

RESEARCH ARTICLE

Two new Brazilian species of Chelodesmidae of the genera *Iguazus* and *Tessarithys* (Diplopoda: Polydesmida)

Rodrigo S. Bouzan¹, João Paulo P. Pena-Barbosa¹, Antonio D. Brescovit¹

¹Laboratório Especial de Coleções Zoológicas, Instituto Butantan. Avenida Vital Brasil 1500, 05503-090 São Paulo, SP, Brazil.

Corresponding author: Rodrigo S. Bouzan (rodrigobouzan@outlook.com)

<http://zoobank.org/739E57D7-535D-4EF3-A6C9-49623563B31E>

ABSTRACT. Two new species of Chelodesmidae from the Brazilian northeast are described, *Iguazus robustus* **sp. nov.**, from the state of Paraíba, and *Tessarithys exacuminatus* **sp. nov.**, from the states of Pernambuco and Sergipe. *Iguazus robustus* **sp. nov.** differs from other species of the genus by having a constriction in the zone of the gonopodal acropodite tip and an extra branch at the tip of the acropodite. *Tessarithys exacuminatus* **sp. nov.** differs from the other species of the genus by the large and ascending subterminal dorsal branch of the prefemoral process of the gonopod. Brief reviews of the taxonomy, geographic distribution and a key for males of the respective genera are provided.

KEY WORDS. Brazil, Chelodesminae, millipedes, Neotropical, taxonomy.

INTRODUCTION

Among the Diplopoda, with almost 5,000 described species in 31 families, the Polydesmida Leach, 1814 is the most speciose order (Brewer et al. 2012). Within the order, Chelodesmidae constitutes the second largest family, with about 800 described species. Members of this family occur in western Africa (Prepodesminae Cook, 1896) and South America (Chelodesminae Cook, 1895), according to Hoffman (1980). The systematics of Chelodesminae was reviewed by Hoffman (1980), who placed some genera and species in tribes. The remaining species were not reviewed by Hoffman (1980) or described after his classification. As a result, of the 171 genera and ca 800 species in Chelodesmidae, 89 genera and 455 species are currently not assigned to a tribe.

During the examination of the Diplopoda collection of the Instituto Butantan, Brazil, two new species of Chelodesminae from the Brazilian Northeast were found. The first belongs to *Iguazus* Chamberlin, 1952 and the other to *Tessarithys* Hoffman, 1990. Neither genera has been assigned to a tribe within the Chelodesmidae.

Iguazus was proposed by Chamberlin (1952) for a single species, *I. ornithopus* (Brölemann, 1902), described from Cerqueira César, state of São Paulo, Brazil. Hoffman (1965)

noticed that the genus *Hoffmanodesmus* Schubart, 1962 is a junior synonym of *Iguazus*. He then transferred *H. roseofasciatus* Schubart, 1962, from Porto Real do Colégio, state of Alagoas, Brazil, to *Iguazus*.

Hoffman (1990) proposed the genus *Tessarithys* for three species, *T. neoecobius* Hoffman, 1990, the type species, from Senhor do Bonfim, and *T. machaerophorus* (Schubart, 1956), from Juazeiro (both localities are in the state of Bahia, Brazil), and *T. soledadinus* (Attems, 1931) labeled only as “Soledad, Brasilien”, (probably Soledade, in the state of Paraíba, Brazil). The last two species were removed from *Leptodesmus* when Hoffman (1971) reorganized the systematic structure of the genus.

Many members of various groups within the Chelodesmidae share character states in their external morphology, and are mostly differentiated by variations in the structures of the male gonopod. These differences in the gonopod indicate that it has undergone rapid divergent evolution in the genitalia, as evidenced in numerous other arthropod groups (Eberhard 2010). Thus, discrimination among species in many chelodesmid groups depends on the analysis of the male gonopod.

In this work we describe the new species *Iguazus robustus* sp. nov. from Araruna, state of Paraíba and *Tessarithys exacuminatus* sp. nov. from São Caetano, state of Pernambuco and provide a map of their records.

MATERIAL AND METHODS

Morphological observations and illustrations were made using a Leica MZ12 stereomicroscope with a camera lucida. Photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereomicroscope. Extended focal range images were composed with Leica Application Suite version 2.5.0. All measurements are in millimeters. The terminology of the gonopodal structures follows Pena-Barbosa et al. (2013) and Hoffman (1990), while the terminology used to describe somatic traits follows Attems (1898), Brölemann (1900) and Pena-Barbosa et al. (2013). The type material was deposited in the collection of the Instituto Butantan, São Paulo (IBSP, curator: A. D. Brescovit).

