1 Ceciamaralia, a new genus of Dorvilleidae (Annelida) from

2 deep waters of the Southwest Atlantic Ocean and an

3 insight into its relationship within the family

Rafael de Oliveira Bonaldo^{1,2,3*}, Tatiana Menchini Steiner^{3,4}, André Rinaldo Senna 4 Garraffoni^{2,4} 5 6 7 ¹ Programa de Pós-Graduação em Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. 8 9 ² Laboratório de Evolução de Organismos Meiofaunais, Instituto de Biologia, Universidade 10 Estadual de Campinas, Campinas, São Paulo, Brazil. 11 ³ Laboratório de Biodiversidade Bentônica Marinha, Departamento de Biologia Animal, 12 Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. ⁴Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, 13 Campinas, São Paulo, Brazil. 14 15 16 *Corresponding Author: Rafael Bonaldo 17 de Oliveira Rua Bertrand Russell, 1251 - Cidade Universitária, Campinas - SP, Brazil, 13083-865. 18 Email address: rafael.o.bonaldo@gmail.com 19 20 **Abstract** 21 22 Dorvilleidae, Chamberlin, 1919 is a family of Annelida grouping containing some of the 23 smallest 'polychaetes' species, being poorly studied worldwide, and with little knowledge 24 regarding its diversity and occurrence. Samples obtained in oceanographic campaigns 25 performed in the Southwest Atlantic Ocean (Brazilian coast) revealed a high number of specimens of dorvilleids, aidding to increase our knowledge of the family's biodiversity 26 27 A detailed morphological analysis of these organisms has revealed a new genus, Ceciamaralia 28 gen. nov., with two new species The new genus, which differs from other Dorvilleidae genera in i) the robust and enlarged pharynx which are frequently everted [CG1], 29 ii) unique 30 composition of maxillae, with an elongated pair of serrated basal plates and one pair

with

long and thin anterior spine and iii) ventral

31

of anterior free maxillary plates

- 32 cirrius present only in the few first chetigers. Ceciamaralia lanai gen. et sp. nov. is 33 characterized by the presence of a broad and large dorsal cirrus on a few anterior parapodia and 34 of by a furcate chaetae [cg2]in supra-acicular fascicles. While - Ceciamaralia nonatoi gen. 35 et sp. nov. presents a one geniculate chaeta instead of a one furcate chaeta cg3, the absence of dorsal cirri and, in some specimens, the absence of palps. A cladistic analysis supported the 36 monophyly of Ceciamaralia gen. nov. by four synapomorphies related to the unique 37 38 morphology of its maxillae, pharynx and appendages. This study is part of several recent increase the knowledge of Dorvilleidae since 39 taxonomic studies aiming to elucidate and 40 it is part of a Ph.D project focused on the family CG4].
- Key words: marine worms , Eunicida, 'Polychaeta', morphology, new species, new genus,
 taxonomy, cladistics

Introduction

The Order Eunicida

43

44

45

52

53

54

55

56

57

58

59

60

61

composed of ventral mandibles and dorsal maxillae (Zanol et al., 2021). <u>Dorvilleidae</u>

Chamberlin, 1919 encompass Some of the smallest—bodied eunicid species belong to

Dorvilleidae Chamberlin, 1919, a <u>The family with exhibits</u> varied life-styles, from free-living worms to some—commensal and/or parasitic species, inhabiting unconsolidated and

(Annelida) comprises 'polychaetes' that have an internal jaw apparatus

- 50 consolidated substrates, from the intertidal zones to great depths (Martin & Britayev, 1998;
- 51 Martin & Britayev, 2018 ; Zanol et al., 2021).
 - Dorvilleidae is characterized mainly by being the only extant group of Eunicida that has a ctenognath-type jaw apparatus: two or four rows of symmetrical or subsymmetrical denticulate maxillary plates, upper comb-like jaws, and an unpaired posterior carrier-like structure (Zanol et al., 2021). Despite the small size of some dorvilleids, a great morphological heterogeneity among species is observed. Body appendages on the (like prostomiumal, parapodial and pygidium,al), important for the initial identification of species, present a diversity of sizes and shapes. A detailed look reveals even more the morphological diversity, not only in smaller structures as tThe number and shape of chaetae, and but also in the internal jaw apparatus also shows great morphological diversity , which is important for delimiting genera and species within the family (Paxton, 2009).

Currently, Dorvilleidae comprises about 200 species distributed in 32 genera, of which 13 are monotypic, including the most recently described *Ikosipodoides* Westheide, 2000, while, almost ½ of the family species belong to the genus Ophryotrocha Claparède & Mecznikow, 1869. More than half of the Ophryotrocha diversity was described in the last 25 years (Read & Fauchald, 2024), as well as other studies encompassing biology, natural history, genetics and systematics (Zhang et al., 2023).

68

69

70

71

72

73

74

75

76

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

94

Meanwhile the rRelationships among genera and species of Dorvilleidae are also understudied. The In a broad morphologicalest cladistic study (comprising all genera of the family known at theat time), Eibye-Jacobsen & Kristensen (1994) analyzeding the relationships within Dorvilleidae was performed by Eibye-Jacobsen & Kristensen (1994), using genera as terminal , recovering several generic groupings CG51 based on the morphology of genera. Other taxa studies were have focused on accessing the monophyly of some genera and its their relationship with closely related genera; for as example of the work by de Oliveira Bonaldo (2022) on Eliberidens Wolf, 1986a, which recovered the monophyly of the genus and discussed its morphological similarities with some other genera. There are also studies including morphological and molecular data of generaus, like Parougia Wolf, 1986b (Yen & Rouse, 2020) and Ophryotrocha (Kvalø Heggøy, Schander & Åkesson, 2007) and one focused on the monotypic parasitic species Veneriserva pygoclava Rossi, 1984, exploring molecular data to analyze its relationship with some other Dorvilleidae genera, mainly Ophryotrocha (Tilic & Rouse, 2024). Thus These latter studies reveal, the scarcity of molecular data and viable specimens from which to extract such data from are an obstacle to advancements in this field.

Among the reasons for the_scarcity of knowledge on species of this family are_: i) the difficulty to perform sampling in_deep waters, ii) the rarity of some groups in the samples and iii) the lack of taxonomists specialized in this group. Theis knowledge gap ion Dorvilleidae systematics is a-worldwide reality ; and exemplified like-on the Brazilian coast, where, currently, there are only nineteen species registeredrecorded: Dorvillea angolana (Augener, 1918), Dorvillea moniloceras (Moore, 1909), D. sociabilis (Webster, 1879), Eliberidens forceps Wolf, 1986, E. hartmannschroederae Hilbig, 1995, Meiodorvillea hartmanae Bonaldo, Steiner & Amaral, 2022, M. jumarsi Bonaldo, Steiner & Amaral, 2022, M. minuta (Hartman, 1965), M. penhae Bonaldo, Steiner & Amaral, 2022, Ophryotrocha pueri lis Claparède & Mecznikow, 1869, O. zitae Miranda, Raposo & Brasil, 2020, Pettiboneia sanmartini Aguirrezabalaga & Ceberio, 2003, Pettiboneia sanmatiensis Orensanz, 1973, Protodorvillea

