

# Foveavelia, a new South American genus of Veliinae (Hemiptera: Heteroptera: Veliidae)

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**Background.** Semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha) are worldwide distributed and play fundamental roles in limnic ecosystems. They are the most successful group of organisms to occupy the air-water interface, are important models to study ecology and evolution, and can be relevant tools in biomonitoring. Veliidae is the second most speciose family of semiaquatic bugs, but it and some of the included subfamilies and genera are artificial sets based on plesiomorphies. One of these non-monophyletic entities is Paravelia Breddin, 1898, the largest genus in the subfamily Veliinae. Results. In an effort to better classify the Veliinae, we describe Foveavelia to hold five South American species previously placed in *Paravelia*. The new genus is characterized by the following combination of features: the unusual coarse cuticular punctures throughout the thorax and abdomen; the pair of small, frosty, pubescent areas formed by a very dense layer of short setae on the anterior lobe of the pronotum; the fore tibial grasping comb present only in males; the middle tibia with a row of elongate dark-brown trichobothria-like setae on the posterior third, decreasing in size distally; the macropterous specimens with the apical macula of the forewings elongate and slightly constricted at mid-length, reaching the wing apex; and the male proctiger with a pair of anterodorsal projections. Besides the description, a key to the species of Foveavelia is provided, accompanied by illustrations and a distribution map.

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#### 1 Foveavelia, a new South American genus of Veliinae (Hemiptera:

2 Heteroptera: Veliidae)

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14	Abstract
15	<b>Background.</b> Semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha) are worldwide
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17	of organisms to occupy the air-water interface, are important models to study ecology and
18	evolution, and can be relevant tools in biomonitoring. Veliidae is the second most speciose
19	family of semiaquatic bugs, but it and some of the included subfamilies and genera are artificial
20	sets based on plesiomorphies. One of these non-monophyletic entities is Paravelia Breddin,
21	1898, the largest genus in the subfamily Veliinae.
22	Results. In an effort to better classify the Veliinae, we describe Foveavelia to hold five South
23	American species previously placed in Paravelia. The new genus is characterized by the
24	following combination of features: the unusual coarse cuticular punctures throughout the thorax
25	and abdomen; the pair of small, frosty, pubescent areas formed by a very dense layer of short
26	setae on the anterior lobe of the pronotum; the fore tibial grasping comb present only in males;
27	the middle tibia with a row of elongate dark-brown trichobothria-like setae on the posterior third,
28	decreasing in size distally; the macropterous specimens with the apical macula of the forewings
29	elongate and slightly constricted at mid-length, reaching the wing apex; and the male proctiger
30	with a pair of anterodorsal projections. Besides the description, a key to the species of
31	Foveavelia is provided, accompanied by illustrations and a distribution map.
32	
33	Introduction
34	Veliidae (Hemiptera: Heteroptera: Gerromorpha) is a family of small to medium-sized insects
35	that live essentially on the surface of the water. Some of them occur on stagnant waters, such as
36	lakes and puddles, while others occupy rivers and streams, and a few can be found in terrestrial
37	environments relatively far from the water (Schuh & Slater, 1995). Andersen (1982) established
38	a phylogeny for Veliidae based on morphology and proposed the division into six subfamilies:
39	Ocellloveliinae, Haloveliinae, Microveliinae, Perittopinae, Rhagoveliinae and Veliinae.
40	Subsequently, Damgaard (2008) proposed a phylogeny for Gerromorpha based on morphological
41	and molecular data. He demonstrated that the subfamilies Microveliinae and Haloveliinae were
42	actually closer to Gerridae than to Veliidae, and found low support for other clades of Veliidae,
43	such as the subfamily Veliinae.



14	More recently, Armisén et al. (2022) obtained a phylogeny of the Gerromorpha based on	
<del>1</del> 5	transcriptomes and corroborated with Haloveliinae + Microveliinae forming a clade sister to	
46	other Gerridae, leaving Veliidae with only four subfamilies. Within Veliidae, the same authors	
17	did not recover the monophyly of Veliinae. Currently, this subfamily includes 11 valid genera,	
<b>1</b> 8	eight of which occur in America: Altavelia D. Polhemus & Moreira, 2019; Callivelia D.	
19	Polhemus, 2021; Oiovelia Drake & Maldonado-Capriles, 1952; Paravelia Breddin, 1898;	
50	Platyvelia J. Polhemus & D. Polhemus, 1993; Steinovelia J. Polhemus & D. Polhemus, 1993;	
51	Stridulivelia Hungerford, 1929; and Veloidea Gould, 1934. The other three genera that occur in	
52	the Palearctic, Afrotropical, and Indo-Malay regions are Angilia Stål, 1865; Angilovelia	
53	Andersen, 1981; and Velia Latreille, 1804.	
54	The Neotropical genus Paravelia is the most speciose of the Veliinae, with 51 valid	
55	species (Rodrigues & Moreira, 2022; Rodrigues, Moreira & Morales, 2022). The paraphyly of	
56	this genus was hypothesized by different authors (e.g., J. Polhemus & D. Polhemus, 1993;	
57	Rodrigues et al., 2014; Rodrigues & Moreira, 2016; D. Polhemus, 2021), but without a	
58	phylogenetic basis. Armisén et al. (2022) recovered the genus as polyphyletic, but assessing the	
59	relationships among its species is still premature, because only a few representatives were	
30	included in their analysis.	
31	The study of Veliinae species and their respective type specimens allowed us to define a	
62	distinct group of five species within Paravelia that share unique characteristics. The new genus	
3	Foveavelia is here proposed for this group, based mainly in a distinct feature: the coarse cuticular	
64	punctures found throughout the body. We also present an illustrated taxonomic key and a	
35	distribution map for the included species.	
66		
67	Materials & Methods	
86	Museum visits. Pinned specimens were examined at the following public collections: <b>DPIC</b> -	
69	Departamento de Parasitologia, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil;	
70	INPA - Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; MZUSP - Museu de	
71	Zoologia, Universidade de São Paulo, São Paulo, Brazil; <b>NMNH</b> - National Museum of Natural	
72	History, Smithsonian Institution, Washington D.C., United States.	
73	Morphological study. All measurements are given in millimeters. Antennomeres and abdomina	
74	segments numbers are expressed as Roman numerals. We used standard entomological	