Museum acronyms: FMNH, Field Museum of Natural History, Chicago, USA; IBSP, Instituto Butantan, São Paulo, Brazil; MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; NHMW, Naturhistorisches Museum, Wien, Austria.

TAXONOMY

Chelodesmidae Cook, 1895

Chelodesminae Cook, 1895

Iguazus Chamberlin, 1952

Camptomorpha (non Silvestri, 1897), Attems 1938: 73 (in part, *ornithopus* Brölemann); Schubart 1943: 147 (in part, *ornithopus* and *phoenicopterus*).

Iguazus Chamberlin, 1952: 568. Type species: *I. leius* Chamberlin 1952, by original designation.

Hoffmanodesmus Schubart, 1962: 255. Type species: *H. ornithopus* (Brölemann, 1902), by original designation; synonymized by Hoffman 1965: 219.

Iguazus: Hoffman 1965: 219.

Diagnosis. Males of *Iguazus* differ from other chelodesmid genera by the following combination of characters: gonopodal acropodite slender, unbranched and sinuously curved, prefemoral process massive in form of a narrow blade or branch, with one or two secondary processes arising proximally from the midlength region (Figs 1-3).

Distribution. Known from the states of Paraíba, Alagoas and São Paulo, Brazil and in Misiones, Argentina.

Composition. Three species, *Iguazus ornithopus* (Brölemann, 1902), *I. roseofasciatus* (Schubart, 1962), *I. robustus* sp. nov.

Iguazus ornithopus (Brölemann, 1902)

Leptodesmus ornithopus Brölemann, 1902: 87, figs 90-92 (One male and two females syntypes from Cerqueira César, 49°16'59"W, 23°03'85"S, São Paulo, deposited in MZSP, not examined).

Camptomorpha ornithopus: Attems 1938: 73.

Camptomorpha phoenicopterus Schubart, 1943: 147, figs 46-47 (Male holotype from Itapura, São Paulo, deposited in MZSP,

not examined); synonymized by Schubart 1962: 255 under *ornithopus*.

Iguazus leius Chamberlin, 1952: 568 fig. 17 (Male holotype, one male and six female paratypes from Iguazu Falls, Misiones, deposited in FMNH #274, not examined). The type lot contains fragments of a single specimen, gonopods missing (Sierwald et al. 2005). Synonymized by Hoffman 1965: 221.

Hoffmanodesmus ornithopus: Schubart 1962: 254.

Iguazus ornithopus: Hoffman 1965: 221, fig. 1.

Distribution. State of São Paulo, Brazil and Misiones, Argentina.

Iguazus roseofasciatus (Schubart, 1962)

Hoffmanodesmus roseofasciatus Schubart, 1962: 255, fig. 2 (Male holotype, one male and two female paratypes from Porto Real do Colégio, 36°83'78"W, 10°18'53"S, Alagoas, deposited in MZSP, not examined).

Iguazus roseofasciatus: Hoffman 1965: 221.

Distribution. State of Alagoas, Brazil.

