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The troglomorphic adaptations of Namanereidinae (Annelida, Nereididae) revisited, including a redescription of *Namanereis cavernicola* (Solís-Weiss & Espinasa, 1991), and a new Caribbean species of *Namanereis* Chamberlin, 1919

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Abstract

Most species belonging to *Namanereis* Chamberlin, 1919 live in freshwater and subterranean waters, even in water bodies several meters above sea level. A new species belonging to the stygobiont *Namanereis* group is described here; it shares the common morphological characters of absence of eyes and pigmentation, bifid jaws, elongation of chaetae and cirri, which have been recently regarded as troglomorphies. Because these features are used in evaluations of phylogenetic affinity in *Namanereis*, a review of these features was made for all known namanereidins, and it was extended to include species in *Namalycastis* Hartman, 1959. It is shown that elongation of tentacular and dorsal cirri, or elongation of upper sub-acicular falcigers in pre- or post-acicular fascicles, are not exclusive or restricted to species living in subterranean habitats or to *Namanereis*, because these features are also present in several *Namalycastis* species. However, the presence of bifid jaws, and the absence of eyes are exclusively found in namanereidins living in subterranean habitats. A hypothetical evolutionary derivation of bifid jaws is proposed, based upon observations of jaw morphology of several species. These exclusive troglomorphic characters (bifid jaws, eyeless) are regarded as convergent features to aphotic environments, and they should be discouraged as indicators of common ancestry. The new species, herein described as *Namanereis christopheri* **sp. n.**, was collected in a cave 435 m above sea level in Saint Vincent, Caribbean Sea. The species resembles *N. cavernicola* but it differs because it has shorter tentacular cirri, margin of prostomium entire, rounded neuropodial lobes and broader dorsal cirri throughout body. A key to identify all known *Namanereis* species is included.

Keywords

Troglomorphic features, convergence, elongation of appendages, evolution of jaws

Introduction

Troglomorphism comprises a set of convergent features found in organisms living in subterranean, aphotic environments, presumably resulting from similar selective pressures (Christiansen 1962, Culver and Pipan 2009b); such features are called troglomorphies, while the species showing them are called troglomorphs (Culver and Pipan 2009b). The troglomorphies often include a mixture of reductions and gains; the former includes loss of eyes and body pigmentation, and the latter relate to over-development of non-optic sensory structures, and elongation of appendages (Culver and Pipan 2009b). During many years, the troglomorphism was considered as resulting from selective factors operating in caves linked to modified patterns of nutrient availability and type of habitat. However, because the absence of light is the only common factor in all cases (Culver et al. 2010), these modifications might not be related exclusively with cave environments.

In an ecological classification, obligate residents of subterranean habitats are called troglobionts, and specifically stygobionts if they live in aquatic systems; interestingly, not all organisms living in subterranean environments are troglomorphs, nor are all organisms showing troglomorphic features are troglobionts (Sket 2008, Culver and Pipan 2009b, Pipan and Culver 2012, Konec et al. 2015). The fact that troglomorphic features are present in species living in non-cave environments indicates that their evolution is more complex than supposed (Heads 2010); therefore, the assumption of features as troglomorphic just because some morphologically modified species have current subterranean distributions deserves critical attention.

Oligochaetes are the most common annelid troglobionts, but polychaetes can also be so, especially those species belonging to the family Nereididae de Blainville, 1818 and specifically the subfamily Namanereidinae Hartman, 1959 (Glasby and Timm 2008, Glasby et al. 2009). This subfamily includes two genera, *Namanereis* Chamberlin, 1919 and *Namalycastis* Hartman, 1959, including a *incertae sedis* species and genus *Lycastoides alticola* Johnston, 1903 (Glasby 1999, Alves and Santos 2016). While most nereidids are estuarine or marine, namanereidins typically occur in freshwater and groundwater habitats, while a few can even thrive in semi-terrestrial ones. In contrast with other nereidids with complex parapodial morphology, the parapodia of namanereidins are reduced, possessing one main chaetal lobe carrying both noto- and neuroaciculae and a few chaetae, with a consequent reduction of taxonomically useful characters (Glasby 1999). Nevertheless, 43 namanereidin species have been described, and the usual diagnostic features are the shape of antennae and jaws, presence of a cleft in anterior margin of prostomium, presence of eyes, relative length of dorsal cirri along body, and arrangement and shape of chaetae (Glasby 1999).

A group of at least 12 stygobiont *Namanereis* (from a total of 18 in the genus) have interestingly shared morphological features, such as the absence of body pigmentation and eyes and the elongation of appendages (cirri and chaetae), including some other features not present in all species as the presence of distally bifid and edentate jaws, and heterogomph falcigers in sub-preacicular fascicles increasing their length posteriorly, even being replaced with spinigers (Glasby et al. 2014). Glasby et al. (2014) made an analogy between these features and those present in other hypogean organisms, arguing that those features could be regarded as troglomorphies; also, they detailed several hypotheses about possible origins and colonization of extant *Namanereis* based mainly on jaw morphology and the current distributions of species.

However, the same troglomorphic features are present at least in one other epigean species from another genus living within mangrove leaves litter, *Namalycastis occulta* Conde-Vela, 2013, as already noted in a previous contribution (Conde-Vela 2013: 481). A recent phylogenetic study challenged the generic placement of this species, suggesting that *N. occulta* is more related to *Namanereis* than to any described *Namalycastis*, forming a strongly supported clade with *Namanereis hummelincki* (Alves and Santos 2016: 509–510). However, the synapomorphies supporting such clade (absence of eyes, presence of bifid jaws and elongated falcigers in preacicular position) are precisely those regarded as troglomorphic features. It means that morphological resemblance could be due to common ancestry but also to convergence, and therefore they must be evaluated cautiously to avoid misleading interpretations (Wiens et al. 2003). Because the supposedly troglomorphic features are not restricted to stygobitic *Namanereis* group, a re-assessment of these features, as a result of living in subterranean habitats is required.

On the other hand, in the *Namanereis* stygobitic group, three species were found in groundwater at several meters above sea level (asl): *N. beroni* (Hartmann-Schröder & Marinov, 1977) from Papua New Guinea, 1700 m asl, *N. cavernicola* (Solís-Weiss & Espinasa, 1991) from Mexico, 1650 m asl and *N. gesae* Fiege & Van Damme, 2002 from Yemen, 700 m asl, while the top record of altitude is for *Lycastoides alticola*, found at 2150 m asl in Mexico (Johnson 1903, Glasby et al. 2014). Glasby (1999: 83) extended the distribution of *N. cavernicola* after based on morphological similarities of specimens from Saint Vincent, Hispaniola and Cuba, Caribbean Sea, and comparison with type material. Subsequently, Glasby et al. (2014: 34) suggested that the current distribution of *N. cavernicola* in Mexico could be explained from a littoral species subsequently becoming 'trapped' in water bodies during orogenic uplifting, a hypothesis that matches well with the tectonic history of the Mexican region (Padilla y Sánchez 2007), but that it could not explain the current disjunct distribution of a single putative species across Caribbean islands with distinct geologic histories (Bouysse 1984, Bouysse et al. 1990). Even restricted distribution is expected in *N. cavernicola* due to the very exclusive environment it inhabits, the altitude and the limited or non-existent connection with the sea, but it currently has amphiamerican status. A preliminary examination of material from the Caribbean Sea and type material of *N. cavernicola*, some morphological differences were observed, suggesting the present study: a reassessment of the amphiamerican status of *N. cavernicola*.

The main goal of this contribution is the re-assessment of troglomorphic morphology in namanereidins. As an introduction to the troglomorphic morphology in stygobitic namanereidins, the systematic section is presented first, addressing the description of a new species of *Namanereis* and the redescription of *N. cavernicola*, and including a key to identify all known species of the genus. After, the discussion of troglomorphic features is presented, focused on the elongation of cirri and chaetae, the arrangement of chaetae and the morphology of the jaws.

Materials and methods

For the morphology re-assessment, specimens of 7 species were examined and are deposited in the National Museum of Natural History, Smithsonian Institution (**USNM**), the Natural History Museum of Los Angeles County (**LACM-AHF**), and in the Reference Collection of El Colegio de la Frontera Sur, Chetumal (**ECOSUR**). They include paratypes of *Namanereis cavernicola* from Mexico (USNM 136559), topotypes of *Namanereis hummelincki* from Bonaire (USNM 29715, 29716), holotype (USNM 178870) and paratypes (USNM 31011) of *Namalycastis intermedia* from the Gulf of Mexico, and topotypes of *Namalycastis occulta* (ECOSUR P-2649), and non-type specimens of *Namanereis* cf. *amboinensis* (ECOSUR P-2902) and *Namalycastis borealis* (ECOSUR P-2651) from Chetumal Bay.

Specimens were examined under stereomicroscope (Olympus SZ40) and compound microscope with differential interference contrast (Olympus BX51). The photographs were made with a digital camera (Canon T5i) with adaptor for both microscopes. Plates and images were made with Adobe Photoshop® and Illustrator®. If not everted, pharynx was dissected to examine interior structures and, in some specimens, jaws were removed, mounted and observed in compound microscope. Parapodia from anterior, middle and posterior chaetigers were removed and mounted in semi-permanent slides, and examined under compound microscope. Some specimens were whole-mounted for examination of chaetal changes along body.

For descriptions, parapodial and chaetal terminology provided by Glasby (1999) and Conde-Vela (2013) were followed. In addition to the examined specimens, and in order to achieve an almost exhaustive discussion of the namanereidin morphology, all pertinent literature including original descriptions, revisions, notes about ecology and distribution, were taken into account. Morphological ratios and measurements used in some sections were obtained mainly from descriptions by Glasby (1999), and only from original descriptions for species described in other publications (Glasby 1997, Fiege and Van Damme 2002, Glasby et al. 2007, Magesh et al. 2012, Conde-Vela 2013, Glasby et al. 2014, Magesh et al. 2014, Alves and Santos 2016). Only ratios of type material were included and, if a range was declared, the average was used; if not clearly stated in descriptions, measures for ratios were obtained from illustrations. Histograms were made with the ratios obtained, sorted from highest to lowest ratio; in all histograms, *Namalycastis* species were highlighted in boldface and *Namanereis* species in lightface, while stygobiont species were labeled with an asterisk.

For the relative length of parapodial cirri, the ratios between the length of dorsal cirri (**Ld**) and length of neuroacicular lobe (**Ln**), for anterior ($\mathbf{A_{Ld/Ln}}$) and posterior

($\mathbf{P}_{\mathbf{Ld/Ln}}$) chaetigers were used. The subtraction of $\mathbf{P}_{\mathbf{Ld/Ln}}$ and $\mathbf{A}_{\mathbf{Ld/Ln}}$ ($\mathbf{D}_{\mathbf{p-a}}$) is less than or equal to zero if anterior cirri are equal or longer than posterior ones, indicating elongation of anterior cirri; and greater than zero if posterior cirri are longer than anterior ones, indicating elongation of posterior cirri. With $\mathbf{A}_{\mathbf{Ld/Ln}}$ and $\mathbf{P}_{\mathbf{Ld/Ln}}$, two histograms were made, the first explores the distribution of elongation of dorsal cirri in both anterior and posterior chaetigers, whilst the second shows the same distribution but based on anterior chaetigers only.

For the relative length of tentacular cirri, the ratio between length of posterodorsal tentacular cirri (**Lpt**) and wide of prostomium (**Wp**) was used. **Lpt/Wp** was obtained from illustrations directly (excepting *Namalycastis geayi*, *N. longicirris* and *N. siolii*). This measure was preferred over the number of chaetigers reached when posterodorsal tentacular cirri are placed backwards (Glasby 1999), because differences in preparation of specimens and contraction of body during fixation can cause misleading measurements (Oliveira et al. 2010, Bonyadi-Naeini et al. 2016).

