An assessment of the status of Polycirridae genera (Annelida: Terebelliformia) and evolutionary transformation series of characters within the family

KIRK FITZHUGH[1]*, JOÃO MIGUEL DE MATOS NOGUEIRA[2], ORLEMIR CARRERETTE[2] and PAT HUTCHINGS[3]

[1]*Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA*
[2]*Laboratório de Poliquetologia (LaPol), Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, n. 101, São Paulo 05508-900, SP, Brazil*
[3]*The Australian Museum Research Institute, Australian Museum, 6 College Street, Sydney 2010, NSW, Australia*

A phylogenetic analysis was performed to determine the monophyly of non-monotypic genera of the terebelliform family Polycirridae, i.e. *Polycirrus*, *Amaeana*, *Lysilla*, and *Hauchiella*, and the evolution of characters among members of this clade. The monotypic genera, *Enoplobranchus* and *Biremis*, were also included, together with members of both known species in *Hauchiella*. Representative species were included for remaining genera: 14 species of *Polycirrus*, six species of *Amaeana*, and six species of *Lysilla*. Out-groups consisted of representatives of Spionidae, Cirratulidae, and Sabellariidae, as well as several species of Telothelepodidae. A total of 40 in- and out-group species were coded for 50 subjects ('characters') and 117 subject–predicate relationships ('states'). Although results are consistent with recent phylogenetic studies within Terebelliformia that suggest Polycirridae monophyly, only *Hauchiella* was found to be monophyletic, albeit part of the more inclusive clade comprising remaining polycirrid genera. Evolutionary transformation series are discussed for selected characters in relation to the non-monophyly of *Polycirrus*, *Lysilla*, and *Amaeana*. Implications for the use of supraspecific taxa as 'taxonomic surrogates' are highlighted. The definition of Polycirridae is emended.

INTRODUCTION

The Polycirridae *sensu* Nogueira, Fitzhugh & Hutchings (2013) comprise a well-known group of polychaetes characterized by the absence of branchiae, presence of a circular upper lip, at least two types of buccal tentacles, and segment 2 distinctly narrower than the following segments, constricting the body posterior to the mouth, and separating the body into 'head' and 'trunk' regions. The trunk is further divided into an anterior part with paired ventrolateral glandular pads, frequently densely papillate, with pads within pairs separated by a mid-ventral groove extending posteriorly from segments 2 or 3, and a posterior region that only has neuropodia or is achaetous (Nogueira, Hutchings & Fukuda, 2010b; Nogueira *et al*., 2013).

The first polycirrid was described by Grube (1850), to which *Polycirrus medusa* Grube, 1850, refers. Malmgren (1866) formally recognized the more inclusive group, Polycirridea, and Hessle, 1917 changed the name to Polycirrinae. Subsequently, Polycirridae has been considered as a subfamily of Terebellidae (Fauvel, 1927; Day, 1967; Fauchald, 1977; Hutchings & Glasby,

Table 1. Comparisons of characters traditionally used to determine Polycirridae genera

Genus	(a) Notopodia/(b) Notochaetae	(c) Neuropodia/(d) Neurochaetae
Amaeana	(a) Anterior segments	(c) Posterior segments
	(b) Nearly alimbate, winged	(d) Acicular spines
Biremis (monotypic)	(a) Absent	(c) Bilobed, starting segment 15
	(b) Absent	(d) Uncini
Enoplobranchus (monotypic)	(a) Anterior to posterior segments, branched, except for anterior and posteriormost notopodia	(c) Absent
	(b) Pinnate	(d) Absent
Hauchiella	(a) Absent	(c) Absent
	(b) Absent	(d) Absent
Lysilla	(a) Anterior segments	(c) Absent
	(b) Pinnate or nearly alimbate, winged	(d) Absent
Polycirrus	(a) Anterior to mid-body segments	(c) Variable distribution
	(b) Pinnate and/or winged	(d) Uncini

1986a; Colgan, Hutchings & Brown, 2001; Glasby, Hutchings & Hall, 2004; Garraffoni & Lana, 2008; Nogueira *et al*., 2010b), but recently Nogueira *et al*. (2013) raised it to familial level as a consequence of an extensive phylogenetic analysis of Terebelliformia.

Polycirridae contains six genera: *Amaeana* Hartman, 1959; *Biremis* Polloni, Rowe & Teal, 1973; *Enoplobranchus* Webster, 1879; *Hauchiella* Levinsen, 1893; *Lysilla* Malmgren, 1866; and *Polycirrus* Grube, 1850. Of these, *Biremis* and *Enoplobranchus* are monotypic; *Polycirrus* is the most diverse, with 59 known species, followed by *Lysilla* with 17, *Amaeana* with seven, and *Hauchiella* with two species. The morphological characters distinguishing members of these genera are well established in the literature (Table 1). *Polycirrus* has been defined by the presence of notopodia for a limited number of anterior segments, sometimes extending to mid-body, and neuropodia bearing avicular uncini. Neuropodia are absent among members of *Enoplobranchus* and *Lysilla*: members of *Enoplobranchus* have conical notopodia on anterior and posterior parapodia, and branching notopodia on mid-body chaetigers, whereas members of *Lysilla* have bilobed notopodia on some anterior segments only. Members of *Hauchiella* lack both noto- and neuropodia, members of *Biremis* have bilobed neuropodia with avicular uncini and notopodia absent, and members of *Amaeana* have notopodia on a limited number of anterior chaetigers and neuropodia with acicular spines beginning some segments after notopodia terminate. Neither the monophyly of non-monotypic genera nor the phylogenetic relationships, inclusive of the evolutionary transformation series of characters, have been rigorously investigated within this group, however.

Polycirrid monophyly has been empirically recognized in recent phylogenetic analyses on terebelliforms (Colgan *et al*., 2001; Glasby *et al*., 2004; Garraffoni & Lana, 2008; Nogueira *et al*., 2013). Most of these studies considered polycirrids as derived terebellids (Colgan *et al*., 2001; Glasby *et al*., 2004; Garraffoni & Lana, 2008). In the most comprehensive phylogenetic analysis of Terebelliformia to date, Nogueira *et al*. (2013) found polycirrids to be the most plesiomorphic clade of Terebelliformia (Fig. 1). This study was consistent with previous works in recognizing the monophyly of Terebelliformia, but found that clades commonly regarded as subfamilies of Terebellidae required elevation to familial rank (Fig. 1). An additional family, Telothelepodidae, previously considered as part of the Thelepodinae, was required to accommodate individuals with a narrow and elongate upper lip.

In the present study we investigate phylogenetic relationships within the Polycirridae. The principle goals are to determine the status of monophyly among non-monotypic genera and present some of the evolutionary transformation series of polycirrid characters. Consistent with the analysis by Nogueira *et al*. (2013), data comprised morphological characters. The availability of polycirrid DNA sequence data is currently too limited and lacking in reliable coordination with species hypotheses inferred from morphological data to be considered here (cf. Nogueira *et al*., 2013; Fitzhugh, 2014, and literature cited therein regarding the treatment of observations relative to the requirement of total evidence).

MATERIAL AND METHODS

SPECIMENS EXAMINED

Most material was examined during visits to the following institutions: Australian Museum (AM), Sydney, Australia; Museum and Art Gallery of Northern Territory (MAGNT) (NTM), Darwin, Australia; Museum Victoria (MV), Melbourne, Australia; Natural History Museum of Los Angeles County (NHMLAC), Los
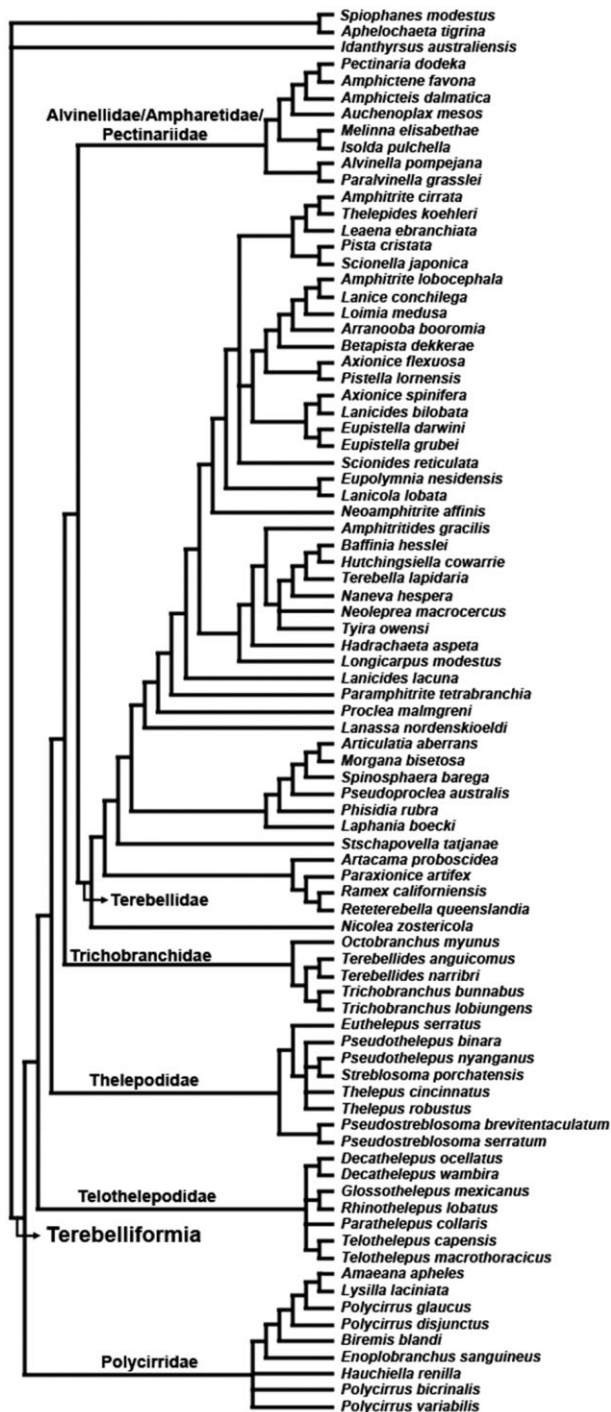
Figure 1. Strict consensus tree from Nogueira *et al*. (2013: fig. 21), indicating phylogenetic relationships among Terebelliformia family-level clades.

Angeles, USA; US National Museum (USNM), Smithsonian Institution, Washington DC, USA; and Yale Peabody Museum (YPM), New Haven, USA. The following museums sent material to be examined at the

AM, the NHMLAC, or the Instituto de Biociências, Universidade de São Paulo (IB-USP) (Table 2): IBUFRJ, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (IB-UFRJ); MZUSP, Museu de Zoologia da Universidade de São Paulo; NHM, Natural History Museum, London, UK; USNM, United States National Museum, Smithsonian Institution, USA; ZMO, Zoologisk Museum, Oslo, Norway; ZMUC, Zoological Museum of the University of Copenhagen (Zoologisk Museum, Københavns Universitet), Copenhagen, Denmark.

Specimens were studied using stereomicroscopes. Notochaetae and small portions of uncini-bearing tori were removed, mounted on slides with polyvinyl-lactophenol (PVLP), and examined using compound microscopes. For examination by scanning electron microscopy (SEM), one or two specimens of some species were critical-point dried, sputter-coated with gold, and examined at the SEM Laboratory, The Australian Museum (AM), Laboratório de Microscopia Eletrônica, IB-USP, and Laboratório de Microscopia Eletrônica, Museu de Zoologia, Universidade de São Paulo (MZUSP). In most instances, specimens prepared for SEM were paratypes, but in some cases non-type specimens were used.

Specimen descriptions were compiled for each available species, and representatives, usually types, of all species were photographed using a stereomicroscope. Noto- and neurochaetae from different regions of the body were mounted and photographed for members of each species, when present. All photographs were edited with Adobe PHOTOSHOP CS.

The nomenclature adopted follows that used by Hutchings & Glasby (1986a, b, 1987) and Glasby & Hutchings (2014), with slight modifications, especially with regards to anterior end characters, as discussed by Nogueira *et al*. (2010b) and Nogueira *et al*. (2013).

OUT-GROUP AND IN-GROUP TAXA

A total of 40 species were considered.

Out-groups

Spionidae
Spiophanes modestus Meissner & Hutchings, 2003

Cirratulidae
Aphelochaeta tigrina Blake, 1996

Sabellariidae
Idanthyrsus australiensis (Haswell, 1883)

Telothelepodidae Nogueira *et al*., 2013

Decathelepus ocellatus Hutchings, 1977
Decathelepus wambira Nogueira & Hutchings, 2007

Table 2. List of material examined for the present study

Taxon	Authorities	Type locality	Collection numbers (status)
Polycirridae			
Amaeana antipoda	(Augener, 1926)	Littelton, New Zealand	Non-types: AM W27469 – King Point, East Lewis Island, Western Australia, Australia; AM W21871, AM W21872 – NW Kurumba, Gulf of Carpentaria, Australia.
Amaeana apheles	(Hutchings, 1974)	South of Yahoo Island (32°17′S, 152°29′E), New South Wales, Australia	Holotype: AM W5239. Paratypes: AM W5237, AM W5238. Non-types: AM W5384, AM W29203 – Kangaroo Island (25°26′S, 152°53′E), Queensland, Australia; AM W10864 – Nerang River (28°6′S 153°18′E) – Queensland, Australia.
Amaeana trilobata	(Sars, 1863)	Slåttholmen i Lofoten, Norway	ZMO C3207, ZMO C3208 – Slåttholmen i Lofoten, Norway.
Amaeana yirrarn	Hutchings, 1997	West Bay, Port Essington (11°16′S 132°09′E) – Western Australia, Australia	Paratype: AM W21888.
Amaeana sp. Brazil	–	–	Undescribed: MZUSP 2349 – Campos Basin (22°11′27″S, 40°55′30″W), Rio de Janeiro, Brazil.
Amaeana sp. Lizard	–	–	Undescribed: AM W46526 – Lizard Island, Great Barrier Reef, Queensland, Australia.
Biremis blandi	Polloni, Rowe & Teal, 1973	Tongue of the Ocean, New Providence Island, Bassau, Bahamas	Holotype: USNM 47976. Paratypes: USNM 170580, USNM 170581.
Enoplobranchus sanguineus	(Verrill, 1873)	Harbour to New Haven and Vineyard Sound – north-east coast of the USA	Syntypes: YPM 181-2, YPM 890, YPM 2723, YPM 40568-70.
Hauchiella renilla	Hutchings & Glasby, 1986	Wreck Bay (35°10′S, 150°41′E) – Australian Capital Territory, Australia	Holotype: AM W199607. Paratypes: AM W199608, AM W199610-11, AM W199614.
Hauchiella tribullata	(McIntosh, 1869)	Off St Magnus Bay, Shetland, UK	Holotype: NHM 1921.5.1.4120.
Lysilla bilobata	Hutchings & Glasby, 1986	Woolooware Bay, Georges River (33°05′S, 151°06′E) – New South Wales, Australia	Holotype: AM W7586. Paratypes: AM W12429, AM W13963, AM W18947, AM W195466, AM W199531, AM W199514.
Lysilla jennacubinae	Hutchings & Glasby, 1986	Caloundra (26°48′S, 153°08′E) – Queensland, Australia	Holotype: AM W199643. Paratype: AM W199644.
Lysilla laciniata	Hutchings & Glasby, 1986	Coffin Bay (34°28′S, 135°19′E) – South Australia, Australia	Holotype: AM W199626. Paratype: AM W199627. Non-types: AM W202415, AM W202416, AM W202417 – Port Pirie, Spencer Gulf (33°12′S, 137°55′E), South Australia, Australia.
Lysilla loveni	Malmgren, 1866	Atlantic Ocean, Sweden	Non-types: AM W9143, USNM 49637 – Massachusetts, Cape Cod Bay (41.956°N, 70.321°W) – USA.
Lysilla macintoshi	Gravier, 1907	Port Charcot, Antarctic Ocean, Antarctic	Non-type: USNM 47147 – Weddell Sea, 77°36.2′S, 42°30′W, Antarctica.
Lysilla pacifica	Hessle, 1917	Pacific Ocean, Bonin Islands, Japan	Non-types: AM W5219 – Carama Creek, New South Wales, Australia, AM W 199619 – Wallis Lake, New South Wales, Australia, AM W12290 – Towra Pt. Botany Bay, New South Wales, Australia, AM W199622 – Botany Bay, New South Wales, Australia.
Polycirrus abrolhensis	Garraffoni & Costa, 2003	Abrolhos Archipelago (17°58′44″S, 38°42′41″W), Bahia	Holotype: IBUFRJ–0481. Paratype: IBUFRJ 0482.
Polycirrus bicrinalis	Hutchings & Glasby, 1986	Lizard Island (14°40′S, 141°28′E), Queensland, Australia	Holotype: AM W199637. Paratypes: AM W199638, AM W199639, AM W199640.
Polycirrus breviuncinatus	Carrerette & Nogueira, 2013	Campos Basin (22°3′37″S 40°24′15″W), Rio de Janeiro, Brazil	Holotype: MZUSP 1220. Paratypes: MZUSP 1245, ZUEC 11816.
Polycirrus disjunctus	Hutchings & Glasby, 1986	Solitary Island (29°56′S, 153°25′E), New South Wales, Australia	Holotype: AM W199632. Paratypes: AM W199633, AM W199634.
Polycirrus glaucus	Hutchings, 1993	Rottnest Island (31°58′24″S, 115°31′48″E), Western Australia, Australia	Holotype: AM W20937. Paratype: AM W20966
Polycirrus "clavatus"	Carrerette & Nogueira, 2013	Campos Basin (21°56′7″S, 39°57′51″W), Rio de Janeiro, Brazil	Holotype: MZUSP 1221. Paratype: MZUSP 1246.
Polycirrus nonatoi	Carrerette & Nogueira, 2013	Campos Basin (23°12′4″S, 40°59′41″W), Rio de Janeiro, Brazil	Holotype: MZUSP 1213. Paratypes: MZUSP 1214, MZUSP 1215, MZUSP 1243, LACM-AHF Poly 4983, LACM-AHF Poly 4984, ZUEC 11811, ZUEC 11812, ZUEC 11813, USNM 1195838, USNM 1195839.
Polycirrus octosetus	(Hutchings, 1977)	Moreton Bay Serpentine Creek, (27°24′S, 153°7′E), Queensland, Australia	Holotype: AM W6852. Paratype: AM W8127.
Polycirrus paivai	Garraffoni & Costa, 2003	Abrolhos Archipelago (17°58′44″S, 38°42′41″W), Brazil	Holotype: IBUFRJ-0484. Paratype: IBUFRJ-0486
Polycirrus papillosus	Carrerette & Nogueira, 2013	Campos Basin (21°42′33″S, 40°9′5″W), State of Rio de Janeiro, Brazil	Holotype: MZUSP 1216. Paratypes: MZUSP 1217, MZUSP 1244.
Polycirrus parvus	Hutchings & Glasby, 1986	North West Shelf (20°1′12″S, 116°57′36″E), Western Australia, Australia	Holotype: AM W199628. Paratype: AM W199630.
Polycirrus variabilis	Hutchings & Glasby, 1986	Lizard Island (14°40′S, 141°28′E), Queensland, Australia	Holotype: AM W199538. Paratypes: AM W199477, AM W199539-41, AM W199543-4. Non-types: AM W199479, AM W199481 – Lizard Island (14°40′S, 145°27′E), Queensland, Australia.
Polycirrus sp. Brazil	–	–	Undescribed: MZUSP 2350 – Praia de São Francisco (23°44′S, 45°24′W), São Paulo, Brazil

Glossothelepus mexicanus Hutchings & Glasby, 1986
Parathelepus collaris (Southern, 1914)
Rhinothelepus lobatus Hutchings, 1974
Telothelepus capensis Day, 1955
Telothelepus macrothoracicus Mohammad, 1980

In-group
Polycirridae Malmgren, 1866

Amaeana (six species)
Biremis blandi Polloni, Rowe & Teal, 1973 (monotypic)
Enoplobranchus sanguineus Verrill, 1873 (monotypic)
Hauchiella (two species)
Lysilla (six species)
Polycirrus (14 species)

Out-groups were determined on the basis of phylogenetic relationships among members of Terebelliformia obtained in the study by Nogueira *et al.* (2013). Those relationships are as follows: (Polycirridae (Telothelepodidae (Thelepodidae (Trichobranchidae (Terebellidae (Alvinellidae – Ampharetidae – Pectinariidae)))))) (Fig. 1). Because of the placement of the Polycirridae, the relevant out-groups are the same as those used by Nogueira *et al.* (2013), i.e. *Spiophanes modestus*, *Aphelochaeta tigrina*, and *Idanthyrsus australiensis*. The family Telothelepodidae was also included, given that it is the nearest terebelliform sister group to Polycirridae (Fig. 1).

