907), PR, Marumbi, viii.1946, K. Imaguire col.; 1 ♂ 3 ♀ (MNRJ-HS 264) same data.

Pseudopachylus longipes Roewer, 1912: 2 ♂ 1 ♀ (MZSP 18893b) SP, Santo André. Estação Biológica do Alto da Serra, 27.viii.1999, R. Pinto-da-Rocha leg.

Pseudopachylus martensi Kury, 2006: ♂ holotype, 4 ♀ female paratypes (MNRJ 4435) SP, São José do Barreiro, Serra da Bocaina, Núcleo Senador Vergueiro, 30.x.1967, O. A. Roppa leg. The paratypes were overlooked in the original description.

Pseudopachylus nigripes (Mello-Leitão, 1932): ♂ holotype of *T. nigripes* (MNRJ 1362), RJ, Rio de Janeiro/♀ holotype of *Pseudopachylus lissonotus* (MNRJ 58240), RJ, Rio de Janeiro, Jacarepaguá, R. Arlé leg./4 ♂ 3 ♀ paratypes of *Pseudopachylus lissonotus* (MNRJ 405), Jacarepaguá, R. Arlé leg./1 ♂ 2 ♀ (MNRJ 6309) RJ, Cachoeiras de Macacu, Boca do Mato, 8.x.1988, A. B. Kury & R. Pinto leg./2 ♂ (MNRJ 4768) RJ, Floresta da Tijuca, 3.iii.2001, D. F. Almeida, A. P. L. Giupponi & D. R. Pedroso leg./2 ♂ 1 ♀ (MNRJ 53) RJ, Jacarepaguá, 900 m, H. F. Berla leg. (determined as *Pseudopachylus longipes* Roewer by Mello-Leitão).

Pseudophalangodes unicolor Roewer, 1912: ♀ holotype (wrongly reported as ♂ by Roewer) (SMF RI 231) RJ, without further locality data/1 ♂ (MNRJ 7005) RJ, Mangaratiba, Reserva Ecológica do Rio das Pedras, 29–31.xi.2007, A. P. L. Giupponi & D. R. Pedroso col.

Rezendesius lanei H. Soares, 1945: ♀ holotype (HS 40) RJ, Fazenda Penedo/1 ♀ (MZSP 22085) SP, São José dos Barreiros: PARNA Serra da Bocaina, rio Mambucaba, 1400 m, 21–24.iii.1997, R. Pinto, C. Campaner & S. Vanin leg. Male unknown.

Spinopilar apiacaensis Kury, 1992: ♂ holotype, 2 ♀ 1 ♀ paratypes (MZSP 13742) and 1 ♂ paratype (ZMUC), ES, Apicacá, Fazenda Santa Maria, 20.vii.1991, R. L. C. Baptista & A. B. Kury leg.

Spinopilar armatus Mello-Leitão, 1940: ♂ holotype (MNRJ 94) RJ, Duque de Caxias, Pilar/1 ♂ (MNRJ 04508) RJ, Rio de Janeiro, Floresta da Tijuca, 2001, A. P. L. Giupponi, R. L. C. Baptista & D. R. Pedroso leg./1 ♂ (MNRJ 04796) RJ, Rio de Janeiro, Floresta da Tijuca: Trilha do Alto da Bandeira, 15.x.1999, A. P. L. Giupponi & D. R. Pedroso leg./7 ♂ 6 ♀ (MNRJ 02251), RJ, Nova Iguaçu, Tinguá, farm adjacent to REBIO do Tinguá, 11.iii.2010, A. Chagas Jr, A. P. L. Giupponi, A. B. Kury & C. Sampaio leg.

Spinopilar insignitus (Roewer, 1949) [hitherto in *Segundolus*]: ♂ holotype (SMF RII 8079/18), SC, Seara: Nova Teutônia.

Spinopilar moria Kury & Pérez-González, 2008: ♂ holotype (MNRJ 18986) 3 ♂ 4 ♀ 2 juv. (MNRJ 18985) MG, Cordisburgo: Caverna Morena, 19.vii.2007, A. Pérez, F. Pelegatti-Franco & E. Trajano leg.

Gen. sp. I (*Spinopilar*): 1 ♂ (MNRJ 04952) SP, Serra da Bocaina, 13.x.1957, F. Segadas Vianna leg.

Gen. sp. J (*Spinopilar*): 2 ♂ (MNRJ 2092) RJ, Santa Maria Madalena, PARES do Desengano, Morumbeca, 1000–1400 m, 13–17.v.2008 A. Chagas, A. Kury, C. Sampaio & T. Moreira leg.

Gen. sp. K (*Spinopilar*): 4 ♂ 3 ♀ (MNRJ 19189) RJ, Búzios, Área de Proteção Ambiental do Pau Brasil, 13–15.i.2011, B. Buzatto, A. Giupponi & A. Kury leg.

Taquara bicoloripes (H. Soares, 1974) [hitherto in *Camarana*]: ♀ holotype (MNRJ-HS 365), 1 ♀ paratype (MNRJ-HS 414) Teresópolis, PN Serra dos Órgãos, 28.iv.1964, E. Izecksohn leg./2 ♂ 4 ♀ (MNRJ 4477) same loc., 27.i.2001, A. P. L. Giupponi & R. L. C. Baptista leg./1 ♂ 2 ♀ (MNRJ 4944) same loc., 25.xii.1989, A. B. Kury leg./3 ♂ 2 ♀ (MNRJ 16191) same loc., 4–5.viii.2005, A. B. Kury, A. P. L. Giupponi, D. R. Pedroso & V. D. Orrico leg.

Taquara pilosa Mello-Leitão, 1936: ♂ holotype 1 ♀ allotype of *Therezopachylus fuscus* (MNRJ 5306) RJ, Teresópolis, PARNA Serra dos Órgãos, 30.viii.1957, J. Becker leg.; 1 ♂ 1 ♀ paratypes of *Therezopachylus fuscus* (MNRJ-HS 0397) RJ, Teresópolis, PARNA Serra dos Órgãos, 28–30.viii.1957, Johann Becker leg.; 1 ♂ 2 ♀ paratypes of *Therezopachylus fuscus* (MNRJ 4943)

RJ, Teresópolis, PARNA Serra dos Órgãos, 28–30.viii.1957, J. Becker leg.; 1 ♀ (MNRJ 6465) RJ, Teresópolis, 1.v.1989, R. Sachsse leg.; 1 ♂ (MNRJ 6566) RJ, Teresópolis, PARNA Serra dos Órgãos, 25.xii.1989, A. B. Kury leg.; 1 ♂ 3 ♀ (MNRJ 6577) RJ, Teresópolis, Fazenda Vale da Revolta, 18.vi.1990, A. B. Kury & Entomological Expedition UFRJ leg.; 1 ♂ 3 ♀ (MNRJ 16193) RJ, Teresópolis, PARNA Serra dos Órgãos, Sede, 4–5.viii.2005, A. B. Kury, A. P. L. Giupponi, D. R. Pedroso & V. G. D. Orrico leg.; 3 ♂ 3 ♀ (MNRJ 18720) RJ, Teresópolis: PARNA Serra dos Órgãos, Trilhas Rancho Frio e Pedra do Sino, 20–23.x.2006, Expedição Arachné leg.; 1 ♀ (MNRJ 18836) RJ, Teresópolis: PARNA Serra dos Órgãos Trilha Pedra do Sino, 19–21.xii.2006, A. B. Kury & G. Machado leg.; 1 ♂ 2 ♀ (MNRJ 18878) RJ, Teresópolis: PARNA Serra dos Órgãos Trilha da Pedra do Sino, submontane forest, 30.xii.2006, A. B. Kury, S. B. Rompani & L. A. Vaz leg.; 1 ♀ (MNRJ 42691) RJ, Petrópolis, R. Arlé leg.; 1 ♂ 1 ♀ (IBSP 2511) RJ, Petrópolis, Fazenda Ranchinho da Roça, 8–15.ii.2001, Equipe IBSP leg.; 1 ♂ 1 juv. (MNRJ 1963), SP, Ubatuba, Picinguaba, xi.2003, A. C. Mendes & R. L. C. Baptista leg.

Gen. sp. Q (*Taquara*): ♂ holotype, 4 ♂ 4 ♀ paratypes (MNRJ 2094) RJ, Santa Maria Madalena, PARES do Desengano, Morumbeca, 1000–1400 m 13–17.v.2008 A. Chagas, A. B. Kury, C. Sampaio & T. S. Moreira leg.; 1 ♂ paratype (MNRJ 2210) RJ, Cachoeiras de Macacu, Guapi-Assu, REGUA 23–25.ix.2009 A. P. L. Giupponi & B. Huber leg.; 1 ♂ paratype (MNRJ 6319) RJ, Cachoeiras de Macacu, Boca do Mato, banana trees 8.x.1988 A. B. Kury & R. Pinto-da-Rocha leg.; 1 ♂ 2 ♀ paratypes (MNRJ 6335) RJ, Nova Friburgo, Nova Friburgo, Rio Grande de Cima, Fazenda São João 10.x.1988 A. B. Kury & R. Pinto-da-Rocha leg.

Gen. sp. R (*Taquara*): ♂ holotype, 2 ♂ 1 ♀ 3 juv. paratypes (MNRJ 4754) RJ, Cachoeiras de Macacu: Reserva Ecológica de Guapi-Açu.

Tibangara cocaensis (H. Soares, 1972) [hitherto in *Pseudopachylus*]: ♀ holotype (MNRJ-HS 363) SP, Cocaia: Represa Nova, 28.xi.1947, H. Bueno leg./♂ (MNRJ 11351) SP, Pirassununga: Emas, Otto Schubart (Fig. 2356) leg./1 ♂ (IBSP 7818) SP, Jundiá: Serra do Japi, 15–19.vii.2002, Equipe Curso Pós USP leg., amostra 37./1 ♂ (IBSP 6147) SP, Jundiá: Serra do Japi, 6–10.viii.2001, Equipe Biota leg., noturna 75./1 ♂ (IBSP 6148) SP, Jundiá: Serra do Japi, 6–10.viii.2001, Equipe Biota leg., noturna 90./1 ♀ (IBSP 3886) SP, Jundiá: Serra do Japi, i.1999, A. J. Santos leg./1 ♂ (IBSP 6887) SP, Guarulhos: Cabuçu, Parque Estadual da Cantareira, 16–22.vii.2001, Equipe Biota leg./1 ♂ brittle, colour faded (IBSP 7093) SP, São Paulo: Parque Estadual do Jaraguá, 14–19.x.2002, Equipe Biota leg.

Tibangara fuscomaculata (Soares & Soares, 1947) [hitherto in *Tachusina*]: ♀ holotype (MHNCI 3626, not examined), PR, Piraquara: Banhado, 11.xi.1945, Gert

Hatschbach leg.; 1 ♀ (MNRJ 06301) PR, Quatro Barras, 1.xi.1988 R. Pinto-da-Rocha leg.; 2 ♀ (MNRJ-HS 0154) PR, Morretes, Marumbi, viii.1946, C. N. Gofferj leg.

Tibangara keyserlingii (Sørensen, 1932) [hitherto in *Tachusina*]: ♂ holotype (BMNH) SC, Blumenau.

Tibangara nephelina Mello-Leitão, 1940: 1 ♂ lectotype 1 ♀ paralectotype (MNRJ 215, herein designated) RJ, Mangaratiba: Fazenda do Rubião, Rancho Dr Gurgel, 550 m beneath dead leaves, v.1938, R. Arlé leg./1 ♂ (MNRJ 6537) RJ, Teresópolis, Fazenda Vale da Revolta 2.ix.1989 S. Potsch & R. Sachsse leg./1 ♂ (IBSP 2516) RJ, Petrópolis. Fazenda Ranchinho da Roça, 8–15.ii.2001, Equipe IBSP/1 ♀ (IBSP 2516) RJ, Petrópolis, Fazenda Ranchinho da Roça, Cascata, pitfall 12–14.ix.1999, F. S. Cunha *et al.* leg./3 ♂ 5 juv. (MNRJ 1964) SP, Ubatuba, Picinguaba, xi.2003, A. C. Mendes & R. L. Baptista leg./1 ♂ 1 ♀ (MNRJ 18867) RJ, Teresópolis: Parque Nacional da Serra dos Órgãos Trilha Mozart Catão – ‘baixo’ (floresta sub-montana), 31.xii.2006, A. B. Kury, S. B. Rompani & L. A. Vaz leg.

Gen. sp. T (*Tibangara*): ♂ holotype (MNRJ 18237), ES, Santa Teresa: REBIO Augusto Ruschi, Tracomal, in leaf litter, 06.ix.2006, T. N. Bernabé, D. Mota, T. G. Souza & E. Soeiro leg.

Gen. sp. U (*Tibangara*): ♂ holotype (MNRJ 6856) Brazil. Rio de Janeiro. Casimiro de Abreu: Barra de São João, Fazendas Reunidas, 21.i.1994, A. F. Duran, M. K. Khalil & A. B. Kury leg.; 4 ♂ 2 ♀ 3 juv. paratypes (MNRJ 17554) Fazendas Reunidas, 21–24.iii.2003, Expedition Arachné (A. C. Mendes, A. B. Kury *et al.*).

Gen. sp. V (*Tibangara*): ♂ holotype, 2 ♀ 2 juv. paratypes (MNRJ 6911) BRAZIL. Rio de Janeiro. Rio de Janeiro: Parque Estadual da Pedra Branca, Estrada do Pau da Fome, 27.v.1995, M. S. Baptista, A. B. Kury & M. G. Vogt leg.; ♂ paratype (MNRJ 17468), Duque de Caxias: Xerém, 11.ii.2001, A. P. L. Giupponi leg.

Gen. sp. W (*Tibangara*): ♂ holotype (MNRJ 4436), Brazil. Rio de Janeiro. Rio de Janeiro: Urca, Praia Vermelha, in leaf litter, 18.xi.1991, R. L. C. Baptista leg.; 1 ♀ paratype (MNRJ 5822), RJ, Morro da Urca, 15.xi.1990, R. L. C. & A. Baptista leg. 2 ♂ (MNRJ 1977) Brasil, RJ, Nova Iguaçu, Parque Natural Municipal de Nova Iguaçu, sifting leaf litter, 24.iii.2004, C. Lima leg. 1 ♂ 1 ♀ (MNRJ 7002) Brasil, RJ, Rio de Janeiro, PARNA da Tijuca, Archer, sifting leaf litter, 19.i.2005, T. S. Moreira leg.

Zalanodius bicornutus Mello-Leitão, 1936: 2 ♂ 4 ♀ 6 juv. (MNRJ 06726), RJ, Nova Friburgo, Três Picos, 16.xi.1991, R. L. C. Baptista leg./1 ♂ 1 ♀ (MNRJ 02095), RJ, Santa Maria Madalena, PARES do Desengano, Morumbeca, 1000–1400 m, 13–17.v.2008, A. Chagas, A. Kury, C. Sampaio & T. Moreira leg.

Zalanodius convexus (Mello-Leitão, 1940) [hitherto in *Berlesecaptus*]: ♂ neotype, 1 ♂ 2 ♀ paraneotypes (MNRJ 4878), RJ, Rio de Janeiro, PN Tijuca, Sumaré, 29.v.1969, H. Schubart & J. Becker leg.

Zalanodius latifemur (Soares & Soares, 1954) [hitherto in *Simonoleptes*]: ♂ holotype (MZSP 1203, not examined), RJ, Rio de Janeiro: Corcovado, 10.iii.1946, P. Wygodzinsky leg./1 ♂ 2 ♀ (IBSP 8346), RJ, Nova Iguaçu: Reserva Biológica do Tinguá, 15.v.2002, E. F. Ramos leg./1 ♂ 1 ♀, (IBSP 8340), same place, 5.viii.2002, E. F. Ramos leg.

CLADISTIC ANALYSIS

OUTGROUP TERMINALS

In order to test the monophyly of Tricommatinae and its inclusion in Gonyleptidae, a broad sample of Gonyleptoidea was used. A Stygnopsidae was used to root the tree. Other outgroups include: *Globibunus rubrofemoratus* Roewer, 1912 a basal Agoristenidae (Kury, 2012); *Prostygnus vestitus* Roewer, 1913, a basal Cranaidae recently treated in the literature (Kury, 2012); *Incasarcus diana*, a Metasarcidae, sister group to Cosmetidae (Pinto-da-Rocha *et al.*, 2014; also Kury's unpubl. data, Gonyleptoidea project), but with rather gonyleptid facies. The present analysis also included *Ampycus telifer* (Butler, 1873) as type species of the type genus of Ampycinae, a recently described gonyleptid subfamily thought to be a basal branch in the phylogeny of the family (Kury, unpubl. data, Gonyleptoidea project) and *Pseudopucroliia mutica* (Perty, 1833), representing the Heteropachylinae, another ‘basal lineage’ of Gonyleptidae (Kury, 1994). Finally, three species of Pachylinae, the most diverse gonyleptid subfamily, and one Mitobatinae (which presents sexual dimorphism in leg IV similar to that in *Camarana*, *Pseudopachylus*, and *Tibangara*) were chosen to increase the diversity of the outgroup.

INGROUP TERMINALS

For this project a large number of specimens from various museums (see Conventions section) were examined, but the bulk of the material was collected by the Arachnology team of Museu Nacional/UFRJ on many expeditions. Representatives of all genera of Tricommatinae *s.l.* were chosen (except for the extremely poorly known *Rezendesius*), along with many undescribed species of larger genera such as *Camarana* and *Pseudopachylus*. In addition, Gen. sp. C, which has a ‘sturdy pachyline’ facies was included because it has sexual secondary dimorphism similar to *Vorix popeye*, although the somatic and genitalic features do not indicate any particular similarity between them.

SETTINGS OF PARSIMONY ANALYSIS

The character states were tabulated in a matrix using MESQUITE v. 2.5 (Maddison & Maddison, 2008). The annotated list of characters is in Appendix 1. The matrix

Table 1. Summary of the four cladistic analyses performed here

Concavity value	Number of trees retained	Length (under equal weights)	Best score – fit
1	1	(756)	69.97984
3	1	(731)	50.69308
6	1	(725)	36.80109
None – equal weights = 1	1232	723	NA

of characters states and terminals is in Appendix 2. Trees were searched using TNT (Goloboff, Farris & Nixon, 2008) using parsimony under implied weights (Goloboff, 1993) with the traditional search algorithm and Subtree pruning and regrafting branch-swapping. Four searches were conducted with TNT using interactive weighting with K concavity values of 1, 3, and 6 as well as a nonweighted analysis (based on prior equal weights). Space was allocated for 10 000 trees in the memory and ten replicates with 10 000 trees each were carried out. A summary of the results of the five analyses is in Table 1. Absolute Bremer support (decay analysis) and bootstrap resampling values (1000 replicates) were calculated using TNT. Values are shown in Figures 6 to 9.

MAIN RESULTS OF THE ANALYSIS

The single tree obtained under concavity 3 is here used to discuss the phylogenetic hypothesis proposed and to label the clades, whereas the differences compared with the other analyses are shown by means of ‘Navajo rugs’. More details may be found in the Discussion. Although a myriad of useful information was extracted from the analysis (Figs 6–10), only the general lines of the phylogenetic hypotheses herein proposed are listed below.

1. Tricommatinae *s.l.* is not a monophyletic group, but rather two unrelated groups – the Tricommatinae proper and the new family Cryptogeobiidae.
2. The Tricommatinae are a microdiverse clade containing the genus *Tricommatus* (including the pachyline *Pherania*), *Caramaschia*, and the new genus *Voriax*, with only five described Brazilian species (Fig. 6).
3. Although the sampling of Gonyleptidae is rather small, it appears monophyletic, either in the traditional concept of Kury (2003a) or in the recent concepts of SG11 or PA14, because the successively farther sister groups to the Gonyleptidae *s.s.* are: Cranaidae and Metasarcidae [here representing the Metasarcidae–Cosmetidae (ME-CO) clade].

This enlarged Gonyleptidae, containing also Manaosbiidae and Cranaidae is called Greater Gonyleptidae (GG; Fig. 6).

4. The clades GG + ME-CO are jointly retrieved as a monophylum (Figs 6, 10) here called the Microsetata unranked new taxon (because of the conspicuous covering of simple microsetae on the ventral surface of the ventral plate of the penis).
5. Most genera of the former Tricommatinae are retrieved as a clade, here named and described as the new family Cryptogeobiidae, with *Huralvioides* as sister group (both well supported, see Figs 6 and 10, and see Discussion for more details).
6. Many hitherto monotypic genera of Cryptogeobiidae (*Bissulla*, *Taquara*, *Tibangara*) cluster with undescribed species, granting them meaningful status as supraspecific entities.
7. The pattern ((Cryptogeobiidae, *Huralvioides*-group) (Agoristenidae (Stygnidae, Microsetata)) is obtained, which is congruent with SG11 (but only because of lacking taxa) but not fully congruent with PA14 (Figs 6, 10).
8. The Cryptogeobiidae themselves are divided into two rather asymmetrically diverse clades A and B, both weakly supported (Figs 7, 8) – which is a reason for them to remain unnamed. It is out of question in the present state of knowledge to try to propose subfamilies for Cryptogeobiidae, as deep relationships are only inadequately substantiated.
9. In group A of Cryptogeobiidae the branching pattern is (unnamed group (*Paratricommatus* (*Heteromeloleptes* (*Pseudophalangodes* *Zalanodius*))))).
10. *Zalanodius* here includes the two current species of this genus plus the monotypic *Berlesecaptus* and the type species of *Simonoleptes* (Fig. 7).
11. *Heteromeloleptes* has a few species of subtle distinction, plus two that are deemed undescribed and are used here as terminals. Monophyly of the genus does not present problems, but internal relationships are complicated and deserve further study.
12. *Paratricommatus* here includes the type species *Paratricommatus modestus* and the other species of the genus, *Paratricommatus mahnerti*, plus the new species *Paratricommatus nicholasi* and the monotypic genera *Neoarminda* and *Soaresula*.
13. Complementing group A there are seven terminals that form a heterogeneous group with low support (Fig. 7). Together, they might be considered an enlarged *Cryptogeobius*, but as the genital morphology of *Bunostigma* is so radically different from that of *Cryptogeobius* (more similar to some *Taquara*), only *Pirahya* is here confirmed to be in the synonymy of *Cryptogeobius*, leaving *Bunostigma* independent. The other four

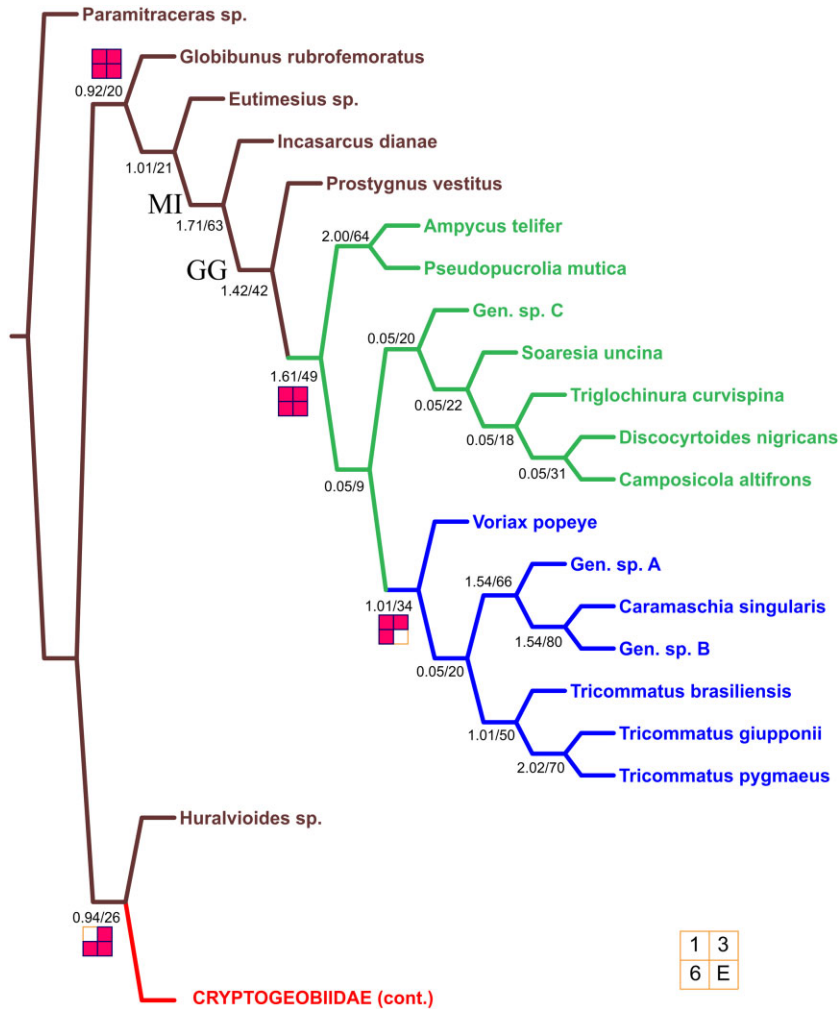


Figure 6. Cladogram depicting proposed phylogenetic relationships for Tricommatinae and Cryptogeobiidae inside Gonyleptoidea (part 1 of 4). The small ‘Navajo rugs’ at selected branches indicate which of the four analyses supports a given clade. A key to the analyses is given in the set of four squares at the bottom, abbreviated as: 1, implied weights, concavity 1; 3, same, concavity 3; 6, same, concavity 6; E, strict consensus of the analysis under equal weights. Numerals at branches represent absolute Bremer support/standard bootstrap resampling percentage values. GG, Greater Gonyleptidae; MI, Microsetata.

terminals are undescribed species with uncertain affinities.