For the relative length of blades of chaetae, the ratio between length of blade (**Lb**) and the width of shaft (**Ws**), standardized to chaetiger 10, was used; only the ratio of the dorsalmost (**Dm**) and ventralmost (**Vm**) falcigers in sub-acicular fascicle were considered. The subtraction of **Dm** and **Vm** ($\mathbf{D}_{\mathbf{d\text{-}v}}$) is zero or nearly so if both falcigers have subequal length, and greater than zero if **Dm** is greater than **Vm**, indicating elongation in **Dm**.

Results

Systematics

Family Nereididae de Blainville, 1818
Subfamily Namanereidinae Hartman, 1959
Genus *Namanereis* Chamberlin, 1919

Namanereis cavernicola (Solís-Weiss & Espinasa, 1991)

Fig. 1

Lycastilla cavernicola Solís-Weiss & Espinasa, 1991: 632–635, figs 1a–e, 2a–f.
Namanereis cavernicola Glasby, 1999: 83–86 (*partim*).

Type locality. Izote Cavern, Guerrero, Mexico, 1650 m above sea level.

Material examined. Paratypes USNM 136559 (2), Izote Cavern, (18°36'40"N, 99°33'25"W), Guerrero, Mexico 1650 m above sea level, 20 November 1988, Coll. L. Espinasa.

Description. Paratypes in excellent condition, one complete; 29 mm long, 1.1 mm wide at chaetiger 10, 69 chaetigers. Body pale, without pigmentation (Fig. 1A, C). Prostomium wider than long, anterior margin incised, groove present

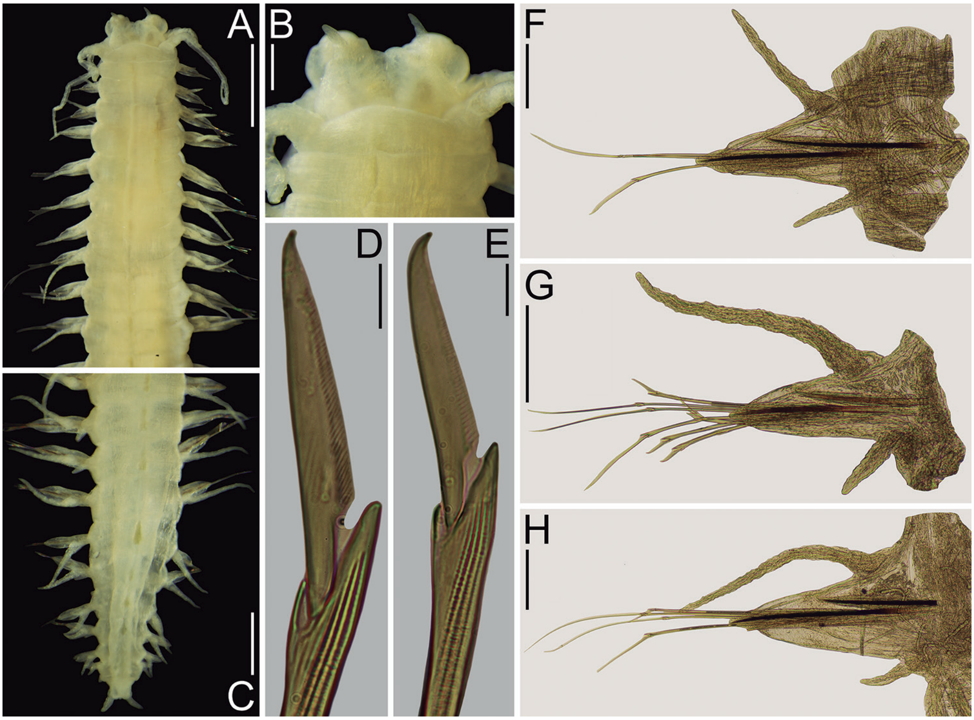

Figure 1. *Namanereis cavernicola* (Solís-Weiss & Espinasa, 1991). **A–H** Paratype USNM 136559 **A** Anterior end, dorsal view **B** Close-up of prostomium **C** Posterior end, dorsal view **D** Supra-acicular falciger, chaetiger 62 **E** Sub-acicular falciger, chaetiger 62 **F** Chaetiger 5, right parapodium **G** Chaetiger 20, right parapodium **H** Chaetiger 62, right parapodium. Scale bars: 1 mm (**A**); 0.2 mm (**B**, **F–H)**; 0.5 mm (**C**); 10 µm (**D**, **E**).

(Fig. 1A–B); antennae cirriform, as long as prostomium; eyes absent (Fig. 1B). Tentacular ring as long as first chaetiger; three pairs of tentacular cirri, superficially annulated, longest one reaches chaetiger 4 (Fig. 1A); cirrophores 1.5-2.0 times longer than wide.

Parapodial cirri pattern: Dorsal cirri sub-equal to neuroacicular lobes in anterior chaetigers, becoming longer than neuroacicular lobes toward posterior end, basally inserted throughout body. Ventral cirri shorter than neuropodial lobes, basally inserted throughout body.

In anterior chaetigers (Fig. 1F), dorsal cirri subequal to neuropodial lobes; neuropodial lobes subconical, twice longer than wide, twice longer than ventral cirri; ventral cirri half as long as dorsa cirri ones. In middle chaetigers (Fig. 1G), dorsal cirri twice longer than neuropodial lobes; neuroacicular lobes subconical, twice longer than wide, twice longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones. In posterior chaetigers (Fig. 1H), dorsal cirri 1.2 to 1.5 times longer than neuropodial lobes; neuropodial lobes subconical, 1.5 times longer than wide, 3 times longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones.

Notochaetae absent. Neurochaetae in type D arrangement, i.e. supra-acicular chaetae heterogomph falcigers (Fig. 1D) and sesquigomph spinigers in pre- and post-acicular fascicles respectively; sub-acicular chaetae heterogomph falcigers with short (Fig. 1E) or long blades and spinigers in pre-acicular fascicles. Supra-acicular sesquigomph spinigers pectinated, teeth minute, decreasing in size towards tip; sub-acicular heterogomph falcigers pectinated, teeth minute, tip falcate, decreasing in length towards tip (Fig. 1D–E).

Pygidium tripartite; a pair of anal cirri cirriform, short, as long as pygidium (Fig. 1C).

Remarks. Solís-Weiss and Espinasa (1991) proposed *Lycastilla* with this species based on the presence of jointed antennae, cleft prostomium and notoaciculae with recurved tips. Posteriorly, Glasby (1999) regarded such features as insufficient and synonymized *Lycastilla* with *Namanereis* Chamberlin, 1919. The original description matches well with the species examined. Glasby (1999) redescribed the species with paratypes and non-type material from the Caribbean; however, part of his Caribbean material is herein regarded as a distinct undescribed species (see below).

Namanereis christopheri sp. n.

http://zoobank.org/FFA8CE1A-AF4A-48F7-96D7-CB2392E8F2ED

Fig. 2

Namanereis cavernicola Glasby, 1999: 83–86, figs 8c, 35a–g (*partim, non* Solís-Weiss and Espinasa 1991).

Type locality. Saint Vincent, Lesser Antilles.

Etymology. The specific name is after Christopher J. Glasby, in recognition of his numerous contributions in polychaete taxonomy, especially about nereidid taxonomy, and because he identified this species as new after his first evaluation (see below).

Type material. Holotype LACM-AHF 1227 and paratypes LACM-AHF 1228 (1), and LACM-AHF 1229 (10), Golden Grove, near Chateaubelair Bay (13°17'18"N, 61°14'25"W), Saint Vincent, Saint Vincent and the Grenadines, 31 July 1972, 435 m above sea level, spring pool in *Colocasia* (Araceae) swamp, Coll. J.J. Rankin.

Description. Holotype complete, 32 mm long, 1 mm wide at chaetiger 10, 95 chaetigers; body with several parapodia removed in middle region, otherwise in good condition. Paratypes complete, in good conditions, 10–30 mm long, 1–2 mm wide, 62–95 chaetigers. Body pale, without pigmentation (Fig. 2A, B).

Prostomium wider than long, anterior margin entire, groove present; antennae cirriform, as long as prostomium; eyes absent (Fig. 2A, C). Tentacular ring as long as first chaetiger; three pairs of tentacular cirri, longest one reach chaetiger 3 (Fig. 2A, C); cirrophores 1.5–2.0 times longer than wide. Pharynx dissected; jaws with layer running throughout cutting edge, two distal teeth, with bifid appearance (Fig. 2E). Pharynx with cushion-shaped papillae on area VI (Fig. 2D), papillae rounded, laterally fused; other areas smooth.