- 95 biarticulata Day, 1963, P. kefersteini (McIntosh, 1869), Schistomeringos annulata (Moore,
- 96 1906), S. anoculatus (Hartman, 1965), S. longicornis (Ehlers, 1901), and S. rudolphi (delle
- 97 Chiaje, 1828) (Amaral et al., 2006-2022); seven of them were recorded in three recent
- 98 taxonomic studies (de Oliveira Bonaldo, Steiner & Amaral, 2022; de Oliveira Bonaldo et al.,
- 99 2022; Miranda, Raposo & Brasil, 2020).
- 100 Recent o Ocean (Brazilian Recent o Ocean
- 101 coast) resulted in the collection of a a high number of Dorvilleidae specimens in their samples,
- allowing for an increase in the ing knowledge on the biodiversity of the family in this region.
- By applying an integrative approach, with light and scanning electron microscopy and
- 104 cladistic analysis, we identified and described a new genus of Dorvilleidae, Ceciamaralia
- gen. nov. with two new species, Ceciamaralia lanai gen. et sp. nov. and Ceciamaralia nonatoi
- gen. et sp. nov., that present unique, external and internal (jaw apparatus), morphological
- 107 characters.

110

118

109 Materials & Methods

Sampled area

- The specimens analyzed were collected in two broad oceanographic campaigns carried out in
- Brazilian waters (Southwest Atlantic Ocean), coordinated by CENPES/PETROBRAS:
- 113 (AMBES: Environmental Characterization of the Espírito Santo Basin (18°-21°S/37°-40°W)
- and HABITATS: Assessment of the Environmental Heterogeneity of the Campos Basin (21°-
- 115 24°S/38°-45°W) (Lavrado & Brasil 2010) . The collections were done between 2008
- and 2013 at depths ranging from 12 to 3301 meters; the organisms were previously
- fixed in 4% formalin and then preserved in 70% ethanol.

Morphological analysis

- The external morphology of the specimens was analyzed in using a ZEISS Axioscop 2 Plus
- 120 compound microscope and drawings were made with a camara lucida attached to the
- microscope. The images were captured with a ZEISS AxioCam MRc attached to a ZEISS

- 122 Axio Imager M2 and Axio Zoom V.16. All images and figures were edited using Adobe®
- 123 Photoshop and Inkscape®.
- To perform the scanning electron microscopy (SEM), specimens were previously immersed in
- ethanol baths at the following concentrations: 70% ethanol (five 5 min), 80%, 90%, 95%
- 126 (15 min each) and in absolute ethanol, in three3 changes (15, 30 and 60 min). Critical point
- drying (Balzers CPD-30) was performed at 37 °C and at a 70 BAR of CO2 gas input,
- followed by gold coating using SPD-050 sputter coater (Steiner & Santos, 2004). Specimens
- on stubs were observed in a JEOL JSM-5800 LV scanning electron microscope and
- images were taken with the software Semafore (v_.5.2). Critical point drying, gold-coating and
- 131 SEM analysis were all performed at the Laboratório de Microscopia Eletrônica, Instituto de
- 132 Biologia, Universidade Estadual de Campinas (LME-IB/UNICAMP).
- The jaw apparatus was analyzed using two different methodologies : i) placing
- the entire specimens on a drop of Hoyer solution (trichloroacetaldehyde) or Aquatex® on a
- slide and coverslip, or ii) placing the specimens between slide and coverslip, waiting for it
- to dry and analyzing the jaws by tissue transparency (not without damaging the specimens,
- and recovering theirits integrity by putting themit back in the ethanol). All observations were
- done in-using the ZEISS Axio Imager M2 and Axioscop 2 Plus microscopes

Cladistic analysis

139

140 To analyze the relationships of *Ceciamaralia* gen. nov. with the morphologically similar

141 genera of Dorvilleidae, we performed a cladistic analysis utilizing the character matrix and data

developed in the study of de Oliveira Bonaldo et al., (2022), which analyzed the cladistic

- relationships of the following genera: Dorvillea Parfitt, 1866, Eliberidens Wolf, 1986,
- 144 Gymnodorvillea Wainwright & Perkins, 1982 Marycarmenia Núñez, 1998, Meiodorvillea
- 145 Jumars, 1974, Pettiboneia Orensanz, 1973, Protodorvillea Pettibone, 1961 and
- 146 Schistomeringos Jumars, 1974. We added four new characters to the matrix (characters 43
- 147 to 46) and inserted a new character state for character 40 , to fit *Ceciamaralia* gen.
- 148 **nov.** (Table 1). We also followed the methodologies of de Oliveira Bonaldo et al. (2022),
- keeping the characters coded as binary or multistate, coded as '-' when the character is non-
- applicable and '?' when the state of the character is unknown. All characters are unweighted.
- The final matrix compriseds 21 species (Table 2), including the same outgroups from Oliveira

.

¹ The letter 'i' was skipped from all illustrations to avoid confusion with scale bars of the images.

152	de Bonaldo et al. (2022) (Pettiboneia urciensis Campoy & San Martín, 1980, Pettiboneia
153	wui Carrasco & Palma 2000 (Dorvilleidae) and Ninoe jessicae Hernández-Alcántara, Pérez-
154	Mendoza & Solís-Weiss, 2006 (Lumbrineridae)). The matrix has 46 morphological
155	characters.
156	The character matrix was assembled using the Mesquite® software (Maddison & Maddison,
157	2019) and the parsimony analysis was performed through the software TNT® (Goloboff &
158	Morales, 2023), with the heuristic search by the traditional search function starting with 10000
159	Wagner trees and utilizing the TBR (tree bisection reconnection) algorithm. We also used
160	TNT® to analyze branch support by standard bootstrap with 1000 replicates and Beremer
161	absolute support analysis, with 40 steps retaining suboptimal trees Finally, to view and edit the
162	resulting tree we used Winclada® software (Nixon, 2002).
163	Deposition of specimens
164	The specimens , SEM stubs and slides, including the type series, were deposited in the
165	Polychaeta Collection (ZUEC-POL) of the Museu de Diversidade Biológica of the Institute of
166	Biology of the Universidade Estadual de Campinas (MDBio - IB/UNICAMP), Campinas,
167	Brazil. Some paratypes were deposited elsewhere in Brazil: Museu de Zoologia of the
168	Universidade de São Paulo, São Paulo (MZUSP) and Museu Nacional do Rio de Janeiro, Rio
169	de Janeiro, Brazil (MNRJ).
170	The electronic version of this article in Portable Document Format (PDF) will represent a
171	published work according to the International Commission on Zoological Nomenclature
172	(ICZN), and hence the new names contained in the electronic version are effectively published
173	under that Code from the electronic edition alone. This published work and the nomenclatural
174	acts it contains have been registered in ZooBank, the online registration system for the ICZN.
175	The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information

viewed through any standard web browser by appending the LSID to the prefix

http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:A1EF2E10-

4863-49C1-A2E7-CF80BDFE6249. The online version of this work is archived and available

from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

180

181

176

177

178

179

Results

182 **Taxonomy**

- 183 **Phylum** Annelida, Lamarck 1802
- 184 **Order** Eunicida, Fauchald 1977
- 185 **Family** Dorvilleidae Chamberlin, 1919