As one of the objectives of this study was to investigate the monophyly of non-monotypic Polycirridae genera, the ideal condition would be the inclusion of data from members of all available species. As it was not feasible to make the present study as comprehensive, the species included were regarded as sufficient to address the issue of monophyly.

CHARACTER DATA

A total of 117 characters, among 50 subjects (colloquially but incorrectly referred to as 'states' and 'characters,' respectively; cf. Fitzhugh, 2006a, 2008a) were included (Table 3). The characters, *qua* subject–predicate relationships, observed among members of the 40 species are presented in Table 4. Except for *Aphelochaeta tigrina*, which was coded from the literature (Blake, 1996), and *Polycirrus medusa*, which was based on Glasby & Hutchings' (2014) description of the neotype, all characters were coded from observations of specimens, and in most cases type material or material from or near the corresponding type localities. Three undescribed species are included in the analysis (Table 2); specimens examined for the present study will be designated as types when those descriptions are formally published. A number of these characters were included by Nogueira *et al.* (2013) for the more comprehensive phylogenetic analysis of family-level relationships in Terebelliformia. As the present study is of more limited scope, modifications of some characters were necessary, together with the addition of new ones. Thus, descriptions of all characters are provided here.

1. General shape of body (subject 1): Terebelliforms have a body divided into a wider anterior region that tapers to a cylindrical posterior region. The transition between regions is usually characterized by termination of notopodia, but this is not always the case. The use of the terms 'thorax' and 'abdomen' has been associated in the literature with the termination of notopodia (Nogueira *et al.*, 2010b). Thus, in cases in which notopodia distribution and body-shape demarcation do not occur at same segment, i.e. taxa with few pairs of notopodia or with notopodia extending posteriorly, the names 'thorax' and 'abdomen' refer to the distribution of notopodia instead of body shape. Although the numbers of pairs of notopodia are variable within the family, the general shape of the body among polycirrids is the same as other terebelliforms, with a wider anterior region and tapering, almost uniformly cylindrical, posterior region [character 1(1); Figs 2A–I, 3, 4, 5A–C]. Nogueira *et al.* (2013) distinguished between body regions on the basis of notopodia distribution, as has been traditional for the group, but the present study treats body shape more specifically. Members of *Glossothelepus mexicanus* are only known from incomplete specimens, so overall body shape is currently unknown. Members of non-terebelliform out-groups have bodies that are more uniformly cylindrical throughout [character 1(0)].

Anterior end characters: prostomium and peristomium (subjects 2–16)
The prostomial and peristomial characters in this study follow Nogueira *et al.* (2013), although with some differences, as discussed below. The names 'tentacular membrane' or 'tentacular lobes' have been widely used in the literature, including recent papers (Holthe, 1986; Hutchings & Glasby 1986a, b; Glasby & Hutchings, 2014); however, as discussed by Nogueira *et al.*, 2010b), that name actually refers to two different structures, the upper lip and the prostomium, attached to the dorsal surface of the lip. For this reason we prefer to treat each of those structures separately in the present paper.

Zhadan & Tzetlin (2002) considered the prostomium of Terebellidae *s.l.* and Trichobranchidae as fused to the peristomium and indistinguishable in adults, and the 'zone of tentacular attachment' at the base of the upper lip as peristomial; however, as discussed by Nogueira *et al.*, 2010b) and Nogueira *et al.* (2013), we disagree with that opinion because, although this 'zone of tentacular attachment' is fused to the dorsal surface of the upper lip, it is clearly a region distinct from the

Table 3. Character matrix

	1 0	2 0	3 0	4 0	5 0
Outgroup taxa:					
Spiophanes modestus	00–010–0—	00–1–11000	0—0–0—02	42000–2010	10————0
Aphelochaeta tigrina	00–000–0—	00–1–10000	0—0–0—02	42000–20–0	–0————0
Idanthyrsus australiensis	00–010–0—	00–1–00000	0—0–0—02	42000–22–2	–0————0
Decathelepus ocellatus	110111110–	1100202001	11–1110002	01100–0111	110100110?
Decathelepus wambira	110110–10–	1100202001	11–110—02	01100–0111	110100110?
Glossothelepus mexicanus	?101011111	1100000101	11–1?10002	01100–0111	111100110?
Parathelepus collaris	110110–10–	1100212001	11–110—02	01100–0111	111100120?
Rhinothelepus lobatus	110111110–	1100011101	11–1110102	01100–0111	111100110?
Telothelepus capensis	1101011111	1100210001	11–1110102	31100–0111	1111001100
Telothelepus macrothoracicus	110101110–	1100210001	11–1110102	31100–0111	110100110?
Ingroup taxa:					
Amaeana antipoda	1101010111	1110105010	1011012202	2001101101	02————1
Amaeana apheles	1101010110	1110100010	1011012202	2001101101	02————1
Amaeana trilobata	1101010111	1110105010	1011012202	2001101101	02————?
Amaeana yirrarn	1101010110	1110100010	1011012202	2001101101	02————?
Amaeana sp. Brazil	110100–110	1110100010	1011012202	2001101101	02————?
Amaeana sp. Lizard	110100–110	1110105010	1011011202	2001101101	02————?
Biremis blandi	111100–111	1110200010	1001010101	—————	–100000010
Enoplobranchus sanguineus	111100–111	1110102010	100100—00	–1010–22–2	————1
Hauchiella renilla	110100–111	1110203010	101100—1–	—————	————1
Hauchiella tribullata	111100–111	1110203010	101101021–	—————	————?
Lysilla bilobata	1101010111	1110100010	1011011200	–0011012–2	————1
Lysilla jennacubinae	110100–11?	1110100010	1011012200	–001101101	0————1
Lysilla laciniata	1101010111	1110100010	1011012200	–0011012–2	————1
Lysilla loveni	110100–111	1110105010	101100—00	–001101101	0————?
Lysilla macintoshi	110100–111	1110105010	1011012200	–0011012–2	————?
Lysilla pacifica	1101010110	1110100010	1011012200	–0011012–2	————1
Polycirrus abrolhensis	110100–111	1110105010	1001011202	01011012–2	–110110011
Polycirrus bicrinalis	110100–111	1110200010	101100—02	31011112–1	1100000010
Polycirrus breviuncinatus	110100–111	1110203010	100100—02	1101101111	110000001?
Polycirrus disjunctus	110100–111	1110100010	1001011202	30011012–2	–110110010
Polycirrus glaucus	110100–111	1110100010	1001012202	30011012–2	–110110011
Polycirrus "clavatus"	110100–111	1110100010	1011011202	01011012–2	–110110011
Polycirrus medusa	110100–111	1110100010	1001010202	30011112–1	1100000010
Polycirrus nonatoi	111100–111	1110203010	1011011202	31011112–1	1100000011
Polycirrus octosetus	111100–111	1110202010	1001012202	2001111111	1110110011
Polycirrus paivai	111100–111	1110100010	1001011202	10011112–1	1100000011
Polycirrus papillosus	111100–111	1110100010	101100—02	30011012–1	1100000011
Polycirrus parvus	110100–111	1110203010	100100—02	3001111111	110000001?
Polycirrus variabilis	111100–111	1110100010	101100—02	3101101111	1100000011
Polycirrus sp. Brazil	111100–111	1110203010	10010?—02	01011112–1	1100000010

See text for a discussion of outgroup and ingroup taxa, and character descriptions (cf. Table 4); –, inapplicable; ?, unknown.

lip, frequently bearing eyespots (absent among polycirrids), which are considered prostomial in origin among members of several other Terebelliformia families, and nuchal organs are present among members of some species in which the peristomium extends dorsally, such as several telothelepodids and thelepodids.

As also discussed by Nogueira *et al.*, 2010b) and Nogueira *et al.* (2013), the eyespots frequently found among members of several families of Terebelliformia are located at the basal part of prostomium, and are therefore of prostomial origin, instead of peristomial, as stated by some authors.

Table 4. Characters, as subject–predicate relationships (often incorrectly referred to as 'characters' and 'states,' cf. Fitzhugh, 2006a, 2008a) used in the present study

1. General shape of body:
   (0) uniformly cylindrical
   (1) anterior end widest, then tapering to cylindrical, tapering posterior end
2. Location of prostomium:
   (0) mid-dorsal (Spionidae, Sabellariidae) or anterior to (Cirratulidae) peristomium
   (1) transverse across dorsal surface of peristomium (upper lip)
3. Transverse prostomium [cf. character 2(1)]:
   (0) restricted to base of upper lip
   (1) extending to near anterior margin of upper lip
4. Prostomium:
   (0) entire, undivided
   (1) distinct basal and distal parts
5. Prostomial eyespots:
   (0) absent
   (1) present
6. Mid-dorsal process on anterior margin of prostomium:
   (0) absent
   (1) present
7. Length of mid-dorsal process on anterior margin of prostomium [cf. character 6(1)]:
   (0) short
   (1) elongate
8. Prostomial buccal tentacles:
   (0) absent
   (1) present
9. Prostomial buccal tentacles shape [cf. character 8(1)]:
   (0) all similar
   (1) at least two types
10. Distal ends of longest buccal tentacles among individuals with two types [cf. character 9(1)]:
    (0) expanded
    (1) spatulate
11. Peristomial palps:
    (0) present
    (1) absent
12. Anterior margin of mouth:
    (0) low ridge
    (1) distinct tissue extension ('upper lip')
13. Large upper lip shape [cf. character 12(1)]:
    (0) elongate, narrow
    (1) circular
14. Lower lip shape:
    (0) expanded
    (1) low ridge
15. Expanded lower lip [cf. character 14(0)]:
    (0) segment like
    (1) rounded, mid/ventral
    (2) cushion like, across ventrum
16. Peristomium composition:
    (0) restricted to lips
    (1) lips and complete annulation
17. Visibility of segment 1:
    (0) all around body
    (1) laterally/ventrally
    (2) laterally/dorsally
    (3) dorsally
    (4) ventrally
    (5) dorsally/ventrally

Table 4. *Continued*

18. Segment 2:
    (0) complete ring
    (1) incomplete ring
19. Segment-2 width:
    (0) same as adjacent segments
    (1) distinctly narrower than adjacent segments
20. Segmental branchiae:
    (0) absent
    (1) present
21. Ventral surfaces of anterior segments:
    (0) similar to more posterior segments or slightly glandular
    (1) strongly glandular
22. Glandular ventral surfaces of anterior segments [cf. character 21(1)]:
    (0) discrete paired ventrolateral pads
    (1) entire surface distinctly glandular
23. Paired glandular ventrolateral pads surfaces [cf. character 22(0)]:
    (0) lightly papillate
    (1) densely papillate
24. Mid-ventral groove:
    (0) absent
    (1) present
25. Distribution of mid-ventral groove [cf. character 24(1)]:
    (0) near anterior end (segments 2–5) to pygidium
    (1) posterior region with notopodia to pygidium
26. Nephridial/genital papillae:
    (0) absent
    (1) present
27. Genital papillae distribution [cf. character 26(1)]:
    (0) some anterior segments (up to segment 11) of region with notopodia
    (1) terminating well before termination of notopodia
    (2) extending to end (or close to) of region with notopodia
28. Genital papillae position [cf. characters 26(1), 27(0–2)]:
    (0) posterodorsal/lateral to notopodia
    (1) posteroventral to notopodia
    (2) anterior to and at bases of notopodia
29. Lateral body margins:
    (0) with parapodia
    (1) similar to dorsal and ventral margins, i.e. parapodia absent
30. Parapodia [cf. character 29(0)]:
    (0) only notopodia
    (1) only neuropodia
    (2) noto- and neuropodia
31. Start of neuropodia relative to notopodia [cf. character 30(2)]:
    (0) anterior segments (up to segment 11) of region with notopodia
    (1) posterior region with notopodia
    (2) at least three segments after notopodia terminate
    (3) first or second segment after notopodia terminate
    (4) chaetiger 1
32. Number of pairs of notopodia [cf. characters 30(0), 30(2)]:
    (0) up to 10–12
    (1) extending to mid-body, terminating well before pygidium
    (2) present throughout
33. Anterior notopodia origin [cf. character 32(0)]:
    (0) laterally on segments
    (1) dorsolateral on segments
34. Notopodia shape [cf. characters 30(0), 30(2)]:
    (0) short
    (1) elongate

