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ANIMAL SCIENCE

A new species of *Euclymene* (Maldanidae, Annelida) from Brazil, with new combinations, and phylogenetic implications for Euclymeninae

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Abstract: Maldanids are tube-building polychaetes, known as bamboo-worms; inhabit diverse marine regions throughout the world. The subfamily Euclymeninae was proposed to include forms with anal and cephalic plates, a funnel-shaped pygidium, and a terminal anus. *Euclymene,* the type genus of Euclymeninae, has about 18 valid species. *Euclymene vidali* sp. nov. is defined and members of the species described from Northeastern Brazil. Members of this species have 23 chaetigers, and one pre-pygidial achaetous segment; nuchal grooves extend through three quarters of the cephalic plate, and there is one acicular spine with a denticulate tip. *Euclymene africana*, and *E. watsoni*, are here recognized, respectively, as *Isocirrus africana* comb. nov., and *I. watsoni* comb. nov. Three monotypic genera are invalid: *Macroclymenella, Eupraxillella*, and *Pseudoclyemene*; their species should be recognized as *Clymenella stewartensis* com. nov., *Praxillella antarctica* com. nov., and *Praxillela quadrilobata* com. nov., respectively. An identification key and a comparative table for all species of *Euclymene* are provided. A comparative table for all genera of Euclymeninae is also furnished. The paraphyletic status of *Euclymene* and Euclymeninae is discussed. The taxon Maldanoplaca is not code compliant and should only be regarded as an informal name.

Key words: Euclymeninae, Maldanidae, new species, polychaeta, systematics.

INTRODUCTION

Maldanids are sedentary, tube-building polychaetes, commonly known as bamboo worms (Fauchald 1977, Imajima & Shiraki 1982, Lee & Paik 1986, Fauchald & Rouse 1997, Rouse 2001, De Assis & Christoffersen 2011). Their tubes are constructed either horizontally, with sand and shell fragments under rocks, or vertically in sandy bottoms with fine sand in marine regions, or with mud in estuaries (Day 1967, Jiménez-Cueto & Salazar-Vallejo 1997, De Assis et al. 2007). Tubes are mucus-lined or have an inner organic sheath secreted by the worm. The internal fibers of this sheath may become hardened by the incorporation of fine sediment (e.g., mud), and these may become agglutinated into several layers (Pilgrim 1977, Shcherbakova et al. 2017). Individual species are found in estuaries, or from other intertidal habitats to the deep sea (Arwidsson 1906, Chamberlin 1919, De Assis et al. 2007).

Arwidsson (1906) presented a revision of maldanids based on the Scandinavian and Arctic fauna. He proposed the subfamily Euclymeninae to include forms with cephalic and anal plates, and a funnel-shaped pygidium bordered by cirri or crenulated. All euclymenins present a terminal anus, and members of some species have a ventral valve. In this revision, Arwidsson proposed *Isocirrus* to include species with members that have anal cirri of the same length. On the other hand, comparisons among members of species have shown that members of *Euclymene* have at least one midventral cirrus longer than remaining cirri (Salazar-Vallejo 1991).

Members of *Euclymene* present the following features: 18–24 chaetigers, and one or more achaetous preanal segments; longitudinal glandular stripes can be present among members of some species. The presence of a midventral cirrus that is longer than remining cirri has been the main feature used to distinguish this genus (Quatrefages 1865, 1866, Arwidsson 1906, Day 1955, 1967, De Assis & Christoffersen 2011, De Assis et al. 2012). However, *Euclymene* is paraphyletic (De Assis, pers. obs.) and this character is not unique to members of the genus (see below).

Members of *Euclymene* occur from estuarine and intertidal regions to the deep sea, in sandy bottoms or on coral reefs (Jiménez-Cueto & Salazar-Vallejo 1997). They have been reported from all oceans, especially in shallow coastal regions. However, most reports are from European waters, the North Atlantic and Mediterranean (Fauvel 1927, Read & Fauchald 2020). Members of the following species have been recorded from Brazil: *E. droebachiensis* (M. Sars, 1872), described originally from Faroe Island, North Atlantic; and *E. coronata* Verrill, 1900, described originally from Castle Island, Boston, USA, were subsequently reported from the north coast of the State of São Paulo; *E. oerstedii* (Claparède, 1863), described originally from Normandy, Atlantic Ocean, and reported from the northern coast of São Paulo and Guanabara Bay, State of Rio de Janeiro; *E. lombricoides* (Quatrefages, 1865), described originally from Boulogne-Sur-Mer and Calais Beach, France, have been collected in Bacia de Campos, Rio de Janeiro (Amaral et al. 2013), and *E. coronata* are reported from northeastern Brazil (De Assis et al. 2012).

The aim of this study is to present a new *Euclymene* species, with members from northeastern Brazil, and to transfer *E. africana* (Gravier, 1905) and *E. watsoni* (Gravier, 1905) to *Isocirrus* Arwidsson, 1906. In addition, we discuss the status of Euclymeninae as a phylogenetic hypothesis.

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MATERIALS AND METHODS

Specimens of the new species were collected in the estuary of Diogo Lopes Macau, Rio Grande do Norte, and the estuary from Barra de Mamanguape River, Rio Tinto, Paraíba, both in northeastern Brazil (Fig. 1). Specimens were fixed in 10% seawater-formalin, and later rinsed with fresh water, then preserved in 70% ethanol. Specimens were observed with a Zeiss stereo microscope. Rostrate and acicular hooks were observed with an Olympus BX41 compound microscope. For scanning electron microscopy, worms were washed twice in a 0.1 M phosphate buffer (pH 7.2) for 2 h at room temperature. They were then fixed again in 1% osmium tetroxide with a phosphate buffer for 1 h at room temperature. All worms were dehydrated into 100% ethanol, critical-point-dried in CO_2, mounted on stubs, coated with gold, and examined using a JEOL 25SII scanning electron microscope. The type material is deposited in Universidade Federal da Paraíba, CIPY-POLY-UFPB. All line drawings were made using a camera lucida. Illustrations were prepared using CorelDraw. Measurements are in millimeters and microns.

The treatment of taxa in this paper follows from the view that they are explanatory hypotheses, as opposed to being ontological entities, individuals, things, or just groupings of individuals (Fitzhugh 2005, 2008, 2009,