- In group B of Cryptogeobiidae (Figs 8, 9) the branching pattern is (*Spinopilar* (*Pararezendesius* (*Bresslavius* (*Camarana* (*Taquara* (a difficult-to-represent pectinate pattern (*Tibangara* (*Pseudopachylus* *Bissulla*)))))))).
- Spinopilar* terminals include three of the four described species plus three undescribed. The monotypic genera *Segundolus* and *Machairoscelis* appear firmly clustered with *Spinopilar*, especially because there is an undescribed *Segundolus*, which bridges the gap between them. Therefore, these three terminals of *Segundolus* plus six terminals of *Spinopilar* are joined into an augmented *Spinopilar*.
- Bresslavius* and *Pinocchio* – two originally monotypic genera, synonymized to each other by Kury (2003a) – form a clade with reasonable support, also containing four undescribed species.
- The type species of *Arruda* clusters with the type species of *Camarana*, supporting the synonymy of both genera, although two other *Camarana* lie outside this group.
- The monotypic *Taquara* clusters with one species of *Camarana*, augmented by two undescribed species.
- Within Cryptogeobiidae group B there is a subgroup C that is also ill-supported but that contains a clade with three better-supported genera – *Tibangara*, *Pseudopachylus*, and *Bissulla*.

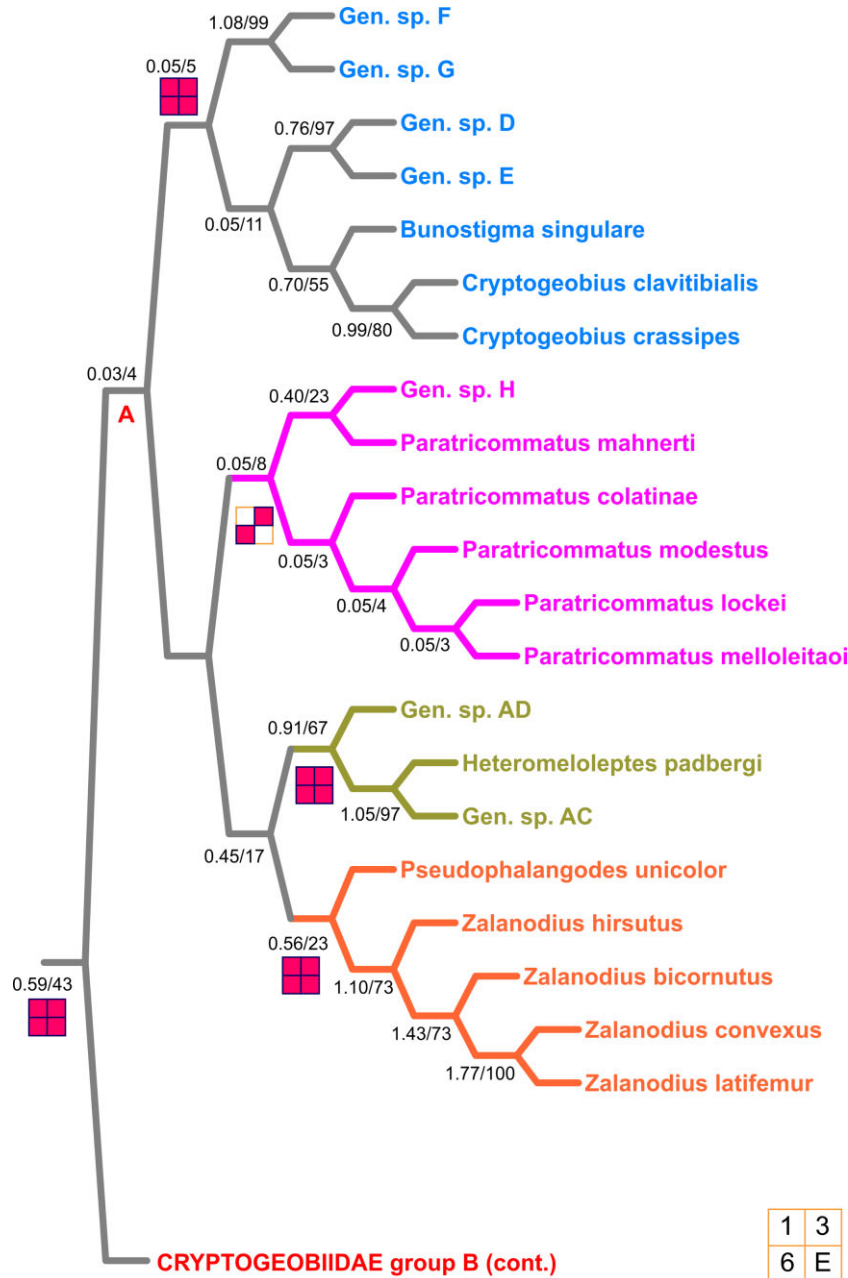


Figure 7. Cladogram depicting proposed phylogenetic relationships for Tricommatinae and Cryptogeoibiidae inside Gonyleptoidea (part 2 of 4). The small ‘Navajo rugs’ at selected branches indicate which of the four analyses supports a given clade. A key to the analyses is given in the set of four squares at the bottom, abbreviated as: 1, implied weights, concavity 1; 3, same, concavity 3; 6, same, concavity 6; E, strict consensus of the analysis under equal weights. Numerals at branches represent absolute Bremer support/standard bootstrap resampling percentage values.

20. In subgroup C of Cryptogeoibiidae there is a pectinate sequence of described and undescribed species in which the only name-bearer is *Lanesoares*.
21. The hitherto monotypic *Tibangara* (Phalangodinae at first, brought into Tricommatinae by Kury, 2003a) forms a strongly supported clade with *Paramitraceras cocaiensis* (Phalangodinae, brought

- into *Pseudopachylus* by Kury, 2003a) plus four undescribed species. The monotypic *Tachusina* is the sister group of this, also with moderate support, granting its synonymy.
22. *Pseudopachylus* currently has six nominal species – apart from *Pseudopachylus cocaiensis* (here included in *Tibangara*) and two other species

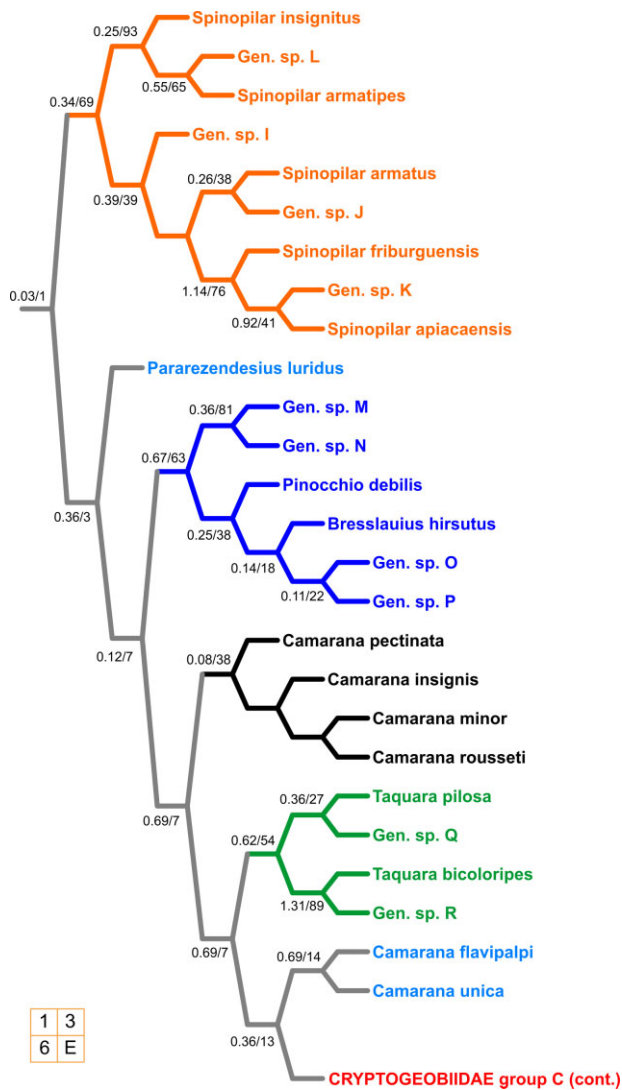


Figure 8. Cladogram depicting proposed phylogenetic relationships for Tricommatinae and Cryptogeobiidae inside Gonyleptoidea (part 3 of 4). The small 'Navajo rugs' at selected branches indicate which of the four analyses supports a given clade. A key to the analyses is given in the set of four squares at the bottom, abbreviated as: 1, implied weights, concavity 1; 3, same, concavity 3; 6, same, concavity 6; E, strict consensus of the analysis under equal weights. Numerals at branches represent absolute Bremer support/standard bootstrap resampling percentage values.

(isolated), the remnant three species, including the type species, form a clade.

23. Finally, the monotypic genus *Bissulla* is enlarged by the accretion of six undescribed species, themselves forming two subclades of three species each, and being extremely well supported. The creation of two new genera was an alternative to denote this topology, but the decision to recognize an enlarged *Bissulla* prevailed.

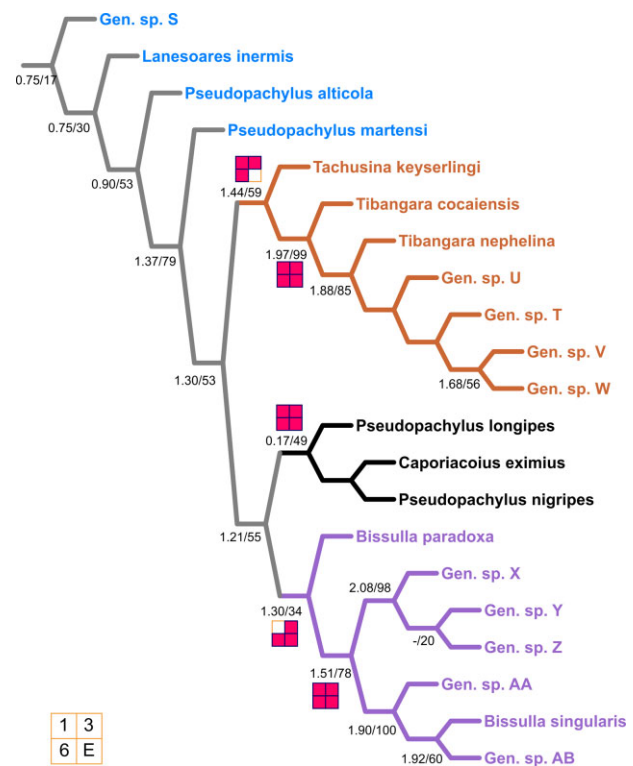


Figure 9. Cladogram depicting proposed phylogenetic relationships for Tricommatinae and Cryptogeobiidae inside Gonyleptoidea (part 4 of 4). The small 'Navajo rugs' at selected branches indicate which of the four analyses supports a given clade. A key to the analyses is given in the set of four squares at the bottom, abbreviated as: 1, implied weights, concavity 1; 3, same, concavity 3; 6, same, concavity 6; E, strict consensus of the analysis under equal weights. Numerals at branches represent absolute Bremer support/standard bootstrap resampling percentage values.

TAXONOMY

Only a summary of the literature listings is given here. Exhaustive citations may be found in Kury (2003a).

GONYLEPTIDAE INCERTAE SEDIS

Some genera, insufficiently characterized, have been assigned to the Tricommatinae in the past, but there is no evidence to keep them in this group or to assign them to the Cryptogeobiidae as diagnosed here. Most of the descriptions were based upon females, and presently are difficult to relate to other groups. They were not included in the present analysis, pending more study, preferably with the discovery and examination of males.

Included genera: *Bebedoura* (probably Escadabiidae), *Lussanvira* Mello-Leitão, 1935, *Otuquisa* Roewer, 1928, *Saladonus* Roewer, 1928.

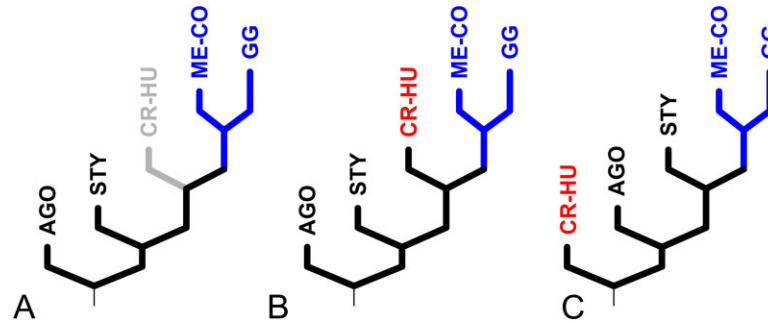


Figure 10. Comparison amongst the recent hypotheses on the placement of the Cryptogeobiidae in the phylogeny of Gonyleptoidea. A, Sharma & Giribet (2011). B, Pinto-da-Rocha *et al.* (2014). C, herein. Abbreviations: AGO, Agoristenidae; CR-HU, Cryptogeobiidae + Huralvioides-group; GG, Greater Gonyleptidae (including Cranaiidae; Manaosbiidae; abbreviation of clade NOT named after Gonzalo Giribet; it is just a coincidence); ME-CO, Metasarcidae + Cosmetidae; STY, Stygnidae. The clade highlighted in blue is the Microsetata. The greyed out clade indicates that it was not included in analysis A, and it is present here just for comparison and inserted in the same place as the other molecular analysis.

KEY TO THE SPECIES OF TRICOMMATINAE

1. Dorsal scutum trapezoid, without marked constrictions, flaring posteriorly; area I undivided; femur and tibia III of male extremely stout, balloon-like swollen; tibia armed with ventral row of spines; femur IV of male thin, not significantly stouter than femora I-II..... *Voriax popeye* (BA, Figs 12, 13)
 - Dorsal scutum type alpha (Fig. 14A, C); area I divided into left and right halves; femur and tibia III normal, not swollen; femur IV robust, clearly thicker than the others..... 2
2. Pedipalpal femur robust, convex, dorsally armed with a row of ventral and dorsal spines; both basichelecerite and cheliceral hand of male very robust; ocularium extremely flattened, eye widely separated; anterior margin of carapace with three teeth..... *Caramaschia singularis* (BA)
 - Pedipalpal femur weak, unarmed; chelicerae monomorphic, weak; ocularium ovoid normal, eyes placed close together; carapacial margin unarmed..... 3
3. Ocularium unarmed; coxa IV prodorsal armed with short spine; trochanter IV of male unarmed.....
 - *Tricommatum brasiliensis* (SC, Figs 15, 16)
 - Ocularium with a small median acuminate tubercle; coxa IV prodorsal armed with bifid short apophysis; trochanter IV of male with three apophyses..... 4
4. Femur IV of male dorso-apical with short tubercle; patella IV of male with three robust spiniform apophyses, one anvil-shaped..... *Tricommatum giupponii* (SC)
 - Femur IV of male dorso-apical with two stouter tubercles and ventro-apical with robust spine; patella IV of male with three apophyses, two very small..... *Tricommatum pygmaeus* (SC)

TRICOMMATINAE ROEWER, 1912

Diagnosis: The Tricommatinae may be distinguished from all other Gonyleptidae by a combination of features such as lack of tarsal process ('pseudonychium'), unarmed scutum, alpha configuration of scutum; columnar glans, ventral process of glans much reduced or entirely absent. The Tricommatinae may be distinguished from the Cryptogeobiidae (false Tricommatinae) by having a more typical gonyleptid penis (with features such as truncus not swollen distally in a malleus, macrosetae of VP marginal, VP not forming a lamina parva, absence of skirt). In addition, the exomorphology is more generalized, featuring absence of sexual dimorphic elongation of femur IV, ocularium always without strong armature, spines of hooks, absence of modifications on sternite III, stigmatic area or coxa IV ventral.

Included genera: *Caramaschia* Kury, 2002, *Tricommatum* Roewer, 1912, and *Voriax* gen. nov.

Combined distribution (Fig. 11): Hitherto the subfamily was known from Bahia and Santa Catarina states in the Brazilian Atlantic Forest, but there is material currently under study from other intermediate localities.

CARAMASCHIA KURY, 2002

Caramaschia Kury 2002: 210 [type species: *Caramaschia singularis* Kury, 2002, by original designation].

Etymology: The name honours the Brazilian herpetologist Ulisses Caramaschi.

Placement: Originally in Tricommatinae.

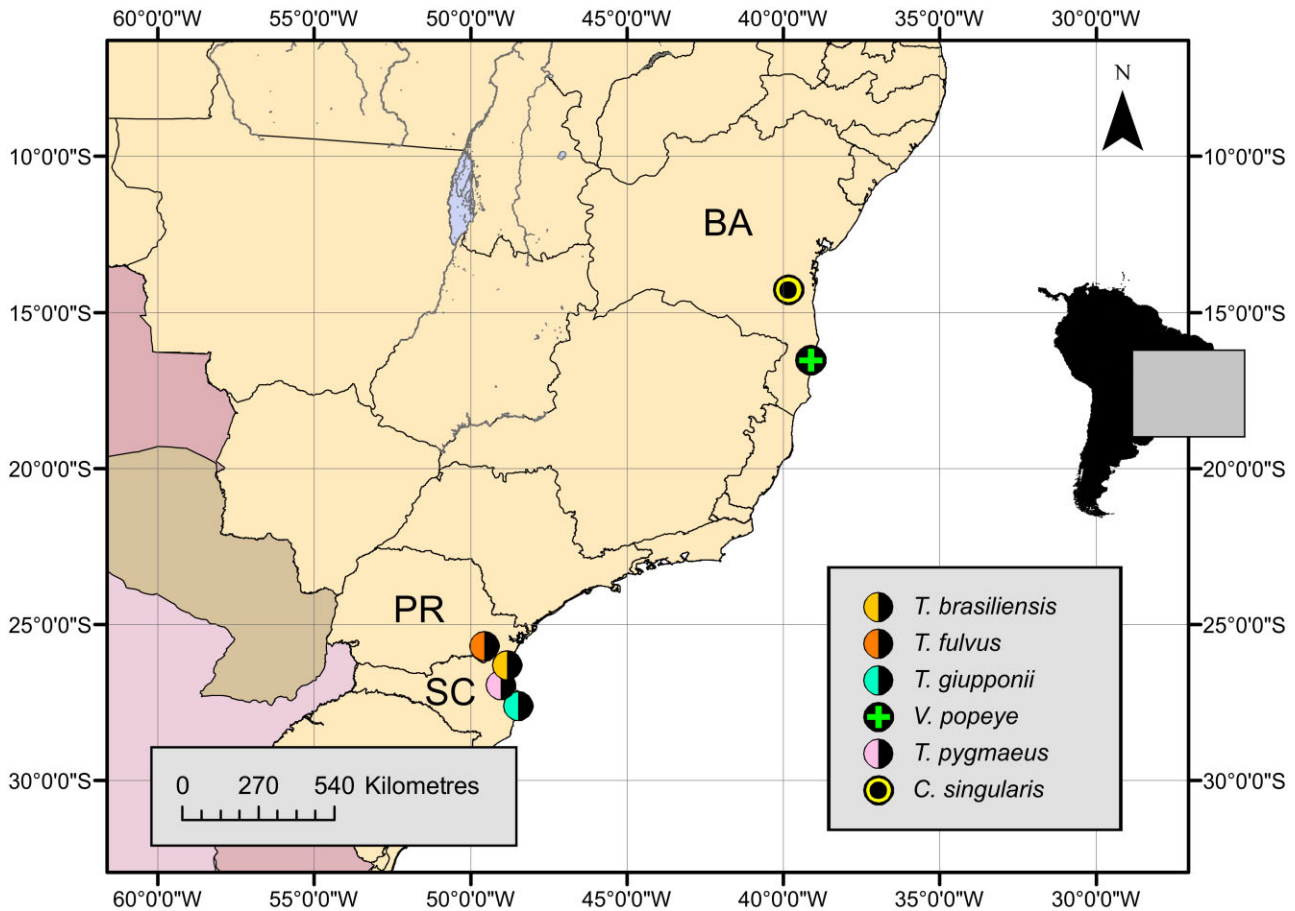


Figure 11. Eastern Brazil, showing the distribution of the Tricommatinae. Black outlines are Brazilian states. Abbreviations: BA, Bahia; PR, Paraná; SC, Santa Catarina.

CARAMASCHIA SINGULARIS KURY, 2002

Caramaschia singularis Kury 2002: 210, figures 1–15.