Table 4. *Continued*

35. Distal ends of notopodia [cf. characters 30(0), 30(2)]:
    (0) conical
    (1) bilobed
36. Relative lengths of pre/ and postchaetal notopodial lobes of elongate notopodia [cf. character 35(1)]:
    (0) same length
    (1) postchaetal lobes longer than prechaetal lobes
37. Notochaetae origin from notopodium [cf. characters 30(0), 30(2)]:
    (0) central core
    (1) between notopodial lobes
    (2) general region on top of notopodia or notopodial branches
38. Type of notochaetae in anterior rows:
    (0) alimbate
    (1) winged
    (2) pinnate
39. Width of wings of winged notochaetae in anterior rows [cf. character 38(1)]:
    (0) narrow
    (1) wide
40. Type of notochaetae in posterior rows:
    (0) alimbate
    (1) winged
    (2) pinnate
41. Width of wings of winged notochaetae in posterior rows [cf. character 40(1)]:
    (0) narrow
    (1) wide
42. Neurochaetae:
    (0) slender or capilliform
    (1) avicular uncini
    (2) tapering spines
43. General dimensions of anterior body avicular uncini [cf. character 42(1)]:
    (0) longer than high
    (1) as high as long
44. Width of neuropodial avicular uncinus base [cf. character 42(1)]:
    (0) narrow
    (1) wide
45. Heel length of neuropodial avicular uncini [cf. character 42(1)]:
    (0) short
    (1) elongate
46. Heel orientation [cf. subject 42(1)]:
    (0) directed posteriorly
    (1) directed downward
47. Inferior margin of neuropodial avicular uncinus base [cf. character 42(1)]:
    (0) nearly straight
    (1) slightly curved
48. Position of neuropodial uncinus dorsal button (in relation to main fang or most proximal tooth and tip of prow) [cf. character 42(1)]:
    (0) distal third
    (1) proximal third
    (2) middle third
49. Neuropodial avicular uncinus prow length [cf. character 41(1)]:
    (0) short
    (1) conspicuous, long
50. Pygidium:
    (0) smooth to crenulate
    (1) papillate
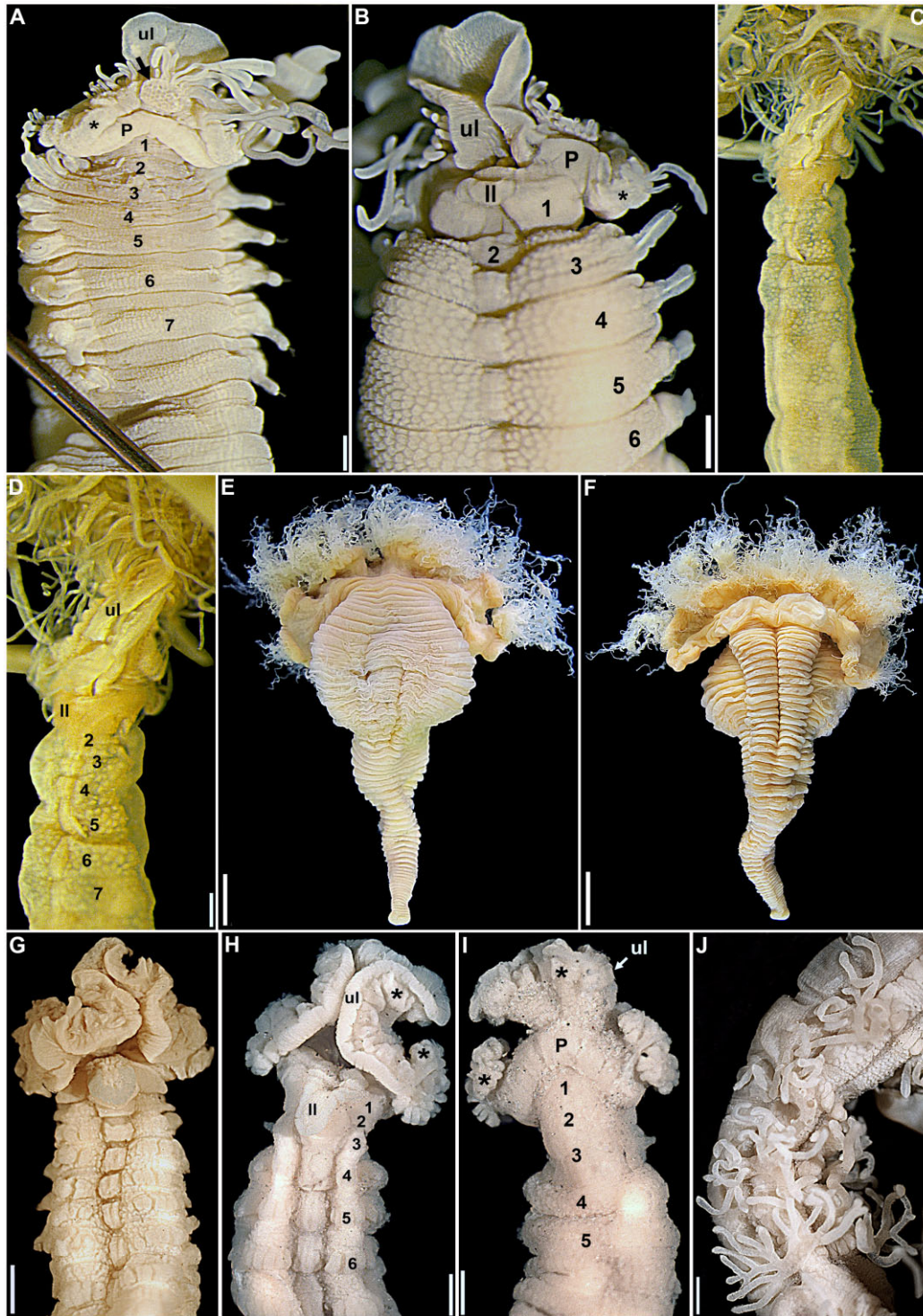
Figure 2. *Amaeana apheles* (holotype, AM W5239): A, anterior end, dorsal view; arrow points to prostomial mid-dorsal process; B, anterior end, ventral view. *Hauchiella renilla* (holotype, AM W199607): C, D, progressively closer ventral views of anterior end. *Biremis blandi* (holotype, USNM 47976): E, F, entire worm, ventral and dorsal views, respectively. *Enoplobranchus sanguineus*: G (syntype, YPM 40569), H (syntype, YPM 40568), anterior end, ventral views; I (syntype, YPM 40568), anterior end, dorsal view; J (syntype, YPM 181), mid-body parapodia. Numbers refer to segments; ll, lower lip; P, basal part of prostomium; *, distal part of prostomium; ul, upper lip. Scale bars: A–C, 0.4 mm; D, 0.2 mm; E–F, 5 mm; G–J, 1 mm.
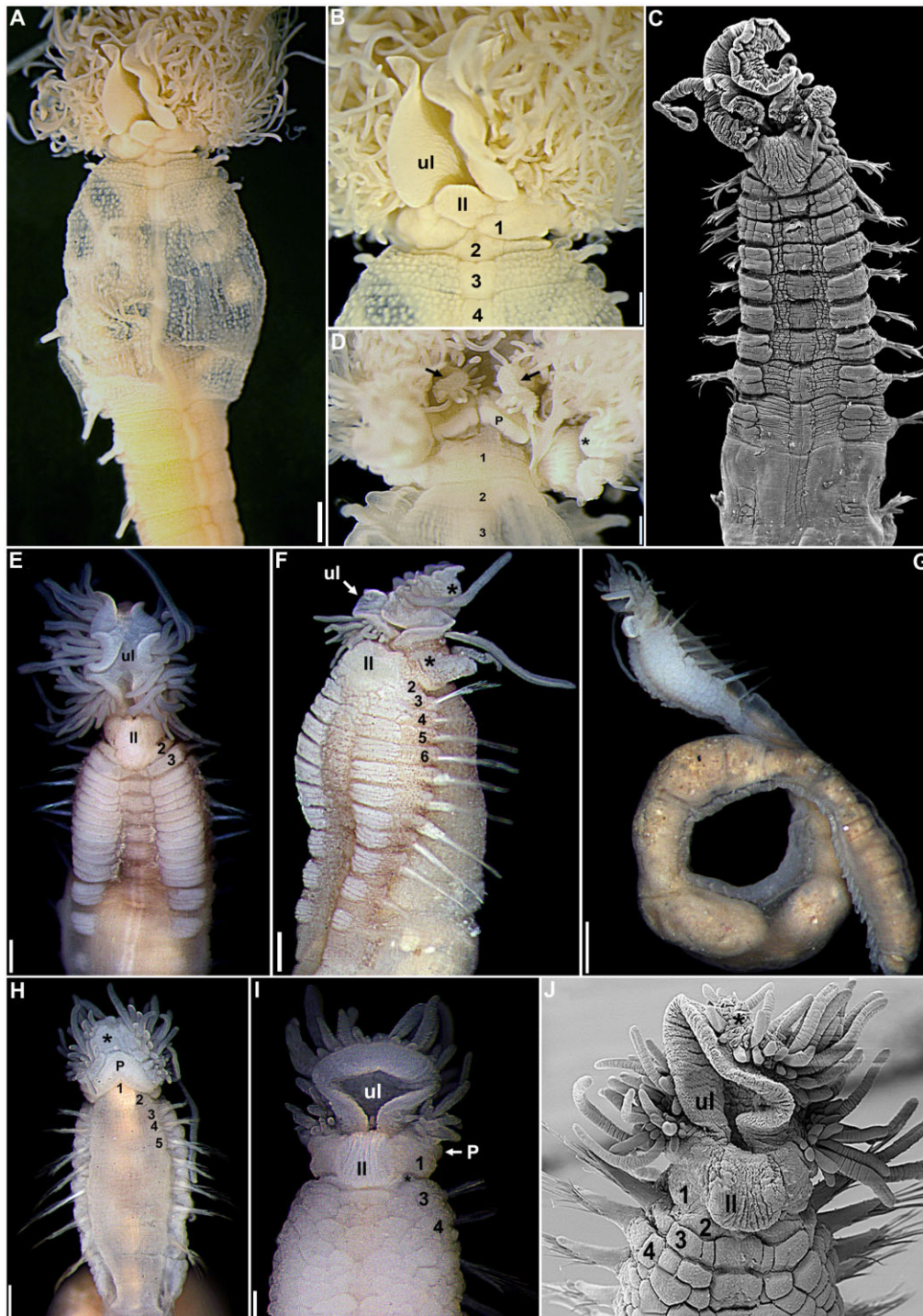
Figure 3. *Lysilla laciniata* (holotype, AM W199626): A, B, progressively closer ventral views of the anterior end; C, close-up view of prostomium to anteriormost segments, dorsal view; arrows point to prostomial process. *Polycirrus nonatoi*: D (paratype, MZUSP 1243), anterior end, ventral view; E, F (holotype, MZUSP 1213), anterior end, ventral and left ventrolateral views, respectively. *Polycirrus papillosus*: G–I (holotype, MZUSP 1216), G, entire worm; H, I, anterior end, dorsal and ventral views, respectively; *segment 2; J (paratype, MZUSP 1244), anterior end, ventral view. Numbers refer to segments; ll, lower lip; P, basal part of prostomium; P* or *, distal part of prostomium; ul, upper lip. Scale bars: A, 1 mm; B, 0.4; C, D, 0.3 mm; E, F, H, J, 0.2 mm; G, 0.5 mm; I, 0.1 mm.
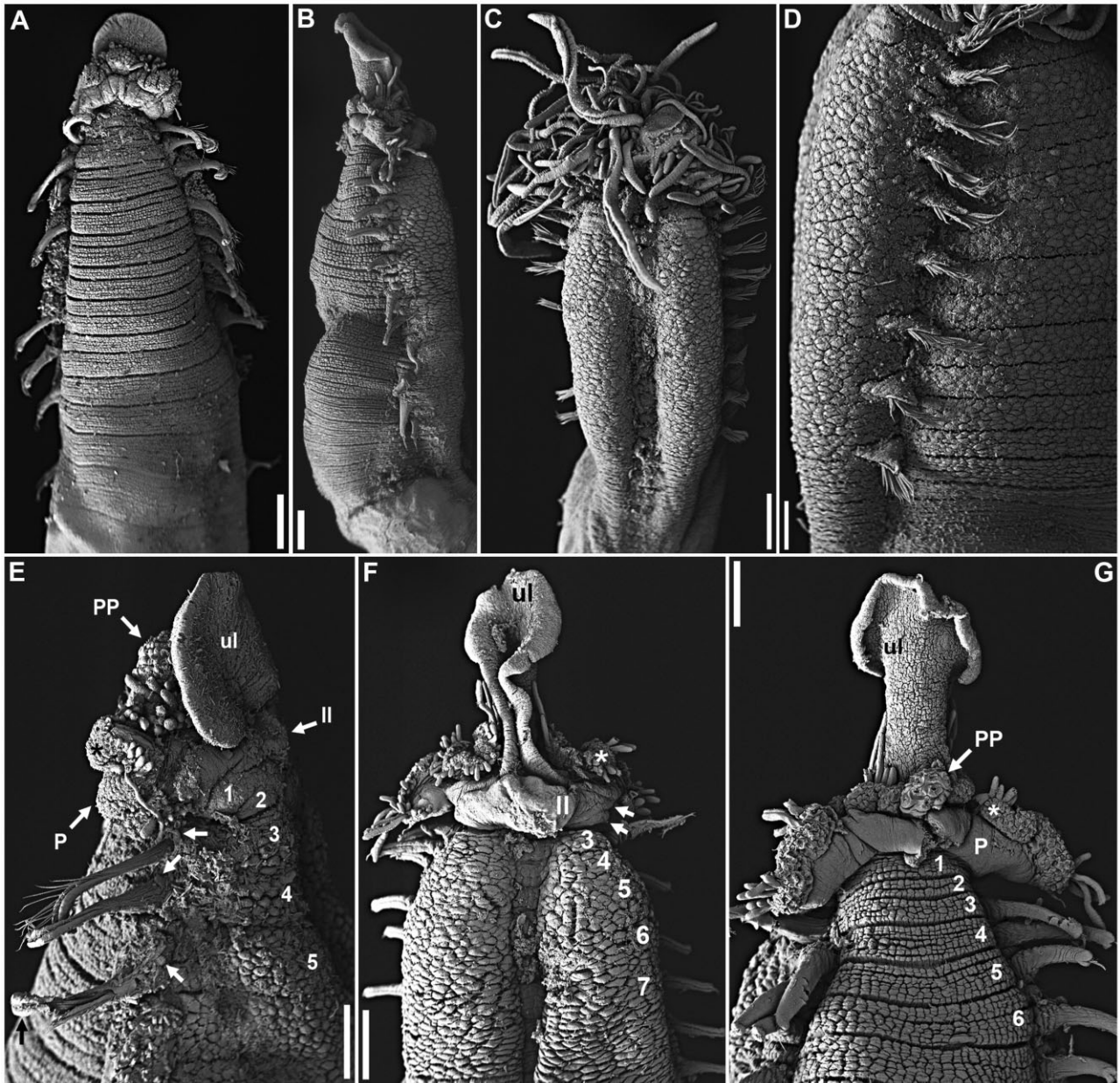
Figure 4. *Amaeana apheles* (AM W10864): A, anterior end, dorsal view; E, close-up view of the anterior end, right lateral view. *Lysilla pacifica* (AM W199622): B, anterior end, right lateral view; F, G, close-up views of the anterior end, ventral and dorsal views, respectively; unspecified arrows point to basal part of prostomium and segment 1. *Lysilla bilobata* (AM W199514): C, anterior end, ventral view; D, left side notopodia. Numbers refer to segments; ll, lower lip; P, basal part of prostomium; *, distal part of prostomium; PP, prostomial process; ul, upper lip. Scale bars: A, 0.5 mm; B–C, G, 0.4 mm; D, 0.2 mm; E–F, 0.3 mm.

2. Location of prostomium: Among members of the Telothelepodidae and Polycirridae, as also occurs in members of Terebellidae and Thelepodidae, the prostomium extends transversely across the dorsal surface of the peristomial 'upper lip' [character 2(1); Figs 2A–B, E–I; 3C–D, F–J; 4A–B, E–G; 5A–E, G–H]. Among some polycirrids, the prostomium extends lat-erally and terminates on either side of the mouth (Figs 2C–D, G–I; 3D–J; 5A–C), but clear visualization of these extensions is strongly dependent on the state of preservation, so this condition was not included. Among out-groups, the prostomium is situated middorsally (Spionidae, Sabellariidae) or directly anterior (Cirratulidae) to the peristomium. Although
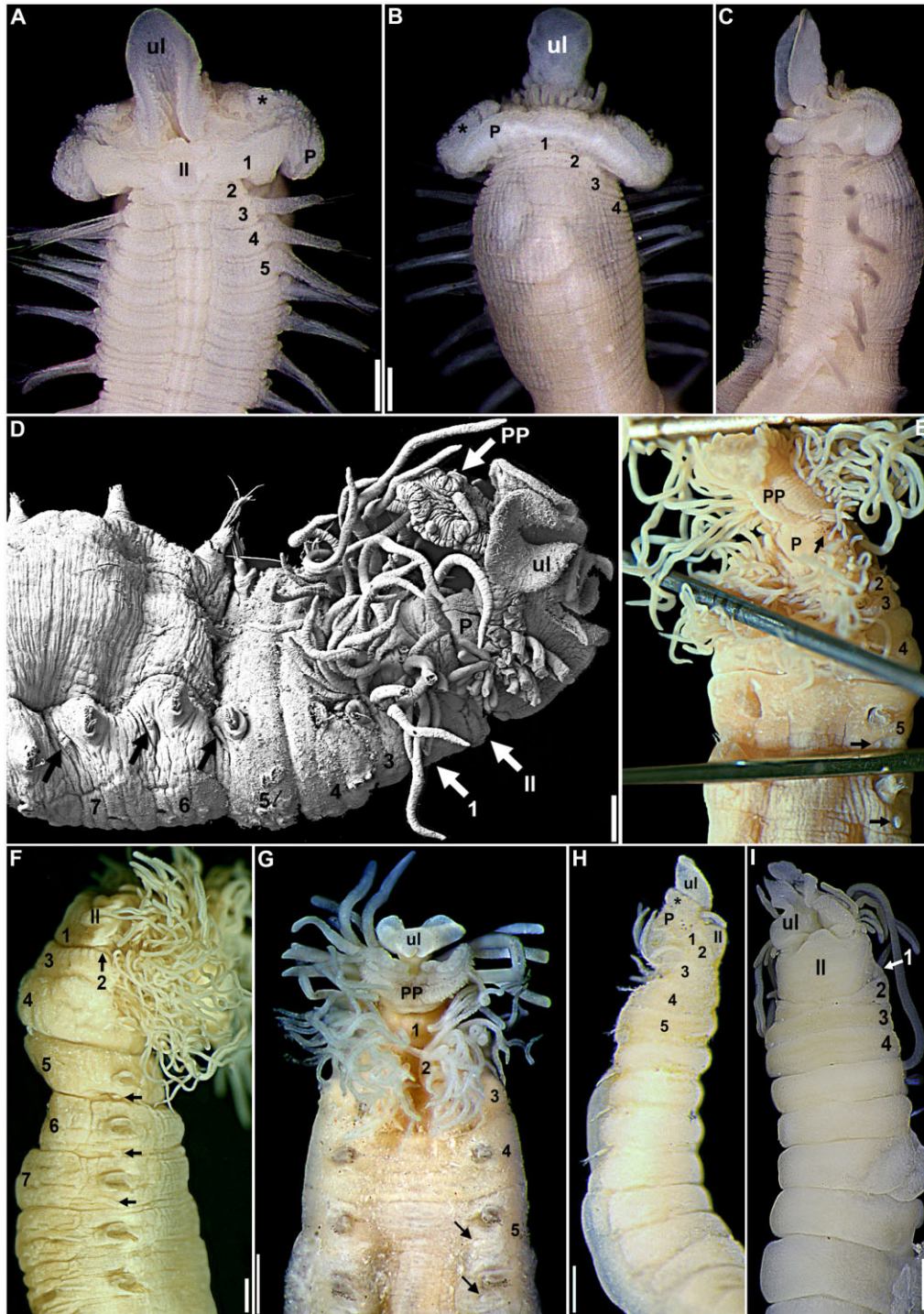
Figure 5. *Polycirrus "clavatus"* (MZUSP 1221): A–C, anterior end, ventral, dorsal, and left lateral views, respectively. *Rhinothelepus occabus*: D (paratype, AM W201904), anterior end, right lateral view; E (holotype, AM W201903), close-up view of the prostomium and anterior segments; unspecified arrow points to eyespots. *Rhinothelepus lobatus*: F (holotype, AM W5234), anterior end, left lateral view. *Glossothelepus mexicanus* (holotype, LACM–AHF Poly 1449): G, anterior end, dorsal view. *Decathelepus wambira* (paratype AM W1749): H, anterior end, right lateral view. *Parathelepus collaris* (specimen BMNH 1983.1696): I, anterior end, ventral view. Numbers refer to segments; unspecified arrows point to nephridial/genital papillae; ll, lower lip; P, basal part of prostomium; *, distal part of prostomium; PP, prostomial process; ul, upper lip. Scale bars: A–C, I = 0.2 mm; D = 0.15 mm; E–F = 0.5 mm; G = 0.4 mm; H = 0.25 mm.

somewhat variable, non-terebelliform out-groups were coded as character 2(0).

3. Transverse prostomium [cf. character 2(1)]: The transverse condition of the prostomium can be limited to the base of the 'upper lip' [character 3(0)], as in members of all telothelepodids (Fig. 5D–H), *Amaeana* (Fig. 2A,B, 4A–B), and *Lysilla* (Figs 3A–C, 4E–F), and members of some *Polycirrus* species (Fig. 5A–C); members of *Hauchiella renilla* Hutchings & Glasby, 1986 have the distal part of the prostomium as a short extension along the 'lip', but ending far from the anterior margin (Fig. 2C,D), as also occurs among members of several species of *Lysilla* (Figs 3A–C, 4C). Alternatively, the prostomium extends to near the anterior margin of the lip [character 3(1)] among some other members of *Polycirrus* (Fig. 3D–J), and members of *Biremis blandi* (Fig. 2E,F), *Enoplobranchus sanguineus* (Fig. 2G–I), and *Hauchiella tribullata* (McIntosh, 1869).

4. Prostomium: The prostomium is clearly divided into basal and distal parts [character 4(1)] among telothelepodids (Fig. 5D–E, G–H) and polycirrids (Figs 2A–I; 3; 4A–B, E–G; 5A–C), as also happens among members of most remaining families of Terebelliformia. In polycirrids, either the basal part or both basal and distal parts are developed as transverse, curved to inverted V-shaped crests (Figs 2A–D, G–I; 3C–I; 4A–C, E–G; 5A–C). Among non-terebelliform out-groups, the prostomium is not divided [character 4(0)].

5. Prostomial eyespots: Eyespots are usually present on the basal part of the prostomium among members of Terebelliformia, but are absent in all polycirrids. Among the taxa used for the present study, the basal region of the prostomium has eyespots [character 5(1)] among members of the telothelepodid genera *Decathelepus* Hutchings, 1977 (Fig. 5H), *Parathelepus* Caullery, 1915, and *Rhinothelepus* Hutchings, 1974 (Fig. 5E). Eyespots are absent [character 5(0)] among members of telothelepodid genera *Glossothelepus* Hutchings & Glasby, 1986 and *Telothelepus* Day, 1955. Among non-terebelliform out-groups, prostomial eyespots are present among members of *Spiophanes modestus* and *Idanthyrsus australiensis*, and are absent among members of *Aphelochaeta tigrina*.

6. Mid-dorsal process on anterior margin of prostomium: The distal part of the prostomium among most polycirrids and some telothelepodids is short and uniform [character 6(0)], and restricted to the origin of buccal tentacles (Figs 2E–I; 3D, F–J; 5A–C). Among members of some species of *Amaeana* [*Amaeana antipoda* (Augener, 1926), *Amaeana apheles* (Hutchings, 1974) (Figs 2A; 4A, E), *Amaeana trilobata* (Sars, 1863),

and *Amaeana yirram* Hutchings, 1997], *Lysilla* [*Lysilla bilobata* Hutchings & Glasby, 1986, *Lysilla laciniata* Hutchings & Glasby, 1986 (Fig. 3C), and *Lysilla pacifica* Hessle, 1917 (Fig. 4B, F)], and most telothelepodids (Fig. 5D–E, G), the anterior margin is developed as a mid-dorsal process [character 6(1)].

7. Length of mid-dorsal process on anterior margin of prostomium [cf. character 6(1)]: Among members of the polycirrid genera *Amaeana* and *Lysilla* the mid-dorsal process is short [character 7(0)]. The process is rounded to roughly squared and button-like (Figs 2A; 4A–B, E–F) among members of *Amaeana*, *Lysilla bilobata*, and *Lysilla pacifica*. The distal margin of the short prostomium among members of *L. laciniata* Hutchings & Glasby, 1986, has a pair of short, mid-dorsal lobes (Fig. 3C). Among telothelepodids, this process is elongate, tongue-like [character 7(1)]; among members of *Rhinothelepus lobatus* Hutchings, 1974 it is attached to the dorsal surface of the upper lip with a free distal lobe (Fig. 5D–E), whereas among members of *Glossothelepus mexicanus* Hutchings & Glasby, 1986 it is completely free from the upper lip (Fig. 5G).