75 techniques to examine the morphology of the specimens used in this study. Abdominal segment VIII and genital capsule of the males were removed using forceps and an entomological pin, 76 77 without the need for clarification. Photographs have been obtained using a Leica DFC420 78 camera attached to a LeicaM165C binocular microscope, processed with the Leica Application Suite V3.7.0, and stacked using Auto-Montage. Scanning electron microscopy photographs 79 (Figs. 5–10) have been provided by Dr. Silvia Mazzucconi. All final figures have been prepared 80 using Adobe Photoshop CS6. 81 82 **Nomenclatural acts.** The electronic version of this article in Portable Document Format (PDF) 83 will represent a published work according to the International Commission on Zoological 84 Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and 85 86 the nomenclatural acts it contains have been registered in ZooBank, the online registration 87 system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the 88 89 prefix http://zoobank.org/. The LSID for this publication is: 90 [urn:lsid:zoobank.org:pub:DAAB68B0-7AB5-4D92-AAE8-A9051CD9EC11]. The online version of this work is archived and available from the following digital repositories: PeerJ, 91 92 PubMed Central SCIE and CLOCKSS. 93 **Results** 94 Foveavelia Rodrigues & Moreira, new genus 95 (Figs. 1–6, 8) 96 97 **Type species.** Velia hungerfordi Drake & Harris, 1933, by present designation. 98 99 **Diagnosis.** Body length 4.80–6.50 mm; body vestiture composed of moderately dense, erect, 100 thin, brown setae (Figs. 1, 4, 6); anterior lobe of pronotum with a pair of small, frosty, pubescent 101 areas formed by a very dense layer of short setae (sometimes indistinct) (as in Fig. 1A); 102 macropterous specimens with apical macula of forewings elongate and slightly constricted at mid-length (Figs. 1A–C, 4E, 6A, 6C); meso- and metasterna each with a pair of tubercles, these 103 104 tubercles meeting at suture, forming a cavity between them; abdominal mediotergites and sterna



105	(except sternum VII) with numerous suboval, coarse cuticular punctures (Fig. 2); male proctiger	
106	with a pair of anterodorsal projections (Figs. 3E-H, 5H).	
107		
108	Description	
109	Medium-sized veliids; macropterous or brachypterous (micropterous and apterous forms	
110	unknown so far); ground color brown, covered by golden pubescence, with weak yellowish	
111	annulations on femora. Body moderately robust, length 4.80-6.50 mm; general characteristics	
112	and size not sexually dimorphic (Figs. 1, 6), except for F. dilatata (Fig. 4).	
113	Head: Declivant anteriorly, not recessed into pronotum, with usual three pairs of trichobothria	
114	and impressed median line; posterodorsal region with a pair of narrow, convergent, impressed	
115	lines between impressed median line and a pair of elliptical indentations (Fig. 2A); gula and	
116	bucculae with several suboval, coarse punctures; gular region visible (Figs. 6B, 6D-E). Eyes	
117	globose, separated by more than an eye width, slightly removed from anterior margin of	
118	pronotum; ocular setae present. Labium extending onto anterior region of metasternum; segment	
119	I almost reaching posterior margin of bucculae; segments I and IV subequal in length, longer	
120	than segment II; segment III about 7 times as long as II (Fig. 1D). Antennae densely covered by	
121	golden pubescence and long brown setae; antennomere I thickest, curved laterally; II slightly	
122	thicker than III-IV; III-IV subequal in width; IV filiform (as in Fig. 1).	
123	Thorax: Pronotum long, completely covering meso- and metanota; covered by fine pubescence	
124	intermixed with elongate brown setae; collar distinct, delineated by coarse punctures; anterior	
125	lobe with pair of small, frosty, pubescent areas formed by a very dense layer of short setae (Figs.	
126	1C, 4A-B, 4D-E, 6C) (sometimes indistinct, as in Figs. 1A-B, 6A); humeri raised, prominent;	
127	posterior lobe with numerous punctures, without rounded or finger-like process at posterior	
128	margin. Forewing with four closed cells, brown, with white macula at basal cells adjacent to	
129	costal margin and at wing apex, without other marks centrally (Figs. 1A-C, 4E, 6A, 6C); some	
130	brachypterous specimens lacking basal macula (Fig. 4C). Thoracic pleura with numerous	
131	suboval, coarse punctures (Figs. 6B, 6D-E). Meso- and metasterna each with a pair of tubercles;	
132	tubercles meeting at suture, forming a cavity between them. Metasternum with posterior margin	
133	convex; metasternal scent gland opening (= omphalium) obscure. Legs moderaly stout, lacking	
134	prominent spines or teeth, light-brown at base, brown distally, with a faint light-brown annulus	
135	on femora, hind femur slightly incrassate, grasping comb occupying approximately half or less	



136 of male fore tibial length, absent in female; middle tibia with a distally decreasing row of 137 elongate dark-brown trichobothria-like setae on posterior third; all tarsi three segmented; 138 segment I shortest; fore leg with segment III longer than II; middle and hind legs with segment II 139 longer than III; claws long, slender, slightly curved. **Abdomen**: Numerous suboval, coarse punctures, except for laterotergites, sterna II–VI adjacent 140 141 to lateral margins, and whole sternum VII (Figs. 2C, 2F) and segment VIII; prominent paired longitudinal carinae present along mediotergites II-III and basally on mediotergite IV (visible 142 with wings open or removed) (Fig. 2C). Sides of abdominal sterna with narrow, roughly ovate 143 144 (sometimes longitudinal) impressed furrows (= striae sensu D. Polhemus 2021) (Figs. 6D–E). Male terminalia of moderate size; black denticles absent; proctiger with a pair of anterodorsal 145 projections (Figs. 3E–H, 5H), lateral lobes without angular projections (Fig. 5F); parameres 146 147 symmetrical, slender, curved (Figs. 3E–H, 5E). Female abdominal segment VIII on same plane as VII; first gonocoxae exposed, plate-like; black denticles absent; proctiger globose, button-like, 148 149 longer than wide (Figs. 6B, 6D). 150 **Etymology.** The generic name *Foveavelia* is derived from *fovea* (Latin), meaning pit, referring 151 to the coarse cuticular punctures present throughout the body, and Velia, the nominate genus of the family. Gender feminine. 152 153 **Distribution.** The genus is distributed throughout South America east of the Andes, with 154 published records from Guyana, Suriname, French Guiana, Brazil, Paraguay and Argentina (Fig. 155 8). **Natural history.** Three of the five species here included in *Foveavelia* are known by one of the 156 157 sexes only, and two of them by just one specimen. Thus, it is a relatively rare genus in 158 collections and not many details are known about its habitat and biology. 159 160 Foveavelia amapaensis (Rodrigues, Moreira, Nieser, Chen & Melo, 2014) n. comb. (Figs. 1A, 3A, 3E, 6E, 8) 161 162 Paravelia amapaensis Rodrigues, Moreira, Nieser, Chen & Melo in Rodrigues et al., 2014: 5–6 163 (original description). 164 **Diagnosis.** Body length 4.80. Distance between basal and apical forewing maculae greater than 165 166 length of basal macula (Fig. 1A). Pair of rounded lobes on male abdominal sternum VII almost at