186

187

- Genus Ceciamaralia gen. nov.
- 188 urn:lsid:zoobank.org:act:22B5ED41-CF25-4A97-8B75-DF336BE1CBE7
- 189 **Type species:** *Ceciamaralia lanai* **gen. et sp. nov.** described herein.
- 190 **Etymology:** Feminine. The genus name "Ceciamaralia" refers to the name Cecília and the
- 191 surname Amaral of Dr. Antônia Cecília Zacagnini Amaral, a Brazilian researcher who
- immensely contributed, and still contributes to the enhancement of Annelida knowledge and to
- 193 the education of zoologists, taxonomists and ecologists, including the three authors of this
- 194 paper.
- 195 **Diagnosis:** Prostomium triangular-shaped with anterior margin rounded. One pair of simple
- antennae, distally clavate, with a long and slender basal portion. One pair of simple, short and
- 197 clavate ventrolateral palps, or absent. Two peristomial rings. First two chaetigers usually
- enlarged to accommodate the large pharynx. Pharynx enlarged, normally protracted [CG6] out of
- the mouth in preserved specimens. First two parapodia shorter than those followings and
- 200 without appendages. Notopodia represented by a large and long dorsal cirrus (with a thin
- 201 notoacicula) present in a few anterior parapodia or entirely absent. Ventral cirri short and
- 202 papilliform, present only in a few anterior parapodia. Supra-acicular chaetae: capillary and
- 203 furcate or geniculate. Sub-acicular chaetae: compound heterogomph falcigers with serrated
- 204 unidentate blades. Two pairs of clavate pygidial cirri. Jaw apparatus with paired mandibles,
- 205 medially connected, without fused or free teeth on the anterior margin. Maxillae composed
- of a posterior ligament fused to a pair of long and serrated basal plates, followed by one
- pair of short, anteriormost free maxillary plates with a long thin spine on the anterior margin.
- 208 Carrier-like structure absent.
- 209 **Remarks:** Ceciamaralia gen. nov. is well distinguished from all Dorvilleidae genera by: i)
- 210 its maxillae composed of a pair of elongated and serrated basal plates and one pair of
- 211 free maxillary plates with an anterior long and thin spine, ii) its enlarged pharynx which

- 212 makes the anterior region of the specimens also enlarged when it is retracted; preserved
- 213 specimens are found usually with the pharynx protracted [CG7], iii) antennae with a long and
- slender basal portion and clavate distal end, iv) first two parapodia slightly shorter and without
- appendages, and v) dorsal cirri present only in a few anterior parapodia.
- 216 The differences of *Ceciamaralia* gen. nov. with some morphologically similar genera of
- 217 Dorvilleidae are analyzed in detail in the Discussion section.

219

- Ceciamaralia lanai gen. et sp. nov. (Figs-1-5)
- 220 urn:lsid:zoobank.org:act:3E16785F-8EDD-47E7-8CF4-34D5BD1F4062
- **Diagnosis:** One pair of palps. Long and large dorsal dorsal cirri with a thin notoacicula present
- on parapodia 3 to 6-9. Supra acicular chaetae: capillary and furcate.
- **Type locality:** Off Espírito Santo State, Brazil, 39°10'17.35"W, 19°36'26.24"S, 392 m, muddy.
- 224 **Type specimens:** Holotype: ZUEC-POL XXX (39°10'17.35"W, 19°36'26.24"S, 392 m,
- 225 muddy, 14 Dec 2011); Paratypes: ZUEC-POL XXX (1 specimen, 39°10'17.35"W,
- 226 19°36'26.24"S, 392 m, muddy, 14 Dec 2011); ZUEC-POL XXX (1 specimen, 38°1'8.43"W,
- 227 19°34'20.42"S, 450 m, sandy mud, 9 Dec 2011); ZUEC-POL XXX (1 specimen 39°36'8.52"W,
- 228 19°49'7.27"S, 158 m, sandy muddy, 14 Jan 2012); ZUEC-POL XXX (3 specimens,
- 229 39°30'25.23"W, 19°45'54.56"S, 144 m, muddy, 15 Jan 2012); ZUEC-POL XXX (2 specimens,
- 230 39°53'47.1"W, 20°35'16.23"S, 410 m, muddy, 8 Jan 2012; ZUEC-POL (1 specimen on slide,
- 231 38°41'18.43"W, 19°34'20.42"S, 450 m, sandy mud, 09 Dec 2011); ZUEC-POL XXX (1
- specimen on slide, 39°36'9.34"W, 19°49'6.26"S, 181 m, mud, 29 Jun 2013); ZUEC-POL XXX
- 233 (1 specimen on slide, 39°30'25.97"W, 19°45'53.43"S, 143 m, muddy, 27 Jun 2013); MZUSP
- 234 (2 specimens, 39°53'47.1"W, 20°35'16.23"S, 410 m, muddy, 8 Jan 2012); MNRJ (2 specimens,
- 235 39°53'47.1"W, 20°35'16.23"S, 410 m, muddy, 08 Jan 2012). SEM Material: (1 stub with 3
- 236 specimens 39°53'47.1"W, 20°35'16.23"S, 410 m, muddy, 8 Jan 2012; 40°14'14.08"W,
- 237 21°4'4.56" S, 141 m, sandy, 11 Jul 2013).
- 238 **Etymology:** Masculine. The specific epithet "lanai" refers to the surname of Dr. Paulo da
- 239 Cunha Lana (in memorian), a Brazilian polychaetologist who immensely contributed to the
- 240 increase of knowledge of Annelida in Brazil and worldwide, and was the supervisor of the
- senior author of this paper.

- **Description of holotype:** Cylindrical body (Fig. 1A). Complete specimen with 46 chaetigers,
- 243 4.18 mm long and maximum width of 0.25 mm in the anterior region (0.16 mm in the
- 244 posterior region), excluding parapodia. First 3-4 chaetigers larger than the rest of the body
- 245 to accommodate the enlarged pharynx (Fig. 1A). Prostomium triangular-shaped, anterior
- 246 margin broadly rounded. Ocelli absent. One pair of simple dorsal antennae in the middle of
- prostomium, distally clavate, with a long and slender basal portion, almost as long as the
- 248 prostomium (Figs. 1B, 4 A and 5 A). One pair of simple ventrolateral, short, and small
- 249 clavate palps, on the base of prostomium, almost half as long as the prostomium (Figs.
- 250 1B, 4 A,B and 5 A). Two peristomial rings without appendages, posterior one longer
- and wider than anterior one. (Figs. 1B, 4 A,B and 5 A,B).
- 252 Parapodia cylindrical, small, and barrel- shaped. First two parapodia smaller than the
- 253 following, without appendages (Figs. 1B and 5 A,B). Large and long dorsal cirrus
- with a thin notoacicula , almost 2.5 times the length of parapodium, present from the 3rd
- 255 to the 7th chaetigers (Figs. 1D, 4 B,D and 5 D). Short and papilliform ventral
- 256 cirri in the middle of parapodium, from the 3rd to the 7th chaetiger (Figs. 1D,
- 257 4 B,D and 5 B,D). Following parapodia slightly larger, longer, and without cirri (Fig
- 258 1E, 4 E and 5 E).
- Supra-acicular chaetae: one long, thin and serrated capillary (Fig. 2A,C) and one furcate with
- asymmetrical prongs, one slightly shorter and more robust than the other; tip of both prongs
- blunt (Figs. 2C, 4 G and 5 G); furcate of first chaetigers with small prongs and
- prominent serration below the shorter prong (Figs. 2A, B and 4 F). Sub-acicular chaetae:
- 263 three compound heterogomph facilgers, slightly different sizes, ventralmost shortest
- and dorsalmost longest; bifid shafts with a subtle serration on the distal end; short,
- robust, serrated, and unidentate blades (Figs. 2A-D, 4 J and 5 F,G). One serrated cultriform
- 266 chaeta occasionally replacing the ventralmost compound chaeta on the last posterior
- 267 chaetigers (Figs. 4 H and 5 F).
- 268 Median and posterior regions moniliform. Pygidium truncate and shorter than the previous
- 269 chaetigers. Two pairs of clavate pygidial cirri, dorsal pair slightly longer than the length of
- pygidium and ventral pair half the length of the dorsal pair (Figs. 1A,C, 4 C and 5 C).
- 271 Paired mandibles medially connected in a region strongly sclerotized; anterior region slightly
- broader and less sclerotized than the slender posterior region (Figs. 3A-D and 4 K).
- 273 Maxillae composed of one pair of elongated and serrated basal plates with small uniform

