Biota Neotropica 23(3): e20231521, 2023
www.scielo.br/bn

biotaneotropica
ISSN 1676-0611 (online edition)

Article

A case of mass occurrence of *Sandalodesmus araujoi* (Schubart, 1946) in a municipality of São Paulo, Brazil and description of the heretofore unknown female (Polydesmida, Chelodesmidae)

***Rodrigo S. Bouzan*[1,2]*, *Jackson C. Means*[3], *Kaloyan Ivanov*[3], *Giovanni B. Pupin*[1], *Antonio D. Brescovit*[1] & *Luiz F. M. Iniesta*[1,4]**

[1]*Instituto Butantan, Laboratório de Coleções Zoológicas, Av.Vital Brasil, 1500, Butantã, 05503-900, São Paulo, SP, Brasil.*
[2]*Universidade de São Paulo, Instituto de Biociências, Pós-Graduação em Zoologia, R. Do Matão, Butantã, 05508-090, São Paulo, SP, Brasil.*
[3]*Virginia Museum of Natural History, Department of Recent Invertebrates, 21 Starling Ave., 24112, Martinsville, VA, United States of America.*
[4]*Universidade Federal do Maranhão, Coordenação do Curso de Licenciatura em Ciências Naturais/Codó, Av. José Anselmo, 2008, 65400-000, Codó, MA, Brasil.*
**Corresponding author: rodrigobouzan@outlook.com*

BOUZAN, R.S., MEANS, J.C., IVANOV, K., PUPIN, G.B., BRESCOVIT, A.D., INIESTA, L.F.M. **A case of mass occurrence of *Sandalodesmus araujoi* (Schubart, 1946) in a municipality of São Paulo, Brazil and description of the heretofore unknown female (Polydesmida, Chelodesmidae).** Biota Neotropica 23(3): e20231521. https://doi.org/10.1590/1676-0611-BN-2023-1521

Abstract: Somatic characters are shared by many Chelodesmidae groups, and generic placement and species identifications traditionally have been based on gonopodal morphology. Female genitalic characters have been largely neglected and are rarely photographed or illustrated. This is rather unfortunate as the morphology of female genitalia presents important characters and may be decisive for developing a more robust family classification. We describe the heretofore unknown female of *Sandalodesmus araujoi* (Schubart, 1946), previously known only from the male holotype collected in São Paulo, Brazil in December 1943; discuss the utility of female genitalic characters for species delineation in *Sandalodesmus*; and report the first case of a mass occurrence in the Chelodesmidae. While an attempt at a formal diagnosis of *Sandalodesmus* females based on genitalic characters is premature, the vulvar morphology of the three taxa examined in this study suggests that female genitalia are species-specific. Some characters (i.e., asymmetric valves, presence of digitiform projections and reduction of setae on the internal basal portion of the valves) are constant between the species, suggesting utility for generic-level delineation. Mass occurrences of millipedes are typically unpredictable and likely related to variations in environmental conditions and/or anthropogenic modifications of natural habitats. Although the mass occurrence of *S. araujoi* reported herein was only observed once, the event coincides with the mating period of millipedes during the rainy season in Brazil. On the other hand, the region where the species was found has been the target of intense urban development, including replacement of natural habitats with residential areas, which may have influenced its population dynamics.
***Keywords*:** *millipedes; Neotropics; population outbreak; Sandalodesmini; swarming; taxonomy.*

Um caso de ocorrência em massa de *Sandalodesmus araujoi* (Schubart, 1946) em um município de São Paulo, Brasil e descrição da fêmea até então desconhecida (Polydesmida, Chelodesmidae)

Resumo: Os caracteres somáticos são compartilhados por muitos grupos de Chelodesmidae, e o posicionamento genérico e as identificações de espécies tradicionalmente têm sido baseadas na morfologia do gonópodo. Carateres genitais das fêmeas foram amplamente negligenciados e raramente são fotografados ou ilustrados. Isso é lamentável, pois a morfologia da genitália feminina apresenta características importantes e pode ser decisiva para o desenvolvimento de uma classificação mais robusta. Neste trabalho, descrevemos a até então desconhecida fêmea de *Sandalodesmus araujoi* (Schubart, 1946), anteriormente conhecida apenas pelo holótipo macho coletado em São Paulo, Brasil, em dezembro de 1943; discutimos a utilidade de caracteres genitais femininos para delineamento de

espécies em *Sandalodesmus*; e relatamos o primeiro caso de ocorrência em massa para Chelodesmidae. Embora uma tentativa de diagnose formal para fêmeas de *Sandalodesmus* com base em caracteres genitais seja prematura, a morfologia vulvar dos três táxons examinados neste estudo, sugere que a genitália feminina é espécie-específica. Alguns caracteres (e.g. válvulas assimétricas, presença de projeções digitiformes e redução de cerdas na margem interna das válvas) são constantes entre as espécies do gênero, sugerindo utilidade para delineamento em nível genérico. Ocorrências em massa de milípedes são tipicamente imprevisíveis e provavelmente relacionadas a variações nas condições ambientais e/ou modificações antropogênicas de habitats naturais. Embora a ocorrência em massa de *S. araujoi* aqui relatada tenha sido observada apenas uma vez, o evento coincide com o período de reprodução dos milípedes durante a estação chuvosa no Brasil. Por outro lado, a região onde a espécie foi encontrada tem sido alvo de intenso desenvolvimento urbano, incluindo substituição de habitats naturais por áreas residenciais, o que pode ter influenciado sua dinâmica populacional.

Palavras-chave: *Milípede; piolho-de-cobra; Neotrópicos; surto populacional; Sandalodesmini; taxonomia.*

Introduction

With over 5,000 described species, Polydesmida is the most diverse order within the class Diplopoda and includes the two most species-rich families of millipedes, Paradoxosomatidae Daday, 1889 (approx. 1,000 described species) and Chelodesmidae Cook, 1895 (750+ described species) (Hoffman 1980, Shelley 2002, Brewer et al. 2012, Nguyen and Sierwald 2013, Enghoff et al. 2015). Chelodesmidae is divided into two subfamilies, Chelodesminae (139 genera) distributed across the Neotropical region, and Prepodesminae (37 genera) known from the Afrotropical and Palearctic regions (Hoffman 1980). Currently, 21 tribes are recognized within the Chelodesmidae, with 19 of them belonging to Chelodesminae, however, more than half of the described genera and species have yet to be assigned to a tribe (Bouzan et al. 2021).

