

This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

Research article

urn:lsid:zoobank.org:pub:92D114FF-94FC-49A0-A83A-08B4E5BF1B3E

Cladistic analysis and description of a new species of the Brazilian genus *Atlantodesmus* Hoffman, 2000 (Diplopoda: Polydesmida: Chelodesmidae)

Rodrigo Salvador BOUZAN^{1,*}, Luiz Felipe Moretti INIESTA² & Antonio Domingos BRESCOVIT³

^{1,2}Pós-graduação em Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brasil.
^{1,2,3}Laboratório Especial de Coleções Zoológicas, Instituto Butantan, Avenida Vital Brasil, 1500, 05503-090, São Paulo, Brasil.

*Corresponding author: rodrigobouzan@outlook.com ²Email: luiz-moretti@hotmail.com ³Email: adbresc@terra.com.br

¹urn:lsid:zoobank.org:author:14A15A7F-730F-4D41-BDAC-D53514FAB85D ²urn:lsid:zoobank.org:author:DEEF048E-97FB-4CCD-875F-5FA6184CA8AB ³urn:lsid:zoobank.org:author:D5B81D79-AFAE-47B1-8A6E-DAB448A24BCC

Abstract. A cladistic analysis of the genus *Atlantodesmus* Hoffman, 2000 is presented. With a total of 11 taxa and 30 morphological characters, and under implied weighting (k = 3), two equally most parsimonious trees (length = 58 steps; total fit = 23.150; CI = 0.64; RI = 0.64) recovered the monophyly of the genus. The resulting synapomorphies are: absence of a ventral projection on the post-gonopodal sternites; presence of folds on the dorsal edge of the prefemoral region of the gonopod; and one homoplastic transformation: presence of a cingulum. In addition, *Atlantodesmus sierwaldae* sp. nov. is described from the state of Minas Gerais, in the Brazilian Cerrado, and a key to the males of the genus is provided.

Keywords. Brazil, Neotropical region, Brazilian Cerrado, Chelodesminae, taxonomy.

Bouzan R.S., Iniesta L.F.M. & Brescovit A.D. 2019. Cladistic analysis and description of a new species of the Brazilian genus *Atlantodesmus* Hoffman, 2000 (Diplopoda: Polydesmida: Chelodesmidae). *European Journal of Taxonomy* 538: 1–17. https://doi.org/10.5852/ejt.2019.538

Introduction

The Chelodesmidae Cook, 1895 is the second largest family in the class Diplopoda de Blainville, 1844, with almost 800 described species (Hoffman 1980). The family is divided into two subfamilies: Chelodesminae Cook, 1895, composed of 19 tribes distributed in the Neotropical region, and Prepodesminae Cook, 1896, with only one tribe from Africa and disjuncts records from Spain (Hoffman 1980).

European Journal of Taxonomy 528: 1–17 (2019)

In the Chelodesminae, the genus *Atlantodesmus* Hoffman, 2000 contains species widely distributed in the Atlantic forest of Brazil (Hoffman 2000; Bouzan *et al.* 2017). The genus is not assigned to any tribe, though Hoffman (2000) suggested a close relationship with members of the genus *Arthrosolaenomeris* Schubart, 1943 in the tribe Arthrosolaenomeridini Hoffman, 1976, due to the presence of a cingulum on the gonopod and a supposedly similar geographic distribution. Recently, *Atlantodesmus* was revised and considered as a senior synonym of *Iemanja* Hoffman, 2000 (Bouzan *et al.* 2017), and is currently composed of the species *A. eimeri* (Attems, 1898), *A. itapurensis* (Schubart, 1943), *A. pickeli* (Schubart, 1946), *A. pintoi* (Schubart, 1946) and *A. teresa* (Hoffman, 2000).

In this study, a morphology-based cladistic analysis is performed to test the monophyly of *Atlantodesmus*. In addition, *Atlantodesmus sierwaldae* sp. nov. from the state of Minas Gerais, Brazil, is described based on several differences in the morphology of the gonopod, and an updated key to the males of the genus is provided.

Material and methods

The material examined is deposited in the following institutions indicated below (curators in parentheses). Photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereo microscope. Focus-staked images were composed with Leica Application Suite version 2.5.0. For the gonopod terminology we follow Pena-Barbosa *et al.* (2013), Koch (2015) for the cyphopod terminology, and Attems (1898) and Brölemann (1900) for other somatic characters.

