New genera and species from the Equatorial Pacific provide phylogenetic insights into deep-sea Polynoidae (Annelida)

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Polynoidae contains ~900 species within 18 subfamilies, some of them restricted to the deep sea. Macellicephalinae is the most diverse among these deep-sea subfamilies. In the abyssal Equatorial Pacific Ocean, the biodiversity of benthic communities is at stake in the Clarion-Clipperton Fracture Zone (CCFZ) owing to increased industrial interest in polymetallic nodules. The records of polychaetes in this region are scarce. Data gathered during the JPI Oceans cruise SO239 made a significant contribution to fill this gap, with five different localities sampled between 4000 and 5000 m depth. Benthic samples collected using an epibenthic sledge or a remotely operated vehicle resulted in a large collection of polynoids. The aims of this study are as follows: (1) to describe new species of deep-sea polynoids using morphology and molecular data (+ COI, 16S and 18S); and (2) to evaluate the monophyly of Macellicephalinae. Based on molecular and morphological phylogenetic analyses, ten subfamilies are synonymized with Macellicephalinae in order to create a homogeneous clade determined by the absence of lateral antennae. Within this clade, the Anantennata clade was well supported, being determined by the absence of a median antenna. Furthermore, 17 new species and four new genera are described, highlighting the high diversity hidden in the deep. A taxonomic key for the 37 valid genera of the subfamily Macellicephalinae is provided.

ADDITIONAL KEYWORDS: deep sea – identification key – molecular systematics – morphology – new genera – new species – phylogeny – Polychaeta.

INTRODUCTION

The family Polynoidae Kinberg, 1856 is one of six families called scale worms (Aphroditiformia). With ~900 species belonging to 167 genera in 18 subfamilies (Wehe, 2006; Norlinder et al., 2012; Read & Fauchald, 2018), polynoids are the most diverse polychaetes in number of genera and the second most diverse in number of species (Hutchings, 2000; Wehe, 2006; Read & Fauchald, 2018). They are errant worms with wide-ranging distribution, from shallow intertidal waters to hadal trenches (Hartmann-Schröder, 1974; Fauchald, 1977; Hutchings, 2000). However, 13 subfamilies appear to be restricted to the deep sea (mostly below 500 m depth), from bathyal to hadal depths, including specialized chemosynthetic habitats and, more rarely, analogous habitats, such as submarine caves in shallow waters (i.e. Admetellinae Uschakov, 1977, Bathydithininae Pettibone, 1976, Bathymacellinae Pettibone, 1976, Branchinotogluminae Pettibone, 1985a, Branchiplicatinae Pettibone, 1985b, Branchipolynoinae Pettibone, 1984a, Eulagiscinae Pettibone, 1997, Lepidonotopodinae Pettibone, 1983, Macelorhaphidinae Hartmann-Schröder, 1971, Macellicephaloidinae Pettibone, 1976, Macelloidinae Pettibone, 1976, Polaruschakovinae Pettibone, 1976 and Vampiropolynoinae Marcus & Hourdez, 2002). Deep-sea polynoids typically have different numbers of cephalic appendices compared with their shallow-water counterparts. The usual form of the polynoid prostomium bears three antennae (one median antenna and two lateral antennae) and is commonly observed in shallow waters but also in few deep-sea subfamilies (i.e. Admetellinae, Bathymacellinae and Eulagiscinae). The main features differentiating the other deep-sea subfamilies are the absence of lateral antennae (Branchinotogluminae, Bathymacellinae, and Eulagiscinae).
Branchiplicatinae, Branchipolynoinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Lepidonotopodinae and Vampiropolynoinae) or the complete absence of antennae (Bathyedithinae and Polaruschakovinae). The subfamilies Branchinotogluminae, Branchiplicatinae, Branchipolynoinae, Lepidonotopodinae, Macellicephalinae (genera Bathykurila Pettibone, 1976 and Levensteiniella Pettibone, 1985c) and Vampiropolynoinae have been successful in exploiting deep-sea chemosynthetic ecosystems, such as hydrothermal vents and cold seeps (Pettibone, 1983, 1984a, 1985a, b, 1986; Marcus & Hourdez, 2002). Many of these thermal vents and cold seeps (Pettibone, 1983, 1984a, 1985b, 1986) have been described in studies of deep-sea chemosynthetic ecosystems, such as hydrothermal vents and cold seeps (Pettibone, 1983, 1984a, 1985a, b, 1986; Marcus & Hourdez, 2002). Many of these vent communities have been successful in exploiting deep-sea chemosynthetic ecosystems, such as hydrothermal vents and cold seeps (Pettibone, 1983, 1984a, 1985a, b, 1986; Marcus & Hourdez, 2002). Many of these deep-sea communities have been successful in exploiting deep-sea chemosynthetic ecosystems, such as hydrothermal vents and cold seeps (Pettibone, 1983, 1984a, 1985a, b, 1986; Marcus & Hourdez, 2002).

The first species described from the deep-sea environment was Polynoe (Macellicepha) mirabilis McIntosh, 1885, collected from off the coast of New Zealand during the Challenger Expedition (1280 m depth, station 169, 37°34′S, 179°22′E). The subfamily Macellicephalinae was erected by Hartmann-Schröder (1971) in order to group the genus Macellicepha McIntosh, 1885 and other representatives from great oceanic depths fitting the following diagnosis: median antenna absent or present; and lateral antennae absent. In a review of the 37 known species, which were attributed, directly or indirectly, to the subfamily Macellicephalinae, Pettibone (1976) erected five new subfamilies (Bathyedithinae, Bathymacellinae, Macellicephalinae, Macellicephaloidinae and Polaruschakovinae) and ten new genera, many of them monotypic. With the production of taxonomic keys for subfamilies, genera and species, this remains the most important work concerning the morphological identity of the subfamily Macellicephalinae. Ussakov (1977, 1982) suggested the presence of derived character states in the worms from this subfamily (e.g. short body and reduction of jaws), hypothesizing that they originated from a common ancestor with genus Bathymoorea Pettibone, 1967. Two studies using combined morphological and molecular data have already suggested the paraphyly of the subfamily Macellicephalinae. Norlinder et al. (2012) showed a well-supported clade (three representatives of deep-sea subfamilies) with members of the subfamilies Macellicephalinae, Branchinotogluminae and Branchipolynoinae. However, owing to the limited number of sequences from deep-sea subfamilies available, no hypothesis about their relationships was developed. In a larger, but still limited, number of seven representative species of deep-sea subfamilies, Gonzalez et al. (2017, 2018) uncovered two main clades: (1) Macellicephalinae, Branchinotogluminae and Branchipolynoinae, similar to Norlinder et al. (2012); and (2) a clade composed only of members of Macellicephalinae. The lack of knowledge about deep-sea polynoids inevitably reflects the small number of samples, particularly DNA friendly, from the deep sea. The relative larger body size, low density and high mobility of polynoids reduce the probability of adequate sampling with the widely used quantitative methods (i.e. box cores, mega-cores; e.g. De Smet et al., 2017). However, a greater abundance of worms can be sampled with qualitative methods, such as an epibenthic sledges (EBS; e.g. Brant & Schnack, 1999; Janssen et al., 2015), which can capture mobile epibenthos, such as polynoids.
Material and Methods

The Clarion-Clipperton Fracture Zone (CCFZ) is the largest polymetallic nodule field in the world, with ~6 million km$^2$ of seabed lying between 4000 and 6000 m depth. Mining these nodules might directly impact 300–800 km$^2$ yr$^{-1}$ of the seafloor, and sediment plume re-deposition might indirectly increase the footprint of mining by a factor two to five (Glover & Smith, 2003).

The polychaete fauna in the CCFZ is highly diverse (up to 113 taxa per 0.25 m$^2$) but remains largely undescribed (~5–10% of worms identified to named species; Glover et al., 2002). The polynoids of CCFZ are virtually unknown.

A large collection of deep-sea polynoids collected from epibenthic sledges and a remotely operated vehicle deployed during the JPI Oceans cruise SO239 led to the discovery of ~80 molecular operational taxonomic units (MOTUs) and, for the first time ever, enabled us to provide insights into the phylogeny of this poorly understood group. In this context, the aims of this work were as follows: (1) to describe 17 new species of deep-sea polynoids using morphology together with molecular data in most cases (COI, 16S and 18S); and (2) to assess the monophyly of the subfamily Macellicephala inae.

Morphology

The specimens were live sorted, photographed with a Canon EOS 700D, fixed in cold (−20 °C) 80% ethanol and kept at −20 °C. In the laboratory, a small piece of tissue (e.g. a few parapodia, an end of the body or tissue from the pharynx when everted) was sampled and fixed in cold 96% ethanol for molecular studies (see DNA extraction, amplification, sequencing and alignment). Preserved specimens were examined under a Leica M125 stereomicroscope and a Nikon Eclipse E400 microscope and photographed with a Nikon DS-Ri 2 camera. Body length and width (at segment 4, without parapodia) were measured using Leica LAS Interactive Measurements. Drawings were carried out on stacked (overlapped and aligned) pictures on an iPad Pro using an Apple pencil and Graphic App, with formatting using Adobe Illustrator and Photoshop to assemble them into plates. Specimens examined with scanning electron microscopy (SEM) were prepared by
dehydration with three immersions of 15 min each in 96% ethanol, critical-point drying, and being covered with gold and photographed using the Quanta200 FEI (Ifremer). Morphological characters were coded either from original descriptions or redescriptions; from Gonzalez et al., (2018), who examined specimens of Gesiella jameensis, Halosydnella australis, Harmothoe rarispina and Pelagomacellicephala iliffei; or from morphological examination of type specimens described in this study. From Gonzalez et al. (2018), 50 out of 87 coded characters were used in the present study. In addition, 24 characters were newly included in order to represent the morphological characters of deep-sea subfamilies. Seventy-four characters (Supporting Information, Appendix S1) were included in a morphological data matrix (Supporting Information, Appendix S2). However, the characters that were regularly missing in the literature or were doubtful (e.g. number or size of pharyngeal papillae) were not included in the matrix.

Type specimens were deposited at the Muséum National d’Histoire Naturelle de Paris (MNHN, France) and at the Natural History Museum, London (NHM, UK). Additional material was mostly archived at the MNHN, and a few specimens remain in the private collection of P.B., as recorded in the ‘Material examined’ sections and Table 1.

DNA EXTRACTION, AMPLIFICATION, SEQUENCING AND ALIGNMENT

Subsamples for DNA analysis were removed from live specimens, placed in 96% ethanol and frozen at −20 °C. Extraction of DNA was done with a NucleoSpin Tissue (Macherey-Nagel) kit, following the protocol supplied by the manufacturers. Approximately 450 bp of 16S, 700 bp of COI (cytochrome c oxidase subunit I) and 1800 bp of 18S genes were amplified using the following primers: Ann16SF and 16SbrH for 16S (Palumbi, 1996; Sjölin, et al., 2005); polyLCO, polyHCO, LCO1490 and HCO2198 for COI (Folmer et al., 1994; Carr et al., 2011); and 18SA, 18SB, 620F and 1324R for 18S (Cohen et al., 1998; Medlin et al., 1998; Nygren & Sundberg, 2003) for 18S. The polymerase chain reaction (PCR), with 25 μL mixtures containing: 5 μL of Green GoTaq Flexi Buffer (final concentration of 1×), 2.5 μL of MgCl₂ solution (final concentration of 2.5 mM), 0.5 μL of PCR nucleotide mix (final concentration of 0.2 mM of each dNTP), 9.875 μL of nuclease-free water, 2.5 μL of each primer (final concentration of 1 μM), 2 μL template DNA and 0.125 U of GoTaq G2 Flexi DNA Polymerase (Promega). The temperature profile was as follows: 95 °C for 240 s, followed by [94 °C for 30 s, 52 °C for 60 s and 72 °C for 75 s (for 16S and COI) or 180 s (for 18S) for 35 cycles (for 16S and 18S) or for 40 cycles (for COI)], with a final extension at 72 °C for 480 s, kept at by 4 °C. The PCR products that produced light bands
Table 1. GenBank accession numbers, museum record and Ifremer codes of newly described and sequenced species in the present study using COI, 16S and 18S genes

| Newly sequenced taxa | Status | Ifremer | Voucher | COI       | 16S       | 18S       |
|----------------------|--------|---------|---------|-----------|-----------|-----------|
| Abyssarya acus gen. nov., sp. nov. | Holotype | 632-2 | MNHN-IA-TYPE 1811 | MH233277 | MH233179 | MH233231 |
| Abyssarya acus gen. nov., sp. nov. | Paratype 1 | 632-5 | MNHN-IA-TYPE 1812 | MH233279 | MH233182 | MH233232 |
| Abyssarya acus gen. nov., sp. nov. | Paratype 2 | 632-1 | MNHN-IA-TYPE 1813 | MH233276 | MH233178 | MH233230 |
| Abyssarya acus gen. nov., sp. nov. | Paratype 3 | 632-3 | NHMUK 2018.25346 | MH233278 | MH233180 | –         |
| Abyssarya acus gen. nov., sp. nov. | Additional 1 | 632-4 | P.B.’s collection | – | MH233181 | –         |
| Bathyedithia retierei sp. nov. | Holotype | 451b | MNHN-IA-TYPE 1814 | – | MH233157 | MH233215 |
| Bathyeliaisona mari-aee sp. nov. | Holotype | 107 | MNHN-IA-TYPE 1815 | MH233249 | MH233149 | MH233204 |
| Bathyeliaisona mari-aee sp. nov. | Paratype | 666-4 | MNHN-IA-TYPE 1816 | MH233260 | MH233197 | MH233243 |
| Bathyfauvelia glacigena sp. nov. | Holotype | 521-1 | MNHN-IA-TYPE 1817 | MH233274 | MH233160 | MH233218 |
| Bathyfauvelia glacigena sp. nov. | Paratype 1 | 302 | MNHN-IA-TYPE 1818 | – | MH233152 | MH233208 |
| Bathyfauvelia glacigena sp. nov. | Paratype 2 | 529-2-1 | NHMUK 2018.25347 | – | MH233162 | MH233220 |
| Bathyfauvelia glacigena sp. nov. | Additional 1 | 520-7 | MNHN-IA-PNT 74 | – | MH233159 | MH233217 |
| Bathyfauvelia glacigena sp. nov. | Additional 2 | 529-2-2 | MNHN-IA-PNT 75 | MH233253 | MH233163 | MH233221 |
| Bathyfauvelia glacigena sp. nov. | Additional 3 | 636-5-4 | P.B.’s collection | MH233272 | MH233186 | MH233236 |
| Bathyfauvelia glacigena sp. nov. | Holotype | 674-2 | MNHN-IA-TYPE 1819 | MH233262 | MH233200 | MH233246 |
| Bathyfauvelia glacigena sp. nov. | Paratype 1 | 521-3 | MNHN-IA-TYPE 1820 | MH233252 | MH233161 | –         |
| Bathyfauvelia glacigena sp. nov. | Paratype 2 | 655-1-1 | NHMUK 2018.25348 | MH233287 | MH233188 | –         |
| Bathyfauvelia glacigena sp. nov. | Additional 1 | 665 | MNHN-IA-PNT 76 | MH233289 | MH233196 | –         |
| Bathyfauvelia glacigena sp. nov. | Additional 2 | 694 | P.B.’s collection | MH233264 | MH233202 | –         |
| Bathymoorea lucasi sp. nov. | Holotype | 601-1 | MNHN-IA-TYPE 1821 | MH233267 | MH233166 | –         |
| Bathymoorea lucasi sp. nov. | Paratype 1 | 600 | MNHN-IA-TYPE 1822 | MH233266 | MH233165 | MH233223 |
| Bathymoorea lucasi sp. nov. | Paratype 2 | 601-7 | MNHN-IA-TYPE 1823 | MH233255 | MH233172 | MH233224 |
| Bathymoorea lucasi sp. nov. | Paratype 3 | 601-6 | NHMUK 2018.25349 | – | MH233171 | –         |
| Bathymoorea lucasi sp. nov. | Paratype 4 | 601-2 | MNHN-IA-TYPE 1844 | MH233284 | MH233167 | –         |
| Bathymoorea lucasi sp. nov. | Additional 1 | 601-3 | MNHN-IA-PNT 77 | MH233285 | MH233168 | –         |
| Bathymoorea lucasi sp. nov. | Additional 2 | 601-4 | MNHN-IA-PNT 78 | – | MH233169 | –         |
Table 1. Continued

| Newly sequenced taxa | Status | Ifremer | Voucher COI          | 16S   | 18S   |
|----------------------|--------|---------|---------------------|-------|-------|
| *Bathymoreoa lucasi* sp. nov. | Additional 3 | 601-5 | P.B.’s collection – | MH233170 | – |
| *Bathymoreoa lucasi* sp. nov. | Additional 4 | 667 | P.B.’s collection MH233261 MH233198 MH233244 |
| *Bathypolaria* sp. 173 | Additional 1 | 173 | MNHN-IA-PNT 63 MH233281 MH233151 MH233206 |
| *Bathypolaria* sp. 173 | Additional 2 | 672 | MNHN-IA-PNT 64 – MH233199 MH233245 |
| *Bathypolaria* sp. 173 | Additional 3 | 406 | MNHN-IA-PNT 65 – MH233154 MH233211 |
| *Bathypolaria* sp. 608 | Additional 1 | 608 | MNHN-IA-PNT 66 MH233268 MH233175 MH233227 |
| *Bathypolaria* sp. 608 | Additional 2 | 658-1 | MNHN-IA-PNT 67 – MH233192 – |
| *Bathypolaria* sp. 608 | Additional 3 | 658-2 | MNHN-IA-PNT 68 MH233280 MH233193 MH233241 |
| *Bathypolaria* sp. 608 | Additional 4 | 624 | MNHN-IA-PNT 69 – MH233176 MH233228 |
| *Bathypolaria* sp. 608 | Additional 5 | 625 | MNHN-IA-PNT 70 MH233286 MH233177 MH233229 |
| *Bathykurila gauymosensis* Pettibone, 1989b | Holotype | 512 | MH233158 MH233216 |
| *Bruunilla nealae* sp. nov. | Holotype | 692 | MNHN-IA-PNT 72 MH233263 MH233201 MH233247 |
| *Hodor hodor* gen. nov., sp. nov. | Holotype | 655-2-1 | MNHN-IA-TYPE MH233257 MH233189 MH233238 |
| *Hodor anduril* gen. nov., sp. nov. | Holotype | 655-2-3 | MNHN-IA-TYPE MH233288 MH233191 MH233240 |
| *Hodor anduril* gen. nov., sp. nov. | Paratype | 655-2-2 | MNHN-IA-TYPE MH233258 MH233190 MH233239 |
| *Macellicephaloides moustachu* sp. nov. | Holotype | 633-1 | MNHN-IA-TYPE MH233269 MH233183 MH233233 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 1 | 633-2 | MNHN-IA-TYPE MH233270 MH233184 MH233234 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 2 | 633-3 | NHMUK 2018.25350 MH233271 MH233185 MH233235 |
| *Macellicephaloides parva-fauces* sp. nov. | Holotype | 602 | MNHN-IA-TYPE MH233275 MH233173 MH233225 |
| *Macellicephaloides parva-fauces* sp. nov. | Paratype | 403 | MNHN-IA-TYPE MH233282 MH233153 MH233210 |
| *Macellicephaloides moustachu* sp. nov. | Holotype | 421 | MNHN-IA-TYPE MH233122 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 1 | 520-1 | MNHN-IA-TYPE MH23332 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 2 | 449b | MNHN-IA-TYPE MH233214 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 3 | 529-1 | MNHN-IA-TYPE MH23319 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 4 | 208 | NHMUK 2018.25351 MH233207 |
| *Macellicephaloides moustachu* sp. nov. | Paratype 5 | 538-3 | NHMUK 2018.25352 MH233222 |
| *Macellicephaloides moustachu* sp. nov. | Additional 1 | 422 | MNHN-IA-PNT 79 – – |
| *Macellicephaloides moustachu* sp. nov. | Additional 2 | 423 | MNHN-IA-PNT 80 – – |
| *Macellicephaloides moustachu* sp. nov. | Additional 3 | 682 | MNHN-IA-PNT 81 – – |
| *Macellicephaloides moustachu* sp. nov. | Additional 4 | 460b | P.B.’s collection – – – |
after electrophoresis on 1% agarose gel were sent to the MacroGen Europe Laboratory in Amsterdam (The Netherlands) to obtain sequences, using the same set of primers as used for the PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences using Geneious Pro 8.1.7 2005–2015 (Biomatters Ltd). For COI, the sequences were translated into amino acid alignments and checked for stop codons to avoid pseudogenes. The minimal length coverage was 344 bp for 16S, 531 bp (only one with 345 bp) for COI and 1215 bp (two with < 800 bp) for 18S.

The sequences were blasted in GenBank in order to check for the presence of contamination. Each set of genes was aligned separately using the plugins MAFFT (Katoh et al., 2002) for 16S and 18S, and MUSCLE (Edgar, 2004) for COI. All sequences obtained in this study have been deposited in GenBank (Table 1; http://www.ncbi.nlm.nih.gov/genbank/).