8. Prostomial buccal tentacles: Buccal tentacles are absent [character 8(0)] among members of the non-terebelliform out-groups, whereas they are present among all Terebelliformia [character 8(1)] (cf. discussion in Nogueira *et al.*, 2013), including members of Telothelepodidae (Fig. 5D–I) and Polycirridae (Figs 2A–F; 3A–J; 4A–C, E–G; 5A–C; 6A).

9. Prostomial buccal tentacles shape [cf. character 8(1)]: All members of Polycirridae, as well as telothelepodid out-groups *Telothelepus capensis* and *Glossothelepus mexicanus*, have at least two types of prostomial buccal tentacles [character 9(1)]. Long tentacles are stouter, usually distally spatulate, whereas short tentacles are thin and uniformly cylindrical (Figs 2A–F; 3A–J; 4A–C, E–G; 5A–C; 6A), although sometimes width differences of tips of long tentacles are so slight that distinctions between types are based mostly on tentacle length. On the other hand, several members of *Amaeana* and *Lysilla pacifica* have more elaborate tips (see below). Remaining members of Telothelepodidae have one tentacle type [character 9(0)], all uniformly cylindrical (Fig. 5E, I). Several species of *Polycirrus* have been described as having a single type of buccal tentacle (Hutchings & Glasby, 1986a; Glasby & Hutchings, 2014), but among the specimens examined, including several that have been described as having a single type of buccal tentacle, we always recognize at least two types, although we agree that sometimes these types are separated mostly by tentacle length and thickness.
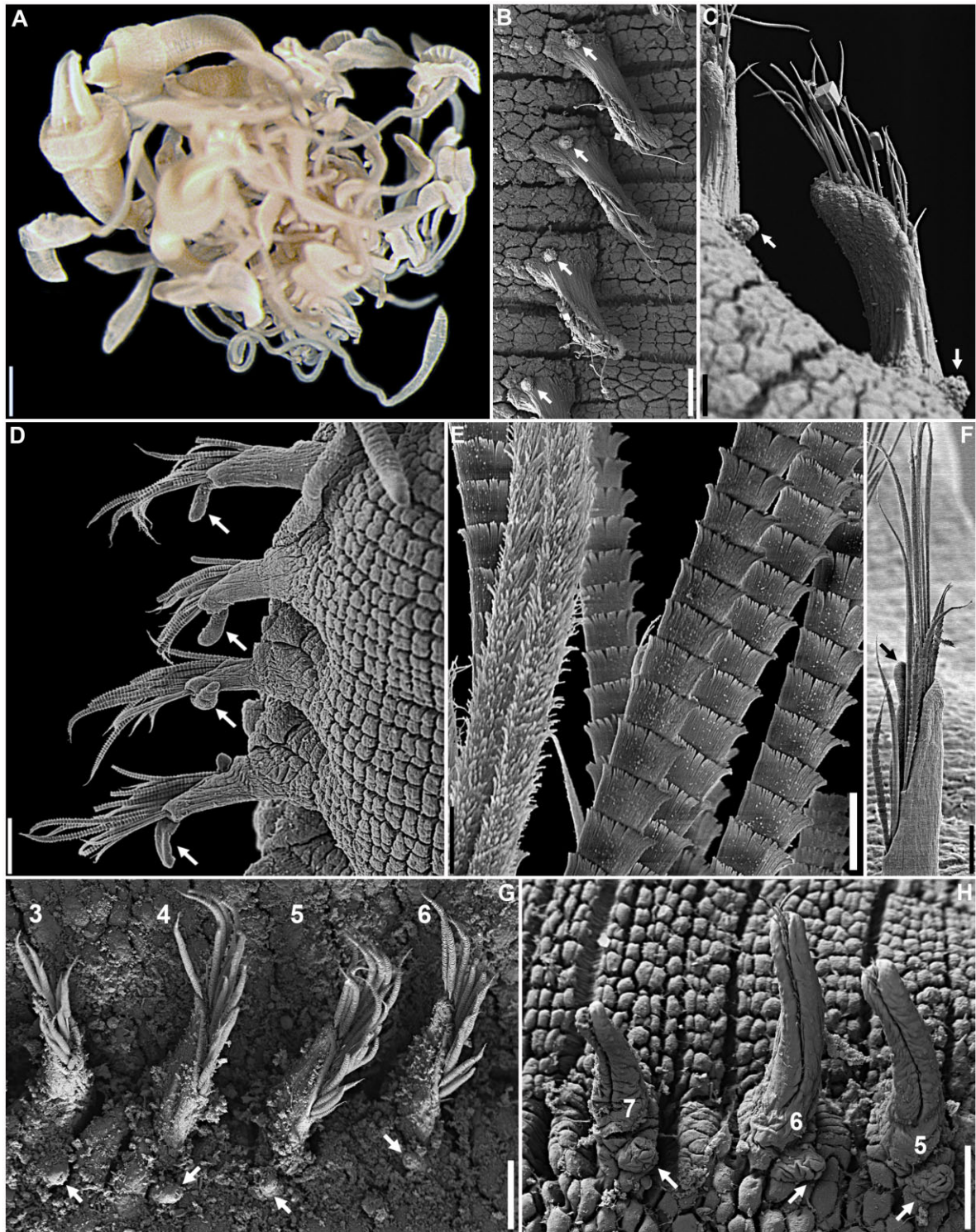
Figure 6. *Amaeana apheles* (holotype AM W5239): A, buccal tentacles. *Amaeana trilobata* (AM W7050): B, C, notopodia, arrows point to nephridial/genital papillae. *Polycirrus nonatoi* (paratype, MZUSP 1243): D, notopodia, arrows point to cirriform process of postchaetal lobe; E, detail of notochaete. *Polycirrus papillosus* (paratype, MZUSP 1244): F, notopodium, arrow points to postchaetal lobe. *Lysilla bilobata* (AM W199514): G, notopodia segments 3–6. *Lysilla pacifica* (AM W199622): H, notopodia segments 5–7. Except for (D) and (F), unspecified arrows point to nephridial/genital papillae. Scale bars: A, 0.5 mm; B, G, 0.1 mm; C, 40 μm; D, 60 μm; E, 7 μm; F, 50 μm; H, 15 μm.

10. Distal ends of longest buccal tentacles among individuals with two types [cf. character 9(1)]: The distal ends of the longest buccal tentacles can exhibit two forms. The tips among most members of *Amaeana* and *Lysilla pacifica* are expanded, with a basal ring and tapering tip (Figs 2A–B; 6A) [character 10(0)]. Among all members of *Polycirrus* (Fig. 3E–J), *Hauchiella* (Fig. 2C–D), *Enoplobranchus sanguineus, Biremis blandi* (Fig. 2E–F), most members of *Lysilla* (Figs 3A–B; 4C), *Amaeana antipoda,* and *Amaeana trilobata,* tips are spatulate [character 10(1)].

11. Peristomial palps: Peristomial palps are present [character 11(0)] among members of all non-terebelliform out-groups, and are absent [character 11(1)] in all Terebelliformia, including members of all species of Telothelepodidae and Polycirridae used for the present study.

12. Anterior margin of mouth: The anterior margin is a low ridge [character 12(0)] among members of the non-terebelliform out-groups. This margin is developed as a distinct tissue extension or 'upper lip' [character 12(1)] among all terebelliforms (Figs 2A–I; 3A–B, D–J; 4A–C, E–G; 5A–D, G–I), except members of the Pectinariidae, which have prostomium and peristomium fused to form a cephalic veil (Nogueira *et al.*, 2010b, 2013).

13. Shape of large 'upper lip' [cf. character 12(1)]: The large upper lip is narrow and elongate [character 13(0)], and often convoluted (Fig. 5D, G–I), among members of Telothelepodidae. The circular condition [character 13(1)], sometimes referred to as 'trilobed' in the literature (e.g. Hutchings & Glasby, 1986b), is characteristic of members of the Polycirridae, although there is some variation in lip width, from circular to elliptical (Figs 2A–I; 3A–B, D–J; 4A–C, E–G; 5A–C).

14. Shape of lower lip: The lower lip is expanded [character 14(0)] among telothelepodids (Fig. 5D, F, H–I) and polycirrids (Figs 2B–E, G–H; 3A–B, D–G, I–J; 4B, E, G; 5A, C) (for an extended discussion of lower lip morphologies among terebelliforms, see Nogueira *et al.*, 2013). Among members of *Spiophanes modestus, Aphelochaeta tigrina,* and *Idanthyrsus australiensis,* the lip is a low ridge [character 14(1)].

15. Expanded lower lip [cf. character 14(0)]: This type of lower lip is rounded and mid-ventral [character 15(1)] among members of *Amaeana, Enoplobranchus sanguineus, Lysilla,* and some *Polycirrus,* frequently with deep, highly ciliated grooves, and sometimes divided into two pieces (Figs 2B, G–H; 3A–B, G, I–J; 4B, E, G; 5A–C). Among members of *Biremis blandi, Hauchiella,* and some *Polycirrus*s, the lower lip is a large, cushion-like shield extending across the ventrum [character 15(2); Figs 2C–E; 3D–F]. Although the type specimens of *Hauchiella renilla* are not well preserved anteriorly, it is apparent that the lower lip has a mid-ventral button-like part, extending laterally as slightly swollen, cushion-like structures (Fig. 2C–D), consistent with character 15(2). Members of the telothelepodid out-groups, *Glossothelepus mexicanus* and *Rhinothelepus lobatus* (Fig. 5D, F), have a segment-like lower lip [character 15(0)]. Members of all other Telothelepodidae have a lower lip that is cushion-like across the ventrum [character 15(2)] (Fig. 5H–I).

16. Peristomium composition: The peristomium bears the upper and lower lips, and forms a complete ring [character 16(1)] among members of the non-terebelliform out-groups *Spiophanes modestus* and *Aphelochaeta tigrina,* but is restricted to the lips [character 16(0)] among members of *Idanthyrsus australiensis.* Both characters occur among members of the Telothelepodidae, whereas among members of Polycirridae the peristomium is restricted to the lips [character 16(0)].

Anterior segments (subjects 17–28)
More extensive, general descriptions of these characters with regard to the Terebelliformia can be found in Nogueira *et al.* (2010b) and Nogueira *et al.* (2013).

17. Visibility of segment 1: As noted by Nogueira *et al.* (2013), the appearance of segment 1 among terebelliforms is variable. In polycirrids, the prostomium frequently extends laterally and ventrally, terminating lateral to the mouth. Segment 1 is usually visible mid-dorsally and ventrally, posterior to the mouth, but the visibility of segment 1 is strongly dependent on the state of preservation of specimens. Segment 1 is not visible ventrally among members of most species that have a cushion-like lower lip, however. Except sometimes for a mid-ventral gap lateral to the lower lip, the entire segment circumference can be visible [character 17(0)], as found among members of the telothelepodids *Glossothelepus mexicanus* (Fig. 5G) and *Telothelepus,* members of *Biremis blandi* (Fig. 2E, F), and some members of *Amaeana* (Figs 2A, B; 4A, E), *Lysilla* (Figs 3A–C; 4B, F–G), and *Polycirrus* (Figs 3G–J; 5A–C). Restricted visibility, i.e. laterally/ventrally [character 17(1)], laterally/dorsally [character 17(2)], dorsally [character 17(3)], ventrally [character 17(4)], or dorsally/ventrally [character 17(5)], can be found among members of Telothelepodidae (Fig. 5D–F, H–I) and Polycirridae (Figs 2C–I; 3D–F; 4A–C). Regarding non-terebelliform out-groups, segment 1 is visible laterally/ventrally [character 17(1)] among members of *Spiophanes modestus,* whereas it is visible all around

[character 17(0)] among members of *Aphelochaeta tigrina* and *Idanthyrsus australiensis*.

18. Segment 2: This segment forms a complete [character 18(0)] or incomplete ring [character 18(1)]. Of taxa considered in this study, the incomplete condition only occurs among members of some Telothelepodidae species, *Rhinothelepus lobatus* (Fig. 4D–F) and *Glossothelepus mexicanus* (Fig. 4G), on which segment 2 terminates laterally, not continuing onto the ventral side of the body, and covered by the expanded lower lip. Among polycirrids, although sometimes segment 2 has a narrow mid-ventral gap, terminating laterally to the expanded lower lip, it is always conspicuous at least dorsally, laterally and ventrolaterally (Figs 2A–I; 3; 4A–B, E–G; 5A–C).

19. Segment 2 width: Segment 2 can be of the same width as adjacent segments [character 19(0)] or distinctly narrower [character 19(1)]. The latter condition is only seen among members of Polycirridae, where the anterior end is clearly separated from the rest of the body by a constriction at segment 2, as it is narrower than segment 1 and subsequent segments (Figs 2A–I; 3; 4A, B, E–G; 5A–C). Members of outgroups have character 19(0) (Fig. 5D–I).

20. Segmental branchiae: Except for members of Polycirridae and some members of Terebellidae (cf. Nogueira *et al*., 2013), where branchiae are absent [character 20(0)], the remaining terebelliforms have branchiae [character 20(1)]. As noted by Nogueira *et al*. (2013), because terebelliform branchiae are disassociated from parapodia, these branchiae are distinguished from the functional equivalents referred to as parapodial branchiae, often seen among other polychaetes. Segmental branchiae *sensu* Terebelliformia were therefore coded as absent [character 20(0)] among members of non-terebelliform out-groups, although parapodial branchiae may be present.

21. Ventral surfaces of anterior segments: The ventral surfaces of anterior segments of all terebelliforms are strongly glandular [character 21(1)], and are involved in tube building or in secreting the mucous layer over which animals glide through the substrate, as in the case of non-tubiculous polycirrids (Nogueira *et al*., 2013). Posterior to this glandular zone, or from its beginning, as occurs among members of Polycirridae, is a mid-ventral groove [cf. character 24(1), below]. Along this groove is one square- to rectangular-shaped area per segment, which does not seem to be glandular (Figs 2B, C–E, G–H; 3A, B, D–G, I–J; 4C, E, G; 5A); these square to rectangular areas were treated as 'mid-ventral shields' by Nogueira *et al*. (2010b), but we prefer not to use this phrase because it could be confused with

the mid-ventral shields of terebellids, which are clearly glandular. The glandular regions among members of the non-terebelliform out-groups are uniform, ranging from non-glandular to slightly glandular [character 21(0)].

22. Glandular ventral surfaces of anterior segments [cf. character 21(1)]: Among members of Telothelepodidae, the ventral surfaces of anterior segments are uniformly and distinctly glandular [character 22(1); Fig. 5D, F, H, I]. The ventral glandular surfaces among members of Polycirridae (Figs 2B–E, G–H; 3A, B, D–G, I, J; 4B–E, G; 5A, C) are arranged as paired, discrete ventrolateral pads [character 22(0)], although frequently these are so densely covered with papillae that individual pads are not distinguishable from each other (Figs 3G, I, J; 4B–E, G); in those cases, we assume the presence of pads rather than considering them absent. The more general occurrences of glandular ventral surfaces among other terebelliforms and the differences among families of Terebelliformia were described by Nogueira *et al*. (2010b) and Nogueira *et al*. (2013).

23. Paired glandular ventrolateral pads surfaces [cf. character 22(0)]: The surfaces of paired ventrolateral pads among members of Polycirridae are either lightly papillate [character 23(0)] or densely papillate [character 23(1)]. Both characters are seen among members of *Polycirrus* (Figs 3D–G, I–J; 5A, C), whereas surfaces are sparsely papillate among members of *Biremis blandi* (Fig. 2E) and *Enoplobranchus sanguineus* (Fig. 2G–H), and densely papillate among members of *Amaeana* (Figs 2B, 4E), *Lysilla* (Figs 3A, B; 4B–D, G), and *Hauchiella* (Fig. 2C, D).

The character 'densely papillate' exhibits variation, from members of species in which papillae are minute and arranged in several transverse rows per segment, to members of species with large irregular papillae, frequently obscuring shield margins. We prefer not to differentiate between these conditions, however, as they are strongly dependent on the state of preservation of specimens, and we have observed significant intraspecific variation that might also be an artifact of preservation.

24. Mid-ventral groove: The mid-ventrum is uniformly smooth [character 24(0)] among members of the non-terebelliform out-groups. Among members of Terebelliformia (cf. Nogueira *et al*., 2013), there is a mid-ventral groove extending posteriorly along part of the length of the body [character 24(1)].

25. Distribution of mid-ventral groove [cf. character 24(1)]: Among the members of Terebelliformia considered in this study (for the full range of character

variation, see Nogueira *et al.*, 2013), the mid-ventral groove extends from the anterior end (segments 2–5) to the pygidium [character 25(0)] among members of Polycirridae (Figs 2B–E, G–H, J; 3A–B, D–G, I–J; 4C, G; 5A, C), or from the posterior region with notopodia to the pygidium [character 25(1)] among members of Telothelepodidae.

The holotype of *Glossothelepus mexicanus* is the longest known specimen, albeit incomplete posteriorly, with 25 segments and notopodia present from segment 3 until the end of the fragment. The specimen has a mid-ventral groove from segment 4, but it is not well defined. As the groove in the remaining members of Telothelepodidae begins from the posterior region with notopodia, or after those structures terminate, and the specimen of *G. mexicanus* has notopodia until the end of the fragment, we coded it as unknown [character 25(?)].

26. Nephridial/genital papillae: Papillae are absent [character 26(0)] among members of non-terebelliform out-groups. Papillae are either absent or present [character 26(1)] among members of the Telothelepodidae, *Polycirrus*, *Lysilla*, and *Hauchiella*. Papillae are present among members of *Biremis blandi* and all species of *Amaeana* included in the study, and absent among members of *Enoplobranchus sanguineus*. In some polycirrids, such as members of *Hauchiella renilla*, papillae are absent but nephridia are visible through the body wall. As visibility of nephridia through the body wall is another character strongly dependent on the state of specimen preservation, we prefer to code for the presence of conspicuous papillae, rather than nephridia, following Nogueira *et al.* (2013), and therefore *H. renilla* was coded as not having papillae [character 26(0)]. Also, it is very difficult to distinguish between the nephridial/genital papillae and those that densely cover the ventral surfaces when both are present.

27. Genital papillae distribution [cf. character 26(1)]: When present, nephridial papillae from segments 3–5 have excretory functions, whereas those from segment 6 onwards are used for discharge of gametes. Nogueira *et al.* (2013) noted that the distribution of nephridial and genital papillae can exhibit intrageneric variation among members of Terebelliformia, and found it useful to recognize papillae absence and presence on a segment-by-segment basis up to segment 11, after which papillae are absent among members of most taxa. The great variability found in the presence of nephridial/genital papillae is only observed among members of the Terebellidae, however, and is not included in this study, with the other families exhibiting some relatively well-established patterns of distribution of papillae. Therefore, the more limited number of taxa

considered here, with the exclusion of Terebellidae, allowed for recognizing the more general patterns of genital papillae distributions, rather than focusing on the presence/absence within each segment. There are three characters regarding genital papillae distributions: genital papillae are limited to some anterior segments (up to segment 11) within the body region with notopodia [character 27(0)]; genital papillae extending further posteriorly, but terminating well before termination of notopodia [character 27(1)]; or genital papillae extending to near the end of notopodia or very close to this termination point [character 27(2)], so that all notopodia, or nearly all, are associated with a papilla.