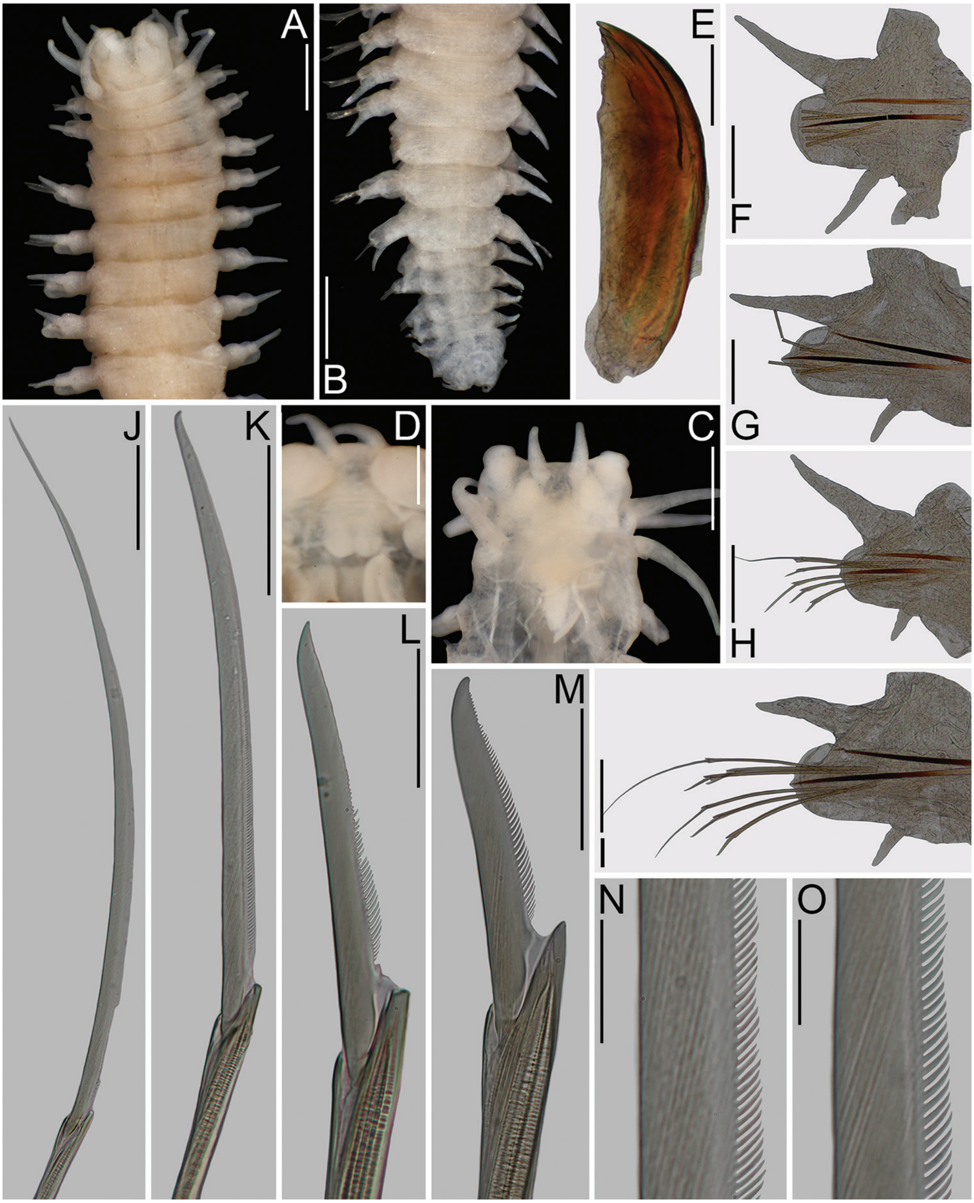

Figure 2. *Namanereis christopheri* sp. n. **A, B, F–O** Holotype LACM-AHF 1227 **C–E** paratype LACM-AHF 1229 **A** Anterior end, dorsal view **B** Posterior end, dorsal view **C** Close-up of prostomium **D** Areas V and VI, pharynx dissected **E** Right jaw, dorsal view **F** Chaetiger 5, right parapodium **G** Chaetiger 21, right parapodium **H** Chaetiger 49, right parapodium **I** Chaetiger 90, right parapodium **J** Supra-acicular sesquigomph spiniger, chaetiger 49 **K** Sub-acicular heterogomph falciger, chaetiger 49 **L** Supra-acicular heterogomph falciger, chaetiger 49 **M** Sub-acicular heterogomph falciger, chaetiger 49 **N** Close-up of blade, supra-acicular sesquigomph spiniger, chaetiger 49 **O** Close-up of blade, supra-acicular heterogomph falciger, chaetiger 49. Scale bars: 0.5 mm (**A–D**); 0.1 mm (**E**); 0.1 mm (**F–I**); 50 µm (**J**, **K**); 30 µm (**L**, **M**); 10 µm (**N**, **O**).

Parapodial cirri pattern: Dorsal cirri longer than neuropodial lobes, basally inserted throughout body. Ventral cirri shorter than neuropodial lobes, basally inserted throughout body.

In anterior chaetigers (Fig. 2F), dorsal cirri 3 times longer than neuropodial lobes; neuropodial lobes rounded, as long as wide, as long as ventral cirri; ventral cirri half as long as dorsal ones. In middle chaetigers (Fig. 2G–H), dorsal cirri twice longer than neuropodial lobes; neuropodial lobes rounded, slightly longer than wide, twice longer than ventral cirri; ventral cirri one-third to one-half as long as dorsal ones. In posterior chaetigers (Fig. 2I), dorsal cirri twice longer than neuropodial lobes; neuropodial lobes rounded, as long as wide, 3 times longer than ventral cirri; ventral cirri half as long as dorsal ones.

Notochaetae absent. Neurochaetae in type D arrangement, i.e. supra-acicular chaetae heterogomph falcigers and sesquigomph spinigers in pre- and post-acicular fascicles respectively; sub-acicular chaetae heterogomph falcigers with short and long blades in pre-acicular fascicles.

Supra-acicular sesquigomph spiniger pectinated, teeth minute, decreasing slightly in size towards tip (Fig. 2J, N); supra-acicular heterogomph falcigers pectinated, teeth minute, decreasing slightly in length towards tip (Fig. 2L). Sub-acicular falcigers pectinated, teeth minute, tip falcate, decreasing slightly in size towards tip; upper heterogomph falcigers long bladed, blades 2–3 times longer than lower ones (Fig. 2K, O), lower falcigers stouter than upper ones (Fig. 2L–M).

Pygidium tripartite; anal cirri cirriform, short, as long as last chaetiger (Fig. 2B).

Remarks. The material of this species was previously examined by Glasby (1999) and identified as *N. cavernicola*. The three vials from the Los Angeles Museum include two labels. One label has the name "*Lycastopsis F*", identified in 1988, and includes the designation of holotypes and paratypes. The other label has another unpublished manuscript name, dated 1990. Likely, Glasby initially regarded it as a new species, but later he changed his mind and included them with *N. cavernicola* (Glasby 1999) resulting in an amphiamerican distribution. The incised anterior margin of prostomium and other features were compared with *Lycastoides alticola* but not with *N. cavernicola*, arguing that the only difference among Caribbean and Pacific materials were the longer dorsal cirri in *N. cavernicola* (Glasby 1999: 85). The result was a description of. *N. cavernicola* with mixed features and encompassing high ranges of variation.

On the other hand, *N. christopheri* sp. n. and *N. cavernicola* share some features as having falcigers with relative long blades and blades with several minute teeth. However, they have some important differences. First, *N. christopheri* sp. n. has an anterior margin of prostomium entire and antennae are shorter than prostomium, while in *N. cavernicola* the anterior margin is incised and antennae are longer than prostomium. Further, tentacular cirri in *N. christopheri* sp. n. are smooth and reach chaetiger 3, while in *N. cavernicola* they are annulated and reach chaetiger 5–6. In addition, *N. christopheri* sp. has jaws much broader than *N. cavernicola*. *N. cavernicola* has neuropodial lobes tapered, subconical with pointed tips, two or three times longer than wide, while in *N. christopheri* sp. n. they are rounded and as long as wide; and parapodial cirri in *N. cavernicola* are thinner than in *N. christopheri* sp. n.

As indicated in the key below, *N. christopheri* sp. n. is also closely related to *N. hummelincki*, differing mainly in chaetal features as Glasby (1999: 85) previously noted. In *N. christopheri* the blades of sub-acicular falcigers and spinigers have several, minute teeth and they have a similar size along the cutting edge, while in *N. hummelincki* they have fewer teeth, and the basal ones are notably longer than medial and distal ones.

Glasby (1999: 85) noted, after the revision of parapodia of *N. cavernicola*, several grades of curvature in notoaciculae and even in neuroaciculae, which are absent in *N. christopheri* sp. n., and considered them as artifacts of preservation. However, since all notoaciculae observed had recurved tips, this feature is regarded here as specific one. Glasby (1999: 74) thought that these features, together with the presence of articulated antennae and tentacular cirri were not sufficient to recognize *Lycastilla* as distinct, and this decision is herein corroborated. Finally, all specimens of *N. christopheri* sp. n. were whole-mounted and examined under microscope, no spinigers were found in sub-acicular fascicles; the long-bladed, uppermost sub-acicular chaetae in Fig. 2H–I have falcate tips, i.e., they are falcigers. The species does not replace upper long-bladed falcigers by spinigers toward posterior chaetigers, sharing this peculiarity with *N. gesae*.

Key for *Namanereis* species from the world

(Modified after Glasby 1999)

1 Four pairs of tentacular cirri **2**
– Three pairs of tentacular cirri **4**
2 Prostomium with entire anterior margin ....
...***N. quadraticeps* (Blanchard *in* Gay, 1849)** (Strait of Magellanes, Chile)[1]
– Prostomium with cleft anterior margin **3**
3 Dorsal cirri shorter than neuroacicular ligule on posterior chaetigers ....
.... ***N. minuta* Glasby, 1999** (Grand'Anse, Haiti)
– Dorsal cirri longer than neuroacicular ligule on posterior chaetigers.............
.... ***N. stocki* Glasby, 1999** (St. Ann's Bay, Jamaica)
4 With antennae **5**
– Without antennae ....
.... ***N. malaitae* (Gibbs, 1971)** (Malaita, Solomon Islands)
5 Eyes present **6**
– Eyes absent **11**
6 Eyes conspicuous, separate 7
– Eyes barely visible, coalesced ....
.... ***N. sublittoralis* Glasby, 1999** (Smoke Alley Well, Sint Eustatius)
7 Supra-acicular spinigers present **8**
– Supra-acicular spinigers absent ....
.... ***N. pontica* (Bobretzky, 1872)** (Bay of Sevastopol, Black Sea)

8 Falcigers with long, strongly falcate tips, one half to one third of cutting edge of blade without teeth **9**

– Falcigers with short, weakly falcate tips, teeth on almost all length of cutting edge of blade **10**

9 Falcigers with blades longer than boss of the joint (i.e. long blades) .... ***N. amboinensis* (Pflugfelder, 1933)** (Ambon Island, Indonesia)

– Falcigers with blades as long as boss of the joint (i.e. short blades) .... ***N. riojai* (Bastida-Zavala, 1990)** (La Paz Bay, Mexico)

10 Jaws with 9 subterminal teeth (6–14) .... ***N. catarractarum* (Feuerborn, 1931)** (Bedali, Java)

– Jaws with 5 subterminal teeth (5–8) .... ***N. littoralis* (Müller & Grube *in* Grube, 1872)** (Santa Catarina Island, Brazil)[1]

11 Jaws with terminal and subterminal teeth **12**

– Jaws with two bifid distal teeth and smooth cutting edge **15**

12 Prostomium with anterior margin entire **13**

– Prostomium with anterior margin cleft .... ***N. tiriteae* (Winterbourn, 1969)** (Turitea Stream, North Island, New Zealand)

13 Dorsal cirri shorter or subequal than neuropodial lobes throughout body.... **14**

– Dorsal cirri longer than neuropodial lobes throughout body .... ***N. beroni* Hartmann-Schröder & Marinov, 1977** (Bem Tem, Papua New Guinea)

14 Supra-acicular falcigers with several, minute teeth (ca. 30) ..... ***N. gesae* Fiege & Van Damme, 2002** (Abd al-Kuri Island, Socotra Archipelago, Yemen)

– Supra-acicular falcigers with few, minute teeth (7–11) .... ***N. pilbarensis* Glasby, Fiege & Van Damme, 2014** (Pilbara Region, Australia)

15 Prostomium with anterior margin cleft **16**

– Prostomium with anterior margin entire **17**

16 Dorsal cirri longer than neuropodial lobes in first chaetigers .... ***N. araps* Glasby, 1997** (Nakhal, Oman)

– Dorsal cirri shorter than to subequal than neuropodial lobes in first chaetigers ....*N. cavernicola* (Solís-Weiss & Espinasa, 1991) (Izote Cavern, Mexico)

17 Supra-acicular falcigers with pectinate, minute teeth **18**

– Supra-acicular falcigers with serrated, coarse teeth .... ***N. serratis* Glasby, 1999** (Étang Saumâtre, Haiti)

18 Upper sub-acicular falcigers with blades two or more times longer than lower falcigers **19**

– Upper and lower sub-acicular falcigers with subequal blades .... ***N. socotrensis* Glasby, Fiege & Van Damme, 2014** (Socotra Island, Yemen)

19 Supra-acicular falcigers with teeth increasing their length greatly basally .... ***N. hummelincki* (Augener, 1933)** (Fontein, Bonaire)

– Supra-acicular falcigers with teeth increasing their length slightly medially .... ***N. christopheri* sp. n.** (Saint Vincent)

[1] Species groups of these species were not considered, but only information of type materials.

Ratios of elongation

Elongation of parapodial cirri. The results of elongation ratios of parapodial cirri are depicted in Fig. 3. Most *Namalycastis* species had high difference between anterior and posterior ratios ($\mathbf{D}_{\mathbf{p-a}} > 1$), whilst five had slight or no difference ($\mathbf{D}_{\mathbf{p-a}} \leq 1$) (Fig. 3A). On the other hand, eight *Namanereis* had posterior dorsal cirri slightly longer than anterior ones, ($1 \geq \mathbf{D}_{\mathbf{p-a}} > 0$) while in 11 they were subequal or shorter ($\mathbf{D}_{\mathbf{p-a}} \leq 0$) (Fig. 3A). In regard to elongation of dorsal cirri towards posterior segments, stygobiont *Namanereis* were not show evident differences in comparison to epigean *Namanereis* (Fig. 3A), excepting *N. cavernicola* having high difference ($4 \geq \mathbf{D}_{\mathbf{p-a}} > 2$).