**Table 1. Continued**

| Newly sequenced taxa | Status       | Ifremer | Voucher 16S | Voucher COI | Voucher 18S |
|----------------------|--------------|---------|-------------|-------------|-------------|
| Nu aakhu gen. nov., sp. nov. | Holotype     | 341     | MNHN-IA-TYPE 1836 | – | MH233209 |
|                      |              |         |              |             |             |
| Polarsuchakov lamellae sp. nov. | Holotype     | 151     | MNHN-IA-TYPE 1837 | MH233250 | MH233205 |
|                      |              |         |              |             |             |
| Polarsuchakov lamellae sp. nov. | Paratype 1   | 659-1-1 | MNHN-IA-TYPE 1838 | MH233259 | MH233242 |
|                      |              |         |              |             |             |
| Polarsuchakov lamellae sp. nov. | Paratype 2   | 607     | MNHN-IA-TYPE 1839 | MH233256 | MH233226 |
|                      |              |         |              |             |             |
| Polarsuchakov limaeae sp. nov. | Holotype     | 639-1   | MNHN-IA-TYPE 1840 | – | MH233187 |
|                      |              |         |              |             |             |
| Polarsuchakov omnesae sp. nov. | Holotype     | 424     | MNHN-IA-TYPE 1841 | MH233283 | MH233213 |
|                      |              |         |              |             |             |
| Polarsuchakov omnesae sp. nov. | Paratype     | 530-1   | MNHN-IA-TYPE 1842 | MH233254 | MH233164 |
|                      |              |         |              |             |             |
| Yodanoe desbruyeresi gen. nov., sp. nov. | Holotype     | 448b    | MNHN-IA-TYPE 1843 | MH233251 | MH233156 |
|                      |              |         |              |             |             |
| Yodanoe sp. 659-3 | Additional 1 | 659-3   | MNHN-IA-PNT 73  | MH233273 | MH233195 |

The model used for all genes was GTR+G (Gonzalez et al., 2018). Each gene set was combined in a partitioned dataset with SequenceMatrix (Vaidya et al., 2011). The Bayesian phylogenetic analysis was performed with MrBayes v.3.2.6 on XSEDE (Ronquist et al., 2012), following standard methods with 60,000,000 generations. At every 1000 generation one chain was sampled; in the end, 25% were discarded as burn-in. At the end, the convergence chain runs were assessed using TRACER v.1.7.1 (Rambaut et al., 2018). The support of nodes is given as Bayesian posterior probability (BPP) values. The maximum likelihood was performed using Randomized Axelerated Maximum Likelihood (RAXML v.8.2.10; Stamatakis, 2014) on XSEDE with rapid bootstrapping (1000 iterations). The support of nodes is given as maximum likelihood bootstrap (MLB) values. MrBayes and RAXML were computed in CIPRES Science Gateway (Miller et al., 2010). Morphological data were analysed using the MK model (Lewis, 2001) in both analyses. The most parsimonious analysis was performed using PAUP v.4.0a (build 161) based only on the morphological data matrix (Supporting Information, Appendix S2), with all observations weighted equally and multistate characters treated as unordered, and the following string was run a few times: hsearch enforce = no start = stepwise addseq = random nreps = 20 000 nchuck = 5 chuckscore = 1 nbest = all. Characters were plotted on the strict consensus tree based on the most parsimonious trees using MacClade v.4 (Maddison & Maddison, 2005). The tree files were analysed with FigTree v.1.4.2 (available at http://tree.bio.ed.ac.uk/software/figtree/).

**PHYLOGENETIC ANALYSES**

Bayesian and maximum likelihood phylogenetic analyses were run with three different datasets (Table 2): a molecular dataset (MDS; 65 taxa) based only on DNA sequences, including COI, 16S and 18S genes; a combined dataset (CDS; 65 taxa) based on the MDS dataset with the addition of morphological data for the species having a complete description for the type species; and a morphological dataset (128 taxa) based only on the 74 coded characters. A dataset with all molecular and morphological data was not possible because of the lack of sequence data for most of the species.
Table 2. List of taxa included in the different datasets: only molecular data (MDS), molecular and morphological data (CDS) and only morphological data.

| Family       | Subfamily | Taxon                  | Reference for morphology | COI          | 16S         | 18S         | Dataset inclusion |
|--------------|-----------|------------------------|---------------------------|-------------|-------------|-------------|------------------|
| Sigalionidae | Sigalioninae | *Neoleanira tetragona* (Orsted, 1845) | Pettibone (1970); Gonzalez et al. (2018) | AY839582   | JN852911    | AY839570    | MDS, CDS and morphological |
| Sigalionidae | Sigalioninae | *Sthenelais boa* (Johnston, 1833) | Barnich & Fiege (2003); Gonzalez et al. (2018) | AY839587   | DQ779635    | AY839575    | MDS, CDS and morphological |
| Polynoidae   | Admetellinae | *Admetella longipedata* (McIntosh, 1885) | Pettibone (1967) | –           | –           | –           | Morphological     |
| Polynoidae   | Admetellinae | *Bathyadmetella commanda* | Pettibone (1967) | –           | –           | –           | Morphological     |
| Polynoidae   | Arctonoinae | *Capitalulinae cf. cupisetis* Hanley & Burke, 1989 | Hanley & Burke (1989); Gonzalez et al. (2018) | KF919303   | –           | KF919301    | MDS, CDS and morphological |
| Polynoidae   | Arctonoinae | *Gastrolepidia clavigera* Schmarda, 1861 | Wehe (2006); Gonzalez et al. (2018) | JN852927   | JN852893    | JN852825    | MDS, CDS and morphological |
| Polynoidae   | Bathedithinae | *Bathyedithia berkeleyi* (Levenstein, 1971a) | Pettibone (1976) | –           | –           | –           | Morphological     |
| Polynoidae   | Bathedithinae | *Bathyedithia retierei sp. nov.* | Present study | –           | MH233157    | MH233215    | MDS, CDS and morphological |
| Polynoidae   | Bathedithinae | *Bathymarina zebra* | Levenstein (1981) | –           | –           | –           | Morphological     |
| Polynoidae   | Bathymacellinae | *Bathymacella ushakovii* (Averincev, 1972) | Pettibone, 1976 | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma burkensis* Pettibone, 1989c | Pettibone (1989c) | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma hessleri* Pettibone, 1985a | Pettibone (1985a) | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma marnanus* (Pettibone, 1989c) | Pettibone, 1989c | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma sandersi* Pettibone, 1985a | Pettibone (1985a); Gonzalez et al. (2018) | JN852923   | JN852889    | JN852821    | MDS, CDS and morphological |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma segonzaci* (Miura & Desbruyères, 1995) | –           | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma trifurcatus* (Miura & Desbruyères, 1995) | –           | –           | –           | –           | Morphological     |
| Polynoidae   | Branchinotogluminae | *Branchinotogluma tunnicliffae* (Pettibone, 1988) | Pettibone (1988) | –           | –           | –           | Morphological     |
| Family          | Subfamily             | Taxon                              | Reference for morphology | COI     | 16S | 18S | Dataset inclusion            |
|-----------------|-----------------------|------------------------------------|--------------------------|---------|-----|-----|-----------------------------|
| Polynoidae      | Branchinotogluminae   | *Peinaleopolynoe santacatalina*    | Pettibone (1993a)        | –       | –   |     | Morphological               |
| Polynoidae      | Branchinotogluminae   | *Peinaleopolynoe sillard*†         | Desbruyères & Laubier (1988); Pettibone (1993a) | –       | –   |     | Morphological               |
| Polynoidae      | Branchicipicatinae     | Branchicipicus cupreus*† Pettibone, 1985b | Pettibone (1985b)        | –       | –   |     | Morphological               |
| Polynoidae      | Branchipolynoinae     | *Branchipolynoe longiennisis* Zhou, Zhang, Lu & Wang, 2017 | Zhou et al. (2017)        | –       | –   |     | Morphological               |
| Polynoidae      | Branchipolynoinae     | *Branchipolynoe pettiboneae* Miura & Hashimoto, 1991 | Miura & Hashimoto (1991) | –       | –   |     | Morphological               |
| Polynoidae      | Branchipolynoinae     | *Branchipolynoe seepensis* Pettibone, 1986 | Pettibone (1986)        | –       | –   |     | Morphological               |
| Polynoidae      | Branchipolynoinae     | *Branchipolynoe symphytilla*† Pettibone, 1984a | Pettibone (1984a); Gonzalez et al. (2018) | AY646048 AF315055 | – |     | MDS, CDS and morphological |
| Polynoidae      | Eulagiscinae          | *Eulagisca gigantea*† Monro, 1939  | Pettibone (1997)         | KJ676633 KJ676608 | – |     | MDS, CDS and morphological |
| Polynoidae      | Lepidastheniinae      | *Hyperhalosydna striata* (Kinberg, 1856) | Wehe (2006); Gonzalez et al. (2018) | JN852932 JN852900 JN852831 | MDS, CDS and morphological |
| Polynoidae      | Lepidastheniinae      | Lepidasthenia elegans*† (Grube, 1840) | Barnich & Fiege (2003); Gonzalez et al. (2018) | JN852933 JN852901 JN852832 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | *Alentia gelatinosa*† (M. Sars, 1835) | Barnich & Fiege (2003); Gonzalez et al. (2018) | AY839577 | – | AY525630.1 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | *Halosydna brevisetosa* Kinberg, 1856 | Salazar-Silva (2013); Gonzalez et al. (2018) | AY894313 JN852895 JN852827 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | *Halosydnellia australis* (Kinberg, 1856) | Barnichet al. (2012b); Gonzalez et al. (2018) | KY823495 KY823480 KY823449 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | *Hermenia verruculosa* Grube, 1856 | Pettibone (1975); Wehe (2006); Gonzalez et al. (2018) | JN852931 JN852899 JN852830 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | Lepidonotus clava*† (Montagu, 1808) | Barnich & Fiege (2003); Gonzalez et al. (2018) | HM473445 DQ779620 AY176290 | MDS, CDS and morphological |
| Polynoidae      | Lepidonotinae         | Lepidonotus squamatus* (Linnaeus, 1758) | Chambers & Muir (1997); Gonzalez et al. (2018) | HM473445 DQ779620 AY176290 | MDS, CDS and morphological |
Table 2. Continued

| Family               | Subfamily          | Taxon                                      | Reference for morphology | COI          | 16S              | 18S              | Dataset inclusion                  |
|----------------------|--------------------|--------------------------------------------|--------------------------|--------------|------------------|------------------|-----------------------------------|
| Polynoidae           | Lepidonotinae      | *Lepidonotus sublevis* Verrill, 1873        | Barnich & Fiege (2003); Gonzalez et al. (2018) | AY894317 – | –                | AY894301         | MDS, CDS and morphological        |
| Polynoidae           | Lepidonotinae      | *Thormora jukesii* Baird, 1865             | Wehe (2006); Gonzalez et al. (2018)             | JN852941    | JN852910         | JN852840         | MDS, CDS and morphological        |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium atalante* Desbruyères & Hourdez, 2000a | Desbruyères & Hourdez (2000a) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium fimbriatum* Pettibone, 1983 | Pettibone (1983) | AF315056 – | –                | –                | MDS, CDS and morphological        |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium joiunae* Desbruyères & Hourdez, 2000b | Pettibone (1983c) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium minutum* Pettibone, 1983 | Pettibone (1983c) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium okinawae* Sui & Li, 2017 | Sui & Li (2017) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium piscesae* Pettibone, 1988 | Pettibone (1988) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium riftense* Pettibone, 1984b | Pettibone (1984b) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Lepidonotopodium williamsae* Pettibone, 1984b | Pettibone (1984b) | –            | –                | –                | Morphological                     |
| Polynoidae           | Lepidonotopodinae  | *Thermopolyne branchiata* Miura, 1994      | Miura (1994)             | –            | –                | –                | Morphological                     |
| Polynoidae           | Macellicephalinae  | *Abyssarya acus* gen. nov., sp. nov.       | Present study             | MH233279     | MH233179         | MH233231         | MDS, CDS and morphological        |
| Polynoidae           | Macellicephalinae  | *Austropolaria magnicirrata* Neal, Barnich, Wiklund & Glover, 2012 | Neal et al. (2012); Gonzalez et al. (2018) | –            | –                | –                | MDS, CDS and morphological        |
| Polynoidae           | Macellicephalinae  | *Bathybahamas charlenea* Pettibone, 1985d | Pettibone (1985d) | –            | –                | –                | Morphological                     |
| Polynoidae           | Macellicephalinae  | *Bathybaculina filamentsa* (Moore, 1910)   | Pettibone (1976) | –            | –                | –                | Morphological                     |
| Polynoidae           | Macellicephalinae  | *Bathyeliasona abyssicola* (Fauvel, 1913)   | Pettibone (1976) | –            | –                | –                | Morphological                     |
| Polynoidae           | Macellicephalinae  | *Bathyeliasona kirgeaardi* (Uschakov, 1971) | Pettibone (1976) | –            | –                | –                | Morphological                     |
| Polynoidae           | Macellicephalinae  | *Bathyeliasona mariae sp. nov.*            | Present study             | MH233249     | MH233149         | MH233204         | MDS, CDS and morphological        |
| Polynoidae           | Macellicephalinae  | *Bathyeliasona nigra* (Hartman, 1967)      | Pettibone (1976) | –            | –                | –                | Morphological                     |
| Family         | Subfamily | Taxon                                      | Reference for morphology | COI       | 16S       | 18S       | Dataset inclusion       |
|---------------|-----------|--------------------------------------------|---------------------------|-----------|-----------|-----------|-------------------------|
| Polynoidae    | Macellicephalinae | *Bathyfauvelia affinis* (Fauvel, 1914a)   | Pettibone (1976)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathyfauvelia glacigera* sp. nov.        | Present study             | MH233274  | MH233160  | MH233218  | MDS, CDS and morphological |
| Polynoidae    | Macellicephalinae | *Bathyfauvelia grandelytris* (Levenstein, 1975) | Levenstein (1975)         | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathyfauvelia ignigna* sp. nov.          | Present study             | MH233262  | MH233196  | MH233246  | MDS, CDS and morphological |
| Polynoidae    | Macellicephalinae | *Bathykermadea hadalis* (Kirkegaard, 1956) | Pettibone (1976)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathykermadea turnerae* Pettibone, 1985d | Pettibone (1985d)         | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathykurila guaymasensis* Pettibone, 1989b | Pettibone (1989b); Gonzalez et al. (2018) | MH233265  | MH233203  | MH233248  | MDS, CDS and morphological |
| Polynoidae    | Macellicephalinae | *Bathykurila zenkevitchi* (Uschakov, 1955) | Pettibone (1976)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathyolevensteina bicornis* (Levenstein, 1962) | Pettibone (1976)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathypolaria carinata* (Levenstein, 1981) | Present study             | MH233281  | MH233151  | MH233206  | MDS and CDS            |
| Polynoidae    | Macellicephalinae | *Bathypolaria sp. 173* Levenstein, 1981   | Not coded for morphology  | MH233268  | MH233175  | MH233227  | MDS and CDS            |
| Polynoidae    | Macellicephalinae | *Bathypolaria sp. 608*                    | Not coded for morphology  | MH233268  | MH233175  | MH233227  | MDS and CDS            |
| Polynoidae    | Macellicephalinae | *Bathyovitiazia pallida* (Levenstein, 1971b) | Pettibone (1976)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bathyovitiazia pettiboneae* Kirkegaard, 1995 | Kirkegaard (1995)         | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Bruunilla natatan* Hartman, 1971 | Hartman (1971); Pettibone (1979) | MH233158  | MH233216  | MH233216  | MDS, CDS and morphological |
| Polynoidae    | Macellicephalinae | *Bruunilla nealeae* sp. nov.               | Present study             | MH233263  | MH233201  | MH233247  | MDS and CDS            |
| Polynoidae    | Macellicephalinae | *Gesiella jameensis* (Hartmann-Schröder, 1974) | Pettibone (1976); Gonzalez et al. (2018) | KY454429  | KY454413  | KY454404  | MDS, CDS and morphological |
| Polynoidae    | Macellicephalinae | *Levensteiniella intermedia* Pettibone, 1990 | Pettibone (1990)          | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Levensteiniella iris* Hourdez & Desbruyères, 2003 | Hourdez & Desbruyères (2003) | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Levensteiniella kincaidi* Pettibone, 1985c | Pettibone (1985c)         | –         | –         | –         | Morphological           |
| Polynoidae    | Macellicephalinae | *Levensteiniella plicata* Hourdez & Desbruyères, 2000 | Hourdez & Desbruyères (2000) | –         | –         | –         | Morphological           |
Table 2. Continued