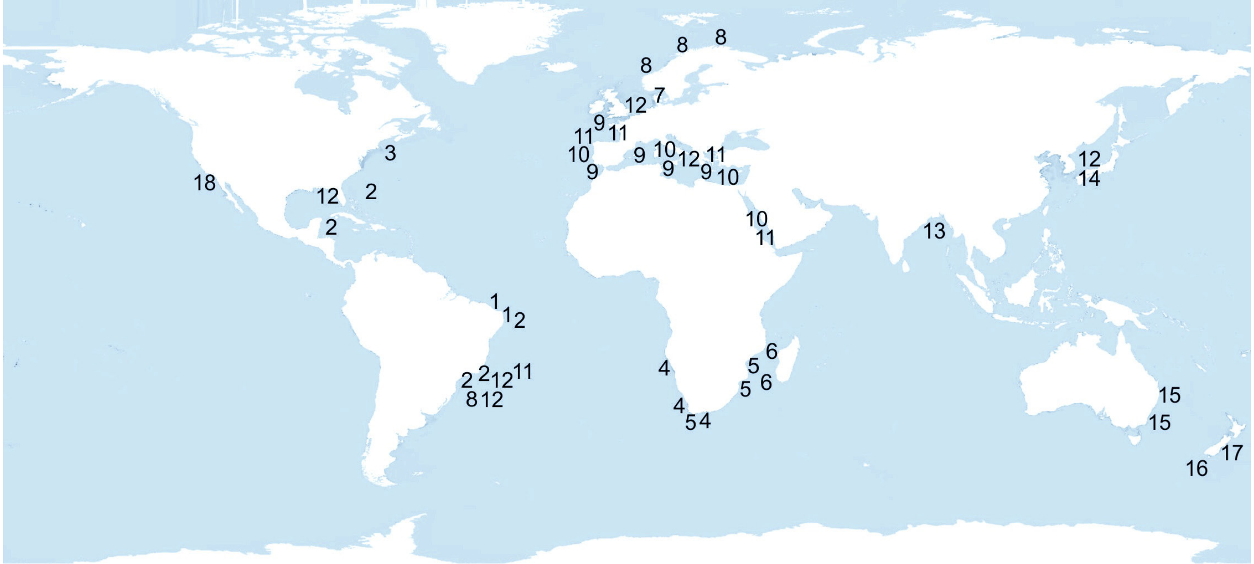

Figure 1. Map of distribution of *Euclymene* species, including the new species described in this paper. (1) *E. vidali* sp. nov., (2) *E. coronata*, (3) *E. dispar*, (4) *E. luderitziana*, (5) *E. natalensis*, (6) *E. mossambica*, (7) *E. lindrothi*, (8) *E. droebachiensis*, (9) *E. palermitana*, (10) *E. collaris*, (11) *E. lombricoides*, (12) *E. oerstedii*, (13) *E. annandalei*, (14) *E. uncinata*, (15) *E. trinalis*, (16) *E. aucklandica*, (17) *E. insecta*, (18) *E. delineata*.

2010a-b, 2012, 2013, 2015, 2016a-b, Fitzhugh et al. 2015, Nogueira et al. 2010, 2013, 2017, 2018). If possible, formal definitions of relevant taxa will be presented, per the International Commission on Zoological Nomenclature (1999) Article 13.1.1, as referring to either phylogenetic or specific hypotheses.

RESULTS

Systematics

Family Maldanidae Malmgren, 1867
Subfamily Euclymeninae Arwidsson, 1906
Genus Euclymene Verrill, 1900

Euclymene Verrill, 1900, p. 654–655; Arwidsson 1906, pp. 220–221, Day 1967, p. 134, Fauchald 1977, p. 40, Salazar-Vallejo 1991, pp. 275–276, De Assis & Christoffersen 2011, p. 242.

Type-species: Clymene amphistoma Lamarck, 1818: p. 341.

Definition: There is no phylogenetic hypothesis to which *Euclymene* refers (cf. Fitzhugh 2008) since this taxon denotes a paraphyletic group. Thus, a formal definition of the name cannot be provided at this time.

The following characters differentiate individuals to which the name *Euclymene* refers from individuals to which other Maldanidae genera refer: body with 18–24 chaetigers; 1–2 acicular spines on first three chaetigers, with smooth or dentate tips; cephalic plate with deep or slight lateral notches; posterior edge of cephalic plate smooth or crenulated; notochaetae include limbate capillaries and slender forms; uncini with 3–7 teeth above rostrum; 1–4 pre-pygidial achaetous segments; midventral cirrus longer than other cirri; anus close to anal plate.

Remarks: The inability to define the name *Euclymene* as representing a phylogenetic hypothesis is due the fact that the taxon is currently presumed paraphyletic; there are no synapomorphies currently recognized (cf. Table I). A future phylogenetic analysis involving members of *Euclymene* species will be required to resolve this issue.

Euclymene vidali sp. nov.

Table I. **Comparative table to all genera of Euclymeninae. Note that some genera are not present exclusive characters. N/A = Not applicable. * *Heteroclymene* is the unique taxon of Euclymeninae that species present acicular spine on chaetiger 4.**

Genera	Characters													References
	Cephalic plate	Cephalic plate rim	Cephalic rim notches. Lateral, posterior	Acicular spines, chaetigers 1–3	Chaetigers 1–3 uncini	Circular collar	Glandular ventral shield, chaetiger 8	Campanulate chaetigers	Paired lobules on posterior chaetigers	Vascular cirri on median/posterior chaetigers	Anal funnel	Anal plug	# of chaetigers/achaetigers	
Aclymene Buzhinskaj, 1995	Present	Weakly developed	Present	Absent	Present	Absent	Absent	Absent	Present	Absent	Present	Present	18/4	Buzhinskaja 1995, De Assis et al. 2012
Axiothella Verrill, 1900	Present	Well developed	Present	Absent	Present, >3 uncini	Absent	Absent	Absent	Absent	Absent	Present	Absent	19–22/0–2	Day 1967, Jiménez-Cueto & Salazar-Vallejo 1997
Clymenella Verrill, 1873	Present	Well developed	Present	Present	Absent	Present	Absent	Absent	Absent	Absent	Present	Present	18–39/0–5	Day 1967, Imajima & Shiraki 1982
Clymenura Verrill, 1900	Present	Well developed; weakly developed, or some times, absent	Present/absent	Absent	Present	Absent	Yes	Absent	Absent	Absent	Present/absent	Present/Absent	17–19/1–6	Imajima & Shiraki 1982, Read 2011
Euclymene Verrill, 1900	Present	Well developed	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	18–24/1–4	Arwidsson 1906, Day 1967
Eupraxillella Hartmann-Schröder & Rosenlfelft, 1989	Present	Well developed	Present	Absent	Present	Absent	Absent	Present	Absent	Absent	Present	Present	More tan 30/4	Hartmann-Schröder & Rosenlfelft 1989
Gravierella Fauvel, 1919	Present	Well developed	Present	Absent	Present	Absent	Absent	Present	Absent	Absent	Present	Absent	60–70/0	Day 1967, De Assis et al. 2012
Heteroclymene Arwidsson, 1906	Present	Well developed	Present	* Present, on chaetigers 1–4	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	19/5	Arwidsson 1906, Garwood 2007, Jirkov 2001
Isocirrus Arwidsson, 1906	Present	Well developed	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	19–20/1–2	Salazar-Vallejo 1991, De Assis et al. 2012
Jonhstonia Quatrefages, 1866	Present	Well developed	Present	Present	Absent	Absent	Absent	Absent	Absent	Present	Present	Present	19–22/1–3	Mackie & Gobim 1993, De Assis et al. 2012
Leiochone Grube, 1868	Absent	N/A	Absent	Absent	Present	Absent	Present	Absent	Absent	Absent	Absent	Present/absent	19–29/1–5	Read 2011, De Assis et al. 2012

Table I. **Continuation.**

Macroclymene Verrill, 1900	Present	Weakly developed	Present	Absent	Present	Absent	Absent	Present	Absent	Absent	Present	Absent	31–40/0–1	Day 1967, De Assis et al. 2012
Macroclyemenlla Augener, 1926	Present	Well developed	Present	Absent	Present on 1–3	Present	Absent	Absent	Absent	Absent	Absent	Absent	31–34/1	Augener 1926
Maldanella McIntosh, 1885	Present	Weakly developed	Present	Absent	Present on chaetigers 2–3	Absent	Absent	Absent	Absent	Absent	Present	Absent	19/2–3	Day 1967, Detinova 1982
Microclymene Arwidsson, 1906	Present	Weakly developed	Absent	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	19/0–3	Arwidsson 1906, Annekova 1937, De Assis et al. 2012
Petaloclymene Augener, 1918	Present	Well developed	Present	Absent	Present	Absent	Absent	Absent	Absent	Absent	Present	Present	38/0	Augener 1918, Green 1997
Praxillella Verrill, 1881	Present	Well developed	Present	Absent	Present	Absent	Absent	Absent	Absent	Absent	Present/ absent	Present	18–19/3–4	Garwood 2007, Imajima & Shiraki 1982
Pseudoclymene Arwidsson, 1906	Present	Well developed	Present	Absent	Present	Absent	Absent	Absent	Absent	Absent	Present	Present	19/5	Arwidsson 1906

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(Figures 2a-f, 3a-f, 4a-b, 5a-d, 6a-d)

Johnstonia sp. De Assis & Christoffersen, 2011, p. 234, Figures 2, 3, 5, 6.