Among telothelepodids, except for *Decathelepus wambira* Nogueira & Hutchings, 2007 and *Parathelepus collaris*, members of all remaining taxa have nephridial/genital papillae on segments 5–7, posterior to notopodia (Fig. 5D–G), and are therefore coded as character 27(0).

Among polycirrids, as also happens with several other characters, the number of pairs of nephridial/genital papillae is directly related to the number of pairs of notopodia (J.M.M. Nogueira, pers. observ.). Three patterns of distribution of nephridial/genital papillae are found: papillae present on a few anterior segments [character 27(0)] among members of *Biremis blandi*, *Hauchiella tribullata*, and *Polycirrus medusa*; papillae extend further posteriorly, but terminate well before termination of notopodia [character 27(1)], as in *Lysilla bilobata* and several species of *Polycirrus*; or papillae are located at anterior bases of all or the great majority of notopodia [character 27(2)], which occurs among most members of Polycirridae (Figs 2A, B; 4B–E).

28. Genital papillae position [cf. characters 26(1) and 27(0–2)]: When present, genital papillae among members of the Polycirridae are anterior to the bases of notopodia and longitudinally aligned with them [character 28(2)], except for *Biremis blandi*, in which individuals do not have notopodia and have papillae at posterior margins of segments 7–10, a position that we consider equivalent to the posterioventral bases of notopodia [character 28(1)]. Members of several species have anterior segments so compacted that pairs of notopodia are very close to each other; as intersegmental lines are often poorly marked, it is very easy to misinterpret what are anterior and posterior margins of notopodia (what looks like the posterior margin of a notopodium is in fact the anterior margin of the adjacent notopodium). Also, as anterior segments are shorter among members of some species, the first two or three pairs of papillae may be lateral to notopodia or even posterior, but usually from segment 5 all papillae are at the anterior bases of notopodia (Figs 4B–E; 6B, G–H). We have examined members of some species described as having

[character 34(1)], when present, among members of the Polycirridae (Figs 2A, B, G–J; 3; 4; 5A–C; 6B–D, F–H).

35. Distal ends of notopodia [cf. characters 30(0), 30(2)]: The ends of notopodia are either conical [character 35(0)] or bilobed [character 35(1)]. The conical condition occurs among members of out-groups as well as members of *Enoplobranchus sanguineus*. When present, notopodia among the remaining polycirrids have bilobed distal ends.

36. Relative lengths of pre- and postchaetal notopodial lobes of elongate notopodia [cf. character 35(1)]: Elongate notopodia of members of Polycirridae are distally oblique, and thus higher dorsally. Tips of notopodia are folded around chaetae, closed dorsally, with anterior (prechaetal) and posterior (postchaetal) lobes [cf. character 35(1)], the latter sometimes with cirriform processes (Figs 3D, 6D). Pre- and postchaetal notopodial lobes are the same length [character 36(0)] among members of *Amaeana* (Figs 2A–B; 4A, E; 6B–C) and *Lysilla* (Figs 3A–C; 4B–D, F–G; 6G–H). Lobes are either the same length (Figs 3J, 6F) [character 36(0)] or postchaetal lobes are longer (Figs 3D, 6D) [character 36(1)] among members of *Polycirrus*, sometimes with cirriform processes originating from postchaetal lobes (Fig. 6D). Although members of *Enoplobranchus sanguineus* have elongate notopodia, they are highly branched and the distal ends are blunt [cf. character 35(0)], with chaetae originating at the tips of each branch, thus lacking pre- and postchaetal lobes (Figs 2J, 10C).

37. Notochaetae origin from notopodium [cf. characters 30(0, 2)]: Patterns of notochaetae emergence from notopodia are of three forms. Notochaetae extend from a central core [character 37(0)], usually retractile, as among all members of Telothelepodidae (Fig. 5D–G); from between notopodial lobes [character 37(1); cf. character 35(1)], as occurs among most members of Polycirridae (Figs 3D, J; 4; 6B–D, F–H); or from a general region at the ends of notopodia or notopodial branches [character 37(2)], as among members of the monotypic polycirrid *Enoplobranchus sanguineus*, which has a small fascicle of two pinnate chaetae on each row at the ends of each notopodial branch (Figs 2J; 10A, C). Members of the non-terebelliform out-groups also exhibit character 37(2).

38–41. Notochaetal characters [cf. characters 30(0, 2)]: These characters were also included in the study by Nogueira *et al.* (2013) for the Terebelliformia, so that paper should be consulted for additional details. As noted by Nogueira *et al.* (2013), notochaetae are arranged in two transverse rows on notopodia of all terebelliforms. Notochaetae in posterior rows are usually longer than those in anterior rows, and the types of chaetae in adjacent rows are not necessarily the same (Figs 6D–G; 7A, C). Whereas members of some terebelliform taxa present chaetal variation from anterior to posterior notopodia, this has not been considered in the present study because such variation does not occur among polycirrids, at least not among those included in the present study. Also, Nogueira *et al.* (2013) coded for regions of chaetae, because members of several taxa of terebelliforms have medially winged and distally serrate chaetae; however, such chaetae do not occur among members of Polycirridae, which only have either pinnate or winged chaetae.

Members of some species of *Polycirrus* were described as having hirsute chaetae, which would be a third type of notochaetae (see Hutchings & Glasby, 1986a; Glasby & Hutchings, 2014). We do not agree with this, however. According to our observations winged notochaetae are always hirsute, when viewed using SEM, because of the deposition of chitin in layers. Depending on the state of preservation of chaetae those layers may separate from each other, particularly in specimens preserved in ethanol, conferring on them a hirsute appearance, but they are the same winged type of chaetae. We have noticed this in several specimens observed with SEM, with 'hirsute' and winged notochaetae sometimes occurring side by side along the same row of chaetae.

As in Nogueira *et al.* (2013), notochaetal features were recognized in this study according to anterior versus posterior row within a notopodium. As already mentioned, notochaetae of polycirrids are of two types, winged or pinnate, and sometimes both types are present on the same notopodium, one in each row (Figs 6D–F; 7A, C). Among terebelliforms pinnate chaetae are only found in members of some Polycirridae, and these chaetae do not have wings, but instead have successive rings of relatively rigid bristles arranged in circles along lengths of chaetae, excepting the very distal tips (Figs 6D–G; 7A, C–D, G; 8A).

With regards to the width of wings of limbate notochaetae, they may be very narrow, inconspicuous when viewed with light microscopy, and visible as minute spines using SEM, as is the case among members of *Amaeana* (Figs 4E; 6B–C; 8B–E; for example, compare the chaetae of *Amaeana apheles* as observed using both light microscopy and SEM in Fig. 8B–D) and among some members of *Lysilla*. Members of *Polycirrus* have wings that are always conspicuous when viewed with light microscopy and considered 'wide,' varying from narrower than shaft width, along each side, to the same width or wider than shaft width (Figs 6F; 7A–C, E–F). This wide wing condition is different from 'broad' wings *sensu* Nogueira *et al.* (2013) that only occur among some members of Terebellidae and Thelepodidae, families not included
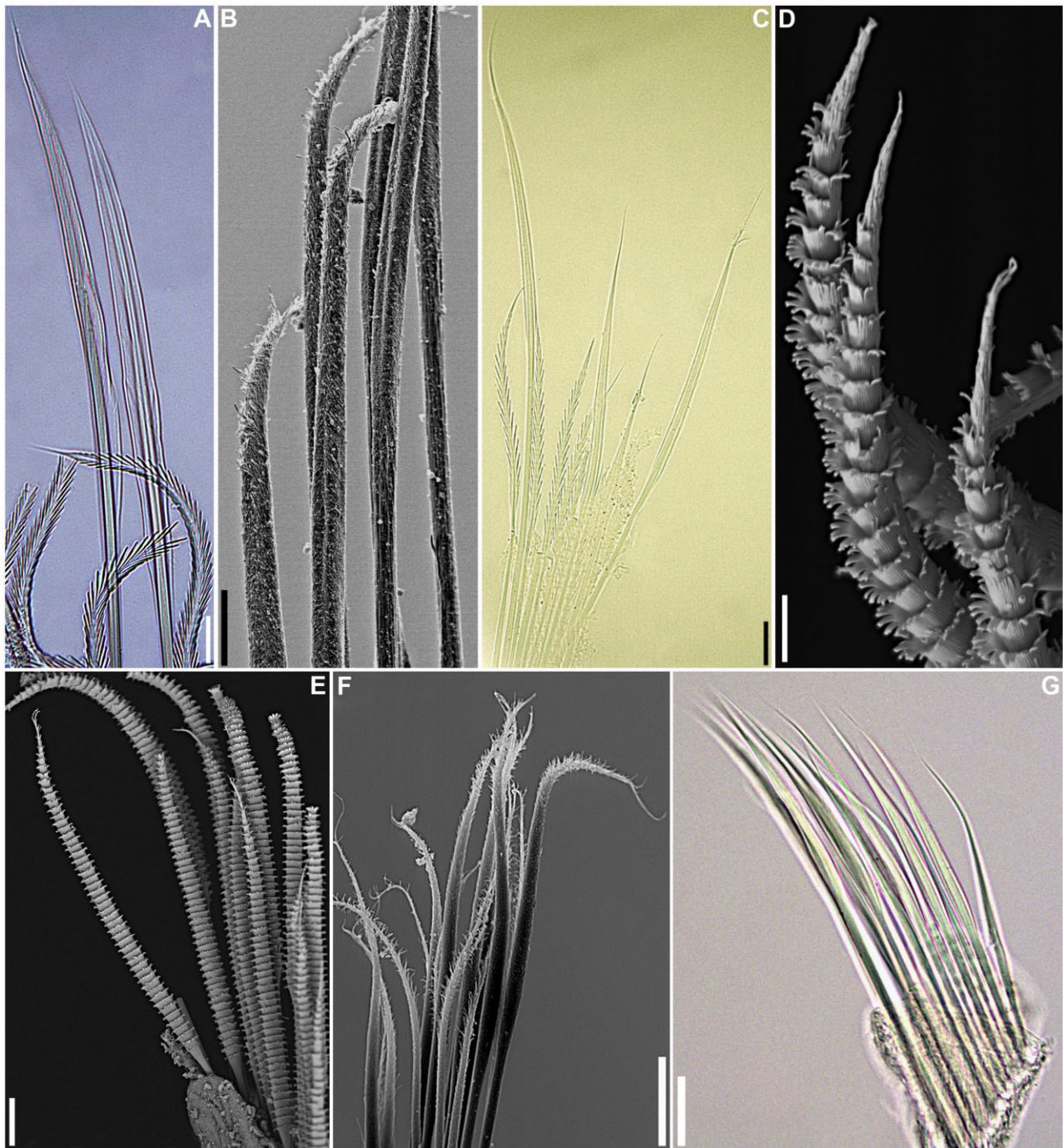
Figure 7. *Polycirrus papillosus*: A (holotype, MZUSP 1216), tips of notochaetae; B (paratype, MZUSP 1244), tips of notochaetae from the posterior row. *Polycirrus bicrinalis* (paratype, AM W199638): C, notochaetae from segment 13. *Lysilla bilobata* (AM W199514): D, E, notochaetae. *Polycirrus breviuncinatus*: F (paratype, MZUSP 1245), G (holotype, MZUSP 1220), notochaetae. Scale bars: A–C, E–G, 20 µm; D, 6 µm.

in the present study. Chaetae are alimbate, smooth capillaries among members of the non-terebelliform outgroups, *Spiophanes modestus* and *Aphelochaeta tigrina*, and pinnate among members of *Idanthyrsus australiensis*. Wide-winged capillaries are present in telothelepodids, referred to as bayonet chaetae by Nogueira *et al.* (2010b; Fig. 8F). Chaetal characters are as follows.
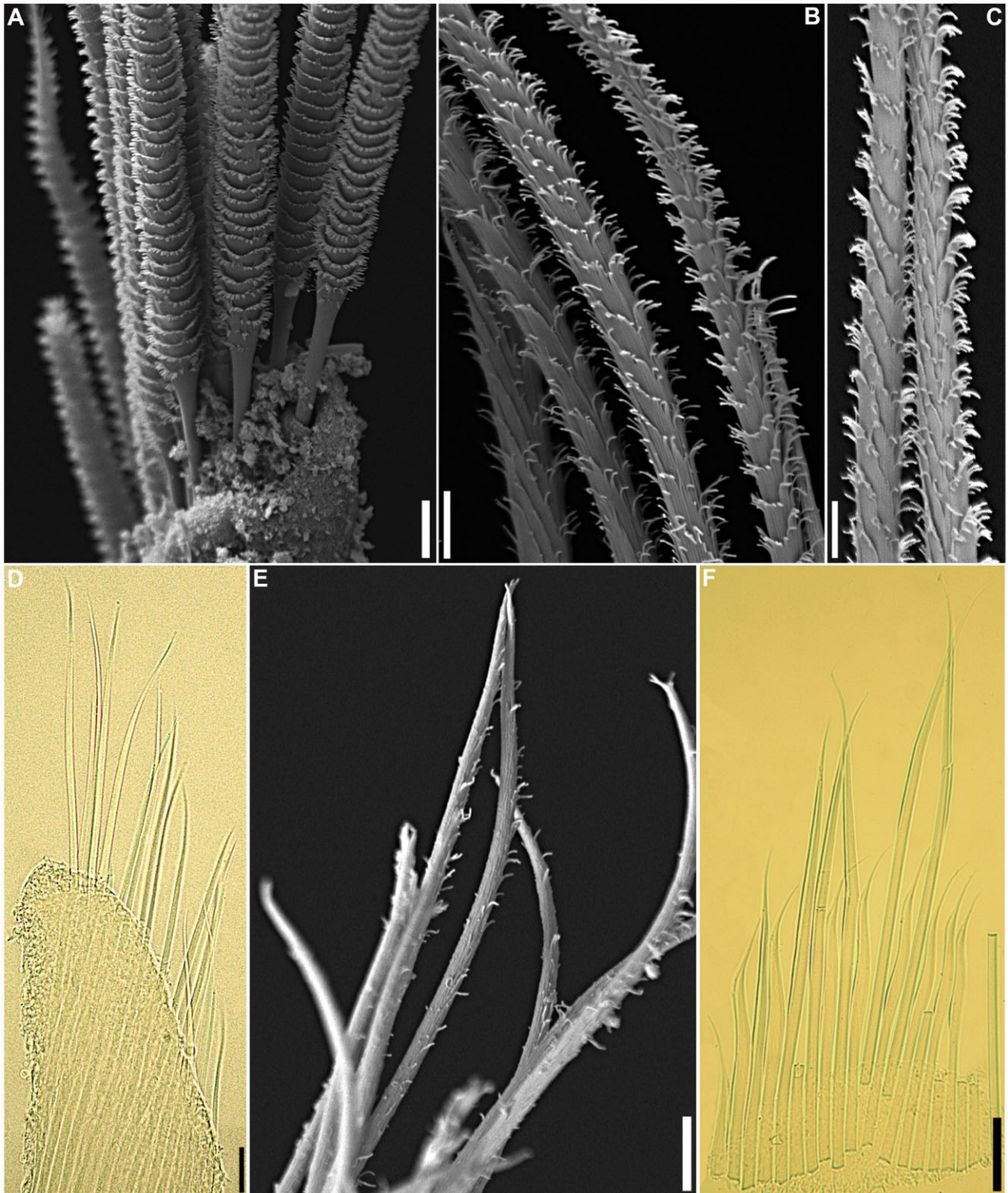
Figure 8. *Lysilla bilobata* (AM W199514): A, base of notochaetae. *Amaeana apheles*: B, C (AM W10864), D (AM W5384): notochaetae. *Amaeana trilobata* (AM W7050): E, notochaetae. *Glossothelepus mexicanus* (holotype, LACM–AHF Poly 1449): F, notochaetae, segment 6. Scale bars: A, E–F, 10 μm; B, C, 6 μm; D, 20 μm.

38. Type of notochaetae in anterior rows: (0) alimbate; (1) winged; (2) pinnate.

39. Width of wings of winged notochaetae in anterior rows [cf. character 38(1)]: (0) narrow; (1) wide.

40. Type of notochaetae in posterior rows: (0) alimbate; (1) winged; (2) pinnate.

41. Width of wings of winged notochaetae in posterior rows [cf. character 40(1)]: (0) narrow; (1) wide.

Neurochaetae (subjects 42–49)
42. Neurochaetae: Members of the non-terebelliform outgroups have slender or capilliform neurochaetae [character 42(0)]. As is typical of terebelliforms (cf. Nogueira *et al.*, 2013), neurochaetae among members of the Telothelepodidae and Polycirridae, when present, are usually avicular uncini [character 42(1)], except in the case of *Amaeana*, where they are tapering spines [character 42(2)] (Fig. 9C–F, I). Following the methodology adopted by Nogueira *et al.* (2013), uncini were coded by the regions defined by Nogueira *et al.* (2010b). As discussed by Glasby & Glasby (2006) and Glasby & Hutchings (2014), two types of uncini are present among polycirrids, sometimes referred to as types 1 and 2. Both types of uncini have a nearly straight base, elongate and distally pointed prow, and dorsal button located at the base of the main fang, although this latter character is usually reduced, frequently almost inconspicuous. The two types of uncini differ in that type 1 are distinctly longer than high and have a short heel, directed posteriorly (Fig. 9J–K), whereas type 2 are about as long as high because of an elongate neck, defined as the distance between the base and the main fang and crest, and have a developed heel, directed downwards (Fig. 9G, L–M). In telothelepodids, neurochaetae are always uncini, and neuropodia in the region with biramous parapodia are low ridges, whereas neuropodia posterior to the termination of notopodia are somewhat more raised (Fig. 9H), but still distinctly lower than in members of the other families of Terebelliformia. Telothelepodid uncini are about as long as high, with slightly curved bases, dorsal buttons at the anterior third of uncini, close to the anterior margin, and with the main fang remarkably long and acute (Fig. 10B).

43. General dimensions of anterior body avicular uncini [cf. character 42(1)]: Uncini can be longer than high [character 43(0)] (Fig. 9J–K), or as high as long [character 43(1)] (Fig. 9G, L–M). Members of species of Polycirridae with type-1 uncini *sensu* Glasby & Glasby (2006) have longer than high uncini, whereas those with type-2 uncini have as long as high uncini because of the greater distance between the base of the uncini and the origin of the main fang in this latter group.

The condition higher than long, found in several members of other families of Terebelliformia (Nogueira *et al.*, 2013), is not present among members of Polycirridae or Telothelepodidae, so it is not included in this study.

44. Width of neuropodial avicular uncinus base [cf. character 42(1)]: The bases of uncini among members of the Telothelepodidae are wide [character 44(1); Fig. 10B], when compared with those of members of the Polycirridae, i.e. *Polycirrus* and *Biremis*, which have narrow bases [character 44(0); Fig. 9G, J–M].

45. Heel length of neuropodial avicular uncini [cf. character 42(1)]: The heel is short [character 45(0)] among members of Telothelepodidae (Fig. 10B) and members of Polycirridae with type-1 uncini *sensu* Glasby & Glasby (2006) (Fig. 9J–K). Members of species of *Polycirrus* with type-2 uncini *sensu* Glasby & Glasby (2006) have elongate heels [character 45(1)], i.e. *Polycirrus "clavatus"* (Fig. 9G, L), *Polycirrus glaucus* (Fig. 9M), *Polycirrus disjunctus*, and *Polycirrus abrolhensis*.