| Family                  | Subfamily                  | Taxon                                      | Reference for morphology | COI   | 16S | 18S | Dataset inclusion       |
|-------------------------|----------------------------|--------------------------------------------|--------------------------|-------|-----|-----|------------------------|
| Polynoidae              | Macellicephalinae          | *Levensteiniella raisae* Pettibone, 1989c  | Pettibone (1989c)        | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal aiculata* (Moore, 1910)     | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal atlantica* Step-Bowitz, 1948 | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal australis* Wu & Wang, 1987  | Wu & Wang (1987)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal clarionensis* sp. nov.      | Present study            | MH233269 | MH233183 | MH233235 | MDS, CDS and morphological |
| Polynoidae              | Macellicephalinae          | *Macellicephal galapagensis* Pettibone, 1985c | Pettibone (1985c)        | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal laubieri* Reys, 1971        | Reys (1971); Pettibone (1976) | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal longipalpa* Uschakov, 1957  | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal mirabilis*† (McIntosh, 1885) | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal parafauces* sp. nov.        | Present study            | MH233275 | MH233173 | MH233225 | MDS, CDS and morphological |
| Polynoidae              | Macellicephalinae          | *Macellicephal remigata* (Moore, 1910)     | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Macellicephal sp.* MB1                    | Not coded for morphology | KX867447 | KX867371 | –   | MDS and CDS           |
| Polynoidae              | Macellicephalinae          | *Macellicephal sp.* MB2                    | Not coded for morphology | –     | KX867380 | –   | MDS and CDS           |
| Polynoidae              | Macellicephalinae          | *Macellicephal violacea* (Levinsen, 1886)  | Pettibone (1976)         | JX119016 | –     | –   | MDS, CDS and morphological |
| Polynoidae              | Macellicephalinae          | *Natopolynoe kensmithi* Pettibone, 1985c   | Pettibone (1985c)        | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephalinae          | *Pelagomacellicephal iliffi* Pettibone, 1985d | Pettibone (1985d); Gonzalez et al. (2018) | KX454435 | KX454420 | KX454408 | MDS, CDS and morphological |
| Polynoidae              | Macellicephalinae          | *Yodano desbruyeresi* gen. nov. sp. nov.   | Present study            | MH233251 | MH233156 | –   | MDS, CDS and morphological |
| Polynoidae              | Macellicephalinae          | *Yodano sp. 659-3*                         | Not coded for morphology | MH233273 | MH233195 | –   | MDS and CDS           |
| Polynoidae              | Macellicephaloidinae       | *Macellicephaloides alvini* Pettibone, 1989b | Pettibone (1989b); Gonzalez et al. (2018) | –     | –   | –   | Morphological          |
| Polynoidae              | Macellicephaloidinae       | *Macellicephaloides grandicirra*† Uschakov, 1955 | Pettibone (1976)         | –     | –   | –   | Morphological          |
| Family         | Subfamily          | Taxon                                      | Reference for morphology | COI   | 16S | 18S | Dataset inclusion          |
|---------------|--------------------|--------------------------------------------|--------------------------|-------|-----|-----|---------------------------|
| Polynoidae    | Macellicephaloidinae | *Macellicephaloides moustachu* sp. nov. | Present study            | –     | –   | –   | MDS, CDS and morphological |
|               | Macellicephaloidinae | *Macellicephaloides* sp. MB1             | Not coded for morphology | KX867448 | KX867334 | –   | MDS and CDS                |
| Polynoidae    | Macellicephaloidinae | *Macellicephaloides uschakovi* Levenstein, 1971b | Pettibone (1976) | –     | –   | –   | Morphological              |
| Polynoidae    | Macellicephaloidinae | *Macellicephaloides verrucosa* Uschakov, 1955 | Pettibone (1976) | –     | –   | –   | Morphological              |
| Polynoidae    | Macellicephaloidinae | *Macellicephaloides vitiasi* Uschakov, 1955 | Pettibone (1976) | –     | –   | –   | Morphological              |
| Polynoidae    | Macelloidinae       | *Macelloides antarctica*† Uschakov, 1957  | Pettibone (1976) | –     | –   | –   | Morphological              |
| Polynoidae    | Polaruschakovinae   | *Bathycanadina diaphana* Levenstein, 1981 | Levenstein (1981) | –     | –   | –   | Morphological              |
| Polynoidae    | Polaruschakovinae   | *Bathymiranda microcephala* Levenstein, 1981 | Levenstein (1981) | –     | –   | –   | Morphological              |
| Polynoidae    | Polaruschakovinae   | *Diplaconotum paucidendatum* (Eliason, 1962) | Loshann (1981) | –     | –   | –   | Morphological              |
| Polynoidae    | Polaruschakovinae   | *Nu aakah* gen. nov., sp. nov.             | Present study            | –     | –   | MH233209 | MDS, CDS and morphological |
| Polynoidae    | Polaruschakovinae   | *Polaruschakov lamellae* sp. nov.          | Present study            | MH233250 | MH233150 | MH233205 | MDS, CDS and morphological |
| Polynoidae    | Polaruschakovinae   | *Polaruschakov limaeae* sp. nov.           | Present study            | –     | MH233187 | MH233237 | MDS, CDS and morphological |
| Polynoidae    | Polaruschakovinae   | *Polaruschakov omenae* sp. nov.            | Present study            | MH233283 | MH233155 | MH233213 | MDS, CDS and morphological |
| Polynoidae    | Polaruschakovinae   | *Polaruschakov polaris*† (Uschakov, 1957)  | Pettibone (1976)         | –     | –   | –   | Morphological              |
| Polynoidae    | Polaruschakovinae   | *Polaruschakov reyssi* Pettibone, 1976     | Pettibone (1976)         | –     | –   | –   | Morphological              |
| Polynoidae    | Polynoinae          | *Acholoe squamosa* (Delle Chiaje, 1827)    | Barnich & Fiege (2003); Wehe (2006); Gonzalez et al. (2018) | AY839576 | JN852888 | AY839567 | MDS, CDS and morphological |
| Polynoidae    | Polynoinae          | *Antarctinoe ferox* (Baird, 1865)          | Barnich et al. (2006); Gonzalez et al. (2018) | KJ676611 | KF713463 | KF713423 | MDS, CDS and morphological |
| Polynoidae    | Polynoinae          | *Bylgides elegans* (Théel, 1879)          | Pettibone (1993b); Gonzalez et al. (2018) | JN852924 | JN852890 | JN852822 | MDS, CDS and morphological |
| Polynoidae    | Polynoinae          | *Bylgides sarsi* (Kinberg in Malmgren, 1866a) | Pettibone (1993b); Gonzalez et al. (2018) | JN852925 | JN852891 | JN852823 | MDS, CDS and morphological |
| Family        | Subfamily | Taxon                          | Reference for morphology            | COI          | 16S          | 18S          | Dataset inclusion                      |
|---------------|-----------|--------------------------------|-------------------------------------|--------------|--------------|--------------|----------------------------------------|
| Polynoidae    | Polynoinae| *Eunoe nodosa* (M. Sars, 1861) | Barnich & Fiege (2003); Gonzalez et al. (2018) | JN852926     | JN852892     | JN852824     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Gattyana ciliata* (Moore, 1902) | Moore (1902); Gonzalez et al. (2018) | AY894312     | –            | AY894297     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Gattyana cirrhosa* (Pallas, 1766) | Fauvel (1923); Gonzalez et al. (2018) | JN852928     | JN852894     | JN852826     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Harmothoe glabra* (Malmgren, 1866b) | Barnich & Fiege (2009); Gonzalez et al. (2018) | JN852929     | JN852896     | JN852828     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Harmothoe imbricata* (Linnaeus, 1767) | Barnich & Fiege (2009); Gonzalez et al. (2018) | HQ023527     | AY340463     | AY340434     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Harmothoe impar* (Johnston, 1839) | Barnich & Fiege (2009); Gonzalez et al. (2018) | JN852930     | JN852897     | JN852829     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Harmothoe ocularum* (Storm, 1879) | Barnich & Fiege (2009); Gonzalez et al. (2018) | AY894314     | JN852898     | AY894299     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Harmothoe rarisipina* (M. Sars, 1861) | Barnich & Fiege (2009); Gonzalez et al. (2018) | KY657659     | KY657641     | KY657611     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Malmgrena mcintoshi* (Tebble & Chambers, 1982) | Pettibone (1993c); Gonzalez et al. (2018) | JN852935     | JN852804     | JN852834     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Mesoenis loceni* Malmgren, 1866b | Uschakov (1982); Gonzalez et al. (2018) | JN852936     | JN852805     | JN852835     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Neopolyne paradoxa* (Anon, 1888) | Loshamn (1981); Gonzalez et al. (2018) | JN852937     | JN852906     | JN852836     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Paradyte crinoidicola* (Potts, 1910) | Pettibone (1969b); Barnich & Fiege (2003); Gonzalez et al. (2018) | JN852938     | JN852907     | JN852837     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Paralepidonotus amplifferus* (Grube, 1878) | Hanley (1991); Gonzalez et al. (2018) | JN852939     | JN852908     | JN852838     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Polyeunoa laevis* McIntosh, 1885 | Barnich et al. (2012a); Gonzalez et al. (2018) | KU738212     | KU738160     | KU738176     | MDS, CDS and morphological               |
| Polynoidae    | Polynoinae| *Polynoe scolopendrina*† Savigny, 1822 | Barnich & Fiege (2003); Gonzalez et al. (2018) | JN852940     | JN852909     | JN852839     | MDS, CDS and morphological               |
The morphological dataset of Gonzalez et al. (2018), used to investigate the phylogeny of the Aphroditiformia, was used as basis for the present study. From Gonzalez et al. (2018), most of the polynoids were included in the present analysis; two sigalionids were added as an outgroup (Table 2). For all taxa, at least one sequence of one of the three targeted genes (COI, 16S or 18S) was available in GenBank (Table 2). All new Linnaean-named polynoids in the present study were included in the morphological and molecular analysis; informally named species were excluded (Table 2).

DNA sequences were available for species from 12 subfamilies (Arctonoinae Hanley, 1989, Bathyedithinae, Branchinotogluminae, Branchipolynoinae, Eulagiscinae, Lepidastheniinae, Lepidonotinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Polaruschakovinae and Polynoinae Kinberg, 1856). Morphological data only were available for the following six subfamilies: Admetellinae, Bathymacellinae, Branchiplicatinae, Macelloidinae, Vampiropolynoinae and Uncopolynoinae Wehe, 2006. Most species (i.e. 89 species; Table 2) fitting the Macellicephalinae description sensu Hartmann-Schröder (1971), having a median antenna present or absent and lateral antennae absent, were coded and included in the morphological analysis. The descriptions of the following species were not available because the descriptions have not been translated from Russian: Bathytasmania insolita Levenstein, 1982a, Macellicephaloides imprivosa Levenstein, 1983, Macellicephaloides sandwichensis Levenstein, 1975 and Macellicephaloides villosa Levenstein, 1982b.

For our purposes, polynoids from the following subfamilies: Arctonoinae, Eulagiscinae, Lepidastheniinae, Lepidonotinae, Polynoinae and Uncopolynoinae, were considered as a reference group in order to evaluate the evolutionary relationship within the deep-sea subfamilies represented by Admetellinae, Bathymacellinae, Bathymacellidae, Branchinotogluinae, Branchipolynoinae, Branchiplicatinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Macellicephalinae, Polaruschakovinae and Vampiropolynoinae. Out of the 18 currently valid subfamilies, 12 were included in molecular analyses, and all 18 were included in morphological analysis.

### Genetic Divergence

Molecular operational taxonomic units were recognized using a threshold of 97% similarity between COI sequences (Hebert et al., 2003a, b). The similarity of sequences within species is given in the ‘Genetic data’ sections in order to compare with this general threshold. Furthermore, the average evolutionary divergence over sequence pairs was calculated within species (intraspecific variation) and between species (interspecific variation) using the Kimura two-parameter (K2P; Kimura, 1980) model in MEGA7 (Kumar et al., 2016). This analysis allowed for the comparison of genetic distance, mainly between closely related species.
species. For instance, Brasier et al. (2016), studying a cryptic species of Macellicephalina, observed an average K2P distance for intraspecific variation of < 1% for COI and 16S; and < 4% for COI and < 13% for 16S for interspecific variation.

RESULTS
PHYLOGENY

The molecular dataset with COI, 16S and 18S was composed of ~3100 bp, with longest sequences of 658 bp for COI, 517 bp for 16S and 1931 bp for 18S. The morphological dataset was composed of 74 characters (63 characters with two states, five with three states, six with six states and one with five states). Bayesian and maximum likelihood analyses of the MDS (COI, 16S and 18S) and the dataset combining molecular and morphological data (CDS) separated most of the polynoids into two major groups (Fig. 2): polynoids with lateral antennae (grey line), which is non-monophyletic; and polynoids without lateral antennae (black line), which is monophyletic. The group having lateral antennae was further subdivided into three main clades with high Bayesian posterior probability (BPP = 0.93–1.0) but low maximum likelihood bootstrap (MLB = 69–91; Fig. 2). Clade a1 included the subfamily Lepidonotinae and one member of Lepidastheniinae. Clade a2 included the subfamily Eulagiscinae and Bathymoorea lucasi sp. nov. (not assigned to a current subfamily). Clade a3 included the subfamily Polynoinae and one member of Lepidastheniinae, two members of the subfamily Lepidonotinae and two members of Arctonoinae. Clade a3a (within clade a3; Fig. 2) was composed of members of the subfamily Polynoinae and one member of Lepidotininae with maximum BPP (1.0) and MLB (100). The positions of Paralepidonotus ampulliferus (Polynoinae) and Hermania verruculosa (Lepidonotinae) with respect to a clade comprising all the remaining Polynoinae and Lepidonotinae, respectively, remain unclear.

The second main clade (black line) assembling all species without lateral antennae (Fig. 2) had a high BPP (1.0) and low MLB (78–81) and was composed of three main clades (Fig. 2). Clade b1 included members of the subfamilies Branchinotogluminae, Branchipolynoinae, Lepidonotopodinae and Macellicephalinae with high BPP (1.0) and low MLB (81–89). Clade b2 included only the subfamily Macellicephalinae with high BPP (1.0) and low MLB (77–79). Clade b3 included members of Bathyedithinae, Macellicephalinae, Poloruschakovinae and Hodor gen. nov. (not assigned to a current subfamily) with high BPP (1.0) and low MLB (61–63). Interestingly, clade b3a (within clade b3; Fig. 2) assembled all taxa without median and lateral antennae (referred to in subsequent text as the Anantennata clade) with high BPP (1.0) and low MLB (53–73). This Anantennata clade included representatives of the subfamilies Bathyedithinae, Poloruschakovinae and Hodor gen. nov. (not assigned to a current subfamily). Within clade b, many members of the subfamilies Macellicephalinae and Macellicephaloidinae remained unsolved, and a few clades showed high BPP (> 0.93) and MLB (> 98): Bathysaffarea glaucigena sp. nov. and Bathysaffera ignigena sp. nov.; Bathypolaria sp. 173, Bathypolaria sp. 608 and Austropolaria magnifica; and Yodane desbruyeresi gen. nov., sp. nov. and Yodanoe sp. 659–3.

The morphological analysis yielded five most parsimonious trees with 396 state changes (strict consensus tree in Fig. 3) rearranged 9 139 993 959 times, with a consistency index of 0.24 and retention index of 0.75. The morphological analysis showed the same patterns as the MDS and CDS analyses. Most polynoids with lateral antennae were subdivided into two main groups without a unique synapomorphy assembling them (grey lines; Fig. 3). Among these groups, only the subfamily Admetellinae (clade c1; Fig. 3) was determined by the unique synapomorphy presence of antennal sheaths in lateral antennae (character 14: 1). The clade without lateral antennae (black lines; Fig. 3) was composed of all members of the subfamilies Bathyedithinae, Bathymacellinae, Branchinotogluminae, Branchipolynoinae, Polynoinae, Lepidonotopodinae, Macellicephalinae, Macellicephaloidinae, Macelloidinae, Polaruschakovinae and Vampiropolynoinae being determined by the unique synapomorphy absence of lateral antennae (character 11: 0). Within this group, five subgroups were supported, each with a unique synapomorphy (Fig. 3). Clade d1 included Brunilha species, being determined by the presence of a lower lip with a wing-like structure (character 6: 1). Clade d2 included only members of the subfamily Macellicephalinae, being determined by the presence of dissimilar dorsal and ventral jaws (character 40: 1). Clade d3 included the Anantennata clade with all members of the subfamilies Poloruschakovinae, Bathyedithinae and the genus Hodor gen. nov. (not assigned to a current subfamily), being determined by the absence of a median antenna (character 7: 0). Clade d4 included Bathysella species, being determined by the presence of very wide neurochaetae (character 60: 1). Clade d5 included only members of the subfamily Branchipolynoinae (Fig. 3), being determined by the absence of ceratophores of the median antenna (character 9: 0).
**Figure 2.** Molecular phylogenetic relationships of subfamilies within Polynoidae based on the molecular dataset (MDS; COI, 16S and 18S genes) and the combined dataset (CDS; MDS and morphology), with tree topology from Bayesian analysis of the CDS. Subfamilies are represented by a colour code. The group with lateral antennae is shown with grey lines, and the group without lateral antennae is shown with black lines. Node values indicate the Bayesian posterior probabilities (BPP) and maximum likelihood bootstrap (MLB) for MDS and CDS. ‘*’ indicates maximal support and ‘–’ indicates low/no support. A taxon with ‘**’ indicates the type species of the genus, and ‘***’ indicates the type genus of the subfamily.

**Subfamilies:**
- Arctonoinae
- Bathyedithinae
- Branchinotoglininae
- Branchipolynoinae
- Eulagiscinae
- Lepidastheniinae
- Lepidonotinae
- Macellicephalinae
- Macellicephaloidea
- Polyruschakovinae
- Uncertain
- Outgroup

**Main groups:**
- with lateral antennae
- without lateral antennae

**Nodes:**
- MDS Bayes/MDS RAxML
- CDS Bayes/CDS RAxML
- * = BPP = 1 or MLB > 50
- # = * in MDS and CDS

**Taxa:**
- * type species of genus
- ** type genus of subfamily

| Taxa | Position | BPP/CDS RAxML |
|------|----------|---------------|
| Paralepidonotus ampulliferus * | 0.93/50 | |
| Lepidonotus squamatus | 0.93/58 | |
| Halosydra brevivertex | 0.93/56 | |
| Halosydra austrovenosa | 0.93/56 | |
| Hyperhalosydra striata * | 0.93/56 | |
| Lepidonotus clava * ** | 0.93/56 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| COI 0.08 | MDS | |
| MDS Bayes/MDS RAxML | 0.93/57 | |
| CDS Bayes/CDS RAxML | 0.93/57 | |
| Neopolynoe paradoxa * | 0.93/57 | |
| Lepidasthenia elegans * ** | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
| Neolecanira tetragona | 0.93/57 | |
| Sthenelais boa | 0.93/57 | |
| Lepidonotus squamatus | 0.93/57 | |
| Halosydra brevivertex | 0.93/57 | |
| Halosydra austrovenosa | 0.93/57 | |
| Hyperhalosydra striata * | 0.93/57 | |
| Lepidonotus clava * ** | 0.93/57 | |
| Hermeniella verruculosa | 0.93/57 | |
Figure 3. Strict consensus tree from five minimum-length trees based on morphological characters with 396 state changes. Subfamilies are represented by a colour code. The group with lateral antennae is shown with grey lines, and the group without lateral antennae in shown with black lines. A taxon with ‘*’ indicates the type species of the genus, and ‘**’ indicates the type genus of the subfamily. Red characters indicate unique synapomorphy, and black or grey characters indicate homoplasies.
Remarks:
with spinous rows; neurochaetae numerous. Notochaetae numerous, elongate acicular lobe; tips of noto- and neuroaciculae shorter than neuropodia; noto- and neuropodia with 26, 29, 32 and 33. Parapodia subbiramous, notopodia pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32 and 33. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae numerous, with spinous rows; neurochaetae numerous.

SYSTEMATICS

POLYNOIDAE KINBERG, 1856

EULAGISCINAe PETTIBONE, 1997

Eulagiscinae Pettibone, 1997: 537.

Diagnosis (emended): Body elongate, up to 41 segments. Prostomium bilobed. Two pairs of eyes (Eulagisca and Pareulagisca) or one pair of large eyes (Bathymoorea). Median and lateral antennae present; lateral antennae present, inserted terminally or subterminally on anterior extension of prostomium. Facial tubercles absent (Pareulagisca) or present (Eulagisca and Bathymoorea). Tentaculophores with acicula and chaetae (Eulagisca and Bathymoorea lucasi sp. nov.), without acicula and with chaeta (Pareulagisca) orachaetous (Bathymoorea renotubulata). Nuchal fold absent (Bathymoorea) or present (Eulagisca and Pareulagisca). Pharynx with two pairs of jaws. Dorsal tubercles present. Elytrophores large, up to 16 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32 and 33. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of nato- and neuroaciculae not penetrating epidermis. Notochaetae numerous, with spinous rows; neurochaetae numerous.

Remarks: Pettibone (1997) has erected this subfamily for Eulagisca McIntosh, 1885 and Pareulagisca Pettibone, 1997. According to Pettibone, the prostomium having lateral antennae inserted terminally or subterminally is a character shared with the subfamilies Lepidonotinae and Lepidastheniinae, but the parapodia shape is distinctive in Eulagiscinae. Indeed, in Lepidonotinae and Lepidastheniinae the notopodia are vestigial to moderately developed, whereas in Eulagiscinae they are well developed (Wehe, 2006). We suggest that Bathymoorea should be included in Eulagiscinae because it has lateral antennae inserted subterminally and well-developed notopodia. Thus, the description has been emended in order to include the characters of Bathymoorea, such as: absence of chaetae on tentacular segment (present in Eulagisca and Pareulagisca as opposed to present or absent in Bathymoorea), the absence of a nuchal fold (present in Eulagisca and Pareulagisca as opposed to absent in Bathymoorea), number and shape of eyes (two small pairs in Eulagisca and Pareulagisca as opposed to one pair of large eyes in Bathymoorea) and shape of dorsal tubercles (bulbous/nodular in Eulagisca and Pareulagisca as opposed to lamelliform/inflated in Bathymoorea).

BATHYMOOREA PETTIBONE, 1967

Bathymoorea Pettibone, 1967: 10. – Fauchald, 1977: 60.

Type species: Polynoe (?) renotubulata Moore, 1910.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 33 segments. Prostomium bilobed. Frontal filaments absent. One pair of large eyes present. Median and lateral antennae present; lateral antennae inserted subterminally on prostomium extensions. Facial tubercles present. Tentaculophores with acicula and chaetae (Bathymoorea lucasi sp. nov.) orachaetous (Bathymoorea renotubulata). Pharynx with two pairs of jaws. Dorsal tubercles present. Elytrophores large, up to 14 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26 and 28. Parapodia subbiramous; nato- and neuropodia with elongate acicular lobe; tips of nato- and neuroaciculae penetrating epidermis. Notochaetae with spinous rows, neurochaetae numerous. Nephridial papillae from segment 5 or 6.

Remarks: Pettibone (1967) erected the genera Bathyadmetella Pettibone, 1967 and Bathymoorea and emended Admetella McIntosh, 1885 based on bathyal specimens from the Central and North-eastern Pacific. According to Pettibone (1967) and Uschakov (1982), these genera share some similarities: prostomium with paired large eyes, lepidonotoid-like ceratophores of the lateral antennae, bulbous facial tubercles, long neuroaciculae lobes and neurochaetae of one type, numerous, long and flattened. Uschakov (1977) created the subfamily Admetellinae to include Admetella and Bathyadmetella, both possessing antennal scales or sheaths. As pointed out by Uschakov (1982), the position of Bathymoorea, without scales or sheaths on the antennae, remained unknown until now. The genus is here emended in order to include the presence of chaetae on the tentacular segment and nephridial papillae from segment 5 or 6 observed in Bathymoorea lucasi sp. nov.

BATHYMOOREA LUCASI SP. NOV.

(Fig. 4A–P; TABLES 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1821 (IFR601-1), complete, length 9.95 mm, width 1.35 mm, 27 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80’S, 128°18.53’W, end 18°48.13’N, 128°18.20’W, 4933–4964

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m depth. Paratype 1, MNHN-IA-TYPE 1822 (IFR600), complete, length 11.30 mm, width 1.35 mm, 29 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 2, MNHN-IA-TYPE 1823 (IFR601-7), complete, in very poor condition but pharynx dissected in good condition, length 8.64 mm, width 1.24 mm, 26 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 3, MNHN-IA-TYPE 1844 (IFR601-2), complete, length 7.66 mm, width 1.08 mm, 25 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 4, MNHN-IA-TYPE 1823 (IFR601-7), complete, length 5.67 mm, width 0.96 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 5, NHMUK 2018.25349 (IFR601-6) for SEM, incomplete, 11 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype 6, NHMUK 2018.25350 (IFR601-8), complete, length 11.30 mm, width 1.35 mm, 29 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI\#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.53′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Description (based on holotype and paratypes): Holotype complete, 9.95 mm long and 1.35 mm wide for 27 segments (including tentacular segment), dorsoventrally flattened, not tapering posteriorly; live specimen coloration pale yellow body and prostomium; ethanol-preserved specimen with pale yellow body (Fig. 4A), dark dots present on middle and posterior margin of prostomium, dark spots sparsely covering mid-ventrum of body and dorsal surface of notopodia, styles of lateral antennae and ventral cirri brownish medially to distally, nephridial papillae brownish.