Based on ratios of anterior chaetigers only (Fig. 3B), most species of both genera had dorsal cirri longer than neuroacicular lobes ($\mathbf{A}_{\mathbf{Ld/Ln}} > 1$). Indeed, *Namanereis araps*, *N. christopheri* sp. n. and *N. serratis* had the greatest $\mathbf{A}_{\mathbf{Ld/Ln}}$ among stygobiont species ($\mathbf{A}_{\mathbf{Ld/Ln}} > 2$), but the epigean species *N. amboinensis* had similar ratios as well. Next, eight stygobiont and three epigean *Namanereis* shared the second range with dorsal cirri slightly longer than neuroacicular lobes ($2 \geq \mathbf{A}_{\mathbf{Ld/Ln}} > 1$), while in three stygobiont and three epigean *Namanereis* they were shorter, occupying the third range ($\mathbf{A}_{\mathbf{Ld/Ln}} \leq 1$). *Namalycastis* species were present in all ranges, with more representatives in the second one ($2 \geq \mathbf{A}_{\mathbf{Ld/Ln}} > 1$).

Elongation of tentacular cirri. The resultant histogram of **Lpt/Wp** ratios is shown in Fig. 4A. Most stygobiont *Namanereis* had high ratios and four occupy the first places with the highest ones (2≥ **Lpt/Wp** >1), but other four species had tentacular cirri subequal or shorter than prostomium (**Lpt/Wp** ≤1); moreover, some *Namalycastis* and epigean *Namanereis* had similar ratios than some stygobiont *Namanereis* in both ranges (Fig. 4A). Excepting *N. pontica*, most epigean *Namanereis* had tentacular cirri subequal or shorter than prostomium.

Elongation of chaetae. The results of $\mathbf{D}_{\mathbf{d-v}}$ for most species is shown in Fig. 4B. Eight stygobiont *Namanereis* species had high distances between **Dm** and **Vm** ($\mathbf{D}_{\mathbf{d-v}} > 1$), occupying the first places (Fig. 4B). At the same range, and between the stygobiont *Namanereis* with the highest difference (~11.3), *N. christopheri* sp. n., and the lowest one (~2.7), *N. stocki*, there are six *Namalycastis* species, four reported with elongated falcigers, excepting *N. hawaiiensis* and *N. fauveli* (Glasby 1999) (Fig. 4B). Following this group, there are four *Namalycastis* species with moderate differences ($3 > \mathbf{D}_{\mathbf{d-v}} > 1$) and ten with lower ones ($\mathbf{D}_{\mathbf{d-v}} \leq 1$), while all epigean *Namanereis* species have low differences ($\mathbf{D}_{\mathbf{d-v}} \leq 1$) (Fig. 4B).

Discussion

Re-assessment of morphological adaptations of Namanereidinae

Typical morphology of stygobiont *Namanereis* are depicted in figures of *N. cavernicola* Solís-Weiss & Espinasa, 1990 and *N. christopheri* sp. n. (Figs 1 and 2, respectively). In

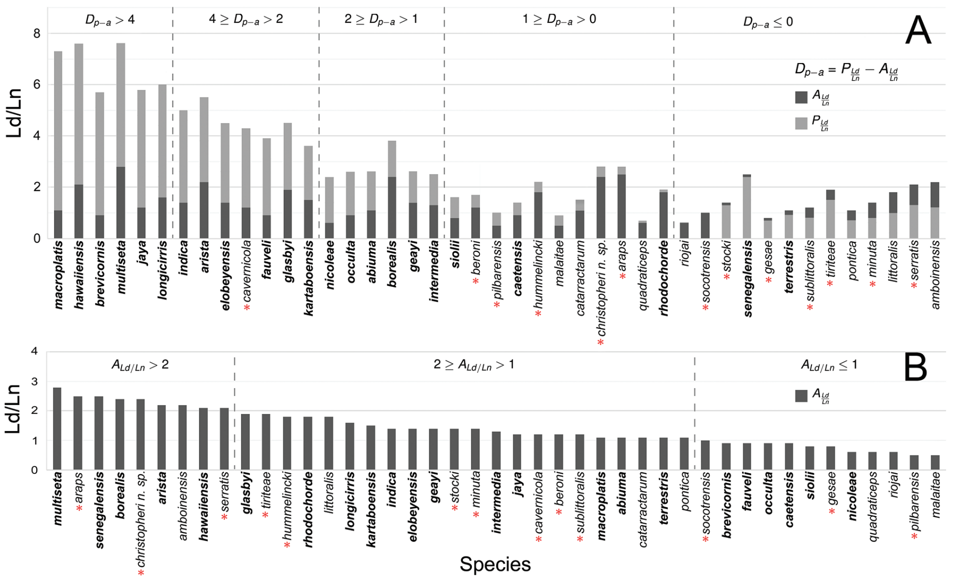

Figure 3. Histograms showing length ratios of parapodial cirri among *Namalycastis* (boldface) and *Namanereis* (lightface) species. **A** Ratios between length of dorsal cirri (Ld) and length of neuroacicular lobe (Ln) at anterior ($A_{Ld/Ln}$) and posterior chaetigers ($P_{Ld/Ln}$), and difference among them (D_{p-a}) **B** Ratios between length of dorsal cirri (Ld) and length of neuroacicular lobe (Ln) at anterior chaetigers ($A_{Ld/Ln}$) only. Sorted from highest to lowest ratios; asterisks highlight stygobiont *Namanereis*.

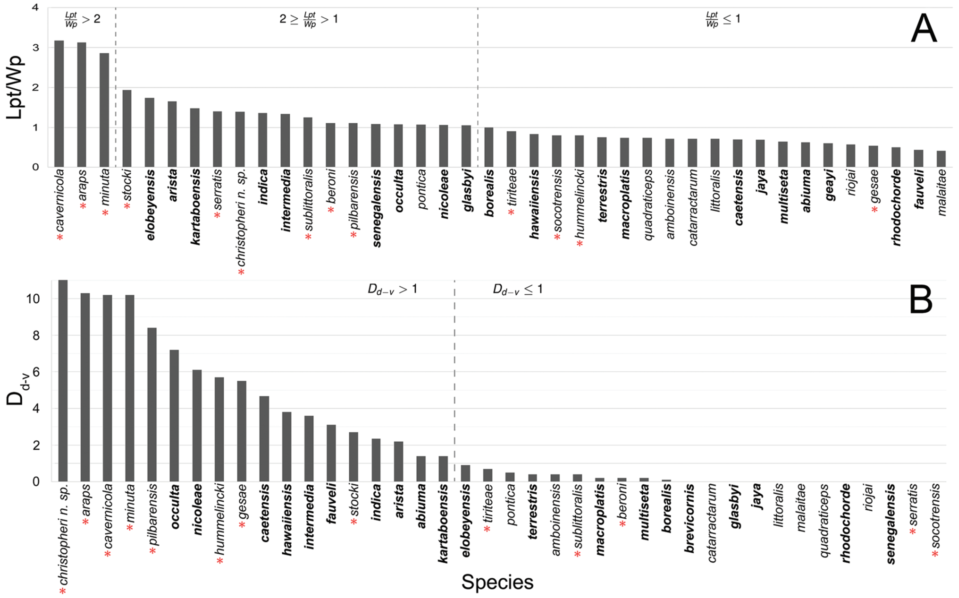

Figure 4. Histograms showing length ratios of some troglomorphic features among *Namalycastis* (boldface) and *Namanereis* (lightface) species. **A** Ratios between length of tentacular cirri (Lpt) and wide of prostomium (Wp) **B** Difference (D_{d-v}) between ratios of dorsalmost (Dm) and ventralmost (Vm) falcigers at chaetiger 10. Sorted from highest to lowest ratios; asterisks highlight stygobiont *Namanereis*.

order to illustrate troglomorphic features in other namanereidins and facilitate comparison, a species from Bonaire, *Namanereis hummelincki* (Augener, 1933), and three other namanereidins from Chetumal Bay, Mexican Caribbean, *Namalycastis occulta* Conde-Vela, 2013, *N. borealis* Glasby, 1999 and *Namanereis* cf. *amboinensis*, were examined (Fig. 5). None of the specimens of the last four species were found in caves but in aphotic environments: Bonaire specimens were found in a cement gutter from a spring with mud and decayed leaves (Wesenberg-Lund 1958: 4–5), whereas Chetumal Bay specimens were found in muddy and sandy bottoms under red mangrove decayed leaves, and in sheltered, shaded places by dense mangrove patches.

Notably, *N. hummelincki*, *N. occulta*, *N. cavernicola*, and *N. christopheri* sp. n. share loss of both eyes and body pigmentation (Figs 5A, C, 1A and 2A, respectively), the presence of bifid jaws (Figs 2E, 5J, 7D–F) and clear elongation of blades in sub-acicular falcigers from the dorsalmost position regard to ventralmost ones (Figs 2J–M, 5M). On the other hand, *Namanereis* cf. *amboinensis* shares the loss of pigmentation with species above mentioned, but its parapodial morphology (Fig. 5F) is quite similar to *N. hummelincki* and *N. christopheri* sp. n. regarding the relative length and shape of dorsal cirri along body (Figs 5E and 2F–I, respectively). In contrast, *N. occulta* is more similar to *N. borealis* in regard to those features (Fig. 5G, H, respectively). Furthermore, *N.* cf. *amboinensis* and *N. borealis* share presence of eyes, serrated jaws and sub-acicular falcigers with subequal blades (Fig. 5B, I, L and 5D, K, N, respectively). Finally, length and shape of both tentacular and parapodial cirri of *N. cavernicola* (Fig. 1A, F–H) do not resemble to any of the last species.

Glasby et al. (2014: 31) used *Namanereis araps* as example of the elongation of appendages observed in subterranean *Namanereis* species and absent in their "marine surface-dwelling counterparts": the tentacular cirri are long and annulated and its posterodorsal pair extends beyond chaetiger 4; dorsal cirri generally are slender and subequal to, or longer than, respective neuroacicular lobes; and all have neuropodial heterogomph falcigers increasing in blade's length toward posterior chaetigers (Glasby 1997). If elongation was restricted to stygobiont *Namanereis* species, a clear clustering of these ones in the histograms is expected, having the highest ratios. Indeed, *N. araps* and three or four stygobiont *Namanereis* had the highest ratios of elongation of tentacular cirri and chaetae, but not for elongation of dorsal cirri in anterior chaetigers, and even most stygobiont *Namanereis* were ranked along with epigean *Namanereis* and *Namalycastis* in all ranges (Figs 3A–B, 4A–B). Therefore, not all stygobiont *Namanereis* have evident elongation of dorsal cirri in anterior segments, but even they have similar ratios than epigean *Namanereis*.