- same level of posterior margin (Fig. 3A). Male proctiger with a pair of non-bilobed projections
- anterodorsally. Male paramere not widened on distal half (Fig. 3E).
- 169 Type locality. Brazil: Amapá: Santana, Porto Santana, I.C.O.M.I.
- 170 **Repository.** The male holotype was deposited at the Museu Nacional, Universidade Federal do
- 171 Rio de Janeiro, Rio de Janeiro, Brazil. However, it was destroyed together with most of the
- entomological collection of the institution in the 2018 fire (Kury *et al.*, 2018).
- 173 **Published records.** Brazil: Amapá (Rodrigues *et al.*, 2014).
- 174 **Distribution.** This species is known only from the type-locality (Fig. 8). The acronym
- 175 I.C.O.M.I. refers to "Indústria e Comércio de Minérios S/A", a mining company that was
- 176 contracted by the government of the state of Amapá in the 1950s to build an ore loading dock at
- 177 Porto Santana, on the estuary of the Amazon River (Bastos, Valente & Oliveira, 2021).
- 178 **Discussion.** This species was described based solely on the male holotype and some structures
- were not examined, either because the specimen was glued to a paper card or because it was no
- possible to dissect the male abdominal segment VIII. The diagnostic features used here to
- separate it from congeners need to be better studied when more specimens become available,
- since variations are expected. In the original description, the authors neglected the pair of small
- lobes present near the posterior margin of male abdominal sternum VII (Fig. 3A), which are
- similar to those of *P. bilobata* (Fig. 3B).

- 186 Foveavelia anta (Mazzucconi, 2000) n. comb.
- 187 (Figs. 2, 3F, 8)
- 188 *Paravelia anta* Mazzucconi, 2000: 130–134 (original description).

- 190 **Diagnosis** [based on original description]. Body length 5.40–5.70. Distance between basal and
- 191 apical forewing maculae greater than length of basal macula. Male fore tibial grasping comb
- occupying 1/6 of the tibial length. Male abdominal sternum VII with a pair of medial gibbosities
- 193 (see Mazzucconi 2000, page 131, fig. 10). Male proctiger with a pair of distinct, divergent,
- 194 spinose projections anterodorsally (Fig. 3F).
- 195 **Type locality.** Argentina: Salta: Anta, 50 km East of Las Lajitas.
- 196 **Repository.** Museo Argentino de Ciências Naturales "Bernardino Rivadavia", Buenos Aires,
- 197 Argentina.



Published records. Argentina: Salta (Mazzucconi, 2000). Paraguay: Concepción (Mazzucconi, 2000).
Distribution. The two records of this species are located in the Río de La Plata basin, in southern South America (Fig. 8).

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- 203 Foveavelia bilobata (Rodrigues, Moreira, Nieser, Chen & Melo, 2014) n. comb.
- 204 (Figs. 1B–D, 3B–D, 3G, 8)
- 205 Paravelia bilobata Rodrigues, Moreira, Nieser, Chen & Melo in Rodrigues et al., 2014: 8–10
- 206 (original description).

- 208 **Diagnosis.** Body length 5.03–5.07. Distance between basal and apical forewing maculae greater
- than length of basal macula (Figs. 1B–C). Male fore tibial grasping comb occupying 1/4 of tibial
- 210 length. Pair of rounded lobes on male abdominal sternum VII extended posteriorly (Fig. 3B).
- 211 Male proctiger with a pair of bilobed projections anterodorsally. Male paramere slightly widened
- 212 on distal half (Fig. 3G).
- 213 Type locality. Brazil: Mato Grosso: Nova Xavantina, Reserva Biológica Municipal Mário Viana
- 214 (Parque Municipal do Bacaba), Córrego Bacaba.
- 215 **Repository.** DPIC.
- 216 **Published records.** Brazil: Ceará and Mato Grosso (Rodrigues *et al.*, 2014; Rodrigues &
- 217 Moreira, 2022).
- 218 **Distribution.** This species has been recorded from the Caatinga and Cerrado biomes in
- 219 northeastern and central-western Brazil, respectively. Here, we extend its distribution
- considerably to the west, based on material from the Colombian Amazon (Fig. 8).
- **Discussion.** We examined a macropterous female (Figs. 6C–D) from northeastern Brazil
- deposited in the NMNH that most likely belongs to this species. However, because the sample
- 223 lacked a male for studying the terminalia and given that F. amapaensis and F. bilobata are very
- similar, we refrained from definitely assigning such female to the latter species.
- 225 Type material examined. HOLOTYPE: BRAZIL, Mato Grosso, Nova Xavantina, Parque
- 226 Municipal do Bacaba, Córrego Bacaba, 14°43'14.80"S, 52°21'35.63"W, 11.X.2003, S.O.
- 227 Pagioro col. (macropterous of, DPIC). PARATYPE: **Mato Grosso**, Córrego da Mata, quarta

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- 228 ordem, 15°01'32"S, 52°26'29"W, 17.XI.2005, H.S.R. Cabette *et al.* col. (1 macropterous ♂,
- 229 MZUSP).
- 230 Additional material examined. COLOMBIA, Amaz. [=Amazonas], Leticia, III-12-15-1969, P.
- 231 & P. Spangler (1 macropterous ♂, NMNH).

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- 233 Foveavelia dilatata (J. Polhemus & D. Polhemus, 1984) n. comb.
- 234 (Figs. 3H, 4–5, 8)
- 235 Paravelia dilatata J. Polhemus & D. Polhemus, 1984: 498 (original description).

- **Diagnosis.** Body length 5.35–6.50. Sexually dimorphic; pronotum distinctly widened anteriorly
- in the male (Figs. 4D–E), but not in the female (Figs. 4A–B). Male fore tibial grasping comb
- 239 male occupying almost half of tibial length. Forewing basal macula of macropterous specimens
- short, roughly ovate (Fig. 4E). Male abdominal segment VIII poorly sclerotized; posterodorsal
- 241 margin almost straight medially; posterolateral corners rounded, slightly extended posteriorly;
- 242 posterolateral margin excavated; posteroventral margin narrowed centrally, rounded (Figs. 5A–
- 243 C). Male abdominal sternum VII with a weak median carina extending along segment, without
- rounded lobes posteriorly. Male proctiger with a pair of spinose anterodorsal projections,
- 245 directed laterally (Figs. 3H, 5H).
- 246 **Type locality.** Suriname: Para: Coesewijneproject, 12 km West of Saramacca-brug.
- **Repository.** Zoölogisch Museum, Rijksuniversiteit te Utrecht, Utrecht, The Netherlands.
- 248 Published records. Brazil: Amazonas, Pará (J. Polhemus & D. Polhemus, 1984; Pereira &
- 249 Melo, 2007; D. Polhemus, 2014; Rodrigues *et al.*, 2014; Rodrigues & Moreira, 2016; dos Santos
- et al., 2021). French Guiana: Saint-Georges (Armisén et al., 2022). Guyana: Upper Demerara-
- Berbice (D. Polhemus, 2014). Suriname: Para (J. Polhemus & D. Polhemus, 1984).
- **Distribution.** This species is distributed from the Guianas to the northern portion of the
- 253 Brazilian Amazon (Fig. 8).
- 254 **Discussion.** This species was described based on brachypterous specimens from Suriname and
- 255 Brazil (J. Polhemus & D. Polhemus, 1984). Rodrigues et al. (2014) illustrated the macropterous
- 256 male, and Rodrigues & Moreira (2016) illustrated the brachypterous female. The size and shape
- of the forewing maculae change according to the wing condition. In macropterous specimens, the
- basal and apical maculae are larger; the basal macula is roughly ovate and the apical macula is