Based chiefly on gonopodal characters, Hoffman (1982) proposed the tribe Sandalodesmini to include the South American *Oncoleptodesmus* Schubart, 1958 and *Sandalodesmus* Silvestri, 1902. Members of the tribe are small to moderately sized chelodesmids (25-45mm in length) with relatively slender bodies and reduced gonopods, characterized by the presence of a shield-like acropodite which conceals the solenomere in the lateral view, a subspatulate prefemoral process that partially envelops the acropodite, the presence of a spiniform process on the gonocoxa, and a modified, hook-like cannula (Hoffman 1982). *Sandalodesmus* differs from *Oncoleptodesmus* by the presence of only two macrosetae on the dorsal side of the gonocoxae and by the absence of spinulations on the lateral margin of the acropodite [except in *Sandalodesmus repandus* (Schubart, 1985); Silvestri 1902, Schubart 1958, Hoffman 1982, Rojas-Buffet et al. 2022]. *Sandalodesmus* includes 14 species distributed across Argentina, Brazil, Paraguay, and Uruguay and *Oncoleptodesmus* includes four species only known from the Brazilian state of Rio Grande do Sul (Attems 1931, 1938; Schubart 1958; Hoffman 1982; Rojas-Buffet et al. 2022). *Sandalodesmus* was reviewed by Hoffman (1982) and recently Rojas-Buffet et al. (2022) provided an updated key to the males.

Somatic characters are shared by many genera within the Chelodesmidae and generic placement and species identification have been traditionally based on gonopodal morphology (Hoffman 1971, Pena-Barbosa et al. 2013, Bouzan et al. 2017a). Female genitalic characters have been largely neglected, seldom examined, and rarely photographed or illustrated (Brölemann 1902; Schubart 1946; Hoffman 1990a, 1990b, 2000; Pena-Barbosa et al. 2013; Bouzan et al. 2017b, 2018a, 2018b). *Sandalodesmus* is no exception, and the females of only six of the 14 known species have been described in some, often very abbreviated, manner. To date, only the females of *Sandalodesmus joachimadisi* Rojas-Buffet and Bouzan, 2022 have been described in detail, including description of genitalic characters, and illustrated (Rojas-Buffet et al. 2022). This is rather unfortunate as the morphology of the female genitalia presents important characters and may be decisive for developing a more robust classification of the Chelodesmidae (see Hoffman 2012).

Mass occurrences (seemingly sudden increases in local abundance) in the Diplopoda are a result of natural cycles (reproduction swarming or lifecycle periodicity) or unpredictable changes in climate, resource availability, or fragmentation of natural habitat (David 2015, Niijima et al. 2021). Such events have been reported from Africa, Eurasia, and The Americas, and vary in magnitude from localized occurrences of hundreds of individuals to millions of individuals covering extensive areas (Cloudsley-Thompson 1949, Niijima et al. 2021). While small scale swarms can occasionally be a nuisance near human habitations in urban and suburban areas, large outbreaks have been reported to impact livestock, crop production, and even interfere with transportation (Cloudsley-Thompson 1949, Niijima et al. 2021). In an attempt to provide a more robust classification of millipede mass occurrences, Niijima et al. (2021) proposed the separation of these events into swarming (hundreds of individuals), mass emergence (thousands), and outbreak (millions), based on the number of individuals observed.

One of the largest millipede outbreaks ever recorded, occurred in West Virginia, USA in June, 1918 when an estimated 65,340,000 *Apheloria virginiensis corrugata* (Wood, 1864) covered 75 acres of farmland for over a month (Cloudsley-Thompson 1949). During this event, farmers were reportedly nauseated by the defensive chemicals released by the millipedes and cattle refused to graze in the impacted areas (Cloudsley-Thompson 1949). An equally impressive series of mass outbreaks have been reported for *Parafontaria laminata* (Attems, 1909) in Japan where mass occurrences of this species have caused multiple road and railroad obstructions between 1920 and 1984 (Niijima and Shinohara 1988, Niijima 1998, Niijima et al. 2021). Interestingly, *Parafontaria laminata armigera* Verhoeff, 1936 was recently shown to have a lifecycle akin to periodical cicadas with an outbreak event occurring every eight years (Niijima et al. 2021).

In Brazil, millipede population outbreaks are most commonly associated with non-native species including the Asian *Oxidus gracilis* (C. L. Koch, 1847) and *Orthomorpha coarctata* (Saussure, 1860)

(Polydesmida, Paradoxosomatidae), and more recently the Portuguese millipede, *Ommatoiulus moreleti* (Lucas, 1860) (Julida, Julidae) (Iniesta et al. 2020, 2021, 2022). Although all three species reach high densities in urban areas of southeastern Brazil, *O. gracilis* and *O. coarctata* have also become established in rural and natural environments, including forests, caves, and islands (Iniesta et al. 2021). There is little published information regarding population outbreaks of native millipedes in Brazil, except for those regarded as agricultural pests. The majority of these accounts concern species of Spirostreptida (Spirostreptidae and Pseudonannolenidae) in cultivated areas where they have been reported to cause damage to seedlings, tubers, and fruits (Schubart 1942; Boock and Lordello 1952; Lordello 1954; Boccardo et al. 1997, 2002). To date, there have been no published accounts of swarming or population outbreaks in the Chelodesmidae.

We report the first case of a mass occurrence in the Chelodesmidae and describe the heretofore unknown female of *Sandalodesmus araujoi* (Schubart, 1946), previously known only from the male holotype collected in the state of São Paulo, Brazil in 1943. In addition, we discuss the utility of female genitalic characters for species delineation in *Sandalodesmus* and provide additional information on male characters, including measurements and SEM images.

Materials and Methods

The material examined is deposited in the following collections (curators in parentheses): Instituto Butantan, São Paulo, Brazil (IBSP; A.D. Brescovit), Arachnida and Myriapoda collection of Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (FCE-Myr; M. Simó). Scanning electron micrographs were taken using a FEI Quanta 250 SEM (FEI, Oregon, USA) with an attached SLR digital camera at Instituto Butantan. Specimens selected for scanning electron imaging were cleaned two times (30 sec. each) ultrasonically, transferred to an ascending series of ethanol dilutions (70, 80, 90, and 100%), bathed for 15 minutes at each step, and critical-point dried. The samples were mounted on aluminum stubs and coated with gold in a sputter coater for 240 seconds. In addition, relevant morphological features were photographed with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereomicroscope and measured to the nearest 0.01 mm with Leica Application Suite ver. 2.5.0 (Leica Camera, Wetzler, Germany). Body-rings were measured in dorsal view, and antennomere lengths were measured in lateral view.

Female genitalic characters of *S. araujoi* (five specimens), *S. joachimadisi* Rojas-Buffet and Bouzan, 2022 (two specimens) and *Sandalodesmus* sp. (two specimens from Estação Ecológica Jureia/Itatins, São Paulo, Brazil) were examined and photographed in order to explore their utility in species delineation and classification.

Distribution maps were generated using the freeware DIVA-GIS ver. 7.5.0 (Hijmans *et al.* 2001).

Terminology of sexual and somatic characters follows Attems (1898), Brölemann (1900), Pena-Barbosa et al. (2013), and Koch (2015).