- sharp teeth on one margin, posteriorly fused to a weakly sclerotized posterior elongated
- 275 ligament. Basal plates anteriorly followed by one pair of anteriormost free maxillary
- 276 plates a long, thin and prominent spine on its anterior margin (Figs. 3A-D and 4 L).
- Variation: Complete specimens ranging from 2.9 mm to 7.6 mm in length and 33 to 61
- 278 chaetigers. All specimens ranging from 0.135 to 0.26 mm in maximum width
- 279 Dorsal cirri present from chaetiger 3 to 6-9 . The presence of ventral cirri usually follows
- 280 the parapodia in which the dorsal cirrus is present, but in some specimens the ventral cirri can
- be present in the following one or two parapodia. The presence of the cultriform chaeta is
- occasional in posterior chaetigers, but it is also present in the median region of some specimens,
- and in some specimens it is absent . The enlarged pharynx is characteristic of the genus and
- 284 it appears protracted cospout of the mouth in most preserved specimens (Figs. 4 B and 5
- 285 B) but when it is retracted the specimen presents an enlarged anterior region to accommodate
- 286 the pharynx (Fig. 1A and 4 A).
- 287 **Location and bathymetrics:** Off the s tates of Espírito Santo and Rio de Janeiro, Brazil,
- 288 141 450 m, substrates: mud, sandy mud, muddy or sandy.
- 289 **Remarks:** F. Ceciamaralia lanai gen. et. sp. nov. differs from C. nonatoi gen. et sp. nov. by
- 290 the presence of a large and long dorsal cirri on a few anterior chaetigers and the presence of
- 291 furcate chaeta in supra-acicular fascicle. The median and posterior regions of specimens are
- 292 usually moniliform.
- 293
- 294 Ceciamaralia nonatoi gen. et sp. nov. (Figs. 6 -9)
- 295 urn:lsid:zoobank.org:act:EFF6CD0C-2071-48A2-915D-6F2F8530A343
- **Diagnosis:** One pair of palps present or absent. Dorsal cirri absent. Supra-acicular chaetae:
- 297 capillary and geniculate.
- 298 **Type locality:** Off Espírito Santo State, Brazil, 40°12'52.126"W, 21°11'12.073"S, 680 m.
- 299 **Type specimens:** Holotype: ZUEC-POL XXX (40°12'52.126"W, 21°11'12.073"S, 680 m 04
- 300 Feb 2009). Paratypes: ZUEC-POL XXX (1 specimen, 40°12'52.126"W, 21°11'12.073"S, 680
- 301 m 04 Feb 2009); ZUEC-POL XXX (2 specimens, 40°1'55.373"W, 21°47'26.771"S, 780 m, 06
- 302 Feb 2009), ZUEC-POL XXX (3 specimens, 41°18'33,045"W, 23°39'21.880"S, 692.7 m, 28

- 303 Jan 2009); ZUEC-POL XXX (2 specimens 40°26'37.449"W, 22°33'35.143"S, 401 m, 31 Jan
- 304 2009); ZUEC-POL XXX (1 specimen, 40°26'40.289"W, 22°33'33.805"S, 393.4 m, 11 Jul
- 305 2008); ZUEC-POL XXX (1 specimen, 40°17'33.343"W, 22°25'59.389"S, 387.1 m, 31 Jan
- 306 2009); ZUEC-POL XXX (1 specimen, 40°5'18.066"W, 21°44'21.493"S, 401.6 m, 07 Jul 2008);
- 307 ZUEC-POL XXX (3 specimens 39°30'4.65"W, 19°46'34.99"S, 428 m, muddy, 14 Jan
- 308 2012); ZUEC-POL (1 specimen on slide, 40°2'13.825"W, 21°47'26.324"S, 730.5 m, 28 Jun
- 309 2008); MZUSP XXX (1 specimen, 41°18'33.045"W, 23°39'21.880"S, 692.7 m, 28 Jan 2009);
- 310 MZUSP XXX (1 specimen, 40°12'52.126"W, 21°11'12.073"S 680 m, 04 Feb 2009); MNRJ
- 311 XXX (38°41'19.8"W, 19°34'20.47"S, 449 m, mud, 30 Jun 2013); MNRJ XXX (1 specimen,
- 312 40°1'45.543"W, 22°19'45.730"S, 701.7 m, 30 Jan 2009); MNRJ XXX (1 specimen,
- 313 40°26'37.585"W, 22°33'35.276"S, 400 m, 31 Jan 2009); ZUEC-POL XXX (3 specimens, 40°
- 314 2' 13,825" W, 21° 47' 26,324" S, 730.5 m, 28 Jun 2008). <u>SEM Material</u>: ZUEC-POL XXX (1
- 315 stub with 3 specimens, 40°2'13.825"W, 21°47'26.324"S, 730.5 m, 28 Jun 2008 /
- 316 40°12'52.126"W, 21°11'12.073"S 680 m, 04 Feb 2009 / 39°30'4.65"W, 19°46'34.99"S, 428 m,
- 317 muddy, 14 Jan 2012).
- 318 **Etymology:** Masculine. The specific epithet "nonatoi" refers to the surname of Dr. Edmundo
- Ferraz Nonato (*in memorian*), one of the greatest Brazilian naturalists and oceanographers who
- 320 was the pioneer of Brazilian polychaetology, responsible for the education and inspiration
- 321 of generations of zoologists.
- 322 **Description of holotype:** Cylindrical body (Fig. 6 A). Complete specimen with 55
- 323 chaetigers, 6.27 mm long and maximum width of 0.41 mm in the anterior region (0.25 m m
- 324 in the posterior region), excluding parapodia. First 3-4 chaetigers larger than the rest of the
- body to accommodate the enlarged pharynx (Fig. 6 A). Prostomium triangular-shaped,
- anterior margin broadly rounded. Ocelli absent. One pair of simple dorsal antennae in the
- 327 middle of prostomium, distally clavate, with a long and slender basal portion, almost as long
- 328 as the prostomium (Figs. 6 B,C, 8 A,B, 9 A,B). One pair of simple, ventrolateral,
- 329 short, and small clavate palps on the base of prostomium, almost half as long as the
- 330 prostomium (Fig. 6 B). Two peristomial rings without appendages, posterior wider
- and longer than anterior (Figs. 6 B,C, 8 A,B and 9 A,B).
- 332 Parapodia cylindrical, small and barrel- shaped. First two parapodia smaller than the
- followings, without appendages (Figs. 6 B, 8 A and 9 B). Dorsal cirri absent on all
- parapodia. Short and papilliform ventral cirri in the middle of the parapodium, from the