- elongate and slightly constricted at mid-length (Fig. 4E). The maculae can be smaller and fainter
- in brachypterous specimens (Figs. 4A–B, 4D); the basal macula, when present, is oval, and the
- apical macula can be small and rounded (Fig. 4B, 4D) or display the typical shape seen in
- 262 macropterous specimens (Fig. 4C).
- 263 Type material examined. PARATYPES: BRAZIL, Amazonas, Reserva Ducke, 25 km NNE
- 264 Manaus, 120 m, July 21, 1973, R.T. Schuh / impounded area in forest stream / Paratype
- 265 Paravelia digitata J.T. & D.A. Polhemus / J.T. Polhemus Collection 2014 C.J. Drake Accession
- 266 (1 brachypterous ♀, NMNH).
- 267 Additional material examined. BRAZIL, Amazonas: Igarape [=Igarapé] da Anta, Reserva
- 268 Ducke, 25 km NE of Manaus, 60 m, 24.5°C, 25 August 1989, CL2472, D.A. & J.T. Polhemus (4)
- brachypterous  $\circlearrowleft$ , 3 brachypterous  $\circlearrowleft$ , NMNH); Manaus, Reserva Florestal Adolpho Ducke,
- poça temporária na trilha para o igarapé Barro Branco, 02°53'S, 59°58'W, 27.XI.2012, U.G.
- 271 Neiss col. (1 brachypterous  $\stackrel{\circ}{+}$ , MZUSP); Barcelos, Serra do Aracá, Igarapé Ataiana, tributário
- 272 do Rio Negro, 00°88'56.57"S, 62°54'13.90"W, 10.VIII.2009, N. Hamada, R.L. Ferreira-Keppler,
- 273 A.M.O. Pes & C.A.S. Azevêdo col. (1 macropterous  $\sqrt[3]{}$ , INPA).

- 275 Foveavelia hungerfordi (Drake & Harris, 1933) n. comb.
- 276 (Figs. 6A–B, 8)
- 277 Velia hungerfordi Drake & Harris, 1933: 46 (original description).
- 278 Paravelia hungerfordi: J. Polhemus 1976: 512 (changed combination).

- 280 **Diagnosis.** Body length 4.80. Distance between basal and apical forewing maculae smaller than
- 281 the length of the basal macula (Fig. 6A).
- 282 **Type locality.** In the original description, the authors mentioned only "Chapada, Brazil", without
- additional data. The locality very likely corresponds to Chapada do Guimarães, state of Mato
- 284 Grosso, and the type material was probably collected by Herbert Huntington Smith (Moreira et
- 285 *al.*, 2011).
- **Repository.** Carnegie Museum of Natural History, Pittsburgh, United States.
- **Published record.** Brazil: Mato Grosso (Drake & Harris, 1933).
- 288 **Distribution.** Known only from the type-locality in central-western Brazil (Fig. 8).



- **Discussion.** Drake & Harris (1933) described this species based on two female specimens.
- 290 Because only the type series is known, the comparison with males of other species is not
- possible. Mazzucconi (2000) provided a redescription of this species and compared it with F.
- 292 anta. She distinguished the two based mainly on the length and width of the body, the shape of
- 293 the anterolateral margin of the pronotum, and the size of the forewing maculae. Female
- 294 Foveavelia are very similar to each other, and the condition of the forewing maculae is the only
- 295 viable character to identify *F. hungerfordi*.
- **Type material examined.** PARATYPE: BRAZIL, **Mato Grosso**: Chapada, Brazil, Acc. No.
- 297 2966, Paratype Velia hungerfordi D&H, CJ Drake Coll. 1956, Velia hungerfordi D&H. (1 \subseteq
- 298 macropterous NMNH).

#### 300 Key to the species of Foveavelia

- 301 Foveavelia amapaensis and F. bilobata are known only from the male, whereas F. hungerfordi is
- 302 known only from the female. As in other Neotropical Veliinae genera, males should be
- prioritized for identification purposes, as they usually display the most informative diagnostic
- 304 features.

- 306 1. Distance between basal and apical forewing maculae in macropterous specimens smaller than
- 307 length of basal macula (Fig. 6A).....*F. hungerfordi*
- 308 Distance between basal and apical forewing maculae in macropterous specimens greater than
- 309 length of basal macula (Figs. 1A–C, 4E).....2
- 2. Pronotum sexually dimorphic, widened anteriorly in the male (Figs. 4D–E) but not in the
- 311 female (Fig. 4A–B); male fore tibial grasping comb occupying almost half of tibial length; male
- 312 proctiger with a pair of small, spinose, laterally directed, anterodorsal projections (Figs. 3H,
- 313 5H).....*F. dilatata*
- Pronotum not sexually dimorphic, not widened anteriorly (Figs. 1A–C); male fore tibial
- 315 grasping comb occupying 1/6–1/4 of tibial length; male proctiger with pair of distinct, upward
- 316 directed, anterodorsal projections, (Figs. 3E–G).....3
- 3. Male abdominal sternum VII with a pair of medial gibbosities, without rounded lobes at
- 318 posterior margin; male proctiger with a pair of long, lateral, divergent spines on anterodorsal
- 319 region (Fig. 3F)..... *F. anta*

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- Male abdominal sternum VII without pair of medial gibbosities, with a pair of rounded lobes at
- or near posterior margin (Figs. 3A–B); male proctiger with a pair of lateral, almost parallel
- 322 projections on anterodorsal region (Figs. 3E, 3G).....4
- 4. Pair of rounded lobes on male abdominal sternum VII almost at same level of posterior margin
- 324 (Fig. 3A); projections of male proctiger not bilobed (Fig. 3E); paramere not widened on distal
- 325 half (Fig. 3E)..... F. amapaensis
- Pair of rounded lobes on male abdominal sternum VII extended posteriorly (Fig. 3B);
- projections of male proctiger bilobed (Fig. 3G); paramere slightly widened on distal half (Fig.
- 328 3G)..... F. bilobata