Material examined: Holotype: Brazil: Diogo Lopes, Macau -Rio Grande do Norte, northeastern Brazil, in tidal creek and mud (1.8–5.2 m). CIPY-POLY-UFPB 1745: José Eriberto De Assis and André Vidal col., September 2007, (5°05´02.95” S; 36°27´13.50” W).

Paratypes: CIPY-POLY-UFPB 1746 (1 complete specimen), (2) 1747, (5°04´27.23” S; 36°27´32.02” W); CIPY-POLY-UFPB 1748, (3 complete specimens) (4 anterior and posterior fragments) CIPY-POLY-UFPB 1749: (5°04´55.01” S; 36°26´31.85” W); Barra do Rio Mamanguape, Rio Tinto, Paraíba, tidal creek and mud: CIPY–POLY–UFPB 1749 (5: 2 complete specimens, 3 broken specimens): José Eriberto De Assis, André Vidal, and Carmen Alonso Col. January 2018 (6°46’04.07” S; 34°56’05.0” W).

Definition: A specific hypothesis, accounting for the following characters: presence of 23 chaetigers, cephalic plate with smooth posterior margin, and serrate capillary chaetae on chaetiger 9 arranged as dense bundle. Hypothetically, each of these characters arose among members of an ancestral population, eventually becoming fixed, resulting in individuals observed in the present.

Description of adult semaphoronts: The holotype is a complete specimen, length 50 mm, 1.5 mm wide. Paratypes 48–62 mm long, 1.7–2.0 mm wide. Body cylindrical; 23 chaetigers, one pre-pygidial achaetous segment, one thinner callus ring, pygidial funnel. Anterior end with oval cephalic plate bordered by well-developed cephalic rim. Cephalic rim smooth, with two deep lateral notches and one posterior notch. Prostomium broadly rounded, forming slightly arched keel; about 10 red-brown ventrolateral ocelli. Nuchal grooves parallel, extending through three-quarters of cephalic plate length. Mouth below prostomium, with wrinkled lower

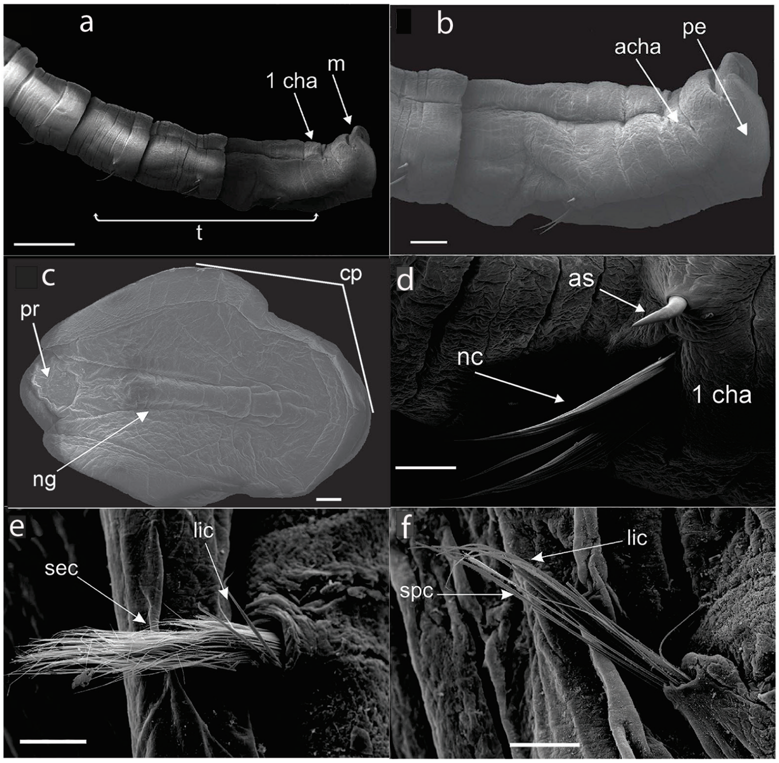

Figure 2. ***Euclymene vidali*** **sp. nov. (a), Anterior end showing the first four chaetigers and mouth; (b) anterior end showing first achaetigerous segment, and peristomium; (c) Cephalic plate showing nuchal grooves and length of prostomium (Modified from De Assis & Christoffersen 2011); (d) Parapodium showing acicular spine and capillary chaetae (Modified from De Assis & Christoffersen 2011); (e) Parapodium from chaetiger 9, showing modified serrate capillary chaetae, and limbate capillary chaetae; (f) Parapodium from chaetiger 15 showing spinose, and limbate capillaries chaetae. Abbreviations: acha, achaetiger head; as, acicular spine; cha, chaetigers; cp, cephalic plate; sec, serrate capillary chaetae; lic, limbate capillary chaetae; spc, spinose capillary chaetae chaetae; m, mouth; nc, notochaetae; ng, nuchal groove; pe, peristomium; pr, prostomium; sc, spinose capillary. Scales bars: (a) = 1 mm; (b) = 300 µm, (c, d, e, f) = 100 µm.**

lip. Proboscis a smooth eversible sac (Figs. 2a-c, 5a). Chaetigers 1–7 varying from 1.5–2.0 mm long, 1.5 mm wide. Chaetigers 8–9 two times longer than anterior chaetigers; chaetigers 10–16 three times longer than first chaetiger; posterior chaetigers decreasing in length. Notochaetae emerge from depressions; neurochaetae project directly from body wall on anterior half of each segment (Fig. 2d-f). Remaining chaetigers with small raised notopodia and conspicuous neuropodial tori. Notopodia of chaetigers 1–23 with fascicles of long, fine capillary chaetae, each with attached microalgal filaments. Notochaetae of all chaetigers with posterior row of long, sheathed capillaries, and anterior row of shorter modified capillaries (Figs. 2e-f). These chaetae have a short base and are of three types: limbate; spinose; modified serrate (Figs. 3a-c, 6b-c). Chaetae on chaetiger 9 arranged in dense bundle (Fig. 2e). Neuropodia of chaetigers 1–3 each with one acicular hook, with small denticles above main fang (Figs. 3d, 6a). Posterior to chaetiger 3, neuropodia with row of rostrate hooks, present to chaetiger 23 (Figs. 3e-f); each hook with rostrum surmounted by 4 smaller denticles; single thick barbule, bent upwards, present below rostrum. Hook rows arranged perpendicular to body wall, with long, curved posterior shaft, and prominent manubrium on posterior half. Neuropodial tori with variable number of rostrate hooks (4: 11, 5: 15, 6: 22) (Figs. 3e-f; 6d). Pre-pygidial segment about one half length of last chaetiger, with reduced torus at posterior end. Distinct callus ring in posterior region of segment (Fig. 4a-b). Pygidial funnel extended posteriorly, bearing 22 subconical anal cirri of slightly variable length (paratypes with 19–27); midventral cirrus two times longer than other cirri. Anus terminal, central, surrounded by divergent folds (Figs. 4a-b, 5d).