Results

The mass occurrence reported herein was brought to the lead author's attention in October 2021 when videos of the event were sent to him by Nicoly Calcagniti (Supplementary Material 1). Subsequently, several male and female specimens were received by the authors and identified as *S. araujoi*. The mass occurrence took place in the municipality of Pardinho (–23.0825, –48.3852), approx. 30 km southeast of the type locality of *S. araujoi* in the municipality of São Manuel (–22.7423, –48.6191) (Figure 1). According to the residents of the municipality, thousands of individuals were observed around house entrances, gardens, and on pavement in the morning and afternoon hours.

The locality where the mass occurrence took place is part of a transitional zone between the Cerrado and Atlantic Forest biomes in the state of São Paulo (Coutinho 2006). The area has a subhumid temperate climate and is characterized by a patchwork of herbaceous and forested habitats which have resulted from retractions and transgressions during the Quaternary (Coutinho 2006, Alvares et al. 2014, Smith and Mayle 2017). Since the second half of the 20th Century, the region has been severely impacted by human activities, including deforestation, farming practices, livestock production, and accelerated urbanization (Ratter et al. 1997).

Order Polydesmida Pocock, 1887

Family Chelodesmidae Cook, 1895

Subfamily Chelodesminae Cook, 1895

Tribe Sandalodesmini Hoffman, 1982

Genus *Sandalodesmus* Silvestri, 1902

Sandalodesmus araujoi (Schubart, 1946)

(Figures 1–17)

Leptodesmus araujoi Schubart 1946: 171, figure 4 (male holotype from São Manuel [-22.7423, -48.6191], São Paulo, Brazil, 09–11.xii.1943, R. L. Araujo leg., deposited at MZSP, examined); Schubart 1955: 516.

Leptodesmus (Gonioleptodesmus) araujoi:-- Schubart 1958: 29.

Gonioleptodesmus araujoi:-- Hoffman 1967: 34.

Sandalodesmus araujoi:-- Hoffman 1982: 251; Bouzan et al. 2018c: 11; Rojas-Buffet et al. 2022: 266.

New record. BRAZIL, São Paulo, Pardinho; –23.0825, –48.3852; 900 m; October 2021; N. Calcagniti leg.; in urban areas, around house entrances, gardens, and on pavement; 1♂ (IBSP 14277); 1♀ (IBSP 14278); 6♂♂, 6♀♀ (IBSP 14279).

Diagnosis. Males of *S. araujoi* can be separated from those of *Sandalodesmus gasparae* (Schubart, 1944) (Schubart 1944, figures 22-23) and *Sandalodesmus hippocampus* (Schubart, 1944) (Schubart 1944, figures 25-26), the only other *Sandalodesmus* species known from the state of São Paulo, by the presence of a prominent subtriangular, secondary process on the lateral side of the acropodite (Figures 4A, C). In addition, males of *S. araujoi* can be separated from those of *Sandalodesmus salvadorii* (Silvestri, 1895), the only other member of the *salvadorii* species group (see Hoffman [1982]), based on the rounded, mesally curving acropodite (Figures 4A, C), which is subtriangular and curving cephalad in *S. salvadorii* (Hoffman 1982, Rojas-Buffet et al. 2022).

Description. Male (new data; IBSP 14277): With characteristics typical for the genus. Coloration in life: body rings dark brown,

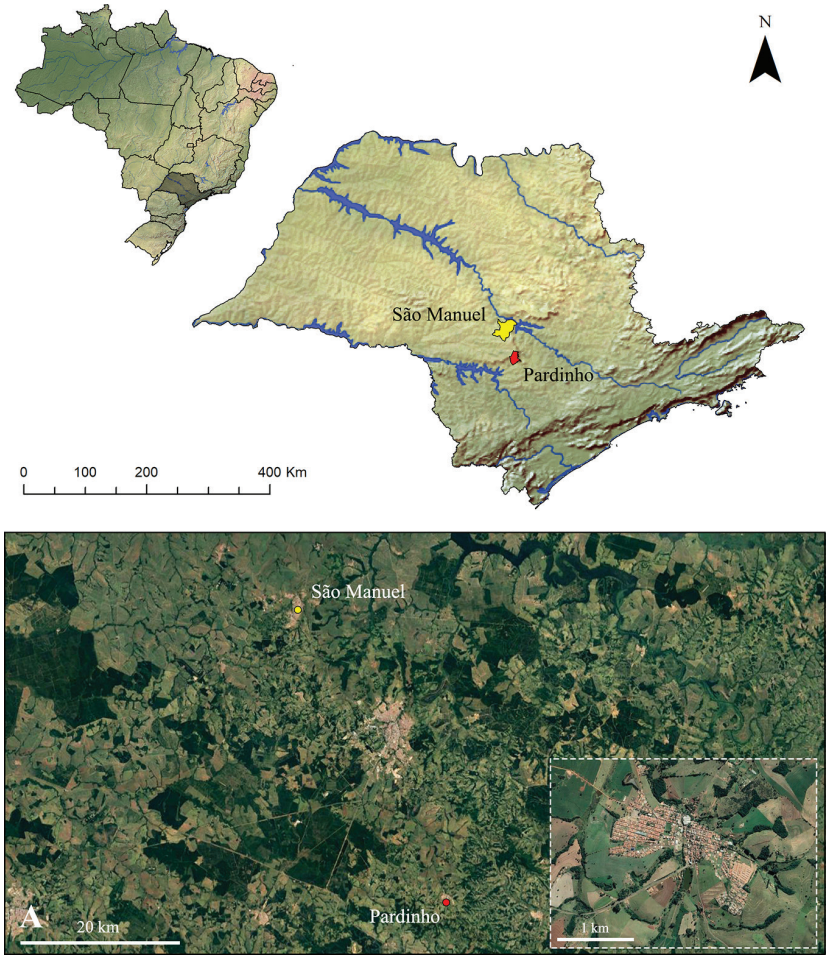

Figure 1. Known distribution of *S. araujoi* with the São Manuel type locality shown in yellow and the new record from Pardinho shown in red.

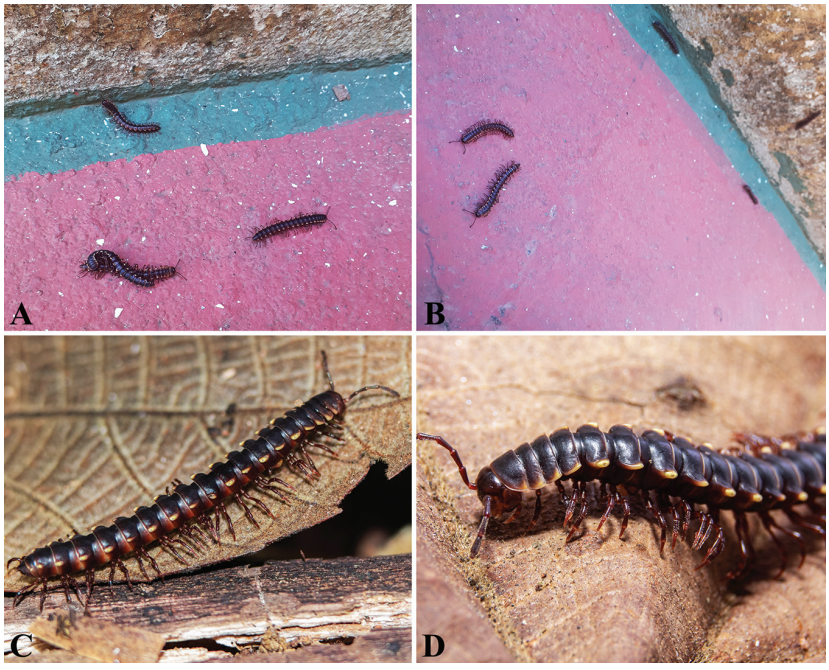

Figure 2. A–D. Living specimens of *S. araujoi* from Pardinho, São Paulo, Brazil.