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#### Discussion

- 331 After examining all described Veliinae from the Neotropical region to study the phylogenetic
- relationships of *Paravelia*, it was possible to define a set of features shared by only five species
- here included in the new genus Foveavelia: F. amapaensis (Rodrigues, Moreira, Nieser, Chen &
- 334 Melo, 2014) **n. comb.**, F. anta (Mazzucconi, 2000) **n. comb.**, F. bilobata (Rodrigues, Moreira,
- 335 Nieser, Chen & Melo, 2014) **n. comb.**, *F. dilatata* (J. Polhemus & D. Polhemus, 1984) **n. comb.**,
- and F. hungerfordi (Drake & Harris, 1933) **n. comb.** (see Table 1). Foveavelia is defined by the
- following combination of characteristics: (1) the unusual coarse cuticular punctures found
- throughout the thorax and abdomen (Fig. 2); (2) the pair of small, frosty pubescent areas formed
- by a very dense layer of short setae on anterior lobe of the pronotum (Figs. 1A, 4A–B, 4D–E);
- 340 (3) the fore tibial grasping comb present only in males, occupying 1/4 (Fig. 1D) to half of the
- 341 fore tibial length; (4) the middle tibia with a row of elongate dark-brown trichobothria-like setae
- on the posterior third, decreasing in size distally; (5) the macropterous specimens with the apical
- macula of the forewings elongate and slightly constricted at mid-length, reaching the wing apex;
- 344 (Figs. 1A–C, 4E, 6A, 6C); (6) the meso- and metasterna each with a pair of tubercles, these
- tubercles meeting at suture, forming a cavity between them (Fig. 1D); (7) the metasternum with
- 346 the posterior margin convex (Fig. 1D); (8) the male abdominal segment VIII acuminating
- posteroventrally (Figs. 2F, 3C–D, 5A–B); and (9) the male proctiger with a pair of anterodorsal
- 348 projections (Figs. 3E–H, 5H).
- Rodrigues et al. (2014) and Rodrigues & Moreira (2016) had already indicated the
- 350 similarities shared by these species, but did not propose any taxonomic changes. The main



diagnostic feature of *Foveavelia* is the presence of coarse cuticular punctures along the body (Fig. 2). As described by Mazzucconi (2000), these structures are cuticular depressions with deep, transverse grooves, and a sensilla-like seta placed eccentrically to these grooves, or sometimes centrally. Although the arrangement of this seta varies, its size is similar among different punctures. Unlike the structure described above, the pronotal punctures typical of most Veliidae, including *Foveavelia*, are rounded and covered by a cluster of centrally directed microtrichia along the puncture rim, making the transverse grooves and sensilla-like seta difficult to see (Figs. 2A–B). On the other hand, the distinctive punctures of *Foveavelia* lack clusters of microtrichia along the puncture rim (Figs. 2D–E). These punctures usually do not touch each other (Figs. 2C, 2F), although in some regions of the body, such as on the sides of abdominal mediotergites I–III, they are conjoined, forming larger, flower-like structures (Figs. 2A, 2D).

Because *Paravelia* is not monophyletic and due to the morphological heterogeneity among its species, it is difficult to detect diagnostic characters for the entire genus. *Paravelia basalis* (Spinola, 1837) (Fig. 7A), the type species, differs from *Foveavelia* in several characteristics, including the absence of coarse cuticular punctures throughout the body, the absence of frosty pubescence on the anterior lobe of the pronotum, the different shape and color of the forewing maculae, the presence of a pair of distinct projections on male abdominal sternum VII, the different shape of male abdominal segment VIII (Figs. 7B–C), and the presence of anterodorsal and anterolateral projections on the male proctiger (Fig. 7D).

Paravelia foveata J. Polhemus & D. Polhemus, 1984 (Figs. 7F–G) displays a pattern of cuticular punctures on the body similar to *Foveavelia*. However, because this species has several characteristics that are not present in other species here assigned to *Foveavelia*, it is not included in the new genus. The following features are exclusive to *P. foveata*: (1) general body color reddish-brown, with short pubescence; (2) antennomere IV very small, fusiform; (3) anterior lobe of pronotum with a pair of yellowish-white markings; (4) forewings with differently shaped closed cells, with an additional macula basally, and apical macula crescent-shaped, not reaching wing apex (5) male fore tibial grasping comb occupying about two-thirds of the tibial length (Fig. 7G); (6) row of elongate dark-brown trichobothria-like setae on the middle tibia occupying half of the segment; (7) coarse punctures present on abdominal sternum VII; and (8) male proctiger without anterodorsal projections. The cuticular modifications found along the body of *P. foveata*, especially those present on the abdomen, are very likely not homologous to those



382	displayed by Foveavelia. Cuticular modifications similar to those of Foveavelia, but probably	
383	also not homologous, are found in members of Microveliinae (Gerromorpha: Gerridae), such as	
384	Neoalardus typicus (Distant, 1903) and Hebrovelia singularis Lundblad, 1939.	
385	In terms of phylogenetic relationships, the only species of Foveavelia heretofore included	
386	in a study is F. dilatata (Armisén et al., 2022). It was recovered as sister to the genus	
387	Stridulivelia, which displays different types of cuticular modifications on the thorax and	
388	abdomen (glabrous longitudinal striae or elongate lacunae). In the future, expanding the	
389	taxonomic scope of Veliinae in a phylogenetic analysis would be interesting to test whether all	
390	taxa with cuticular modifications, including Stridulivelia, Foveavelia and P. foveata are indeed	
391	closely related.	
392		
393	Conclusions	
394	After examination of all american species within the subfamily Veliinae, a new Neotropical	
395	genus has been established to accommodate five species previously classified in <i>Paravelia</i> . This	
396	new genus has been characterized morphologically using SEMs and photographs. Future	
397	phylogenetic hypotheses are required to elucidate the closely related lineages of this new genus.	
398		
399	Acknowledgements	
400	We are grateful to Dr. Silvia Mazzucconi (Universidad de Buenos Aires, Buenos Aires,	
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403		
404	access to their institutional collections.	
405		
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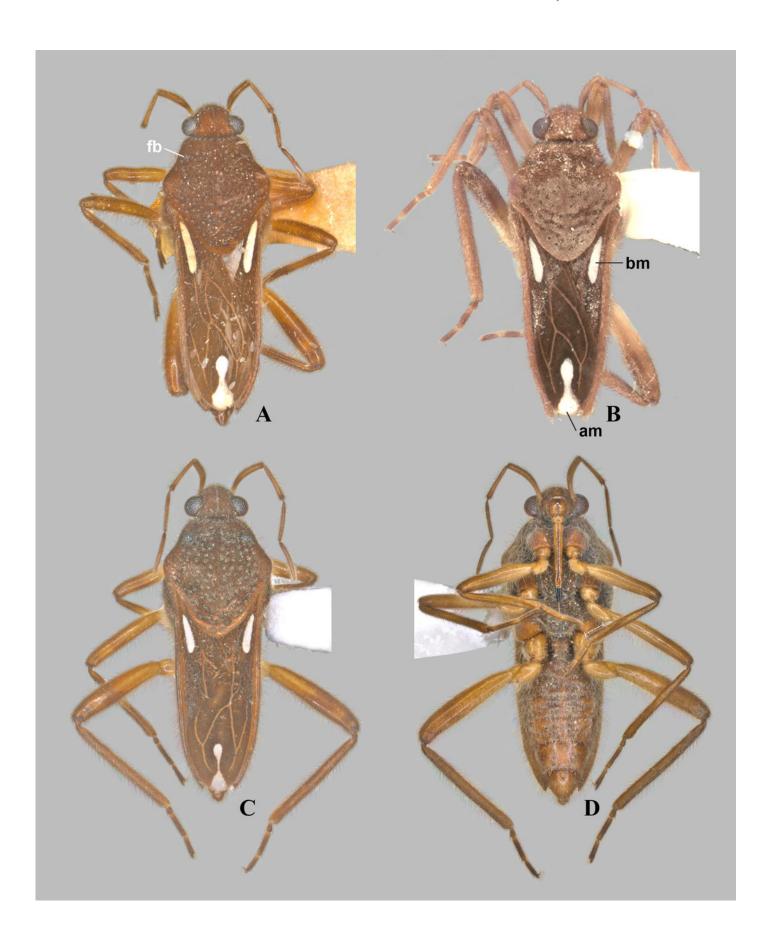