46. Heel orientation of neuropodial avicular uncini [cf. character 42(1)]: The orientation of the heel is correlated with its length, and these are two important characters to define type-1 and -2 uncini *sensu* Glasby & Glasby (2006), together with the distance between the base and main fang ('neck'). Heels are short [cf. character 45(0)] and directed posteriorly [character 46(0)] in members of species with type-1 uncini *sensu* Glasby & Glasby (2006) (Fig. 9J–K), and heels are elongate [cf. character 45(1)] and oriented downwards along the main uncinus axis [character 46(1)] among members of species with type-2 uncini *sensu* Glasby & Glasby (2006) (Fig. 9M).

47. Inferior margin of neuropodial avicular uncinus base [cf. character 42(1)]: The bases of uncini, when present (i.e. *Polycirrus* and *Biremis*), are nearly straight [character 47(0)] among members of Polycirridae (Fig. 9G, J–M). Bases are slightly curved [character 47(1)] among members of Telothelepodidae (Fig. 10B).

48. Position of neuropodial uncinus dorsal button (in relation to main fang or most proximal tooth and tip of prow) [cf. character 42(1)]: Members of the Polycirridae have reduced, sometimes nearly inconspicuous, dorsal buttons located along the distal third [character 48(0)], close to the base of the main fang or most proximal tooth (Fig. 9G, J–M). The dorsal button among members of the Telothelepodidae is well developed and located along the proximal third [character 48(1); Fig. 10B] or middle third [character 48(2)] of the distance between the base of the main fang and tip of the prow.
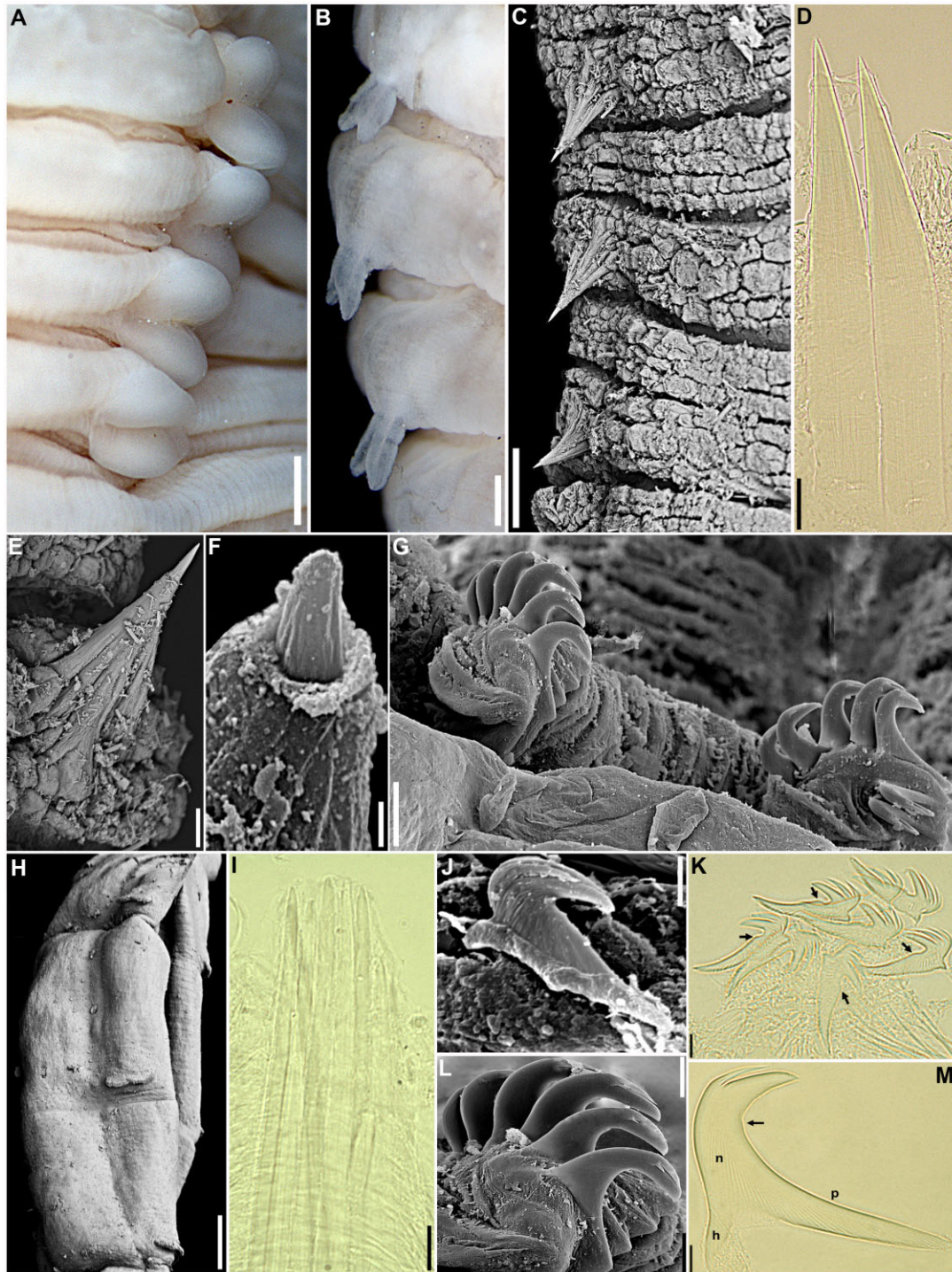
Figure 9. *Biremis blandi* (holotype, USNM 47976): A, B, neuropodia from anterior and posterior body, respectively. *Amaeana apheles* (C, E, AM W10864; D, AM W5384): neuropodia and neurochaetae. *Amaeana* sp. Brazil (MZUSP 2349): F, neurochaeta. *Polycirrus "clavatus"* (MZUSP 1246): G, posterior neuropodia; L, uncini from posterior neuropodium. *Rhinothelepus occabus* (paratype, AM W201904): H, neuropodia from region after notopodia terminate. *Amaeana trilobata* (neotype, ZMO C3207-8): I, neurochaetae from segment 45. *Polycirrus breviuncinatus* (paratype, MZUSP 1245): J, uncinus from posterior neuropodium. *Polycirrus bicrinalis* (paratype, AM W199638): K, uncini from posterior neuropodium. *Polycirrus disjunctus* (paratype, AM W199633): M, uncinus from region after notopodia terminate; b, base; h, heel; n, neck; p, prow. Unspecified arrows point to dorsal buttons. Scale bars: A, 2 mm; B, 4 mm; C, 100 μm; D, 20 μm; E, H, 200 μm; F, 2 μm; G, 30 μm; I, L, 10 μm; J–K, 5 μm; M, 7 μm.

© 2015 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2015, **174**, 666–701
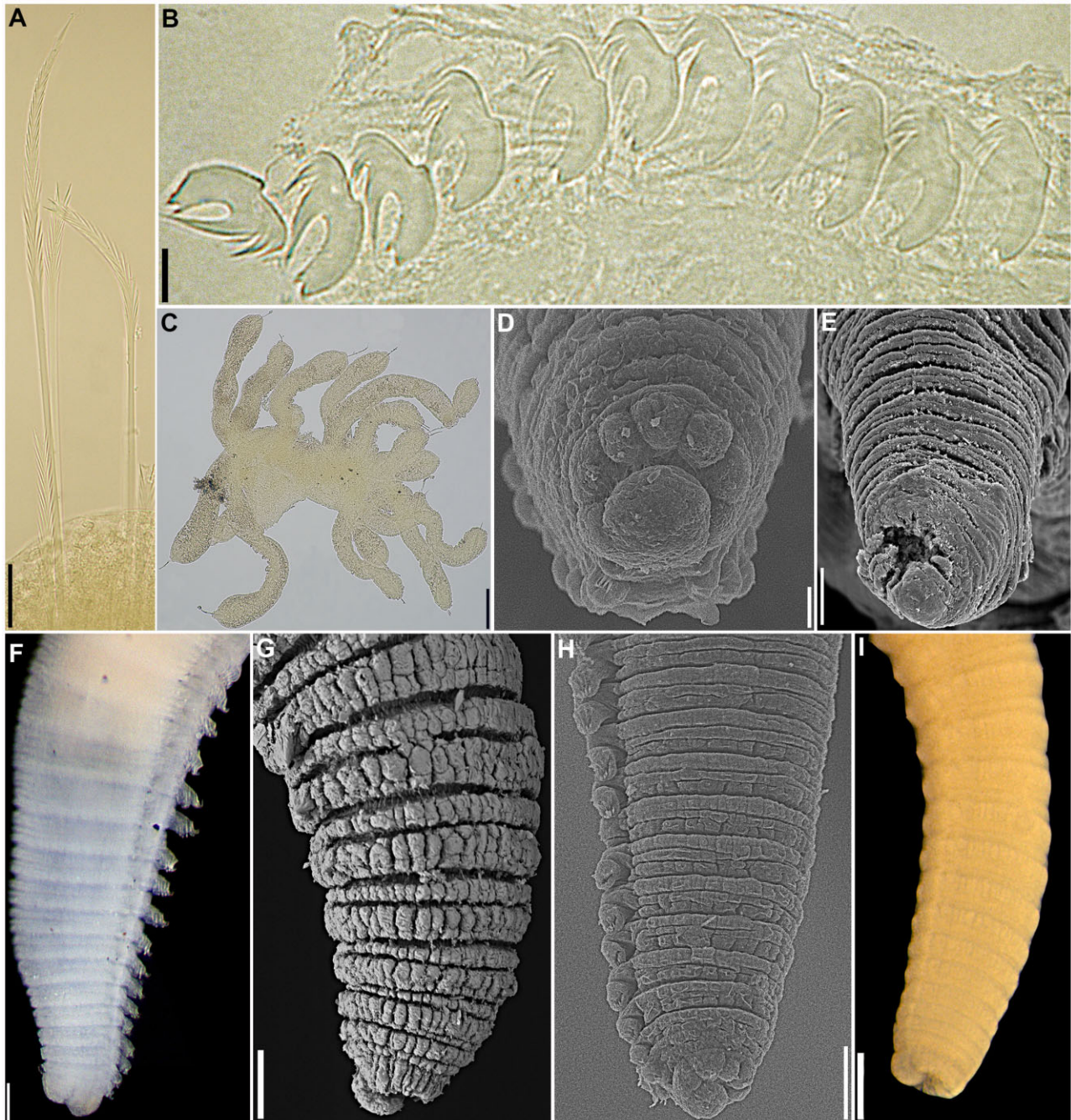
Figure 10. *Enoplobranchus sanguineus* (syntype, YPM 181): A, notochaetae; C, notopodium from mid-body segment. *Decathelepus ocellatus* (holotype, AM W6782): B, uncini, segment 18. *Polycirrus* sp. Hawaii (LACM-AHF): D, posterior end, frontal view; H, posterior end, dorsolateral view. *Polycirrus nonatoi* (paratype, MZUSP 1243): E, posterior end, frontal view. *Polycirrus "clavatus"* (MZUSP 1221): F, posterior end, right dorsolateral view. *Amaeana trilobata* (AM W7050): G, posterior end, left dorsolateral view. *Lysilla laciniata* (holotype, AM W199626): I, posterior end, right lateral view. Scale bars: A, C, 30 μm; B, 6 μm; D, 50 μm; E, G–H, 100 μm; F, 200 μm; I, 0.3 mm.

49. Neuropodial avicular uncinus prow length [cf. character 42(1)]: The prow is the region between the dorsal button and the anteriormost border of an uncinus, or when the dorsal button is absent, the area between the base of the main fang and the distalmost border, in which case the margin is usually pointed or rounded (Nogueira *et al.*, 2013). The prow is long [character 49(1)] among members of the Polycirridae

(Fig. 9G, J–M), and short [character 49(0)] among members of the Telothelepodidae (Fig. 10B).

50. Pygidium: The pygidium is either smooth to crenulate [character 50(0)] or papillate [character 50(1)]. Unfortunately, the pygidium is unknown among members of most of the Telothelepodidae used in this study. Members of the Polycirridae exhibit both characters, but most have at least one large, round, ventral papilla, frequently surrounded by shorter papillae laterally and dorsally (Fig. 10D–I).

INFERENCES OF PHYLOGENETIC HYPOTHESES

Phylogenetic inferences were performed using PAUP* 4.0b10 (Swofford, 2001), with all observations weighted equally and multiple subject–predicate relationships ('multistate characters') treated as 'unordered'. The following command string was implemented (cf. Larkin, Neff & Simpson, 2006; Fitzhugh, 2010; Nogueira, Fitzhugh & Rossi, 2010; Nogueira *et al.*, 2013): hsearch enforce = no start = stepwise addseq = random nreps = 100 000 nchuck = 5 chuckscore = 1; hsearch enforce = no start = current chuckscore = no.

RESULTS

The analysis produced 54 minimum-length trees, of 128 steps each, with consistency index (CI) 0.551 and retention index (RI) 0.813. The strict consensus tree is shown in Figure 11. The individual topologies are uniform in that the Telothelepodidae and Polycirridae are monophyletic. Variation among Polycirridae genera, as indicated by the consensus tree, is the result of ambiguities among most of the non-monotypic genera, i.e. *Polycirrus*, *Lysilla*, and *Amaeana*.

The monophyly of Polycirridae is unambiguously indicated by segment 2 distinctly narrower than adjacent segments [character 19(1)]. An additional character establishing the Polycirridae clade includes the presence of elongate notopodia [character 34(1)], albeit notopodia are absent among members of *Hauchiella* [cf. character 29(1)] and *Biremis blandi* [cf. character 30(1)]. Notochaetae emerging between notopodial lobes [character 37(1)] is a synapomorphy for Polycirridae, albeit notopodia are absent among members of *Biremis blandi* and *Hauchiella*, and notochaetae extend from the nondescript ends of branched notopodia [character 37(2)] among members of *Enoplobranchus sanguineus*. Depending on the transformation series, the Polycirridae clade is also determined by three additional characters (Fig. 12): the upper lip [cf. character 12(1)] is circular [character 13(1)]; glandular ventrolateral pads [cf. character 21(1)] are discretely paired [character 22(0)]; and the mid-ventral groove [cf. character 24(1)] extends from anterior segments 2–5 to the pygidium [character 25(0)]. Alternative transformation series for these three characters present them as plesiomorphic for the Terebelliformia.

Of the non-monotypic Polycirridae genera, *Polycirrus* is paraphyletic among all topologies relative to all remaining genera. Although the clade lies within the *Polycirrus* grade, *Hauchiella* is monophyletic based on the absence of noto- and neuropodia [character 29(1)]. Among all topologies, *Amaeana* is part of the *Lysilla* grade. *Amaeana* can be monophyletic by way of the presence of noto- and neuropodia [character 30(2)], and neurochaetae as distally tapering spines [character 42(2)], or paraphyletic by the inclusion of *Lysilla jennacubinae* Hutchings & Glasby, 1986. *Lysilla* is either para- or polyphyletic relative to *Amaeana*. The *Lysilla–Amaeana* clade is determined by the presence of densely papillate, paired ventral glandular ventrolateral pads [character 23(1)].

DISCUSSION

The principle conclusion to be drawn from the present study is that the status of the phylogenetic hypotheses implied by the names *Polycirrus*, *Amaeana*, and *Lysilla* are empirically unfounded. At least with regard to *Polycirrus*, the present results are consistent with the results obtained by Nogueira *et al.* (2013: fig. 21; Fig. 1) in suggesting the paraphyly of the genus. Although the questionable standing of these genera might be seen as problematic, in fact they are revelations: the tradition of not focusing on monophyly can have detrimental consequences for polychaete systematics.

The equivocal monophyly of *Amaeana* and paraphyly of *Lysilla* obtained in the present study are at least in part attributable to the inherent limits of phylogenetics algorithms, wherein 'inapplicable' entries are not realistically factored into inferences of evolutionary transformation series. Coding to represent 'unknown' ('?', 'inapplicable', and '–') are incorrectly treated as being equivalent(Platnick, Griswold & Coddington, 1991; Strong & Lipscomb, 2005), culminating in hypothetically assigning characters as though unknown and inapplicable are empirically identical. Thus, the instances of para- or polyphyly for *Lysilla* are probably artifacts stemming from the absence of neuropodia and neurochaetae. The artifactual assignments of characters to compensate for 'inapplicable' entries among members of *Lysilla* are probably the cause of *Lysilla jennacubinae* being part of the *Amaeana* clade among some topologies (e.g. Fig. 12). The presence of neurochaetae as tapering spines [character 41(2)] among members of *Amaeana* would seem a clear synapomorphy, but the absence of neurochaetae among members of *Lysilla* [cf. character 30(0)] allow for a spurious transformation series.
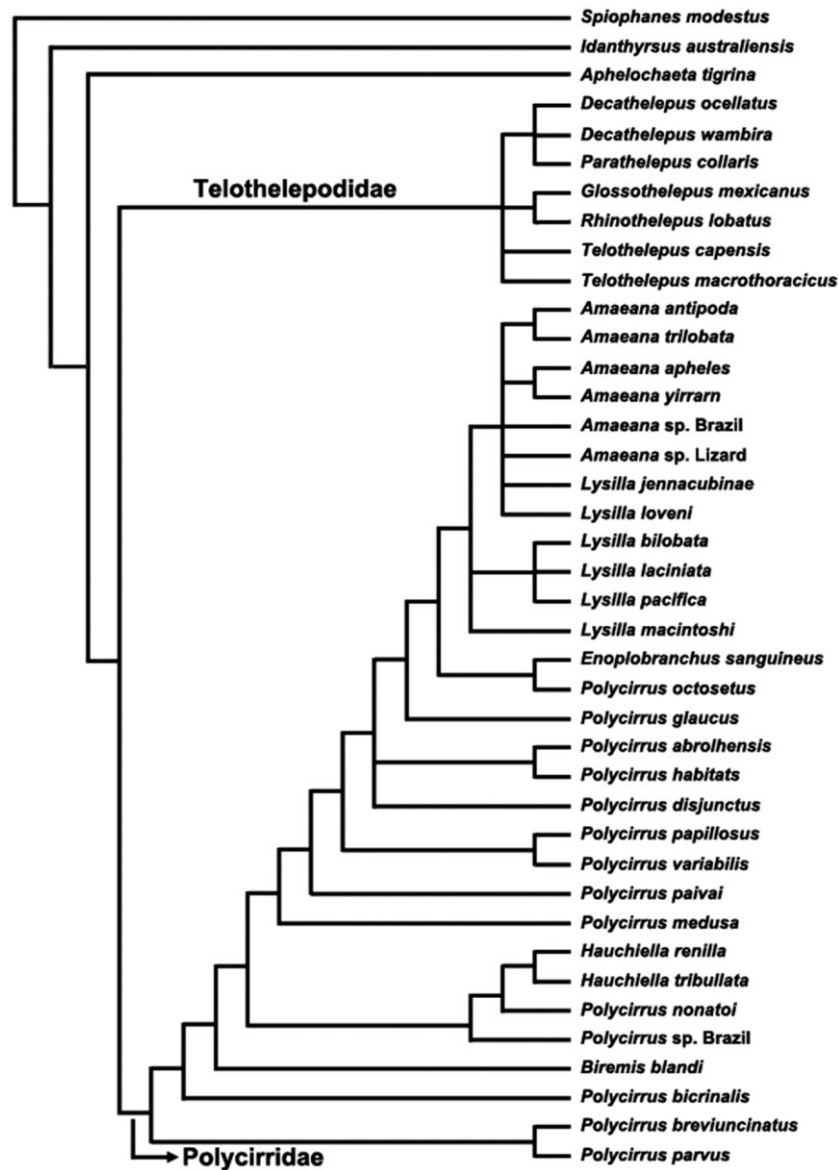
Figure 11. Strict consensus tree of 54 minimum-length cladograms. Note that except for *Hauchiella*, non-monotypic ingroup genera are either para- or polyphyletic, i.e. *Polycirrus*, *Amaeana*, and *Lysilla*.