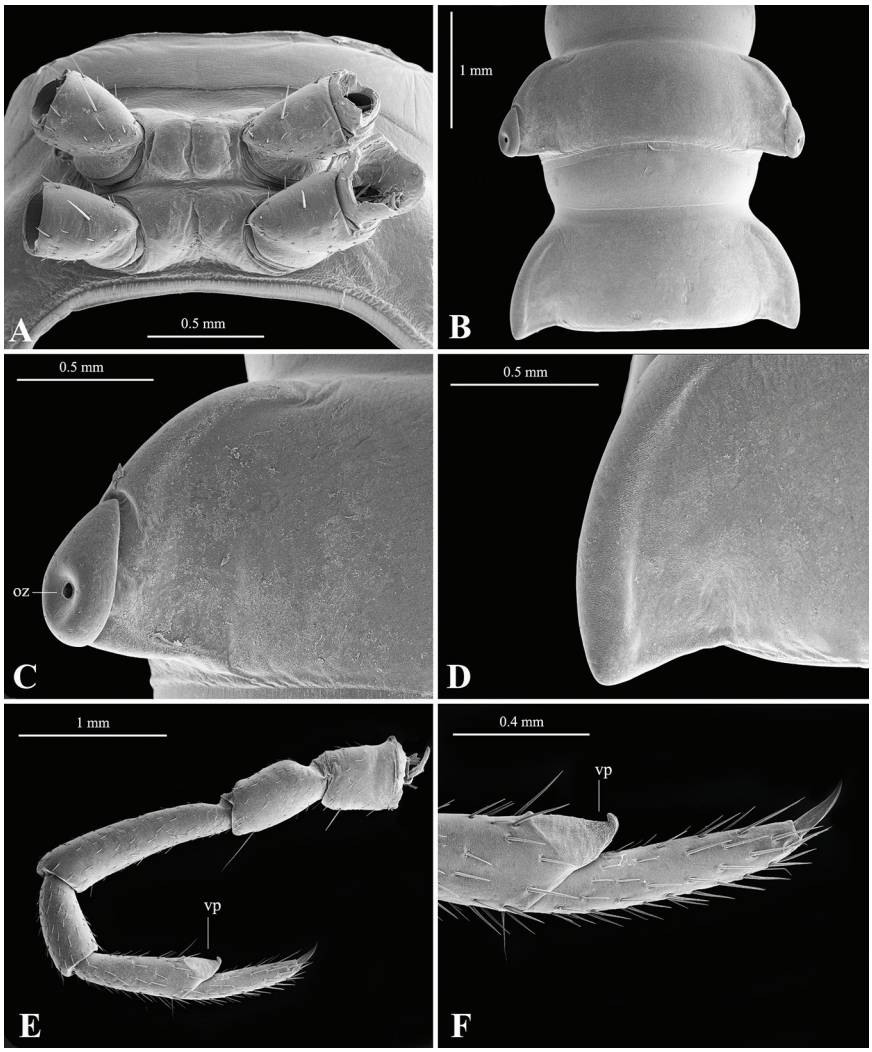

Figure 3. A–F. SEM images of somatic characters of *S. araujoi* (IBSP 14279). A, Projections of sternite 4, ventral view. B, Midbody rings, dorsal view. C, Paranota with ozopore, dorsal view. D, Paranota, dorsal view. E, Midbody leg. F, Detail of tibial ventral pad. Abbreviations: vp= ventral pad, oz= ozopore.

head, antennae, and legs reddish-brown, paranota tips yellowish (Figures 2A–D). *Head:* epicranial macrosetae 2–2, interantennal macrosetae 1–1, frontal macrosetae 1–1. *Body:* rings smooth; paranota subtriangular, with standard polydesmidan pore formula (5, 7, 9, 10, 12, 13, 15–19; Figures 3B–D); ozopores situated posteriorly (Figure 3C); sternite of 4th body ring with two pairs of partly appressed projections (Figure 3A). *Legs:* with ventral tibial pads, except for the last leg pair (Figures 3E–F).

Gonopods: prefemoral process (pfp) subtriangular, slightly twisted, and parallel to acropodite (ap) (Figures 4A, C); cannula (ca) hook-shaped (Figure 4C); seminal groove (sg) S-shaped along the acropodite, ending at apex of solenomere (Figure 4C); prefemoral region (pf) densely setose (Figures 4A, C); acropodite (ap) broad, elongated, strongly curved mesad (Figures 4A, C), with part of its margin serrated mesally (Figures 4A–B, white arrow), and with a prominent subtriangular secondary process; solenomere (s) sickle-shaped, curved mesad (Figure 4C).

Measurements (mm): Body: total length (n = 3), average = 34.1 (range = 29.1 – 38.5); width of 10th body ring (n = 3), average = 3.6 (range = 3.3–3.8). Antennomere lengths (1–7): 0.33, 0.91, 0.87, 0.80, 0.88, 0.82, 0.21. Telson length: 0.6.

Female (IBSP 14278): Coloration in life as in male. Similar to male in general body outline and somatic characters, except sternite of 4th body ring with less conspicuous and separate projections, all remaining sternites and all legs without modification. Posterior margin of vulvar aperture smooth, without projections. *Vulvae* (Figures 4D–F): densely setose, ovoid in ventral view and subrectangular in lateral view. External and internal valves asymmetrical, projecting ventrad. External valve (Ev) projecting distad, distinctly longer than the internal valve (Iv). Internal margins of valves irregular medially, with digitiform projections (Figure 4F). Internal basal portion of valves, in ventral view without setae. Operculum (Op): small, flattened, with setae at the base, approximately 1/6 size of valves.

Measurements (mm): Body: total length (n = 3), average = 30.1 (range = 29.2 – 30.8); width of 10th body ring (n = 3), average = 3.3 (range = 3.2–3.4). Antennomere lengths (1–7): 0.32, 0.81, 0.67, 0.70, 0.74, 0.73, 0.20. Width of posterior margin of vulvar aperture 1.4. Vulvae: ventral length 0.88, ventral width 0.53. Valves asymmetrical.