Prostomium bilobed, wider than long, with large pair of whitish ocular areas (Fig. 4H, A). Median and lateral antennae present; ceratophore of median antenna large, bulbous, inserted near anterior margin, style missing; lateral antennae inserted on anterior extension of prostomium subterminally to ceratophore of median antenna, styles smooth, tapering, short (about one-quarter length of palps). Palps smooth, tapering distally to thin tips, short (reaching to segment 4; Fig. 4H). Facial tubercle present, bulbous.

Tentacular segment with short lobe, inserted laterally and slightly ventral to prostomium; acicula not penetrating epidermis, with chaetae; tentaculophores large, cylindrical, equal sized (Fig. 4H); tentacular styles missing. Mouth lips strongly developed, protruding when pharynx not everted. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1823), with nine pairs of subtriangular, equal-sized distal papillae, two pairs of jaws, each with main fang, margin smooth (Fig. 4I). Second segment with eyltrophores, subbiramous parapodia, chaetae and ventral cirri.

Thirteen pairs of large, bulbous eyltrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23 and 26 (all elytra missing); eyltrophores large, bulbous.

Cirrigerous segments with distinct, bulbous dorsal cirrophores (Fig. 4H, J, K), inserted basally on notopodia; styles (mostly missing) sparsely papillated, tapering, very short on segment 2 (shorter than neuroacicula tip), long on segment 6 (longer than neuroacicula tip); dorsal tubercle lamelliform, short (as long as dorsal cirrophore; Fig. 4H, J, K).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicula lobe); in subsequent segments inserted medially and basally on neuropodia of posterior segments (Fig. 4J, L), style short (shorter than tip of neuroacicula lobe).
Figure 4. *Bathymoorea lucasi* sp. nov., holotype MNHN-IA-TYPE 1821 (A, H, J–P), paratype 3 NHMUK 2018.25349 (B–G) and paratype 2 MNHN-IA-TYPE 1823 (I). A, dorsal view of a preserved complete specimen. B, notochaeta. C, detailed view of same. D, upper neurochaeta. E, detailed view of same. F, upper neurochaeta tip. G, lower neurochaeta tip. H, anterior end, dorsal view, chaetae omitted. I, inner view of half side of dissected jaws. J, left parapodia, anterior view, segment 6. K, dorsal view of segments 20 and 21 with dorsal tubercle and elytrophore on notopodia, chaetae omitted. L, ventral view of segments 11 and 12 with nephridial papillae on neuropodia, chaetae omitted. M, short notochaeta with developed spinous rows, segment 6. N, long notochaeta with developed spinous rows, segment 6. O, middle neurochaeta, frontal view, segment 6. P, middle neurochaeta, lateral view, segment 6. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elytrophore; ft, frontal tubercle.
Parapodia subbiramous, notopodia shorter than neuropodia (Fig. 4J). Notopodia subtriangular, tapering into long acicular lobe, tip of notochaeta not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroaculata not penetrating epidermis. Notochaetae moderate in number (≥20 observed), short or long, stout, distally curved, with distinct, well-developed spinous rows on convex side, with pointed tips (Fig. 4B, C, M, N); notochaetae stouter than neurochaetae. Neurochaetae very numerous (~60 observed), very long, distally tapering into long acicular lobe, tip of neuroaculata not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of notochaeta not penetrating epidermis. Notochaetae moderate in number (≥20 observed), short or long, stout, distally clustering into two groups.

Nephridial papillae present from segment 5 (in paratype MNHN-IA-TYPE 1844, from segment 6) to end of body, small, bulbous (Fig. 4L). Pygidium small, rounded, not enclosed by last segment (Fig. 4A); with terminal anus. Anal cirri lost, scars not seen.

Morphological variation: Specimens with 25, 26, 27 and 29 segments were found. The form of the prostomial appendages, shape of parapodia and form of chaetae were similar to those of the types. However, specimens with 25 and 29 segments possessed 12 and 13 pairs of elytrophores, respectively. Differences are probably linked to size or growth/development stages of the animals, because DNA confirmed that all specimens belonged to the same species. Furthermore, variation in the first occurrence of nephridial papillae is also linked to size; in animals with 25 segments the nephridial papilla started from segment 5 or 6, whereas in animals with >25 segments the nephridial papilla always started from segment 5. Worms also differed in having short and long dorsal cirri in the anterior part of the body, but in the posterior body the observed dorsal cirri were always long. Loss and regeneration could explain the very short dorsal cirri observed in the anterior body.

Remarks: Bathymoorea has contained a single species, Bathymoorea renotubulata (Moore, 1910) since its erection by Pettibone (1967). The specimens found in the CCFZ are similar to Bathymoorea renotubulata as follows: short body, large ocular areas, similar prostomial shape and form of distally flattened neurochaetae with faint spinous rows, which appear bidentate in lateral view as opposed to unidentate in Bathymoorea lucasi sp. nov. Bathymoorea lucasi sp. nov. differs from Bathymoorea renotubulata in having fewer segments (≤29), very short lateral antennae, short palps, presence of acicula and notochaetae on the tentacular segment, short neuropodial lobes and very reduced (bulbous) nephridial papillae. In comparison, Bathymoorea renotubulata has 33 segments, long antennae, long palps, achaetous tentaculophores, elongate neuropodial lobes and elongate nephridial papillae. With regard to chaetae, notochaetae are robust with well developed rows of spines in Bathymoorea lucasi sp. nov. instead of the delicate and fine spines in Bathymoorea renotubulata.

Etymology: This species is dedicated to Lucas Lisboa, cousin of P.B., for his friendship.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S, respectively sharing at least 98.6, 99.3 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.8% for COI and 0.2% for 16S.

Distribution: Based on the material examined (nine specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled at two stations in APEI#3 nodule area (type locality).

Ecological notes: During the sampling at station 189, 11 Hexactinellida sponges were sampled together with a few ophiuroids and alcyonaceans, all conditioned in the biobox of the ROV. At station 200, six Hexactinellida sponges were sampled together with anthipatharians, crinoids, hydrozoans, ophiuroids and tunicates. The specimens of the new species Bathymoorea lucasi sp. nov. were found by sieving water from the biobox, which indicates a possible commensalism with the sponges.

MACELLICEPHALINAE HARTMANN-SCHRÖDER, 1971

Macellicephalinae Hartmann-Schröder, 1971: 75. – Hartmann-Schröder, 1974: 75. – Pettibone, 1976: 6. – Uschakov, 1982: 108 (translated version). – Pettibone, 1985d: 129. – Pettibone, 1994: 609. – Jirkov, 2001: 127. – Barnich & Fiege, 2003: 90.

Bathyedithinae Pettibone, 1976: 53.

Branchinotogluminae Pettibone, 1985a: 447.

Pettibone, 1993a: 679.

Branchiplicatinae Pettibone, 1984b: 150.

Branchipolynoinae Pettibone, 1984a: 227.

Lepidonotopodinae Pettibone, 1983: 392.

Pettibone, 1984b: 850.

Macellicephaloidinae Pettibone, 1976: 42.

Macellicephalinae Pettibone, 1976: 48.

Vampiropolynoinae Marcus & Hourdez, 2002: 342.
**Type genus:** Macellicephalinae McIntosh, 1885.

**Diagnosis:** Median antenna absent (Bathycanadina Levenstein, 1981, Bathyedithia Pettibone, 1976, Bathymariana Levenstein, 1978, Bathymiranda Levenstein, 1981, Diplaconotum Loshann, 1981, Hodor gen. nov., Nu gen. nov. and Polaruschakov Pettibone, 1976) or present (Abyssarya gen. nov., Austropolaria Neal, Barnich, Wiklund & Glover, 2012, Bathymbahamas Pettibone, 1985d, Bathycatalina Pettibone, 1976, Bathylisaiosa Pettibone, 1976, Bathythauvelia Pettibone, 1976, Bathykermadeca Pettibone, 1976, Bathykuri Petra Pettibone, 1976, Bathylevensteina Pettibone, 1976, Bathymacella Pettibone, 1976, Bathypolaria Levenstein, 1981, Bathyvitiizia Pettibone, 1976, Bathytasmania Levenstein, 1982a, Branchinotogluma Pettibone, 1985a, Branchiplicatus Pettibone, 1985b, Branchipolynoe Pettibone, 1984a, Bruunilla Hartman, 1971, Gesiella Pettibone, 1976, Lepidonotopodium Pettibone, 1983, Levensteinella Pettibone, 1985c, Macellicephalinae McIntosh, 1885, Macellicephaloidinae Uschakov, 1955, Macelloides Uschakov, 1957, Natopolyne Pettibone, 1985e, Peinaleopolynoe Desbruyès & Laubier, 1988, Pelagomacellicephal Pettibone, 1985d, Thermopolyne Miura, 1994, Vampiropolynoe Marcus & Hourdez, 2002 and Yodane gen. nov.); and lateral antennae absent.

**Remarks:** Pettibone (1976) has reviewed numerous species directly or indirectly related to Macellicephalinae and erected four new subfamilies (i.e. Bathypedithinae, Macellicephaloidinae, Macelloidinae and Polaruschakovinae). Uschakov (1982), however, did not agree with this rearrangement. Based on molecular (Fig. 2) and morphological phylogenetic analyses (Fig. 3), our data support previous studies (Hartmann-Schröder, 1971; Uschakov, 1982), which suggest grouping polynoids with or without a median antenna and without lateral antennae into a single subfamily (see Discussion for more details). Consequently, the above subfamilies, characterized by the synapomorphic absence of lateral antennae, are here synonymized with Macellicephalinae sensu Hartmann-Schröder, 1971.

**ABYSSARYA GEN. NOV.**

**Type species:** Abyssarya acus gen. nov., sp. nov.

**Gender:** Feminine.

**Diagnosis:** Short body, dorsoventrally flattened, up to 18 segments. Prostomium anteriorly extending, as oval projection, ventrally directed. Frontal filaments present. Eyes absent. Median antenna present, lateral antennae absent. Facial tubercles absent. Tentacular segment fused to prostomium. Tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws; smooth margin. Dorsal tubercles absent. Elytrophores large, up to nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subirruramious, notopodia reduced, much shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae of two types: upper group, distally with spinous rows; lower group, distally falcate, with spinous rows, modified along body. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae from segment 5. Pygidium with terminal anus.

**Remarks:** Genetic analysis suggests that Abyssarya gen. nov. is a member of the Macellicephalina species clade, which is supported by the number of segments, the number of elytraulophore pairs and the presence of dorsal ridges. However, Abyssarya gen. nov. presents important morphological differences from other members of the clade: prostomium lobes are ventrally directed, presence of well-developed lanceolate pre-chaetal lobes, presence of ventral lobes and falcate neurochaetae modified along the body. Well-developed pre-chaetal lobes have been observed in a few species of Parahololepidella Pettibone, 1969a and Paradyte Pettibone, 1969b, but they are conical in shape (Wehe, 2006; Britayev et al., 2014), while differentiation in neurochaetae between the anterior and the posterior body has been shown for Uncopolynoe coralicola (with the first segments having more bent neurochaetae than subsequent ones). The presence of modified falcate neurochaetae along the body of Abyssarya gen. nov. might be related to a commensal life mode, probably with corals.

**Etymology:** This genus is dedicated to Arya Stark, one of P.B.’s favourite characters in the novel ‘A song of ice and fire’ by George R. R. Martin. The name is composed by ‘abyss’ from the Latin word ‘abyssus’ meaning ‘bottomless’ and Arya.

**ABYSSARYA ACUS GEN. NOV., SP. NOV.**

**(Fig. 5A–Q, TABLES 1, 2)**

**Type material:** Holotype, MNHN-IA-TYPE 1811 (IFR632-2), complete, length 4.77 mm, width 0.40 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212,
collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 1, MNHN-IA-TYPE 1812 (IFR632-5), complete, length 3.50 mm, width 0.36 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 2, MNHN-IA-TYPE 1813 (IFR632-1), complete, length 4.64 mm, width 0.53 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 3, NHMUK 2018.25346 (IFR632-3), posterior fragment, used for molecular analysis and SEM, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

**Additional material:** P.B.’s collection (IFR632-4), complete, length 2.77 mm, width 0.29 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. P.B.’s collection (IFR632-4), complete, length 2.77 mm, width 0.29 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

**Description (based on holotype and paratypes):**

Holotype complete, 4.77 mm long and 0.40 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly (Fig. 5A); colour of live animal not known; ethanol-preserved specimen pale white.

Prostomium bilobed, about as wide as long, lobes moderately pronounced, anteriorly extending as oval projections, ventrally directed; small, oval frontal filaments present, inserted at innermost margin of prostomial lobes, between lobes and oval projections; median notch between prostomial lobes moderately wide and deep (Fig. 5A, H, I); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, large, inserted anteromedially on prostomium (in the notch); style smooth, tapering into thin tips, long (reaching segment 4). Palps smooth, tapering, short (reaching around segment 2), ventrally directed, shorter than all tentacular appendages (Fig. 5I). Facial tubercles absent.

Tentacular segment fused to prostomium, with short lobe, inserted laterally and slightly ventral to prostomium; achaetous; tentaculophores large, cylindrical, equal sized; tentacular styles smooth, tapering, long, dorsal tentacular style (reaching segment 6) longer than ventral style (Fig. 5H). Pharynx not everted on holotype, dissected in paratype (MNHN-IA-TYPE 1812); the pharyngeal papillae could not be counted; two pairs of jaws, each with main fang, margin smooth (Fig. 5J). Second segment with elytrophores, subbimamous parapodia, chaetae and ventral cirri.

Nine pairs of large, bulbous elytrophores, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17; elytra large (covering dorsum and parapodia; the largest overlapping about four to five segments), thin, translucent, rounded (Fig. 5H); margin smooth; surface covered uniformly, moderate number of rounded microtubercles (Fig. 5K).

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 5L), inserted subdistally on notopodia; styles smooth, tapering to thin tips, long (longer than neuropodial pre-chaetal lobe); dorsal tubercles absent (Fig. 5L).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (as long as neuropodial pre-chaetal lobe); in subsequent segments inserted medially on neuropodia (Fig. 5L, M), style short (much shorter than distal neuropodial pre-chaetal lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 5L). Dorsal ridges with one to three folds in all segments. Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of notoacicular not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicular not penetrating epidermis, neuroacicular reaching midway of pre-chaetal lobe; pre-chaetal lobe expanded, lanceolate (usually approaching the end of neurochaetae in length); postchaetal lobe poorly developed, short, pointed; ventral lobe, oval, small (Fig. 5L, M). Notochaetae very few (one or two observed), short, slightly curved, distally with distinct, faint spinous rows on convex side, with blunt tips (Fig. 5B, C, N); notochaetae more slender than neurochaetae. Neurochaetae of two types: (1) upper and middle groups, moderate in number (24 observed), long, slightly curved, distally, with distinct, faint spinous rows on convex side, with slightly bent blunt tip (occasionally presenting a very small secondary apical tooth; Fig. 5D, E, O); and (2) lower group, few (eight to ten observed), short, distally falcate, with faint spinous rows on convex side, with slightly bent blunt tip (Fig. 5F, G, P, Q); on segment 2, the lower group with strongly bent tips (Fig. 5Q); on segments 17 and 18 slightly more bent than on preceding segments.

Nephridial papillae present from segment 5 to end of body, small, bulbous (Fig. 5M); slightly enlarged, digitiform in mid body. Pygidium rounded, inflated dorsally, not enclosed by last segment; with terminal anus.
Figure 5. *Abyssarya acus* gen. nov., sp. nov., holotype MNHN-IA-TYPE 1811 (A, H, I, K–Q), paratype 3 NHMUK 2018.25346 (B–G) and paratype 1 MNHN-IA-TYPE 1812 (J). A, dorsal view of a preserved complete specimen. B, notochaeta. C, detailed view of the same. D, upper neurochaeta. E, detailed view of the same. F, lower neurochaeta. G, detailed view of the same. H, anterior end, dorsal view, chaetae omitted. I, anterior end, ventral view, chaetae and elytra omitted. J, inner view of half side of dissected jaws. K, microtubercles of elytron. L, right parapodia, posterior view, segment 12. M, ventral view of segments 10 and 11 with nephridial papillae on neuropodia, chaetae omitted. N, notochaeta with faint spinous rows, segment 12. O, upper neurochaeta, segment 12. P, lower neurochaeta, segment 12. Q, lower neurochaeta, segment 2. Abbreviations: dr, dorsal ridges folded; fil, frontal filament; np, nephridial papilla; prl, pre-chaetal lobe; vl, ventral lobe.

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(Fig. 5A). In paratype (MNHN-IA-TYPE 1812) anal cirri observed, smooth, tapering to thin tips, very long (reaching segment 9).

**Morphological variation:** The specimens differing in number of segments (16 and 18) otherwise showed great morphological similarities, including: size of appendages, form of prostomium and its appendages, first occurrence of nephridial papillae, form of parapodia and type of chaetae. However, animals with 16 segments had eight pairs of elytrophores instead of nine pairs, probably related to size.

**Remarks:** No other genera of Macellicephalinae show neuropodia with lanceolate pre-chaetal lobes and falcate neurochaetae differing between segment 2 and subsequent segments. In Uncopolynoinea the species *Uncopolynoe corallicola* likewise shows strongly curved hooks present in anterior segments (Wehe, 2006). This character might be linked to the life history of these worms, which are always found living on alcyonarian corals. Furthermore, *Parahololepidella greeffi* (Augener, 1918) is commensal on antipatharians (Britayev et al., 2014) and shows neurochaetae rather similar to *Abyssarya acus* gen. nov., sp. nov. This evidence reinforces a possible commensal relationship between *Abyssarya acus* gen. nov., sp. nov. and corals recovered from the same sampling biobox.

**Etymology:** The species name came from Latin ‘ācus’ meaning ‘needle’. It refers to modified neurochaetae present on segment 2 similar to a ‘crochet needle’.

**Genetic data:** DNA sequencing for this species was successful for COI, 16S and 18S, respectively sharing at least 99.1, 99.8 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.5% for COI and 0.1% for 16S.

**Distribution:** Only five specimens were sampled and all at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 seamount area (type locality).

**Ecological notes:** These worms were found in the water sieved from the ROV biobox at station 212, which contained sponges (Hexactinellidae), alcyonaceans, antipatharians and pennatulacean corals, in addition to ophiuroids. *Abyssarya acus* gen. nov., sp. nov. is likely to be commensal with one of these taxa, and more studies in the area are needed to identify the host.

**BATHYEDITHIA PETTIBONE, 1976**

*Bathyedithia* Pettibone, 1976: 53. – Levenstein, 1978: 167. – Uschakov, 1982: 133 (translated version). – Jirkov, 2001: 128.

**Type species:** *Macellicephaloides berkeleyi* Levenstein, 1971a.

**Diagnosis (emended):** Short body, dorsoventrally flattened, up to 26 segments. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercle absent. Large palpophores. Tentacular segment fused with prostomium, tentaculophores without acicula or chaetae. Pharynx with seven to nine pairs of distal papillae; two pairs of jaws with serrated margin. Dorsal tubercles large (*Bathyedithia tuberculata*) or absent (*Bathyedithia berkeleyi* and *Bathyedithia retierei* sp. nov.). Elytrophores prominent, up to ten pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicula lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neuropodia numerous, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present (*Bathyedithia berkeleyi* and *Bathyedithia retierei* sp. nov.) or absent (*Bathyedithia tuberculata*). Pygidium small, with dorsal (*Bathyedithia tuberculata* and *Bathyedithia berkeleyi*) or terminal anus (*Bathyedithia retierei* sp. nov.).

**Remarks:** The diagnosis of genus *Bathyedithia* is emended to include a character observed in the species described below and the species *Bathyedithia tuberculata* Levenstein, 1981: ten pairs of elytrophores; as well as with characters observed in the new species: the presence of a terminal anus and the number of pairs of pharyngeal papillae.

**BATHYEDITHIA RETIEREI SP. NOV.** (Fig. 6A–G; Tables 1, 2)

**Type material:** Holotype, MNHN-IA-TYPE 1814 (IFR451b), complete, length 3.81 mm, width 0.71 mm, 20 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge suprapnet, start 14°3.411′ N, 130°7.989′ W, end 14°3.813′ N, 130°6.481′ W, 4946–4978 m depth, 3789 m trawling distance.

**Description (based on holotype):** Holotype complete, 3.81 mm long and 0.71 mm wide for 20 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; live specimen bluish, transparent (Fig. 6A); ethanol-preserved specimen pale white.