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Foveavelia species, dorsal and ventral views.

(A) Foveavelia amapaensis (Rodrigues, Moreira, Nieser, Chen & Melo, 2014), dorsal habitus of male holotype (specimen destroyed). (B-D) Foveavelia bilobata amapaensis (Rodrigues, Moreira, Nieser, Chen & Melo, 2014), (B) dorsal habitus of male from Colombia, (C) dorsal and (D) ventral habitus of male paratype from Brazil, dashed line indicates length of grasping comb. am = apical macula, bm = basal macula, fb = frosty pubescence.



Structures of Foveavelia anta (Mazzucconi, 2000). Scanning electron microscopy.

(A) Dorsal view of head, pronotum and part of abdomen (wings removed). (B) Pronotal punctures. (C) Male abdomen in dorsal view (wings and genital capsule removed). (D) Part of abdominal mediotergite II with suboval punctures. (E) Suboval puncture of abdominal mediotergite IV in detail. (F) Male abdomen in lateral view (wings and genital capsule removed), white arrow indicates posteroventral margin of abdominal segment VIII acuminating distally. mt = mediotergite, It = laterotergite. Figures provided by Dr. Silvia Mazzucconi.

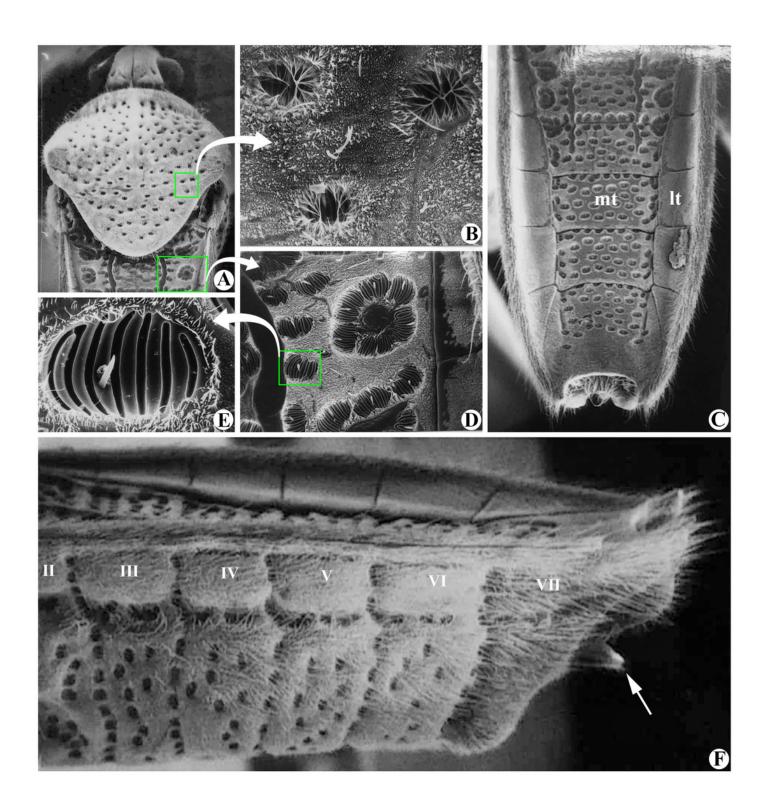
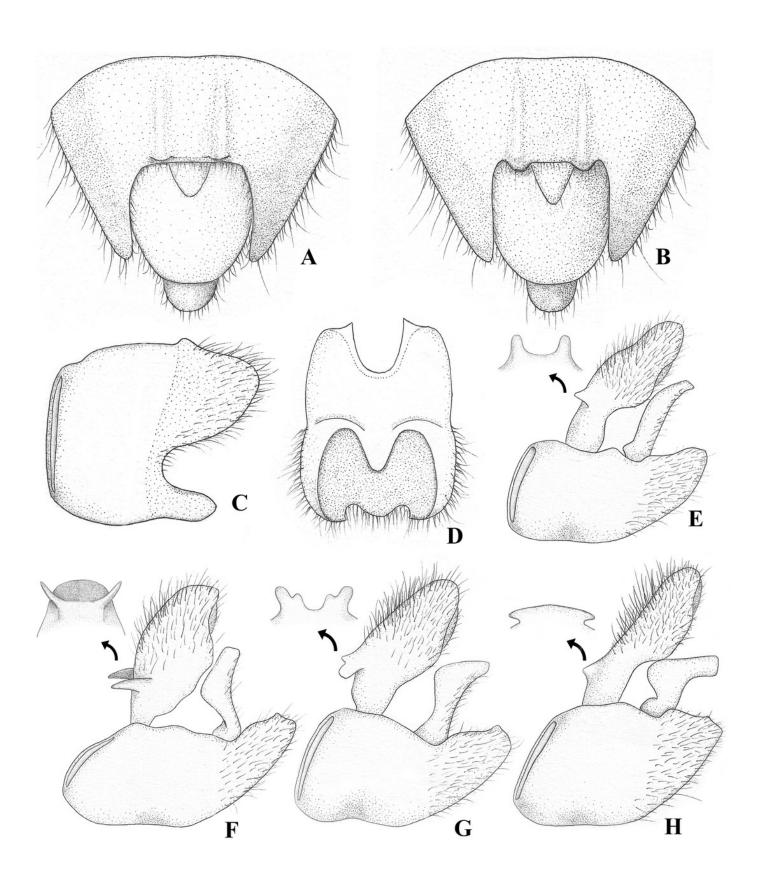




Figure 3. Foveavelia species, male structures.