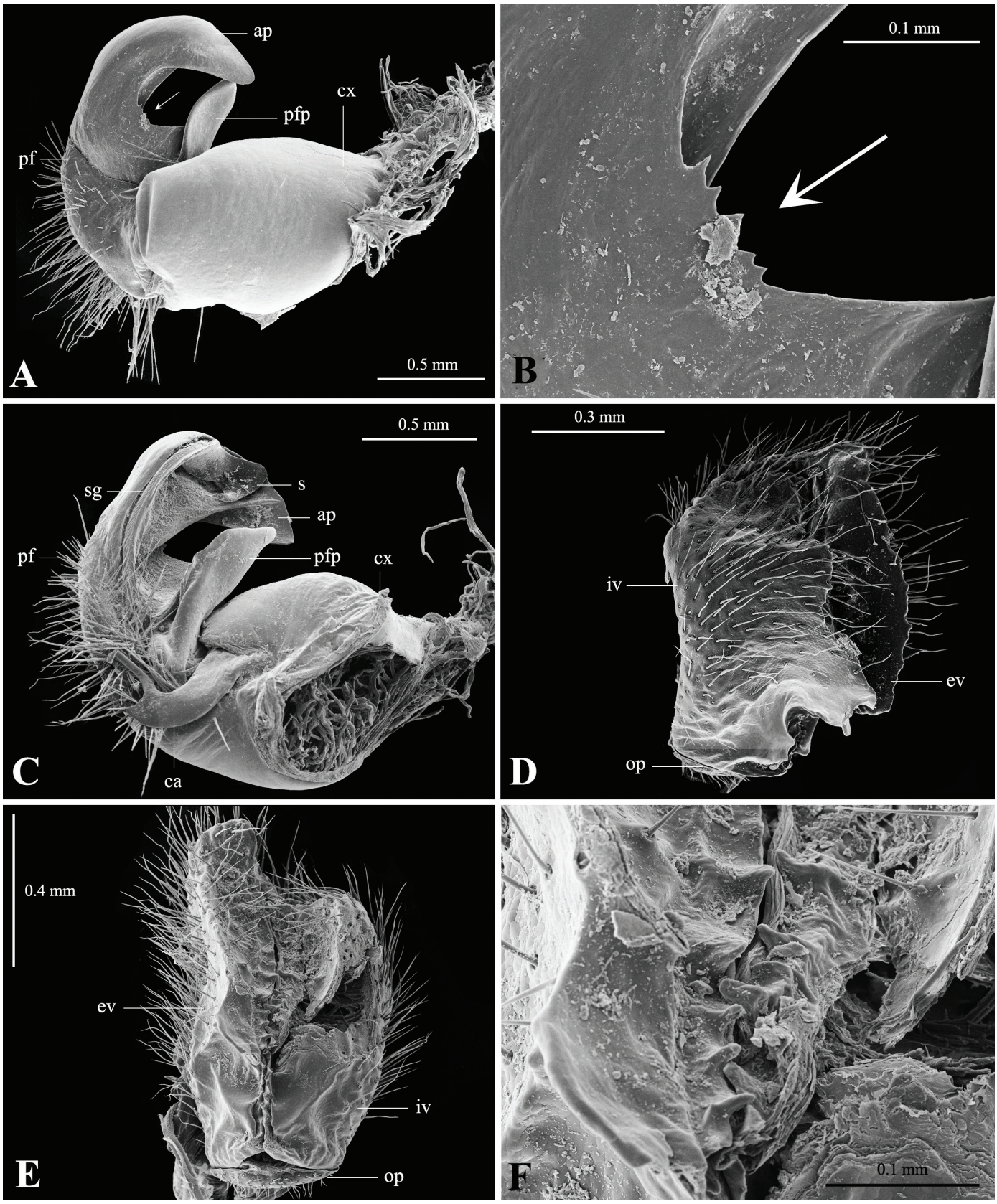

Figure 4. A–F. SEM images of genitalic characters of *S. araujoi* (IBSP 14279). A, Left gonopod, ectal view. B, Detail of mesal portion of the acropodial process, ectal view. C, Right gonopod, mesal view. D, Left vulva, ectal view. E, Right vulva, ventral view. F, Detail of the junction of the valves, ventral view. Abbreviations: ap= acropodital process, ca= cannula, cx= gonocoxa, ev= external valve, iv= internal valve, op= operculum, pf= prefemur, pfp= prefemoral process, s= solenomere, sg= seminal groove. The subtriangular secondary process is hidden by the prefemoral process in ectal and mesal view.