Type data: ♂ holotype (MNRJ 4409, examined), from Brazil, Bahia, Itagibá, Fazenda Pedra Branca, 14°17'S 39°51'W, elevation 270 m.

TRICOMMATUS ROEWER, 1912

Tricommatum Roewer 1912: 158; Kury 2003a: 205 [type species: *Tricommatum brasiliensis* Roewer, 1912, by monotypy].

Phera Sørensen in Henriksen 1932: 228 [junior homonym of *Phera* Stål, 1864 (Hemiptera); type species: *Phera pygmæa* Sørensen, 1932, by monotypy].

Pherania Strand 1942: 399 [valid replacement name for *Phera*]; Kury 1995a: 75; Kury 2003b: 2. **syn. nov.**

Etymology: *Tricommatum*, probably from Greek *tri* ('three times') + *kommatos* ('that which is cut off, piece'); thus 'divided into three pieces'. Surely referring to the tripartite distitarsus I of which *Tricommatum* was the paradigm contrasting with the bipartite *Phalangodes*. Gender masculine. *Phera* from Latin *fera* (wild beast),

the initial ph- seems to be an archaism/classicism. Gender feminine.

Placement: *Tricommatum* originally the type genus of Tricommatinae. *Phera* originally in Minuidae. Removed to Gonyleptidae Pachylinae by Kury (1995a).

Diagnosis: Dorsal scutum outline alpha, with well-marked posterior constriction. Pedipalpal femur unarmed dorsally and ventrally and not especially flattened. Femora/tibiae III and IV of male not incrassate. Distal margin of penis ventral plate with shallow (about 1/4 of its length) V-shaped cleft.

TRICOMMATUS BRASILIENSIS ROEWER, 1912

Tricommatum brasiliensis Roewer 1912: 159; Mello-Leitão 1923: 108 [non Roewer, 1912 – misidentification of *Pseudopachylus eximius* (Mello-Leitão, 1936) as noted by B. Soares 1946: 524]; Kury 2003a: 205.

Type data: ♂ Holotype (SMF RI 220, examined), Brazil, Santa Catarina, without further locality data.

False records: Mello-Leitão (1932) stated this is a 'common species from Santa Catarina to Rio de Janeiro',

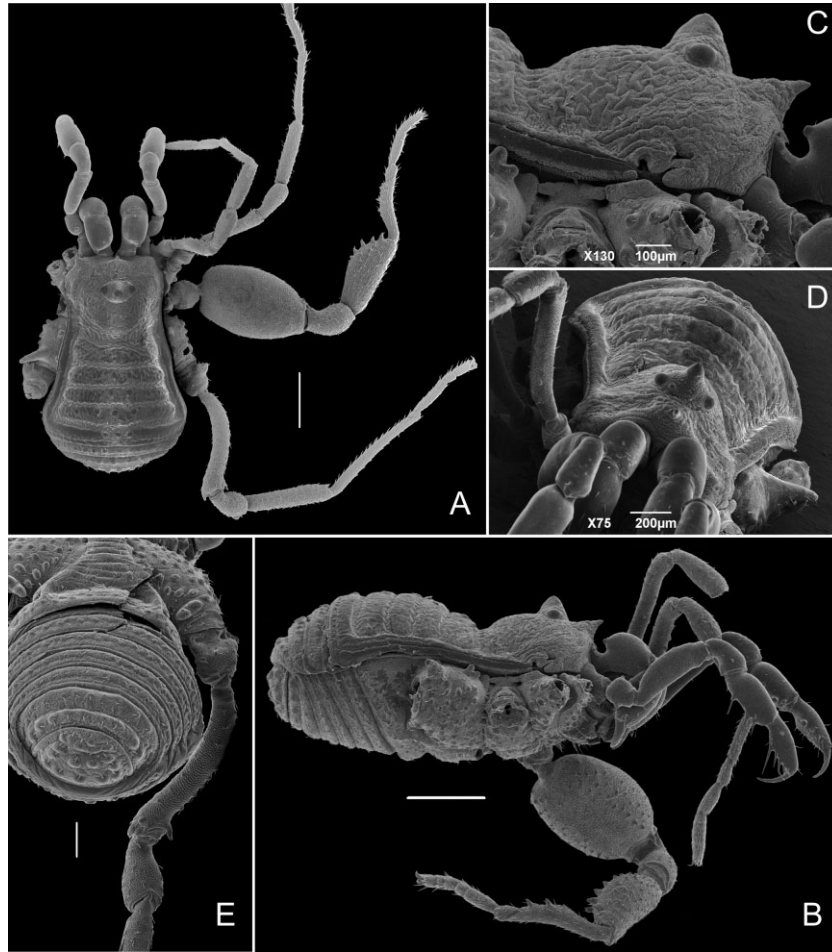


Figure 12. *Voriax popeye* sp. nov., male paratype (MNRJ 17722). A, habitus, dorsal view; B, same, lateral view; C, carapace, coxae I–III, lateral view; D, dorsal scutum, frontodorsal view; E, coxa IV, stigmatic area, free sternites, ventral view. Scale bars = 0.5 mm (A, B), 0.2 mm (D, E), 0.1 mm (C).

but actually only the holotype is known, all other cited specimens are misidentifications (Kury, 2003a).

Diagnosis: Distinguished from the other two species by ocularium unarmed (instead of with a median small acuminate tubercle); coxa IV prodorsal armed with short spine (with bifid short apophysis); trochanter IV of male unarmed (with three apophyses).

Remarks: (1) When received for study, the holotype was already dissected, and the penis was not accompanying the loaned material. Much later, it was learned that the specimen was examined by Michael Weber for a monograph (Weber, 1988). At my request, Dr Weber kindly provided scans of his genitalia drawings (used here as Fig. 16C–E), low-resolution versions of which are on his website. (2) Study of the published descriptions of *Pherania pygmaea* (Kury, 1995a) and *Pherania giupponii* (Kury, 2003b) revealed that the male genitalia of these species are virtually identical to those of *T. brasiliensis*. The latter is mostly distinguished from the other two by impoverished armature of leg IV, which

suggests that the holotype could be a beta male, maybe even belonging to one of the other two species.

TRICOMMATUS GIUPPONII (KURY, 2003) **COMB. NOV.**

Pherania giupponii Kury, 2003b: 2, figures 1–14.

Type data: ♂ holotype, 2 ♂ 3 ♀ paratypes (MNRJ 4494, examined), from Brazil, Santa Catarina, Florianópolis, Ilha de Santa Catarina, forest on hill behind buildings of APAE, ÚNICA and SESI (27.61°S, 48.49°W).

TRICOMMATUS PYGMAEUS (SØRENSEN, 1932)
COMB. NOV.

Phera pygmaea Sørensen in Henriksen, 1932: 229.

Phera pygmaea: Mello-Leitão, 1935b: 90.

Pherania pygmaea: Strand, 1942: 399; Kury, 1995a: 75, figures 1–6; Kury, 2003a: 187.

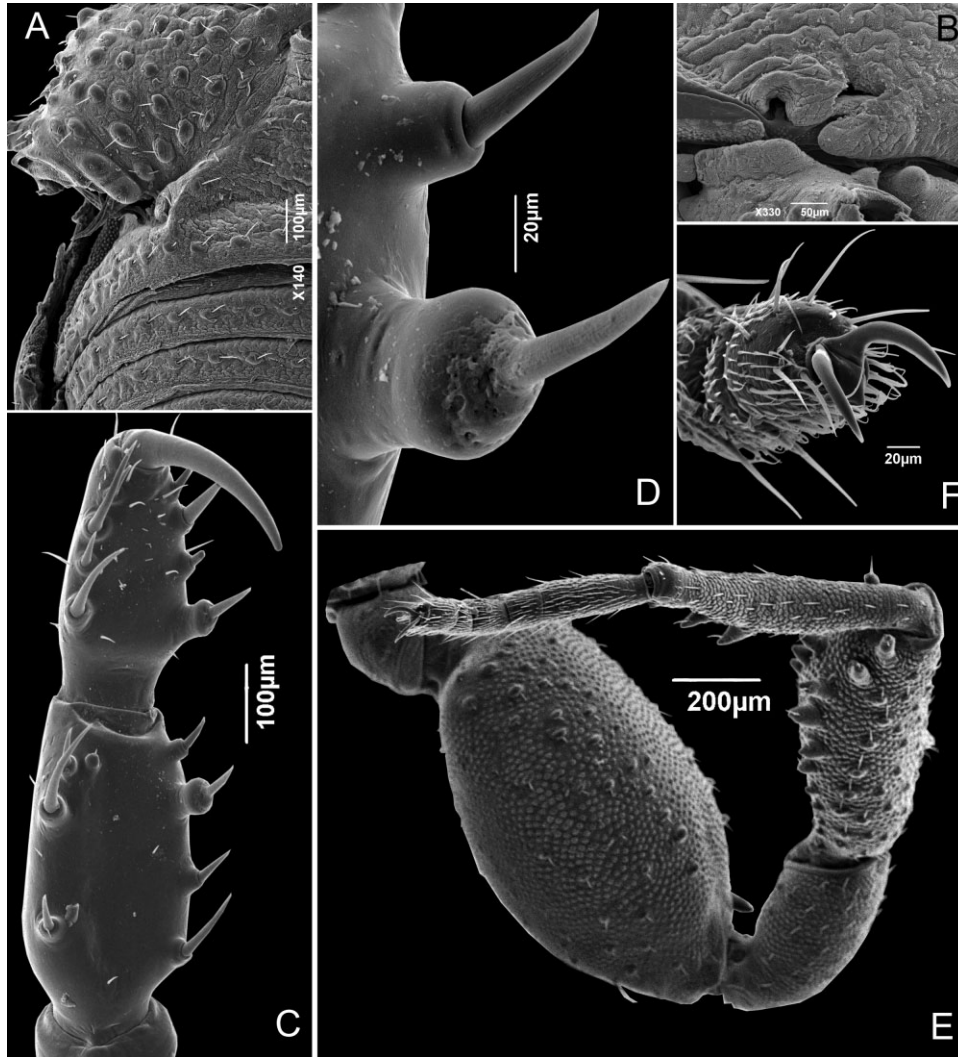


Figure 13. *Voriax popeye* sp. nov., male paratype (MNRJ 17722). A, stigmatic area showing 'encased' position of stigma; B, right ozopore, lateral view; C, right pedipalpal tibia-tarsus, ventral view; D, same, detail of mesal tibial setiferous tubercles; E, left leg III whole, prolateral to dorsal views; F, left distitarsomere + claws III, latero-apical view.

Type data: ♂ holotype, (BMNH, examined), from Brazil, Santa Catarina, Blumenau.

VORIAX GEN. NOV.

Etymology: Lord Voriac, the coronal, is a fictional character of the 'Majipoor' series of books written by the fantasy/sci-fi master, Robert Silverberg. Gender masculine.

Diagnosis: Tricommatinae with dorsal scutum trapezoid, without marked constrictions, flaring posteriorly; area I undivided; femur and tibia III of male extremely stout, balloon-like swollen; tibia with spines; femur IV of male thin, not signifi-

cantly stouter than femora I–II; ventral plate of penis with subtle concavity (instead of deep, V-shaped notch).

Type species: *Voriac popeye* sp. nov.

VORIAX POPEYE SP. NOV.

Etymology: Popeye the sailor is a cartoon fictional character created by Elzie Crisler Segar, and whose most distinctive feature are his massive forearms. Noun in apposition.

Type data: ♂ holotype, 15 ♂ 49 ♀ [2 ♂ mounted on stubs with scanning electron microscopy (SEM)] Porto Seguro: Arraial d'Ajuda, Fazenda do Sr. Valter: 16°32'18.24"S, 39°8'35.52"W, A. Kury *et al.* leg.

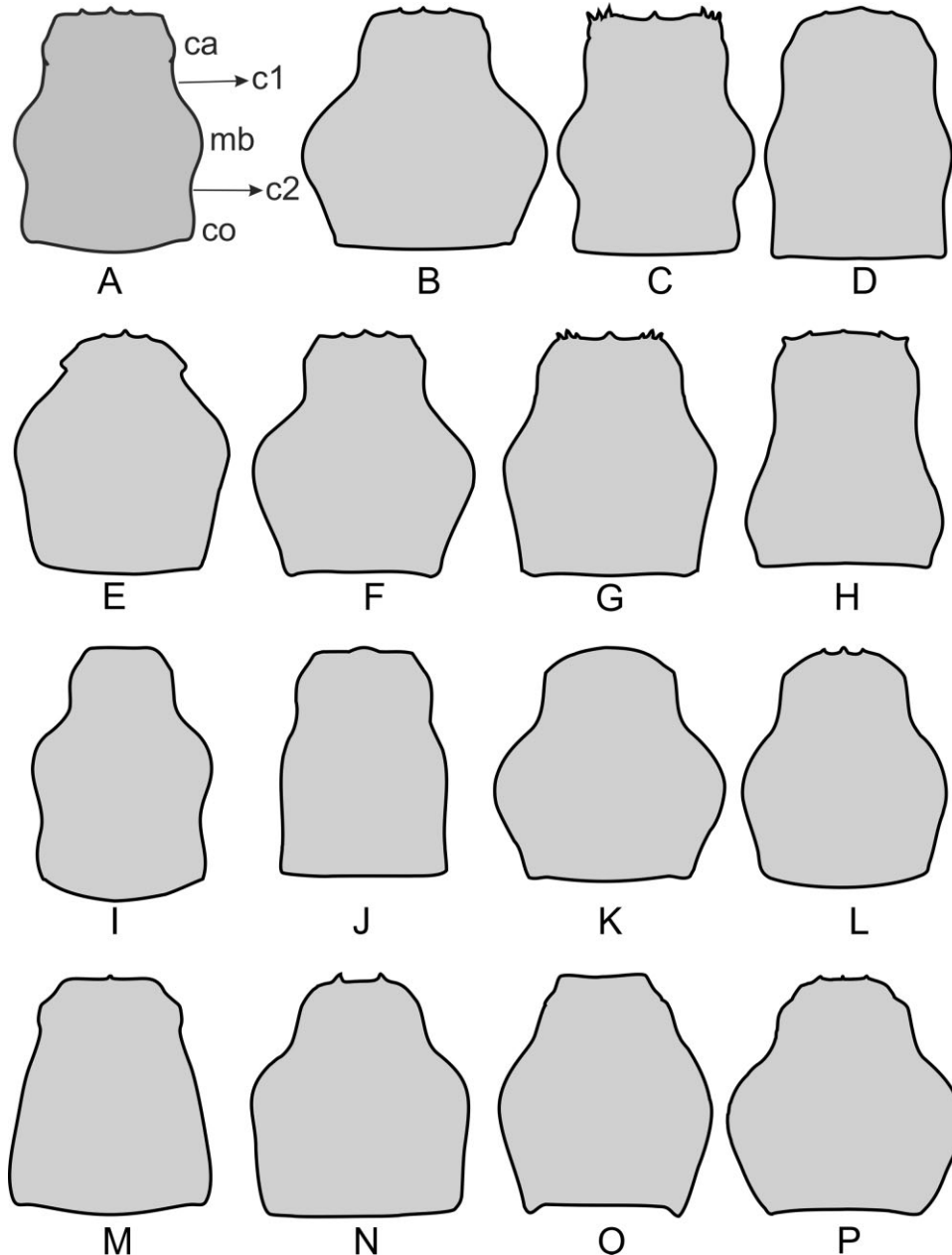


Figure 14. Cryptogeobiidae and other relevant taxa. Sample of the diversity of dorsal scutum outlines (schematic, not to scale). A, *Tricommatius brasiliensis*; B, *Soaresia uncinata*; C, *Caramaschia singularis*; D, *Pseudophalangodes unicolor*; E, *Bunostigma singulare*; F, *Cryptogeobius crassipes*; G, Gen. sp. D; H, Gen. sp. G; I, *Zalanodius bicornutus*; J, *Heteromeloleptes padbergi*; K, *Camarana insignis*; L, Gen. sp. S; M, *Bissulla paradoxa*; N, *Tibangara nephelina*; O, *Bissulla singularis*; P, Gen. sp. X. Abbreviations: c1–2, constrictions 1 and 2; ca, carapace; co, coda; mb, mid-bulge.

Description, male holotype: Dorsum. Carapace subrectangular, posterior border penetrating strongly into abdominal scutum (Fig. 12A). Abdominal scutum without meaningful constrictions, steadily widening posteriorly. Tegument deeply wrinkled, grooves very deep, especially the scutal groove, separating carapace from abdominal scutum (Fig. 12B). Ocularium narrow and

high, ending in a sturdy, short spine. Frontal hump strongly projected into a point (Fig. 12C, D). Ozopore with two openings (Fig. 13B). Mesotergum divided into four areas, with straight grooves. Areas II to V with a pair of paramedian low, blunt tubercles. Anal opercle densely covered with stout setiferous tubercles (Fig. 12E). Venter. Stigmatic area short. Stigmata small, partly

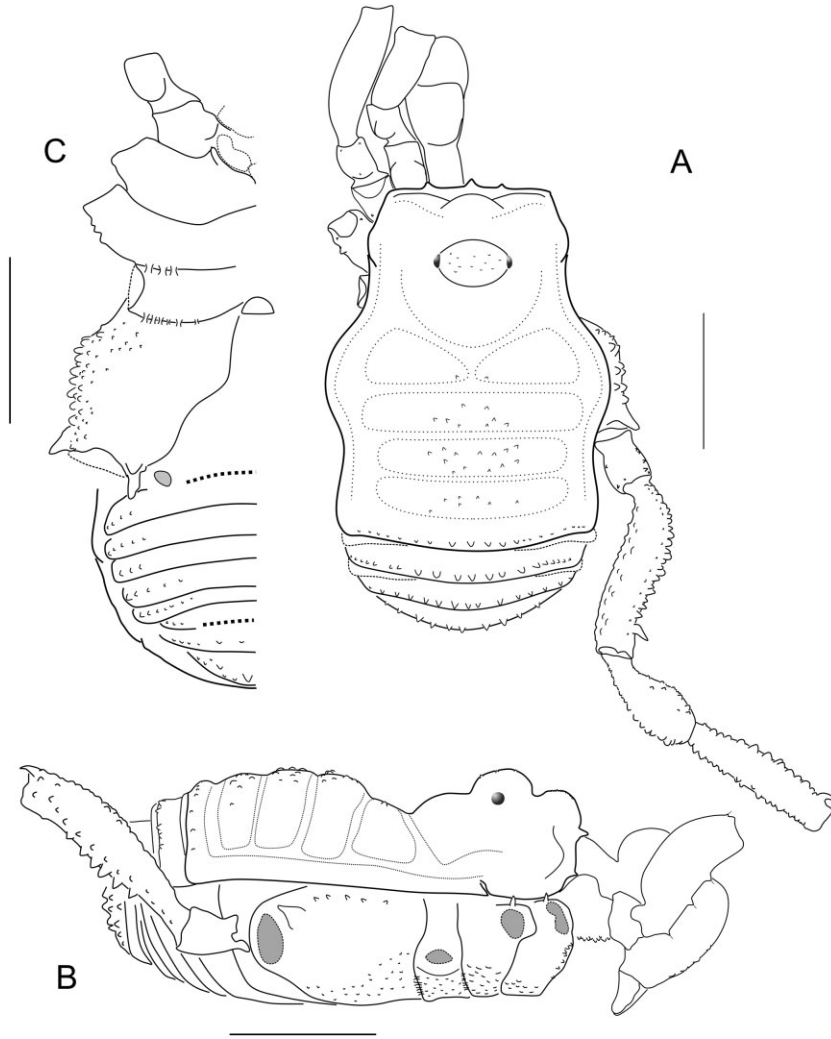


Figure 15. *Tricommatus brasiliensis* Roewer, 1912, male holotype (SMF RI 220). A, habitus, dorsal view; B, same, lateral view; C, sternal region, coxae, stigmatic area, and sternites, ventral view. Scale bars = 1 mm.

sunken (Fig. 13A). Coxae I–IV covered with large, rounded tubercles similar to those of anal opercle. Free sternites with one transverse row of small, setiferous tubercles each (Fig. 12E). Chelicera. Monomorphic, weakly developed, basichelicerite short, bulla with posterior apophysis (Fig. 12B). Pedipalpus. Without remarkable features, without elongate or incrassate articles. Ordinary spines on tibia and tarsus (Fig. 13C). Tibia ventromesal IiIi, ventro-ectal Iii. Tarsus both sides IiIi. Some mesal spines of tibia and tarsus have unusually strongly swollen bases (Fig. 13C, D). Legs. Legs I, II, and IV relatively short and unarmed, with femora gently sinuous (Fig. 12A). Leg III with femur, tibia immensely swollen. Femur with only a few ventral rows of small granules. Tibia and metatarsus armed with robust setiferous tubercles (Fig. 13E). Coxa IV armed with robust prodorso-apical acuminate apophysis. Trochanter IV

armed with prodorsal conic apophysis. Tarsal claws III–IV without tarsal process (Fig. 13F). Tarsal counts: 4(3)/5(3)/5/6. Genitalia (Fig. 17A–D). Ventral plate very flat, subrectangular with rounded sides and basal half wider (Fig. 17A, B). Ventral surface of ventral plate with rows of microsetae present only on the laterals. Macrosetae A1–A2 short, robust, and somewhat spatulate, B1 minuscule, a little more ventral. D very small, lateral, mid-way between A and C. E1–E2 minuscule on the flange. Stylus C-shaped, without any process or ornament, atop a short glans. Podium overlapping ventral plate in lateral view, occupying half of its width in dorsal view. Colour. Appendage background 67 Brilliant Orange Yellow densely honeycombed with a darker tone, especially on legs I, II, and IV. Scutum background 69 Deep Orange Yellow with darker mottling of 38 Dark Reddish Orange, especially on the scutal areas.