Live specimens dark red in anterior region, light yellow in median and posterior regions. Preserved specimens (in alcohol) uniformly yellow. Tubes composed of sand, shells, fine

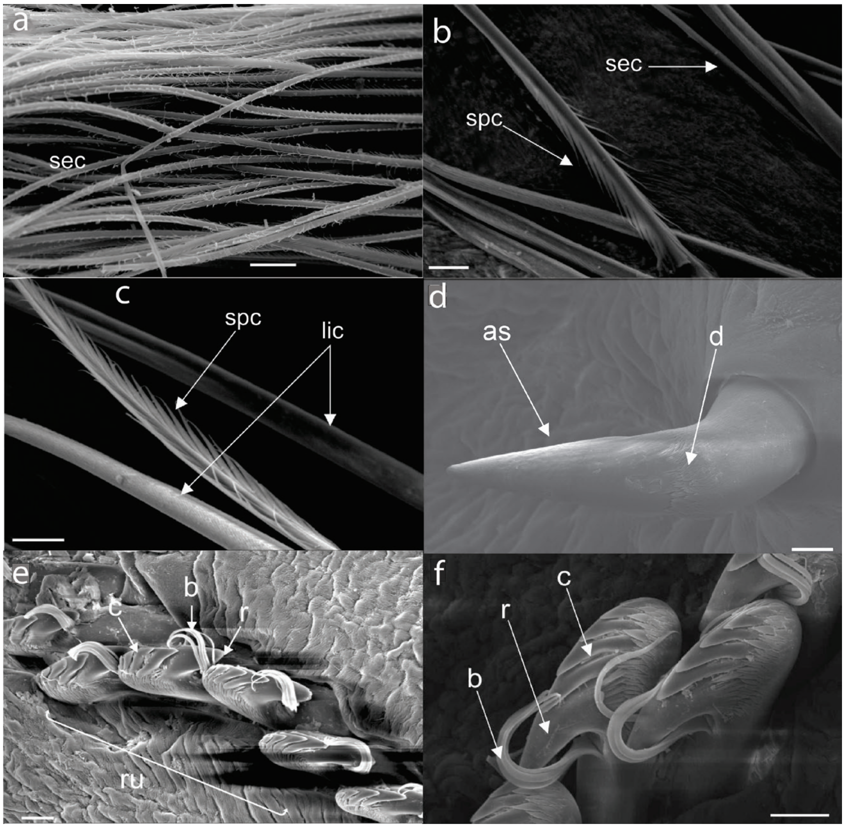

Figure 3. **(a) Tufts of modified serrate capillary chaetae from chaetiger 9; (b-c) spinose and limbate capillaries chaetae from chaetiger of segment 15; (d) acicular spine of first chaetigerous segment, with denticulate tip; (e) Row of rostrate uncini from chaetigerous segment 15; (f) Rostrate uncini from chaetigerous segment 15 showing capitium, rostrum and barbules. Abbreviations: as, acicular spine; b, barbules; c, capitium, d, denticules; sec, serrate capillary chaetae; lic, limbate capillary chaetae; r, rostrum, ru, rostrate uncini; sc, spinose capillary chaetae. Scales bars: (a-f) = 10 µm.**

wood fragments, small stones, all adhered to mucous matrix. Chaetigers 8–13 with strongly marked stripes, neuropodial regions glandular, arranged into four equidistant, longitudinal glandular bands (one dorsal, one ventral, two lateral). Dorsal glandular stripes extend to chaetiger 13; ventral strips to chaetiger 14 (Fig. 5b). Low, rounded nephridial papillae below posterior regions of neuropodial tori on chaetigers 7–9 (Fig. 5c).

Distribution: Specimens live in sandy mud, intertidal (type locality) to 1.8–5.2 m depth. Known only from Brazilian northeastern littoral, for the Rio Grande do Norte and Paraíba States.

Etymology: The species name is after the companion of the first author, André Vidal, who assisted in the collection of material.

Remarks: Members of *Euclymene vidali* sp. nov. differ from members of *E. aucklandica* Augener, 1923, in that the latter has 21 chaetigers, cephalic plate with crenulated posterior edge, uncini with 4–5 teeth on the rostrum, and midventral cirrus two times longer than other anal cirri. Members of *E. vidali* sp. nov. differs from members of *E. coronata* as the latter has 22 chaetigers, deep lateral notches, cephalic plate with a strongly crenulated posterior edge, and uncini with 3 teeth on the rostrum. Members of other species of *Euclymene* differ from *E. vidali* sp. nov. in having 2–4 pre-pygidial achaetigerous segments, and the number of chaetigers (Table II).

Key to species of *Euclymene* Verrill, 1900

1. One pre-pygidial achaetous segment........................2

– More than one pre-pygidial achaetous segment......................................4

2. Midventral cirrus two times longer than other anal cirri................................3

– Midventral cirrus four times longer than other anal cirri; 21 chaetigers; posterior edge of

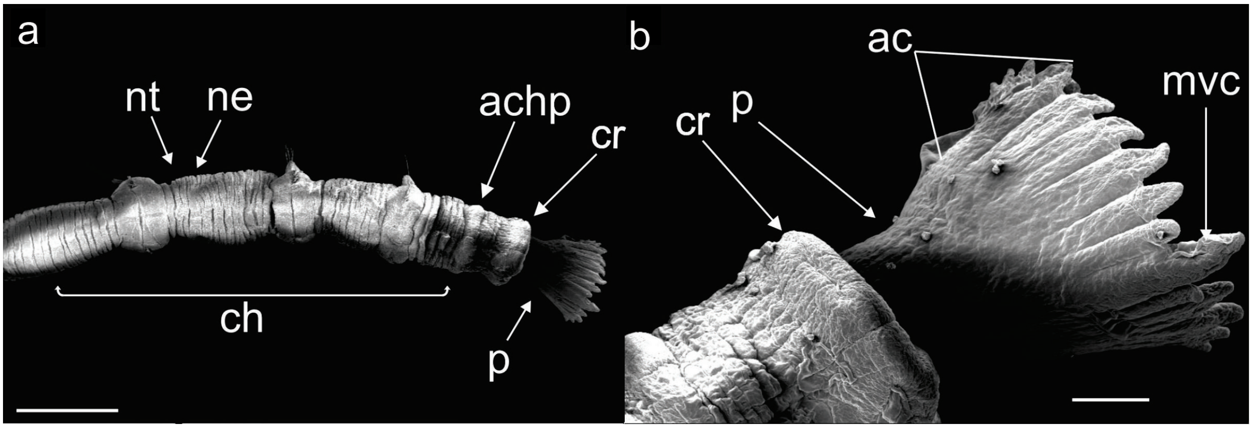

Figure 4. **(a) Posterior end of *Euclymene vidali* sp. nov. Showing the pre-pygidial achaetous segment and pygidium (Modified from De Assis & Christoffersen 2011); (b) Anal funnel with sub-triangular cirri showing a long midventral cirrus (Modified from De Assis & Christoffersen 2011). Abbreviations: ac, anal cirri; ppa, pre-pygidial achaetiger; ch, chaetigers; cr, callus ring; mvc, medioventral cirrus; ne, neuropodium; nt, notopodium; p, pygidium. Scales bars: (a) = 1 mm, (b) = 200 µm.**

cephalic plate slightly crenulated; uncini with 4–5 teeth above rostrum.....................................*E. aucklandica* Augener, 1923

3. Twenty-two chaetigers; deep lateral notches; cephalic plate strongly crenulated edge; uncini with three teeth above rostrum................. *E. coronata* Verrill, 1900

– Twenty-three chaetigers; slight lateral notches; cephalic plate with smooth edge; uncini with four teeth above rostrum; midventral cirrus two times longer than other anal cirri.................... ....*E. vidali* sp. nov.