Prostomium bilobed, wider than long, anteriorly rounded, lobes not developed; frontal filaments absent;
median notch between prostomial lobes narrow and shallow (Fig. 6A, B); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching to segment 2–3), inserted on rounded palpophores (Fig. 6B). Facial tubercle absent.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching to segment 4), dorsal and ventral tentacular cirri of similar length (Fig. 6B). Pharynx dissected, with seven pairs of subtriangular distal papillae of similar size; two pairs of jaws with main fang, serrated margin (one pair of jaws with nine to 11 teeth and the other pair with 13 teeth; Fig. 6C). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Ten pairs of distinct, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19 (elytron still attached on segment 7); elytra very small (approaching the margins of preceding and subsequent segments, covering notopodia), smooth margin; surface with sparse, rounded microtubercles.

Cirrigerous segments with distinct, small dorsal cirrophores (Fig. 6D), inserted subdistally on notopodia; styles of dorsal cirri smooth, tapering into thin tips, short (as long as tip of neuroacicular lobe); dorsal tubercles absent.

Segment 6–8 without any structures.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 6D). Notopodia narrow, subtriangular, tapering into short acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, lanceolate, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae very few (one or two observed), short, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by smooth margin (Fig. 6E); notochaetae more slender than neurochaeta. Neurochaetae of two types: (1) variable in number (three to 20 observed), long, distally flattened to concave, serrated along both margins, with abrupt pointed tips (Fig. 6F); and (2) middle group mostly in anterior segments, few (five observed), slightly stouter, long, distally flattened to concave, coarsely serrated along both margins, with blunt tips (Fig. 6G). The neurochaetae present a central rib that is more or less evident.

Nephridial papillae present on segments 10 and 11, small, digitiform. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 6A). Anal cirri lost, scars not seen.

Remarks: The new species is very close to Polaruschakov species having seven pairs of pharyngeal papillae, but even closer to Bathyedithia in having serrated jaws and rounded palpophores. Bathyedithia retierei sp. nov. differs from the two other species of Bathyedithia in having seven pairs of pharyngeal papillae and lanceolate neuropodia. Furthermore, in Bathyedithia retierei sp. nov. the nephridial papillae are present on segments 10 and 11, whereas in Bathyedithia tuberculata they are present from segment 7 to the end of the body, and they are absent in Bathyedithia berkeleyi.

Etymology: This species is dedicated to Professor Christian Retière (Muséum National d’Histoire Naturelle, Dinard, France) for his many contributions to French benthic research.

Genetic data: DNA sequencing for this species was successful for 16S and 18S (only 720 bp) but not for COI.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

BATHYELIASONA PETTIBONE, 1976
Bathyeliasona Pettibone, 1976: 23.

Type species: Macellicepsula abyssicola Fauvel, 1913.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 18 segments. Prostomium bilobed. Frontal filaments present. Eyes absent. Nuchal organs absent (Bathyeliasona abyssicola, Bathyeliasona kirkegaardi and Bathyeliasona nigra) or present (Bathyeliasona mariaeae sp. nov.). Median antenna present, lateral antennae absent. Facial tubercles absent. Tentaculophores with acicula and chaetae. Pharynx with two pairs of jaws; smooth margin; with nine pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores prominent, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae stout, distally with spinous rows; notochaetae stouter (Bathyeliasona mariaeae sp. nov.) or more slender (Bathyeliasona abyssicola, Bathyeliasona kirkegaardi and Bathyeliasona nigra) and narrower than neurochaetae. Neurochaetae greatly expanded and flattened distally, serrated on both sides. From
segment 3, ventral cirri inserted subdistally on neuropodia. Nephridial papillae present (Bathyeliasona nigra) or absent (Bathyeliasona mariae sp. nov.). Pygidium prominent, with dorsal anus.

Remarks: The diagnosis of the genus is emended to add the following characters observed in the new species described below: nuchal organs present and nephridial stouter than neurochaetae.
**Bathyeliasona mariae sp. nov.**  
(FIG. 7A–J; TABLES 1, 2)

*Type material:* Holotype, MNHN-IA-TYPE 1815 (IFR107), complete, length 9.86 mm, width 1.88 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 50, collected 26 March 2015, epibenthic sledge supra-net, start 11°49.592′N, 117°30.786′W, end 11°49.756′N, 117°29.574′W, 4360–4328 m depth, 2469 m trawling distance. Paratype, MNHN-IA-TYPE 1816 (IFR666-4), complete, length 2.90 mm, width 0.44 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance.

*Description (based on holotype and paratype):* Holotype complete, 9.86 mm long and 1.88 mm wide for 17 segments (including tentacular segment), dorsoventrally slightly flattened, not tapering posteriorly; live specimen iridescent, purplish in colour dorso-ventrally slightly flattened, not tapering 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 50, collected 26 March 2015, epibenthic sledge supra-net, start 11°49.592′N, 117°30.786′W, end 11°49.756′N, 117°29.574′W, 4360–4328 m depth, 2469 m trawling distance. Paratype, MNHN-IA-TYPE 1816 (IFR666-4), complete, length 2.90 mm, width 0.44 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′N, 128°22.753′W, end 18°49.088′N, 128°21.289′W, 4805–4823 m depth, 2529 m trawling distance.

*Remarks:* Only three species belonging to Bathyeliasona are known: Bathyeliasona kirkegaardi (Uschakov, 1971), Bathyeliasona abyssicola (Fauvel,
Figure 7. *Bathyeliasona mariaae* sp. nov., holotype MNHN-IA-TYPE 1815 (A–C, E–J) and paratype MNHN-IA-TYPE 1816 (D). A, dorsal view of a live complete specimen. B, anterior end, dorsal view of a live specimen. C, anterior end, dorsal view, chaetae omitted. D, inner view of half side of dissected pharynx with papillae. E, posterior end, dorsal view, chaetae omitted. F, left parapodia, posterior view (ventral cirri lost), segment 8. G, notochaeta with distinct spinous rows, segment 8. H, notochaeta with developed spinous, segment 8. I, upper neurochaeta, segment 8. J, lower neurochaeta, segment 8. Abbreviation: nu, nuchal organ.
1913) and Bathyeliasona nigra Hartman, 1967. These species were reviewed by Pettibone (1976), who separated them using characters such as the number of segments, type of notochaetae and development of notopodia/neuropodia in the last segments. Although not mentioned by Pettibone (1976), differences in the shape of pygidium can be highlighted from her drawings, which can also be used to separate species. The species Bathyeliasona abyssicola and Bathyeliasona nigra have 18 segments (including tentacular segment), whereas Bathyeliasona kirkegaardi has 17 segments, like Bathyeliasona mariaae sp. nov. Additional similarities between the latter two species are: shape of jaws, shape of pygidium and notopodial lobes shorter than neuropodia in the last segments. However, while Bathyeliasona mariaae sp. nov. has prostomial lobes anteriorly extending into long frontal filaments that reach the distal end of the ceratophore of the median antenna, in Bathyeliasona kirkegaardi the prostomial lobes are anteriorly rounded and the frontal filaments are minute and filiform, shorter than the ceratophore of the median antenna. Furthermore, in Bathyeliasona kirkegaardi, Bathyeliasona abyssicola and Bathyeliasona nigra the length of the ventral cirri is much shorter than the neuroacicular tip and the notochaetae are of one type only (stout with distinct spinous rows), whereas in Bathyeliasona mariaae sp. nov. the length of the ventral cirri is approaching the neuroacicular tip and the notochaetae are of two types (stouter with distinct spinous rows and slender with developed spinous rows). Pettibone (1976) described all the Bathyeliasona species with notochaetae more slender than neurochaetae, but in Bathyeliasona mariaae sp. nov. one notochaeta per notopodium can be stouter (and always narrower) than the neurochaetae. Furthermore, in Bathyeliasona mariaae sp. nov. the middle and lower neurochaetae show a kind of central rib distally that gives the neurochaetae a bilimbate appearance.

Etymology: This species is dedicated to Maria Silva, mother of P.B., for her love.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S, with all three genes sharing 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.0% for both COI and 16S.

Distribution: Based on the material examined (two specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR license (type locality) and APEI#3 areas.
Type material: Holotype, MNHN-IA-TYPE 1817 (IFR521-1), complete, length 5.43 mm, width 0.91 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317'N, 123°15.442'W, end 13°52.622'N, 123°14.263'W, 4498–4521 m depth, 3129 m trawling distance. Paratype 1, MNHN-IA-TYPE 1818 (IFR302), complete, length 3.31 mm, width 0.61 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296'N, 119°40.825'W, end 11°2.612'N, 119°39.512'W, 4398–4402 m depth, 2529 m trawling distance. Paratype 2, NHMUK 2018.25347 (IFR529-2-1), complete, length 2.70 mm, width 0.56 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317'N, 123°15.442'W, end 13°52.622'N, 123°14.263'W, 4498–4521 m depth, 3129 m trawling distance.

Additional material: Specimen 1, MNHN-IA-PNT 74 (IFR520-7), incomplete, length 1.38 mm, width 0.30 mm, nine segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317'N, 123°15.442'W, end 13°52.622'N, 123°14.263'W, 4498–4521 m depth, 3129 m trawling distance. Specimen 2, MNHN-IA-PNT 75 (IFR529-2-2), incomplete, length 1.13 mm, width 0.26 mm, eight segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317'N, 123°15.442'W, end 13°52.622'N, 123°14.263'W, 4498–4521 m depth, 3129 m trawling distance. Specimen 3, P.B.’s collection (IFR636-5-4), incomplete, length 1.10 mm, width 0.30 mm, eight segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 158, collected 15 April 2015, epibenthic sledge epi-net, start 14°3.813'N, 130°7.989'W, end 14°3.813'N, 130°6.481'W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype and paratypes): Holotype complete, 5.43 mm long and 0.91 mm wide for 18 segments (including tentacular segment), slightly dorsoventrally flattened, slightly tapering posteriorly; live specimen bluish, slightly translucent (Fig. 8A); ethanol-preserved specimen pale white, prostomium transparent with two large white patches interiorly. Prostomium bilobed, wider than long, lobes not so pronounced, anteriorly tapering to short pointed cephalic peaks (Fig. 8B); frontal filaments absent; median notch between prostomial lobes wide and moderately deep; eyes absent; a pair of internal white ganglia visible through translucent epidermis. Median antennae present, lateral antennae absent; ceratophore of median antenna bulbous, small, short (shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch, style missing in holotype; in paratype (MNHN-IA-TYPE 1818) style papillated (Fig. 8L), tapering into thin tips, short (reaching to segment 4); Palps smooth, tapering, short (reaching to segment 5–6; Fig. 8B). Facial tubercle absent. Upper lip with few folds. Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores distinct, small, equal sized, inserted subdistally (Fig. 8B); styles missing in holotype; in paratype (MNHN-IA-TYPE 1818) dorsal tentacular style papillated, tapering into thin tips, long (reaching to segment 2), ventral tentacular cirri missing. Pharynx not everted in holotype; dissected in paratype (NHMUK 2018.25347), with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang, outer margin with few (four to six) smaller teeth (Fig. 8E). Second segment with elyrophores, subbibramous paraphidia, chaetae and ventral cirri. Nine pairs of massive, large elyrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing in holotype); in paratype (MNHN-IA-TYPE 1818), elytra still attached on segments 2 and 7, large, covering dorsal and paraphidia, the largest overlapping about six segments, milky, translucent, kidney-shaped (Fig. 8C); almost entire margin papillated, except on anterior and inner parts, papillae smooth, thin, short to long, rather well spaced (Fig. 8D); surface densely and uniformly covered by microtubercles, except for overlapping parts; microtubercles rounded, covered by one to numerous button-like papillae, some microtubercles with distal long papillae, uniformly present on surface (Fig. 8D). Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 8F), inserted subdistally on notopodia; styles missing in holotype; in paratype (MNHN-IA-TYPE 1818) style papillated, tapering into thin tips, long (much longer than tip of neuroacicular lobe); dorsal tubercles forming lamelliform branchial-like processes (Fig. 8F), small on segment 3, becoming longer from segment 6–8 (shorter, smaller than elyrophores).
Figure 8. *Bathyfauvelia glacigena* sp. nov., holotype MNHN-IA-TYPE 1817 (B, F–K), paratype 1 MNHN-IA-TYPE 1818 (A, C, D, L) and paratype 2 NHMUK 2018.25347 (E). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, elytron from segment 9. D, detail of the same elytron. E, inner view of half side of dissected jaws. F, left parapodia, anterior view, segment 6, most upper neurochaeta broken. G, notochaeta with distinct spinous rows, segment 6. H, notochaeta with well-developed spinous rows, segment 6, frontolateral view. I, upper neurochaeta, frontal view, segment 6. J, middle neurochaeta, frontolateral view, segment 6. K, lower neurochaetae, segment 6. L, papillated median antenna. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elytrophore; pa, papilla.
Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing on holotype, in paratype (MNHN-IA-TYPE 1818) long (slightly longer than tip of neuroacicular lobe); in subsequent segments (Fig. 8F) inserted medially on neuropodia of mid-body and basally on neuropodia of anteroposterior body, styles very short (shorter than tip of neuroacicular lobe); last ventral cirri about as long as neuropodial lobe of same segment.

Parapodia subbiparamous; notopodia shorter than neuropodia (Fig. 8F). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae of two types: (1) few (five or six observed), short to long, stout, slightly curved with distinct spinous rows on convex side, with blunt tips (Fig. 8G); and (2) moderate in number (five to 13 observed), long to very long, slender, slightly curved with distinct, well-developed spinous rows, with blunt tips (Fig. 8H); notoacicula stouter than neurochaetae. Neurochaetae of two types: (1) upper group, few (five observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 8I); and (2) middle and lower group, moderate in number (20 observed), long to short, stouter, distally concave to folded, with spines (three to 19 observed) along both margins, with gently curved pointed tips (Fig. 8J); the lower neurochaetae in fascicle much shorter, with fewer lateral spines (about three observed; Fig. 8K), not present on segments 2–4; in last segment, neurochaetae can be very thin.

Nephridial papillae present on segments 12 and 13, globular. Pygidium rounded, enclosed by last segment; with dorsal anus (Fig. 8A). Anal cirri lost, scars not seen.

**Morphological variation:** Only one specimen shows an adult size, confirmed by the presence of nephridial papillae. All the other specimens appear to be juveniles sharing many similarities with the adult: long palps (reaching to segment 4–5) and form of notochaetae and neurochaetae. However, the prostomium in juveniles shows a wider notch, and peaks are poorly developed.

**Remarks:** Currently, only two species belonging to *Bathyfauvelia* are valid: *Bathyfauvelia affinis* and *Bathyfauvelia grandelytris* (Levenstein, 1975). Both species share the presence of pointed cephalic peaks (anterior end), presence of cirriform dorsal tubercle and only one type of neurochaetae, whereas the new species described here presents a similar prostomium shape and dorsal tubercle but has two types of neurochaetae present (Table 3). *Bathyfauvelia glacigena* sp. nov. is very similar to *Bathyfauvelia ignigena* sp. nov., and the two species can be easily confused (Table 3), but evidence from DNA shows that they are distinct species (Fig. 2). This was confirmed by the average K2P distance between them (14.0% for COI and 7.8% for 16S). Adult specimens of *Bathyfauvelia glacigena* sp. nov. have 18 segments, prostomial lobes anteriorly tapering to pointed cephalic peaks, palps slightly longer (reaching to segment 5–6) and the last ventral cirri about as long as the neuropodial lobe. In contrast, *Bathyfauvelia ignigena* sp. nov. has 19 segments, prostomial lobes anteriorly tapering to rounded cephalic peaks, palps slightly shorter (reaching to segment 3–4) and the last ventral cirri slightly longer than the neuropodial lobe. Only one adult specimen of *Bathyfauvelia glacigena* sp. nov. with 18 segments has been observed, and it is unclear whether this is the maximal number of segments for the species. More specimens are needed to confirm this character. It should be noted that prostomial lobes anteriorly tapering to blunt cephalic peaks were also observed in a few juvenile specimens of *Bathyfauvelia glacigena* sp. nov., suggesting that this character is ontogenetic and should be used only to differentiate adult specimens. The length of palps and ventral cirri on the last segment appear to be more consistent characters for separating these two species. Both species have overlapping distributions in the IOM and GSR license areas. In addition, *Bathyfauvelia glacigena* sp. nov. was also sampled in the Ifremer license area, and *Bathyfauvelia ignigena* sp. nov. was also sampled in APEI#3.

**Etymology:** The species name *glacigena* means ‘ice-born’, which is composed by borrowing from the Latin word ‘*glāciēs*’ meaning ‘ice’ and the Greek word ‘*γεννῶ*’ meaning ‘born’. It refers to white ganglia like ice.

**Genetic data:** DNA sequencing for this species was successful for COI, 16S and 18S, respectively sharing at least 98.6, 99.5 and 100% of genetic material between the specimens. The average K2P distance for intraspecific variation was 1.6% for COI and 0.2% for 16S.

**Distribution:** Based on the material examined (six specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in the IOM, GSR (type locality) and Ifremer license areas.
"BATHYFAUVELIA IGNIGENA SP. NOV.
(P. 9A–R; TABLES 1–3)
Polychaeta sp. NB-Po595 (GenBank KJ736540) Janssen et al. (2015).

Type material: Holotype, MNHN-IA-TYPE 1819 (IFR674-2), complete, length 5.65 mm, width 0.80 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 81, collected 1 April 2015, epibenthic sledge supra-net, start 11°3.900′ N, 119°37.812′ W, end 11°4.171′ N, 119°36.661′ W, 4365–4346 m depth, 2739 m trawling distance. Paratype 1, MNHN-IA-TYPE 1820 (IFR521-3), complete, length 5.80 mm, width 1.08 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′ N, 123°15.442′ W, end 13°52.622′ N, 123°14.263′ W, 4498–4521 m depth, 3129 m trawling distance. Paratype 2, NHMUK 2018.25348 (IFR655-1-1) for SEM, complete, length 5.67 mm, width 0.91 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′ N, 128°22.753′ W, end 18°49.088′ N, 128°21.289′ W, 4805–4823 m depth, 2529 m trawling distance.

Additional material: Specimen 1, MNHN-IA-PNT 76 (IFR665), incomplete, length 4.89 mm, width 0.88 mm, 13 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′ N, 128°22.753′ W, end 18°49.088′ N, 128°21.289′ W, 4805–4823 m depth, 2529 m trawling distance. Specimen 2, P.B.’s collection (IFR694), complete juvenile specimen, length 1.27 mm, width 0.28 mm, 12 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659′ N, 128°22.753′ W, end 18°49.088′ N, 128°21.289′ W, 4805–4823 m depth, 2529 m trawling distance.

Description (based on holotype and paratypes): Holotype complete, 5.65 mm long and 0.80 mm wide for 19 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly; colour of live animal not known; ethanol-preserved specimen pale white, prostomium transparent with two large white patches interiorly (Fig. 9A). Prostomium bilobed, wider than long, lobes not so pronounced, anteriorly tapering to short rounded cephalic peaks (Fig. 9B, H); frontal filaments absent; median notch between prostomial lobes wide and moderately deep; eyes absent; a pair of internal white ganglia visible through translucent epidermis. Median antennal present, lateral antennae absent; ceratophore of median antenna bulbous, small, short (shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch; style missing. Palps smooth, distally tapering abruptly, short (reaching around segment 4; Fig. 9H). Facial tubercle absent. Upper lip with few folds.

Tentacular segment with elongate aciculae, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, with chaetae; tentaculophores distinct, small, equal sized, inserted subdistally; dorsal tentacular style missing; ventral tentacular style papillated, tapering into thin tip, long (reaching segment 5), thin (Fig. 9H). Pharynx not

References for species are provided in Table 2. ‘?’ indicates uncertain information.