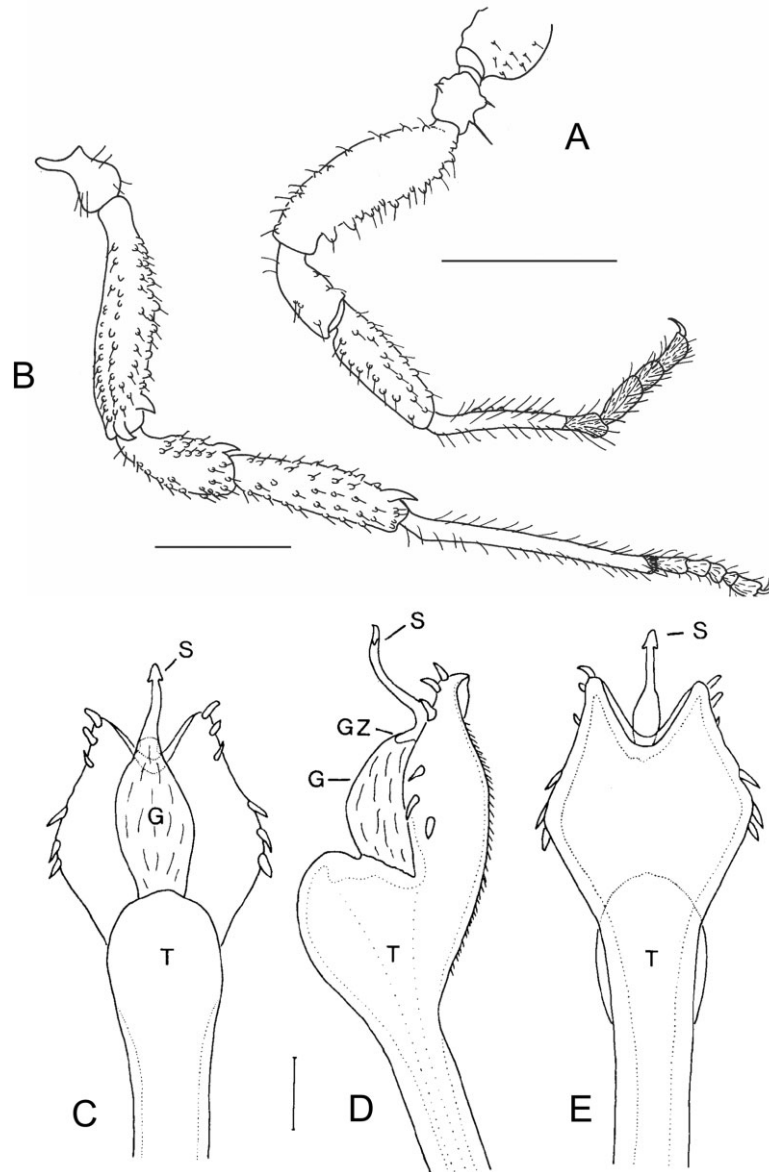


Figure 16. *Tricommatus brasiliensis* Roewer, 1912, male holotype (SMF RI 220). A, left leg I, retrolateral view; B, right leg IV, prolateral view; C, penis, distal part, dorsal view; D, same, lateral view; E, same, ventral view. Figures C–E from Weber (1988). Abbreviations: G, glans; GZ, gelenk-zone (articular zone); S, stylus; T, Truncus. Scale bars = 1 mm (A, B); 0.05 mm (C–E).

CRYPTOGEOBIIDAE FAM. NOV.

Type genus: *Cryptogebius* Mello-Leitão, 1935. It should be noted that the oldest genus is *Pseudopachylus* Roewer, 1912. However, as there is a large number of gonyleptid genera ending in -pachylus, or containing pachylo-, which could potentially be used for family types (besides the existing Heteropachylinae, Pachylospeleinae), and the International Code of Zoological Nomenclature (ICZN, 1999) allows the use of any valid generic name to typify a family group name, a further component ending in -pachylinae is avoided here.

Diagnosis: (1) Dorsal scutum outline extremely variable, from alpha (e.g. *Zalanodius*), gamma (e.g. *Cryptogebius*) to campaniform (e.g. *Pseudopachylus*), passing through many diverse shapes often showing posterior constriction of abdominal scutum attenuate or lost (instead of typical alpha in Tricommatinae and gamma in most Gonyleptidae); (2) ocularium extremely variable, it may be extremely depressed (e.g. *Pararezendesius*), normal elliptical (e.g. *Bressladius*), extremely narrow (e.g. *Bunostigma*), as a huge warty mound (undescribed genus), or marginal with strong hook (e.g. *Bissulla*); (3) frontal hump of carapace either

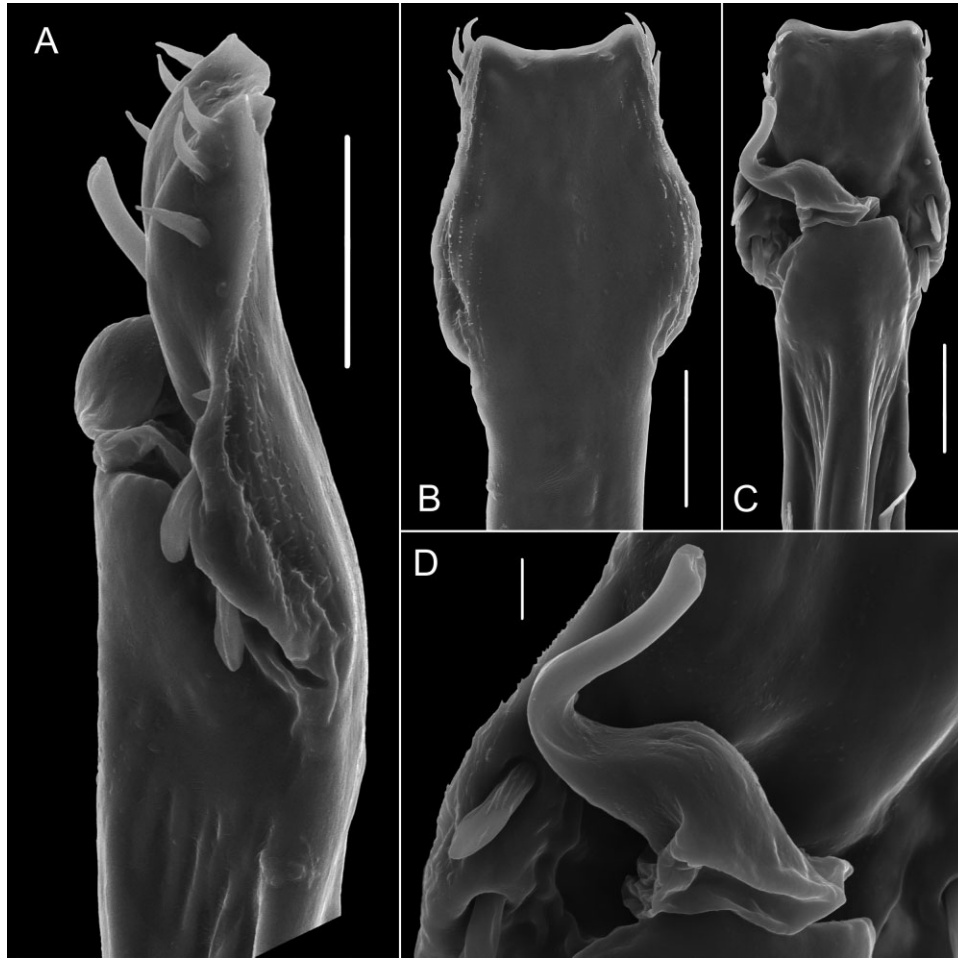


Figure 17. *Voriax popeye* sp. nov., male paratype (MNRJ 17722). Distal part of penis. A, lateral view; B, ventral view; C, dorsal view; D, detail of glans, laterodorsal view. Scale bars = 0.05 mm (A, B, C), 0.01 mm (D).

very high or entirely absent, ocularium either marginal or interior; (4) scutal areas mostly unarmed, in some species either area III or IV armed with paramedian or single spiniform apophysis; (5) mesotergal area I entire, without median longitudinal groove (instead of present, dividing area I into left and right halves); (6) stigmatic area fused with coxa IV along most of their area of contact (instead of clearly marked), sometimes with unique armature; (7) stigmata in some species may be significantly developed, placed on mounds or variedly orientated; (8) sternite II may bear lobes connected to coxal apophyses in male; (9) pedipalpus mostly generalized, with cylindrical articles and no special armature or elongation, but in some genera femur strongly concave and bearing mesal stridulatory grate (e.g. *Pseudopachylus*); (10) chelicerae monomorphic; (11) calcaneus of metatarsus IV of male swollen only in *Taquara*; (12) leg I with all podomeres very thickened in male only in one species of *Tibangara*; (13) distitarsus of leg I mostly trimerous, dimerous

in *Berlesecaptus* for example; (14) leg II very elongate in male in some *Paratricommatus*; (15) coxa II in situ much longer than coxa III; (16) coxa IV sexually dimorphic, larger in male and armed with dorso-apical spiniform apophysis and most important, varied and bizarre ventrodiscal apophyses (often with fasciolate hyaline ones); (17) trochanter IV often with elaborate ventral and retrolateral armature (often with fasciolate hyaline apophysis), but without dorsal armature as in gonyleptids; (18) femur IV may show sexual dimorphism either in armature, swelling, or elongation, in some species being mitobatine-like – extremely long, straight, and unarmed; (19) tibia IV clavate or incrassate in some species; (20) coloration mostly shades of brown, never with white secretion patches or areas vividly coloured in yellow or green; (21) ventral plate of penis not defined as a single flattened plate, but as a malleus + lamina parva; (22) macrosetae A and B forming a girdle around the truncus; (23) secondary distal macrosetae (E1–E2)

inserted ventrally on lamina parva (LP), forming a rectangle; (24) stylus with a skirt attached to its middle (instead of a gonyleptid flabellum arising from its base).

Included genera (number of described species): *Bissulla* Roewer, 1929 (2), *Bresslavius* Mello-Leitão, 1935 (2), *Bunostigma* Mello-Leitão, 1935 (1), *Camarana* Mello-Leitão, 1935 (4, incl. *Arruda* Mello-Leitão, 1940), *Cryptogeobius* Mello-Leitão, 1935 (2, incl. *Pirahya* Roewer, 1949), *Heteromeloleptes* Mello-Leitão, 1931 (2), *Lanesoares* Roewer, 1949 (1), *Pararezendesius* H. Soares, 1972 (1), *Paratricommatus* Piza, 1943 (8, incl. *Corcovadesia* Soares & Soares, 1954, *Neoarminda* Özdikmen & Kury, 2006, *Soaresula* Roewer, 1949), *Pseudopachylus* Roewer, 1912 (3), *Pseudophalangodes* Roewer, 1912 (1), *Rezendesius* H. Soares, 1945 (1), *Spinopilar* Mello-Leitão, 1940 (7, incl. *Machairoscelis* Kury, 2003, *Segundolus* Roewer, 1949), *Taquara* Mello-Leitão, 1936 (2), *Tibangara* Mello-Leitão, 1940 (2, incl. *Tachusina* Strand, 1942), *Zalanodius* Mello-Leitão, 1936 (6, incl. *Berlesecaptus* Mello-Leitão, 1940, *Simonoleptes* Soares & Soares, 1954). Uncertain genus: four species in *Camarana* and *Pseudopachylus*.

Taxonomic notes: In contrast to the Tricommatinae, which are much less diverse, taxonomy is not treated here in detail, except for the description of the new *Paramitraceras* and redescription of *Zalanodius convexus*, which was hitherto unillustrated and lacked type material. A detailed synopsis of literature records may be found in Kury (2003a). Only nomenclatural acts derived from (or justified by) the new proposed hypothesis of phylogeny are listed below. The equals sign (=) used here means 'newly considered a senior subjective synonym of'.

All included genera cited above are newly transferred from Tricommatinae to Cryptogeobiidae, except for *Berlesecaptus* Mello-Leitão, 1940, and *Simonoleptes* Soares & Soares, 1954, newly transferred respectively from Grassatores incertae sedis and Phalangodidae to Cryptogeobiidae.

Bissulla singularis (Soares & Soares, 1949) **comb. nov.** made for *Paramitraceras singularis* Soares & Soares, 1949, currently in *Machairoscelis*.

Camarana Mello-Leitão, 1935 = *Arruda* Mello-Leitão, 1940 **syn. nov.**

Camarana insignis (Mello-Leitão, 1940) **comb. nov.** made for *Arruda insignis* Mello-Leitão, 1940.

Camarana pectinata (Mello-Leitão, 1940) **comb. nov.** made for *Arruda pectinata* Mello-Leitão, 1940.

Camarana minor Mello-Leitão, 1935 = *Arruda mutilata* Mello-Leitão, 1940 **syn. nov.**

Paratricommatus Piza, 1943 = *Liops* Mello-Leitão, 1940 [invalid, junior homonym, see Kury & Alonso-Zarazaga, 2011], = *Poecilosophus* Mello-Leitão, 1948, = *Soaresula* Roewer, 1949, = *Arminda* Roewer, 1949, = *Corcovadesia* Soares & Soares,

1954, = *Buzioleptes* H. Soares, 1966, = *Neoarminda* Özdikmen & Kury, 2006, all **syn. nov.** (some of them transferred from other synonyms).

Paratricommatus colatinae (Soares & Soares, 1946) **comb. nov.** made for *Phalangodella colatinae* Soares & Soares 1946.

Paratricommatus hexabunus (Mello-Leitão, 1940) **comb. nov.** made for *Liops hexabunus* Mello-Leitão, 1940.

Paratricommatus inermis (Soares & Soares, 1954) **comb. nov.** made for *Corcovadesia inermis* Soares & Soares, 1954.

Paratricommatus melloleitai (H. Soares, 1945) **comb. nov.** made for *Paratricommatus melloleitai* H. Soares, 1945.

Paratricommatus veneficus (H. Soares, 1966) **comb. nov.** made for *Buzioleptes veneficus* H. Soares, 1966.

Spinopilar de Mello-Leitão, 1940 = *Segundolus* Roewer, 1949 = *Machairoscelis* Kury, 2003 **syn. nov.**

Spinopilar armatipes (B. Soares, 1972) **comb. nov.** made for *Corcovadesia armatipes* B. Soares, 1972.

Spinopilar insignitus (Roewer, 1949) **comb. nov.** made for *Segundolus insignitus* Roewer, 1949.

Taquara bicoloripes (H. Soares, 1974) **comb. nov.** made for *Camarana bicoloripes* H. Soares, 1974.

Tibangara de Mello-Leitão, 1940 = *Tachusina* Strand, 1942 **syn. nov.**

Tibangara cocaiensis (H. Soares, 1972) **comb. nov.** made for *Paramitraceras cocaiensis* H. Soares, 1972.

Tibangara fuscomaculata (Soares & Soares, 1947) **comb. nov.** made for *Paramitraceras fuscomaculatus* Soares & Soares, 1947.

Tibangara keyserlingii (Sørensen, 1932) **comb. nov.** made for *Tachus keyserlingii* Sørensen, 1932.

Zalanodius Mello-Leitão, 1936 = *Berlesecaptus* de Mello-Leitão, 1940, = *Simonoleptes* Soares & Soares, 1954 **syn. nov.**

Zalanodius convexus (Mello-Leitão, 1940) **comb. nov.** made for *Berlesecaptus convexus* de Mello-Leitão, 1940

Zalanodius insulanus (H. Soares, 1966) **comb. nov.** made for *Simonoleptes insulanus* H. Soares, 1966

Zalanodius latifemur (Soares & Soares, 1954) **comb. nov.** made for *Simonoleptes latifemur* Soares & Soares, 1954.

Zalanodius obstectispiracula (Soares & Soares, 1954) **comb. nov.** made for *Simonoleptes obstectispiracula* Soares & Soares, 1954.

PARATRICOMMATUS PIZA, 1943

PARATRICOMMATUS LOCKEI SP. NOV.

Type data: ♂ holotype (MNRJ 07582) RJ, Cachoeiras de Macacu, Reserva Ecológica de Guapi-Açu (REGUA), 28.ii–01.iii.2012, A. P. L. Giupponi & J. S. Silva leg./1 ♂ 1 ♀ paratypes (MNRJ 0475) same loc., 11.iii.2001, R. L. C. Baptista *et al.* leg./3 ♂ 3 ♀ paratypes (MNRJ

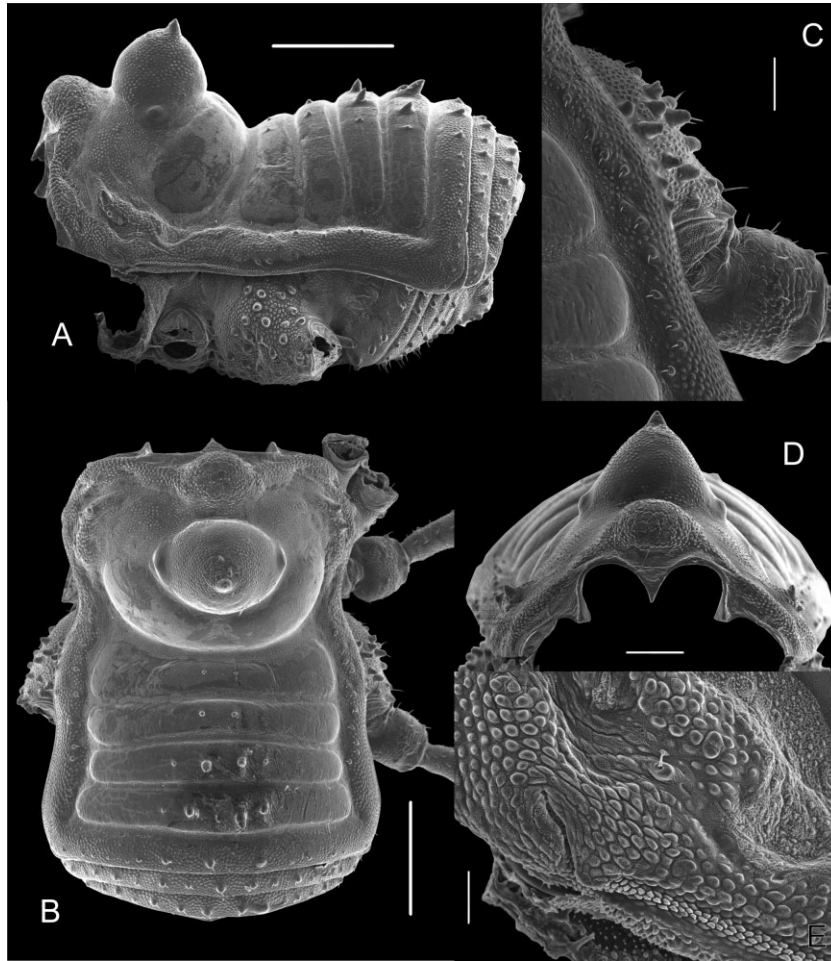


Figure 18. *Paratricommatus lockei* sp. nov., male paratype, MNRJ 7583, from Guapi-Açu. A, habitus, left lateral view; B, same, dorsal view; C, detail of border of dorsal scutum and right coxa IV, dorsal view; D, carapace and ocularium, frontal view; E, ozopore region, left lateral view. Scale bars = 500 µm (A, B), 200 µm (D), 100 µm (C), 50 µm (E).

07517) same loc., 09–11.ii.2012, A. P. L. Giupponi & J. S. Silva leg./4 ♂ 9 ♀ paratypes (MNRJ 08204) same loc., 01–02.ix.2012, A. P. L. Giupponi & J. S. Silva leg./3 ♂ 5 ♀ paratypes (MNRJ 07583) same loc., 28.ii–01.iii.2012, A. P. L. Giupponi & J. S. Silva leg.

Etymology: Named after Mr Nicholas Locke, who continuously struggles for the integrity of the REGUA natural reserve.

Diagnosis: Similar to *P. modestus* in the skirt being acorn-shaped, greatly folded (as a tricorn fan or parabolic erect in the other species). Similar to *P. colatinae* in the scutal groove II being straight (arched frontwards in all other species). Separated from all other species by the ocularium being wide and very high (instead of ordinary ovoid) and the acuminate tubercles on scutal areas II to IV. Tarsal counts slightly higher than most *Paratricommatus* – Ta II, IV higher than pentamerous. Patella II not particularly elongate (as in *P. modestus*); pedipalpus of male not massive (as in

Gen. sp. H); stylus C-shaped (instead of substraight in *P. modestus*). Basicheicerite sturdy (instead of elongate slender as in *P. mahnerti* and sp. H).

Description, male holotype: Dorsum. Dorsal scutum subrectangular with constrictions well marked and coda wide (Figs 18B, 19A). Carapace slightly convex and projected anterolaterally and almost as long as abdominal scutum. Frontal hump strongly developed, unarmed (Fig. 18A). Ocularium located far from the anterior margin of scutum, very wide and high, armed with a single median sturdy spine (Fig. 18D). Mesotergum divided into four areas separated by straight grooves. Area I entire. Scutal areas II to IV armed with slightly asymmetrical paramedian acuminate tubercles (Fig. 18A, B). All scutum finely granular with a transverse row of setiferous tubercle on each of the free tergites. Ozopore single. Venter (Fig. 19E). Stigmatic area short, partly fused with coxae IV. Coxa IV armed with proventral apical spiniform apophysis matching

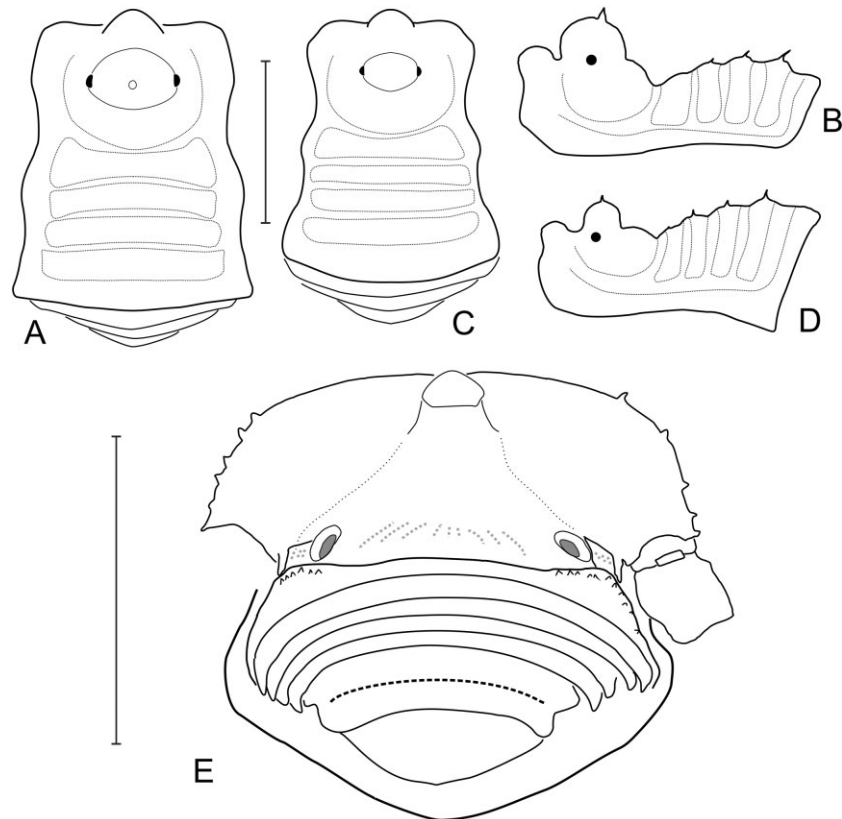


Figure 19. *Paratricommatus lockei* sp. nov., schematic dorsal scutum, showing the dimorphism in the ocularium. A, B, male holotype (MNRJ 7582); C, D, female paratype (MNRJ 7583), dorsal and lateral views; E, male holotype, sternites, ventral view. Scale bars = 1 mm.

lobe on sternite II. Chelicera (Fig. 20A, E). Basichelecerite short, with well-developed bulla. Hand not swollen. Pedipalpus (Fig. 20B). Without particularly elongate or incrassate articles. Trochanter armed with dorsal protuberance and two ventral setiferous tubercles. Femur slightly compressed and slightly convex dorsally, with a ventral row of three small, setiferous tubercles on proximal half. Tibia and tarsus with the usual armature of setiferous tubercles – tibia ectal with III, mesal with IiIi, tarsus ectal and mesal with IiIi. Legs (Fig. 20C–E). Legs short, without armature, except for ventral row of setiferous tubercles on femur I. Femur IV sinuous, unarmed. Tarsal counts 4(3)/6(3)/5/6. Genitalia. Distal part of truncus shaped as an oblique kidney-shaped malleus and an erect LP. Malleus with one pair of robust, ventral, ridged prostrate setae pointing basally. Lamina parva tongue-shaped, covered with numerous median dorsal and lateral acuminate short spines. LP with broad base, base with two pairs of robust, ridged setae, one ventrolateral with massive sockets and pointing laterobasally, another dorsolateral, flanking glans and pointing dorsally. Laterodistal margins of LP each with four long, ridged setae parallel to each other. Ventral face of LP with rectangle

of four setae, two short, distal and two long immediately basal to those. Malleus functions as a support from where arise the rigid ‘finger’, which is the LP, and the soft sac, which is the follis of the glans. Follis almost without folds, with a well-marked dorsal furrow dividing it into left and right halves. Stylus smooth and simple, without head, mounted atop glans, with short pedestal and arising candelabrum-like from it. Skirt ungrooved, without an axis, pentagonal in dorsal view, folding over itself, with shallow-serrate margins. Coloration. Body and appendages uniform 53 Moderate Orange.