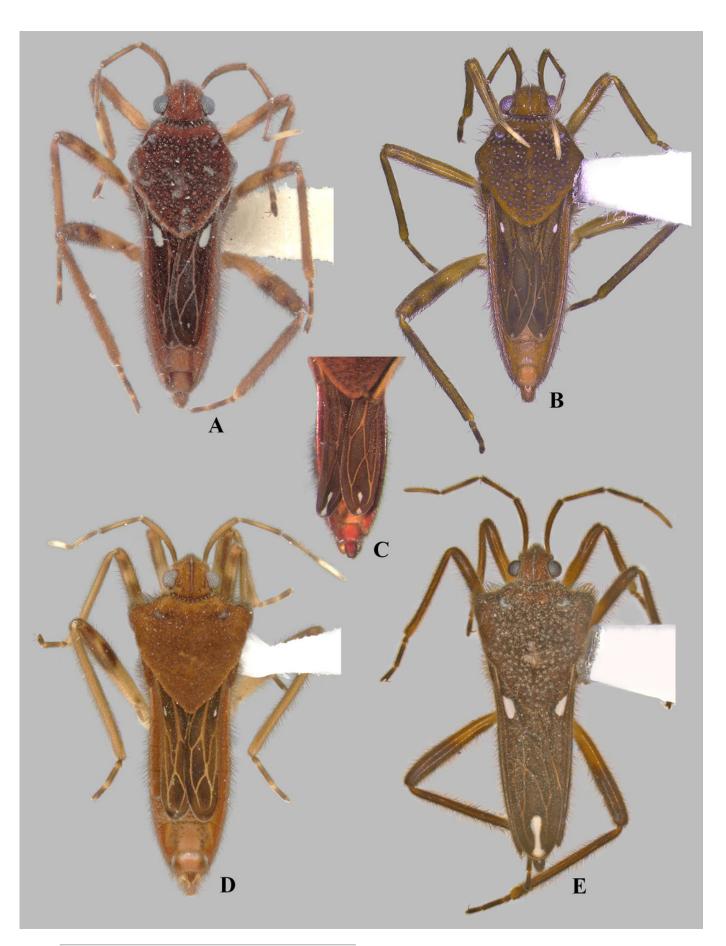
(A–B) Ventral view of abdominal apex, (A) *F. amapaensis* (Rodrigues, Moreira, Nieser, Chen & Melo, 2014), (B) *F. bilobata* (Rodrigues, Moreira, Nieser, Chen & Melo, 2014). (C–D) Abdominal segment VIII of *F. bilobata*, (C) lateral and (D) ventral views. (E–H) Genital capsule in lateral view, showing proctiger projections detailed in frontal view, (E) *F. amapaensis*, (F) *F. anta* (Mazzucconi, 2000), (G) *F. bilobata*, (H) *F. dilatata* (Polhemus & Polhemus, 1984).





Foveavelia dilatata (Polhemus & Polhemus, 1984), dorsal views of female and male.

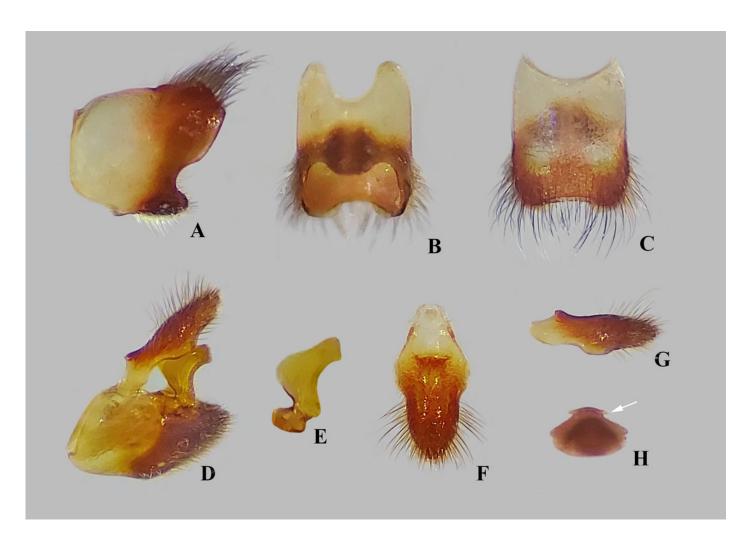
(A-B) Dorsal habitus of brachypterous females, (A) paratype from Brazil, (B) specimen from Brazil. (C) Dorsal view of abdomen of brachypterous female, specimen from Brazil. (D) Dorsal habitus of brachypterous male, paratype from Brazil. (E) Dorsal habitus of macropterous male, specimen from Brazil.



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Figure 5. Male structures of *Foveavelia dilatata* (Polhemus & Polhemus, 1984), paratype from Brazil.

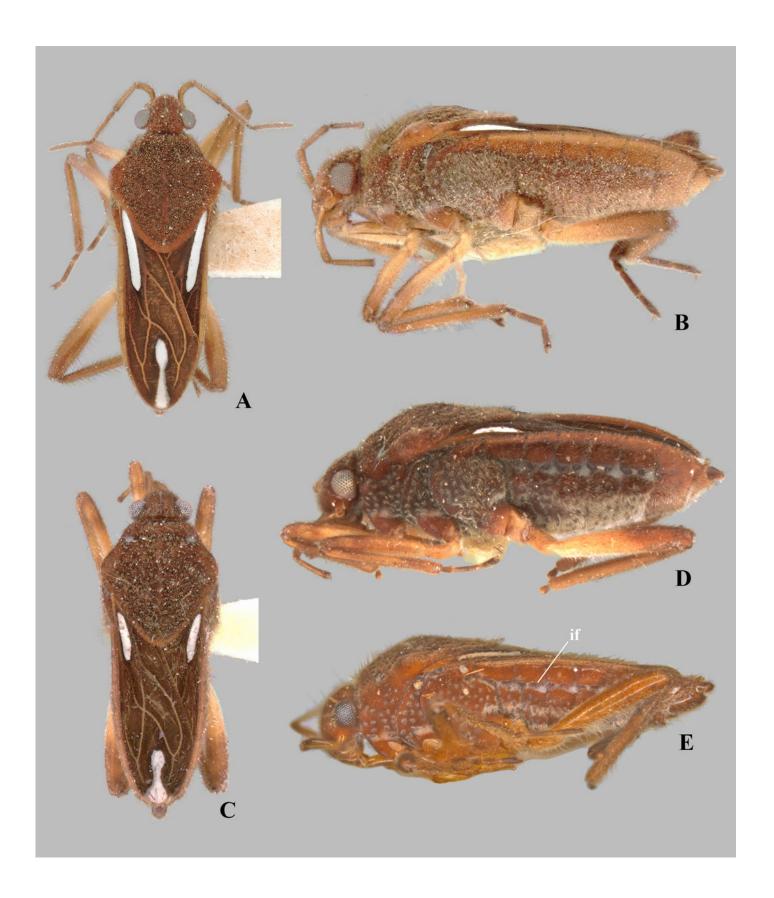
(A-C) Abdominal segment VIII, (A) lateral, (B) ventral and (C) dorsal views. (D) Genital capsule in lateral view. (E) Left paramere in lateral view. (F-H) proctiger, (F) dorsal, (G) lateral and (H) frontal views, white arrow indicates pair of anterodorsal projections.