4. Two pre-pygidial achaetous segments...5

– Three or more pre-pygidial achaetous segments...14

5. Posterior edge of cephalic plate smooth..6

– Posterior edge of cephalic plate crenulated..11

6. Less than 20 chaetigerous segments..7

– Twenty-four chaetigers; uncini with 6–7 teeth above rostrum; midventral anal cirrus three times longer than other cirri......*E. luderitziana* Augener, 1918

7. Nineteen chaetigers...8

– Eighteen chaetigers; midventral anal cirrus four times longer than other cirri............................ ....*E. dispar* (Verril, 1873)

8. Midventral cirrus three times longer than other anal cirri...9

– Midventral cirrus two times longer than other anal cirri...10

9. Cephalic plate with slightly lateral and posterior notches; uncini with four teeth above rostrum..............................*E. trinalis* Hutchings, 1974

– Cephalic plate with deep lateral and posterior notches; uncini with five teeth above rostrum.......................*E. droebachiensis* (Sars, 1872)

10. Cephalic plate with well-developed edge; anal cirri all of similar length; uncini with five teeth above rostrum.............*E. natalensis* Day, 1957

– Cephalic plate with low edge; anal cirri alternating in length; uncini with 5–6 teeth above rostrum.........................*E. oerstedii* (Claparède 1863)

11. Less than 20 chaetigers.................................12

– Twenty-one chaetigers ....*E. annandalei* Southern, 1921

12. Nineteen chaetigers.......................................13

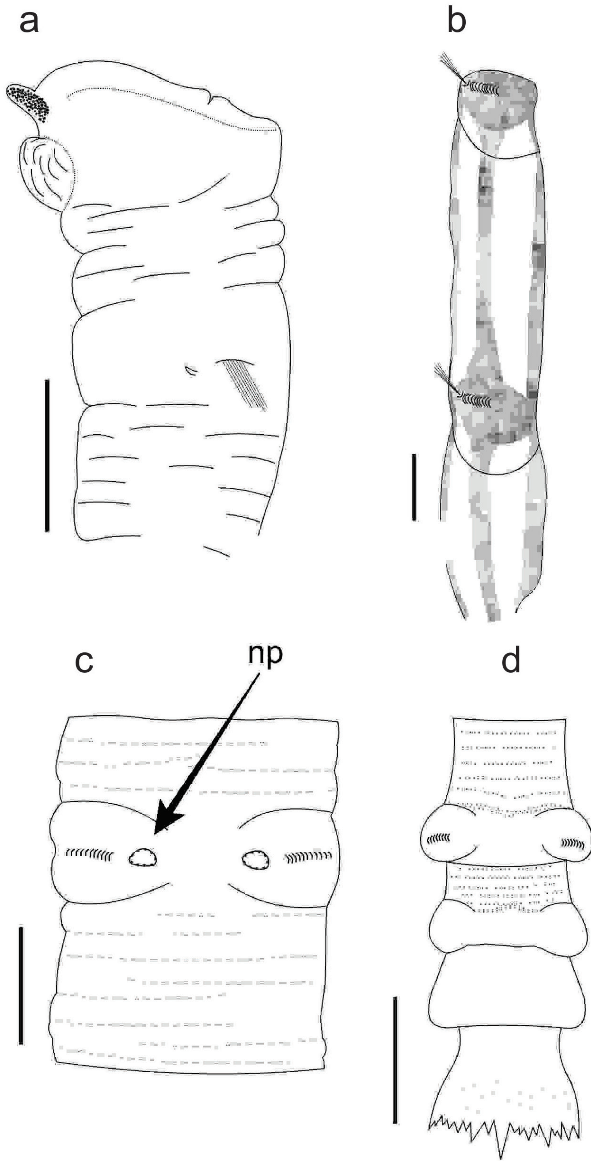

Figure 5. (a) anterior end of *Euclymene vidali* sp. nov. showing the first chaetigerous segment and prostomium with ocelli; (b) Median segments of *Euclymene vidali* sp. nov. showing longitudinal glandular strips; (c) Nephridial papillae from chaetigerous segment 6; (d) Posterior end of *Euclymene vidali* sp. nov. with one preanal achaetigerous segment and pygidium. Abbreviation: Np, nephridial papillae. Scales bars: (a and d) = 1 mm, (b and c) = 300 µm.

– Ten chaetigers; cephalic plate with slight lateral notches; posterior edge slightly crenulated ....*E. delineata** Moore, 1923

13. Posterior edge of cephalic plate slightly crenulated; with very small midventral anal cirrus; other cirri short, subconical and of similar length..............*E. uncinata* Imajima & Shiraki, 1982

– Posterior edge of cephalic plate strongly crenulated; first three chaetigers with 1–2 rostrate hooks; midventral anal cirrus two times longer than other anal cirri, conical, of similar length....................................*E. mossambica* Day, 1957

14. Three pre-pygidial achaetous segments...15

– Four pre-pygidial achaetous segments; cephalic plate slightly crenulated; midventral anal cirrus two times longer than other anal cirri, remaining cirri of similar length.......*E. lindrothi* Eliason, 1962

15. Posterior edge of cephalic plate smooth...16

– Posterior edge of cephalic plate crenulated; midventral anal cirrus two times longer than others similar lengths.....*E. lombricoides* (Quatrefages, 1865)

16. Nineteen chaetigers.......................................17

– Twenty chaetigers; cephalic plate with deep lateral notches; midventral anal cirrus three times longer than other cirri...........*E. palermitana* (Grube, 1840)

17. Cephalic plate with shallow notches; uncini with five teeth above rostrum; midventral anal cirrus two times longer than other cirri ....*E. insecta* (Ehlers, 1905)

– Cephalic plate with strong lateral notches; uncini with four teeth above rostrum; midventral anal cirrus two times longer than other cirri ....*E. collaris* (Claparède, 1869)

* Members of *E. delineata* were described on the basis of anterior and posterior body fragments, which indicates that the numbers furnished do not represent the actual number of chaetigers. The species is included in this group since individuals have two achaetous