Repositories

CZUFMT MYR	=	Coleção Zoológica da Universidade Federal do Mato Grosso, Cuiabá, Mato
		Grosso, Brazil (A. Chagas-Jr)
IBSP	=	Instituto Butantan, São Paulo, Brazil (A.D. Brescovit)
MZSP	=	Museu de Zoologia, Universidade de São Paulo, Brazil (R. Pinto da Rocha)

Abbreviations

- A = Acropodite C = Cingulum
- Cn = Cannula
- Pfp = Prefemoral process
- $S^{T} = Solenomere$
- Sg = Seminal groove

Cladistic analysis

All recognized species in the genus *Atlantodesmus* were included in the cladistic analyses. Members of the tribes Strongylomorphini: *Brasilodesmus paulistus paulistus* (Brölemann, 1902), Macrocoxodesmini: *Macrocoxodesmus marcusi* Schubart, 1947, and Arthrosolaenomeridini: *Arthrosolaenomeris pantalanensis* Schubart, 1943 were included as outgroups, as well as two species not assigned to any tribe (*Leiodesmus* sp. and *Plectrogonodesmus gounellei* (Brölemann, 1902)), hypothesized to be closely related to *Atlantodesmus*, according to Hoffman (2000) and Bouzan *et al.* (2017, 2019).

The character construction was based on established procedures for morphological cladistic analyses, such as topological correspondence between the structures, similarity, and hierarchy and independence between characters and states (Rieppel & Kearney 2002). Contingent character construction was employed in some cases (Strong & Lipscomb 1999), due to the relationship concerning the presence/absence of structures (neomorphic feature) and their possible shapes (transformational) (Sereno 2007). The character matrix (Tables 1–2) was constructed using the program ASADO ver. 1.89 (Nixon 2004). All characters were

Table 1. Morphological matrix for the cladistic analysis of the genus *Atlantodesmus* Hoffman, 2000. - = inapplicable characters; ? = unobserved characters. All characters were treated as nonadditive.

											hai	ract	ers													1
0	0	0	0	0	0	0	-	1		-	-	-	-	-	1	7	7	7	7	7	7	7	7	7	7	3
3	4	S	9	٢	æ	6	0	-	(1) (1)	4	5	9	7	8	6	0	1	7	e	4	S	9	٢	æ	6	0
0 (0	1	0	0	0	1	1 () (0	1	1	0	0	0	0	1	0	Ι	Ι	0	0	0	0	1	0	
0 (0	1	1	1	1	1	1		-	3	0	1	0	0	1	0	0	Ι	Ι	0	0	0	1	5	1	C
- 0	Ι	1	1	1	0	Ι	-	-	-	1	0	1	0	0	0	0	0	T	Т	0	0	0	-	0	1	0
0	0	1	1	1	1	-	0	_	-	2	0	1	1	0	0	0	0	Ι	Ι	0	0	0	0	I	ċ	~:
0	0	-	1	-	-	-	0	_	0	-	0	1	1	0	0	-	-	Ξ	0	0	0	0	0	I	1	0
-	1	0	0	0	0	0	1	2) 1	1	1	1	0	1	-	0	1	0	2	0	0	0	-	_	1	0
0	1	1	0	0	0	0	1	2) 1	1	0	1	0	-	Τ	0	-	-	-	0	-	-	1	—	-	C
0 (Ι	0	0	0	0	0	1	2) 1	3	0	0	0	0	-	0	1	0	2	0	1	0	-	-	, T	I
0	0	0	0	0	0	0	1	2) 1	0	0	0	0	1	-	0	-	0	2	-	-	0	-	-	2	-
- 0	0	Η	0	0	0	0	1 () () 1	1	0	1	0	1	0	0	1	-	3	-	0	0	1	-	2	-
0	-	0	0	0	0	0	1			-	0	-	0		0	0					0		_			ı I
	$\neg m \mid \circ \circ \circ \circ \circ \neg \circ \circ$	• • • • • • • • • • • • • • • • • • •	3 4 5 3 4 5 0 0 1 0 0 1 1 1 0 1 1 0 0 1 1 0 1 1 0 1 0 0 0 0 0 1 0 1 1 0 0 1 1 0 1 1 0 1 1 0 0 1 0 1 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3 4 5 6 7 8 9 0 0 0 1 0 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 1 1 0 0 0 1 1 1 1 1 0 1	0 0 0 0 1 1 3 4 5 6 7 8 9 1 1 0 0 1 1 0 0 1 10 0 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1	0 0 0 0 1 1 3 4 5 6 7 8 9 0 1 2 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 0 0 1	0 0 0 0 1	0 0 0 0 1	0 0 0 0 1 0 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1 1 0 1	0 0 0 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1	0 0 0 1 0	0 0 0 0 1	0 0 0 1	0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 3 4 5 6 7 8 9 0 1 1 0 1 1 0 1 1 0 1 1 0 0 1	0 0 0 0 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1	0 0 0 1 1 1 1 1 1 2 3 3 3 3 3 3 3 3 3 3 3 3 4 5 6 7 8 9 0 1 2 3 3 3 4 5 6 7 8 9 0 1 2 3 3 4 5 6 7 8 9 0 1 2 3 3 5 6 7 8 9 0 1 2 3 4	0 0 0 1 1 1 1 1 1 1 1 2 3 4 0 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 1 1 0 0 1 1 0 1 1 0 0 1	0 0 0 0 1 1 1 1 1 1 1 2 3 4 5 3 4 5 3 4 5 3 4 5 3 4 5 3 4 5 3 4 5 3 4 5 3 4 5 5 5	0 0 0 1 1 1 1 1 1 1 1 2 3 4 5 6 0	0 0 0 1 	0 0 0 1 2 	3 4 5 6 7 8 9 0 1