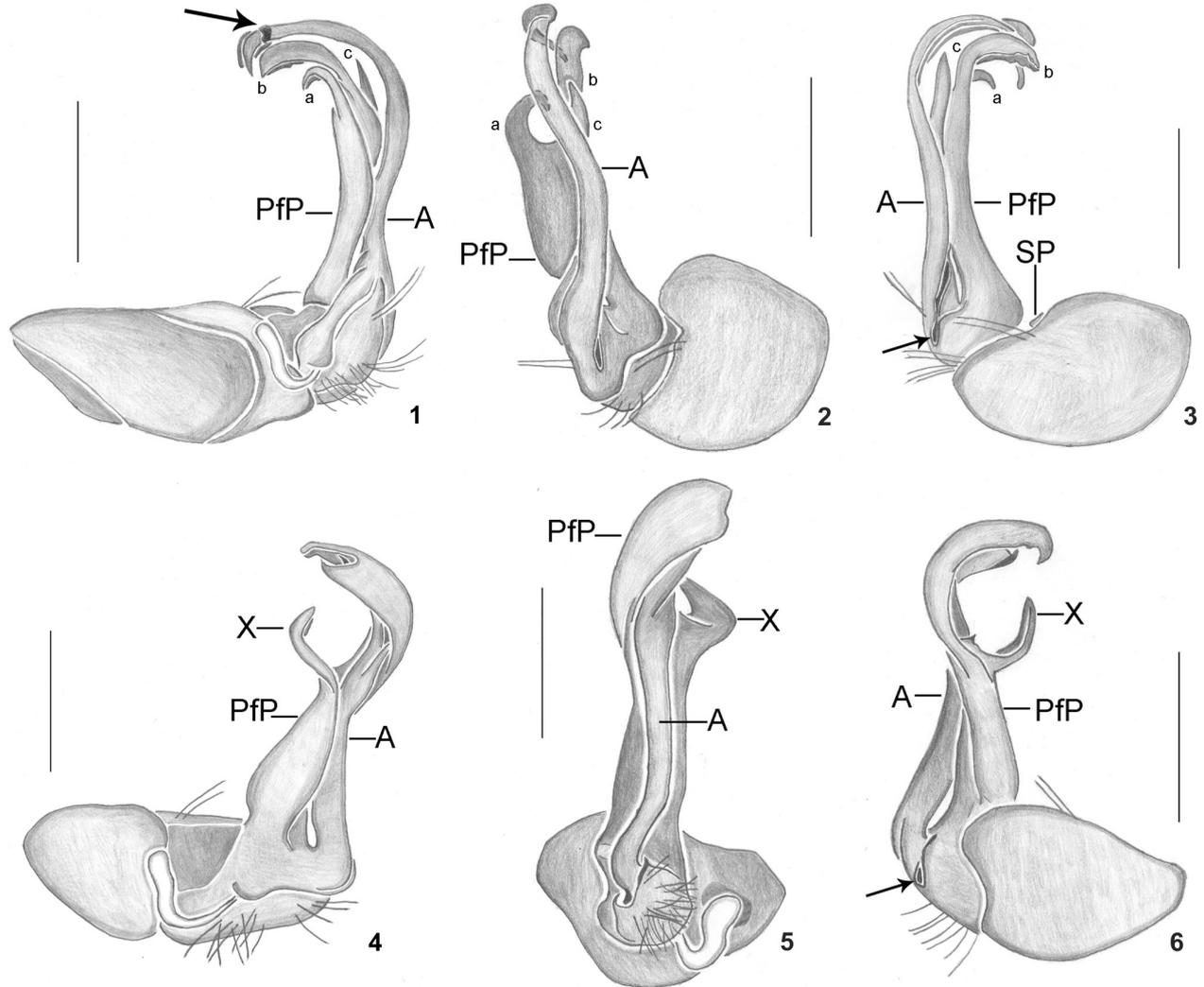
Iguazus robustus sp. nov.

<http://zoobank.org/CE310199-8C38-444C-9A0D-644298CDBED5>

Figs 1-3, 7-12, 19-21, 28

Diagnosis. Males of this species differ from those of other species of the genus by having a constriction in the zone of the gonopodal acropodite tip (Fig. 1, arrow) and an extra branch at the tip of the acropodite.

Description. Female: Unknown. Male (Holotype, IBSP 4397): Head reddish with a yellow labrum, Tömösvary organ suboval in shape. Antennae reddish brown, terminal antennomere with invaginations between the four apical sense cones. Body reddish brown and paranota tip yellow, gradually losing the brown color towards the posterior body rings, reddish brown color in the mid-body ring restricted to the anterior and posterior edge and yellow filling the remaining portion (Figs 19-21). Body rings: tegument smooth; alignment of paranota ventrally curved; paranota with posterior edges acutely produced from body ring 5; ozopore centrally situated on body ring 5; and posteriorly situated on the other body rings; ozopore arrangement at the edge of paranota: 5, 7, 9, 10, 12, 13, 15-19 (following the standard polydesmid pore formula). Penultimate body ring with reduced paranota (Fig. 12, arrows). Stigma oval and elongated. Coxae of leg pair 2nd with rectangular shaped genital papilla (Fig. 7, arrows). Sternite of body ring 5 with a pair of elongated projections (Fig. 8). Sternite of body ring 8 presenting two pairs of pointed projections in the zone anterior to the coxae (Fig. 9, arrows). Gonopod aperture on seventh body ring: elliptical, posterior edge without folds. Legs whitish yellow, with rounded ventro-apical process on the prefemur and with an apical-ventral



Figures 1–6. (1–3) *Iguazus robustus* sp. nov., left gonopod: (1) mesal view (arrow = insertion point, zone of acropodite); (2) ventral view; (3) ectal view (arrow = groove near the first portion of the acropodite). (4–6) *Tessarithys exacuminatus* sp. nov., left gonopod: (4) mesal view; (5) ventral view; (6) ectal view (arrow = groove near the first portion of the acropodite). Scale bars = 0.5 mm. (a) Process A, (A) acropodite, (b) process B, (c) process C, (PfP) prefemoral process, (SP) spiniform projection on gonopod coxae, (X) subterminal dorsal branch.

membranous projection on the tibia (Figs 10–11), leg modifications are present in all pairs except the last. Telson yellowish with dark brown edges. Total length: 39. Collum 2.08 long, 5.46 wide. Antennomere length: 0.26; 1.14; 1.23; 1.15; 1.27; 1.00; 0.21. Gonopod aperture 1.66 long, 2.56 wide. Telson 0.85 long.