Sexual dimorphism (Fig. 19A–D): Ocularium of male is hugely developed in width and height, whereas that of female is normal-sized. Dorsal scutum of female is more rounded and has sharper constrictions.

ZALANODIUS MELLO-LEITÃO, 1936
 ZALANODIUS CONVEXUS (MELLO-LEITÃO, 1940)
 COMB. NOV.

Berlesecaptus convexus Mello-Leitão, 1940: 101; Kury 2003a: 23 (removed from Phalangodidae to Grassatores incertae sedis).

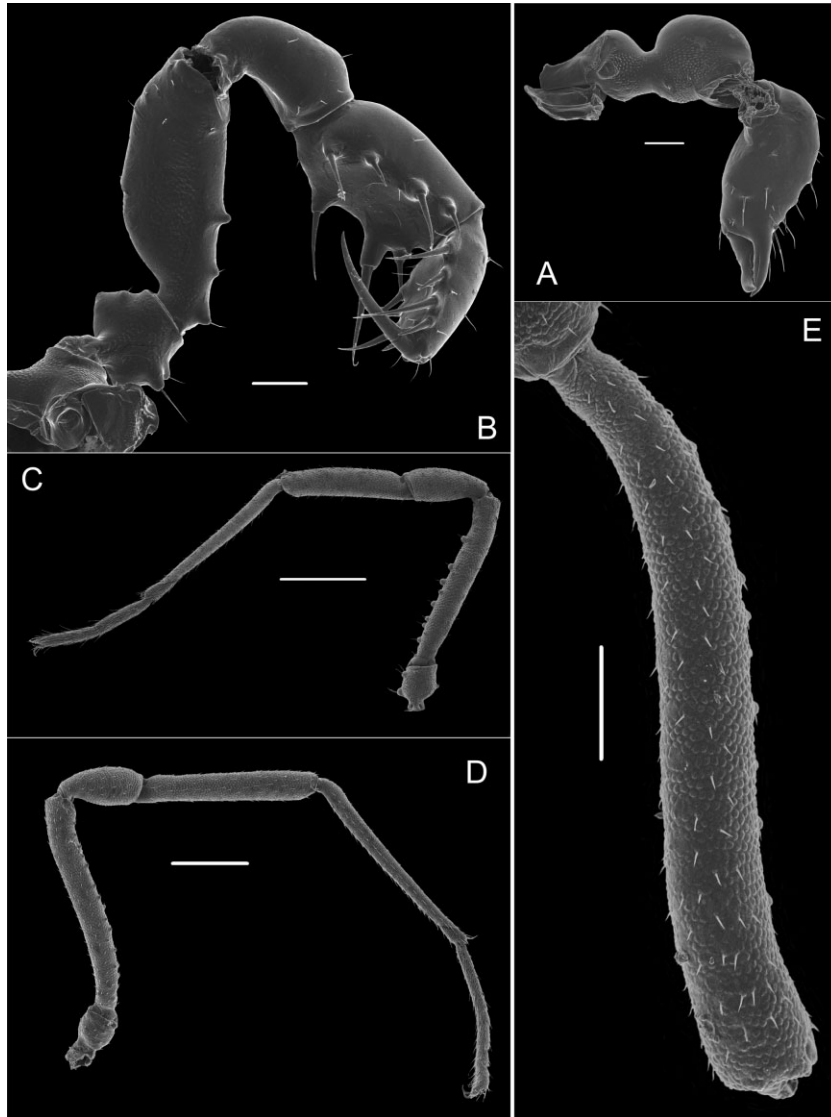


Figure 20. *Paratricommatus lockei* sp. nov., male paratype (MNRJ 7517), from Guapi-Açu. A, left chelicera, mesal view; B, left pedipalpus, mesal view; C, left leg I, retrolateral view; D, left leg IV, prolateral view; E, right femur IV, dorsal view. Scale bars = 500 μ m (C, D), 200 μ m (A, B, E).

Diagnosis: Closest to *Z. latifemur*, in the compact shape and short legs (as opposed to slender body with longer legs in *Z. bicornutus* and *Z. hirsutus*) but with tegument much more finely granular and not wrinkled. Leg IV densely covered by small, long-haired setiferous tubercles (instead of covered by very large ones in *Z. latifemur*). Metatarsus IV normal (instead of incrassate with a powerful spur in *Z. bicornutus*).

Description, male neotype: Dorsum (Figs 21A, B, 22A–D). Dorsal scutum outline classic alpha, carapace elongate, scutal groove posterior margin in obtuse angle. Mesotergum divided into four areas, area I entire, larger than the others, expanded to the sides. All areas unarmed, covered by irregular, large setiferous tuber-

cles. Posterior border of scutum and free tergites each with a single transverse row of setiferous tubercles. Ocularium high, inclined frontwards, topped by a short protuberance, placed far from the anterior margin of carapace. Frontal hump low, unarmed. Venter (Figs 21C, 23A–C). Coxa IV with ventro-apical, rod-like ventral apophysis connected to sternite II. Sternite II with small, anterior projections partly covering the stigmata. Chelicera (Fig. 22B). Weakly developed, basichelicerite short. Pedipalpus (Fig. 23F). Articles short, trochanter with ventral setiferous tubercle, femur with one ventrobasal setiferous tubercle, tibia and tarsus armed with very weak ventro-ectal and ventromesal spines. Legs (Fig. 23D, E). Legs I–III short, unarmed.

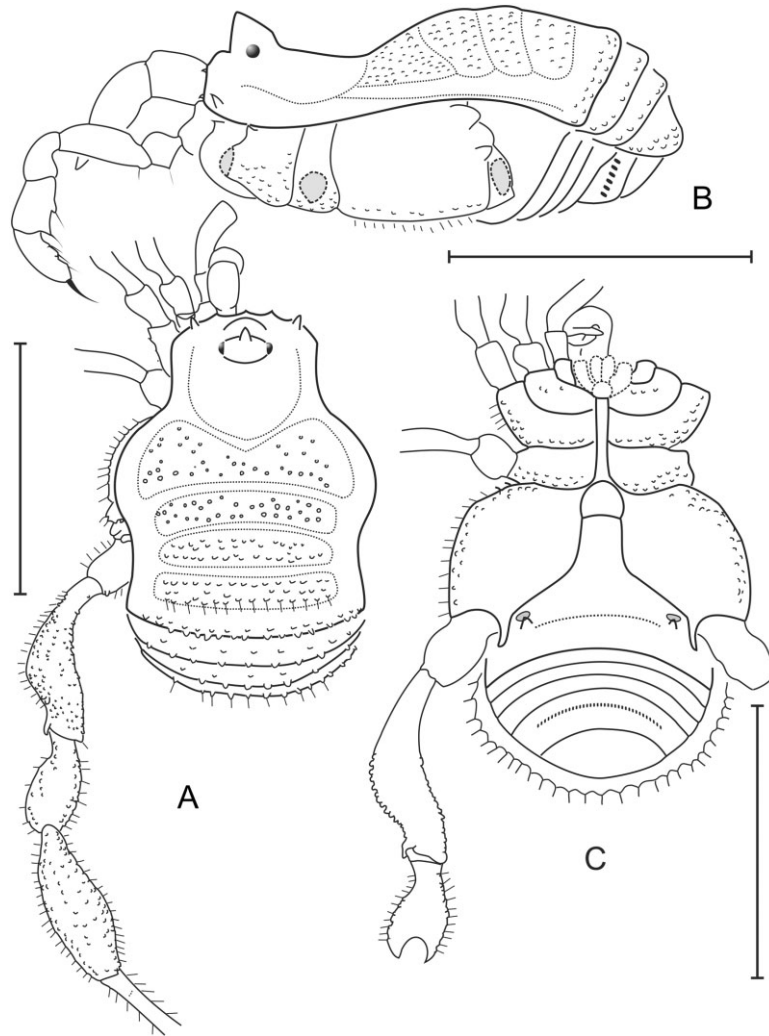


Figure 21. *Zalanodius convexus* (Mello-Leitão, 1940). Male neotype (MNRJ 4878). A, habitus, dorsal view; B, same, lateral view; C, sternal region, coxae, stigmatic area, and sternites, ventral view. Scale bars = 0.5 mm.

Leg IV considerably stouter than the others, trochanter unarmed, femur and tibia IV incrassate, femur to tibia densely covered with coarse, long-haired setiferous tubercles. The distitarsus I has three articles (as can be clearly seen on Fig. 23E), but the suture between the two distal-most is very shallow, and led to the count of only two by Mello-Leitão (1940; the nearest species, *Z. latifemur* has clearly only two articles, without any suture, and other species have three articles, so it appears that *Z. convexus* shows an intermediate state: trimerous in the process of becoming bimerous). Tarsal counts 4(3) or 3(2) (depending on the interpretation)/6(3)/5/5. Genitalia (Fig. 24A–C). Distal setigerous part of truncus divided into a basal malleus and a distal LP. LP slender, gently curved ventrally. Prepodium extremely elongate, forming angle with truncus. Malleus ventrally with longitudinal wide ditch.

Macrosetae A1–A2 inserted laterally on malleus. Macroseta B ventral on malleus. Macrosetae C1–C3 short, D very small on the laterals of LP. Macrosetae E1–E2, short, forming rectangle on ventral surface of LP. Skirt flabellar, expanded laterally, with deeply serrate margins. Stylus C-shaped. Coloration. Body and appendages uniform 53 Moderate Orange.

DISCUSSION

BRANCHING PATTERN IN GONYLEPTOIDEA

The focus of this analysis concentrated on the relationships and definitions of the genera of Tricommatinae and Cryptogeobiidae. Therefore, both deeper relationships (of families in Gonyleptoidea) and fine positioning of species in each genus were not thoroughly

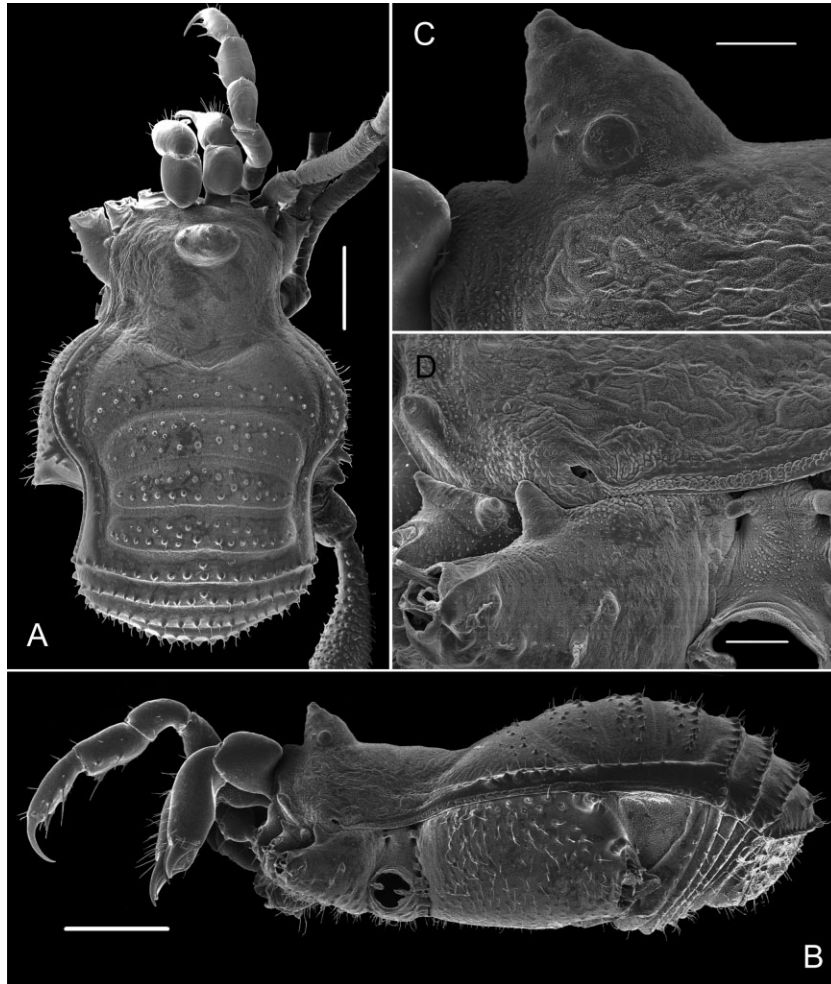


Figure 22. *Zalanodius convexus* (Mello-Leitão, 1940). Male neotype (MNRJ 4878). A, habitus, dorsal view; B, same, lateral view; C, sternal region, coxae, stigmatic area, and sternites, ventral view. Scale bars = 0.5 mm (A, B), 0.1 mm (C, D).

investigated. As for the basal relationships, the branching structure obtained in SG11 and PA14 was only partly retrieved.

It is out of the scope of the present project to address the relationships of families in Gonyleptoidea, although the result obtained is remarkably congruent with SG11 and PA14. It is not trivial to compare the three data sets because of the disparity of taxonomic focus (one was designed to study the internal relationships of Laniatores, another to test the monophyly of Gonyleptidae, and this one has done the same for the traditional Tricommatinae), which reflects the low coincidence of shared terminals. The results obtained by Caetano & Machado (2013), in which Cryptogeobiidae (there called 'Tricommatinae') appear deeply nested within Gonyleptidae are an artefact, probably caused by the lack of true external outgroups.

An expanded Gonyleptidae was retrieved in all three analyses (SG11, PA14, and here), and also a

monophyletic group named herein Microsetata (that is Metasarcidae + Cosmetidae and the complex Gonyleptidae).

TRICOMMATINAE – INTERNAL AND EXTERNAL RELATIONSHIPS

The pertinence of a much diminished Tricommatinae to the Gonyleptidae is strongly supported by Bremer and bootstrap values and appeared consistently in all four analyses performed here (Fig. 6). The monophyly of *Tricommatius* + *Pherania* is supported confidently enough to propose the synonymy of both genera, whereas the interrelationships of the three genera of Tricommatinae are much less secure. The decision to describe the monotypic *Voriax* was based on the large morphological gap as well as its position as sister group to two nonmonotypic genera.

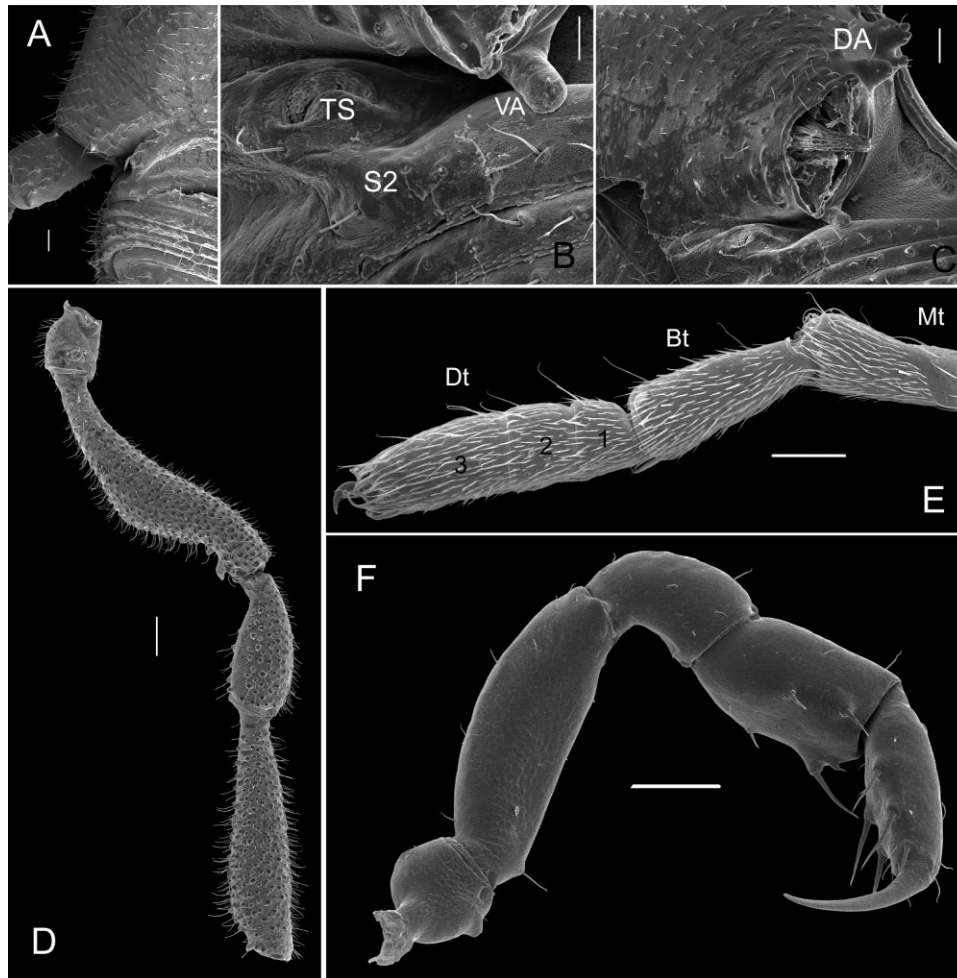


Figure 23. *Zalanodius convexus* (Mello-Leitão, 1940). Male neotype (MNRJ 4878). A, right coxa IV and stigmatic area, partial, ventral view; B, same, detail of rod-like ventral apophysis of coxa IV (VA) resting on sternite II (stigmatic area, S2), oblique view; C, left coxa IV, lateroposterior view, showing multiple dorsal apophyses (DA) of coxa IV; D, left trochanter to tibia of leg IV, dorsal view; E, left tarsus of leg I, showing very faint sutures separating pseudo-articles (1, 2, 3) of distitarsus, lateral view; F, left pedipalpus, mesal view. Other abbreviations: Bt, basitarsus; Dt, distitarsus; Mt, metatarsus; TS, tracheal stigma. Scale bars = 0.2 mm (D, F), 0.1 mm (A, C, E), 0.05 mm (B).

THE SISTER GROUP OF CRYPTOGEOBIIDAE

The *Huralvioides* group has been speculated to be closest to 'Tricommatinae' for almost 20 years (Kury, 1995b), and this relationship was also retrieved in PA14. Here, in spite of the poor bootstrap and moderate Bremer performances, this sister-group relationship appeared in three of the four analyses, failing only in the weighting with concavity = 1, which entails strong distortions.

GENERIC LIMITS IN CRYPTOGEOBIIDAE

In the classification and choice of generic limits, a delicate balance was sought amongst the recognition of

traditional generic names, the branching phylogenetic structure proposed here, and the support for each clade, avoiding production of unwarranted new genera (especially monotypic ones). The proposed taxonomy has already been explained in general lines in the 'Main results of the analysis' section. Here a few comments are added.

1. *Zalanodius*: In group A, the monotypic *Berlesecaptus* and the type species of *Simonoleptes* are sister groups, with strong support, sustaining the new synonymy of both genera. They are also more loosely clustered with three other terminals. However, keeping *Berlesecaptus* separated would turn the genus *Zalanodius* (with two species, as defined by

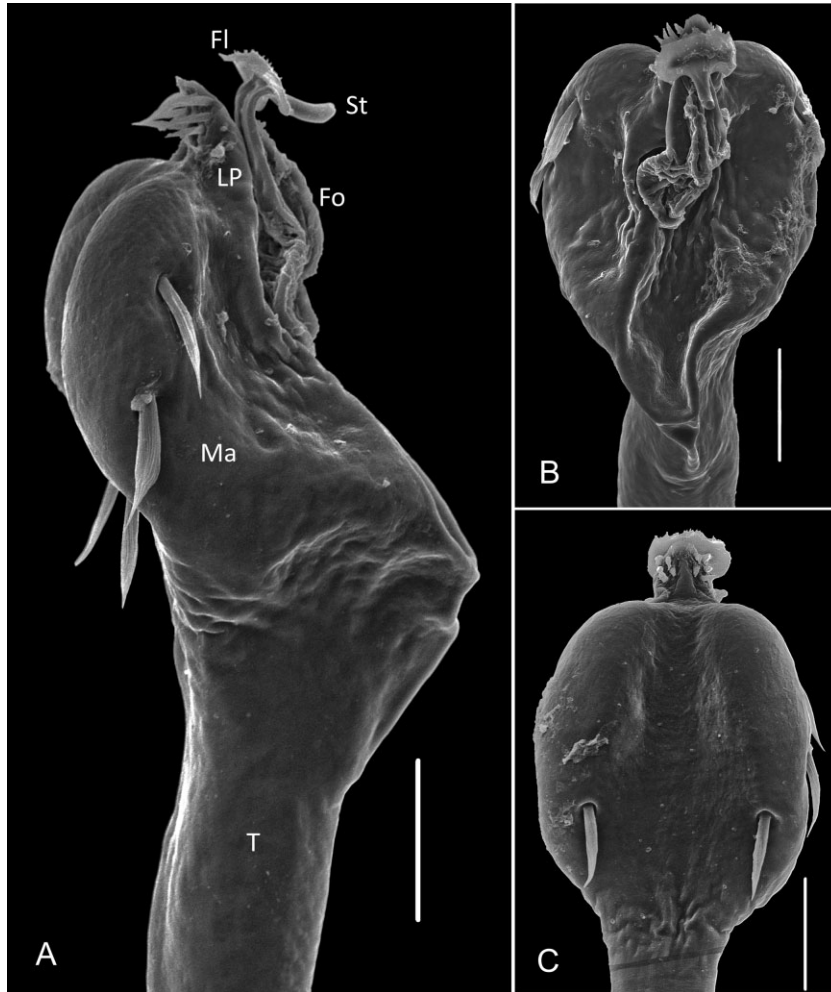


Figure 24. *Zalanodius convexus* (Mello-Leitão, 1940). Male neotype (MNRJ 4878). Distal part of penis. A, lateral view; B, dorsal view; C, ventral view. Abbreviations: Fl, flabellum; Fo, follis ('glans'); LP, lamina parva; Ma, malleus; St, stylus; T, truncus. Scale bars = 0.05 mm.