uniform (Fig. 3).

 Table 2 (continued next page). List of character and character states used in the cladistic analysis of the genus *Atlantodesmus* Hoffman, 2000.

Character Character state (1) Coloration of the body rings (Pena-Barbosa et al. 2013, character #6): 0 – Uniform; 1 – Not

- (2) Patches of color on the paranota: 0 On lateral margin (Fig. 4A); 1 Extended to posterior edge (Fig. 4C); 2 On central area (Fig. 4B).
- (3) Tegument of the body rings: 0 Smooth (Fig. 4A–C); 1 Granular (Fig. 4D).
- (4) Edge of the lateral projection on the seventh sternite: 0 Smooth (Fig. 4A); 1 Serrated (Fig. 4B).
- (5) Ventral projection on the fourth sternite: 0 Absent; 1 Present (Fig. 5C).
- (6) Ventral projection on the fifth sternite: 0 Absent; 1 Present (Fig. 5D).
- (7) Ventral projection on the sixth sternite (Pena-Barbosa et al., 2013, character #9): 0 Absent; 1 Present.
- (8) Ventral projection on the seventh sternite (Pena-Barbosa et al., 2013, character #10): 0 Absent; 1 – Present.
- (9) Ventral projection on the sternites just after the gonopods (Pena-Barbosa et al., 2013, character #18): 0 Absent; 1 Present.
- (10) Shape of the posterior edge of the paranota (Pena-Barbosa et al., 2013, character #21): 0 Rounded (Fig. 5E); 1 Acuminate (Fig. 5F).
- (11) Paranota alignment in oral view (Pena-Barbosa et al., 2013, character #13): 0 Straigth; 1 – Curved ventrad; 2 – Curved dorsad.
- (12) Dorsal lobe on the prefemur of the fifth leg (Pena-Barbosa et al., 2013, character #16): 0 Absent; 1 – Present.
- (13) Folds on the aperture of the gonopod (Pena-Barbosa et al., 2013, character #20): 0 Absent; 1 Present (Fig. 6A).
- (14) Posterior edge of gonopod aperture (Pena-Barbosa et al., 2013, character #23): 0 Not extended to coxae of the legs; 1 Extended up to half of the coxae; 2 Exceeding the coxae.
- (15) Coxal apophysis (Pena-Barbosa et al., 2013, character #27): 0 Absent; 1 Present.
- (16) Setae on the gonocoxae: 0 Two setae; 1 A row of setae.
- (17) Shape of the projection on the gonocoxae: 0 Oval; 1 Subtriangular; 2 Digitiform.
- (18) Folds on dorsal edge of the prefemoral region: 0 Absent; 1 Present (Fig. 6B).
- (19) Prefemoral process: 0 Smooth (Fig. 6C); 1 Serrated (Fig. 6D).
- (20) Projection on prefemoral process (Pena-Barbosa et al., 2013, character #47): 0 Absent; 1 – Present.

 Table 2 (continued). List of character and character states used in the cladistic analysis of the genus

 Atlantodesmus Hoffman, 2000.