Gonopods (Figs 1–3): gonopod coxae equivalent to about half the length of the telopodite and prominent in ectal view (Fig. 3). Coxae with two bristles in the distal dorsal side. Spiniform projection present. Cannula (Fig. 1): hook-shaped. Prefemoral region ventrally developed and short, 1/3 the size of telopodite. In ectal view, presence of a conspicuous groove near the beginning of the acropodite (Fig. 3, arrow). Prefemoral process (PfP) long, massive,

blade-like. In the middle portion, the prefemoral process divides into three different projections: the first projection, mesal view, sickle-shape (Figs 1–3, a); the mid-projection, the largest among them, boat-shaped (Figs 1–3, b); the last is the spine-shaped lower projection (Figs 1–3, c). Acropodite (A) elongated and slender, carrying the seminal groove; acropodite is unbranched and sinuously-curved (Figs 1–3); its distal portion, mesal view, displays a constriction, that resembles a cingulum where a moveable branch is attached, that results in a pointed tip and in a blade which seems to have the function of protecting this acute blade on the lateral side, thus the tip of acropodite is constituted for two branches (Figs 1, 3).

Type material. Male holotype from Parque Estadual Pedra da Boca, Araruna (6°45'95"S, 35°67'78"W, 228 m), Paraíba, Brazil, 01-02.VI. 2012, I.L.F. Magalhães & J.L. Chavari col., deposited in IBSP 4397.

Distribution. Known only from the type locality (Fig. 28).

Etymology. The species epithet, *robustus*, is a reference to the massive prefemoral process and derives from the Latin word "robustus", "robusta".

Key to males of *Iguazus*

- 1 Prefemoral process trifurcated..... 2
- 1' Prefemoral process bifurcated (Schubart 1962: fig. 2)
.....*I. roseofasciatus*
- 2 Apical portion of acropodite with two branches (Fig. 1)....
.....*I. robustus*
- 2' Apical portion of acropodite single branch (Hoffman, 1965: fig. 1).....*I. ornithopus*

Tessarithys Hoffman, 1990

Tessarithys Hoffman, 1990: 159–166. Type species: *T. neoecobius* Hoffman, 1990, by original designation.

Diagnosis. Males of *Tessarithys* differ from other chelodesmid genera by the combination of the following characters: sternite of body ring 5 with four projections (Fig. 14). Legs with apical-ventral projection on the tibia (Fig. 17). Gonopodal prefemoral process exceeding the acropodite apex and forming a distinct sheath on the ectal side, also displaying a subterminal dorsal branch on the middle portion. Acropodite are divided into two slender and acuminate branches (Figs 4–6).

Distribution. Known from the states of Pernambuco to Bahia.

Composition. Four species, *Tessarithys neoecobius* Hoffman, 1990, *T. machaerophorus* (Schubart, 1956), *T. soledadinus* (Attems, 1931), *T. exacuminatus* sp. nov.

Tessarithys neoecobius Hoffman, 1990

Tessarithys neoecobius Hoffman, 1990: 161, figs 7 (Male holotype and three female paratypes from Senhor do Bonfim, 40°18'68"W, 10°45'97"S, Bahia, deposited in MZSP, not examined).

Distribution. State of Bahia, Brazil.

Tessarithys machaerophorus (Schubart, 1956)

Leptodesmus machaerophorus Schubart, 1956: 424, figs 5-6 (Male holotype, two males and six female paratypes from Joazeiro, 40°50'58"W, 09°42'78"S, Bahia, deposited in MZSP, not examined).

Tessarithys machaerophorus: Hoffman 1990: 1965.

Distribution. State of Bahia, Brazil.

Tessarithys soledadinus (Attems, 1931)

Pseudoleptodesmus soledadinus Attems, 1931: 30, fig. 43-45 (Male holotype, labeled only "Soledad", Brazil, deposited in NHMW, not examined).

Leptodesmus (Pseudoleptodesmus) soledadinus: Attems 1938: 43.

Leptodesmus soledadinus: Schubart 1946: 196.

Tessarithys soledadinus: Hoffman 1990: 163.

Distribution. Labeled only as from "Soledad", Brazil.

Tessarithys exacuminatus sp. nov.