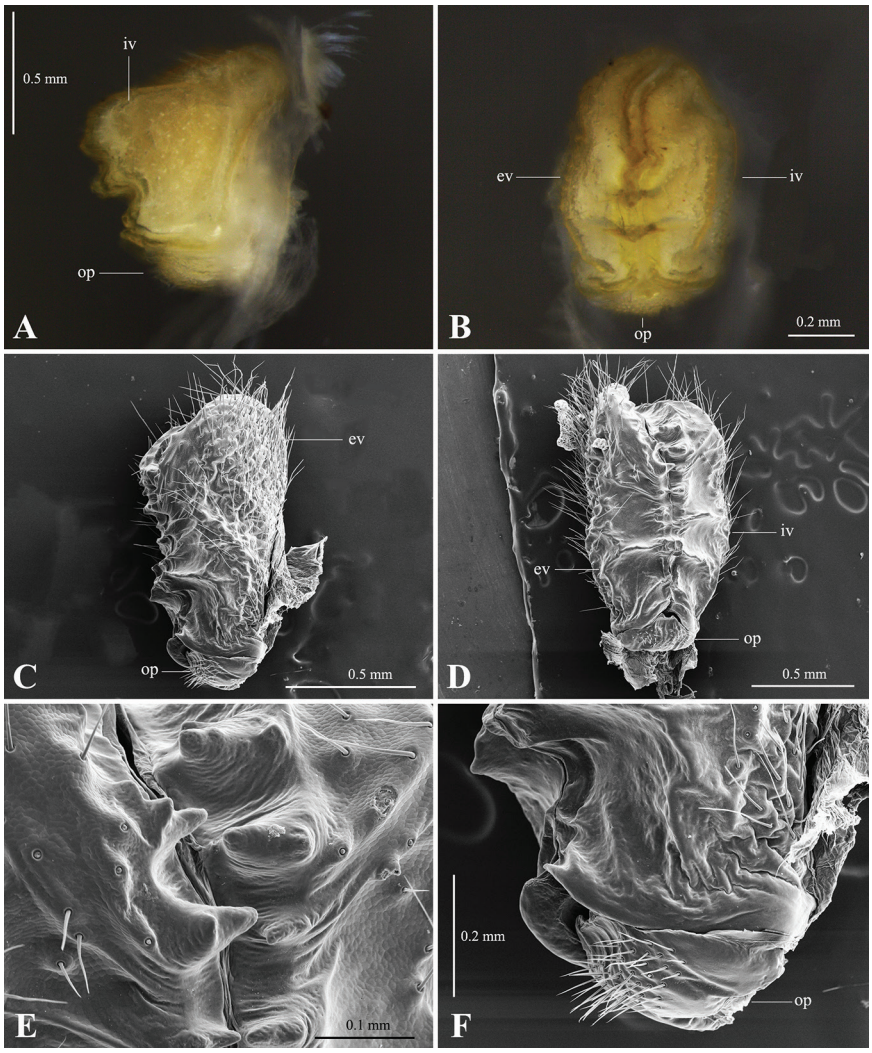

Figure 5. A–F. Steromicroscope (5A–B) and SEM images (5C–F) of vulvae of *Sandalodesmus* species: A, Right vulva of *S. joachimadisi* (FCE-Myr 0664), ectal view; B, Right vulva of *S. joachimadisi* (FCE-Myr 0664), ventral view. C, Left vulva of *Sandalodesmus* sp. (IBSP 3741), ectal view. D, Right vulva of *Sandalodesmus* sp. (IBSP 3741), ventral view. E, Detail of the junction of the valvae of *Sandalodesmus* sp. (IBSP 3741), ventral view. F, Detail of the operculum of *Sandalodesmus* sp. (IBSP 3741), ectal view. Abbreviations: ev= external valve, iv= internal valve, op= operculum.

External valve: lateral length 0.72, lateral width 0.61. Internal valve: lateral length 0.61, lateral width 0.59. Operculum: ventral length 0.14, ventral width 0.34. Telson length: 0.6.

In comparison to *S. araujoi*, the size difference between the external and internal valves of *Sandalodesmus* sp. (from Estação Ecológica Jureia/Itatins, São Paulo, Brazil) is less pronounced, and those of *Sandalodesmus* sp. have larger and fewer digitiform projections which continue to the apical portion of the valves (Figures 4E-F; 5B, 5D-F). In addition, the vulvae of *Sandalodesmus* sp. have a pronounced horizontal ridge spanning both valves and delineating the bottom third of each (Figures 5C–D). As compared to the previous two species, the valves of *S. joachimadisi* are relatively symmetrical, with only a slight enlargement of the external valve, and with fewer and more robust digitiform projections on the internal margin (Figures 5A–B). In addition, the lateral profile of the valves of *S. joachimadisi* is distinctly subtriangular while those of both *S. araujoi* and *Sandalodesmus* sp. are subrectangular, narrower near the operculum and widening towards the apex (Figures 4D, 5A, 5C).

Discussion

Although numerous collection events have targeted the area surrounding the type locality of *S. araujoi*, until the mass occurrence reported herein, this species was known only from the single male holotype collected in the municipality of São Manuel in December 1943 (Schubart 1946).

Millipede female genitalia undoubtedly contain valuable taxonomic information, however, they have been historically neglected and have been rarely included in species descriptions. Genitalic characters of female *Sandalodesmus* remain poorly known, and only those of *S. joachimadisi* have been described and properly illustrated (Rojas-Buffet et al. 2022: figure 3D). While an attempt at a formal diagnosis of females based on genitalic characters is premature, the vulvar morphology of the three taxa examined herein suggests that *Sandalodesmus* female genitalia are species-specific. In addition, some characters, such as the asymmetric (to different degrees) valves, and the presence of digitiform projections and the reduction or absence of setae on the internal basal portion of the valves, are constant between the species, suggesting utility for generic-level

delineation. Additional studies on the morphology of *Sandalodesmus* female genitalia are needed to assess their systematic importance.

With the exception of the population outbreaks of the Japanese *P. laminata armigera*, mass occurrences of millipedes are typically unpredictable and likely related to variations in environmental conditions and/or anthropogenic modifications of natural habitats. Although the mass occurrence of *S. araujoi* reported herein was only observed once, the timing of the event coincides with the mating period of millipedes during the rainy season (October–April) in Brazil (see Alvares et al. 2013). On the other hand, the region where the species was found has been the target of intense urban development, including replacement of natural vegetation with residential areas, which may have influenced its population dynamics. More detailed studies are needed to tease apart the factors contributing to these largely unpredictable events.

The original communities of the Cerrado and the Atlantic Forest in southeastern Brazil, two of the world's premier biodiversity hotspots, have been severely altered by anthropogenic activities, such as medium to large-scale farming practices, livestock production, and accelerated urbanization, and are rapidly disappearing (Fonseca 1985, Durigan et al. 2007). To date, approximately 50% of the Cerrado has been destroyed by human activities (Rodriguez-Zorro et al. 2022), and only 10% of the original vegetation of the Atlantic Forest remains (Colombo and Joly 2010, Joly et al. 2014, Rezende et al. 2018). The region, long known for its vertebrate and invertebrate diversity and high levels of endemicity, was also recently shown to contain the highest species richness and the highest concentration of threatened Spirostreptida in Brazil making its conservation vital for the protection of numerous plant and animal taxa (Iniesta et al. 2023).

Supplementary Material

The following online material is available for this article:
Supplementary Material 1

Acknowledgments

We thank Beatriz Mauricio (Laboratório de Biologia Celular of the Instituto Butantan) for her help with the SEM imaging, Carolina Rojas-Buffet for the *S. joachimadisi* vulvae photographs, and Nicoly Calcagniti and Leandro Lisardo for alerting us regarding the mass occurrence of *S. araujoi* and for sending us the specimens used in this study. Comments from Antonio Parra-Gomez and an anonymous reviewer improved the manuscript. This study was financially supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (grant to RSB; 88887.510007/2020-00). LFMI was supported by grant 162977/2020-4 from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and ADB by the grant CNPq (303028/2014-9) and by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; 2022/12588-1). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES - Finance Code 001).

Associate Editor

Gustavo Graciolli

Author Contributions

Rodrigo Salvador Bouzan: formulated the idea; data collection; manuscript preparation and revision.

Jackson C. Means: data collection; manuscript preparation and revision.

Kaloyan Ivanov: data collection; manuscript preparation and revision.

Giovanni B. Pupin: manuscript preparation and revision.

Antonio D. Brescovit: manuscript preparation and revision.

Luiz F. M. Iniesta: data collection; manuscript preparation and revision.

Conflicts of Interest

The authors declare that there is no conflict of interest related to the publication of this manuscript.

Data Availability

The data used in this study are available at Biota Neotropica Dataverse
https://doi.org/10.48331/scielodata.W9CXON

References

ALVARES, C. A., J. Z. STAPE, P. C. SENTELGA, J. L. MORAES-GONÇALVES, AND G. SPAROVEK. 2013. Köppen's climate classification map for Brazil. Meteorologische zeitschrift 22(6): 711–728.

ATTEMS, C. M. T. GRAF VON. 1898. System der Polydesmiden. I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften zu Wien, Mathematisch-Naturwissenschaftliche Classe 67: 221–482.

ATTEMS, C. M. T. GRAF VON. 1931. Die Familie Leptodesmidae und andere Polydesmiden. Zoologica Stuttgart (79): 1–150.