# Ch	aracter Character state
(21)	Cingulum: 0 – Absent; 1 – Present.
(22)	Shape of the cingulum: 0 – Reduced; 1 – Well-developed (Fig. 2E–F).
(23)	Cingulum position: 0 – Medial; 1 – Proximal; 2 – Submedial.
(24)	Acropodite incision in mesal view: 0 – Absent; 1 – Present.
(25)	Lobe on the basis of the solenomere: 0 – Absent; 1 – Present.
(26)	Lateral membrane of the process of the acropodite: 0 – Absent; 1 – Present.
(27)	Solenomere branching: 0 – Absent; 1 – Present.
(28)	Position of the solenomere branching: 0 – Apical; 1 – Medial; 2 – Proximal.
$\langle 20\rangle$	Stand of the standard standard (Deep Protocol of 1, 2012) the standard (146) 0. Circular

- (29) Shape of the vulva in ventral view (Pena-Barbosa et al., 2013, character #46): 0 Circular; 1 Oval; 2 Triangular.
- (30) Shape of the apex of the vulva: 0 Rounded; 1 Triangular.

treated as nonadditive. The search for the most parsimonious cladograms were carried out heuristically in TNT ver. 1.5 (Goloboff & Catalano 2016). The searches of the trees were conducted under implied weights of the characters (Goloboff 1993; Goloboff *et al.* 2008a, 2017) and with different values for the constant k (1–7). The analysis was conducted following the Traditional search, with 1000 replications and 100 trees held per replicate. Concerning the different topologies for different values of k, the tree topology that shared the highest number of nodes with the other trees was considered the most stable, and thus, used for the our discussion. The measurement of the sharing was made by subtree prune and regraft [SPR-distances] (Goloboff *et al.* 2008b). Branch support was calculated through relative Bremer support (Bremer 1994; Goloboff & Farris 2001) and by Symmetric Resampling approach (Goloboff *et al.* 2003) under implied weights of the characters, using the Traditional search with 700 replications and 2000 resampled matrices. The strict consensus of the two most parsimonious trees is presented in Fig. 1 with only unambiguous changes. The list of terminal taxa scored for the cladistic analysis is presented in Appendix 1.

Results

Taxonomy

Order Polydesmida Pocock, 1887 Suborder Leptodesmidea Brölemann, 1916 Family Chelodesmidae Cook, 1895 Subfamily Chelodesminae Cook, 1895

Genus Atlantodesmus Hoffman, 2000

Atlantodesmus Hoffman, 2000: 102. Type species: Leptodesmus eimeri Attems, 1898, by original designation.

Iemanja Hoffman, 2000: 106. Type species: *I. teresa* Hoffman, 2000, by original designation. Synonymized by Bouzan *et al.* 2017: 271.

Diagnosis

Modified from Bouzan *et al.* (2017): males of *Atlantodesmus* differ from other chelodesmid genera by the combination of the following characters: absence of ventral projections on the sternites (except *A. itapurensis* and *A. teresa*, which have a pair of projections on the fourth sternite; Fig. 5C); presence of folds on the dorsal edge of the prefemoral region of the gonopod (Fig. 6B), except *A. pickeli*; presence of a cingulum (Fig. 2E–F); acropodite branching, forming a long, thin, falciform solenomere, and a large acropodite process with a broadened apical region overreaching the tip of the solenomere (Fig. 2C–F).

Distribution

Occurring in the Atlantic rain forest (states of Paraná, Santa Catarina, São Paulo, Minas Gerais, Espírito Santo and Bahia) and in the Cerrado (states of São Paulo, Mato Grosso do Sul and Minas Gerais) areas of Brazil. See map in Bouzan *et al.* (2017).

Composition

Six species: Atlantodesmus eimeri (Attems, 1898), A. itapurensis (Schubart, 1943), A. pickeli (Schubart, 1946), A. pintoi (Schubart, 1946), A. teresa (Hoffman, 2000) and A. sierwaldae sp. nov.



Fig. 1. Strict consensus of the two most parsimonious trees obtained with implied weighting of the characters (k = 3) (length = 58 steps; total fit = 23.150; CI = 0.64; RI = 0.64). Black circles correspond to unique transformations and white circles to homoplastic transformations. Values below branches refer to the GC values (Symmetric Resampling) and relative Bremer support. Only unambiguous changes are shown in this topology.

Key to the males of *Atlantodesmus*

1. _	Body coloration concolorous to paranota edge Coloration at paranota edge lighter	
2.	Tubercles present on dorsal surface of metazonites Tubercles absent on dorsal surface of metazonites	
3. _	Median stripe on metazonite present Median stripe on metazonite absent	
4. -	Prefemoral process serrated distally Prefemoral process unserrated distally	
5. -	Prefemoral process densely serrated distally Prefemoral process slightly serrated distally	

Atlantodesmus sierwaldae sp. nov.

urn:lsid:zoobank.org:act:499BF939-82E7-4191-AD2D-5E3B4240FF1E

Figs 2–4C

Diagnosis

Males differ from all other species of the genus by the following features: paranota and posterior border of the metaterga whitish (Fig. 2A); tip of acropodite hood-shaped, covering the solenomere only in mesal view (Fig. 2C, E); prefemoral process of the gonopod without serrated margin (Fig. 2E–F).