A possible explanation of the similar $\mathbf{A}_{\mathbf{Ld/Ln}}$ in stygobiont *Namanereis* and epigean *Namanereis* and *Namalycastis* species is related to the shape of neuroacicular lobes. In some species, neuroacicular lobes are subconical, i.e., longer than wide with pointed tips, while in other they are rounded, i.e., as long as wide with rounded tips; then, species with relatively short dorsal cirri and rounded neuroacicular lobes have high ratios because rounded lobes are shorter respect to subconical ones. The effect of this difference is appreciable in *N. araps*, *N. amboinensis* and *N. christopheri* sp. n.: they have similar $\mathbf{A}_{\mathbf{Ld/Ln}}$ but with evident subconical neuroacicular lobes in the former spe-

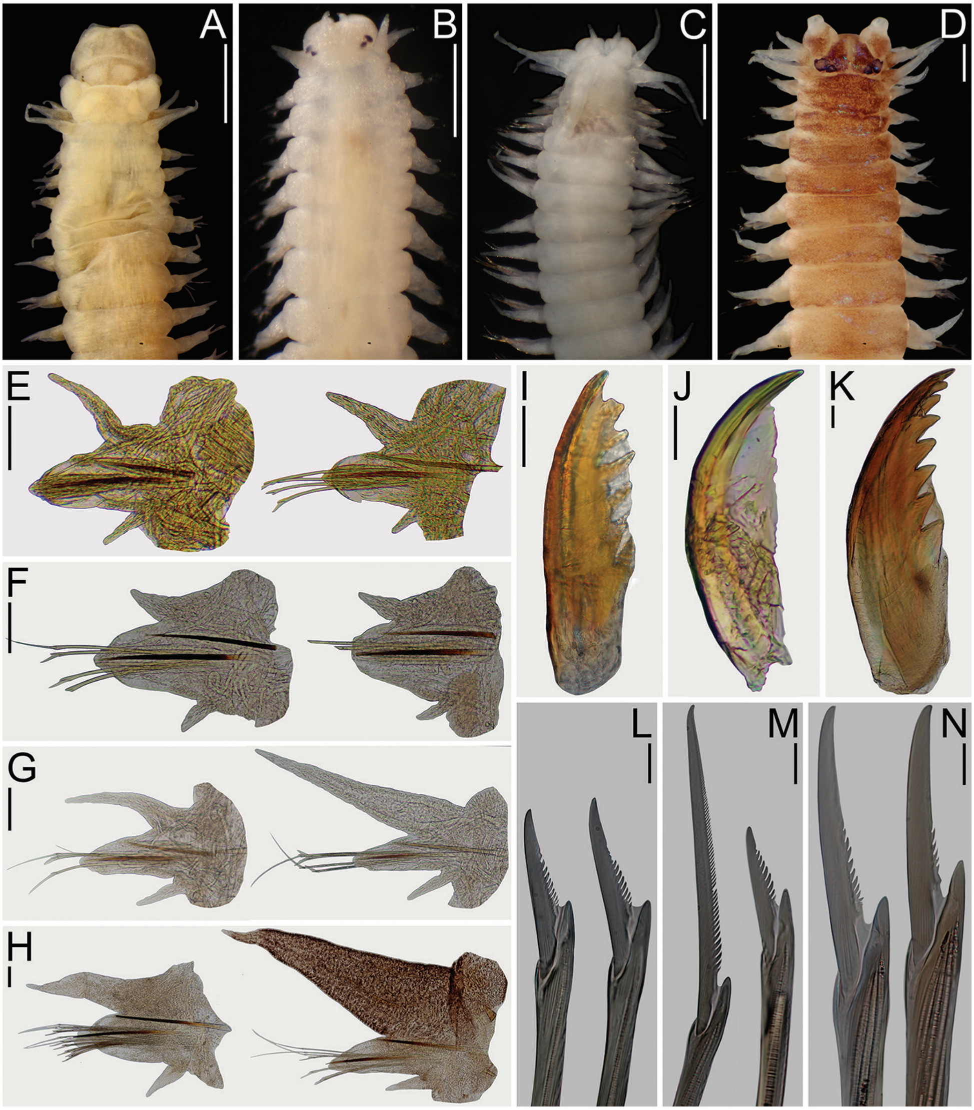

Figure 5. Morphological comparison among namanereidins. *Namanereis hummelincki* (**A, E**) (USNM 29715, 29716); *N.* cf. *amboinensis* (**B, F, I, L**) (ECOSUR P-2902); *Namalycastis occulta* (**C, G, J, M**) (ECOSUR P-2649); *N. borealis* **D, H, K, N. A–D** (ECOSUR P-2651). Anterior ends, dorsal view **E–H** Right parapodia from anterior (10, left) and posterior (right) chaetigers **I–K** Left jaws, dorsal view **L–M** Dorsalmost (left) and ventralmost (right) sub-acicular, heterogomph falcigers from chaetiger 10. Scale bars: 0.5 mm (**A–D**); 0.1 mm (**E–H**); 50 µm (**I–K**); 10 µm (**L–N**).

cies and rounded ones in the last two (Glasby 1997; 1999; this paper). However, most *Namalycastis* species have subconical neuroacicular lobes and dorsal cirri longer than lobes, while only *N. araps*, *N. minuta* and *N. tiriteae* have remarkable subconical lobes (Glasby 1997, 1999).

As expected, most *Namalycastis* had high values of $\mathbf{D}_{p-a}$ since elongation of dorsal cirri toward posterior chaetigers is usual of that genus (Glasby 1999), but in *N. caetensis*, *N. rhodochorde*, *N. senegalensis*, *N. siolii* and *N. terrestris* there is no evident elongation of dorsal cirri in posterior chaetigers ($\mathbf{D}_{p-a} \leq 1$). Although, they have a notable basal widening and flattening in comparison to anterior chaetigers (Glasby 1999), being a remarkable morphological change used as diagnostic for the genus (Glasby 1999). In other species such as *N. nicoleae* Glasby 1999, *N. occulta* and in *N. intermedia* Glasby, 1999, this feature is weakly developed, and the three had similar $\mathbf{D}_{p-a}$ (Fig. 3A). On the other hand, eight *Namanereis* have posterior dorsal cirri slightly longer than anterior ones, while in 11 they are subequal or shorter. Notably, *N. cavernicola* is the only species ranked together with *Namalycastis* species with high differences, however dorsal cirri do not become foliose as in the latter ones. In regard to elongation of dorsal cirri towards posterior segments, stygobiont *Namanereis* do not show evident differences in comparison to epigean *Namanereis* (Fig. 3A).

Based on the results of the analysis performed (Fig. 4A, B), the elongation of both sub-acicular, dorsalmost falcigers and tentacular cirri are not restricted to stygobiont *Namanereis*. As expected, the eight *Namanereis* species with $\mathbf{D}_{d\text{-}v} > 1$ are those ones previously described as bearing elongated neuropodial falcigers. Only four *Namalycastis* have been described with elongated falcigers (*N. caetensis*, *N. intermedia*, *N. occulta* and *N. nicoleae*), but six more had similar ratios as well (Fig. 4B). Similarly, most stygobiont *Namanereis* had elongated tentacular cirri (Fig. 4A), and even the first four species (including *N. araps*) have jointed tentacular cirri (Glasby 1997, 1999), but this feature cannot be regarded exclusively as an adaptation to subterranean habitats, because it is also present in epigean species such as *Namalycastis elobeyensis*, *N. indica* and *N. kartaboensis* (Glasby 1999), and even outside namanereidins. All *Namalycastis* and epigean *Namanereis* with clear elongation of upper neuropodial falcigers occur in freshwater or brackish environments as ponds, streams and estuaries, and in muddy to sandy sediments (Glasby 1999, Conde-Vela 2013, Alves and Santos 2016), but not in subterranean habitats.

As shown above, the elongation and articulation of appendages are not restricted neither to *Namanereis* species nor stygobiont ones, but are rather present in several species occurring in different habitats. Some confusion can be led by evaluating the elongation of appendages *a priori* as troglomorphic features. For example, Heads (2010) described a new fossil spider cricket (Insecta: Orthoptera), *Araneogrillus dylani*, embedded into amber, showing troglomorphic features as the elongation of structures, as in other closely related troglobitic genera. Given its inclusion in amber, *A. dylani* presumably lived in plant litter, so such troglomorphies were not obtained the result of troglobitic habits. His phylogenetic analysis of subtribe Amphicustina showed that the troglomorphic features are not restricted to troglobitic species, and that those troglomorphies evolved at least twice (Heads 2010). Therefore, the presence of elongated structures resulted from exaptation and were later conserved in recent troglobitic species, and not the result of adaptation to current cave habitats. So, at least the elongation of appendages in namanereidins seems to respond to independent selective pressures and not exclusively generated in cave environments. Furthermore, since most species showing elongation do not have a close phylogenetic relationship (Glasby 1999, Alves and Santos 2016), and the diversity of habitats they currently occur, it suggests that this feature evolved at least twice, asynchronously and in distinct scenarios.

While the factors driving the elongation of appendages in namanereidins are elusive, the evidence in other groups is weak or inconclusive. For example, the elongation of some segments of legs seems to be unique among stygobiont millipedes, but not the elongation of antennae (Liu et al. 2017). On the other hand, Delić et al. (2016: 46) found for the stygobiont amphipod *Niphargus croaticus* (Jurinac, 1887) that elongation in legs is more related with local factors as low of absent water flow and interspecific competition, rather than food availability or time of colonization; moreover, they found a high differentiation among closely related populations, suggesting a fast morphological change regarding this feature (p. 46). It is unknown the function of evident elongation of specific sub-acicular falcigers, especially after relationships among length and shape of chaetae and type of substrate or movement abilities are uncertain (Merz and Edwards 1998, Hesselberg and Vincent 2006a, 2006b). Being that most namanereidins (especially *Namanereis* species) have small body size and distinct parapodial morphology when compared with other nereidids, a further experimental evaluation is needed to discard possible relationships with both biotic and abiotic factors.

Neurochaetal arrangement. The arrangement of neurochaetae deserves additional comments. Glasby (1999: 7–8) proposed a classification based on the neurochaetae arrangement respect to the neuroacicula, along discrete bundles or fascicles, depicted in Fig. 5. Four main neuropodial fascicles (Fig. 6A) can be discerned, and six distinct arrangements were observed depending on the type of chaetae in each fascicle; *Namalycastis* has type A or B arrangements, while *Namanereis* has C, D, E or F (Glasby 1999: 7). Some problems with types C and D are herein addressed, and "pre-" or "postacicular" fascicles in the remaining section must be assumed that they are referred as sub-acicular ones, unless otherwise indicated.

By definition, types C and D do not have chaetae in postacicular fascicles (Fig. 6D and 6E, respectively). The main difference between them is that type D has heterogomph spinigers and heterogomph falcigers with elongated blades in preacicular positions (Fig. 6B), whereas type C presents heterogomph falcigers without elongated blades only. These falcigers with elongated blades are commonly called "pseudospinigers" and, if parapodium is mounted laterally, they are the dorsalmost falcigers, occupying this position in all cases, notably longer than remaining falcigers but shorter that spinigers (Figs 5M, 6B), and having a terminal hook or falcate tip, as is the case for falcigers (Glasby 1997: 160). However, they are just long-bladed falcigers as indicated by their falcate tips, such that the dismissal of the term had been proposed (Conde-Vela 2013, Alves and Santos 2016). Some inconsistences were highlighted by Glasby (1999: 87) about the type D present in some *Namanereis* species; he found that it is difficult to state if "pseudospinigers" are in pre- or postacicular position, and he regarded them as preacicular for cladistics analysis; moreover, Fiege and Van Damme (2002: 241) and Conde-Vela (2013: 481) found the same problem for *Namanereis gesae* and *Namalycas-*