ATTEMS, C. M. T. GRAF VON. 1938. Myriapoda 3. Polydesmoidea II. Fam. Leptodesmidae, Platyrhachidae, Oxydesmidae, Gomphodesmidae. Das Tierreich 69: 1–487.

BOCCARDO, L., R. JUCÁ-CHAGAS, AND C. H. S. PENTEADO. 2002. Migration and Population Outbreaks of Millipedes in the Coffee Plantations, Region of Alto Paranaiba, MG, Brazil. Holos Environment 2(2): 220–223.

BOCCARDO, L., C. H. S. PENTEADO, AND R. JUCÁ-CHAGAS. 1997. Swarming of millipedes, a new case noticed in the district of Patrocínio – MG - Brazil. Journal of Advanced Zoology 18: 62–63.

BOOCK, O. J. AND L. G. E. LORDELLO. 1952. Diplópoda depredador de tubérculos de batatinha. Bragantia12: 343–348. doi:10.1590/S0006-87051952000400006.

BOUZAN, R. S., J. P. P. PENA-BARBOSA, AND A. D. BRESCOVIT. 2017a. Two new Brazilian species of Chelodesmidae of the genera *Iguazus* and *Tessarithys* (Diplopoda: Polydesmida). Zoologia 34: 1−8. doi:10.3897/zoologia.34.e19986.

BOUZAN, R. S., J. P. P. PENA-BARBOSA, AND A. D. BRESCOVIT. 2017b. Taxonomic review of the genus *Atlantodesmus* Hoffman, 2000 (Polydesmida: Chelodesmidae). Zootaxa 4236(2): 269−290. doi:10.11646/zootaxa.4236.2.3.

BOUZAN, R. S., L. F. M. INIESTA, AND A. D. BRESCOVIT. 2018a. A review of the millipede genus *Rupidesmus* Schubart, 1952 (Polydesmida: Chelodesmidae). Zootaxa 4434(3): 589−599.

BOUZAN, R. S., L. F. M. INIESTA, C. A. R. SOUZA, AND A. D. BRESCOVIT. 2018b. A new record after a century and description of the female of *Plectrogonodesmus gounellei* (Brölemann 1902) (Polydesmida: Chelodesmidae). Studies on Neotropical Fauna and Environment 54(1): 61−68. doi:10.1080/01650521.2018.1536018.

BOUZAN, R. S., L. F. M. INIESTA, J. P. P. PENA-BARBOSA, AND A. D. BRESCOVIT. 2018c. Annotated checklist of the millipede family Chelodesmidae Cook, 1895 from São Paulo state, Brazil (Diplopoda: Polydesmida). Papéis Avulsos de Zoologia 58: 1–19. doi:10.11606/1807-0205/2018.58.06.

BOUZAN, R. S., L. F. M. INIESTA, AND A. D. BRESCOVIT. 2021. Cladistic analysis and taxonomic review of the millipede tribe Arthrosolaenomeridini Hoffman, 1976 (Polydesmida: Chelodesmidae). Zootaxa 4970(2): 201-256.

BREWER, M. S., P. SIERWALD, AND J. E. BOND. 2012. Millipede taxonomy after 250 years: classification and taxonomic practices in a mega-diverse yet understudied arthropod group. PLoS ONE 7(5): e37240. doi:10.1371/journal.pone.0037240

BRÖLEMANN, H. W. 1900. Myriapodes d'Amérique. Mémoires de la Société Zoologique de France 13: 89–131.

BRÖLEMANN, H. W. 1902. Myriapodes recueillis par M. E. Gounelle au Brésil. Annales de la Société Entomologique de France 71: 649–694.

CLOUDSLEY-THOMPSON, J. L. 1949. The significance of migration in myriapods. The Annals and Magazine of Natural History 12(2): 947–62.

COLOMBO, A. F., AND C. A. JOLY. 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian Journal of Biology 70: 697–708. doi:10.1590/S1519-69842010000400002.

COUTINHO, L. M. 2006. O conceito de bioma. Acta Botanica Brasilica 20(1): 13–23. doi:10.1590/S0102-33062006000100002.

DAVID, J. F. 2015. Diplopoda – ecology, pp. 303–327. *In* Minelli, A., ed. Treatise on Zoology - Anatomy, Taxonomy, Biology. The Myriapoda. Boston: Brill. 498 pp.

DURIGAN, G., M. F. SIQUEIRA, G. A. D. C. FRANCO. 2007. Threats to the Cerrado remnants of the state of São Paulo, Brazil. Scientia Agricola 64(4): 355–363. doi:10.1590/S0103-90162007000400006.

ENGHOFF, H., S. I. GOLOVATCH, M. SHORT, P. STOEV, AND T. WESENER. 2015. Diplopoda - taxonomic overview, pp. 363 – 454. *In* A. Minelli (Ed), Treatise on Zoology - Anatomy, Taxonomy, Biology. The Myriapoda. Brill, Boston. 498 pp.

FONSECA, G. A. B. 1985. The vanishing Brazilian Atlantic forest. Biological Conservation 34: 17–34. doi:10.1016/0006-3207(85)90055-2.

HIJMANS, R. J., M. CRUZ, E. ROJAS AND L. GUARINO. 2001. DIVA-GIS, Version 1.4. A geographic information system for the management and analysis of genetic resources data. Manual. International Potato Center, Lima, Peru.

HOFFMAN, R. L. 1967. Chelodesmid Studies III. Notes on the status of *Gonioleptodesmus*, the description of a new species from Minas Gerais, and a key to the presently known members of the genus (Diplopoda, Polydesmida). Papéis Avulsos de Zoología 21(4): 33–42.

HOFFMAN, R. L. 1971. Chelodesmid studies V. Some new, redefined, and resurrected Brazilian genera. Arquivos de Zoologia, São Paulo 20(4): 225–277. doi:10.11606/issn.2176-7793.v20i4p225-277.

HOFFMAN, R. L. 1980. Classification of the Diplopoda. Múseum d'histoire naturelle, Genève. 237 pp.

HOFFMAN, R. L. 1982. Chelodesmid studies. XVIII. A synopsis of the genus *Sandalodesmus* Silvestri, 1902, and proposal of the new tribe Sandalodesmini (Polydesmida: Chelodesmidae). Spixiana 5(3): 247–259.

HOFFMAN, R. L. 1990a. Chelodesmid studies XX. Millipeds of the new Brazilian tribe Cornalatini (Polydesmida: Chelodesmidae). Papéis Avulsos de Zoología, São Paulo 37(2): 23–37.

HOFFMAN, R. L. 1990b. Chelodesmid studies XXIII. Proposal of a new tribe for the disjunct Brasilian genus *Macrocoxodesmus* (Diplopoda, Polydesmida, Chelodesmidae). Papéis Avulsos de Zoologia 37(11): 167–172.

HOFFMAN, R. L. 2000. A synopsis of the Telonychopodini, a tribe of Pantanalian chelodesmid millepeds (Polydesmida: Chelodesmidae). Myriapodologica 7(1): 1–13.