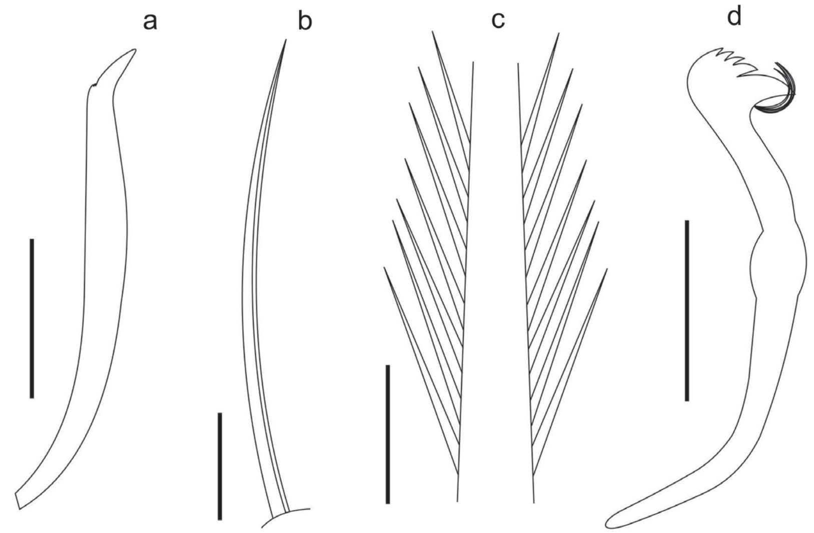

Figure 6. ***Euclymene vidali*** **sp. nov. (a) Acicular spine from chaetiger 2; (b) Limbate capillary from chaetiger 15; (c) Spinose capillary from chaetiger 15, (d) Rostrate uncinus from chaetiger 15. Scales bars: (a-d) = 10 μm.**

pre-pygidial segments and a crenulated posterior edge of the cephalic plate.

DISCUSSION

Genera of Euclymeninae can be distinguished by several characters, summarized in Table I. Three monotypic genera are synonymized here: *Macroclymenella* Augener, 1926, *Eupraxillella* Hartmann-Schröder & Rosenlfelft, 1989, and *Pseudoclymene* Arwidsson, 1906.

Members of *Macroclymenella* were described as having 31–34 chaetigers, one pre-pygidial achaetiger, and a circular collar on chaetiger 4. The last character is unique for members of *Clymenella*. Yet, the number of chaetigers among members of *Clymenella* varies between 18 and 39, and there are 0 to 5 pre-pygidial achaetigers (Table II). In fact, the presence of a circular collar on chaetiger 4 indicates that *Macroclymenella* is a junior synonym of *Clymenella*, and thus, *M. stewartensis* Augener, 1926, must thus be recognized as *Clymenella stewartensis* comb. nov.

Members of *Eupraxillella* Hartmann-Schröder & Rosenlfelft, 1989, were described with 30 chaetigers, four pre-pygidial achaetigers, a pygidium with a short edge, and with a ring of cirri; anus on the cone, with anal ventral valve. The form of the pygidium (with an anal pore located over the cone), and anal valve are typical for members of *Praxillella*. The number of chaetigers among members of *Praxillella* varies from 18 to 19, and there are 3–4 pre-pygidial achaetigers. Based especially on the pygidium, position of the anus and anal valve, *Eupraxillella* is a junior synonym of *Praxillella*, and *Eupraxillella antarctica* Hartmann-Schröder & Rosenlfelft, 1989, must be recognized as *Praxillella antarctica* com. nov.

Pseudoclyemene Arwidsson 1906 was erected on the basis of the length of the nuchal grooves. This is a unique character for the genus. However, members of this species have a pygidium with a short edge, and a ring of cirri of different lengths; the anus is located on the cone. Although Arwidsson (1906) does not describe the presence of an anal valve, the original figures resemble typical specimens of *Praxillella*. In this case, we recognize *Pseudoclyemene* as a junior synonym of *Praxillella*, and *P. quadrilobata* Arwidsson, 1906, must be recognized as *Praxillella quadrilobata* com. nov.

Members of *Euclymene africana* (Gravier 1905, p. 198–201, Figs. 214–216), and *E. watsoni* (Gravier 1905, p. 201–203, Figs. 2017–2219) were

Table II. **Comparative table of *Euclymene* species that have midventral cirrus longer than other anal cirri. The sequence of species is according to the number of pre-pygidial achaetigerous segments.**

Species	Cephalic plate border	No. of chaetigers	No. of pre-pygidial achaet-igers	Uncini apical teeth	Anal funnel cirri	Type Locality	Distribution	References
E. aucklandica Augener, 1923	Deep lateral notches; posterior crenulated	21	1	4–5	Midventral cirrus 4 times longer than other cirri of different lengths	New Zealand, Auckland Islands	Type locality	Augener 1923, Glasby et al. 2009
E. coronata Verrill, 1900	Deep lateral notches; posterior strongly crenulated	22	1	3	Midventral cirrus 2 times longer than other cirri; triangular cirri alternating lengths	Castle Island Boston, USA	Bermuda to Northeastern Caribbean; northeastern Brazil, João Pessoa, Paraíba Brazil	Verrill 1900, Jones et al. 1986, Jiménez-Cueto & Salazar-Vallejo 1997, De Assis et al. 2012, Amaral et al. 2013
E. vidali sp. nov.	Slight lateral notches, 1 posterior notch; smooth edge	23	1	4	Midventral cirrus 2 times longer than other cirri; subequal triangular cirri	Diogo Lopes, Macau, Rio Grande do Norte, Brazil	Rio Mamangua pe, Rio Tinto, Paraíba, Brazil	This paper
E. annandalei Southern, 1921	Slight lateral notches; crenulated edge	21	2	5–6	Midventral cirrus 2 times longer than other cirri, triangular cirri of same length	Chilka Lake, India	Tropical Indian Ocean	Southern 1921, Day 1967
E. delineata Moore, 1923	Slight lateral notches; posterior edge slightly crenulated	10	2	4	Midventral cirrus one third length of anal cup; other cirri of similar length	Santa Rosa Island, California, USA	Type locality	Moore 1923
E. díspar (Verrill, 1873)	Slight lateral notches; posterior edge smooth	18	2	?	Midventral cirrus 4 times longer than other cirri; shorter cirri of different lengths	Massachu-setts, USA	Type locality	Verrill 1873, Arwidsson 1906
E. droebachiensis (Sars, 1872)	Slight lateral notches; posterior edge smooth	19	2	5	Midventral cirrus 3 times longer than others; shorter cirri of different lengths	Faeroe, Iceland	Type locality	Arwidsson 1906, Jirkov 2001, Amaral et al. 2013
E. luderitziana Augener, 1918	Slight lateral notches, and 1 posterior notch; smooth edge	24	2	6–7	Midventral cirrus 3 times longer than remaining cirri, which are of different lengths	Southwest Africa, Lambert's Bay, Lüderitzbucht, Namibia	South Africa, Cape	Augener 1918, Day 1955, 1967
E. mossambica (Day, 1957)	Slight lateral notches; crenulated edge	19	2	6	Midventral cirrus 2 times longer than other, triangular cirri, that alternate in length	Mozambique-que Is., South Africa	Type locality	Day 1957, 1967

Table II. Continuation.