- 335 3rd to the 6th chaetiger (Figs. 6 E, 8 D and 9 B,C). Following parapodia slightly
- larger, longer and without cirri (Figs. 8 E and 9 D).
- Supra-acicular chaetae: one long, thin and serrated capillary (Figs. 7A and 9 F,G) and
- one geniculate with distal region robust and slightly serrated (Figs. 7A,B , 8 F and
- 9 C,F). Sub-acicular chaetae: three compound heterogomph falcigers, almost equal length,
- 340 ventralmost slightly shortest; bifid shafts with a subtle serration on the distal end;
- 341 short, robust, serrated and unidentate blades (Figs. 7A,B, 8 G,H and 9 E,G). One
- 342 serrated cultriform chaeta occasionally replacing the ventralmost compound in the last
- posterior chaetigers (Figs. 7B , 8 J and 9C).
- 344 Median and p osterior regions moniliform. Pygidium truncate and shorter than the previous
- chaetigers. Two pairs of clavate pygidial cirri; dorsal pair slightly longer than the length of
- pygidium and ventral pair half the length of the dorsal pair (Figs. 6 D and 8 C).
- Paired mandibles medially connected in a region strongly sclerotized; anterior region slightly
- broader and less sclerotized than the slender posterior region (Figs. 7C-E and 8 K).
- 349 Maxillae composed of one pair of elongated and serrated basal plates with small uniform
- 350 sharp teeth on one inner margin, posteriorly fused to a weakly sclerotized posterior elongated
- 351 ligament. Basal plates anteriorly followed by one pair of anteriormost free maxillary plates
- 352 with a long, thin and prominent spine on its anterior margin (Figs. 7C-E and 8 L).
- 353 Variation: Complete specimens ranging from 3.23 to 6.27 mm in length and 46 to 62
- 354 chaetigers. A variation within this species, which was observed through the analysis of some
- specimens, is the presence or absence of palps. Ceciamaralia nonatoi sp. nov. has small and
- 356 fragile palps, but many specimens do not present them (Figs. 5C and 7A,B). The small size
- of palps and the enlarged pharynx protracted cospout of the mouth are obstacles to clearly
- 358 <u>observe would obscure</u> the scar of a possible broken palp. Therefore, it is debatable whether
- 359 this is a variation or a methodological problem, so we decided to diagnose the species with
- presence/absence of palps. The ventral cirri are always present, from the parapodia 3 to 5-7.
- The presence of the cultriform chaeta is occasional in posterior chaetigers, but it is also present
- in the median region of some specimens, and in some specimens it is absent. The enlarged
- pharynx is characteristic of the genus and it appears protracted [CG10] out of the mouth in most
- preserved specimens, but when it is retracted the specimen presents an enlarged anterior region
- 365 to accommodate the pharynx.

- 366 Location and bathymetrics: Off the states of Espírito Santo and Rio de Janeiro, Brazil,
 367 387.1 780 meters deep, substrates: mud or muddy.
- 368 **Remarks:** Ceciamaralia nonatoi sp. nov. differs from its congener by the absence of dorsal
- 369 cirri and by the presence of a geniculate chaeta instead of a furcate in the supra-acicular fascicle.
- The variation of the length of the blades of the compound chaetae is very subtle, while in
- 371 Ceciamaralia lanai gen. et sp. nov. it is more distinguished distinctive. The bathymetric
- 372 distribution is also a difference between the two species; Ceciamaralia nonatoi gen. et sp.
- 373 **nov.** is registered in deeper waters (387.1 780 m) than *Ceciamaralia lanai* **gen. et sp. nov.**
- 374 (141 450 m).

376

Cladistic results

- 377 The cladistic analysis resulted in one most parsimonious cladogram from 467,210
- 378 rearrangements, with best score (length) of 79 steps, consistency index (ci) of 74 , retention
- index (ri) of 87 (Fig. 10). The cladogram shows the monophyly of Ceciamaralia gen.
- **nov.**, supported by the following synapomorphies: character 40 : only one pair of free
- 381 maxillary plates; character 44 : enlarged pharynx/enlarged anterior region; character 45
- ventral cirri present only on a few anterior parapodia and character 46 : presence of a
- long and thin spine on the anteriormost maxillary plate. The genera Ceciamaralia gen. nov.,
- Protodorvillea and Dorvillea were well supported by the Bbremer absolute support index (9,
- 385 12 and 16 respectively) as well as the bootstraps values (87, 92 and 90 respectively) (Fig. 11).
- The inclusion of Ceciamaralia lanai gen. et sp. nov. and Ceciamaralia nonatoi gen. et sp.
- **nov.**, as well as the addition of four new characters to the matrix of characters in the study
- of de Oliveira Bonaldo et al. (2022), did not substantially affect the results obtained in the
- previous study. Ceciamaralia gen. nov. was placed as a sister group of all other genera
- analyzed, except *Eliberidens* and *Gymnodorvillea*, in presenting the synapomorphy of the
- 391 character 22: the chaeta which accompanies the capillary in the supra-acicular fascicle does
- 392 not change along the body.

393

394

Discussion

- At the first glance, *Ceciamaralia* **gen. nov.** specimens are hard to differentiate from other small-sized dorvilleids, but a closer look reveals their morphological differences and unique morphology. Below, these differences are discussed with some morphologically similar genera, specifically those present in the cladistic study of this work and also presented in de Oliveira Bonaldo et al. (2022). —Prostomial *appendages*
- Ceciamaralia gen. nov. presents a cylindrical and small-400 sized body, with small body 401 appendages and triangular prostomium , as in Protodorvillea, Meiodorvillea, 402 Eliberidens, and Pettiboneia. Those genera also appear closely related in cladistic studies 403 (Eibye-Jacobsen & Kristensen, 1994; de Oliveira Bonaldo et al., 2022). *Protodorvillea* has long 404 and biarticulated palps, while Ceciamaralia gen. nov. has simple, small, clavate and 405 papilliform palps, when present. The palps of *Pettiboneia* are shorter than in *Protodorvillea* 406 but are still biarticulated and also longer and larger than the palps of Ceciamaralia gen. nov. The small clavate palps in Ceciamaralia gen. nov. are similar to those observed in 407 408 Meiodorvillea and Eliberidens. The antennae are described here as simple and clavate, as in 409 some Dorvilleidae genera, but, in *Ceciamaralia* **gen. nov.** they are unique in having a longer
- 411 Parapodial appendages

416

417

418

419

420

421

422

423

424

425

426

Ceciamaralia **gen. nov.** presents small papilliform ventral cirri only on a few anterior parapodia, while *Meiodorvillea Protodorvillea, Pettiboneia, Dorvillea, Schistomeringos* and *Eliberidens* present it on all parapodia, except the first; on the other hand, Eliberidens hartmannschroederae Hilbig, 1995 does not have ventral cirri.

and slender basal portion than the antennae from other genera.