The most notable issue with the current standing of Polycirridae genera is that *Polycirrus* is not only paraphyletic, but is a grade inclusive of remaining genera. No synapomorphies are known to which any phylogenetic hypotheses refer that warrant the formal name *Polycirrus*. This finding is consistent with results from the extensive revisionary work on the genus by Glasby & Hutchings (2014), and had also been suggested by Hutchings & Glasby (1991). In point of fact, as the objective of inferences in systematics is to causally account for differentially shared features among organisms, the present paper succeeds regardless of not meeting anticipations that particular 'groups' *qua* genera should be delineated. There is a popular view that efforts should be made to salvage as many of the current genera as possible by way of searching for more character data. Regardless of the potential success of introducing more characters, the worthiness of the present taxa are determined by the fact that they are the best hypotheses, given the available observations. The real difficulty at the moment is the inadequacy of phylogenetics algorithms to serve as inference generators that cogently answer the questions implied by data matrices (Fitzhugh, 2006a, 2008a, 2012, 2013).
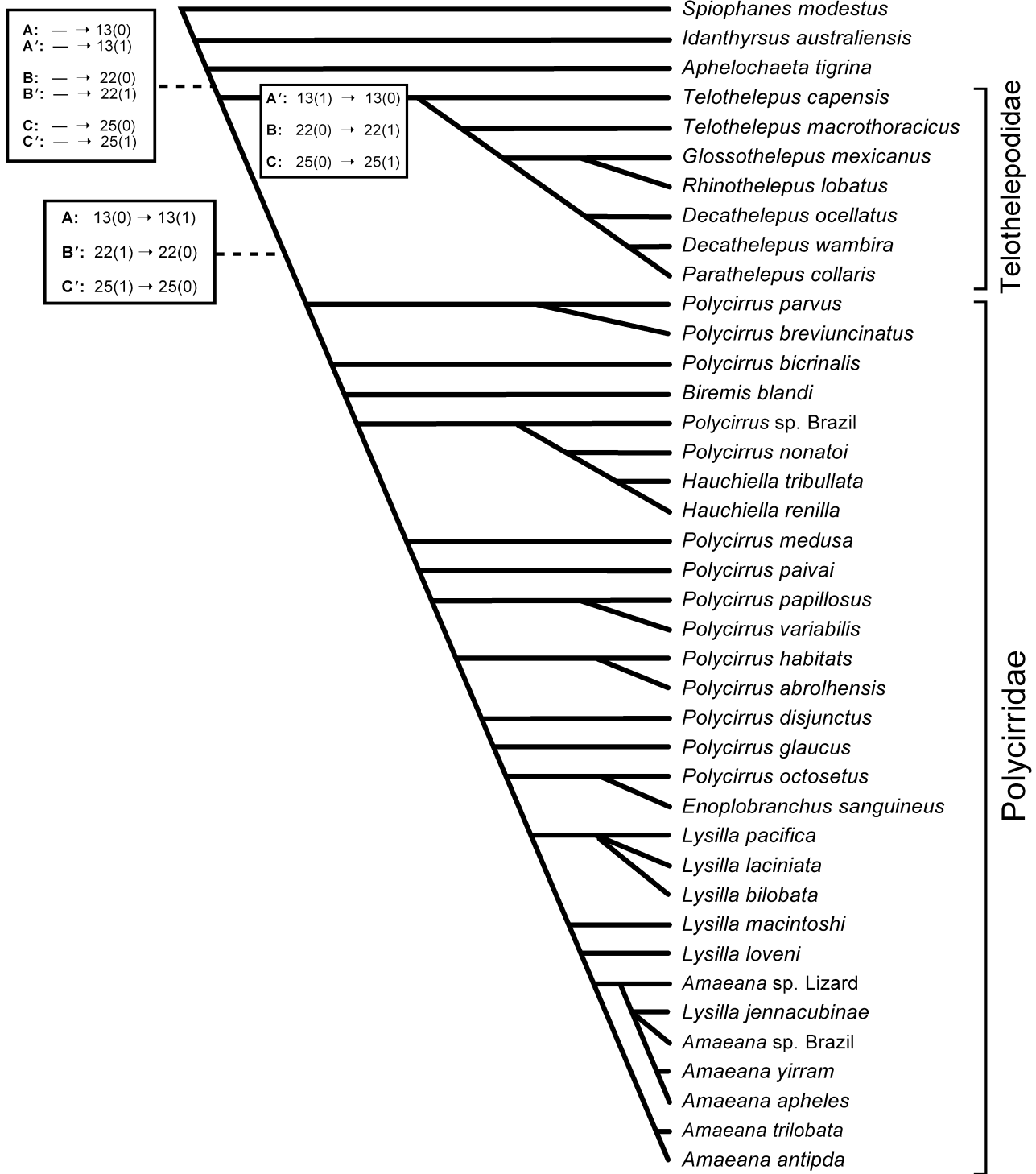
Figure 12. One of the 54 minimum-length cladograms, showing transformation series for characters potentially relevant to defining Polycirridae. A–C and A'–C' refer to respective alternative transformation series.

EVOLUTIONARY TRANSFORMATION SERIES OF
POLYCIRRIDAE CHARACTERS

We alluded to the issue of 'inapplicable' coding as a possible cause of the non-monophyly of *Lysilla* relative to *Amaeana*, as well as the fact that there are no synapomorphies currently recognized for *Polycirrus*. In this section we present some of the transformation series of characters that also contribute to the questionable standings of *Polycirrus*, *Lysilla*, and *Amaeana*.

Anterior end (Fig. 13)
Restriction of the transverse prostomium [cf. character 2(1)] to the base of the upper lip [character 3(0)] is plesiomorphic for Polycirridae, whereas the distal part of the prostomium extending to near the anterior margin of the lip [character 3(1)] forms a grade among members of *Biremis blandi*, *Hauchiella tribullata*, and

several *Polycirrus* species, as well as a synapomorphy for the *Polycirrus octosetus*–*Enoplobranchus sanguineus* clade; character 3(0) is then a synapomorphy at the level of more apomorphic members of *Polycirrus*, as well as *Lysilla* and *Amaeana*. The mid-dorsal process on the anterior margin of the prostomium [character 6(1)] within Polycirridae is restricted to three separate clades among members of some *Lysilla* and *Amaeana*. Buccal tentacles with spatulate tips [character 10(1)] is the plesiomorphic condition for Polycirridae. Among members of a clade within *Amaeana*, however, buccal tentacle tips are broad [character 10(0)], which independently occurs among members of *Lysilla pacifica*. The expanded lower lip [cf. character 14(0)] being cushion-like across the ventrum [character 15(2)] is plesiomorphic for Polycirridae, whereas the lip is mid-ventral [character 15(1)] among members
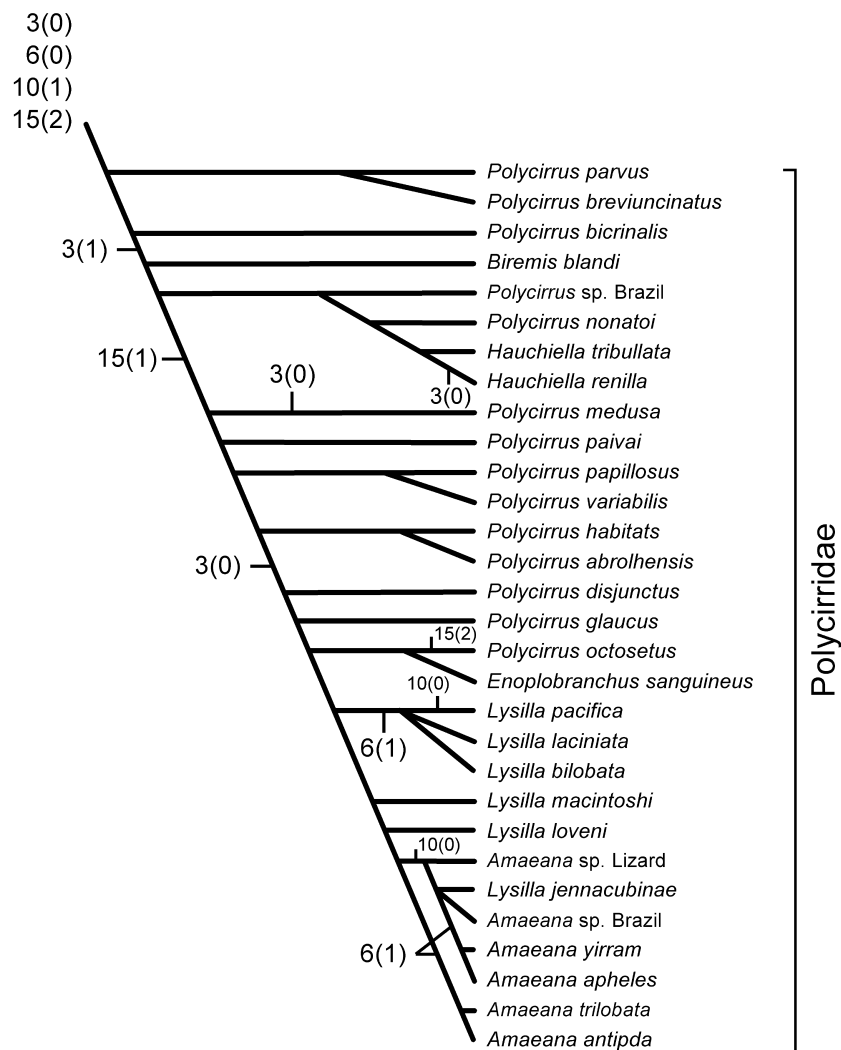

Figure 13. One of the 54 minimum-length cladograms, showing transformation series for selected characters (see also Figs 14–16) that contribute to the non-monophyly of *Polycirrus*, *Lysilla*, and *Amaeana*.

of more apomorphic *Polycirrus* [except for the putative reversal to character 15(2) among members of *Polycirrus octosetus*], *Enoplobranchus*, *Lysilla*, and *Amaeana*.

Anterior segments (Fig. 14)
The visibility of segment 1 (subject 17) presents considerable variation among members of Polycirridae. It is possible that visibility is dependent upon the state of preservation of the specimens, as segment visibility is strongly influenced by the extension of the prostomium, which frequently covers segment 1 laterally, and sometimes also dorsally. Among members of the most plesiomorphic polycirrids, which have a cushion-like lower lip, as discussed above, segment 1 is not usually visible, at least ventrally [characters 17(2) or 17(3)], because of the expanded lip. Among

members of species with a short, mid-ventral lower lip, segment 1 is visible at least ventrolaterally [characters 17(0, 1, 4, or 5)].

Lightly papillate glandular ventrolateral pads [character 23(0)] is the plesiomorphic condition for Polycirridae, but with several independent derivations of the densely papillate condition [character 23(1)] among members of several *Polycirrus* species and *Hauchiella*, as well as a synapomorphy for the *Lysilla–Amaeana* clade.

Nephridial and genital papillae are usually restricted to a few anterior segments [characters 26(1) and 27(0)] among members of Terebelliformia, frequently on segments 5–7 in the telothelepodids and segments 4–7 in the thelepodids, for example. Among the polycirrids, the plesiomorphic condition is absence of papillae [character 26(0)], but with subsequent
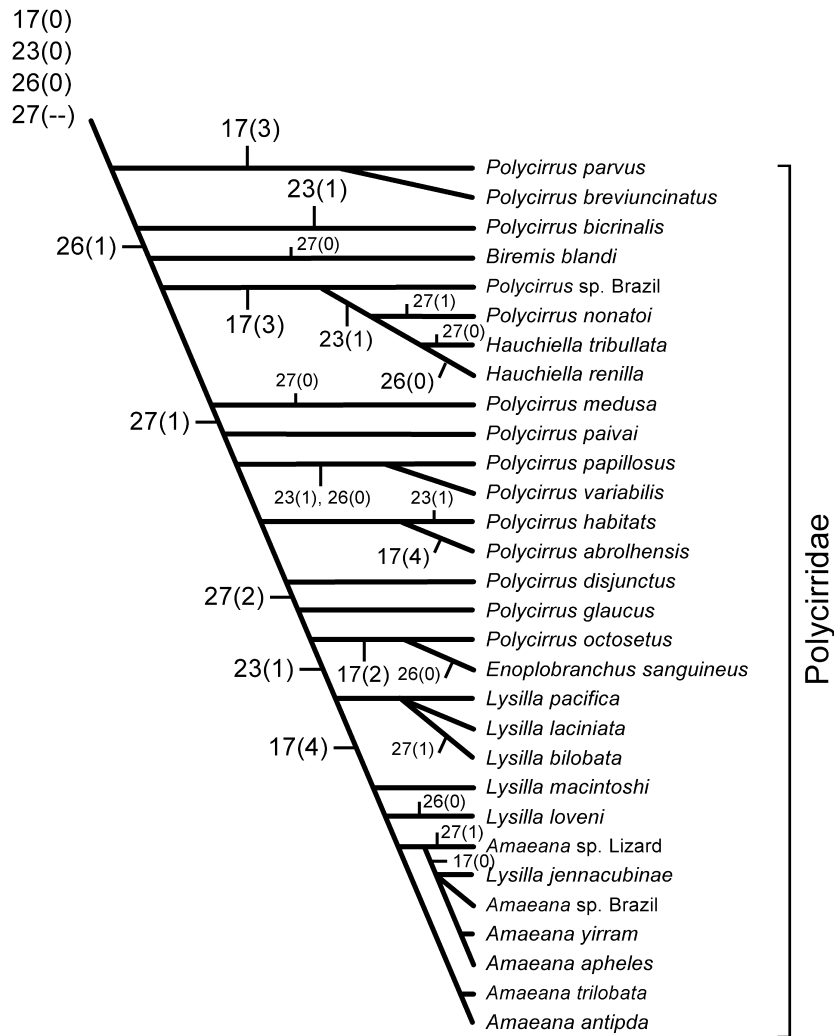

Figure 14. One of the 54 minimum-length cladograms, showing transformation series for selected characters (see also Figs 13, 15–16) that contribute to the non-monophyly of *Polycirrus*, *Lysilla*, and *Amaeana*.

derivation of papillae [character 26(1)] among most members of the family, along with several putative losses among members of some species of *Hauchiella*, *Polycirrus*, *Enoplobranchus*, and *Lysilla*. Regarding the distribution of genital papillae, there is a general tendency towards an increase in the number of pairs of papillae related to the number of pairs of notopodia: from papillae only present on some anterior segments [character 27(0)]; to presence extending to the mid-body but terminating well before notopodia [character 27(1)]; to presence on all, or nearly all, notopodia [character 27(2)].

Parapodia (Fig. 15)
Polycirrids are remarkable for the reduction of parapodia, frequently with loss of one or both parapodial rami. According to our results, the loss of notopodia [character 30(1)] among members of *Biremis blandi*, loss of neuropodia [character 30(0)] among members of *Enoplobranchus* and *Lysilla*, and loss of noto- and neuropodia [character 29(1)] among members of *Hauchiella* occurred independently.

In addition, there is a general tendency towards a reduction in the number of pairs of notopodia among members of Polycirridae species. When present, notopodia begin on segment 3, as is also the case among members of Telothelepodidae. Except for *Polycirrus parvus*, which has fewer pairs, the most plesiomorphic members of polycirrid species have notopodia extending to mid-body [character 32(1)]. Members of more apomorphic taxa have notopodia restricted to 12 segments at most [character 32(0)], usually around ten,
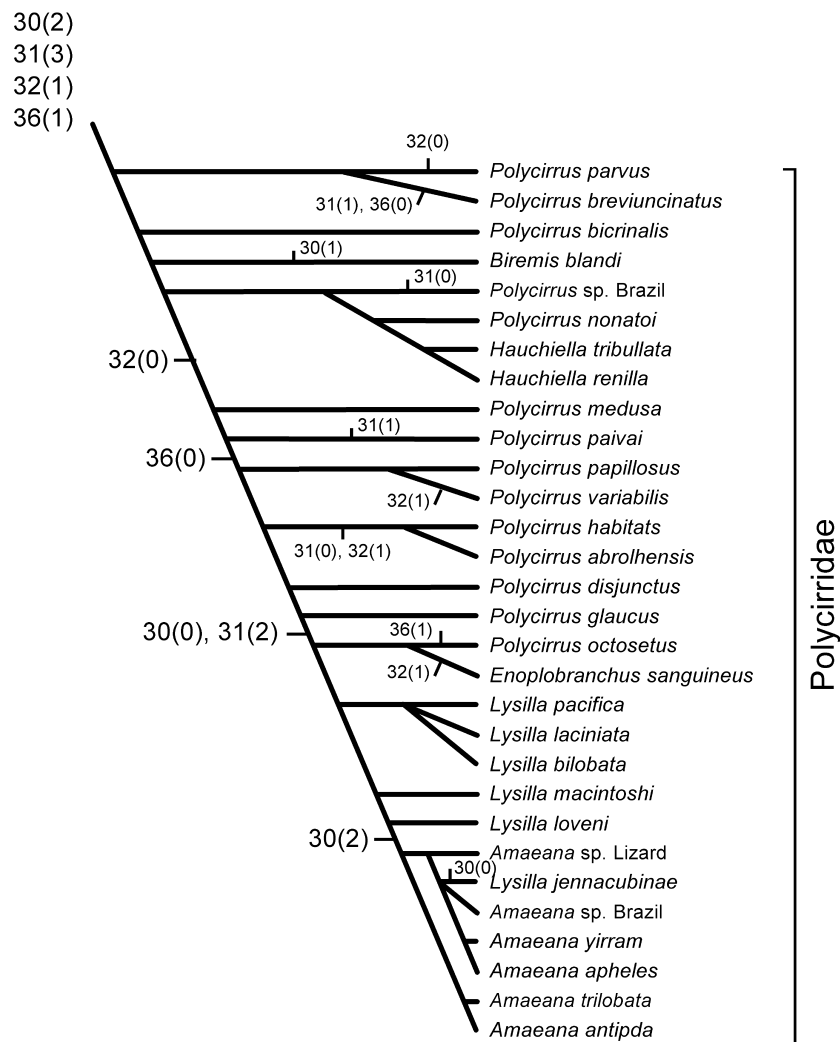

Figure 15. One of the 54 minimum-length cladograms, showing transformation series for selected characters (see also Figs 13–14, 16) that contribute to the non-monophyly of *Polycirrus*, *Lysilla*, and *Amaeana*.

although several independent reversals occur to a greater number. Notable examples of reduced numbers of notopodia occur among *Polycirrus octosetus* and *Lysilla loveni* Malmgren, 1866, each with eight pairs, or *Lysilla macintoshi* Gravier, 1907, with five or six pairs of notopodia extending to segments 7–8.