Table 3. Diagnostic characters for all valid species in the genus Bathyfauvelia

| Character                  | B. affinis | B. glacigena sp. nov. | B. grandelytris | B. ignigena sp. nov. |
|----------------------------|------------|-----------------------|-----------------|----------------------|
| Median antenna surface     | Papillated | Papillated            | ?               | ?                    |
| Cephalic peak              | Pointed    | Pointed               | Pointed         | Rounded              |
| Frontal filaments          | Present?   | Absent                | ?               | Absent               |
| Pulp length                | ?          | Until segment 5–6     | ?               | Until segment 3–4    |
| Shape of dorsal tubercles  | Cirriform  | Lamelliform            | Cirriform       | Lamelliform           |
| First segment with         | Segment 6  | Segment 12            | ?               | Segment 12           |
| nephridial papillae        |            |                       |                 |                      |
| Notochaetae                | One type?  | Two types (short, robust and long, slender) | One type (long, slender) | Two types (short, robust and long, slender) |
| Neurochaetae               | One type   | Two types             | One type        | Two types            |
| Length of ventral cirri on | ?          | About as long as the neuropodial lobe | ?               | Longer than neuropodial lobe |

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Figure 9. Bathyfauvelia ignigena sp. nov., holotype MNHN-IA-TYPE 1819 (A, H–J, L–R) and paratype 2 NHMUK 2018.25348 (B–G, K). A, dorsal view of a preserved complete specimen. B, prostomium, dorsal view. C, dorsal tubercles on segments 6 and 8, elytrophores on segments 7 and 9. D, short notochaeta with distinct spinous rows. E, long notochaeta with well-developed spinous rows. F, distal part of upper neurochaeta. G, lower neurochaeta. H, anterior end, dorsal view, chaetae omitted. I, elytron from segment 4. J, detail of the same elytra. K, inner view of half side of dissected pharynx with few papillae. L, right parapodia, posterior view, segment 12. M, notochaeta with distinct spinous segment 12. N, notochaeta with well-developed spinous rows, segment 12. O, upper neurochaeta, segment 12. P, lower slender neurochaeta, segment 3. Q, lower neurochaetae, segment 12. R, lower neurochaeta, segment 12. Abbreviations: ci, cirrophore; dt, dorsal tubercle; el, elyphore.
everted on holotype; dissected in paratype (NHMUK 2018.25348), with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang, margin serrated with few (four or five) smaller teeth (Fig. 9K). Second segment with elytraphores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of massive, large elytraphores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (on holotype elytra present on segments 2 and 4); exytra large (covering dorsum and parapodia, the largest overlapping about four to five segments), milky, translucent, kidney shaped (Fig. 9I); almost entire margin papillated, except on anterior and inner parts, papillae smooth, thin, long, rather well spaced (Fig. 9J); surface densely and uniformly covered by microtubercles, except overlapping parts; microtubercles rounded, few covered distally with one to few button-like papillae, few papillae present on surface (Fig. 9J).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 9L), inserted subdistally on notopodia; styles missing; dorsal tubercles forming lamelliform branchial-like processes (Fig. 9C, L), small on segment 3, becoming longer from segment 6 (approaching cirrophore; Fig. 9C).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicula lobe); in subsequent segments inserted medially on neuropodia but basally on neuropodia of posterior segments (Fig. 9L), styles very short (shorter than tip of neuroacicula lobe); last ventral cirri longer than neuropodial lobe of same segment.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 9L). Notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neupropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae of two types: (1) few (six to eight observed), short to long, stout, slightly curved with distinct spinous rows on curved side, with blunt tips (Fig. 9D, M); and (2) moderate in number (13 observed), long to very long, slender, slightly curved with distinct, well-developed spinous rows, with blunt tips (Fig. 9E, N); notoacicula stouter than neuroaciculae. Neuroaciculae of two types: (1) upper group, moderate in number (~12 observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 9F, O); and (2) middle and lower group, moderate in number (25 observed), long to short, stout, distally concave to folded, with spines (two to 19 observed) along both margins, with gently curved pointed tips (Fig. 9G, P–R); the lower neuroaciculae in fascicle much shorter (Fig. 9Q, R), with fewer lateral spines (two or three observed), not present on segments 2–4; in last segment neurochaetae can be very thin.

Nephridial papillae on segments 12 and 13, globular. Pygidium rounded, slightly enclosed by last segment; with dorsal anus (Fig. 9A). Anal cirri lost, scars not seen.

Morphological variation: Most of the specimens have an adult size with 19 segments, with few morphological variations. Only one adult specimen presents a very short palp (MNHN-IA-PNT 76, reaching segment 2), which might be regenerating. The only juvenile specimen, with 12 segments, already has the two types of both notochaetae and neurochaetae present in adults but less numerous. However, the prostomial lobes (slightly wider), the prostomial peaks (poorly developed) and the dorsal tubercles (poorly developed) differ from the adults.

Remarks: Bathyfauvelia ignigena sp. nov. differs from Bathyfauvelia glacigena sp. nov. in having 19 segments, rounded cephalic peaks, slightly shorter palps (reaching to segment 3–4) and slightly longer ventral cirri than neuropodial lobes on the last parapodia. See Remarks on Bathyfauvelia glacigena sp. nov. and Table 3 for more details.

Etymology: Species named from the ‘ignīgēna’, a poetical epithet of Bacchus meaning ‘fire-born’, which is composed by borrowing from the Latin word ‘ignis’ meaning ‘fire’ and the Greek word ‘γεννώ’, γεννώ meaning ‘born’.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S (only one specimen). The specimens shared ≥ 99.3% for COI and 100% and for 16S. The average K2P distance for intraspecific variation was 0.4% for COI and 0.0% for 16S.

Distribution: Based on the material examined (five specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in IOM (type locality), GSR, Ifremer (Janssen et al., 2015) and APEI#3 areas.

**BATHYPOLARIA LEVENSTEIN, 1981**

*Bathypolaria Levenstein*, 1981: 27. – Jůrkov, 2001: 130.

Type species: Bathypolaria carinata Levenstein, 1981.

Diagnosis: Short body, 15 segments. Prostomium bilobed. Frontal filaments absent. Eyes absent. Median antenna present, lateral antennae absent. Facial
tubercle absent. Tentaculopores without chaetae. Pharynx with two pairs of jaws, small secondary tooth in margin; with seven pairs of pharyngeal papillae. Dorsal tubercles absent. Elytrophores small, eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous; notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae flattened, with spines on convex side, smooth on straight side, stout; notochaetae stouter than neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted subdistally on neuropodia. Posterior end with a ventral keel.

**Bathypolaria sp. 173**
(Fig. 10A, E; Tables 1, 2)

*Material examined:* Specimen 1, MNHN-IA-PNT 63 (IFR173), complete, length 3.45 mm, width 0.80 mm, probably 15 segments (including prostomium segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 20, collected 21 March 2015, epibenthic sledge supra-net, start 11°50.15′N, 117°58.49′W, end 11°50.18′N, 116°58.46′W, 4144–4093 m depth, 2769 m trawling distance. Specimen 2, MNHN-IA-PNT 64 (IFR672), incomplete, length 1.80 mm, width 0.38 mm, nine segments (including prostomium segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 81, collected 1 March 2015, epibenthic sledge supra-net, start 11°3.90′N, 119°37.81′W, end 11°4.17′N, 119°36.66′W, 4365–4346 m depth, 2739 m trawling distance. Specimen 3, MNHN-IA-PNT 65 (IFR406), incomplete, length 3.54 mm, width 0.93 mm, 11 segments (including prostomium segment), originally complete with 15 segments, but the end was cut for molecular analysis; Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 133, collected 10 April 2015, epibenthic sledge supra-net, start 13°50.75′N, 123°15.64′W, end 13°51.12′N, 123°14.13′W, 4516–4427 m depth, 2289 m trawling distance.

*Description (based on all specimens):* Fragile worms, all damaged; parapodia, prostomium and parapodial appendages often missing. Body dorsoventrally cylindrical; live specimen with body surface translucent to milky, prostomium whitish, pharynx red; ethanol-preserved specimens with body surface pale white, prostomium white, pharynx internally red, longitudinal ventral whitish line (Fig. 10A).

Prostomium bilobed, wider than long, lobes slightly pronounced, anteriorly rounded; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 10A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna small (not surpassing anterior end of prostomial lobes), inserted near median notch, style missing. Palps smooth, tapering, very long (reaching around segment 11). Facial tubercle bilobed. Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculopores small; styles smooth, tapering; dorsal tentacular style very short (reaching segment 2); ventral tentacular style long (reaching around segment 4). Pharynx dissected, with seven pairs of distal subtriangular papillae; two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt). Lips of mouth in a bulbous projection when pharynx not everted. Probably eight knob-like elytrophores present (all elytra missing).

Cirri of ventral cirrophores and elytrophores small, absent; ceratophores small, cylindrical; ceratophores with pointed tips (Fig. 10E). Neurochaetae all missing. Ventrally smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroaciculae lobe); missing in subsequent segments. Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuropodic lobe not penetrating epidermis. Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips (Fig. 10E). Neurochaetae all missing. Nephridial papillae not seen. Ventral keel present on last segments.

*Remarks:* The sampled specimens belong to Bathypolaria and share many characters with the single species described in this genus (Bathypolaria carinata): short body (15 segments), flattened noto- and neuropodia; posterior end of prostomial lobes, inserted near median notch, style missing. Palps smooth, tapering, very long (reaching around segment 11). Facial tubercle bilobed. Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculopores small; styles smooth, tapering; dorsal tentacular style very short (reaching segment 2); ventral tentacular style long (reaching around segment 4). Pharynx dissected, with seven pairs of subtriangular papillae; two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt). Lips of mouth in a bulbous projection when pharynx not everted. Probably eight knob-like elytrophores present (all elytra missing).

Cirri of ventral cirrophores and elytrophores small, absent; ceratophores small, cylindrical; ceratophores with pointed tips (Fig. 10E). Neurochaetae all missing. Ventrally smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroaciculae lobe); missing in subsequent segments. Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuropodic lobe not penetrating epidermis. Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips (Fig. 10E). Neurochaetae all missing. Nephridial papillae not seen. Ventral keel present on last segments.

*Remarks:* The sampled specimens belong to Bathypolaria and share many characters with the single species described in this genus (Bathypolaria carinata): short body (15 segments), flattened noto- and neuropodia; posterior end of prostomial lobes, inserted near median notch, style missing. Palps smooth, tapering, very long (reaching around segment 11). Facial tubercle bilobed. Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculopores small; styles smooth, tapering; dorsal tentacular style very short (reaching segment 2); ventral tentacular style long (reaching around segment 4). Pharynx dissected, with seven pairs of subtriangular papillae; two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt). Lips of mouth in a bulbous projection when pharynx not everted. Probably eight knob-like elytrophores present (all elytra missing).

Cirri of ventral cirrophores and elytrophores small, absent; ceratophores small, cylindrical; ceratophores with pointed tips (Fig. 10E). Neurochaetae all missing. Ventrally smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroaciculae lobe); missing in subsequent segments. Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuropodic lobe not penetrating epidermis. Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips (Fig. 10E). Neurochaetae all missing. Nephridial papillae not seen. Ventral keel present on last segments.

*Genetic data:* DNA sequencing for this species was successful for COI (only one specimen), 16S and 18S. The specimens shared at least 99.5% and 99.9% of
genetic material in 16S and 18S genes, respectively. The average K2P distance for intraspecific variation was 0.3% for 16S.

**Distribution:** Based on the material examined (three specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR, IOM and GSR license areas.

**Bathypolaria sp. 608**

(Fig. 10B–D, F; Tables 1, 2)

Polychaeta sp. NB-Po581 (GenBank KJ736683) Janssen et al. (2015).

**Material examined:** Specimen 1, MNHN-IA-PNT 66 (IFR608), complete, length 3.80 mm, width 0.80 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°34.612′N, 128°17.809′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 2, MNHN-IA-PNT 67 (IFR658-1), complete, length 3.73 mm, width 0.74 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 3, MNHN-IA-PNT 68 (IFR658-2), incomplete, length 3.84 mm, width 0.80 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Specimen 4, ...
MNHN-IA-PNT 69 (IFR624), incomplete, length 0.43 mm, width 0.74 mm, not possible to count the number of segments, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 210, collected 24 April 2015, epibenthic sledge supra-net, start 18°49.271′N, 128°25.804′W, end 18°49.926′N, 128°24.401′W, 4700–4740 m depth, 3399 m trawling distance. Specimen 5, MNHN-IA-PNT 70 (IFR625), complete, length 0.38 mm, width 0.75 mm, not possible to count the number of segments, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 210, collected 24 April 2015, epibenthic sledge supra-net, start 18°49.271′N, 128°25.804′W, end 18°49.926′N, 128°24.401′W, 4700–4740 m depth, 3399 m trawling distance.

**Description (based on all specimens):** Fragile worms, all damaged; parapodia, prostomial and parapodial appendages often missing. Body dorsoventrally cylindrical; live specimen with body surface translucent to milky, prostomium whitish, pharynx red; ethanol-preserved specimens with body surface pale white, prostomium white, pharynx internally red, longitudinal ventral whitish line (Fig. 10B).

Prostomium bilobed, wider than long, lobes slightly pronounced, anteriorly rounded; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 10B); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna small (not surpassing anterior end of prostomial lobes), inserted near median notch, style missing. Palps missing.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; tentaculophores distinct, small; dorsal tentacular style very short (reaching segment 2), smooth, tapering. Pharynx everted, with seven pairs of distal subtriangular papillae, equal sized (Fig. 10B); two pairs of jaws, each one with one main fang, outer margin with a secondary very small tooth (pointed or blunt; Fig. 10D). Lips of mouth in a bulbous projection when pharynx not everted.

Probably eight knob-like elytrophores present (all elytra missing).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores (Fig. 10C); elongated, and anteriorly directed on segment 3, not seen in subsequent segments; styles missing; dorsal tubercles absent.

Ventral cirr smooth, tapering; inserted basally on neuropodia of segment 2, style short (much shorter than tip of neuroacicular lobe); in subsequent segments inserted subdistally on neuropodia, styles short (approaching tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 10C). Notopodia tapering into long acicular lobe, tip of notoacica not penetrating epidermis. Neuropodia rectangular, tapering into long acicular lobe, tip of neuroacicular not penetrating epidermis.

Notochaetae flattened, short, few (two observed), with spines on convex side, smooth on straight side, with pointed tips. Neurochaetae long, slender, distally flattened, serrated along both margins, with pointed tips (Fig. 10F).

Nephridial papillae not seen. Anal cirr lost, scars not seen. Ventral keel present on last segments.

**Remarks:** See Remarks on Bathypolaria sp. 173 for more details.

**Genetic data:** DNA sequencing for this species was successful for COI, 16S and 18S, respectively sharing at least 99.6, 99.5 and 99.9% of genetic material between the specimens. The average K2P distance for intraspecific variation was 0.2% for COI and 0.1% for 16S.

**Distribution:** Based on the material examined (five specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled at two stations in APEI#3 area.

**Bruunilla Hartman, 1971**

Bruunilla Hartman, 1971: 1411. – Pettibone, 1979: 384.

**Type species:** Bruunilla natalensis Hartman, 1971.

**Diagnosis (emended):** Short body, dorsoventrally flattened, up to 18 segments. Prostomium bilobed. Frontal filaments present (Bruunilla nealae sp. nov.) or absent (Bruunilla natalensis). Eyes absent. Median antenna present, lateral antennae absent. Facial tubercles present. Wing-like structure present on ventral side of lower lip. Tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws, serrated margin. Dorsal tubercles absent. Elytrophores small, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Neuropodial papillae present. Notochaetae few, slender, distally flattened to concave, serrated along both margins; notochaetae more slender than neurochaetae. Neurochaetae numerous, with distal part flattened to concave, serrated along both margins. From segment 3, ventral cirr inserted subdistally on neuropodia. Pygidium with dorsal anus.

**Remarks:** This genus was first classified as a Fauveliopsidae Hartman, 1971, but the unique specimen...
(without any chaetae) was reviewed by Pettibone (1979), who transferred it to Macellicephalinae. The genus **Bruunilla** is easily recognized by the presence of a wing-like structure located ventrally on segments 1–3. The generic diagnosis is emended here in order to include characters observed in the new species described below, such as: presence of frontal filaments, neuropodial papillae and types of notochaetae and neurochaetae. Pettibone (1979) did not mention the presence of neuropodial papillae, although Hartman (1971) drew it as a short papilla on segment 7 (Hartman, 1971: 1412, fig. 3). This kind of papilla has been observed before in species of *Diplaconotum* Loshann, 1981 (Loshann, 1981: 12, fig. 5C), as a small, short papilla also on the neuropodia. However, this latter genus belongs to Polarschakovinae, not having median or lateral antennae. This fact could explain the closer relationship between *Bruunilla* and taxa without antennae. The genus *Bruunilla* has been monotypic for almost four decades since its erection (Pettibone, 1979). Increased exploration of the deep ocean has led to the discovery of several new forms that possess wing-like structures on their ventrum, a hallmark of this genus. One species is described here, but several others (seven MOTUs) were recognized by DNA only. Unfortunately, those specimens were in too poor condition to allow for a morphological description (data not presented). Our findings suggest that there is a much greater diversity of this genus in the deep sea than previously thought.

**BRUUNILLA NEALAE** **SP. NOV.**

**(FIG. 11A–G; TABLES 1, 2)**

**Type material:** Holotype, MNHN-IA-TYPE 1824 (IFR512), complete, length 3.00 mm, width 0.69 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 171, collected 17 April 2015, epibenthic sledge supra-net, start 14°2.687'N, 130°5.951'W, end 14°3.205'N, 130°4.606'W, 5024–5017 m depth, 2979 m trawling distance.

**Description (based on holotype):** Holotype complete, 3.00 mm long and 0.69 mm wide for 17 segments (including tentacular segment), dorsoventrally flattened, slightly tapering posteriorly; live specimen pale white, slightly translucent; ethanol-preserved specimen pale yellow.

Prostomium bilobed, wider than long, lobes not pronounced, anteriorly rounded; with short, ovoid frontal filaments; median notch between prostomial lobes narrow and shallow (Fig. 11A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, very short (shorter than anterior end of frontal filaments), inserted near posterior margin of prostomium; style smooth, tapering, long (reaching segment 7). Palps smooth, tapering, short (reaching segment 4; Fig. 11A). Facial tubercle not seen. A pair of wing-like structures on ventral side, like a prolongation of lower lip, separated longitudinally until segment 3; median notch between lobes narrow and deep; each lobe oval, with blunt tips, with most longitudinal folds anteriorly, and most horizontal folds posteriorly, partially covering first four or five segments (Fig. 11B, G).

Tentacular segment with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores small, cylindrical, equal sized; tentacular styles smooth, tapering, dorsal tentacular style (reaching segment 7) slightly longer than ventral tentacular cirri (Fig. 11A). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Eight pairs of knob-like, bulbous elytrophores on segments 2, 4, 5, 7, 9, 11, 13 and 15 (elytron still attached on segment 2, both sides and on segment 4, on the left side); elytra in poor condition, thin, fragile, translucent, surface and margin smooth. Cirrigenous segments with distinct, small dorsal cirrophores, inserted subdistally on notopodia; styles smooth, tapering, long (as long as the neuropodial lobe), longest on segments 3 and 14 (much longer than tip of neuroacicula lobe); dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, long (much longer than tip of neuroacicula lobe); in subsequent segments inserted subdistally on neuropodia (Fig. 11C), styles long (about as long as tip of neuroacicula lobe).

Parapodia subbiramous, notopodia reduced, much shorter than neuropodia (Fig. 11C). Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; posteriorly post-chaetal lobe becoming ventrally pointed; segments 11–14 with long (slightly shorter than tip of neuroacicula lobe) cirriform neuropodial papilla present, inserted in upper part of neuropodia lobe, smooth, tapering, long, blunt tips. Neurochaetae few (one to six observed), short to long, slender, distally flattened to concave, serrated along both sides, with blunt tips (Fig. 11D); notochaetae more slender than neurochaetae. Neurochaetae moderate in number (16 observed), long to short, with distal part flattened to concave, serrated along both margins, with pointed tips (Fig. 11E, F); upper group stouter, longer than lower group (Fig. 11F).
Nephridial papillae absent. Pygidium small, rounded, enclosed by last segment; with dorsal anus. Anal cirri lost, scars not seen.

Remarks: *Bruunilla natalensis* is the only species described in this genus until now. *Bruunilla nealae* sp. nov. is unique in having frontal filaments and long neuropodial papillae on segments 11–14, which are absent in *Bruunilla natalensis* (papilla maybe present on segment 7; see Remarks on *Bruunilla*). In addition, the blunt tips of the wing-like structure in *Bruunilla nealae* sp. nov. differ from the protruding tips of the wing-like structure in *Bruunilla natalensis*. Furthermore, the average K2P distance between *Bruunilla nealae* sp. nov. and *Bruunilla* sp. 692 was very high (27.3% for 16S).
**Etymology:** This species is dedicated to Lenka Neal (Natural History Museum, London) for her friendship, discussion and comments during this project.

**Genetic data:** Gene sequencing for this species was successful for 16S and 18S (only 1200 bp) but not for COI.

**Distribution:** Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

**BRUUNILLA sp. 692**

(Fig. 11H, Tables 1, 2)

**Material examined:** MNHN-IA-PNT 72 (IFR692), complete, length 3.16 mm, width 0.55 mm, segment count not possible because of poor condition, Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 197, collected 22 April 2015, epibenthic sledge epi-net, start 18°48.659' N, 128°22.753' W, end 18°49.088' N, 128°21.289' W, 4805–4823 m depth, 2529 m trawling distance.

**Description:** Complete, 3.16 mm long and 0.55 mm wide, dorsoventrally flattened; colour of live animal not known; ethanol-preserved specimen pale yellow; poor condition, most chaetae and parapodia missing (Fig. 11H).