Etymology

The specific epithet is a patronym in honor of Dr. Petra Sierwald, for her friendship and outstanding contributions to our knowledge concerning millipedes.

Material examined

Holotype BRAZIL • ♂ adult; Minas Gerais, Paracatu; 17°14′41.6″ S, 46°50′38.0″ W; K. Lenko leg.; IBSP 180.

Description

Male (holotype)

MEASUREMENTS. Total length: 47.6 mm. Width (body ring 5): 7.2 mm. Collum length 1.3 mm, width 5.5 mm. Antennomeres in mm (1–7): 0.8; 1.5; 1.6; 1.4; 1.3; 1.3; 0.4. Podomeres in mm (1–6): 0.9; 0.9; 2.0; 1.1; 1.1; 1.5. Tarsal claw: 0.3. Gonopod aperture: 1.1 mm length, 1.9 mm width. Telson 1.2 mm.

COLORATION (in 70% ethanol). Head light brown with whitish labral region (Fig. 2A). Antennae whitishyellow. Body brown; paranota and posterior margin of metaterga whitish.

BODY RINGS. Integument slightly rough; alignment of paranota curved slightly dorsad; anterior corners rounded, posterior edges acutely produced; ozopores and peritremata situated on the posterior edge of paranota (Fig. 4C). Sterna without modifications.

LEGS. Whitish yellow and without modifications, with thin and slightly elongated setae. Gonopod aperture transversely oval; posterior edge excavated and with folds. Telson light brown with whitish apex (Fig. 2B); hypocroct triangular, with two setae.

European Journal of Taxonomy 528: 1–17 (2019)

GONOPODS (Fig. 2C–F). Gonopod: length 2.22 mm, width 1.79 mm. Coxae: length 0.61 mm, width 0.93 mm. Telopodite: length 1.99 mm, width 0.61 mm. Coxae equivalent to about half the length of telopodite and prominently rounded in ectal view (Figs 2F, 3C); with two or three long setae on distal dorsal side and with two or four short setae above cannula; without a spiniform process. Cannula hook-shaped (*Cn*; Figs 2C, 3A). Prefemoral region $\frac{1}{3}$ the size of telopodite; dorsal side with folds. Prefemoral process a long and broad, smooth blade, with the terminal portion expanded, acuminate at apex (*PfP*; Figs 2C–F, 3). Conspicuous cingulum present below bases of solenomere and acropodite (*C*; Figs 2E–F, 3). Solenomere long and falciform, tapering to acuminate tip; carrying the seminal groove to apical point (*S*; Figs 2E–F, 3B–C). Acropodite long, obscuring solenomere in most of its length in ectal view;



Fig. 2. *Atlantodesmus sierwaldae* sp. nov., holotype, \mathcal{E} (IBSP 180). **A**. Anterior region in dorsal view. **B**. Posterior region in dorsal view. **C**–**F**. Left gonopod. **C**. Mesal view. **D**. Ventral view. **E**. Ectal view. **F**. Detail of the distal portion in ectal view. Scale bars: A–B = 2 mm; C–D = 250 µm. E–F = 500 µm.

overreaching the solenomere; hood-shaped. Prefemoral process covering the solenomere in most of its length in mesal view. Acropodite process weakly sclerotized and covering the apical part of the solenomere, in ectal view and also is irregular.

Female

Unknown.

Distribution

The species is known only from the type locality.



Fig. 3. *Atlantodesmus sierwaldae* sp. nov., holotype, $\stackrel{\circ}{\bigcirc}$ (IBSP 180), schematic drawings of the gonopods. **A**. Mesal view. **B**. Ventral view. **C**. Ectal view. Scale bars: A–B = 250 µm; C = 500 µm.