The plesiomorphic condition for neuropodia distribution is that they begin immediately after the termination of notopodia [character 31(3)]. This condition is found among most members of *Polycirrus*, but within this grade are several independent modifications: neuropodia beginning on last one or two segments with notopodia [character 31(1)], neuropodia on anterior segments [character 31(0)], or neuropodia limited more posteriorly [character 31(2)]. Neuropodia are absent among all members of *Lysilla*, but are present among all members of *Amaeana*, beginning after notopodia terminate [character 31(2)], resulting in an achaetous gap of several segments.

The plesiomorphic condition for the distally bilobed condition of notopodia [cf. character 35(1)] is that the postchaetal lobes are longer than prechaetal lobes [character 36(1)], with more apomorphic members of *Polycirrus* [except *Polycirrus octosetus*, with character 36(1)], *Lysilla*, and *Amaeana*, with lobes of about the same length [character 36(0)].

Chaetae (Fig. 16)
Notochaetae are winged [characters 38(1), 40(1)], with relatively wide wings [characters 39(1), 41(1)] among members of the Telothelepodidae and plesiomorphic Polycirridae. Anterior notochaetal rows are pinnate [character 38(2)] among most members of *Polycirrus* and *Lysilla*. A reversal to the winged character occurs in the clade comprising the most apomorphic members of *Lysilla*, *L. loveni* and *L. jennacubinae*, as well as all members of *Amaeana*, but chaetae are narrowly winged in this latter clade. The pattern of distribution of pinnate notochaetae in posterior rows [character 40(2)] among members of *Polycirrus* differs from that in anterior rows in that they are limited to more apomorphic members.

The traditional definitions of *Amaeana* and *Lysilla* are the absence of neuropodia [cf. character 30(0); Table 1] among members of *Lysilla*, whereas members of *Amaeana* bear neuropodial acicular spines [character 42(2)]. The present results deny such a distinction given the paraphyletic status of *Lysilla* relative to *Amaeana*. Regarding the types of neurochaetae, type-1 uncini [characters 42(1), 43(0), 45(0), and 46(0)] are plesiomorphic, occurring among members of *Biremis blandi* and most included members of *Polycirrus*, whereas more apomorphic members of *Polycirrus* species have type-2 uncini [characters 42(1), 43(1), 45(1), and 46(1)].

Posterior end (Fig. 16)
The plesiomorphic condition for the pygidium among members of Polycirridae is smooth to crenulate [character 50(0)], with the papillate condition [character 50(1)] present among members of most included *Polycirrus* species, *Hauchiella*, *Enoplobranchus*, *Lysilla*, and *Amaeana*. The overall transformation series is, however, quite tentative as in many cases the specimens examined were not complete and the pygidium is unknown.

TAXONOMIC SURROGACY REDUX

The status of Polycirridae genera determined in the present study reinforces the view (cf. Bertrand, Pleijel & Rouse, 2006; Fitzhugh, 2013) that taxonomic surrogacy carries with it distinct epistemic problems. All taxa, including species, are explanatory hypotheses specifically inferred to account for particular sets of characters shared among groups of organisms (Fitzhugh, 2012). Phylogenetic hypotheses are but one class of hypothesis to which the phrase 'supraspecific taxon' applies. Linnean ranks are then recognized for some but not necessarily all of those phylogenetic hypotheses. But as it is generally the case that not all phylogenetic hypotheses are formally named and thus not assigned a rank, it is not possible to equate one taxon at a particular rank with another taxon of the same rank, much less regard the epistemic standing of phylogenetic-level hypotheses as representations or surrogates of species hypotheses. And there is also the disparity between genera with regard to the number of species hypotheses entailed by those phylogenetic hypotheses.

The results in Figure 11 point to another dimension to the problem of taxonomic surrogacy, illustrating the historic consequences of not specifically defining supraspecific taxa in terms of monophyly. If, for instance, one were to accept at face value the generic composition of Polycirridae as part of an environmental characterization of a particular region, those conclusions would be entirely spurious. The fact that polycirrid genera, other than *Hauchiella*, cannot be formally recognized as conveying phylogenetic hypotheses offers a strong case against taxonomic surrogacy. A related problem is the consequence of the requirement of binomial nomenclature imposing the necessity of monotypic taxa. Such taxa lack empirical content as they do not refer to any phylogenetic hypotheses (Fitzhugh, 2008c, 2010). Coupled with the artificial recognition of most polycirrid genera, the monotypic genera *Enoplobranchus* and *Biremis* contribute to the argument that taxonomic surrogacy is lacking in any sound scientific justification.
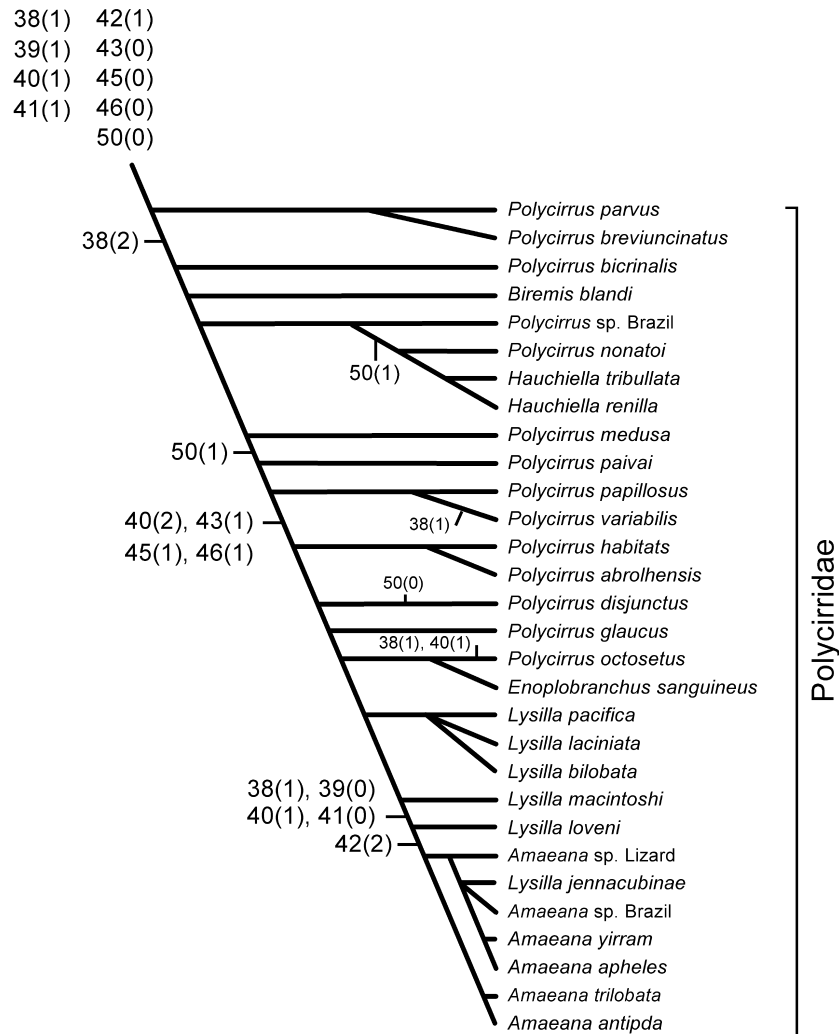
Figure 16. One of the 54 minimum-length cladograms, showing transformation series for selected characters (see also Figs 13–15) that contribute to the non-monophyly of *Polycirrus*, *Lysilla*, and *Amaeana*.

SYSTEMATIC ACCOUNT

Although the results presented in Figure 11 are consistent with those of Nogueira *et al.* (2013: fig. 1) regarding the formal recognition of Polycirridae, the definition is in need of emendation. The format used below follows from the principles of systematics outlined by Fitzhugh (2006b, 2006c, 2008b, 2008c, 2012) and implemented by Fitzhugh (2010), Nogueira *et al.* (2010a), and Nogueira *et al.* (2013). The intent is to convey the causal events, vague as they are, implied by the cladograms. These past events typically only refer to novel character origins and subsequent character fixation within reproductively isolated ancestral populations, followed by population splitting events ('speciation'; cf. Fitzhugh, 2009, 2013). Formal names imply these sets of events (Fitzhugh, 2005a, 2005b, 2006b, 2006c, 2008a, 2008b, 2008c, 2009, 2012).

ORDER TEREBELLIFORMIA

FAMILY POLYCIRRIDAE MALMGREN, 1866 *EMEND.*

Type genus. *Polycirrus* Grube, 1850.

Definition
A phylogenetic hypothesis, unambiguously accounting for segment 2 being distinctly narrower than adjacent segments [character 19(1)]. Also offering explanatory accounts for the following characters (which can also be explained at the level of Terebelliformia, depending on transformation series; cf. Fig. 12): (1) expanded upper lip [cf. character 12(0)] rounded and mid-ventral [character 13(1)]; (2) ventral surfaces of anterior segments [cf. character 21(1)] with discrete, paired glandular ventrolateral pads [character 22(0)]; and (c) mid-ventral groove [cf. character 24(1)] distributed from anterior segments 2–5 to pygidium [character 25(0)].

The presence of notopodia [cf. characters 29(0), 30(0), 30(2)] that are elongate [character 34(1)] is plesiomorphic for Polycirridae; notopodia are, however, absent among members of *Biremis* [character 30(1)] and *Hauchiella* [character 29(1)].

Within a reproductively isolated population of individuals, the distinctly narrower segment 2 [character 19(1)] originated by unspecified mechanism(s) among individuals with the segment of the same width as adjacent segments [character 19(0)], subsequent to which character 19(1) became fixed in the population by an unspecified mechanism(s), and elongate notopodia [character 34(1)] originated by unspecified mechanism(s) among individuals with short notopodia [character 34(0)], subsequent to which character 34(1) became fixed in the population by unspecified mechanism(s) (with subsequent losses of notopodia among members of *Hauchiella* and *Biremis blandi*). Additional tentative causal events (cf. Fig. 12) include: (1′) the expanded upper lip [cf. character 12(1)] being rounded and mid-ventral [character 13(1)], originated by unspecified mechanism(s) among individuals with an elongate, narrow upper lip [character 13(0)], subsequent to which character 13(1) became fixed in the population by unspecified mechanism(s); (2′) ventral surfaces of anterior segments [cf. character 21(1)] with discrete, paired glandular ventrolateral pads [character 22(0)], originated by unspecified mechanism(s) among individuals with a generalized glandular surface [character 21(1)], subsequent to which character 22(0) became fixed in the population by unspecified mechanism(s); and (3′) the mid-ventral groove [cf. character 24(1)] extending from posterior segments with notopodia to the pygidium [character 25(0)], originated by unspecified mechanism(s) among individuals with a groove extending from anterior segments to the pygidium [character 25(1)], subsequent to which character 25(0) became fixed in the population by unspecified mechanism(s). Following the character origin/fixation events in (1′)–(3′) were a series of population splitting events, leading to individuals to which lower-level systematics hypotheses refer (i.e. phylogenetic and specific).

Remarks

The emended definition of Polycirridae is perhaps excessively liberal in that it not only includes an explanation of segment 2 [character 19(1)] as an unambiguous synapomorphy, but also includes explanations of the presence of the rounded, mid-ventral upper lip [character 13(1)], discrete, paired glandular ventrolateral pads [character 22(0)], mid-ventral groove along most of the body length [character 25(0)], and elongate notopodia [character 34(1)]. As noted above, although character 34(1) can be regarded as a synapomorphy for Polycirridae, notopodia/notochaetae are absent among members of *Hauchiella* and *Biremis*. Characters 13(1), 22(0), and 25(0) are synapomorphies for Polycirridae under one possible set of evolutionary transformation series, but can be explained at the more general level of Terebelliformia in the other transformation series (Fig. 12).

The present definition differs from that provided by Nogueira *et al.* (2013) by the inclusion of the rounded, mid-ventral lower lip [character 13(1)] and notopodia, when present, being elongate [character 34(1)]. The following characters are no longer regarded as synapomorphies: presence of two types of prostomial buccal tentacles [character 8(1)]; neuropodia beginning after termination of notopodia [character 31(2)]; and papillate pygidium [character 5(1)]. The only character that is consistent between this study and that of Nogueira *et al.* (2013) is segment 2 distinctly narrower than adjacent segments [character 19(1)].

visiting their institutions and fruitful discussions. The SEM photos were taken by Sue Lindsay, from the AM, by Lara Guimarães, from the MZUSP, and by Enio Mattos and Phillip Lenktaitis, from the IB-USP. Leslie Harris (LACMNH) generously hosted JMMN and OC at her house during visits to the LACMNH, allowed them to use her stereomicroscope and camera, and also provided fruitful discussions and many other kind favours.

REFERENCES

Bertrand Y, Pleijel F, Rouse G. 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnean ranks. *Systematics and Biodiversity* **4:** 149–159.

Blake JA. 1996. Family Cirratulidae Ryckholdt, 1851. Including a revision of the genera and species from the eastern north Pacific. In: Blake JA, Hilbig B, Scott PH, eds. *Taxonomic atlas of the benthic fauna of the santa maria basin and the western santa barbara channel. volume* 6: *the Annelida part 3, Polychaeta: Orbiniidae to Cossuridae.* Santa Barbara: Santa Barbara Museum of Natural History, 263–384.

Colgan DJ, Hutchings PA, Brown S. 2001. Phylogenetic relationships within the Terebellomorpha. *Journal of Marine Biological Association UK* **81:** 765–773.

Day JH. 1967. A monograph on the Polychaeta of southern Africa. *British Museum of Natural History* **656:** 1–878.

Fauchald K. 1977. The polychaete worms. Definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County, Science Series* **28:** 1–188.

Fauvel P. 1927. Polychètes sédentaires. Addenda aux Errantes, Archiannélides, Myzostomaires. *Faune de France* **16:** 1–494.

Fitzhugh K. 2005a. Les bases philosophiques de l'inférence phylogénétique: une vue d'ensemble. *Biosystema* **24:** 83–105.

Fitzhugh K. 2005b. The inferential basis of species hypotheses: the solution to defining the term 'species.'. *Marine Ecology* **26:** 155–165.

Fitzhugh K. 2006a. The philosophical basis of character coding for the inference of phylogenetic hypotheses. *Zoologica Scripta* **35:** 261–286.

Fitzhugh K. 2006b. The abduction of phylogenetic hypotheses. *Zootaxa* **1145:** 1–110.

Fitzhugh K. 2006c. The 'requirement of total evidence' and its role in phylogenetic systematics. *Biology & Philosophy* **21:** 309–351.

Fitzhugh K. 2008a. Clarifying the role of character loss in phylogenetic inference. *Zoologica Scripta* **37:** 561–569.

Fitzhugh K. 2008b. Fact, theory, test and evolution. *Zoologica Scripta* **37:** 109–113.

Fitzhugh K. 2008c. Abductive inference: implications for 'Linnean' and phylogenetic' approaches for representing biological systematization. *Evolutionary Biology* **35:** 52–82.

Fitzhugh K. 2009. Species as explanatory hypotheses: refinements and implications. *Acta Biotheoretica* **57:** 201–248.

Fitzhugh K. 2010. Revised systematics of *Fabricia oregonica* Banse, 1956 (Polychaeta: Sabellidae: Fabriciinae): an example of the need for a uninomial nomenclatural system. *Zootaxa* **2647:** 35–50.

Fitzhugh K. 2012. The limits of understanding in biological systematics. *Zootaxa* **3435:** 40–67.

Fitzhugh K. 2013. Defining 'species,' 'biodiversity,' and 'conservation' by their transitive relations. In: Pavlinov IY, ed. *The species problem? Ongoing problems.* Rijeka: InTech, 93–130.

Fitzhugh K. 2014. Character mapping and cladogram comparison versus the requirement of total evidence: does it matter for polychaete systematics? *Memoirs of Museum Victoria* **71:** 67–78.

Garraffoni ARS, Lana PC. 2008. Phylogenetic relationships within the Terebellidae (Polychaeta: Terebellida) based on morphological characters. *Invertebrate Systematics* **22:** 605–626.

Glasby CJ, Glasby TM. 2006. Two types of uncini in *Polycirrus* (Polychaeta: Terebellidae: Polycirrinae) revealed using geometric morphometrics. *Journal of Natural History* **40:** 237–253.

Glasby CJ, Hutchings P. 2014. Revision of the taxonomy of *Polycirrus* Grube, 1850 (Annelida: Terebellida: Polycirridae). *Zootaxa* **3877:** 1–117.

Glasby CJ, Hutchings PA, Hall K. 2004. Phylogeny of the polychaete order Terebellomorpha (Polychaeta: Terebellidae) based on morphology. *Journal of Marine Biological Association UK* **84:** 961–971.

Grube A-E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte, Berlin* **16:** 249–364.

Hessle C. 1917. Zur Kenntnis der terebellomorphen Polychaeten. *Zoologiska bidrag från Uppsala* **5:** 39–258.

Holthe T. 1986. Evolution, systematics, and distribution of the Polychaeta Terebellomorph, with a catalogue of the taxa and a bibliography. *Gunneria* **55:** 1–236.

Hutchings PA, Glasby CJ. 1986a. The Polycirrinae (F. Terebellidae) of Australia. *Records of the Australian Museum* **38:** 319–350.

Hutchings PA, Glasby CJ. 1986b. A new genus of Thelepinae (F. Terebellidae) *Glossothelepus* from Mexico. *Proceedings of the Biological Society of Washington* **99:** 84–87.

Hutchings PA, Glasby CJ. 1987. The Thelepinae (F. Terebellidae) from Australia together with a discussion of the generic and specific characters of the family. *Bulletin of the Biological Society of Washington* **7:** 217–250.

Hutchings PA, Glasby CJ. 1991. A cladistic analysis of the Polycirrinae (Polychaeta: Terebellidae) and the genus *Polycirrus* (Terebellidae: Polycirrinae). *Bulletin of Marine Science* **48:** 589. (abstract only).

Larkin LL, Neff JL, Simpson BB. 2006. Phylogeny of the *Callandrena* subgenus of *Andrena* (Hymenoptera: Andrenidae) based on mitochondrial and nuclear DNA data: polyphyly and convergent evolution. *Molecular Phylogenetics and Evolution* **38:** 330–343.

Malmgren AJ. 1866. Nordiska Hafs-Annulater. *Oefversigt Kongliga Vetenskaps Akademien Stockholm, Forhandlingar* **22:** 355–410. pls. 18–29.

Nogueira JMM, Fitzhugh K, Hutchings P. 2013. The continuing challenge of phylogenetic relationships in

Terebelliformia (Annelida: Polychaeta). *Invertebrate Systematics* **27:** 186–238.

Nogueira JMM, Fitzhugh K, Rossi MCS. 2010a. A new genus and new species of fan worms (Polychaeta: Sabellidae) from Atlantic and Pacific Oceans – the formal treatment of taxon names as explanatory hypotheses. *Zootaxa* **2603:** 1–52.

Nogueira JMM, Hutchings PA, Fukuda MV. 2010b. Morphology of terebelliform polychaetes (Annelida: Polychaeta: Terebelliformia), with a focus on Terebellidae. *Zootaxa* **2460:** 1–185.

Platnick N, Griswold CE, Coddington JA. 1991. On missing entries in cladistic analysis. *Cladistics* **7:** 337–343.

Strong EE, Lipscomb D. 2005. Character coding and inapplicable data. *Cladistics* **15:** 363–371.

Swofford DL. 2001. *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4.0b10*. Sunderland: Sinauer Associates.

Zhadan AE, Tzetlin AB. 2002. Comparative morphology of the feeding apparatus in the Terebellida (Annelida: Polychaeta). *Cahiers de Biologie Marine* **43:** 149–164.