Pettiboneia and Ceciamaralia gen. nov. also share the presence of dorsal cirri on anterior parapodia inserted at the base of parapodia, but they have two evident differences: i) Ceciamaralia lanai gen. nov. presents the dorsal cirri from parapodium 3 reaching the 9th, while in Pettiboneia they are present from parapodium 2 reaching at least the 7th, but in some species they can reach as far as the 25th, as in Pettiboneia sanmartini Aguirrezabalaga & Ceberio, 2003; ii) Ceciamaralia lanai gen. et sp. nov. has very long and large dorsal cirri, reaching more than three times the length of parapodia, while in Pettiboneia they are distinctively slender and shorter. Some species of Meiodorvillea, as Meiodorvillea minuta (Hartman, 1965), also present dorsal cirri in few anterior parapodia, but they small, papilliform/globular, from the 2nd parapodium and inserted in the middle of parapodium. Dorvillea and Schistomeringos also present a cylindrical dorsal cirri, but they are slender,

- biarticulated and absent only on the first parapodium. In contrast, Ceciamaralia nonatoi gen. et
- 428 sp. nov. does not have dorsal cirri.
- 429 *Dorsal cirri x notopodium x notopodial lobe x branchiae*
- 430 The presence of the dorsal cirri in Ceciamaralia lanai gen. et sp. nov. generated a debate
- 431 regarding the origin of this appendage. It resembles the same structure observed in species of
- 432 Pettiboneia, Diaphorosoma Wolf, 1986a and Westheideia Wolf, 1986a, but they are named
- differently. All species of these genera present this cylindrical appendage inserted at the base
- of parapodia. In Diaphorosoma magnavena Wolf, 1986a and Westheideia minutimala Wolf,
- 435 1986a, it is described as a notopodium bearing an internal acicula, and the former having an
- internal vascular loop, similar to a branchia. It is important to note that both species also present
- an appendage described as branchia inserted distally on the neuropodium and it also
- 438 presents a vascular loop in that from *D. magnavena*. The notopodium in *Pettiboneia* species
- 439 is described as a dorsal cirrus, also having internal acicula; some species, like *P. dibranchiata*
- 440 (Armstrong & Jumars, 1978), also have a distal appendage in the neuropodium described
- 441 as branchia, exactly as in D. magnavena and W. minutimala. Notopodium of
- 442 Ceciamaralia lanai gen. et. sp. nov., it shows a vascularized tissue and an acicula barely
- visible, so we decided to describe it as a dorsal cirrus because of its position and in agreement
- 444 with whathow it is described in the literature.
- 445 Chaetae
- 446 The presence and format of furcate and geniculate chaeta shows a great diversity in
- Dorvilleidae. Of the two species of *Ceciamaralia* gen. nov., *C. lanai* gen. et sp. nov. has
- 448 furcate chaetae, while *C. nonatoi* gen. et sp. nov. has geniculate chaetae. This variation can
- also be observed in species of *Meiodorvillea*; *M. minuta* possesses furcate and *M. apalpata*
- possesses geniculate chaetae, while *M. penhae* and *M. jumarsi* present both types. Dorvillea
- and Schistomeringos are two similar genera, the former does not have lacking furcate while the
- latter has them. All species of Protodorvillea and Eliberidens present furcate chaeta.
- The blades of the compound chaeta of *Ceciamaralia* **gen. nov.** are smaller, straighter and more
- robust than in species of other genera in which the dorsalmost compound chaeta can be very
- 455 long and spinigerous.
- 456 Jaw apparatus

The jaw apparatus of Ceciamaralia gen. nov. presents a distinct and specific morphology differing from that of all other species of the family. Protodorvillea and Dorvillea present a broad and robust jaw apparatus with a maxillae composed of strong basal plates, a carrierlike structure and four rows of many robust maxillary plates. The maxillae of *Pettiboneia* and smaller, presenting only two rows of similar maxillary plates (species of Meiodorvillea are Pettiboneia have some poorly sclerotized additional plates and they lack basal plates). On the other hand, the maxillae of *Eliberidens* do not have maxillary plates at all; they are composed only of superior and inferior long basal plates. The jaw apparatus of Ceciamaralia gen. nov. presents the posterior ligament fused to only one pair of long and serrated basal plates followed anteriorly by one pair of free maxillary plates presenting a long and thin distinct spine.

Cladistic analysis

457

458

459

460

461

462

463

464

465

466

467

468

469

470

471

472

473

474

475

476

477

478

479

480

481

482

483

484

485

486

487

488

The scarcity of taxonomic knowledge of Dorvilleidae is an obstacle to conduct phylogenetic analysis . But some studies were have been performed to elucidate relationships within the family; the most comprehensive was a cladistic one carried out by Eibye-Jacosbsen & Kristensen (1994) where they utilized all known genera of Dorvilleidae at that time as terminal taxa. Even with slow progress, molecular data is already aiding in the clarification of the phylogenetic relationships of dorvilleids, mainly *Ophryotrocha* (Heggøy, Schander & Åkesson, 2007), which is the genus with most sequence data. The gap lack of in-molecular data of in other genera of the family opens space to specific cladistic studies with morphological data like Pleijel & Eide (2007), de Oliveira Bonaldo et al. (2022) and this present one. Those studies are important to subside provide data and results to future studies about the systematics of Dorvilleidae.

Ceciamaralia gen. nov. morphologically resembles other small—sized dorvilleids presented in the cladistics analysis by de Oliveira Bonaldo et al., 2022; hence we included both new species described here in the matrix—of that study. The new genus appeared as monophyletic by the specific synapomorphies discussed here: , which ranked it as a new genus, the unique maxillae with only one pair of free—maxillary plates,—presenting a specific long and thin spine,—the enlarged pharynx making the anterior region enlarged when it is retracted, which is not observed in others genera—of the family, and the ventral cirrus present only in few anterior parapodia. The results of de Oliveira Bonaldo et al., 2022 placed Meiodorvillea as a sister group of all other genera—presented in the analysis except Eliberidens and

Gymnodorvillea. The inclusion of the *Ceciamaralia* **gen. nov** species and the new characters in the analysis did not affect the previous relationship results among the genera or their monophyly .

Present and future

The study of small annelids has some obstacles like the difficulty to collect and identify them. In Brazil only nineteen species were registered before the present study, but this number does not reflect the true diversity of this family on the Brazilian coast. The continuous increase of scientific advancements and the development of new techniques and tools, researchers can perform new and more detailed analyses of unidentified species. These studies increase the systematic knowledge of the species and reveal the biodiversity of the group.