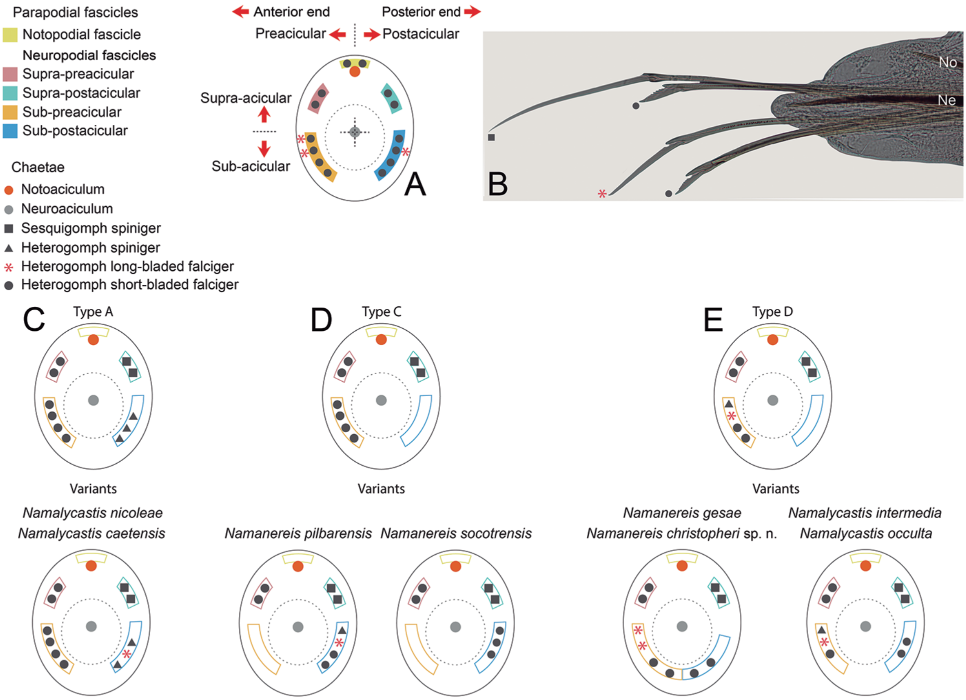

Figure 6. Chaetal arrangement of some namanereidins referred in this study. **A** Scheme showing the parapodial fascicles and their positions in relation to neuroaciculum **B** Neuropodial lobe of right parapodium from chaetiger 10 of *Namalycastis occulta*, showing the position of chaetae in type D species when mounted **C–E** Chaetal arrangement of types A, C and E, and their variants found in literature (modified from Glasby 1999, Fig. 1).

tis occulta, respectively. A possible variant of type D is found in *N. gesae* and *N. christopheri* sp. n. (Fig. 6E), where sub-preacicular heterogomph spinigers were not found.

On the other hand, type A arrangement, typical of *Namalycastis* species, is characterized by having only falcigers in both supra- and sub-preacicular fascicles, and only spinigers in both supra- and sub-postacicular ones (Fig. 6C). Before *N. occulta*, the only *Namalycastis* species described with "pseudospinigers" was *N. nicoleae* Glasby, 1999 that has them in postacicular fascicles, together with spinigers, but considered as a type A arrangement without further explanation (Glasby 1999: 65). Later, Glasby et al. (2014: 31) stated that the position of these "pseudospinigers" is not homologous with those found in *Namanereis* species in preacicular fascicles. In the same work (p. 25), the new species *Namanereis pilbarensis* was described as having falcigers and "bifid pseudospinigers" in postacicular fascicles and type C arrangement without further explanation; the other new species, *N. socotrensis*, was described as having type C arrangement but with falcigers in postacicular fascicles instead of preacicular ones (p. 29), requiring a reassessment in both species. In order to avoid confusion, a term should not be used for two structures with likely distinct origin or function. Since "pseudospinigers" might not be homologous structures, this is another indication that such term must be dismissed (Conde-Vela 2013, Alves and Santos 2016).

Another species from the Gulf of Mexico, *Namalycastis intermedia*, was described as having a type A arrangement, but heterogomph falcigers in both supra- and sub-preacicular fascicles are replaced by heterogomph spinigers toward posterior chaetigers (Glasby 1999: 55); also, elongated falcigers ("pseudospinigers-like") were described in upper, sub-acicular position (Glasby 1999, fig. 22g) and since it has a type A arrangement, these elongated falcigers must be present in preacicular fascicles, as corroborated after the revision of type material. The replacement of falcigers (short blades) by spinigers (long blades) in posterior chaetigers in both supra- and sub-preacicular fascicles is also shown by *Namalycastis arista*, *N. macroplatis* and *N. senegalensis* (Glasby 1999: 57). In a recent contribution, Alves and Santos (2016: 504) pointed out the presence of "elongated falcigers" in postacicular fascicles in their new species *Namalycastis caetensis*, regarded it as a relevant feature (p. 505) and included in the diagnosis of the genus (p. 502); the type of arrangement in this species was not stated, but based on the description it corresponds to a modified type A.

Summarizing, *Namalycastis caetensis*, *N. intermedia* and *N. nicoleae* are species with type A arrangements but also with elongated falcigers or "pseudospinigers" in pre- or postacicular fascicles, resembling the type D arrangement. However, in type A species, typically the chaetae are clearly positioned in their fascicles and are abundant (e.g. Glasby 1999: 124–125), whereas in type D their position sometimes is ambiguous and they are in low number (pp. 126–127). Based on revision of type material, here *Namalycastis intermedia* is stated as having type D arrangement instead of type A (Glasby 1999: 55). A similar analysis is required for *Namanereis pilbarensis* and *N. socotrensis*, both described with type C neurochaetae, although it can be advanced that *N. pilbarensis* has type D neurochaetae after the presence of "pseudospinigers" and that *N. socotrensis* has sub-acicular falcigers in preacicular fascicles; if not, additional new types or arrangement might be needed.

Jaws. The jaws of nereidids are formed by a cross-linked matrix of proteins, where the hardness and stiffness properties are due to the presence of high levels of glycine and histidine, halogens (especially chlorine) and zinc; the distribution of these elements is not homogeneous throughout jaw, but is more concentrated at the tip (Lichtenegger et al. 2003, Birkedal et al. 2006, Broomell et al. 2006, 2008), and this unequal distribution is presumably related to the pigmentation gradient from tip (darker) to base (lighter) (Khan et al. 2006). This tendency in distribution of elements is observed in other polychaetes and even in fossils, suggesting a functional significance (Eriksson and Elfman 2000), although direct corroboration in nereidids could not be possible due to their easy degradation (Colbath 1988). On the other hand, the jaws grow throughout worm's life, and this growth seems to be restricted to the basal section (Paxton 1980). This agrees with the ontogenetic development, where the terminal or 'primary' tooth is formed first, with subsequent addition of basal teeth (Bass and Brafield 1972, Tzetlin and Purschke 2005, Fischer et al. 2010).

It has been suggested that bifid jaws in stygobiont *Namanereis* are a derived condition from the typically serrated jaws in nereidids, implying that species with bifid jaws arise from other *Namanereis* or *Namalycastis* ancestor with serrated jaws (Glasby 1999: 23, Glasby et al. 2014: 32–33). There are some evidences supporting this hypothesis. All namanereidins have 'ensheathed' teeth, i.e., basal and most subterminal teeth are surrounded by a layer, always lighter than remaining jaw (e.g. Fig. 5I–K); this layer can be observed in other nereidids but it has been less frequently recorded (pers. obs.). In most cases, terminal and some subterminal teeth are not covered by the layer, and since the terminal teeth are formed first, it follows that the layer appears in later stages. Further, because this layer is lighter than remaining jaw, the ensheathed teeth can be seen when jaws are mounted for observation under light microscope, but from the surface teeth cannot not be seen. This clearly occurs in *N. tiriteae* (Winterbourn, 1969) that has several teeth observed by transparency, but show up as a smooth cutting edge on SEM photographs (Gray et al. 2009, Fig. 3), and in *N. stocki* Glasby, 1999 (Glasby 1999, Fig. 48b). Furthermore, some species as *N. socotrensis* Glasby, Fiege & Van Damme, 2014 have remnants of teeth, now fully covered and fused with the layer (Glasby et al. 2014, Fig. 6E).

Glasby et al. (2014: 32) proposed that bifid jaws are formed by sclerotization of subterminal teeth, leading to some likely scenarios of formation. Initially, the spaces among original teeth would be "filled" by growth of new layers of proteins, forming a continuous plate. This means that jaws with deeply incised, but ensheathed teeth, as *N. tiriteae* and *N. stocki* arise from another one with that kind of teeth, however there are no records about neither namanereidin nor even nereidid species with so sharp teeth. Also, it means that remnants of original teeth must be clearly visible in the plate as in the last two species, but this does not occur in most cases. Conversely, in the second scenario, the original teeth had an overgrowth and filled the spaces among them. If true, the resulting plate must have a similar pigmentation (and consistence) than the remnant jaw, but in fact, this plate is always lighter. Moreover, this scenario cannot explain the observed jaws in *N. tiriteae* and *N. stocki* with remnant ensheathed teeth.

Based upon these previous ideas, another plausible scenario leading to bifid jaws is a hypothetical reduction or loss of teeth (Fig. 7). In the first stage (Fig. 7A), the jaws have a fully dentate cutting edge, with an incipient, barely visible layer running along a few of the most-basal teeth; tips of teeth are rounded or near so, and barely separated from other adjacent teeth or having shallow incisions along the cutting edge. In subsequent stages, the layer continues developing by extending itself along other teeth, and by growing towards tips of teeth; first the layer becomes a slight cover between basal, adjacent teeth (Fig. 7B), and then the layer completely covers basal teeth (Fig. 7C). Simultaneously, during these two latter stages, the teeth start to reduce and become narrower, resulting in incisions along the cutting edge becoming deeper. Further growth of the layer would increase its extension, covering all teeth except the two distal ones, such that the jaw has a smooth cutting edge but with visible remnant teeth (Fig. 7D). The layer does not grow between the two most-distal teeth, perhaps due to the distance with the basal section and their hardness, or because of a more intense erosion. Either case, in the

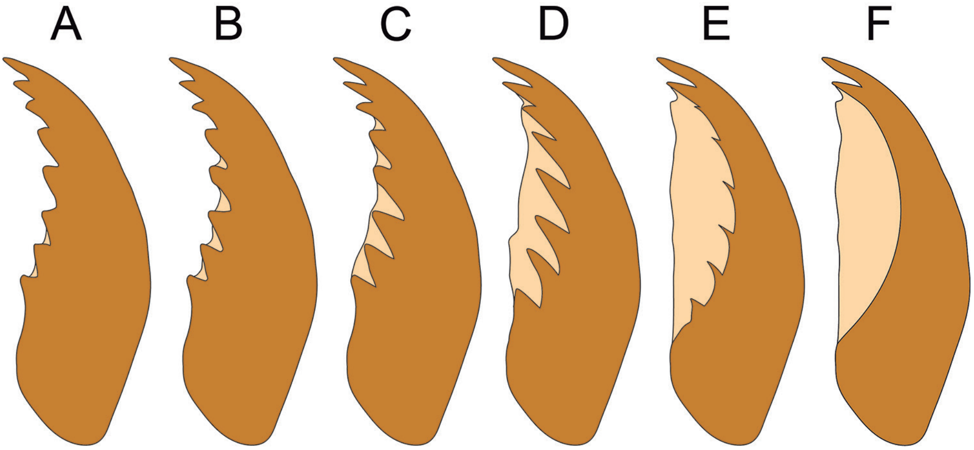

Figure 7. Proposed evolution of jaws in Namanereidinae. **A** Jaws with fully dentate cutting edge, layer almost inconspicuous in basal teeth **B** Layer increases their extension among basal teeth and reaches medial ones **C** Layer covers completely basal and medial teeth, and reaches subterminal ones **D** Teeth recede and become narrow, layer covers subterminal teeth excepting the last two **E** Just remnants of teeth are visible if any, layer increases its extension **F** Teeth fully replaced by the layer. Stages B and C in most *Namalycastis* species and *Namanereis* with serrated cutting edge; stage D as in *Namanereis stocki* and *N. tiriteae*; stage E as in *Namanereis socotrensis*; stage F as in *Namanereis* with bifid jaws and *Namalycastis occulta*.

final stages (Fig. 7E–F) most teeth progressively become into smaller, sharper structures, and then completely disappear, such that only the two distal teeth remain uncovered, giving a bifid appearance. The nature of the layer is uncertain, but it is expected to have a lower hardness compared with the tip and outer edge because both are darker.