Phylogenetic relationships

The cladistic analysis returned two equally most parsimonious trees under value of the constant k = 3, which showed the highest number of nodes shared (strict consensus presented in Fig. 1; and the two trees in Appendix 2), with the genus *Atlantodesmus* recovered as a monophyletic group, as suggested by Bouzan et al. (2017). The clade is supported by two synapomorphies and one homoplastic transformation: absence of ventral projection on the sternite just after the gonopods (char. 9 [0]), folds on dorsal edge of the prefemoral region (char. 18 [1]) and presence of a cingulum (char. 21, a presence shared with Arthrosolaenomeris pantalanensis). Despite forming a monophyletic group, the relationships of the species within the genus still remain unclear. Based on the topology, the species Atlantodesmus teresa was the first to diverge, and the latter group (A. eimeri + (A. itapurensis + A. sierwaldae) + (A. pickeli + A. pintoi)) was recovered as a trichotomy. In the strict consensus, the trichotomy is supported by two synapomorphies and one homoplastic transformation: absence of ventral projection on the fourth sternite (char. 5 [0]), paranota dorsally curved (char. 11 [2]) and a serrated prefemoral process (char. 19 [1], although reversed to the smooth aspect in A. sierwaldae). In the two trees obtained, the trichotomy was resolved with the grouping (A. eimeri + (A. pickeli + A. pintoi)) supported by a reduced cingulum (char 22 [0]) (Appendix 2, A), and with the grouping (A. eimeri + (A. itapurensis + A. sierwaldae)) by a serrated lateral projection on the seventh sternite (Appendix 2, B).



Fig. 4. Details of the tergites in the genus *Atlantodesmus* Hoffman, 2000. A. *A. pickeli* (Schubart, 1946). B. *A. pintoi* (Schubart, 1946). C. *A. sierwaldae* sp. nov. D. *A. eimeri* (Attems, 1898). Scale bars = 2 mm.

Discussion

As suggested by Hoffman (2000), the genus *Atlantodesmus* is possibly related to *Leiodesmus* Silvestri, 1897, and the presence of a well-defined cingulum on the telopodite (specified for the junior synonym *Iemanja*) would indicate a possible relationship with the genus *Arthrosolaenomeris*. However, based on our topology, neither genus was recovered close to *Atlantodesmus*. Although we found that the



Fig. 5. A–B. Lateral projection on the seventh sternite. A. Smooth in *Atlantodesmus eimeri* (Attems, 1898). B. Serrated in *A. pintoi* (Schubart, 1946). C. Ventral projection on the fourth sternite in *A. teresa* (Hoffman, 2000). D. Ventral projection on the fifth sternite in *Arthrosolaenomeris pantalanensis* Schubart, 1943. E–F. Shape of the posterior edge of the paranota. E. Rounded in *A. pantalanensis*. F. Acuminate in *Atlantodesmus eimeri* (Attems, 1898). Scale bars: A–B = 250 µm; C–F = 500 µm.

genus *Atlantodesmus* is a well-supported clade, no inference concerning its tribal position was possible.

The phylogenetic relationship of the genus allows first insights into its biogeographic origin. The clade *A. itapurensis* + *A. sierwaldae* occurs mainly in areas containing the biome Cerrado, while the other taxa are distributed exclusively in the Atlantic rain forest. Concerning the cingulum, our results corroborate the suggestion made by Hoffman (2000), in which the presence of the structure is merely a recurrent homoplasy in different groups within the family. Importantly, phylogenetic relationships of the Chelodesmidae still require more investigation to achieve a better understanding of the morphological characters (Pena-Barbosa *et al.* 2013), as well as the delineation of its generic and tribal limits. This work presents important results about the evolution of the characters for *Atlantodesmus*, corroborating hypotheses from previous taxonomic treatments (Hoffman 2000; Bouzan *et al.* 2017).

Acknowledgements

We are grateful to Ricardo Pinto da Rocha and Mauro Cardoso Júnior (MZSP) and Amazonas Chagas-Jr (UFMT) for their hospitality during the visits, Beatriz Mauricio for helping with the SEM images in the Laboratório de Biologia Celular of the Instituto Butantan, and to R. Bassini Silva (IBSP) for his



Fig. 6. A. Folds on the gonopod aperture in *Atlantodesmus pintoi* (Schubart, 1946). **B**. Folds on dorsal edge of the prefemoral region in *A. pintoi*. **C**. Smooth-edged prefemoral process in *A. itapurensis* (Schubart, 1943). **D**. Serrated prefemoral process in *A. teresa* (Hoffman, 2000). Scale bars: A-B = 2 mm; $C = 500 \mu$ m; $D = 200 \mu$ m.

suggestions. Thanks to the Willi Hennig Society for allowing the use of the software TNT, and to J.P.P. Pena-Barbosa for making available his unpublished PhD thesis (2015): "Phylogenetic Framework for the Tribes of the Subfamily Chelodesminae Hoffman, 1980, Based on Morphological Characters (Diplopoda, Polydesmida, Chelodesmidae)". A special thanks to Derek Hennen (Virginia Tech) for all suggestions and for critical readings of the English, and to Ross Thomas for the second review. Thanks to the reviewers for all the suggestions. This study was financially supported by CNPq (130092/2018-5) grant to RSB and grant 2018/00103-8 from the São Paulo Research Foundation (FAPESP). LFMI was supported by grant 2016/24248-0 from FAPESP. ADB was supported by the grant CNPq (301776/2004-0). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES - Finance Code 001).