E. natalensis (Day, 1957)	Slight lateral notches; smooth edge	19	2	6	Midventral cirrus slightly longer than cirri of alternating lengths	Inhaca Island, Delagoa Bay City	Cape Region and Natal, South Africa:	Day 1957, 1967
E. oerstedii (Claparède 1863)	Slight lateral notches; smooth edge	19	2	5–6	Midventral cirrus 2 times longer than other cirri that alternate in length	**Normandy**, Atlantic Ocean	North Sea and English Channel, Mediterranean, South America, Brazil; Western Africa Japan	Fauvel 1927, Day 1967, Imajima & Shiraki 1982
E. trinalis Hutchings, 1974	Slight lateral notches; posterior edge smooth	19	2	4	Midventral cirrus 4 times longer than other cirri; triangular, of similar length	South of Godwin Is., Wallis Lake NSW	New South Wales (Marimbula, Jervis Bay, Port Hacking, Botany Bay, Lake Macquarie, Port Stephens)	Hutchings 1974, Hutchings & Murray 1984
E. uncinata Imajima & Shiraki, 1982	Deep lateral notches; posterior edge crenulated	19	2	6	Midventral cirrus 2 times longer than other cirri; very small; others short, subtriangular, of similar length	Kashima Sea, Japan	Known only from type locality	Imajima & Shiraki 1982
E. collaris (Claparède, 1869)	Without lateral notches; a deep posterior incision	19	3	4	Midventral cirrus 2 times longer than other cirri; of similar length	Gulf of Naples, Italy	Northeastern Atlantic: North America and Canada; Northwestern Atlantic: Portugal and Spain; Mediterranean: Italy and Greece; Rea Se	Claparède 1869, Arwidsson 1906, Fishelson & Rullier 1969, Brunel et al. 1998
E. insecta (Ehlers, 1905)	Slight lateral notches; posterior edge smooth	19	3	5	Midventral cirrus slightly longer than other anal cirri, with different lengths	Chatham Island, New Zealand	Type locality	Ehlers 1905, Hartman 1959, Glasby et al. 2009, Liu 2008
E. lombricoides (Quatrefages, 1865)	Slight lateral notches; crenulated edge	19	3	5–6	Midventral cirrus 2 times longer than other cirri that alternate in lengths	Boulogne-Sur-Mer and Calais beach, France	North Atlantic, Scotland, English Channel to Morocco; Mediterranean Sea	Quatrefages 1865, Fauvel 1927, Day 1967, Imajima & Shiraki 1982, Amaral et al. 2013
***E. palermitana* (Grube, 1840)**	Slight notches lateral, and deep posterior notch; posterior edge smooth	20	3	5	Midventral cirrus 3 times longer than others cirri, other cirri of different lengths	Palermo, Italy, Mediter-anean	North Atlantic, Portugal and Spain; France, Monaco; Italy, Naples; Africa, coast of Tunisia.	Grube 1840, Orlandi 1898, Arwidsson 1906, Fauvel 1927, Bellan 2001
E. lindrothi Eliason, 1962	Slight lateral notches; posterior edge slightly crenulated	19	4	5–6	Midventral cirrus 2 time longer than other cirri; cirri with different lengths	North Atlantic, Geounit Skagerrak Strait.	Type locality	Eliason 1962, Bellan 2001

originally described from Djibouti, Gulf of Aden, East Africa. In the original descriptions and illustrations, the specimens presented a pygidium with an anal funnel bordered by several anal cirri of equal length. This condition is part of what characterizes members of *Isocirrus* (Arwidsson 1906, Salazar-Vallejo 1991, De Assis & Christoffersen 2011, De Assis et al. 2012). From both the text and figures, it is clear that members of the species do not present a midventral cirrus that is longer than the remaining cirri, a condition that is part of the definition of *Euclymene*. Therefore, these species are herein transferred to *Isocirrus*: *I. africana* (Gravier, 1905) comb. nov., and *I. watsoni* (Gravier, 1905) comb. nov.

Comments on monophyly of Euclymeninae: In their inferences of phylogenetic hypotheses explaining morphological characters among members of Maldanidae, De Assis & Christoffersen (2011) found Euclymeninae to be monophyletic. Kobayashi et al. (2018) subsequently inferred phylogenetic hypotheses for only sequence data and obtained a paraphyletic Euclymeninae due to members of Nicomachinae within the former clade. Based on their results, Kobayashi et al. (2018) concluded that the morphological characters used by De Assis & Christoffersen (2011) are not synapomorphies for Euclymeninae. We will first comment on inherent limitations to inferring phylogenetic hypotheses for sequence data, the error of relying on phylogenetic hypotheses for sequence data as the means of determine explanatory hypotheses for other classes of characters, then address those characters that establish monophyly of Euclymeninae.

It has become fashionable in polychaete systematics to focus on inferences of phylogenetic hypotheses based only on sequence data (e.g. Struck et al. 2011, 2015, Borda et al. 2012, Glasby et al. 2012, Goto et al. 2013, Weigert et al. 2014, Aguado et al. 2015, Goto 2016, Weigert & Bleidorn 2016, Kobayashi et al. 2018, Nygren et al. 2018, Langeneck et al. 2019, Shimabukuro et al. 2019, Alves et al. 2020, San Martín et al. 2020, Stiller et al. 2020, Tilic et al. 2020), and often to then comment on other classes of characters in relation to those hypotheses, typically through the process called 'character mapping.' Two significant, interrelated problematic questions arise with these approaches: can inferences of phylogenetic hypotheses causally account for sequence data, and can other classes of characters be explained through mapping on the basis of those inferred hypotheses? In-depth treatments of these topics can be found for instance in Fitzhugh (2014, 2016a), so only a brief overview will be presented here.

In accordance with the goal of scientific inquiry, which is to obtain causal understanding (e.g. Hanson 1958, Hempel 1965, Rescher 1970, Popper 1983, 1992, Salmon 1984, Van Fraassen 1990, Strahler 1992, Mahner & Bunge 1997, Hausman 1998, Thagard 2004, Nola & Sankey 2007, de Regt et al. 2009, Hoyningen-Huene 2013, Potochnik 2017, Currie 2018, Anjum & Mumford 2018), we regard this as the intent of inferring both specific and phylogenetic hypotheses. While it is common in systematics to claim that the purpose of inferring such hypotheses is to obtain 'the phylogeny' for a particular group of organisms, this is something of a misnomer, just as it is erroneous to say one has inferred a 'molecular phylogeny.' Inferring explanatory hypotheses that causally account for a set of differentially shared characters (cf. Fitzhugh 2006a, 2008b, 2009, 2012, 2013, 2016a-c), implied by cladograms, cannot be equated with being 'a phylogeny' much less 'the phylogeny.' The term phylogeny incorrectly connotes that one can attain comprehensive explanatory constructs regardless of the number of observations used to infer those constructs. This, along with not acknowledging the requirement of total evidence (Fitzhugh 2006b), has led to the tendency to only infer phylogenetic hypotheses from sequence data and assume, incorrectly, that those hypotheses extend to other observed characters. This does not work because the reasoning involved in producing explanatory hypotheses only pertains to the characters involved in inferring those hypotheses. Other characters in need of explanation should not be excluded simply out of conformity with uncritical or popular methodological trends.

Computer algorithms for inferring phylogenetic hypotheses are entirely agnostic with regard to what causal mechanisms contribute to fixation of novel characters among individuals in ancestral populations or the nature of population splitting events (Fitzhugh 2016a). This does not present problems when explaining morphological characters since at a minimum either natural selection or genetic drifts are possible causes of fixation. When considering sequence data, however, drift can directly explain shared nucleotides or amino acids; but selection does not operate at the level of those molecules since they have no direct emergent properties that manifest fitness differences among individuals. Instead, selection occurs at higher organizational levels and indirectly affects intergenerational occurrences of associated nucleotides and amino acids; a phenomenon known as downward causation (Campbell 1974, Vrba & Eldredge 1984, Salthe 1985, Lloyd 1988, Ellis 2008, 2012, 2013, Auletta et al. 2008, Jaeger & Calkins 2011, Ellis et al. 2011, Laland et al. 2011, Martínez & Moya 2011, Davies 2012, Okasha 2012, Walker et al. 2012, Griffiths & Stotz 2013, Martínez & Esposito 2014, Walker 2014, Fitzhugh 2016a, Mundy 2016, Callier 2018, Pouyet et al. 2018, Salas 2019, Yu et al. 2020). While it would be unrealistic to explain all sequence data by way of drift, invoking selection first requires associating those sequence data to be explained, via downward causation, with morphological characters upon which selection has been hypothesized as operative. If such an association is available, then those relevant sequence data would be excluded from the data matrix used to infer phylogenetic hypotheses, since those characters already would be accounted for via downward causation by the morphological characters. In the absence of evidence for discriminating sequence data to be explained by drift or downward causation, the only viable option is to acknowledge that those data should be excluded from phylogenetic inferences. For these reasons, we do not regard the phylogenetic hypotheses presented by Kobayashi et al. (2018) to be plausible or provide a basis for concluding that Euclymeninae is paraphyletic.