Based on the literature already cited, *Namanereis* and *Namalycastis* include species in various stages along these hypothetical evolutionary stages. This pattern in jaw morphology has been explained as a shift towards deposit-feeding habits for shovelling (Glasby et al. 2014: 33), but an alternative hypothesis might be related to the scarcity of trace elements needed for hardening of the jaw, or the energetic cost expended in formation of jaws.

Glasby et al. (2014: 33) also proposed how namanereidins colonized brackish and freshwater habitats based on the jaws morphology. The marine ancestor of serrated-jaw *Namanereis* group reached epigean environments in the late Jurassic in a single event with subsequent speciation by vicariance, whereas the widely distributed, marine ancestor of bifid-jawed *Namanereis* group colonized semiterrestrial and groundwater environments in the Cretaceous in a second, independent event, implying that this last ancestor had serrated jaws as well (Glasby et al. 2014: 34). The hypothesis here proposed of jaws evolution is in full agreement with the proposed shift of jaws morphology, and more important, it does not restrict formation of bifid jaws to *Namanereis* species, so that any ancestral namanereidin with serrated jaws might derive into that type of jaw. Consequently, it is likely that some *Namalycastis* ventured into subterranean habitats and their jaws derived to bifid jaws, as in *N. occulta*.

Additional considerations. Although elongation of appendages is not restricted to stygobitic namanereidins, the bifid jaws and absence of eyes are the only features present in namanereidin species living in aphotic environments. Up to date, all bifid-jawed species are blind, whereas some blind species have serrated jaws. A possible explanation to the distribution of troglomorphic features among extant namanereidins is that such features appeared in their ancestors before reaching subterranean habitats, in intermediate habitats called superficial subterranean habitats (SSHs) (Culver and Pipan 2009a). Specifically, elongation of parapodial and chaetal appendages, even loss of body pigmentation, evolved in SSHs, whereas loss of eyes and bifid jaws evolved once species reached deeper caves. This reasoning fits well with the hypotheses by Glasby et al. (2014: 34) about colonization of subterranean realm, and also suggested for troglobitic opilions by Derkarabetian et al. (2010: 11).

However, the current epigean distribution of *Namalycastis occulta* in Yucatan Peninsula likely is due to a secondary invasion of those habitats. Most land of Yucatan Peninsula uplifted from Jurassic, but it was submerged from Upper Cretaceous through Eocene, and progressively emerged since Oligocene (López-Ramos 1975). During these events, shoreline changed along Cenozoic as well as the distribution of organisms occupying coastal environments, allowing them to reach the vast subterranean realm along Yucatan Peninsula. In this way, the hypothetical ancestor of *N. occulta* colonized coastal habitats such as mangroves, where likely it developed elongated appendages. After, during uplifting events, this ancestor was trapped and obligated to colonize the subterranean realm (Glasby et al. 2014). Once it reached caves, ancestor lost eyes and developed bifid jaws, and after reached coastal environments again by dispersion through subterranean flows seawards as it currently occurs (e.g. Gondwe et al. 2010). In this manner, epigean species such as *Namalycastis occulta* could gain elongation of appendages without living in caves but in aphotic environments, nor by being closely related to other *Namanereis* species with similar troglomorphies. What is more interesting here is to wonder why the other two species cohabiting with *N. occulta* in mangrove litter leaf, *Namanereis* cf. *amboinensis* and *Namalycastis borealis*, do not show these features. This could indicate a longer time of association to this aphotic environment by *N. occulta,* and a recent colonization by the other species.

Moreover, this also means that the use of troglomorphic features as evidence of phylogenetic affinity must be avoided since they could be convergent features, in disagreement with previous studies (Glasby 1999: 87, Alves and Santos 2016: 510). In his phylogenetic analysis including most namanereidins, Glasby (1999) obtained a clade that groups all eyeless namanereidins, that although the large number of trees obtained in the analysis, is was formed 94 (Nelson consensus) to 95 (50% majority rule consensus) percent of the times (Glasby 1999: 21–22). *Namanereis tiriteae* was the most basal species, having serrated jaws and cleft prostomium, followed by *N. beroni*, a species with serrated jaws as well but with entire prostomium. The group formed by Caribbean species was always recovered and supported by the character bifid jaws (Glasby 1999: 23); *N. serratis*, followed by *N. hummelincki*, both species with entire prostomium, were the sister of the most-derived, sister species in this clade, *N. stocki* and *N. minuta*, both species with four pairs of tentacular cirri and cleft prostomium. *N. cavernicola* had uncertain relationship with the later species, perhaps by their polymorphic character of cleft and entire prostomium associated to this species (Glasby 1999: 16, 83).

The use of some disregarded morphological features, as the number of tentacular cirri, could help to find better delimited groups. Chamberlin (1919: 196) proposed the genus *Namanereis* for *Lycastis quadraticeps* Blanchard *in* Gay, 1849, a namanereidin with four pairs of tentacular cirri. After, Augener (1922: 42) proposed the genus *Lycastopsis* for species with three pairs, a decision followed by other authors (Glasby 1999: 74). Hartman (1959: 162) suggested the synonymy of *Lycastopsis* with *Namanereis*; perhaps she thought *N. quadraticeps* had three pairs instead of four ones (Glasby 1999: 102). Further, Glasby (1999) obtained a clade containing species with four and three pairs, and therefore validating the suggestion by Hartman. In the same analysis, four pairs of tentacular cirri was regarded as a plesiomorphic character, that combined with the plesiomorphy presence of notochaetae, positioned *N. quadraticeps* as the most-basal species of *Namanereis* (Glasby 1999: 103). Interestingly, character four pairs of tentacular cirri appears again in *Namanereis stocki* and *N. minuta*, but they are positioned in the clade containing the most-derived *Namanereis* (Glasby 1999: 20). The number of tentacular cirri was not considered in the phylogenetic analysis by Alves and Santos (2016).

Among all nereidids, only some *Namanereis* species and *Lycastonereis indica* Rao, 1981 have three pairs of tentacular cirri (Rao 1981, Misra 1999). However, *Namanereis* and *Lycastonereis* are very different genera, just similar in the tendency to simplify their morphology (pers. obs.). We must wonder why the posteroventral pair of tentacular cirri has disappeared. The formation of tentacular cirri occurs in larval stages and following developmental programs distinct to postlarval stage, where the posteroventral pair is the last one to be developed (Kulakova et al. 2007, Fischer et al. 2010, Bakalenko et al. 2013). Consequently, a scenario where this later pair of cirri can appear and disappear selectively among congeneric species becomes very difficult to explain, even if it is supported by a phylogenetic analysis (Glasby 1999). As the number of tentacular cirri seems to be highly conservative among nereidids, its use as a diagnostic generic feature deserves a new evaluation.

Namalycastis occulta clearly resembles *Namanereis minuta* and *N. stocki* by having four pairs of tentacular cirri. Their main difference is the evident elongation of dorsal cirri toward posterior chaetigers and that it becomes flattened in the former species, whereas in the last species they are subequal and cirriform throughout body. Conde-Vela (2013: 481) argued about the elongation of dorsal cirri as part of diagnostic features of *Namalycastis*, but after the comparison made above, neither elongation is restricted to *Namalycastis* nor subequal dorsal cirri are distinctive for *Namanereis*. Based on this feature only, it is possible that 1) *Namanereis minuta* and *N. stocki* be *Namalycastis* as well as *N. occulta*, or 2) the former two species are more related to *Namanereis quadraticeps* than remaining *Namanereis* by having four pairs of tentacular cirri. Since foliose dorsal cirri are absent in both species, the second option is more likely, and if true, then genus *Lycastopsis* would be reinstated containing species with three pairs of tentacular cirri and *Namanereis* should be restricted for species having four pairs. Since the reinstatement of *Lycastopsis* and restriction of *Namanereis* is beyond the scope of this study, here the current classification was used.

If *Namalycastis occulta* is to be regarded as belonging into *Namanereis,* some problems could arise, as the mixture of current diagnostic features for both genera, exacerbating the problem of delimitation. Indeed, the elongation of appendages, bifid jaws and absence of pigmentation as stygobitic adaptations could explain the observed morphology, but could not account for the elongation and flattening of dorsal cirri towards the posterior body region only, as well as the elongation of sub-acicular, dorsalmost neurochaetae also matches this anterior-posterior gradient, both occurring in *Namalycastis* species as well (see above). It is true that *N. occulta* has not been recorded in cave environments yet, but other *Namanereis* species regarded as having stygobitic adaptations such as *N. hummelincki, N. serratis* Glasby, 1999 and *N. tiriteae* are in the same condition.

Of course, the most reliable way to test these and other hypotheses is through new phylogenetic analyses; however, there are some problems preventing it. As Glasby et al. (2014: 35) concluded, the inclusion of molecular evidence could reinforce or refuse several of these issues, mainly about what features are truly troglomorphies and which do not. However, there are no available specimens properly fixed for DNA extraction for most species, and there are few sequences available for a number of species, hindering to test morphology-based hypotheses at specific or generic levels (Alves and Santos 2016: 500). Even, if all appear to be troglomorphic, convergent features, it does not mean that they are not phylogenetically informative, but just that their use as diagnostic features or as signals of common ancestry must be avoided. Finally, an additional difficulty is how to code these features correctly; for example, some troglomorphic features were coded as "absent/present" in previous phylogenetic studies (Glasby 1999, Alves and Santos 2016), as the case for eyes, pigmentation and elongated falcigers, driving to mistaken statements (Fitzhugh 2008).

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References

Alves PR, Santos CSG (2016) Description of a new species of *Namalycastis* (Annelida: Nereididae: Namanereidinae) from the Brazilian coast with a phylogeny of the genus. Zootaxa 4144: 499–514. http://dx.doi.org/10.11646/zootaxa.4144.4.3

Augener H (1922) Ueber litorale Polychaeten von Westindien. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, Jahrgang 1922: 38–53.

Bakalenko NI, Novikova EL, Nesterenko Y, Kulakova MA (2013) Hox gene expression during postlarval development of the polychaete *Alitta virens*. EvoDevo 4: 1–17. http://dx.doi.org/10.1186/2041-9139-4-13

Bass NR, Brafield AE (1972) The life-cycle of the polychaete *Nereis virens*. Journal of the Marine Biological Association of the United Kingdom 52: 701–726. http://dx.doi.org/10.1017/S0025315400021664

Birkedal H, Khan RK, Slack N, Broomell CC, Lichtenegger HC, Zok FW, Stucky GD, Walton AS (2006) Halogenated Veneers: Protein cross-linking and halogenation in the jaws of *Nereis*, a marine polychaete worm. ChemBioChem 7: 1392–1399. http://dx.doi.org/10.1002/cbic.200600160

Bonyadi-Naeini A, Rahimian H, Glasby CJ (2016) A new substance to relax polychaete worms (Annelida) prior to morphological study. ZooKeys 594: 1–9. http://dx.doi.org/10.3897/zookeys.594.8061

Bouysse P (1984) The Lesser Antilles Island Arc: Structure and Geodynamic Evolution. In: Biju-Duval B, Moore JC, Bergen JA, Blackinton G, Claypool GE, Cowan DS, Davis D, Guerra RT, Hemleben CHJ, Marlow MS, Pudsey C, Renz GW, Tardy M, Wilson DS, Wright AW (Eds) Initial Reports of the Deep Sea Drilling Project, 78A. Initial Reports of the Deep Sea Drilling Project. U.S. Government Printing Office, 83–103. http://dx.doi.org/10.2973/dsdp.proc.78a.107.1984

Bouysse P, Westercamp D, Andreieff P (1990) The Lesser Antilles Island Arc. In: Mascle A, Moore JC, Taylor E, Underwood MB (Eds) Proceedings of the Ocean Drilling Program, Scientific Results. College Station, Texas (Ocean Drilling Program), 29–44. https://doi.org/10.2973/odp.proc.sr.110.166.1990

Broomell CC, Chase SF, Laue T, Walton AS (2008) Cutting edge structural protein from the jaws of *Nereis* virens. Biomacromolecules 9: 1669–1677. http://dx.doi.org/10.1021/bm800200a

Broomell CC, Mattoni MA, Zok FW, Walton AS (2006) Critical role of zinc in hardening of *Nereis* jaws. The Journal of Experimental Biology 209: 3219–3225. http://dx.doi.org/10.1242/jeb.02373

Chamberlin RV (1919) The Annelida Polychaeta of the *Albatross* Tropical Pacific Expedition, 1891-1905. Memoirs of the Museum of Comparative Zoology at Harvard College 48: 1–514.