References

Attems C.G. 1898. System der Polydesmiden. I. Theil. Denkschriften der Kaiserlichen Akademie der Wissenschaften zu Wien, Mathematisch-Naturwissenschaftliche Klasse 67: 221–482.

Bouzan R.S., Pena-Barbosa J.P.P. & Brescovit A.D. 2017. Taxonomic review of the genus *Atlantodesmus* Hoffman, 2000 (Polydesmida: Chelodesmidae). *Zootaxa* 4236: 269–290. https://doi.org/10.11646/zootaxa.4236.2.3

Bouzan R.S., Iniesta L.F.M., Souza C.A.R. & Brescovit A.D. 2019. 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. https://doi.org/10.1080/01650521.2018.1536018

Bremer K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304. https://doi.org/10.1111/j.1096-0031.1994.tb00179.x

Brölemann H. 1900. Dous myriapodos notáveis do Brazil, Notas Myriapodologicas. *Boletim do Museu Paraense de História Natural e Ethnographia* 3: 65–71.

Goloboff P.A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83–91. https://doi.org/10.1111/j.1096-0031.1993.tb00209.x

Goloboff P.A. & Farris J.S. 2001. Methods for quick consensus estimation. *Cladistics* 17: S26–S34. https://doi.org/10.1111/j.1096-0031.2001.tb00102.x

Goloboff P.A., Farris J.S., Källersjö M., Oxelman B., Ramírez M.J. & Szumik C.A. 2003. Improvements to resampling measures of group support. *Cladistics* 19: 324–332. https://doi.org/10.1111/j.1096-0031.2003.tb00376.x

Goloboff P.A., Carpenter J.M., Arias J.S. & Esquivel D.R.M. 2008a. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 24: 758–773. https://doi.org/10.1111/j.1096-0031.2008.00209.x

Goloboff P.A., Farris S. & Nixon K. 2008b. TNT, a free program for phylogenetic analysis. *Cladistics* 24 (5): 774–786. https://doi.org/10.1111/j.1096-0031.2008.00217.x

Goloboff P.A. & Catalano S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238. https://doi.org/10.1111/cla.12160

Goloboff P.A., Torres A. & Arias J.S. 2017. Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. *Cladistics* 34: 407–437. https://doi.org/10.1111/cla.12205

Hoffman R.L. 1980. Classification of the Diplopoda. Múseum d'histoire naturelle, Genève.

Hoffman R.L. 2000. Two new genera of chelodesmid millipeds from southeastern Brazil (Polydesmida: Chelodesmidae). *Myriapodologica* 6: 101–113.

Koch M. 2015. General morphology. In: Minelli A. (ed.) Treatise on Zoology - Anatomy, Taxonomy, Biology. The Myriapoda. Vol. 2. Leiden & Boston, Brill. https://doi.org/10.1163/9789004188273_003

Nixon K.C. 2004. ASADO version 1.5 Beta. Published by the author. Ithaca, New York, USA.

Pena-Barbosa J.P.P., Sierwald P. & Brescovit A.D. 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

Rieppel O. & Kearney M. 2002. Similarity. *Biological Journal of the Linnean Society* 75: 59–82. https://doi.org/10.1046/j.1095-8312.2002.00006.x

Sereno P.C. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics* 23: 565–587. https://doi.org/10.1111/j.1096-0031.2007.00161.x

Strong E.E. & Lipscomb D. 1999. Character coding and inapplicable data. *Cladistics* 15: 363–371. https://doi.org/10.1111/j.1096-0031.1999.tb00272.x

Manuscript received: 22 April 2019 Manuscript accepted: 12 June 2019 Published on: 19 July 2019 Topic editor: Rudy Jocqué Desk editor: Pepe Fernández

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Zoological Research Museum Alexander Koenig, Bonn, Germany; National Museum, Prague, Czech Republic.

Appendix 1

List of terminal taxa scored for the cladistic analysis.