Prostomium bilobed, wider than long, lobes not pronounced, anteriorly rounded; with ovoid frontal filaments; median notch between prostomial lobes narrow and shallow (Fig. 11H); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna bulbous, very short (shorter than anterior end of frontal filaments), inserted near posterior margin of prostomium, style smooth, tapering, long. Palps missing. A pair of wing-like structures on ventral side (left one broken), like a prolongation of lower lip, separated longitudinally until segment 3; each lobe oval, blunt, with mostly longitudinal folds anteriorly and posteriorly, partly covering at least four segments. Tentacular segment with a pair of short lobes, inserted laterally and slightly below prostomium; tentacularophores small, equal sized; styles missing. Pharynx dissected with pharyngeal papillae not possible to count; two pairs of jaws, each with main fang and serrated margins (18–22 teeth); gradually bigger distally. Second segment with eleytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Cirrigerous segments with small dorsal cirrophores; styles missing; dorsal tubercles absent. Ventral cirri present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style smooth, tapering, long (much longer than tip of neuroacicula lobe); missing in subsequent segments. Parapodia subbiramous, notopodia reduced, much shorter than neuropodia. Notopodia reduced, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; cirriform neuropodial papillae not seen on segments 11–14. Notochaetae missing. Neurochaetae long to short, with distal parts flattened to concave, serrated along both margins, with pointed to blunt tips. Nephridial papillae not seen. Pygidium rounded, with dorsal anus.

**Remarks:** The specimen was too damaged to be described formally as a new species but was successfully sequenced for COI, 16S and 18S.

**Genetic data:** DNA sequencing for this specimen was successful for COI, 16S and 18S.

**Distribution:** Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area.

**HODOR GEN. NOV.**

*Type species:* Hodor hodor gen. nov., sp. nov.

**Gender:** Masculine.

**Diagnosis:** Short body, dorsoventrally flattened, up to 24 segments. Prostomium bilobed, with lobes subtriangular, tapering to blunt peaks. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercles absent. Palpophores enlarged. Tentacular segment fused with prostomium, tentacularophores without acicula or chaetae. Pharynx with two jaws, serrated margin; with seven pairs of pharyngeal papillae. Dorsal tubercles absent. Eleytrophores prominent, nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroaciculae not penetrating epidermis. Notochaetae slender, distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae numerous. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present. Pygidium with dorsal anus.

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**Remarks:** The presence of large palpophores and serrated jaws should place this genus as a member of Bathyedithinae, but the presence of seven pairs of pharyngeal papillae is a character present in Polaruschakovinae. The genus can thus not be assigned to any of the current subfamilies, which supports synonymizing most of the deep-sea subfamilies (see Discussion). The distinctive characters of *Hodor* gen. nov., which separate the genus from *Bathyedithia*, are: seven pairs of similar-sized distal papillae and the presence of stouter modified neurochaetae on segments 3–7, whereas *Bathyedithia* has nine pairs of distal papillae, with the middle one elongated, and lacks modified neurochaetae. In this study, the combined molecular and morphological phylogenetic analysis placed *Hodor* gen. nov. closer to *Polaruschakov* and morphological phylogenetic analysis placed *Hodor* gen. nov. closer to *Polaruschakov*, which is consistent with their morphology, given that in both genera the median and lateral antennae are absent.

**Etymology:** This genus is dedicated to Hodor, one of P.B.’s favourite characters in the novel ‘A song of ice and fire’ by George R. R. Martin.

**HODOR HODOR SP. NOV.**

(Fig. 12A–H; Tables 1, 2)

**Type material:** Holotype, MNHN-IA-TYPE 1825 (IFR655-2-1), complete, length 11.35 mm, width 1.68 mm, 24 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°20.418′W, end 18°45.338′N, 128°21.874′W, 4821–4820 m depth, 2799 m trawling distance.

**Description (based on holotype):** Holotype complete, 11.35 mm long and 1.68 mm wide for 24 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white (Fig. 12A).

Prostomium bilobed, about as long as wide, lobes subtriangular, poorly developed, anteriorly tapering into blunt peaks, extending until superior lip; frontal filaments absent; median notch between prostomial lobes narrow and shallow (Fig. 12C); eyes absent; a pair of internal white ganglia visible through translucent epidermis, dorsolaterally located on prostomium. Median and lateral antennae absent. Palps smooth, tapering, very long (reaching segment 9), inserted on large, rounded palpophores (Fig. 12C). Facial tubercle absent.

Tentacular segment fused to prostomium, well developed, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores large, bulbous, equal sized; dorsal tentacular style smooth, tapering, short (reaching segment 4); ventral tentacular style missing (Fig. 12C). Pharynx not everted. Second segment with elyrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of large, globular elyrophores (Fig. 12B, D) present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing); with dorsal cirrophores on last segments.

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 12B), inserted subdistally on notopodia; styles missing.

Segments 6 and 8 with large, swollen dorsal structure (Fig. 12A, B), located basally to cirrophores, interiorly whitish; smaller on segment 6, bigger on segment 8. Dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (Fig. 12D), style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia reduced, much short than neuropodia (Fig. 12D). Notopodia arising from the dorsum as two thickened ridges; narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Neuroacicaetae variable in number (one to 16 observed), long, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by subdistally smooth margin (Fig. 12E); notoacicaetae more slender than neuroacicaetae. Neurochaetae of two types: (1) moderate in number (12–28 observed), long to very long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 12F); and (2) middle and lower group on segments 3–7 modified, moderate in number (16 observed), stouter, short to long, distally flattened to concave, with coarse spines along both margins, spines concentrated basally and well spaced later, middle part with smooth margins (most of or less of their length), subdistally smooth or with one or two spines, blunt tip, tip margin slightly lighter (Fig. 12G, H).

Nephridial papillae present on segments 11, 12 and 13, small, bulbous. Last segment very reduced. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 12A). Anal cirri lost, scars not seen.

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Remarks: Hodor hodor gen. nov., sp. nov. presents many similarities with Hodor anduril gen. nov., sp. nov., including the number of segments, prostomium and parapodial shape, chaetae and number of nephridial papillae pairs. However, the palps in Hodor hodor gen. nov., sp. nov. are longer (reaching segment 9) than the palps in Hodor anduril gen. nov., sp. nov. (reaching segment 2). Furthermore, the average K2P distance...
between these species was 14.2% for COI and 6.1% for 16S. Interestingly, the morphological variation observed in Hodor anduril gen. nov., sp. nov. specimens could also indicate some dissimilarity within Hodor hodor gen. nov., sp. nov. specimens, which will necessitate care in the identification of any further specimens. In addition, both species have overlapping distribution in APEI#3.

Etymology: This species is dedicated to Hodor, one of P.B.’s favourite characters in the novel ‘A song of ice and fire’ by George R. R. Martin.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

**HODOR ANDURIL GEN. NOV., SP. NOV.**
(Fig. 13A–G; Tables 1, 2)

*Type material:* Holotype, MNHN-IA-TYPE 1826 (IFR655-2-3), complete, length 8.82 mm, width 1.50 mm, 23 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance. Paratype, MNHN-IA-TYPE 1827 (IFR655-2-2), complete, length 6.03 mm, width 0.73 mm, 23 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.4807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

*Description (based on holotype):* Holotype complete, 8.82 mm long and 1.50 mm wide for 23 segments (including tentacular segment), dorsosvertically flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white.

Prostomium bilobed, about as long as wide, lobes subtriangular, poorly developed, anteriorly tapering into blunt peaks, extending until superior lip; frontal filaments absent; median notch between prostomial lobes narrow and shallow (Fig. 13A); eyes absent; a pair of internal white ganglia visible through translucent epidermis, dorsolaterally located on prostomium. Median and lateral antennae absent. Palps smooth, tapering, very short (reaching segment 2), inserted on large, rounded palpophores (Fig. 13A). Facial tubercle absent.

Tentacular segment well developed, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores large, bulbous, equal sized (Fig. 13A); tentacular styles missing. Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri. Pharynx dissected, with seven pairs of subtriangular distal papillae, abruptly tapering, increasing in length gradually towards middle, with middle pair longest; two pairs of jaws with main fang, serrated margin (one pair of jaws with 15–16 teeth and the other with ten or 11 teeth; Fig. 13B).

Nine pairs of large, globular to cylindrical elytrophores (Fig. 13A) present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing); with dorsal cirrophores on last segments.

Cirrigerous segments with large, bulbous dorsal cirrophores (Fig. 13C), inserted subdistally on notopodia; styles smooth, thin, long (longer than tip of neuroacicula lobe).

Segments 6 and 8 with large, swollen dorsal structure (Fig. 13C), located basally to cirrophores, interiorly whitish; similar in size. Dorsal tubercles absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing; in subsequent segments inserted medially on neuropodia (Fig. 13C), style short (shorter than tip of neuroacicula lobe). Parapodia subbiramous; notopodia reduced, much shorter than neuropodia (Fig. 13C). Notopodia arising from the dorsum as two thickened ridges; narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Neurochaetae variable in number (one to 13 observed), long, slender, slightly curved with distinct, faint spinous rows on convex side, with blunt tips preceded by smooth margin (Fig. 13D); neurochaetae more slender than neurochaetae. Neurochaetae of two types: (1) moderate in number (13–21 observed), long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 13E); and (2) middle and lower group on segments 3–7 modified, moderate in number (16 observed), stouter, short to long, distally flattened to concave, with coarse spines along both margins, spines concentrated basally and well spaced later, middle part with smooth margins (most of or less of their length), subdistally smooth or with one or two spines, blunt tips, tip margin slightly lighter (Fig. 13F, G).

Nephridial papillae present on segments 11, 12 and 13, small, globular. Last segment very reduced.
Pygidium rounded, not enclosed by last segment; with terminal anus. Anal cirri lost, scars not seen.

Morphological variation: Holotype and paratype agree in many characters (e.g. number of segments, prostomium and parapodial shape, and form of chaetae) and their DNA (see Genetic data) but they show two important differences. In the holotype, the palps are very short (reaching segment 2), the segments 6 and 8 have swollen dorsal structure, and the nephridial papillae are present on segments 11–13, whereas in the paratype the palps are very long (reaching segment 11), the swollen dorsal structure is absent on segments 6 and 8, and the nephridial papillae are present on segments 10–13. These differences might be linked to sexual dimorphism.

Remarks: Differences in the first segment with nephridial papillae have been observed in Branchipolyneoe seepensis (Jollivet et al., 2000). They suggested that male specimens present one pair of nephridial papillae on segment 11, whereas female specimens present two pairs on segments 10 and 11. Thus, we believe that the differences observed between the holotype and paratype of Hodor anduril gen. nov., sp. nov. are linked to sexual dimorphism. In view of the morphological variation observed in this species, more attention needs to be paid to this genus. The long palps in the paratype resemble those of Hodor hodor gen. nov., sp. nov., but the first segment with nephridial papillae is different. In Hodor anduril gen. nov., sp. nov., nephridial papillae start on segment 10, whereas in Hodor hodor gen. nov., sp. nov. nephridial papillae start on segment 11. Furthermore, the presence of a swollen structure on anterior segments seems to indicate a reproductive feature, which is perhaps temporary.

Etymology: The species name is derived from the sword named 'andúril' meaning ‘Flame of the West’ and belonging to Aragorn in the novel ‘The lord of the rings’ by J. R. R. Tolkien. It refers to the sword-like modified neurochaetae present in this species.
Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S. Holotype and paratype shared 100% of genetic material in COI, 16S and 18S. The average K2P distance for intraspecific variation was 0.0% for both COI and 16S.

Distribution: Only two specimens were sampled and both at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

**Macellicephala McIntosh, 1885**

*Macellicephala* McIntosh, 1885: 121. – Uschakov, 1955: 312. – Uschakov, 1965: 106 (translated version). – Day, 1967: 44. – Hartmann-Schröder, 1971: 76. – Levenstein, 1971b: 18. – Hartmann-Schröder, 1974: 76. – Petitbone, 1976: 8. – Fauchald, 1977: 63. – Uschakov, 1982: 111 (translated version). – Jirkov, 2001: 130. – Barnich & Fiege, 2003: 92.

*Oligolepis* Levinsen, 1886: 292.

Type species: *Polynoe (Macellicephala) mirabilis* McIntosh, 1885, by monotypy.

**Diagnosis:** Short body, dorsally flattened, 18 segments. Prostomium bilobed. Frontal filaments present (*Macellicephala aciculata, Macellicephala australis, Macellicephala clarionensis* sp. nov., *Macellicephala mirabilis, Macellicephala parvafoaces* sp. nov., *Macellicephala remigata* and *Macellicephala violacea*) or absent (*Macellicephala galapagensis, Macellicephala laubieri* and *Macellicephala longipalpata*). Elytrophores without acicula or chaetae. Pharynx with two pairs of jaws, smooth margin; with nine pairs of papillae. Dorsal tubecules present (*Macellicephala galapagensis, Macellicephala remigata* and *Macellicephala violacea*) or absent/inconspicuous (*Macellicephala aciculata, Macellicephala atlantica, Macellicephala australis, Macellicephala laubieri, Macellicephala longipalpata and Macellicephala mirabilis*). Elytrophores prominent, nine pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroacicular not penetrating epidermis. Notochaetae few to moderate in number, smooth or spinous; notochaetae stouter or more slender than neurochaetae. Neurochaetae very numerous. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae present usually large, on segments 10, 11 and 12 (*Macellicephala aciculata, Macellicephala australis, Macellicephala clarionensis* sp. nov., *Macellicephala laubieri, Macellicephala longipalpata, Macellicephala mirabilis, Macellicephala parvafoaces* sp. nov. and *Macellicephala violacea*) or on segments 9, 10 and 11 (*Macellicephala remigata*); or absent (*Macellicephala galapagensis*). Pygidium bulbous, with dorsal anus.

**Macellicephala clarionensis sp. nov.**

*(Fig. 14A–H; Tables 1, 2, 4)*

**Type material:** Holotype, MNHN-IA-TYPE 1828 (IFR633-1), complete, length 4.48 mm, width 0.85 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 1, MNHN-IA-TYPE 1829 (IFR633-2), complete, length 4.03 mm, width 0.74 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth. Paratype 2, NHMUK 2018.25350 (IFR633-3), complete, length 3.67 mm, width 0.80 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 seamount, station 212, collected 24 April 2015, ROV Kiel 6000, biobox, start 18°32.83′N, 128°44.88′W, end 18°32.57′N, 128°44.93′W, 1853–1713 m depth.

Description (based on holotype and paratypes): Holotype complete, 4.48 mm long and 0.85 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, not tapering posteriorly; live specimen slightly translucent, bluish; ethanol-preserved specimen pale; nephridial papillae whitish. Body surface smooth.

Prostomium bilobed, about as wide as long, lobes well pronounced, anteriorly truncated; frontal filaments present, very small, inserted at innermost margin of the lobes; median notch between prostomial lobes very narrow and deep (Fig. 14A); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna large, cylindrical, short (much shorter than anterior margin of prostomial lobes), inserted medially on prostomium, near median notch, style missing. Palps smooth, tapering, short (reaching to segment 5; Fig. 14A, B). Trilobed facial tubercle present, median tubercle not pronounced (Fig. 14B).

Tentacular segment with short lobe, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores large, cylindrical, equal sized (Fig. 14A); tentacular styles missing in holotype; in paratype (MNHN-IA-TYPE 1829) dorsal
tentacular style missing, ventral tentacular style smooth, tapering, short (reaching to segment 4). Pharynx not everted in holotype; dissected in para- type (NHMUK 2018.25350), with pharyngeal papil- lae not possible to count; two pairs of jaws, each with main fang, margin smooth (Fig. 14C). Second segment with elytophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of prominent, bulbous elytophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segment with prominent, bulbous cir-rophore (Fig. 14D), inserted subdistally on notopodia; style smooth, tapering, long (longer than tip of neuroacicular lobe); dorsal tubercles distinct, subconical to oval.

Ventral cirri smooth, tapering, present from seg- ment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, styles very short (shorter than tip of neuroacicular lobe).
Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 14D). Notopodia subtriangular, tapering into long aciculiferous lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangulard to subtriangular, tapering into long aciculiferous lobe, tip of neuroacicula not penetrating epidermis; post-chaetal lobe slightly fleshy. Notochaetae moderate in number (19–25 observed), short to long, distally slightly curved, with very faint spinous rows on convex side, with pointed to blunt tips (Fig. 14E); notochaetae stouter than neurochaetae. Neurochaetae very numerous (45–60 observed), short to very long, very narrow, distally flattened to concave, with very faint spinous rows on the notochaetae. However, in Macellicephala macellicephala parvafauces sp. nov. these neurochaetae are present minute bidentate tips, whereas Macellicephala clarionensis sp. nov. has a moderately wide median notch, a well-developed median facial tubercle and neurochaetae present minute bidentate tips, whereas Macellicephala parvafulce sp. nov. has a moderately wide median notch, a well-developed median facial tubercle and neurochaetae with hooked tips. Macellicephala clarionensis sp. nov. is the only species within Macellicephala having minute bidentate tips (Table 4).

**Distribution:** Only three specimens were sampled and all at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area (type locality).

**Ecological notes:** The specimens were found in the water sieved from the ROV biobox at station 212, which contained several species of sponges (hexactinellid), alcyonaceans, antipatharians and pennatulacean corals, in addition to ophiuroids. Furthermore, spicules were found inserted in the body of the worms, suggesting an artefact of sieving or a commensal life with sponges. More studies in the area are needed to find out which species is the host.

**Macellicephala parvafauces sp. nov.**

(Fig. 15A–I; Tables 1, 2, 4)

**Type material:** Holotype, MNHN-IA-TYPE 1830 (IFR602), complete, length 11.82 mm, width 1.50 mm, 18 segments (including tentacular segment). Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.35′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype, MNHN-IA-TYPE 1831 (IFR403), complete, length 8.02 mm, width 1.05 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 131, collected 9–10 April 2015, ROV Kiel 6000, biobox, start 13°52.39′N, 123°15.03′W, end 13°52.44′N, 123°14.88′W, 4478 m depth.

**Description (based on holotype and paratype):**

Holotype complete, 11.82 mm long and 1.50 mm wide for 18 segments, slightly dorsoventrally flattened, not tapering posteriorly; live specimen whitish anteriorly and slightly brownish posteriorly; ethanol-preserved specimen pale yellow throughout (Fig. 15A, C). Body surface smooth.

Prostomium bilobed, about as wide as long, lobes pronounced anteriorly, truncated; small, oval frontal filaments present, inserted at innermost margin of prostomial lobes; median notch between prostomial lobes moderately wide and deep (Fig. 15D); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna large, cylindrical, short (shorter than anterior margin of prostomial lobes), inserted near median notch, style missing. Palps smooth, tapering, short (reaching segment 4; Fig. 15D). Trilobed facial tubercle present, median tubercle larger than lateral ones (Fig. 15B, D).

Tentacular segment with short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores large, cylindrical,

**Remarks:** Macellicephala clarionensis sp. nov. is the only species of Macellicephala with minute bidentate tips on neurochaetae. In the paratype of Macellicephala clarionensis sp. nov. the median notch is not so pronounced, and the neurochaetae present minute bidentate tips, whereas Macellicephala parvafauces sp. nov., the median notch between the prostomial lobes is very narrow, the median facial tubercle is not so pronounced, and the neurochaetae present minute bidentate tips. However, in Macellicephala clarionensis sp. nov. the median notch between the prostomial lobes is very narrow, the median facial tubercle is not so pronounced, and the neurochaetae present minute bidentate tips, whereas Macellicephala parvafauces sp. nov. has a moderately wide median notch, a well-developed median facial tubercle and neurochaetae with hooked tips. Macellicephala clarionensis sp. nov. is the only species within Macellicephala having minute bidentate tips (Table 4). The average K2P distance between the two new species was high (26.9% for COI and 25.8% for 18S).

**Etymology:** The term ‘clarionensis’ refers to the area of distribution; APEI#3 is crossed by the Clarion Fracture. During the SO239 cruise, the area was sampled for the first time ever.

**Genetic data:** DNA sequencing for this species was successful for COI, 16S and 18S. Specimens shared ≥ 99.3% of genetic material in 16S and 100% of genetic material in COI or 18S. The average K2P distance for intraspecific variation was 0.0% for COI and 0.6% for 16S.

**Morphological variation:** All specimens show great similarities in the shape of the prostomium, form of the chaetae and size of the neuro- and notoacicula on the last segment. However, the paratype has slightly longer frontal filaments.

**Ecological notes:** The specimens were found in the water sieved from the ROV biobox at station 212, which contained several species of sponges (hexactinellid), alcyonaceans, antipatharians and pennatulacean corals, in addition to ophiuroids. Furthermore, spicules were found inserted in the body of the worms, suggesting an artefact of sieving or a commensal life with sponges. More studies in the area are needed to find out which species is the host.