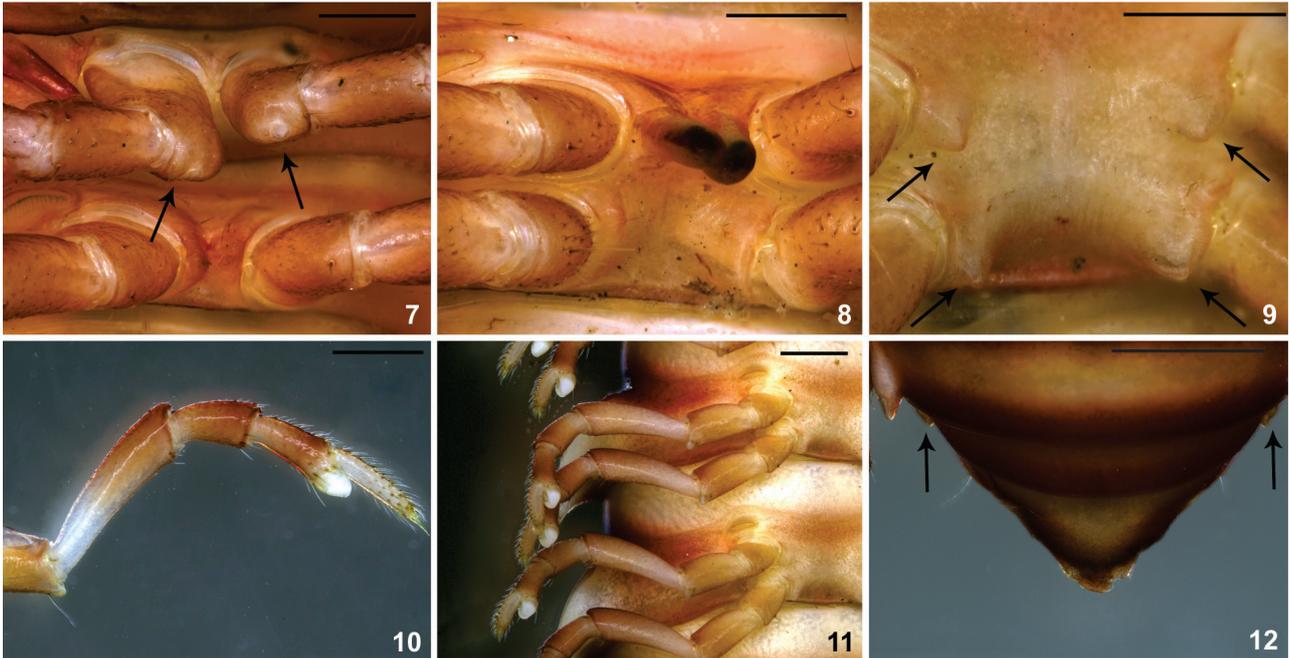
<http://zoobank.org/B511E597-DFD1-45C0-AAC9-F95D21001B5A>

Figs 4–6, 13–18, 22–27, 29

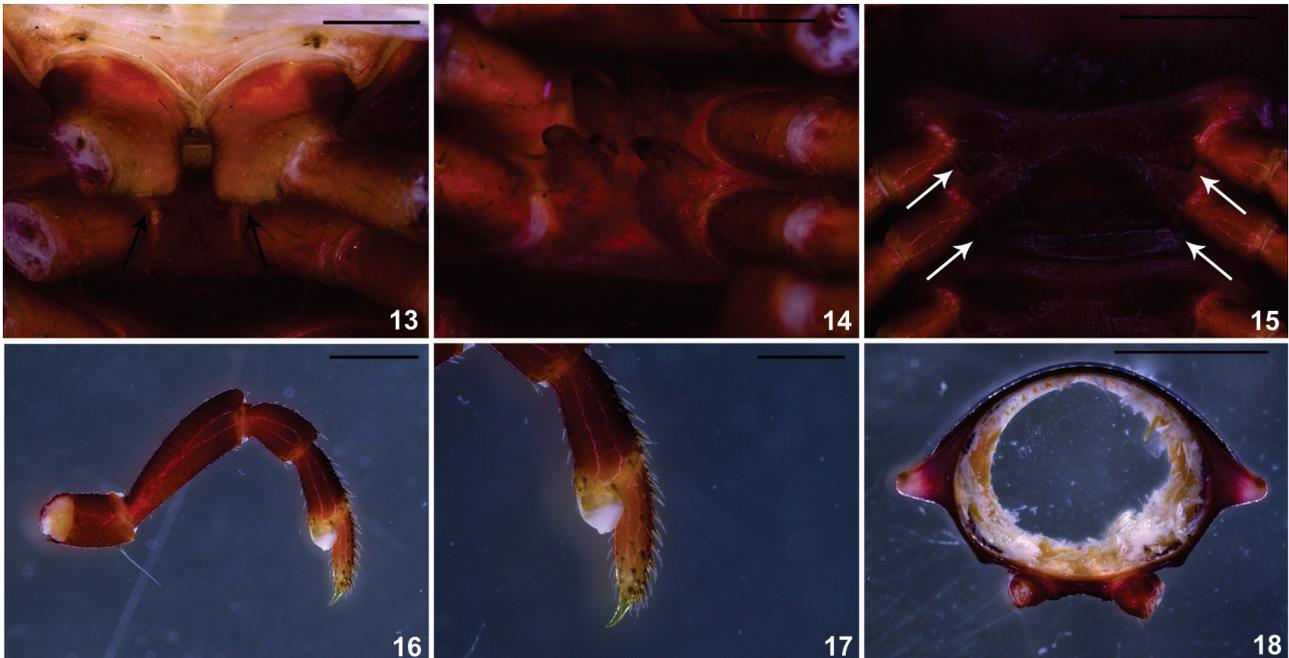
Diagnosis. Males of this species differ from those of other species of the genus by the large and ascending subterminal dorsal branch of the prefemoral process of the gonopod (Fig. 4).