Kury, 2003a) into a paraphylum. As there is also strong support for this augmented *Zalanodius*, it is here considered to include *Berlesecaptus* as well. Besides, as male genitalia are quite uniform for all of those species, this decision is also supported by sheer similarity. The inclusion of *Pseudophalangodes* is not firmly supported, and this genus is kept independent for now (Fig. 7);

2. *Paratricommatus*: There is a weakly supported group of six terminals (Fig. 7), including the two species of *Paratricommatus*, both the very poorly known monotypic genera *Soaresula* (only females) and *Neoarminda*, and two undescribed species, one of them described here as *P. lockei*. An alternative approach would be to describe the new species as a separate monotypic genus because of the lack of convincing ties with other genera. A conservative ap-

proach (as taken here) is to call it a new species of *Paratricommatus*, although this augmented *Paratricommatus* deserves more study regarding its composition. The genus *Corcovadesia* is known only by females and may also belong here;

3. The choice of leaving *Lanesoares* monotypic was chosen over the alternative of creating an exceedingly diverse *Pseudopachylus*, which would deplete the information content of the classification;
4. *Tibangara*, hitherto monotypic, but now with five undescribed species, has the strongest Bremer and bootstrap support and appeared in all four analyses (Fig. 9). The accretion of the poorly known monotypic *Tachusina* is less supported, but still warranted by the present results.
5. There is a lack of resolution in the vicinity of *Pseudopachylus*. The species *Pseudopachylus*

martensi and *Pseudopachylus alticola* form a paraphylum well outside the true *Pseudopachylus*. There is a considerable number of undescribed species of *Pseudopachylus* not included in the present analysis, and to avoid cluttering the taxonomy even more with monotypic genera, for now these are left in a poorly supported *Pseudopachylus*, sister group of an expanded *Bissulla*. This latter genus was monotypic until now, but a group of six morphotypes, five of them as yet undescribed (Gen. sp. X, Y, Z, AA, and AB), are a well-supported clade, sister group of *Bissulla paradoxa*. One species from Paraná, described by Soares & Soares (1949) in *Paramitraceras* is newly combined in *Bissulla*. The *Paramitraceras* species are members of the Stygnopsidae, but Kury (2003a) had already brought this species into the Tricommatinae (in the broad 2003 sense).

CONCLUSION

This first attempt to reconstruct the phylogeny of the Tricommatinae *s.l.* was useful to survey the abundant morphological features for defining genera in this subfamily and the Cryptogeobiidae. The unusual features previously demonstrated for the Tricommatinae *s.l.*, as exemplified by *Pseudopachylus* (Kury, 2006), *Spinopilar* (Kury, 1992, Kury & Pérez-González, 2008), and *Camarana + Pseudopachylus* (Pinto-da-Rocha *et al.*, 2014), in fact refer to the Cryptogeobiidae only. This latter group is well characterized, in spite of the high diversity and variability of features such as the shape of dorsal scutum, ocularium, and skirt of stylus.

The proposal of morphological synapomorphies to support many clades is important to diagnose them, especially the establishment of the unranked group of families in Gonyleptoidea as a named clade, here called Microsetata, also supported by molecular analysis. An important step has been taken with the removal of Cryptogeobiidae, possessing a primitive penis with lamina parva (akin to those of Agoristenidae and Stygnidae), from the Microsetata, which includes species with a true ventral plate. A gradual refinement of the internal relationships will unavoidably follow.

The present survey of homology in the characters is an important step towards a morphological analysis of the Gonyleptoidea. The severe under-sampling of the small Tricommatinae and Cryptogeobiidae causes many gaps in the morphological diversity, that is crucial to phylogenetic reconstruction. Most genera were monotypic to begin with, but much greater diversity is slowly being uncovered as a profusion of material from sifting leaf litter is studied. Many genera are still monotypic, but this will gradually change when more new species are found.

ACKNOWLEDGEMENTS

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APPENDIX 1

CHARACTER DESCRIPTIONS AND STATES USED IN THE PRESENT ANALYSIS

1. DS (dorsal scutum), outline in dorsal view
 0. Type alpha classic [carapace sides straight or slightly convex, mid-bulge central, coda slightly divergent, as wide as carapace; scutum subrectangular, with laterals convex, forming

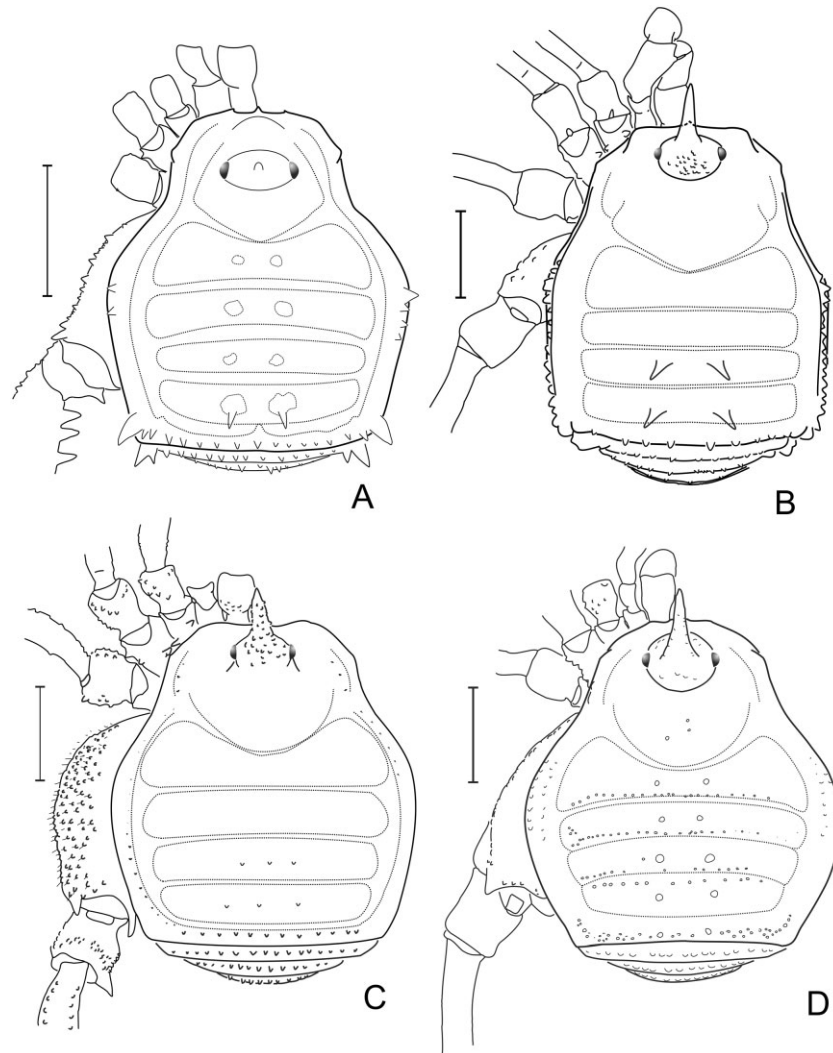


Figure 25. Cryptogeobiidae. Males, habitus, dorsal view. A, Gen. sp. Q (MNRJ 7585); B, *Pseudopachylus eximius* (HS-MNRJ 907); C, Gen. sp. AB (MZSP 14779); D, Gen. sp. Y (ZMUC AK 042a). Scale bars = 1 mm.

- two well-marked constrictions (Kury *et al.*, 2007); as in *Tricommatius*, *Caramaschia*, Figs 7A, 14A, C].
1. Modified-alpha (coda divergent and on average as wide as mid-bulge, as in *Pseudophalangodes*, *Heteromeloleptes*, Fig. 14D, J).
 2. Type gamma [mid-bulge very wide, constriction 2 lacking, coda convergent posteriorly (Kury *et al.*, 2007); as in *Soaresia*, *Cryptogeobius* Fig. 14B, F].
 3. Trapezoid: constrictions 1 and 2 extremely attenuated, coda strongly flaring, much wider than carapace (as in *Voriacx*, Fig. 12A).
 4. Modified-beta, pyriform, mid-bulge strongly displaced backwards (as in Gen. sp. G, Fig. 14H).
 5. Modified-gamma, campaniform (bell-shaped) with coda sides parallel (as in *Bissulla*, *Tibangara*, Fig. 14N–P).
 6. Subrectangular with constrictions well marked, but coda wide (as in *Paratricommatus lockei*, Fig. 18B).
 7. Agoristenid hexagon.
2. Abdominal scutum, posterior constriction
 0. Well marked.
 1. Attenuate, more posterior or lost with outline continuous, but with sides converging (as in Gen. sp. AB, Gen. sp. Y, Fig. 25C, D).
 2. Attenuate, more anterior (as in *Pseudophalangodes*, Fig. 1B).
 3. Lost: abdominal scutum without any constriction, with sides straight and parallel, giving

- the scutum the shape of a bell (as in *Pseudopachylus eximius*, Fig. 25B; Gen. sp. T, Fig. 1C).
3. Carapace, outline of lateral margins
 0. Clearly divergent to posterior side.
 1. Straight or only slightly convex.
 2. Strongly convex.
 4. Carapace, anteroposterior outline
 0. Not projected anterolaterally.
 1. Widely projected anterolaterally on male (as in *Paratricommatus lockei*, Fig. 18B).
 2. Projected anteriorly on male.
 5. Abdomen, length relative to carapace
 0. Subequal to carapace (as in *Paratricommatus lockei*, Fig. 18B).
 1. Much longer than carapace.
 6. Carapace, armature of frontal margin
 0. Two to three pairs of dentiform projections pointed frontwards.
 1. Much reduced projections or entirely wanting.
 2. One pair of strong dorso-anterior teeth (as in *Zalanodius convexus*, Figs 21A, 22A).
 3. One pair of frontal sharp spiniform apophyses (as in *Spinopilar apiacaensis*, Kury, 1992: figs 1, 2).
 7. Carapace, anterolateral triangular lobes
 0. Lobes absent.
 1. Lobes present (as in Gen. sp. F, Fig. 4C).
 8. Carapace, lateral projection of lateral margins
 0. Without acuminate lobes.
 1. With acuminate lobes at the ozopores (as in *Bunostigma*, Figs 1E, 14E).
 9. Abdominal scutum, lateral areas
 0. Smooth and unarmed marginally.
 1. With noticeable cluster of granules that can extend to the posterior border or be restricted to anterior part.
 10. Abdominal scutum, posterior border in males
 0. At most as wide as the rest.
 1. Intermediate.
 2. Much wider than anterior part.
 11. Frontal hump, structure
 0. Low, weakly developed or indistinct (as in *Pararezendesius*, Fig. 4D).
 1. Very high, strongly developed (as in *Spinopilar*, Figs 2C, 26D).
 12. Frontal hump, armature
 0. Unarmed.
 1. With acuminate spiniform apophysis (as in *Spinopilar*, Fig. 26D).
 13. Ocularium, structure
 0. Ovoid, normally developed (as in Gen. sp. H, Fig. 4E).
 1. Extremely depressed and sprawled, eyes migrated backwards (as in *Caramaschia singularis*, Kury, 2002: figs 1–3).
 2. Huge, blunt protuberance at the anterior margin of carapace neither ending on a tubercle nor a spine and inclined frontwards (as in Gen. sp. F, Fig. 4C).
 3. Pointed protuberance oblique frontwards (as in *Zalanodius*, Fig. 22C).
 4. Erect, very high campaniform mound (as in *Spinopilar*, Figs 2C, 26D).
 5. Flattened and wide, *Bourguyia*-like (as in *Pararezendesius luridus*, Fig. 4D).
 6. Wide, high, and swollen mound, far from the anterior margin (as in *Paratricommatus lockei*, Fig. 18A, B, D).
 7. Wide, thick mound (as in Gen. sp. P, Fig. 2B).
 14. Ocularium, position relative to the anterior border of carapace
 0. Remote, space for frontal hump well defined (Figs 4D, E, 15B).
 1. Contiguous with border, frontal hump absent or much reduced (Figs 2D, 4C).
 15. Ocularium, armature
 0. Pair of short tubercles or spines.
 1. Entirely unarmed or with minute median granule (as in *Tricommatus*, Fig. 15B).
 2. Single median pointed spine.
 3. Huge, single hook (as in *Bissulla paradoxa*, Fig. 2D).
 4. Thick spine bent frontwards but more with angle than curve.
 5. Extremely high erect Mello-Leitão's *Pinocchio*-like spine.
 6. Thick and short acuminate protuberance (as in *Voriac*, Fig. 12D).
 16. Single, straight spine of ocularium, inclination
 0. Erect.
 1. Leant backwards.
 17. Mesotergal area I, length relative to other areas
 0. As long as any of the others.
 1. Much longer than each of the others (e.g. *Zalanodius*, Fig. 22A).
 18. Mesotergal area I, longitudinal median groove
 0. Present, area I divided into left and right halves (as in *Tricommatus brasiliensis*, Fig. 15A).
 1. Absent, area I entire (e.g. *Cryptogeobiidae*, Figs 25A–D, 26A–C).
 19. Scutal groove I, shape
 0. U-shaped, elongate, posterior border convex respect to area I but barely deforming it (as in *Zalanodius*, Fig. 22A).
 1. Short U, posterior border broader, not touching A I (as in Gen. sp. D, Fig. 26A).
 2. Reniform attenuate, short, with posterior border substraight, barely deforming A I (as in *Camarana*, Fig. 26C).

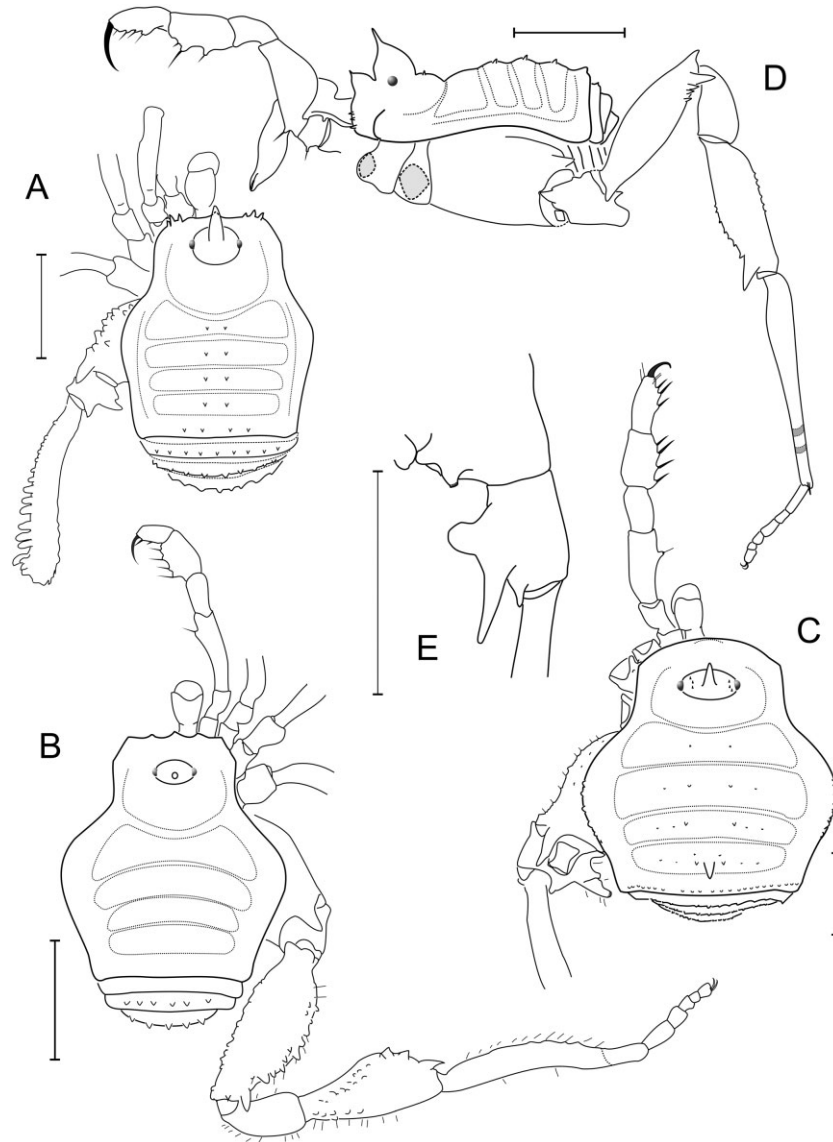


Figure 26. Cryptogeobiidae. A, Gen. sp. D, male (MZSP 14756). Habitus, dorsal view. B, *Cryptogeobius crassipes*, male (MNRJ 6889). Same. C, *Camarana insignis*, male lectotype (MNRJ 58322). Same. D, Gen. sp. K, male (MNRJ 18984). Habitus, lateral view. E, Gen. sp. L, male (MNRJ 17.480). Left trochanter IV, ventral view. Scale bars = 1 mm.

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| <ul style="list-style-type: none"> 3. U-shaped very elongate, posterior border broad, substraight (as in <i>Bissulla</i>, Fig. 25C, D). 4. V-shaped, elongate, but anterior outline dissolving, aggressively intruding into area I. 5. Section of pentagonal. 20. Scutal groove II, shape <ul style="list-style-type: none"> 0. Changing slope, with median projection. 1. Subtly arched pointing frontwards (as in <i>Camarana</i>, Fig. 26C, <i>Cryptogeobius</i>, Fig. 26B). 2. Strongly arched frontwards. 3. Straight (Fig. 25B, C). 4. Median portion concave backwards. 5. Strongly concave backwards. 6. Straight, with the laterals curved backwards. | <ul style="list-style-type: none"> 21. Mesotergal area III, armature <ul style="list-style-type: none"> 0. With a pair of high acuminate spines. 1. Unarmed. 2. With a pair of short tubercles. 3. With pair of high, blunt tubercles. 4. With a transverse row of acuminate tubercles. 22. Mesotergal area IV, armature <ul style="list-style-type: none"> 0. Unarmed. 1. Armed with single acuminate spine (as in <i>Camarana</i>, Fig. 26C). 2. Armed with a pair of blunt short spines (as in <i>Taquara</i>, Fig. 25A). 3. Armed with a mamilliform unpaired spine. |
|--|---|

4. Armed with a pair of short acuminate spines (as in Gen. sp. P, Fig. 2B).
5. Armed with a small median tubercle.
23. Tegument of dorsal scutum
0. Fine granular.
1. Coarsely granular, jagged outline of granules clearly visible on lateral view.
24. Phaneres of mesotergum and free tergites
0. Fine granular.
1. Coarse tubercles densely clustered.
2. Sui generis.
25. Dorsal anal operculum, granulation
0. Smooth or finely granular.
1. Moruliform, densely covered with coarse tubercles.
26. Basichelicerite, length, relative to carapace
0. Much shorter than carapace.
1. Comparable to the carapace.
27. Cheliceral hand, armature of frontal surface
0. Unarmed.
1. With powerful frontal dentiform apophysis.
28. Cheliceral basichelicerite, build
0. Weak and slender.
1. Thick and swollen.
29. Cheliceral hand, sexually dimorphic swell
0. Weak.
1. Kidney-shaped swollen in male.
30. Pedipalpus, total length
0. Much shorter than dorsal scutum.
1. Well developed, at least as long as dorsal scutum.
31. Pedipalpal trochanter, shape
0. Rounded cylinder with neck.
1. Extremely short and compact (as in *Tibangara*, Fig. 27A, *Bissulla*, Fig. 27C, D).
2. Robust and long.
32. Pp femur, presence of median ventral setiferous tubercle
0. Absent.
1. Present.
2. Setiferous tubercles row present.
3. Row of spines.
33. Pedipalpal femur, concavity and grate
0. Cylindrical, base as thick as apex.
1. Strongly compressed, convex dorsally, with ventral stout spines (as in *Caramaschia*, Kury, 2002: fig. 2).
2. Slightly compressed, strongly convex dorsally, with moderate ventral spines.
3. Widest distally, with mesal concavity, ventral crest, and basal stridulatory grate (as in *Tibangara*, Fig. 27F).
34. Stridulatory grate, extension
0. Basal third of Fe (as in *Tibangara nephelina*, Fig. 27A, B).
1. Basal fifth of femur plus trochanter (as in as in *Bissulla paradoxa*, Fig. 27C, D).
35. Distal-most ectal spine of pedipalpal tibia, length relative to basal one
0. Short comparable to the others.
1. Much longer than the others (as in *Paratricommatus*, Fig. 4E).
36. Calcaneus of metatarsus I of male, level of swell
0. Normal.
1. Swollen.
2. Astragalus swollen.
37. Coxa II, length relative to the other coxae
0. in situ only a little longer than coxa III.
1. in situ widely surpassing coxa III in length.
38. Patella II of male, length
0. Short, normal.
1. Very elongate (as in *Heteromeloleptes padbergi*, Fig. 1D).
39. Femur III of male, structure
0. Not swollen.
1. Strongly swollen, with irregular tubercles.
2. Strongly swollen, with two ventral rows of spines (as in *Voriax*, Fig. 12A, B).
40. Tibia III of male, structure
0. Not swollen.
1. Swollen, straight.
2. Swollen, pyriform.
41. Coxa IV of male, development
0. Normal, reaching posterior limit of area II or even middle of area III (as in Gen. sp. Q, Fig. 25A).
1. Very small and short, attaining at most middle of area II (as in *Pseudopachylus eximius*, Fig. 25B).
2. Strong, widely projected outside, attaining posterior limit of area III (as in Gen. sp. AB and Gen. sp. Y, Fig. 25C, D).
42. Coxa IV, lateral margin
0. Oblique to the main axis of body.
1. Straight, parallel to main axis of body.
2. Clearly transverse to main body axis.
43. Coxa IV, granulation of dorsal surface
0. Finely granular.
1. Intermediate – clearly marked granules.
2. Densely covered with pointed setiferous tubercles.
3. With few coarse tubercles.
44. Coxa IV of male, prodorsal armature
0. With dorso-apical acuminate oblique apophysis.
1. Unarmed.
2. With blunt, almost transverse tubercle.
3. With blunt, oblique tubercle, which may be multiple.
45. Coxa IV of male on ventral surface, retrolateral border
0. Unarmed.