Christiansen KA (1962) Proposition pour la classification des animaux cavernicoles. Spelunca 2: 75–78.

Colbath GK (1988) Taphonomy of recent polychaete jaws from Florida and Belize. Micropaleontology 34: 83–89. http://dx.doi.org/10.2307/1485613

Conde-Vela VM (2013) *Namalycastis occulta* n. sp. and a new record of *N. borealis* (Polychaeta: Nereididae: Namanereidinae) from the Northwestern Caribbean Sea. Zootaxa 3721: 475–487. http://dx.doi.org/10.11646/zootaxa.3721.5.3

Culver DC, Holsinger JR, Christman MC, Pipan T (2010) Morphological differences among eyeles amphipods in the genus *Stygobromus* dwelling in different subterranean habitats. Journal of Crustacean Biology 30: 68–74. http://dx.doi.org/10.1651/09-3156.1

Culver DC, Pipan T (2009a) Superficial subterranean habitats – gateway to the subterranean realm? Cave and Karst Science 35: 5–12.

Culver DC, Pipan T (2009b) The biology of caves and other subterranean habitats. Oxford University Press, New York, 254 pp.

Delić T, Trontelj P, Zakšek V, Fišer C (2016) Biotic and abiotic determinants of appendage length evolution in a cave amphipod. Journal of Zoology 299: 42–50. http://dx.doi.org/10.1111/jzo.12318

Derkarabetian S, Steinmann DB, Hedin M (2010) Repeated and time-correlated morphological convergence in cave-dweliing harvestmen (Opiliones, Laniatores) from Montane Western North America Fleischer RC (Ed.) Plos One 5: e10388. http://dx.doi.org/10.1371/journal.pone.0010388

Eriksson M, Elfman M (2000) Enrichment of metals in the jaws of fossil and extant polychaetes - distribution and function. Lethaia 33: 75–81. http://dx.doi.org/10.1080/00241160050150195

Fiege D, Van Damme K (2002) A new species of polychaete (Polychaeta: Nereididae: Namanereidinae) from the Socotra Archipelago, Yemen. Fauna of Arabia 19: 239–244.

Fischer AHL, Henrich T, Arendt D (2010) The normal development of *Platynereis dumerilii* (Nereididae, Annelida). Frontiers in Zoology 7: 1–39. http://dx.doi.org/10.1186/1742-9994-7-31

Fitzhugh K (2008) Clarifying the role of character loss in phylogenetic inference. Zoologica Scripta 37: 561–569. http://dx.doi.org/10.1111/j.1463-6409.2008.00338.x

Glasby CJ (1997) A new species of *Namanereis* (Polychaeta: Nereididae: Namanereididae) in Groundwater of the Sultanate of Oman, Arabian Peninsula. Beaufortia 47: 157–162.

Glasby CJ (1999) The Namanereidinae (Polychaeta: Nereididae). Part 1, Taxonomy and Phylogeny. Records of the Australian Museum, Supplement 25: 1–129. http://dx.doi.org/10.3853/j.0812-7387.25.1999.1354

Glasby CJ, Fiege D, Van Damme K (2014) Stygobiont polychaetes: notes on the morphology and the origins of groundwater *Namanereis* (Annelida: Nereididae: Namanereidinae), with a description of two new species. Zoological Journal of the Linnean Society 171: 22–37. http://dx.doi.org/10.1111/zoj.12130

Glasby CJ, Miura T, Nishi E, Junardi (2007) A new species of *Namalycastis* (Polychaeta: Nereididae: Namanereidinae) from the shores of South-east Asia. The Beagle, Records of the Museums and Art Galleries of the Northern Territory 23: 21–27.

Glasby CJ, Timm T (2008) Global diversity of polychaetes (Polychaeta; Annelida) in freshwater. Hydrobiologia 595: 107–115. http://dx.doi.org/10.1007/s10750-007-9008-2

Glasby CJ, Timm T, Muir AI (2009) Catalogue of non-marine Polychaeta (Annelida) of the World. Zootaxa 2070: 1–52.

Gondwe BRN, Lerer S, Stisen S, Marín L, Rebolledo-Vieyra M, Merediz-Alonso G, Bauer-Gottwein P (2010) Hydrogeology of the south-eastern Yucatan Peninsula: New insights from water level measurements, geochemistry, geophysics and remote sensing. Journal of Hydrology 389: 1–17. http://dx.doi.org/10.1016/j.jhydrol.2010.04.044

Gray DP, Harding JS, Winterbourn MJ (2009) *Namanereis tiriteae*, New Zealand's freshwater polychaete: new distribution records and review of biology. New Zealand Natural Sciences 34: 29–38.

Hartman O (1959) Capitellidae and Nereidae (Marine Annelids) from the Gulf side of Florida, with a review of freshwater Nereidae. Bulletin of Marine Science 9: 153–168.

Heads SW (2010) The first fossil spider cricket (Orthoptera: Gryllidae: Phalangopsinae): 20 million years of troglobiomorphosis or exaptation in the dark? Zoological Journal of the Linnean Society 158: 56–65. http://dx.doi.org/10.1111/j.1096-3642.2009.00587.x

Hesselberg T, Vincent (2006a) A comparative study of the functional morphology of parapodia and setae in nereids (Polychaeta: Nereididae). Animal Biology 56: 103–120. http://dx.doi.org/10.1163/157075606775904704

Hesselberg T, Vincent JFV (2006b) The function of parapodial setae in a nereidid polychaete moving on two different substrata. Journal of Experimental Marine Biology and Ecology 335: 235–244. http://dx.doi.org/10.1016/j.jembe.2006.03.008

Johnson HP (1903) Fresh-water nereids from the Pacific coast and Hawaii, with remarks on fresh-water Polychaeta in general. In: Mark Anniversary Volume. To Edward Laurens Mark, Hersey professor of anatomy and director of the zoölogical laboratory at Harvard university, in celebration of twenty-five years of successful work for the advancement of zoölogy from his former students, 1877–1902. Henry Holt & Co., New York, 205–222.

Khan RK, Stoimenov PK, Mates TE, Walton AS, Stucky GD (2006) Exploring gradients of halogens and Zinc in the surface and subsurface of *Nereis* jaws. Langmuir 22: 8465–8471. http://dx.doi.org/10.1021/la061027k

Konec M, Prevorčnik S, Sarbu SM, Verovnik R, Trontelj P (2015) Parallels between two geographically and ecologically disparate cave invasions by the same species, *Asellus aquaticus* (Isopoda, Crustacea). Journal of Evolutionary Biology 28: 864–875. http://dx.doi.org/10.1111/jeb.12610

Kulakova MA, Bakalenko NI, Novikova EL, Cook CE, Eliseeva E, Steinmetz PRH, Kostyuchenko RP, Dondua AK, Arendt D, Akam M, Addison JA (2007) Hox gene expression in larval development of the polychaetes *Nereis virens* and *Platynereis dumerilii* (Annelida, Lophotrochozoa). Development Genes and Evolution 217: 39–54. http://dx.doi.org/10.1007/s00427-006-0119-y

Lichtenegger HC, Schoberl T, Ruokolainen JT, Cross JO, Heald SM, Birkedal H, Walton AS, Stucky GD (2003) Zinc and mechanical prowess in the jaws of *Nereis*, a marine worm. Pan-American Journal of Aquatic Sciences 100: 9144–9149. http://dx.doi.org/10.1073/pnas.1632658100

Liu W, Golovatch S, Wesener T, Tian M (2017) Convergent evolution of unique morphological adaptations to a subterranean environment in cave millipedes (Diplopoda). Plos One 12: e0170717. http://dx.doi.org/10.1371/journal.pone.0170717

López-Ramos E (1975) Geological Summary of the Yucatan Peninsula. In: Nairn AEM, Stehli FG (Eds) The Gulf of Mexico and the Caribbean. Springer US, Boston, MA, 257–282. http://dx.doi.org/10.1007/978-1-4684-8535-6_7

Magesh M, Glasby CJ, Kvist S (2014) Redescription of *Namalycastis glasbyi* Fernando & Rajasekaran, 2007 (Annelida, Nereididae, Namanereidinae) from India. Proceedings of the Biological Society of Washington 127: 455–465. http://dx.doi.org/10.2988/0006-324x-127.3.455

Magesh M, Kvist S, Glasby CJ (2012) Description and phylogeny of *Namalycastis jaya* sp. n. (Polychaeta, Nereididae, Namanereidinae) from the southwest coast of India. ZooKeys 238: 31–43. http://dx.doi.org/10.3897/zookeys.238.4014

Merz RA, Edwards DR (1998) Jointed setae – their role in locomotion and gait transitions in polychaete worms. Journal of Experimental Marine Biology and Ecology 228: 273–290. http://dx.doi.org/10.1016/s0022-0981(98)00034-3

Misra A (1999) Polychaete. In: Ghosh AK (Ed.) State Fauna Series: Fauna of West Bengal, Part 10. Calcutta, 125–225.

Oliveira VM, Santos CSG, Lana PDC, Camargo M de G (2010) Morphological variations caused by fixation techniques may lead to taxonomic confusion in *Laeonereis* (Polychaeta: Nereididae). Zoologia 27: 146–150. http://dx.doi.org/10.1590/s1984-46702010000100022

Padilla y Sánchez RJ (2007) Evolución geológica del sureste mexicano desde el Mesozoico al presente en el contexto regional del Golfo de México. Boletín de la Sociedad Geológica Mexicana 59: 19–42.

Paxton H (1980) Jaw growth and replacement in Polychaeta. Journal of Natural History 14: 543–546. http://dx.doi.org/10.1080/00222938000770431

Pipan T, Culver DC (2012) Convergence and divergence in the subterranean realm: a reassessment. Biological Journal of the Linnean Society 107: 1–14. http://dx.doi.org/10.1111/j.1095-8312.2012.01964.x

Rao CAN (1981) On two polychaetes (Nereidae: Annelida) from estuarine waters of India. Bulletin of the Zoological Survey of India 3: 213–217.

Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42: 1549–1563. http://dx.doi.org/10.1080/00222930801995762

Solís-Weiss V, Espinasa L (1991) *Lycastilla cavernicola*, a new freshwater nereidid from an inland mexican cave (Polychaeta: Nereididae: Namanereidinae). Proceedings of the Biological Society of Washington 104: 631–639.

Tzetlin AB, Purschke G (2005) Phranyx and intestine. Hydrobiologia 535/536: 199–255. http://dx.doi.org/10.1007/s10750-004-1431-z

Wesenberg-Lund E (1958) Lesser Antillean polychaetes, chiefly from brackish water with a survey and a bibliography of fresh and brackish–water polychaetes. Studies on the Fauna of Curaçao and other Caribbean Islands 8: 1–41.

Wiens JJ, Chippindale PT, Hillis DM (2003) When are phylogenetic analyses misled by convergence? a case study in texas cave salamanders. Systematic Biology 52: 501–514. http://dx.doi.org/10.1080/10635150390218222