Description. Female: Unknown. Male (Holotype, IBSP 4431): Head dark reddish with a yellow labrum, Tömösváry organ suboval in shape. Antennae reddish brown, terminal antennomere with invaginations between the four apical sense cones. Body purple, coloration of paranota tip differing from body ring 5, reddish yellow (Figs 22–24). Body rings: tegument slightly rough. Alignment of paranota: ventrally curved (Fig. 18); paranota with posterior edges acutely produced from body ring 5; ozopore centrally situated on body ring 5, and posteriorly situated on the others; ozopore arrangement at the edge of paranota: 5, 7, 9, 10, 12, 13, 15–19 (following the standard polydesmid pore formula). Penultimate body ring with reduced paranota. Stigma oval and elongated. Coxae of 2nd leg pair with rectangular shaped genital papilla (Fig. 13, arrows). Sternite of body ring 4 with a pair of small rounded projections (Fig. 13). Sternite of body ring 5 with two pairs of elongated projections (Fig. 14). Sternite from body ring 8 presenting two pairs of pointed projections in the zone anterior to the coxae (Fig. 15, arrows). Gonopod aperture on seventh body ring: transversal oval, posterior edge without folds. Legs reddish, with a membranous apical-ventral projection on the tibia (Fig. 16–17); leg modifications are present in all pairs except on the last. Telson purple. Total length: 42.5 (Fragmented). Collum 2.03 long, 5.50 wide. Antennomere length: 0.41; 1.17; 1.28; 1.04; 1.23; 1.01; 0.20. Gonopod aperture 1.40 long, 2.77 wide. Telson 1.58 long.

Gonopods (Figs 4–6): gonopod coxae equivalent to about half the length of the telopodite and prominent in ectal view (Fig. 6). Coxae with two bristles in the distal dorsal side. Spiniform projection absent. Cannula (Fig. 4): hook-shaped. Prefemoral region short, ventrally developed, 1/3 the size of telopodite. Presence of a conspicuous groove near the first portion of the acropodite, in the ectal view (Fig. 6, arrow). Prefemoral process (PFP) long, parallel to the acropodite (A); displays a long and acuminate subterminal dorsal branch on the middle portion (Figs 4–6, X).



Figures 7–12. *Iguazus robustus* sp. nov.: (7) Sternite, body ring 3 (arrow = genital papilla), body ring 4; (8) Sternite of body ring 5; (9) Sternite on body ring 8 (arrow = pairs of projections); (10) Leg, lateral view; (11) Leg, ventral view; (12) Penultimate body ring (arrow = reduced paranota).



Figures 13–18. *Tessarithys exacuminatus* sp. nov.: (13) Sternite, body ring 3 (arrow = genital papilla), body ring 4; (14) Sternite of body ring 5; (15) Sternite on body ring 8 (arrow = pairs of projections); (16) Leg, lateral view; (17) Tibia, membranous projection apico-ventral, detail; (18) Paranota, ventral.



Figures 19–27. (19–21) *Iguazus robustus* sp. nov., body: (19) first body rings; (20) midbody body rings; (21) last body rings. (22–27) *Tessarithys exacuminatus* sp. nov., body (holotype): (22) first body rings; (23) midbody body rings; (24) last body rings; body (paratype): (25) first body rings; (26) midbody body rings; (27) last body rings.