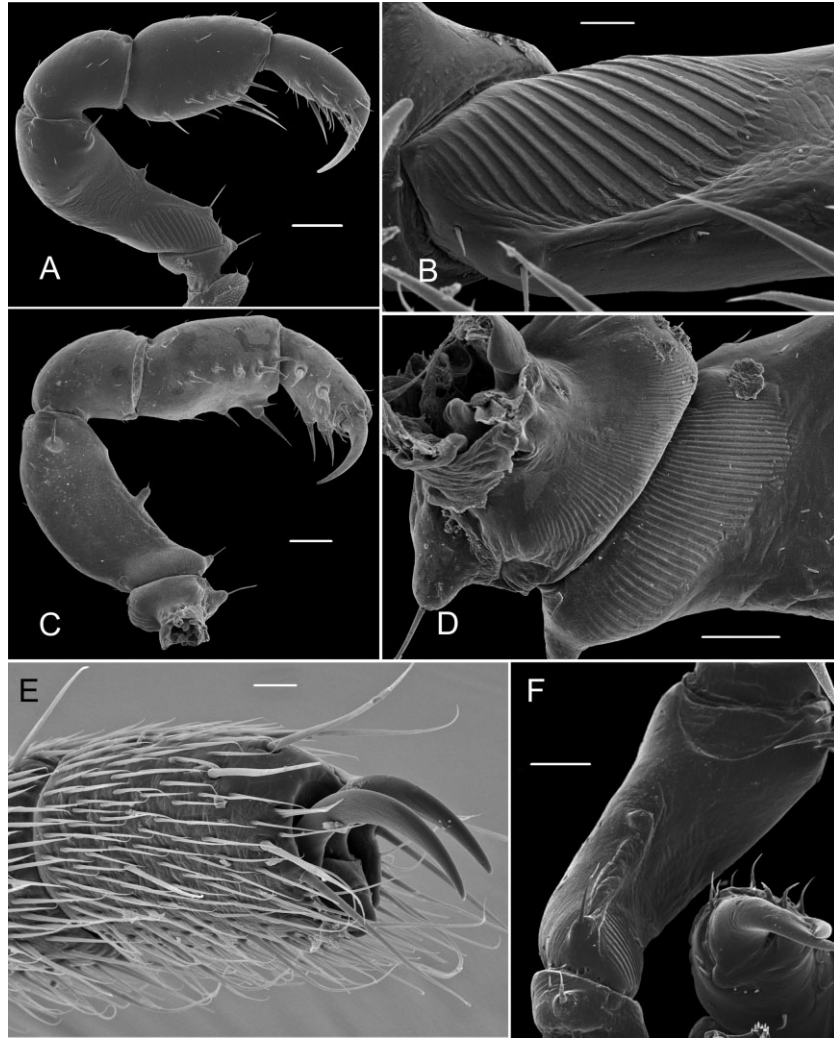


Figure 27. Cryptogeobiidae, appendages: A, *Tibangara nephelina* (MNRJ 1964), left pedipalpus, mesal view; B, same, detail of stridulatory grate on femur; C, *Bissulla paradoxa* (MZSP 432), left pedipalpus, mesal view; D, same, detail of stridulatory grate on trochanter and base of femur; E, Gen. sp. O, male (MNRJ 17557), left distitarsus IV, prolateral view; F, Gen. sp. W, male (MNRJ1977) right pedipalpus, ventral view, showing compression and grate. Scale bars = 0.2 mm (A, C), 0.1 mm (D, F), 0.05 mm (B), 0.02 mm (E).

1. With strong, single-branched apophysis (spear) (Fig. 28H, P).
2. With blunt, subtriangular conic apophysis (Fig. 28I, J, Q).
3. C-shaped or wrench-shaped, with two branches (Fig. 28K, R).
4. Horse head facing outside (Fig. 28L, S).
5. As in 4, but with outer branch extremely elongate running along lobe of sternite (as in *Bunostigma singulare*, Figs 2A, 28M, N, T).
6. With two independent, short spiniform apophyses (as in *Caramaschia*, Fig. 28O).
7. With a single, slender and short spine (as in *Pararezendesius*, Fig. 28V).
8. Horse head facing inside.
9. Taquara-like polygon.
46. Coxa IV in both sexes subapical retrolateral
 0. Without special features.
 1. With very slender, rod-like apophysis applied to free sternite I.
47. Trochanter IV of male sub-basal retrolateral, presence of A-process
 0. Unarmed.
 1. With alpha process, with secondary truncate incisor process alpha 2, which is fasciolate hyaline and matches corresponding hyaline incisor lobe in coxa IV (as in *Pseudopachylus longipes*, Fig. 5A; *Tibangara nephelina*, Fig. 5B).
48. Alpha process of trochanter IV
 0. Short, uniramous dentiform (shark fin-shaped) (Fig. 29C).
 1. Long, curved, and tapering.

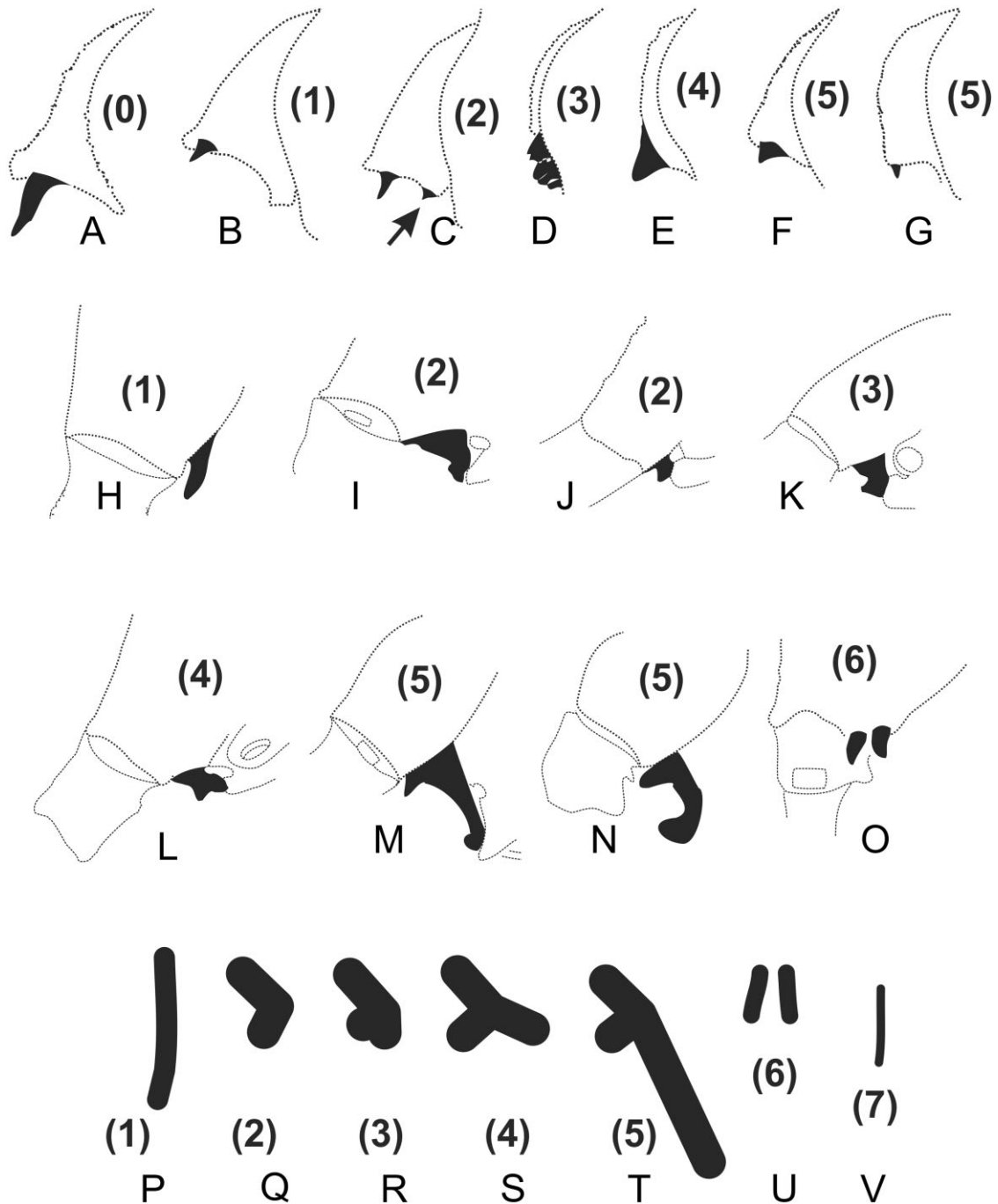


Figure 28. Apophyses of coxa IV of males (schematic). Left dorso-apical apophysis, dorsal view: A, *Camarana insignis*; B, Gen. sp. S; C, Gen. sp. I; D, *Zalanodius convexus*; E, *Caramaschia singularis*; F, Gen. sp. Y; G, Gen. sp. AB. Right ventro-apical apophysis, ventral view: H, Gen. sp. AB; I, *Camarana insignis*; J, *Taquara bicoloripes*; K, *Tibangara cocaiensis*; L, Gen. sp. X; M, *Cryptogeobius crassipes*; N, *Bunostigma singulare*; O, *Caramaschia singularis*. P–V, the same character states (numbered) of ventral apophyses, ultrascematic.

49. Trochanter IV (Tr IV) of male medial retrolateral, presence of B-process
 0. Unarmed.
 1. With beta process (as in *Spinopilar armatus*, Fig. 4B).

50. Beta process of Tr IV of male, shape
 0. Spiniform.
 1. Triangular, broad lobe.
 2. Procurved lobe with or without L-shaped composite branch.

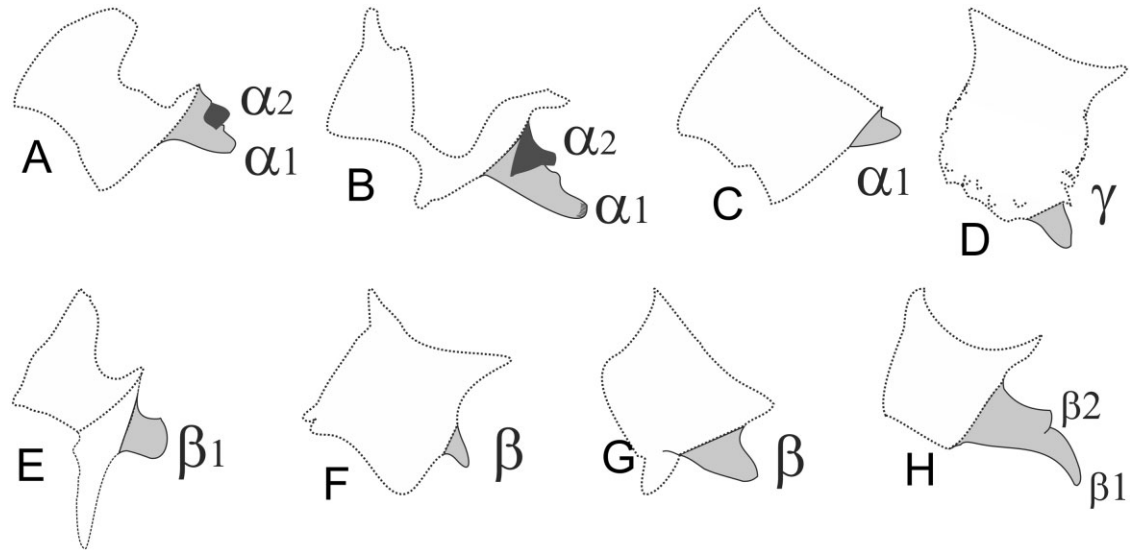


Figure 29. Cryptogeobiidae. Left trochanter IV of male, schematic, dorsal view: A, *Camarana minor*; B, *Camarana insignis*; C, *Tibangara nephelina*; D, Gen. sp. AB; E, Gen. sp. L; F, *Taquara pilosa*; G, *Cryptogeobius crassipes*; H, Gen. sp. AE. Alpha and Beta apophyses as defined in the descriptions of characters 47 and 48 (Appendix 1).

3. Recurved, long pointed lobe, with secondary branch (as in *Spinopilar armatus*, Fig. 4B).
51. Secondary lobe of beta apophysis, presence
 0. Absent.
 1. Present as composing huge L-complex apophysis.
52. Trochanter IV of male subapical retrolateral, presence of G-process
 0. Unarmed.
 1. With stout spiniform gamma process granulous at base (as in *Bissulla*, Fig. 29D).
 2. With short and blunt gamma protuberance.
 3. With simple spiniform apophysis.
53. Trochanter IV of male, dorsal armature
 0. Unarmed.
 1. Armed with small hook curved to the inside.
 2. Armed with dorsodistal strong apophysis.
54. Trochanter IV of male, proateral armature
 0. Unarmed.
 1. With broad, triangular apophysis.
 2. With short, thin apophysis.
55. Femur IV of male, elongation
 0. Relatively short, similar to that of female.
 1. Moderately elongate, slender and sinuous.
 2. Moderately elongate, straight.
 3. Extremely elongate and substraight, almost mitobatiform (as in Gen. sp. S, Fig. 1A).
56. Femur IV of male relatively short and thick, not incrassate, without serrulae or pectination and clearly curved to the proateral side
 0. Absent.
 1. Present.
 2. Same, but curvature more intense in the basal quarter of femur.
3. Same, but with proateral flap along most of the length of femur.
4. Thick in both sexes.
57. Femur IV of male much thicker in distal quarter of its length
 0. Absent.
 1. Present.
58. Femur IV of male on dorsal surface
 0. With fine granulation.
 1. Coarsely tuberculate.
59. Femur IV, level of swell
 0. Not inflated.
 1. Only moderately inflated in males.
 2. Spindle-like, swollen in males only (as in *Cryptogeobius crassipes*, Fig. 26B and *Pseudophalangodes unicolor*, Fig. 1B).
 3. Strongly swollen in both sexes.
 4. With ventral spiny hump in both sexes.
60. Femur IV of male proateral surface
 0. With rows of tubercles and larger apical tooth.
 1. Unarmed.
 2. With row of blunt spines on the distal half of femur.
61. Femur IV of male, lateral curvature
 0. Double, podomere sinuous, attenuate sigmoid.
 1. Single, only one proateral curvature.
 2. No curvature because of elongation and rectification of podomere.
62. Femur IV of male, dorsoventral bend
 0. Absent.
 1. Present in the distal quarter of femur.
63. Patella IV of male, length
 0. Short, normal.

1. Elongate (as in *Heteromeloleptes padbergi*, Fig. 1D).
64. Patella IV of male, armature
0. Unarmed.
 1. With apophyses and/or spines.
65. Tibia IV, thickness
0. As thick as femur IV.
 1. Strongly incrassate in males only (as in *Cryptogeobius crassipes*, Fig. 26B).
 2. Intermediate.
 3. Incrassate in both sexes.
66. Tibia IV of male, armature
0. Unarmed on retrolateral surface.
 1. With a row of stout retrolateral apophyses.
 2. Basal row of six acuminate apophyses decreasing apically.
 3. With a row of many blunt spines.
67. Metatarsus of leg IV of male, thickness
0. Slender and unarmed.
 1. Swollen and armed with two longitudinal ventral rows of tubercles.
 2. Distally swollen in both sexes.
 3. Sinuous, thickened, with a row of tubercles.
 4. Proximally thickened, fusiform.
68. Distitarsus I, number of joints
0. Three.
 1. Two.
69. Basitarsus I, number of joints
0. Three.
 1. Two.
 2. One (as in *Zalanodius*, Fig. 23E).
 3. More than three.
70. Leg II of male, tarsal counts
0. Six or more.
 1. Five.
 2. Four.
 3. Three.
71. Tarsal counts leg III
0. Seven or more.
 1. Six.
 2. Five.
 3. Four.
72. Tarsal counts of leg IV
0. Seven or more.
 1. Six.
 2. Five.
 3. Four.
73. Tarsal process (pseudonychium, ps), presence
0. ps well developed.
 1. ps absent (as in *Voriax*, Fig. 13F).
74. Tubercles of scutum and legs I–IV
0. With short bristles.
 1. With very long bristles giving hirsute aspect.
75. Femur IV of male, dimorphic armature
0. Virtual cross-section of femur as a square, armature when present potentially distributed along four surfaces, but typically restricted to a retrolateral and a prolateral row.
 1. Virtual cross-section of femur as a hexagon, armature when present variedly disposed in rows along six surfaces.
76. Stigmatic area, shape
0. Elongate, with coxa IV running parallel to its axis.
 1. Very short, with coxa IV transverse to its axis.
77. Stigmatic area, posterior border
0. Straight or only very slightly concave.
 1. Deeply concave.
78. Stigmatic area, fusion to coxa
0. Discrete from coxa IV.
 1. Fused with coxa IV along most of their area of contact.
79. Stigmatic opening
0. Sessile.
 1. Placed on a discrete mound (as in *Tibangara*, Fig. 5B).
80. Stigmata, size
0. Small, width around 25–30% of trochanter IV width.
 1. Large, width around 50% of trochanter IV width.
81. Area surrounding stigmata
0. Convex, keeping the outline defined by edges of sternites and coxa.
 1. Receding, strongly concave.
82. Orientation of stigmata
0. Ventral.
 1. Ventroposterior.
 2. Posterior.
 3. Lateral.
83. Sternite II, lateral projection
0. Not projected laterally.
 1. Projected laterally into a lobe matching the apophysis of coxa IV.
 2. Projected laterally in a big apophysis.
 3. Projected laterally into a multiple-protuberance lobe matching the apophysis of coxa IV.
 4. Not projected but lateral thirds well defined by a ridge.
84. Sternite II, anterior projection
0. Not projected anteriorly.
 1. Projected anteriorly as a large semicircular lobe not covering the stigmata, but fusing with the coxal apophysis.
 2. Projected anteriorly as a very small lobe partially covering the stigmata.
 3. Projected anteriorly as a triangular lobe not covering the stigmata, and not fusing with the coxal apophysis.
85. Sternite II, posterior projection
0. Not projected posteriorly.

1. Posterior margin projected posteriorly across all its width as a big rectangular process.
86. Femora I–IV, colour pattern of basal third
 0. Same colour as distal two thirds.
 1. Much lighter, strongly contrasting with distal two thirds.
 2. Ringed.
87. Trochanter I–IV, colour relative to rest of legs
 0. Concolorous.
 1. Clearly lighter (Fig. 1C).
88. Mesotergal areas, colour relative to scutum background
 0. Somewhat darker, brown over light brown background.
 1. Concolorous, both very dark.
 2. Dark brown, sharply contrasting with yellow scutum background (Fig. 1C).
 3. Concolorous, both light tan.
89. Pedipalps, colour relative to chelicerae
 0. Concolorous.
 1. Clearly lighter, typically pale yellow vs. dark yellow.
 2. Clearly darker.
90. Ventral plate of penis, division
 0. Uniform, undivided (as in *Tricommatius*, Fig. 16C–E).
 1. Divided into two regions, a basal hammer and a distal lamina parva (LP; Fig. 3A–D).
 2. Macrosetae inserted directly on truncus, no VP.
91. Ensemble hammer, podium, and LP, arrangement
 0. LP undifferentiated, podium forming platform.
 1. LP fairly medium to small, podium slanted, not well defined, prepodium elongate.
 2. Podium entirely absent, prepodium extremely elongate, with dorsal furrow, VP in lateral view oblique relative to main penis shaft like a crooked walking-stick.
 3. Podium slanted but still defined, basal VP strongly projected dorsally, prepodium greatly enlarged.
 4. Podium slanted, prepodium and basal VP forming a spheroid.
 5. Podium well defined, forming an almost transverse kidney-like protuberance with basal VP, LP massive, medial instead of apical.
 6. LP large, hammer is only a callus in apical truncus, glans sac incumbent on horizontal podium.
 7. No definition of VP, LP, podium, or prepodium – glans arises straight from truncus.
 8. LP extremely thick, glans situated on a podium excavated on truncus.
92. Ventral plate, cleavage of distal border
 0. Entire.
1. With V-shaped cleft (Fig. 16C–E).
2. Only subtle concavity.
3. With deep, U-shaped cleft.
4. With small notch.
93. Ventrodistal bulge of truncus penis
 0. Undifferentiated
 1. Present as a *Brontotherium*-horn or kidney-shaped bifid projection (as in *Heteromeloleptes*, Fig. 30D).
 2. Present as a heart-shaped general swelling of truncus (Fig. 30C).
 3. Present as a V-shaped valley (as in *Pseudopachylus*, Fig. 30A).
 4. Present as apical paired bumps (Fig. 30B).
94. Ventral plate overlapping with distal truncus
 0. Not overlapping.
 1. Truncus reaching about half length of the VP.
 2. Truncus overlapping very little, only at base.
95. Truncus penis, presence of distal dorsal hyaline button
 0. Absent.
 1. Hyaline button present as a haematodocha.
 2. Button much reduced, only as soft folded area.
96. Ventral process of glans penis, reduction
 0. Present as a flabellum (Fig. 31A).
 1. Extremely reduced to a peg.
 2. Entirely absent.
 3. Present as a skirt (Fig. 31B–I).
97. Glans-sac, structure
 0. Soft, many-folded.
 1. Turgid sac.
 2. Balloon.
 3. Canal-shaped, rigid case.
 4. Gaping mouth.
98. Skirt, shape
 0. Gonyleptid flabellum – more or less reduced fan with stem entirely independent from stylus (as in *Discocyrtoides nigricans*, Fig. 31A).
 1. *Tibangara*-like – peacock's tail, with radiating branches and central pit (as in Gen. sp. W, Fig. 31B).
 2. *Bunostigma*-like – parabolic, erect, folded on the sides, with central pit (as in Gen. sp. Q, Fig. 31C).
 3. *Paratricommatus lockei*-like – acorn-shaped strongly folded.
 4. *Bissulla*-like – rectangular, deeply serrate, without pit (as in Gen. sp. AA, Fig. 31D).
 5. *Paratricommatus*-like – tricorn fan (Fig. 31E).
 6. *Spinopilar*-like – short stem, short and wide fan with individual barbels, each one deeply serrate and no pit (Fig. 31F).
 7. *Bresslavius*-like – globose base, erect small fan (Fig. 31G).
 8. *Pseudopachylus*-like – small erect square (Fig. 31H).