The second problem related to inferences of phylogenetic hypotheses from sequence data is the popular tactic of considering additional phylogenetic hypotheses of morphological characters through what is called ‘character mapping’ (cf. Fitzhugh 2014). For instance, Kobayashi et al. (2018) mapped the absence and presence of cephalic and anal plates onto tree topologies they obtained for sequence data, and then proceeded to discuss phylogenetic hypotheses accounting for these characters. Mapping, however, does not lead to results that can be interpreted as legitimate explanatory hypotheses. The reason is because the act of ‘optimizing’ characters on a previously inferred tree topology, i.e. a set of explanatory hypotheses for a set of characters used to infer those hypotheses, is not an action that can be interpreted as an epistemically meaningful inference. Inferring phylogenetic hypotheses involves a form of non-deductive reasoning known as abduction (Peirce 1931, 1932, 1933a-b, 1934, 1935, 1958a-b, Hanson 1958, Fann 1970, Reilly 1970, Thagard 1988, Josephson & Josephson 1994, Magnani 2001, 2009, 2017, Psillos 2002, 2011, Walton 2004, Gabbay & Woods 2005, Aliseda 2006, Schurz 2008, Park 2017, for considerations of abduction in relation to systematics see Fitzhugh 2006a-2006b, 2008, 2009, 2010a, 2012, 2013, 2014, 2015, 2016a-b). At a minimum, the premises of an abductive inference involve the conjunction of some causal theory(ies) and effect(s) to be explained. The conclusion is an explanatory hypothesis stating past causal conditions accounting for observed effects. Phylogenetics computer algorithms serve as surrogates for human abductive reasoning, albeit under incorrect monikers such as 'parsimony,' 'maximum likelihood,' and 'Bayesian' (Fitzhugh 2012, 2016a). Character mapping is not a form of abductive reasoning since the premises of such an 'inference' would only include a previously inferred tree topology and subsequent characters to be explained. In the absence of any actual or implied evolutionary theory(ies) involved in the inference, or the inclusion of all observed characters as part of the premises, per the requirement of total evidence, the conclusion of mapped characters cannot be interpreted as indicating past causal conditions. As such, the evolutionary considerations of cephalic and anal plates by Kobayashi et al. (2018) cannot be regarded as epistemically sound.

With the foregoing overview, the synapomorphies for Euclymeninae called into question by Kobayashi et al. (2018) can be reviewed. Regarding nuchal grooves, members of species of *Maldanella,* including *M. harai* Izuka, 1902, have straight and parallel nuchal groves according to Detinova (1982, p. 66, Fig. 2a-d). Interestingly, one specimen of *M. harai* described and illustrated from Japanese waters by Imajima & Shiraki (1982, p. 55, Fig. 25b) had strongly curved nuchal grooves, in contrast to the description and illustration of Detinova (1982). Members of species of *Clymenella*, including *C. complanata* Hartman, 1969, have straight, parallel nuchal grooves. A specimen of *C. complanata* reported from Japan presented short and curved nuchal grooves (Imajima & Shiraki 1982, p. 48, Fig. 20b), contradicting the original description of Hartman (1969, p. 435, Fig. 2). For both cited species, we suggest they are new species, but only with examinations of material we can confirm this opinion.

Straight, parallel nuchal grooves have been illustrated with details for all Euclymeninae in several important systematics papers in the literature on Maldanidae (Pilgrim 1977, Arwidsson 1906, Fauvel 1927, Day 1967, Fauchald 1977, Imajima & Shiraki 1982, Lee & Paik 1986, Salazar-Vallejo 1991, Jiménez-Cueto & Salazar-Vallejo 1997, Mackie & Gobin 1993, De Assis & Christoffersen 2011, De Assis et al. 2012) (Table I). Curved or J-shaped nuchal grooves have been found in Rhodininae, Notoproctinae, Maldaninae and Nicomachinae (Arwidsson 1906, Day 1967, De Assis & Christoffersen 2011, De Assis et al. 2012). It is possible that the straight, parallel nuchal grooves had reverted in punctual species of Euclymeninae, but it does not seem very clear. The most important here is that straight nuchal grooves arise as a synapomorphy to Euclymeninae.

Subsequent authors (Pilgrim 1977, Hausen & Bleidorn 2006, Tilic et al. 2015), dealing with ontogeny and morphology, presented more detailed characters for Euclymeninae: 1) a double row of notochaetae parallel to the antero-posterior body axis from chaetiger 13 onwards, and 2) a straight chaetal sac visible from chaetiger 13 in adults, in contrast to an involute chaetal sac. A transverse notopodial double row of chaetae represents the primary condition in Maldanidae (Tilic et al. 2015). The stepwise transition between both conditions can always be seen in chaetigers 11 and 12 (Tilic et al. 2015, De Assis & Christoffersen 2011).

The presence of a callus ring preceding the anal funnel is a unique character among members of Euclymeninae (Garwood 2007). This character was not discussed by Kobayashi et al. (2018).

The presence of a terminal anus, enclosed within an anal funnel, and covered by a plate, is a unique character for Euclymeninae and Nicomachinae (Fauvel 1927, Fachauld 1977 Day 1967, Imajima & Shiraki 1982, De Assis & Christoffersen 2011, De Assis et al. 2012). Whether Nicomachinae may represent a taxon included within Euclymeninae, as suggested by Kobayshi et al. (2018), needs to be more thoroughly investigated. Although a cephalic plate has been lost among members of Nicomachinae and some *Leiochone*, the anal plate is a synapomorphy for the clade Notoproctinae + Maldaninae + Euclymeninae + Nicomachinae.

In summary, straight, parallel nuchal organs, double rows of notochaetae parallel to the antero-posterior body axis from chaetiger 13 onwards, chaetal sacs visible from chaetiger 13 in adults, a callus ring preceding the anal funnel, and the anus on an anal plate that is sunk into the anal funnel, are all characters that support the monophyly of Euclymeninae. A more extensive future phylogenetic analysis of Maldanidae will consider those characters establishing monophyly of the remaining subfamilies.

Comment on the status of the taxon ‘Maldanoplaca’

In their phylogenetic study of Maldanidae, De Assis & Christoffersen (2011: Table 3, Fig. 7) introduced the unranked name Maldanoplaca for the clade, (Notoproctinae (Maldaninae (Nicomachinae, Euclymeninae))). Unfortunately, this name was not accompanied by a definition as required by Article 13.1.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). As such, the name Maldanoplaca can only be regarded as an informal placeholder for the phylogenetic hypotheses accounting for characters associated with that clade. We therefore suggest that the name ‘Maldanoplaca’ should no longer be referred to as a formal taxon name. As such, the name can be ignored.

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