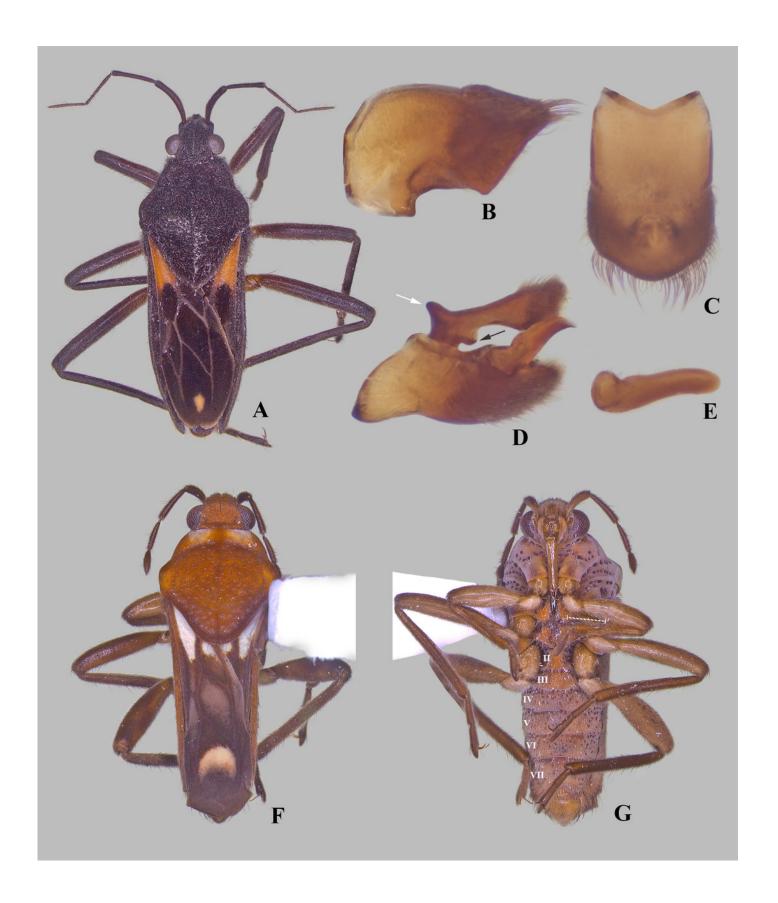
Foveavelia species, dorsal and lateral views.

(A–B) Foveavelia hungerfordi, macropterous female paratype from Brazil, (A) dorsal and (B) lateral views. (C–D) Foveavelia sp., macropterous female from Brazil, (C) dorsal and (D) lateral views. (E) Foveavelia amapaensis, macropterous male holotype in lateral view (specimen destroyed). if = impressed furrow.

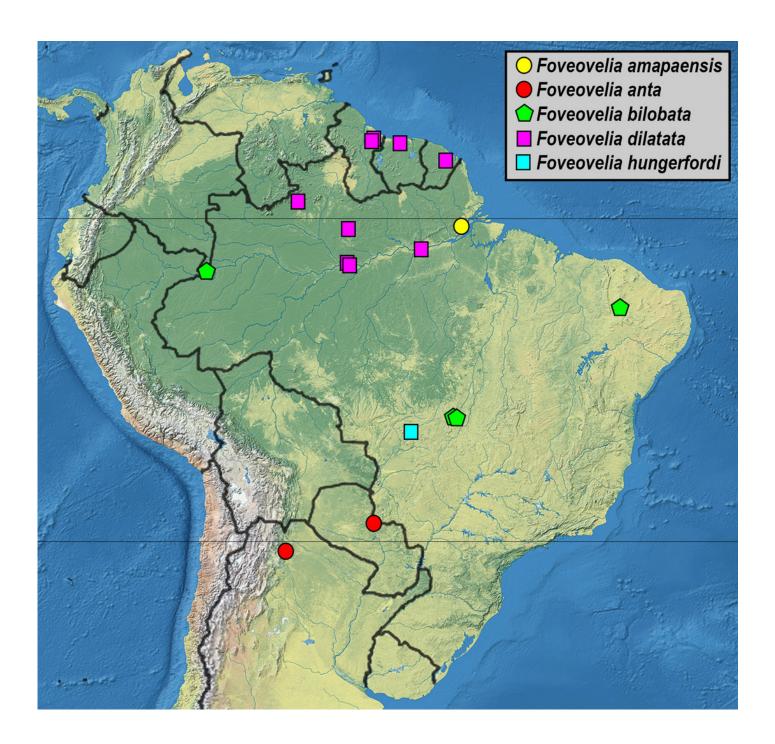


Paravelia species.

(A–E) *Paravelia basalis* (Spinola, 1837), (A) dorsal habitus of male from Brazil, (B–C) male abdominal segment VIII, (B) lateral and (C) dorsal views, (D) male genital capsule, white arrow indicates anterodorsal projection, black arrow indicates anterolateral projection, both in proctiger, (E) left paramere in anterolateral view. (F–G) *Paravelia foveata* Polhemus & Polhemus, 1984, (F) dorsal and (G) ventral habitus of male from Brazil, dashed line indicates length of grasping comb.



Geographic distribution records of Foveavelia species.





#### Table 1(on next page)

Checklist of species of Foveavelia.

All species are removed from the genus *Paravelia*.

Taxon	Distribution
Foveavelia amapaensis (Rodrigues, Moreira, Nieser, Chen & Melo, 2014)	Brazil (Amapá)
Foveavelia anta (Mazzucconi, 2000)	Argentina (Salta), Paraguay (Concepción)
Foveavelia bilobata (Rodrigues, Moreira, Nieser, Chen & Melo, 2014)	Brazil (Ceará, Mato Grosso), Colombia
	(Amazonas)
Foveavelia dilatata (Polhemus & Polhemus, 1984)	Brazil (Amazonas, Pará), French Guiana
	(Saint-Georges), Guyana (Upper
	Demerara-Berbice), Suriname (Para)
Foveavelia hungerfordi (Drake & Harris, 1933)	Brazil (Mato Grosso)