The final portion of the prefemoral process passes on the back of the acropodite, forming a distinct protection on the lateral side, with two blades forking in the terminal portion (Fig. 4). Acropodite (A) long and slender, with solenomere and one additional branch (Fig. 4). Spermatic groove mostly visible in mesal view except at the base of the acropodite where it diverts to the ectal side.

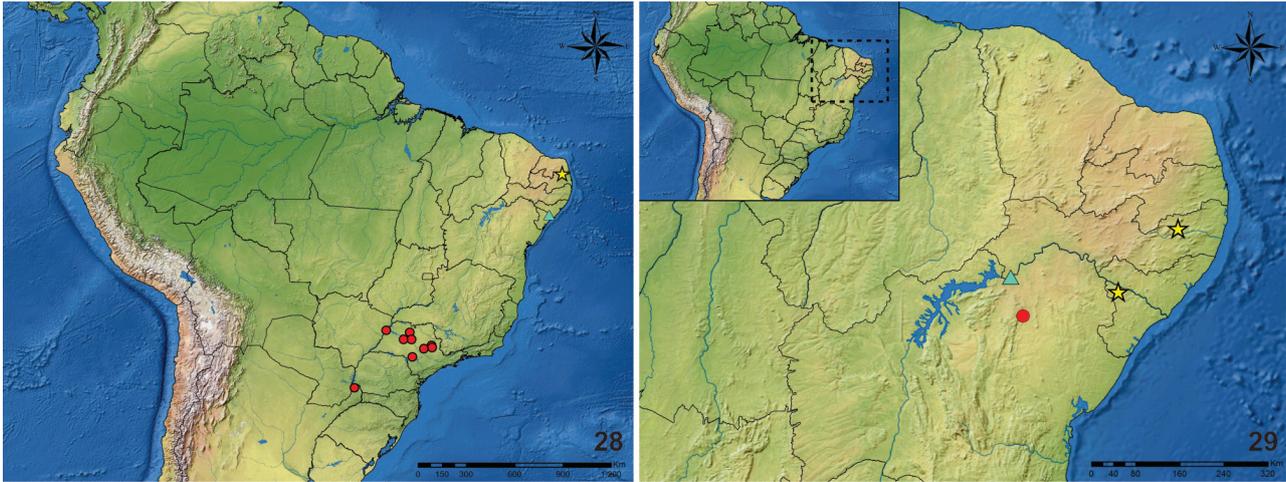
Variation. The body of the paratype (IBSP 4434) shows reddish brown coloration, with the edges of the paranota whitish yellow, tegument smooth and with a median band present, weakly developed (Figs 25–27).

Type material. Holotype: one male (IBSP 4431) from Reserva Particular do Patrimônio Natural Pedra do Cachorro (8°14'22.9"S, 36°11'13.7"W), São Caetano, Pernambuco, Brazil, 26.V.2012, I.L.F. Magalhães & J.L. Chavari coll. Paratypes: one male (IBSP 4434) same data as holotype and one male (IBSP 4634) from Unidade de Conservação Monumento Natural Grota do Angico, Poço Redondo (9°80'65"S, 37°68'36"W), Sergipe, Brazil. I. 2013, R. G. Faria coll.

Distribution. Known only from the type locality (Fig. 29).
Etymology. In reference to the acuminate subterminal dorsal branch, labelled "X" in figs 7-9 in Hoffman 1990.

Key to *Tessarithys* males

- | | | |
|----|--|--------------------------|
| 1 | Prefemoral process: terminal section consisting of a single branch | 2 |
| 1' | Prefemoral process: terminal section consisting of two branches | 3 |
| 2 | Presence of small denticles beyond the base of the subterminal dorsal branch of prefemoral process (Hoffman 1990: fig. 9)..... | <i>T. soledadinus</i> |
| 2' | Base of subterminal dorsal process of prefemoral process smooth (Hoffman 1990: fig. 7) | <i>T. neoecobius</i> |
| 3 | Subterminal dorsal branch pointing upward (Fig. 4) | <i>T. exacuminatus</i> |
| 3' | Subterminal dorsal branch pointing downward (Hoffman 1990: fig. 8)..... | <i>T. machaerophorus</i> |



Figures 28–29. (28) Distribution map. *Iguazus ornithopus* = red circles; *I. roseofasciatus* = blue triangle; *I. robustus* sp. nov. = yellow star. Locality data for *I. ornithopus* and *I. roseofasciatus* taken from the literature. (29) Distribution map. *Tessarithys neoecobius* = red circle; *T. machaerophorus* = blue triangle; *T. soledadinus* = ?; *T. exacuminatus* sp. nov. = yellow stars. Locality data for *T. neoecobius* and *T. machaerophorus* taken from the literature.