Outgroup

Strongylomorphini

Brasilodesmus paulistus paulistus (Brölemann, 1902)

BRAZIL • 1 \Diamond ; São Paulo, Peruíbe, Estação Ecológica Juréia/Itatins; 24°16'38" S, 47°00'44" W; 5 Mar. 1994; A. Eterovic coll.; IBSP 1130 • 1 \Diamond ; same collection data as for preceding; Dec. 1998; A.D. Brescovit *et al.* coll.; IBSP 981.

Macrocoxodesmus marcusi Schubart, 1947

BRAZIL • 1 ♂; Minas Gerais, Manhuaçu, Rio Matipó, Fazenda Floresta; 20°15′30″ S, 42°02′01″ W; Dec. 1919; R. Fonseca coll.; MZUSP.

Arthrosolaenomeridini

Arthrosolaenomeris pantanalensis Schubart, 1943

BRAZIL • 1 \Diamond ; Mato Grosso, São Luiz de Cáceres (now Cáceres); 16°04′15″ S, 57°40′44″ W; Feb. 1940; Passarelli coll.; MZUSP 1085 • 1 \Diamond ; Porto Estrela, E.E. Serra das Araras; 15°19′28″ S, 57°13′39″ W; 12 Nov. 2017; T.F. Conceição coll.; CZUFMT MYR 847.

Without tribal designation

Plectrogonodesmus gounellei (Brölemann, 1903)

BRAZIL • 1 ♂, 1 ♀; Bahia, Guanambi, Aeroporto; 14°13′25″ S, 42°46′52″ W; 14 Dec. 2007; C.A.R. Souza *et al.* coll.; IBSP 3281.

Leiodesmus sp.

BRAZIL • 1 ♂; Mato Grosso do Sul, Miranda, Fazenda Cayman; 20°14′27″ S, 56°22′42″ W; Oct. 1992; A. Eterovic coll.; IBSP1080.

Ingroup

Atlantodesmus eimeri (Attems, 1898)

BRAZIL • 3 $\Diamond \Diamond$, 1 \bigcirc ; Santa Catarina, Blumenau, Nova Rússia; 49°07'17" W, 26°91'65" S; 20 Feb. 2013; R.P. Indicatti and B. Gambaré coll.; IBSP 4367 • 1 \bigcirc ; Paulo Lopes, Parque Estadual da Serra do Tabuleiro; 48°80'35" W, 27°92'22" S; 10–20 Jan. 2003; Equipe Biota coll.; IBSP 2317.

Atlantodesmus itapurensis (Schubart, 1943)

BRAZIL • 1 ♂; São Paulo, Assis, Estação Ecológica de Assis; 50°41′88″ W, 22°66′04″ S; 25–30 Nov. 2002; Equipe Biota coll.; IBSP 2976 • 1 ♀; same collection data; IBSP 2981.

Atlantodesmus pickeli (Schubart, 1946)

BRAZIL • 1 \circlearrowleft ; São Paulo, São Paulo, Jardim São Bento; 46°38′0″ W, 23°33′0″ S; 1939; Dom B.J. Pickel coll.; IBSP 29 • 1 \updownarrow ; same collection data; IBSP 4433.

Atlantodesmus pintoi (Schubart, 1946)

BRAZIL • 1 \bigcirc , 1 \bigcirc ; Bahia, Una, Reserva Biológica de Una; 39°02'98" W, 15°19'54" S; Nov. 2001; A.D. Brescovit coll.; IBSP 1001.

Atlantodesmus teresa (Hoffman, 2000)

BRAZIL • 1 ♀; Espírito Santo, Linhares, Reserva Natural Vale do Rio Doce; 40°06'37" W, 19°13'74" S; 09–15 Jan. 2012; J.P.P. Pena-Barbosa *et al.* coll.; IBSP 4106 • 1 ♂; São Mateus Reserva Florestal do Vale do Rio Doce; 39°85'67" W, 18°71'91" S; 05–12 Jan. 1998; A.D. Brescovit coll.; IBSP 565.

Atlantodesmus sierwaldae sp. nov.

BRAZIL • 1 ⁽³⁾; Minas Gerais, Paracatu; 17°14'41.6" S, 46°50'38.0" W; K. Lenko coll.; IBSP 180.

Appendix 2

The two most parsimonious trees (A and B) obtained in the cladistic analysis under implied weighting (k = 3). Black circles correspond to unique transformations, and white circles correspond to homoplastic transformations. Only unambiguous changes are shown.