Museum collections play an important role since they preserve the organisms previously described and also contain unidentified organisms, which can hold much biological and ecological information aiding in several fields of study, mainly taxonomy and ecology. The specific identification of the organisms reveals records and occurrences of them aiding in biogeographical, ecological and distribution studies and ecological patterns subsidizing data of potential distribution (Budaeva et al., 2024). Morphological analysis can reveal new or different characters and structures supporting a refined description, reveal new species and aid the understanding of the phylogenetic relationship of the species of the group, as was demonstrated in the present study. That is why the education of taxonomists is important as well as encouraging them to identify, describe and study those neglected groups, enhancing the discovery of their biodiversity and knowledge. [CG11]

The incentive towards taxonomic studies and projects resulted in the first description of a new genus of Dorvilleidae in almost 25 years, presented here. Dorvilleids present a great morphological diversity, but our taxonomic knowledge of this group is still limited by the reasons mentioned before and the lack of incentive for taxonomist studies. This incentive is very important to aid researchers to better comprehend and classify those organisms, because their identification and description is not an easy task.

This study is a partial result obtained through the current Ph.D thesis of the first author, which is focused on the taxonomic study of Dorvilleidae; CG12 Pereliminary morphological analysis of museum materials of Dorvilleidae indicates

several new records of the family for the Brazilian coast and also potential new species to the family. In addition, we highlight the importance of the effort to collect new and fresh organisms in view of the fact that they can provide current biodiversity data and can also provide more accurate genetic information through molecular studies, since some groups like the Dorvilleidae present a huge gap in those data.

525

526

520

521

522

523

524

Key to species of Ceciamaralia gen. nov.

532

533

531

Acknowledgements

- We would like to thank all people involved in the collection of the material (projects AMBES
- and HABITATS) and also the MDBio for providing access to it. We would like to acknowledge
- 536 the access to equipment and assistance provided by the Electron Microscope Laboratory
- 537 (LME/UNICAMP). We thank Dr. Yasmina Shah Esmaeili for providing language revision.
- We also express our gratitude for the three reviewers, Dr. Vinicius Miranda, Dr. Danny Eibye-
- Jacobsen and one anonymous, for all the corrections and suggestions which immensely
- 540 contribute to the improvement of this work.

541

542

Funding Statement

- 543 This study was financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
- 544 Brasil (CAPES) Finance Code 001 to Rafael de Oliveira Bonaldo; Conselho Nacional de
- Desenvolvimento Científico e Tecnológico CNPq (301551/2019-7) and The São Paulo
- 546 Research Foundation FAPESP (2018/10313-0).

548 **References** [CG13]

- 549 Aguirrezabalaga F, Ceberio A. 2003. Dorvilleidae (Polychaeta) from the Capbreton Canyon
- 550 (Bay of Biscay, NE Atlantic) with the description of *Pettiboneia sanmartini* sp. nov. *Cahiers*
- 551 *de Biologie Marine* 44(1), 41-48.
- 552 Amaral ACZ, Nallin SAH, Steiner TM, Forroni TO, Gomes-Filho D, Araújo GR, Freitas R,
- 553 Costa CAO, Ruta C, Gomes KRE, Bonaldo RO. 2006-2022. Catálogo das espécies de
- 554 Annelida "Polychaeta" do Brasil. (available from:
- 555 http://www.ib.unicamp.br/museu_zoologia/files/lab_museu_zoologia/Catalogo_Polychaeta_
- Amaral et al 2022.pdf (accessed in 28 July 2023).
- Augener H. 1918. Polychaeta. Beitrage zur Kenntnis der Meeresfauna Westafrikas 2 (2): 67–
- 558 625.
- 559 Armstrong JW, Jumars PA. 1978. Branchiate Dorvilleidae (Polychaeta) from the North Pacific.
- 560 Bulletin, Southern California Academy of Sciences 77(3), 133-138.

561

- Budaeva N, Agne S, Ribeiro PA, Straube N, Preick M, Hofreiter M. 2024. Wide-spread
- dispersal in a deep-sea brooding polychaete: the role of natural history collections in assessing
- 564 the distribution in quill worms (Onuphidae, Annelida). Front Zool 21, 1.
- 565 https://doi.org/10.1186/s12983-023-00520-0.
- 566 Chamberlin RV. 1919. The Annelida Polychaeta. Memoirs of the Museum of Comparative
- 567 *Zoology at Harvard College* 48: 1–514. https://doi.org/10.5962/bhl.title.49195
- 568 Claparède E, Mecznikow E. 1869. Beiträge zur Kenntnis der Entwickelungsgeschichte der
- 569 Chaetopoden. Zeitschrift für wissenschaftliche Zoologie 19, 163–205.
- 570 Day JH. 1963. The polychaete fauna of South Africa. Part 8: New species and records from
- 571 grab samples and dredging. Bulletin of the British Museum (Natural History), Series Zoology
- 572 10(7): 381–445.
- 573 de Oliveira Bonaldo R, Menchini Steiner T, Zacagnini Amaral AC. 2022. Revision of
- 574 Meiodorvillea Jumars, 1974 (Annelida: Dorvilleidae) including descriptions of three new
- species from the Southwestern Atlantic Ocean. *Plos one* 17(3), e0264081.
- 576 de Oliveira Bonaldo R, Steiner TM, Garraffoni ARS, Amaral ACZ. 2022. First record of the
- 577 genus *Eliberidens* (Annelida: Dorvilleidae) from the Southwestern Atlantic Ocean and cladistic
- 578 analysis of the genus. Zoologischer Anzeiger 301, 115-126.
- delle Chiaje S. 1828. Memorie sulla storia e notomia degli animali senza vertebre del Regno di
- 580 Napoli. *Stamperia della Società Tipografica Napoli* 3: 1–232.
- 581 Ehlers E. 1901. Die Polychaeten des magellanischen und chilenischen Strandes. Ein
- 582 faunistischer Versuch. Festschrift zur Feier des Hundertfu nfzigja hrigen Bestehens des