ACKNOWLEDGMENTS

This work was supported by CNPq/PIBIC-IC (105077/2015-1) grant to RSB; CNPq (301776/2004-0) grant to ADB and CNPq (143049/2011-9) grant to JPB. We are grateful to the reviewers and the editor for their valuable comments. We are also grateful to Luiz F.M. Iniesta (IBSP) for his helping during this work. The version of the manuscript was improved by critical readings from Ross Martin Thomas.

LITERATURE CITED

- Attems CG (1898) System der Polydesmiden I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften zu Wien, Mathematisch-Naturwissenschaftliche Klassen 67: 221–482.
- Attems CG (1931) Die Familie Leptodesmidae und andere Polydesmiden. Zoologica 30: 1–150.
- Attems CG (1938) Polydesmoidea II. Families Leptodesmidae, Platyrhacidae, Oxydesmidae, Gomphodesmidae. Das Tierreich 69: 1–487.
- Brewer MS, Sierwald P, Bond JE (2012) Millipede taxonomy after 250 years: classification and taxonomic practices in a mega-diverse yet understudied arthropod group. Plos One 7: 1–12. <https://doi.org/10.1371/journal.003724>
- Brölemann HW (1900) Dous myriapodos notáveis do Brazil, Notas Myriapodologicas. Boletim do Museu Paraense 3: 65–71.
- Brölemann HW (1902) Myriapodes du Musée de São Paulo. Revista do Museu Paulista 5: 35–237. <https://doi.org/10.5962/bhl.part.9824>
- Chamberlin RV (1952) Some American polydesmid millipeds in the collection of Chicago Museum of Natural History. Annals of the Entomological Society of America 45: 553–584. <https://doi.org/10.1093/aesa/45.4.553>
- Eberhard WG (2010) Rapid divergent evolution of genitalia. In: Leonard J, Cordoba-Aguilar A (Eds) The evolution of primary sexual characters in animals. Oxford University Press, New York, 40–78.
- Hoffman RL (1965) Chelodesmid studies I. The status of the generic name *Hoffmanodesmus* Schubart (Diplopoda: Polydesmida). Papéis Avulsos de Zoologia 17: 219–223.
- Hoffman RL (1971) Chelodesmid studies V. Some new, redefined, and resurrected Brazilian genera. Arquivos de Zoologia 20: 225–277. <https://doi.org/10.11606/issn.2176-7793.v20i4p225-277>
- Hoffman RL (1980) Classification of the Diplopoda. Muséum d'histoire naturelle, Geneva, 237 pp.
- Hoffman RL (1990) Chelodesmid studies XXII. Synopsis of *Tessarithys*, a new genus of Brazilian millipeds (Diplopoda: Chelodesmidae). Papéis Avulsos de Zoologia 37: 159–166.
- Pena-Barbosa JPP, Sierwald P, Brescovit AD (2013) On the largest chelodesmid millipedes: taxonomic review and cladistic analysis of the genus *Odontopeltis* Pocock, 1894 (Diplopoda; Polydesmida; Chelodesmidae). Zoological Journal of the Linnean Society 169: 737–764. <https://doi.org/10.1111/zoj.12086>
- Schubart O (1943) Espécies novas das famílias Strongylosomidae e Leptodesmidae da ordem Proterospermophora do interior dos estados de São Paulo e de Mato-Grosso. Papéis avulsos do Departamento de Zoologia 3: 127–164.
- Schubart O (1946) Contribuição ao conhecimento do gênero *Leptodesmus* (Leptodesmidae, Diplopoda). Anais da Academia Brasileira de Ciências 18: 165–202.



Schubart O (1956) Leptodesmidae Brasileiras. IV: Espécies novas da Bahia (Diplopoda, Proterospermophora). *Revista Brasileira de Biologia* 16: 421–428.

Schubart O (1962) Leptodesmidae Brasileiras. IX: Sobre algumas espécies do gênero *Camptomorpha* (Proterospermophora, Diplopoda). *Revista Brasileira de Biologia* 22: 251–261.

Sierwald P, Bond JE, Gurda GT (2005) The millipede type specimens in the collections of the Field Museum of Natural History (Arthropoda: Diplopoda). *Zootaxa* 1005: 1–64. <https://doi.org/10.11646/zootaxa.1005.1.1>

Submitted: 18 August 2016

Received in revised form: 4 January 2017

Accepted: 7 February 2017

Editorial responsibility: Ricardo Pinto da Rocha

Author Contributions: RSB produced all images (drawings, photos and maps) and description; RSB, JPPPB and ADB examined material and wrote the text.

Competing Interests: The authors have declared that no competing interests exist.