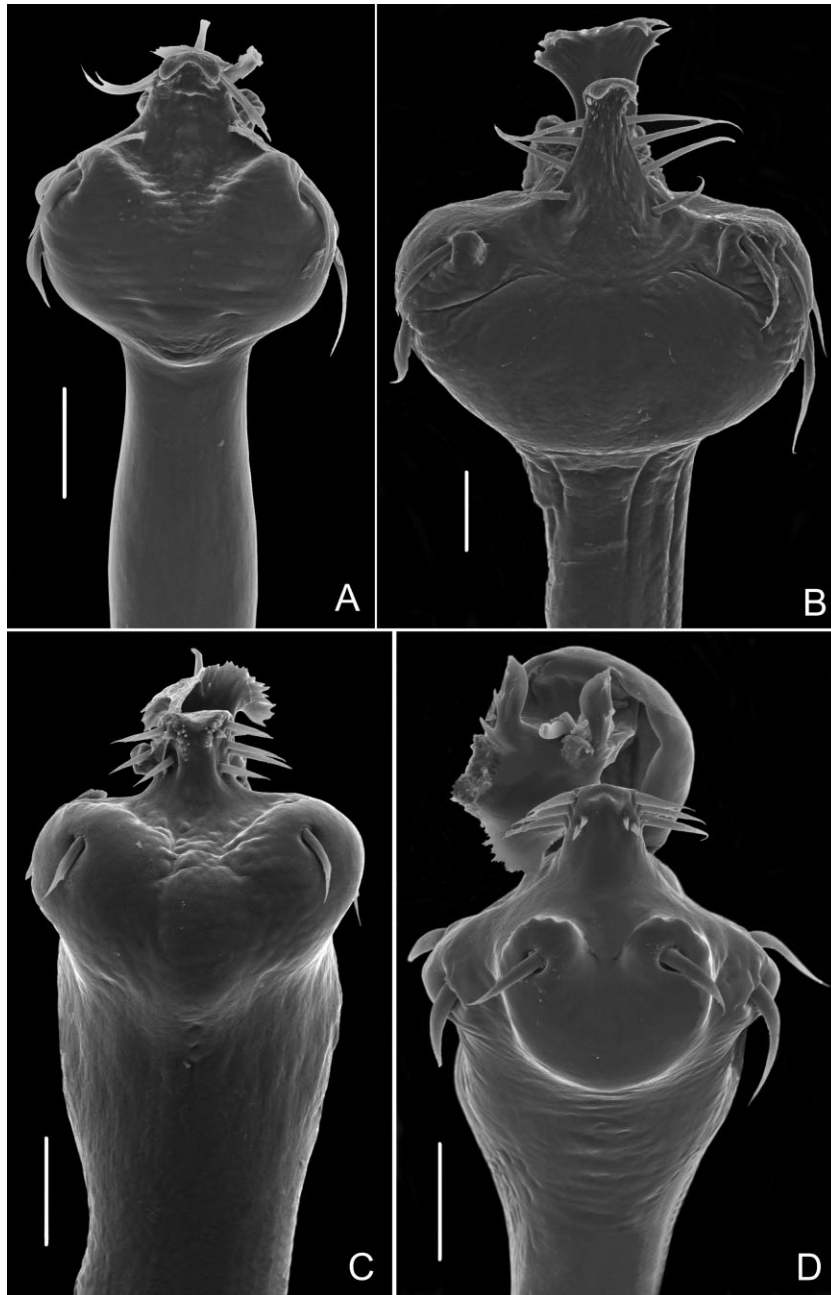


Figure 30. Cryptogeobiidae, distal part of penis, ventral view, showing lamina parva and varied conformations of ventrodistal bulge. A, *Pseudopachylus nigripes* (MNRJ 4768). B, Gen. sp. AA (MZSP 18090). C, Gen. sp. U (MNRJ 17554). D, Gen. sp. AC (MNRJ 7031). Scale bars = 0.1 mm (A), 0.05 mm (B–D).

9. *Heteromeloleptes*-like – with pair of bird-like wings and central wing-like lobe (as in *Heteromeloleptes*, Fig. 31I).
99. Mid-ventral skirt on stylus
0. Absent, only a flabellum, basally inserted and with stem may be present.
 1. Skirt present in the middle of stylus (synapomorphy for Cryptogeobiidae, Fig. 31B–I).
100. Stylus, position of insertion point
0. Apical at glans.
 1. Ventro-subdistal at glans.
101. Basic curvature of stylus
0. Slight, medial to ventral.
 1. Accentuate, medial to dorsal (stylus C-shaped).
 2. None, stylus straight.
 3. Stylus encased.

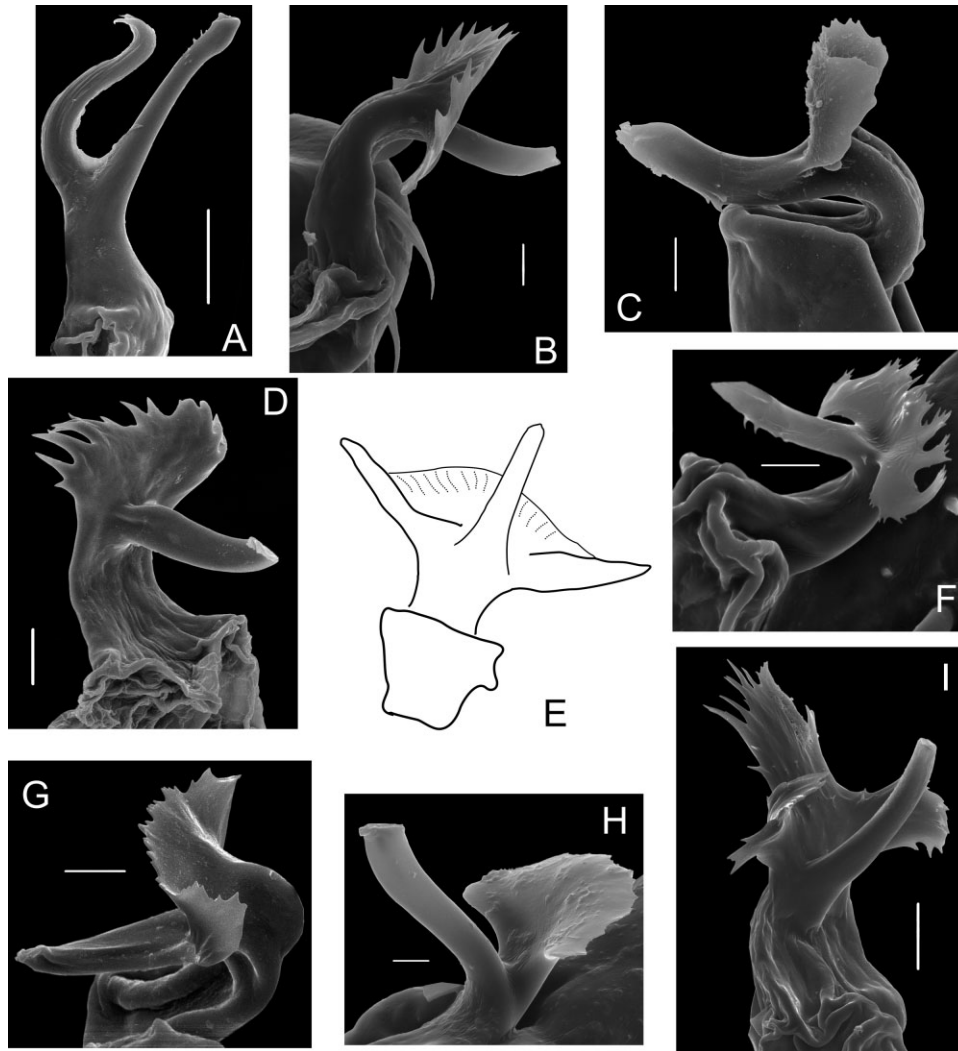


Figure 31. Cryptogeobiidae, detail of varied styli and flabella of glans penis compared with a Gonyleptidae with true ventral process of glans, varied views. A, *Discocyrtoides nigricans* (MNRJ 18884). B, Gen. sp. W (MNRJ 1977). C, Gen. sp. Q (MNRJ 7585). D, Gen. sp. AA (MZSP 18090). E, Gen. sp. H (MZSP 15747). F, Gen. sp. AE (MNRJ 4487). G, Gen. sp. M (MNRJ 17687). H, *Pseudopachylus nigripes* (MNRJ 4768). I, Gen. sp. AD (MNRJ 5592). Scale bars = 0.05 mm (A), 0.2 mm (D, I), 0.1 mm (B, C, F, G, H).

102. Stylus, shape
0. *Discocyrtus*-like, thin with apex slightly swollen.
 1. Thin, long, with apex abruptly bent.
 2. *Graphinotus*-like, thick, truncated.
103. LP, basic shape
0. Trapezoid with sides concave in gentle slope.
 1. Subrectangular (with sides straight).
 2. With neck plus two changes of curvature.
 3. Rectangular, but extremely narrow.
 4. Trapezoid more extreme, with sides more deeply concave.
104. Apical border of LP, aspect of folds
0. Smooth, without fold.
 1. With two widely spaced patches of scaly bristles connected by thin patch.
 2. With two large patches of scaly bristles closely connected (Fig. 30A, B).
 3. With simple stripe (Fig. 30D).
 4. With paired slopes (Fig. 30C).
105. E1–E2 – secondary macrosetae (E) of distal ventral plate (VP), arrangement
0. E1 and E2 minute, marginal on flange region.
 1. E1–E2 forming rectangle strongly displaced to ventral region of VP (as in all Cryptogeobiidae, Fig. 31A–D).
106. Rectangle of four macrosetae on ventral face of LP (E1 to E2), length of basal pair of setae
0. Short (as in *Heteromeloleptes*, *Zalanodius*, *Spinopilar*, Fig. 30D).

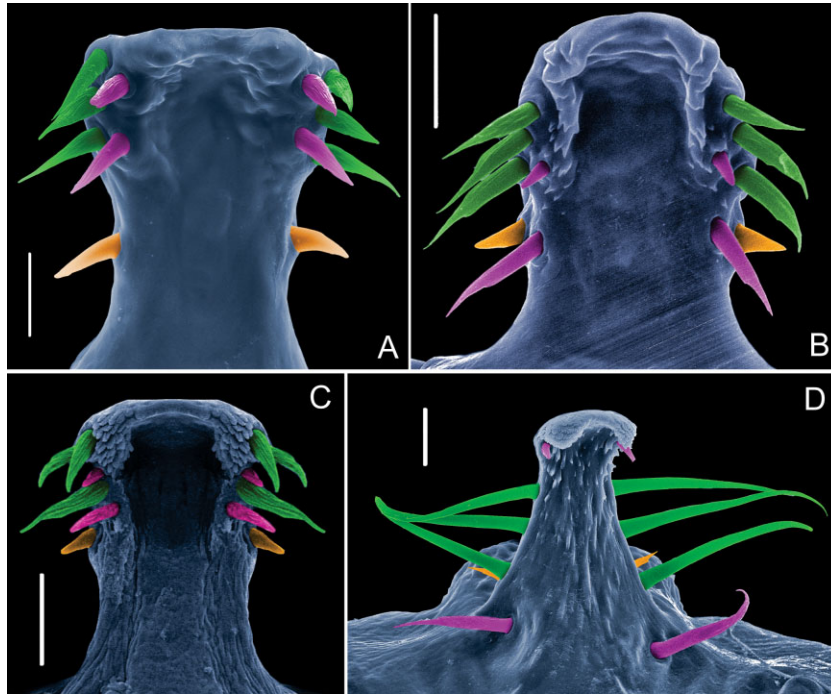


Figure 32. Cryptogeobiidae, details of the ventral surface of the lamina parva, showing the configurations of the rectangle of macrosetae. A, Gen. sp. AD (MNRJ 5592). B, *Taquara bicoloripes* (MNRJ 2218). C, Gen. sp. P (MNRJ 16192). D, Gen. sp. AA (MZSP 18090). Scale bars = 0.2 mm (A, B, C, D).

1. Long (Fig. 30A–C).
2. Macrosetae E absent.
107. Rectangle of four macrosetae on ventral face of LP, arrangement of basal pair of setae (E2)
 0. Close to the distal pair.
 1. Far from distal pair, pointing basally (as in *Tibangara*, *Lanesoares*, *Cryptogeobius*, Gen. sp. R, U, Fig. 30C).
 2. Extremely remotely placed, pointing distal (Fig. 30A, B).
 3. Macrosetae E absent.
108. Ventral plate, basal macrosetae (A and B)
 0. Fairly short and more or less straight.
 1. Very long and prostrate, roughly similar to Agoristenidae (as in Gen. sp. X).
109. Basal-most macrosetae of VP (A3), presence
 0. A1 to A3 present.
 1. only A1 and A2 present.
110. Macrosetae A1 to A3, arrangement relative to B
 0. Arched row close to the loop of VP.
 1. A1 on LP region, A2 on hammer.
 2. Both A1 and A2 in LP.
 3. Both A1 and A2, occasionally A3 inner on hammer.
 4. A1 and A2 on the fringe of LP.
111. Macroseta B, position
 0. Marginal on VP, close and aligned with A.
 1. Marginal on VP, aligned with A, but very far from them, closer to C3.
 2. Strongly displaced to ventral, at apex of hammer, close to A1–2.
 3. Same as 2, but much more proximal than A1–2.
112. Distal macrosetae of lateral border of LP (C1 to C3), length
 0. Much shorter than width of LP (Fig. 32A).
 1. About as long as LP width (Fig. 32B, C).
 2. Clearly longer than width of LP (Fig. 32D).
113. Macrosetae A, position
 0. Inserted on lateral border of VP in longitudinal row.
 1. Encircling VP as a girdle.
114. Ventral plate or ventral surface of penis, microsetae cover
 0. Glabrous, microsetae absent.
 1. Covered by one or two fields or clumps of microsetae of varied shapes (this appears to be a synapomorphy for a group of families, the Microsetata).
 2. With clumps of scale-spines on the laterodistal part only.
115. Styler cradle on dorsal side of LP
 0. Absent.
 1. Present.
116. LP, outline (as in lateral view)
 0. Slender, gently curved or almost erect.

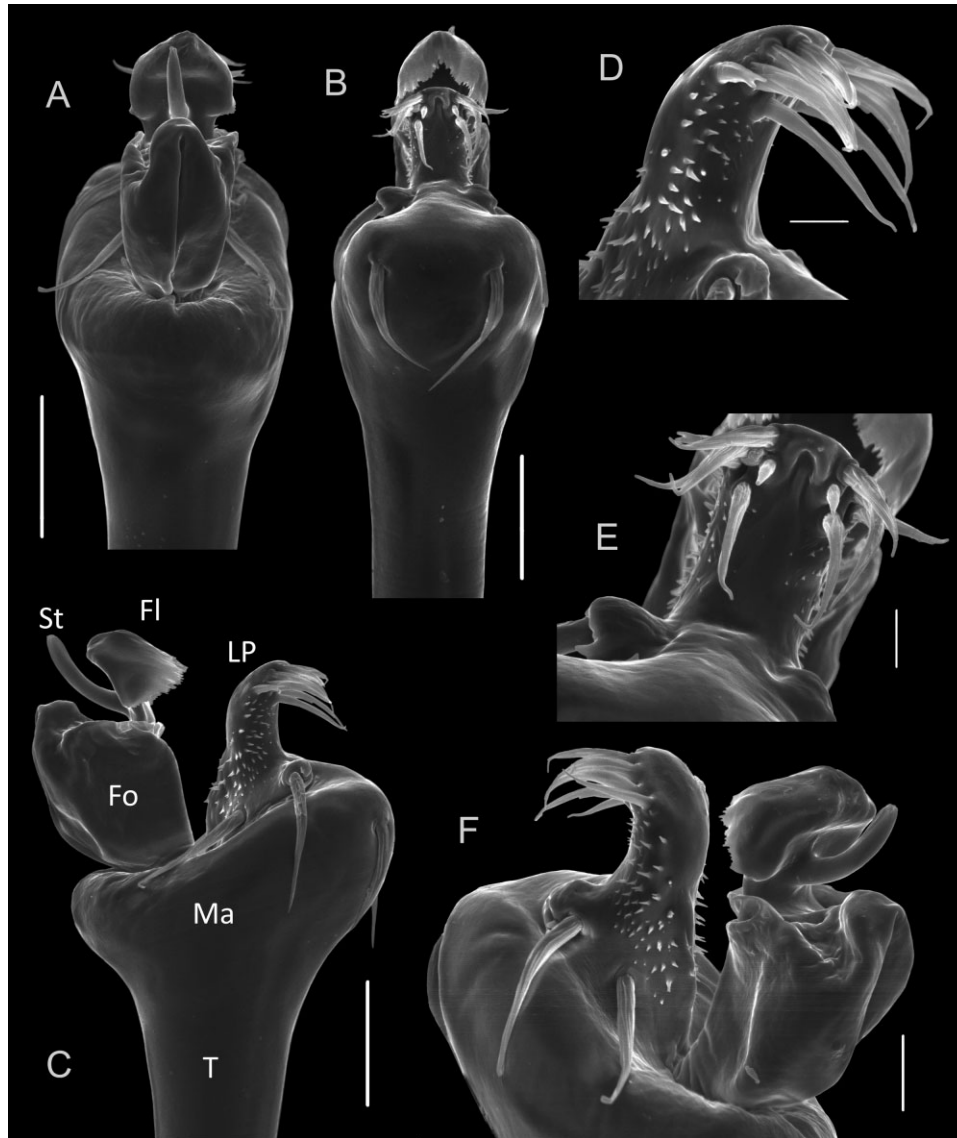


Figure 33. *Paratricommatus lockei* sp. nov., male paratype, MNRJ 7583, from Guapi-Açu. Male genitalia. A, distal part of penis, dorsal view; B, same, ventral view; C, same, lateral view. D, lamina parva, lateral view; E, same, ventral view; F, lamina parva and glans, dorsolateral view. Abbreviations: Fl, flabellum; Fo, follis ('glans'); LP, lamina parva; Ma, malleus; St, stylus; T, truncus. Scale bars = 50 μ m (A–C), 10 μ m (D, E), 20 μ m (F).

- | | |
|--|--|
| <ol style="list-style-type: none"> 1. Massive, angled. 2. Thin, pyramidal, gently curved at the apex. 3. Flattened, resting on projected hammer, separated from it by deep groove. 4. Folded to dorsal. <p>117. Ventral projection of hammer, using LP as parameter</p> <ol style="list-style-type: none"> 0. Hammer with subtle rounded ventral callus, making LP ventral (Fig. 3A–C). | <ol style="list-style-type: none"> 1. Ventral setiferous projection of hammer well developed, angular, making LP medial (Figs 3D, 33C). 2. Ventral setiferous projection of hammer also projected as a pair of buttocks or a boss. |
|--|--|

APPENDIX 2
MATRIX OF CHARACTER STATES FOR THE CLADISTIC ANALYSIS OF THE TRICOMMATINAE S.L.

Table with 2 columns: Genus/Species and Character State Matrix. Rows include Paramitraceras_sp., Globibunus_rubroformoratus, Eutimesius_sp., Incasarcus_dianae, Prostygynus_vestitus, Ampycus_telifer, Pseudopucrobia_mutica, Discocorythoides_nigricans, Triglochitura_curvispina, Soaresia_uncina, Camposicola_altifrons, Gen_sp_C, Vortiox_popeye, Tricommatius_giupponii, Tricommatius_pygmaeus, Tricommatius_brasiliensis, Gen_sp_A, Caramaschia_singularis, Gen_sp_B, Huralioides_sp., Gen_sp_F, Gen_sp_G, Gen_sp_D, Gen_sp_E, Bunostigma_singulare, Cryptogobius_clavittibalis, Cryptogobius_crassipes, Paratricommatius_colatinae, Paratricommatius_modestus, Gen_sp_H, Paratricommatius_mahnerti, Paratricommatius_melloleिताoi, Pseudophalanges_unicolor, Gen_sp_AD, Heteromeloletes_padbergi, Gen_sp_AC, Zalanodius_bicornutus, Zalanodius_hirsutus, Zalanodius_convexus, Zalanodius_latifemur, Spinopilar_ insignitus, Gen_sp_L.

APPENDIX 2 *Continued*

Spinopilar_armatipes	53110100000001-011111000010001000-1010002000300-121000100000000000002121100101000020000001107003167170??1??11120100?1
Gen_sp_I	512101000010001-011111000010001000-1010002000300-130000100000?0?0000?0?0000?100001?00?200000001101013?61010?1??112?10001
Spinopilar_armatus	51210100001000210111000010001000-1010002000300-1300001000010?0020401021100001?00?20000001104013?610102?1??112?10001
Gen_sp_J	51210100001000210111000010001000-1010002000300-13000010000?00000?0?0000?100001?00?2?00001104013?61010?1??112?10001
Spinopilar_friburguensis	512103000011402000111000010001000-1010002000300-13000010000100000040101110000?00?2??00001100013161010?1??1112110001
Gen_sp_K	512001000011402000111000010001000-1010002000300-13000010000000010000002030??1100001100020000001000131610102?10000112010001
Spinopilar_apiaensis	512103000011402000111000010001000-1010002000300-1300001000000000301011100?00?0000?100013?61010?1??112110010
Pararezendesius_huridus	5301010000200501-011111000010001?10-0010002001710-000021000100000070102210000?0?0??0?000001?0?0?3????????????????1?0??
Bresslausius_hirsutus	612101000010705001114011100010?0-1010001000700-0-0000300001200000?010211110?000?00000001?0?0?3????????????????1?0??
Gen_sp_O	612103000011070500111401110001010-1010001001700-0-0000100001000000?0??110?0?0?0?0000110?0113111??0?1??112?10010
Pinocchio_debilis	61010100001107050011124011100010?0-101000200040110-0000300001200000?0?0??11000010?000000011000131?1012??0?0?01000?0
Gen_sp_P	6011010000110705001112401100001020-1210000021710-0-00000100010?002010102210000101000000110002342101221100012010010
Gen_sp_M	61010?0001007050010344011100010?0-101000200030110-000030000120000001021100001100000000011000033710122??0?0?010010
Gen_sp_N	6101010000100705001114401110001010-10100020004011-00003000012000000?0??100010100000000011000033710121011001120100?0
Taquara_bicoloripes	51001100000002001221110000001010-0110002000900-0-00003000012?000002022100100000010011101600003121113110000321100?0
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Gen_sp_Q	51001100000002001211200000010?0-0110000000?0??100000000011210020001?1100?0?0??210012000033211121311000032110030
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Arruda_pectinata	511101000000020121110000001?0-?0?0002000401??0?0?01000010?002?01032?00?0??0?0?1?0?0?3????????????????1?0??
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Camarana_rousetti	51100000000020121110000000?0?0-00?000200040110-00001000010?0000?010220000?000001?0?0?0?3????????????????1?0??
Camarana_flavipalpi	5101010000000200122110000001010-101000200040110-00003000012?0000?010220000?0000010001111600003121112??1100112110010
Camarana_umica	5101010000000200123210000001000-001000000040110-00003000012?0000?010220000?000001000111160?03????????????1?0??
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Lanesoares_inermis	51010100000002001231500000010?0-001000000040100-00003000012000000202210010?10001000111600003?21112??1100112110020
Pseudopachylus_alticola	5300010000004040012310000000010?0-0010000000040100-0000300001200000010221001001000100001022100?13110011201012?
Pseudopachylus_martensi	530001000000404001331000?00000113-0010001001200-0-000030000120000002122100100101?100001111013081011??1?0?0?110?22
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Pseudopachylus_nigripes	5300010000-0413-01333200000000113?0010001001200-0-00003000012000000202210010011010000101030130810114211132110122
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Tibangara_nephelina	5300010000-0413-01451000000001?3?0010001001200-0-0000300001000000121221001001010011?1100003081011??1?0?0?110???
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Gen_sp_V	5300010010-0413-01431000000001?3?001000000040100-0000300001200000?12133100100101?110012210201301101141101110022
Gen_sp_W	5300010010-0413-01431000000001?3?001000000040100-0000300001200000?12133100100101?110012210201301101141101110022
Gen_sp_T	5300010010-0413-01431000000001?3?001000000040100-0000300001200000?12133100100101?110012210201301101141101110022
Tibangara_cocciensis	5300010010-0413-01431000000001?3?001000000040100-0000300001200000?12133100100101?110012210201301101141101110022
Bissulla_paradoxa	5300010010-0413-01331000000001?3100100010001000-0000300001200000?12133100100101?110012210201301101141101110022
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