HOFFMAN, R. L. 2012. New genera for two poorly-known millipeds from Bahia (Polydesmida: Chelodesmidae). Papeis Avulvsos de Zoologia 52(8): 103–110.

INIESTA, L. F. M., R. S. BOUZAN, J. MEANS, K. IVANOV, AND A. D. BRESCOVIT. 2023. Where are they from and where are they going? Detecting areas of endemism, distribution patterns and conservation status of the order Spirostreptida in Brazil (Diplopoda, Juliformia). Biodiversity and Conservation. doi:10.1007/s10531-023-02566-2.

INIESTA, L. F. M., R. S. BOUZAN, P. E. S. RODRIGUES, T. M. ALMEIDA, R. OTT, AND A. D. BRESCOVIT. 2020. Ecological niche modeling predicting the potential invasion of the non-native millipede *Oxidus gracilis* (C. L. Koch, 1847) (Polydesmida: Paradoxosomatidae) in Brazilian Atlantic Forest. Annales de la Société entomologique de France (N.S.) 56(5): 1–8. doi:10.1080/00379271.2020.1834873.

INIESTA, L. F. M., R. S. BOUZAN, P. E. S. RODRIGUES, T. M. ALMEIDA, R. OTT, A. D. BRESCOVIT. 2021. A preliminary survey and range extension of millipedes species introduced in Brazil (Myriapoda, Diplopoda). Papéis Avulsos de Zoologia 61: 1–18. doi:10.11606/1807-0205/2021.61.88.

INIESTA, L. F. M., A. D. BRESCOVIT, D. G. A. JÚNIOR, AND R. S. BOUZAN. 2022. Into the New World: first report of introduction of the Portuguese millipede *Ommatoiulus moreleti* (Lucas, 1860) (Julida: Julidae) in South America and its potential invasion range into the continent. Annales de la Société entomologique de France (N.S.) 58(3): 187–196. doi:10.1080/00379271.2022.2084641.

JOLY, C. A., J. P. METZGER, M. TABARELLI. 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist 204: 459–473. doi:10.1111/nph.12989.

KOCH, M. 2015. General morphology. In: MINELLI, A. (Ed.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda. Brill, Leiden, 7–68.

LORDELLO, L. G. E. 1954. Observação sobre alguns Diplópodos de interesse agrícola. Anais da Escola Superior de Agricultura "Luiz de Queiroz" 11: 69–76. doi:10.1590/S0071-12761954000100004.

NGUYEN A. D. AND P. SIERWALD. 2013. A worldwide catalog of the family Paradoxosomatidae Daday, 1889 (Diplopoda: Polydesmida). *Check List* 9(6): 1132–1353. doi:10.15560/9.6.1132.

NIIJIMA, K. 1998. Effects of outbreak of the train millipede *Parafontaria laminata armigera* Verhoeff (Diplopoda: Xystodesmidae) on litter decomposition in a natural beech forest in Central Japan. 1. Density and biomass of soil invertebrates. Ecological Research 13: 41–53. doi:10.1046/j.1440-1703.1998.00242.x.

NIIJIMA, K. AND K. SHINOHARA. 1988. Outbreaks of the *Parafontaria laminata* group (Diplopoda, Xystodesmidae). Journal of Ecology (Japan) 38: 257–268.

NIIJIMA, K., M. NII, AND J. YOSHIMURA. 2021. Eight-year periodical outbreaks of the train millipede. Royal Society Open Science 8: 201399. doi:10.1098/rsos.201399.

PENA-BARBOSA, J. P. P., P. SIERWALD, AND A. D. BRESCOVIT. 2013. On the largest chelodesmid millipedes: taxonomic review and cladistic analysis of the genus *Odontopeltis* Pocock, 1894 (Diplopoda; Polydemsida; Diplopoda). Zoological Journal of the Linnean Society 169 (4): 737–764. doi:10.1111/zoj12086.

RATTER J. A., J. F. RIBEIRO, S. BRIDGEWATER. 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. Annals of Botany 80: 223–230. doi:10.1006/anbo.1997.0469.

REZENDE, C. L., F. R. SCARANO, E. D. ASSAD, C. A. JOLY, J. P. METZGER, B. B. N. STRASSBURG, M. TABARELLI, G. A. FONSECA, R. A. MITTERMEIER. 2018. From hotspot to hopespot: an opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16: 208–214. doi:10.1016/j.pecon.2018.10.002.

RODRÍGUEZ-ZORRO P. A., M. P. LEDRU, C. FAVIER, E. BARD, D. C. BICUDO, M. GARCIA, G. MARQUARDT, F. ROSTEK, A. O. SAWAKUCHI, Q. SIMON, K. TACHIKAWA. .2022. Alternate Atlantic forest and climate phases during the early Pleistocene 41 kyr cycles in southeastern Brazil. Quaternary Science Reviews 286:107560. doi:10.1016/j.quascirev.2022.107560.

ROJAS-BUFFET, C., R. S. BOUZAN, P. SIERWALD, A. D. BRESCOVIT, M. SIMÓ. 2022. *Sandalodesmus joachimadisi* n. sp., the first Chelodesmidae member from Uruguay with an updated key to species of the genus (Diplopoda: Polydesmida). Zootaxa 5150(2): 260–268. doi:10.11646/zootaxa.5150.2.5.

SCHUBART, O. 1942. Os Myriápodes e suas relações com a agricultura - Com uma bibliografia completa sôbre o assunto. Papéis Avulsos do Departamento de Zoologia 2(16): 205–234.

SCHUBART, O. 1944. Os Diplopodos de Pirassununga. Acta Zoologica Lilloana 2: 321–440.

SCHUBART, O. 1946. Contribuição ao conhecimento do gênero *Leptodesmus* (Família Leptodesmidae, Diplopoda). Anais da Academia Brasileira de Ciências 18: 165–202.

SCHUBART, O. 1955. Materiais para uma fauna do Estado de Sao Paulo - os Leptodesmidae. Arquivos do Museu Nacional, Rio de Janeiro 42: 507–540.

SCHUBART, O. 1958. "Leptodesmidae" Brazileiras. VI: Espécies novas do Estado do Rio Grande do Sul (Diplopoda, Proterospermophora). Revista Brasileira de Biologia 18(1): 23–32.

SHELLEY, R.M. 2002. A revised, annotated, family-level classification of the Diplopoda. Arthropoda Selecta 11(3): 187–207.

SILVESTRI, F. 1902. Viaggio del Dr. A. Borelli nel Matto Grosso. VII. Diplopodi. Bollettino dei Musei di Zoologia e di Anatomia Comparata R. Università di Torino 17(432): 1–25.

SMITH, R. J, AND F. E. MAYLE. 2017. Impact of mid-to late Holocene precipitation changes on vegetation across lowland tropical South America: a paleo-data synthesis. Quaternary Research 89(1): 134–155. doi:10.1017/qua.2017.89.

Received: 01/06/2023
Accepted: 03/08/2023
Published online: 09/10/2023