- 583 Ko niglichen Gesellschaft der Wis-senschaften zu Go tingen, Abhandlungen der
- Mathematisch-Physikalischen Klasse. 1–232, 25 plates.
- Eibye-Jacobsen D, Kristensen RM. 1994. A new genus and species of Dorvilleidae (Annelida,
- Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and
- 587 Dinophilidae. Zool Scr 23(2): 107–131.
- Fauchald K. 1977. The polychaete worms. Definitions and keys to the orders, families and
- 589 genera. Natural History Museum of Los Angeles County, Science Series.
- 590 Goloboff PA, Morales ME. 2023. TNT version 1.6, with a graphical interface for MacOS and
- 591 Linux, including new routines in parallel. Cladistics 39(2), 144-153. DOI
- 592 10.1111/cla.12524.
- Hartman O. 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and
- 594 other North Atlantic areas. Occasional Papers of the Allan Hancock Foundation 28: 1–384
- 595 Hernández-Alcántara P, Pérez-Mendoza AY, Solís-Weiss V. 2006. Description of three new
- 596 species of *Ninoe* and *Cenogenus* (Polychaeta: Lumbrineridae) from the Mexican Pacific.
- 597 *Scientia Marina* 70(S3), 81-90.
- 598 Hilbig B. 1995. A new polychaete Eliberidens hartmannschroederae sp. n. Polychaeta
- 599 Dorvilleidae from the US Atlantic continental slope. Mitt Hambg Zool Mus. Inst 92
- 600 (April), 85–88.
- Jumars PA. 1974. A generic revision of the Dorvilleidae (Polychaeta), with six new species
- from the deep North Pacific. Zool J Linn Soc 54(2): 101–135.
- 603 https://doi.org/10.1111/j.1096-3642.1974.tb00794.x.
- 604 Kvalø Heggøy K, Schander C, Åkesson B. 2007. The phylogeny of the annelid genus
- 605 Ophryotrocha (Dorvilleidae). Marine Biology Research 3(6), 412-420.
- 606 https://doi.org/10.1080/17451000701695361.
- 607 Lamarck JBD. 1802. Discours d'Ouverture, Prononcé le 27 floréal An 10, au Muséum
- d'Histoire naturelle. Recherches sur l'organisation des corps vivans. Bulletin Scientifique de la
- 609 France et de la Belgique 483-517.
- 610 Lavrado HP, Brasil ACS. 2010. In: Lavrado, H.P., Brasil, A.C.S. (Eds.), Biodiversidade da
- 611 região oceânica da Bacia de Campos: Macrofauna, p. 232. Rio de Janeiro, SAG Serv.
- Maddison WP, Maddison DR. 2019. Mesquite: a Modular System for Evolutionary Analysis.
- 613 Version 3.61, 2019.
- Martin D, Britayev TA. 1998. Symbiotic polychaetes: review of known species. Ansell A,
- Barnes M, Gibson RN, Gibson RN. (Eds.). 1998. Oceanography and Marine Biology: An
- 616 annual review Volume 36 (1st ed.). CRC Press. 35(36), 217-340.
- 617 https://doi.org/10.1201/b12646.

- Martin D, Britayev TA. 2018. Symbiotic polychaetes revisited: an update of the known species
- and relationships (1998–2017). In: Hawkins SJ, Evans AJ, Dale AC, Firth LB, Smith, IP.
- 620 (Eds.). 2018. Oceanography and Marine Biology: An annual review Volume 56 (1st ed.). CRC
- 621 Press.. https://doi.org/10.1201/9780429454455.
- McIntosh WC. 1869. On the structure of the British nemerteans, and some new British annelids.
- 623 Trans R Soc Edinb 25 (2), 305–433.
- Moore JP. 1906. Additional new species of Polychaeta from the North pacific. In: *Proceedings*
- 625 of the Academy of Natural Sciences of Philadelphia vol. 58, pp. 217–260.
- Moore JP. 1909. Polychaetous annelids from Monterey Bay and San Diego, California. Proc
- 627 *Acad Nat Sci Phila* 61: 235–295. https://doi.org/10.5852/ejt.2021.736.1251.
- Nixon KC. 2002. WinClada Ver. 1.00. 08. Published by the Author, Ithaca, NY.
- 629 Núñez J. 1998. Marycarmenia lysandrae, a new genus and interstitial species (Polychaeta:
- 630 Dorvilleidae) from Madeira. Bull Mar Sci 62 (1), 115–119.
- Orensanz JM. 1973. Los anelidos poliquetos de la provincia biogeografica Argentina. III.
- 632 Dorvilleidae. *Physis Seccion A Los oceanos y sus organismos* 32(85): 325–342.
- Parfitt E. 1866. Description of a *Nereis* new to science. *Zoologist* 21: 113–114.
- Paxton H. 2009. Phylogeny of Eunicida (Annelida) based on morphology of jaws. Zoosymposia
- 635 2 (1), 241–264. https://doi.org/10.11646/zoosymposia.2.1.18.
- Pettibone MH. 1961. New species of polychaete worms from the Atlantic Ocean, with a
- revision of the Dorvilleidae. *Proceedings of the Biological Society of Washington* 74(19),
- 638 167-186.
- Pleijel F, Eide R. 1996. The phylogeny of *Ophryotrocha* (Dorvilleidae: Eunicida: Polychaeta).
- 640 *Journal of Natural History* 30(5), 647-659. https://doi.org/10.1080/00222939600770361.
- Read G, Fauchald K. 2024. World Polychaeta database. Dorvilleidae Chamberlin, 1919.
- 642 Accessed through: World Register of Marine Species. Available at
- 643 https://www.marinespecies.org/aphia.php?p=taxdetails&id=971 (accessed 31 Jan 2024).
- Rossi MM. 1984. A new genus and species of iphitimid parasitic in an aphroditid (Polychaeta),
- 645 with an emendation of the family Iphitimidae. Bulletin Southern California Academy of
- 646 Sciences 83(3): 163-166.
- 647 Steiner TM, Santos CSG. 2004. A new species of *Neanthes* (Annelida, Polychaeta, Nereididae)
- 648 from Brazil, and some remarks on Neanthes bruaca Lana & Sovierzoski, 1987. Beaufortia
- 649 54 (2), 39–57.
- 650 Tilic E, Rouse GW. 2024. Hardly Venus's servant—morphological adaptations of Veneriserva
- 651 to an endoparasitic lifestyle and its phylogenetic position within Dorvilleidae (Annelida).
- Organisms Diversity & Evolution 24(1), 67-83.

- Wainwright SC, Perkins TH. 1982. Gymnodorvillea floridana, a new genus and species of
- 654 Dorvilleidae (Polychaeta) from Southeastern Florida. Proc Biol Soc Wash 95 (4),
- 655 694–701.
- Webster HE. 1879. The Annelida Chaetopoda of the Virginian coast. Transactions of the
- 657 *Albany Institute* 9: 202–269.
- Westheide W. 2000. Ikosipodoides seychellensis, a new genus and species of interstitial
- polychaetes (Dorvilleidae) from the island of Mahé, Indian Ocean. *Cahiers de biologie marine*
- 660 41(1), 19-24.
- Wolf PS. 1986a. Four new genera of Dorvilleidae (Annelida: Polychaeta) from the Gulf of
- 662 Mexico. *Proc Biol Soc Wash* 99(4): 616–626.
- Wolf PS. 1986b. Three new species of Dorvilleidae (Annelida: Polychaeta) from Puerto Rico
- and Florida and a new genus for dorvilleids from Scandinavia and North America. Proc Biol
- 665 Soc Wash 99(4), 627-638.
- Yen NK, Rouse GW. 2020. Phylogeny, biogeography and systematics of Pacific vent, methane
- seep, and whale-fall *Parougia* (Dorvilleidae: Annelida), with eight new species. *Invertebrate*
- 668 Systematics 34(2), 200-233.
- Zanol J, Carrera-Parra LF, Steiner TM, Amaral ACZ, Wiklund H, Ravara A, Budaeva N.
- 670 2021 The Current State of Eunicida (Annelida) Systematics and Biodiversity. *Diversity* 13(2):
- 671 74. https://doi.org/https://doi.org/10.3390/d13020074.
- 672 Zhang D, Zhou Y, Yen N, Hiley AS, Rouse GW. 2023. Ophryotrocha (Dorvilleidae,
- Polychaeta, Annelida) from deep-sea hydrothermal vents, with the description of five new
- 674 species. European Journal of Taxonomy 864, 167-194.