**Macellicephala parvafauces sp. nov.**

(Fig. 15A–I; Tables 1, 2, 4)

**Type material:** Holotype, MNHN-IA-TYPE 1830 (IFR602), complete, length 11.82 mm, width 1.50 mm, 18 segments (including tentacular segment). Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3 nodules, station 189, collected 20–21 April 2015, ROV Kiel 6000, biobox, start 18°47.80′N, 128°18.35′W, end 18°48.13′N, 128°18.20′W, 4933–4964 m depth. Paratype, MNHN-IA-TYPE 1831 (IFR403), complete, length 8.02 mm, width 1.05 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 131, collected 9–10 April 2015, ROV Kiel 6000, biobox, start 13°52.39′N, 123°15.03′W, end 13°52.44′N, 123°14.88′W, 4478 m depth.

**Description (based on holotype and paratype):**

Holotype complete, 11.82 mm long and 1.50 mm wide for 18 segments, slightly dorsoventrally flattened, not tapering posteriorly; live specimen whitish anteriorly and slightly brownish posteriorly; ethanol-preserved specimen pale yellow throughout (Fig. 15A, C). Body surface smooth.

Prostomium bilobed, about as wide as long, lobes pronounced anteriorly, truncated; small, oval frontal filaments present, inserted at innermost margin of prostomial lobes; median notch between prostomial lobes moderately wide and deep (Fig. 15D); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna large, cylindrical, short (shorter than anterior margin of prostomial lobes), inserted near median notch, style missing. Palps smooth, tapering, short (reaching segment 4; Fig. 15D). Trilobed facial tubercle present, median tubercle larger than lateral ones (Fig. 15B, D).

Tentacular segment with short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores large, cylindrical,
|                      | M. aciculata | M. atlantica | M. australis | M. clarionensis sp. nov. | M. galapagensis | M. kubieri | M. longipalpa | M. mirabilis sp. nov. | M. parvafauces sp. nov. | M. remigata | M. violacea |
|----------------------|--------------|--------------|--------------|--------------------------|----------------|------------|--------------|----------------------|--------------------------|--------------|-------------|
| **Prostomial shape** | ?            | Subretangular | Oval         | Subretangular             | Oval           | Subretangular | Oval         | Subretangular         | Oval                     | Oval         | Oval        |
| **Frontal/facial tubercles** | Absent      | Absent       | ?            | Present                   | Present        | Absent      | Absent       | Absent               | Present                  | Present      | Present     |
| **Frontal filaments** | Present      | Present      | ?            | Present                   | Absent         | Present      | Absent       | Present               | Present                  | Present      | Present     |
| **Dorsal tubercles on non-elytrigerous segments** | Inconspicuous | Inconspicuous | Inconspicuous | Prominent                 | Inconspicuous  | Inconspicuous | Inconspicuous | Prominent            | Prominent                 | Prominent    | Prominent   |
| **Shape of dorsal tubercles** | Bulbous      | –            | –            | Conical                   | Conical        | –          | –            | –                    | Conical                   | Bulbous      | Conical     |
| **Dorsal body surface** | Papillated   | Smooth       | ?            | Smooth                    | ?              | Smooth      | Papillated   | Papillated           | Smooth                    | Smooth       | Smooth      |
| **Ventral body surface** | Smooth       | Smooth       | ?            | Smooth                    | ?              | Smooth      | Papillated   | Smooth               | Smooth                    | Smooth       | Smooth      |
| **First segment with nephridial papillae** | Segment 10   | Segment 10   | Segment 10   | Segment 10                | Segment 10     | Segment 10  | Segment 10   | Segment 9            | Segment 10                | Segment 10   | Segment 10  |
| **Notochaetae development compared to neurochaetae** | Notochaetae stouter than neurochaetae | Notochaetae stouter than neurochaetae | Notochaetae stouter than neurochaetae | About the same | About the same | Notochaetae subequal to or more slender than neurochaetae | Notochaetae stouter than neurochaetae | About the same | Notochaetae stouter than neurochaetae | Notochaetae stouter than neurochaetae |
| **Notochaetae** | With two rows of spines in one side | With two rows of spines in one side, pointed tips | With spinous rows, blunted tips | With faint spinous rows, pointed tips | With spinous rows, rounded tips | With faint spinous rows, pointed tips | Smooth or spinous rows, blunted tips | Smooth or spinous rows, pointed tips | Smooth or spinous rows, pointed tips | Smooth or spinous rows, pointed tips |
| **Neurochaetae** | With spinous pocket on both margins, tapered to blunted tips | With spinous pocket on both margins, hooked tips | With spinous pocket on both margins, minute bidentate hooked tips | With spinous pocket on both margins, minute bidentate hooked tips | With spinous pocket on both margins, hooked tips | With spinous pocket on both margins, blunted tips | With spinous pocket on both margins, pointed tips | Type 1, with spinous pocket more centrally, hooked tips | With spinous pocket on both margins, pointed tips | With spinous pocket more centrally, hooked tips |
|                      |              |              |              |                          |                |            |              |                      |                          |              |             |

References for species are provided in Table 2. The descriptions of the valid species *Macellicephala alia* and *Macellicephala tricornis* were not included (see Taxa selection for detail). ‘?’ indicates uncertain information.
Figure 15. *Macellicephala parvafauces* sp. nov., holotype MNHN-IA-TYPE 1830 (A, B, D, F–I) and paratype MNHN-IA-TYPE 1831 (C, E). A, dorsal view of a preserved complete specimen. B, anterior end, ventral view of a preserved specimen. C, ventral view of a live specimen with nephridial papillae on segments 10–12. D, anterior end, dorsal view, chaetae omitted. E, inner view of half side of dissected pharynx with papillae. F, right parapodium, posterior view, segment 7. G, notochaeta with very faint spinous rows, segment 7. H, upper neurochaeta, segment 7. I, lower neurochaeta, segment 7. Abbreviations: dt, dorsal tubercle; ft, facial tubercle; np, nephridial papilla.
equal sized (Fig. 15D); styles missing. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1831), with nine pairs of rounded to subtriangular, equal-sized distal papillae; two pairs of small jaws with main fang, margin smooth (Fig. 15E). Second segment with eylerophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of large, bulbous eylerophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17; elytron dropped from segment 13 but still attached on segment 15, both elytra in poor condition; moderately large (partly covering preceding segment and subventral two segments), surface smooth; posterior margin papillated, with large, short papillae.

Cirrigerous segments with large, bulbous dorsal cirrophores, inserted subdistally on notopodia; style smooth, tapering, long (reaching three or four subsequent segments, much longer than tip of neuroacicular lobe); dorsal tubercles distinct, conical, small (Fig. 15D).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (longer than tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia (in middle body slightly subdistally on neuropodia), style short (shorter than tip of neuroacicular lobe), style longer than neuropodia lobe in last segment.

Parapodia subbiramous; notopodia shorter than neuropodia (Fig. 15F). Dorsal ridges absent. Notopodia subtriangular, tapering into long acicular lobe, tip of neuroacica not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacica not penetrating epidermis. Notochaetae moderate in number (15–20 observed), short to long, distally straight to slightly curved, with very faint spinous rows, with pointed tips (Fig. 15G); some with slightly hooked tip; notochaetae as stout as neurochaetae. Neurochaetae of two types: (1) upper group, moderate in number (~20 observed), long to very long, distally flattened to concave, with very faint spinous rows along both margins, with pointed tips (Fig. 15H), laterally appearing with hooked tips; and (2) middle and lower groups, moderate in number (~20 observed) long to short, distally flattened to concave with very faint spinous rows on both sides but distally not touching the margins, with minute hooked tips (Fig. 15I).

Nephridial papillae on segments 10, 11 and 12, small, bulbous (Fig. 15C). In last segment, notopodia and neuropodia of similar size. Pygidium rounded, not enclosed by last segment; with dorsal anus (Fig. 15A). Anal cirri lost, scars not seen.

Morphological variation: The specimens found in the CCFZ are highly similar. The only difference between them concerns the chaetae. In the holotype, the chaetae are slightly wilted, giving an impression of flatness, whereas in the paratype the chaetae have the usual appearance. This could be an artefact of the fixation/conservation process.

Remarks: Macellicephaloides parvafauces sp. nov. is closer to Macellicephaloides violacea (Levinsen, 1886) and Macellicephaloides australis Wu & Wang, 1987, having a smooth body surface and neurochaetae with hooked tips (Table 4). However, the styles of the dorsal cirri in Macellicephaloides violacea are shorter than the tip of neuropodial lobe, whereas in Macellicephaloides australis they are longer, as in Macellicephaloides parvafauces sp. nov. This new species also has prodomal lobes anteriorly truncated and conical dorsal tubercles, whereas Macellicephaloides australis has prodomal lobes anteriorly rounded and no dorsal tubercules.

Etymology: The species name came from the Latin ‘parv.fauces’ meaning ‘small jaws’. It refers to the relatively smaller jaws of this species.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S. The holotype and paratype shared 98.6% of genetic material in COI and 100% in 16S or 18S. The average K2P distance for intraspecific variation was 1.4% for COI and 0.0% for 16S.

Distribution: Based on the material examined (two specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in APEI#3 (type locality) and GSR license areas.

Ecological notes: The holotype was extracted from a sponge, Corbitella discasterosa Tabachnick & Lévi, 2004 (Kersken et al., 2018), indicating a commensal life mode with this sponge.

Macellicephaloides Uschakov, 1955

Macellicephaloides Uschakov, 1955: 314. – Levenstein, 1971b: 26. – Hartmann-Schröder, 1974: 81. – Fauchald, 1977: 63. – Uschakov, 1982: 127 (translated version). – Pettibone, 1989b: 161.

Type species: Macellicephaloides grandicirra Uschakov, 1955.

Diagnosis (emended): Short body, dorsally flattened, up to 21 segments. Prostomium bilobed. Frontal filaments present (Macellicephaloides grandicirra...
and *Macellicephaloides moustachu* sp. nov.) or absent (*Macellicephaloides uschakovi, Macellicephaloides verrucosa* and *Macellicephaloides vitiati*). Eyes absent. Median antenna present, lateral antennae absent. Tentacular segment fused to prostomium; tentaculophores without acicula or chaetae. Pharynx with two pairs of jaws; dorsal pair fused; with five pairs of pharyngeal papillae. Dorsal tubercles absent (Macellicephaloides alvini, Macellicephaloides grandicirra, Macellicephaloides moustachu, Macellicephaloides uschakovi and *Macellicephaloides vitiati*) or nodular (*Macellicephaloides verrucosa*). Elytrophores small, eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subirramous. Notopodia reduced, with short to long, slender to stout notaocuilla. Neuropodia with elongate acicular lobe; tips of neuroaciculae not penetrating epidermis. Notochaetae absent. Neurochaetae slender, with serrated margins. From segment 3, ventral cirri inserted distally on neuropodia.

**Remarks:** Currently, eight species have been described (Pettibone, 1989b) in this relatively speciose genus, presenting such particular morphological characters as: modification in prostomium shape, dorsal jaws fused, absence of notochaetae and very short to very long notoacicula. The genus description is emended here in order to include the characters observed in the new species below: very short and slender notoacicula.

**Additional material:** Specimen 1, MNHN-IA-PNT 79 (IFR422), complete, length 2.75 mm, width 0.62 mm, 16 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°50.15′N, 117°58.49′W, end 11°50.18′N, 116°58.46′W, 4144–4093 m depth, 2769 m trawling distance. Paratype 3, MNHN-IA-PNT 80 (IFR423), complete, length 1.84 mm, width 0.44 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 133, collected 10 April 2015, epibenthic sledge supra-net, start 13°50.751′N, 123°15.649′W, end 13°51.126′N, 123°14.131′W, 4516–4427 m depth, 2289 m trawling distance.

**Macellicephaloides moustachu** sp. nov.  
(Fig. 16A–J; Tables 1, 2)

**Type material:** Holotype, MNHN-IA-TYPE 1832 (IFR520-1), complete, length 2.69 mm, width 0.66 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′N, 119°40.825′W, end 11°2.612′N, 119°39.512′W, 4398–4402 m depth, 2529 m trawling distance. Paratype 1, MNHN-IA-TYPE 1833 (IFR529-1), complete, length 1.97 mm, width 0.52 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratyp 2, MNHN-IA-TYPE 1834 (IFR449b), complete, length 1.41 mm, width 0.46 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge supra-net, start 14°3.411′N, 130°7.989′W, end 14°3.813′N, 130°6.481′W, 4946–4978 m depth, 3789 m trawling distance. Paratype 3, MNHN-IA-TYPE 1835 (IFR460b), incomplete, length 1.24 mm, width 0.40 mm, nine segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′N, 123°15.442′W, end 13°52.622′N, 123°14.263′W, 4498–4521 m depth, 3129 m trawling distance. Paratype 4, NHMUK 2018.25351 (IFR208), complete, length 2.19 mm, width 0.52 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 133, collected 10 April 2015, epibenthic sledge supra-net, start 13°50.751′N, 123°15.649′W, end 13°51.126′N, 123°14.131′W, 4516–4427 m depth, 2289 m trawling distance.
Description (based on holotype and paratypes): Holotype complete, 2.69 mm long and 0.66 mm wide for 15 segments (including tentacular segment), slightly dorsoventrally flattened, slightly tapering posteriorly; live specimen bluish; ethanol-preserved pale brown (Fig. 16A), with brownish bands subbasally on palps and medially on dorsal cirri; prostomium whitish.

Prostomium bilobed but continuously fused, wider than long, lobes not pronounced anteriorly but extending to ventral side (Fig. 16A–D); frontal filaments small, inserted anteriorly (Fig. 16A–C); median notch between prostomial lobes absent; eyes absent. Median antenna present, lateral antennae absent; ceratophore of median antenna cylindrical, short (shorter than distance between ceratophore insertion and posterior margin of prostomium), inserted anteriorly in medially on prostomium; style missing in holotype; in paratype (MNHN-IA-TYPE 1833) style smooth, tapering into thin tips, long (reaching segment 5). Palps smooth, tapering, long (reaching segment 4–5), inserted ventrally, directed ventroposteriorly (Fig. 16C, D). Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1833), with pharyngeal papillae not possible to count; two pairs of jaws, dorsal jaw fused, each dorsal jaw with two main blunt teeth, innermost one with a smaller, pointed secondary tooth, margin smooth (Fig. 16E); each ventral jaw with one main blunt tooth, outer margin serrated (four to five small teeth), with two smaller secondary teeth, pointed on each side, margin smooth and short (Fig. 16F). Bilobed facial tubercle, very small, located between palps and upper lip (Fig. 16D). In most specimens, bilobed facial tubercle difficult to see but made visible using forceps to move palps apart.

Tentacular segment very reduced, fused to prostomium, with very short lobe, inserted ventrolaterally to prostomium; without acicula orchaetae; tentaculophores small but distinct, dorsal tentaculophores slightly smaller than ventral tentaculophores; styles missing in holotype; in paratype (MNHN-IA-TYPE 1833), styles smooth, tapering into thin tips, short; dorsal tentacular style shorter than ventral tentacular style (reaching segment 4). Second segment with elytrophores, sub-biramous parapodia, with chaetae and ventral cirri. Segments 3 and 4 medioventrally inflated, forming a truncated structure (Fig. 16C).

Eight pairs of knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13 and 15 (all elytra missing); on segment 2, elytrophores larger.

Cirrigenous segments with large, cylindrical, elongate dorsal cirrophores (Fig. 16G); dorsodistal, pointed projection (Fig. 16G) on cirrophores; styles smooth, tapering into long thin tips, long (much longer than tip of neuroacicular lobe), mostly directed posteriorly; dorsal tubercle absent.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style missing in holotype; in paratypes (MNHN-IA-TYPE 1833 and MNHN-IA-TYPE 1835), style short (shorter than tip of neuroacicular lobe); in subsequent segments inserted distally on neuropodia, styles short on segments 3 and 4 (shorter than tip of neuroacicular lobe) and long from segment 5 (longer than tip of neuroacicular lobe).

Parapodia sub-biramous, notopodia very reduced, much shorter than neuropodia (Fig. 16G). Notopodia with inconspicuous to very short acicular lobe, notoacicular slender, tip of notoacicular not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicular not penetrating epidermis. Notochaetae absent. Neurochaetae moderate in number (nine to 22 observed), short to long, very narrow, distally with spines along both margins, with pointed tips (Fig. 16H–J).

Nephridial papillae present on segments 7–14, small, bulbous. Pygidium rounded, with minute papilla ventrally; slightly enclosed by last segment; with terminal anus (Fig. 16A). Anal cirri lost, scars not seen.

Morphological variation: The specimens vary in the number of segments from 11 (MNHN-IA-PNT 81) to 16 (MNHN-IA-PNT 79) but share many of the morphological characters described above except for the number of pairs of elytra and the presence of nephridial papillae. The specimen with 11 segments presents five pairs of elytrophores and no nephridial papillae; these characters are probably linked to growth.

Methyl Green staining pattern: The paratype (NHMUK 2018.25351) stains slightly but uniformly all along the body (not shown). Two densely stained spots are observed anteriorly on prostomium, located close to the median ceratophore.

Remarks: Among the eight species described in Macellicephaloides only one species, Macellicephaloides improvisa Levenstein, 1983, shows notopodia shorter than neuropodia, with thin notoacicular (Pettibone, 1989b). However, the new species Macellicephaloides moustachu sp. nov. differs from Macellicephaloides improvisa in having up to 16 segments and elongate cirrophores with a distal pointed projection, whereas Macellicephaloides improvisa has 18 segments and short cirrophores without a distal pointed projection. Macellicephaloides
Figure 16. *Macellicephaloides moustachu* sp. nov., holotype MNHN-IA-TYPE 1832 (A–C, G–I), paratype 2 MNHN-IA-TYPE 1834 (D–F) and paratype 3 MNHN-IA-TYPE 1835 (J). A, dorsal view of a preserved complete specimen. B, anterior end, dorsal view, chaetae omitted. C, anterior end, ventral view, chaetae omitted. D, anterior end, ventral view, chaetae omitted. E, inner view of dorsal side of jaws from dissected pharynx, papillae omitted. F, inner view of ventral side of jaws from dissected pharynx, papillae omitted. G, right parapodia, posterior view (ventral cirri lost), segment 6. H, neurochaeta with spines along both margins, frontal view, segment 6. I, neurochaeta with spines along both margins, frontolateral view, segment 6. J, scanning electron micrograph of neurochaeta; up side is the distal part of chaeta. Abbreviations: fil, frontal filament; ft, frontal tubercles; inf, inflated truncate structure; pp, pointed projection.
moustachu sp. nov. is a relatively common species in the CCFZ, with > 38 specimens sampled in four out of the five areas. Unfortunately, only the 18S gene could be sequenced; DNA amplification of the 16S and COI genes was unsuccessful. Consequently, identification of damaged specimens was challenging.

Etymology: The species name came from the French word ‘moustachu’ meaning ‘with a moustache’. It refers to the palps directed ventrally, giving the impression that the worm has a moustache.

Genetic data: DNA sequencing for this species was successful only for 18S but not for COI or 16S, sharing 100% of genetic material between the specimens.

Distribution: Based on the material examined (ten specimens), this species has a wide distribution within Clarion-Clipperton Fracture Zone, being sampled in BGR, IOM (type locality), GSR and ifremer license areas.

Reproductive notes: Paratype MNHN-IA-TYPE 1833 seems to be brooding dorsally; two large interconnected pouches were observed linked to the body through an anterior small hole on the notopodia of segment 10. The sac directly connected to the body is surrounded by a membrane and has visible small ova inside; the second sac shows an agglomerate of small ova without a visible membrane.

NU AAKHU GEN. NOV., SP. NOV.

(type 17A–F; Tables 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1836 (IFR341), complete, length 4.82 mm, width 0.76 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge supra-net, start 13°52.317’N, 123°15.442’W, end 13°52.622’N, 123°14.263’W, 4498–4521 m depth, 3129 m trawling distance.

Description (based on holotype): Holotype complete, 4.82 mm long and 0.76 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened; slightly tapering posteriorly; live specimen translucent, bluish; digestive system and chaetae internally visible, chaetae golden (Fig. 17A); ethanol-preserved specimen pale white, translucent.

Prostomium bilobed, wider than long, lobes not pronounced, short, anteriorly rounded; fused with tentacular segment; frontal filaments absent; median notch between prostomial lobes shallow and moderately wide (Fig. 17A, C); eyes absent. Median and lateral antennae absent. Palps smooth, tapering, short (reaching segment 3), with small, distinct palpophores (Fig. 17C). Facial tubercles absent. Upper lip with minute folds.

Tentacular segment fused to prostomium, with short lobe, inserted ventrolaterally to prostomium; without acicula or chaetae; tentaculophores very short, small, distinct, equal sized; tentacular styles short, smooth, tapering distally into filamentous tip; dorsal tentacular style (reaching segment 4) slightly longer than ventral tentacular style (Fig. 17C). Pharynx not everted. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.
Nine pairs of very small, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segment with distinct, small dorsal cirrophores (Fig. 17D), inserted basally on notopodia; styles smooth, tapering, long to short (anteriorly, longer than tip of neuroacicular lobe; posteriorly, about as long as tip of neuroacicular lobe); dorsal tubercles absent.

Segments 5 and 6 with large, swollen dorsal structure (Fig. 17A, B), interiorly whitish; smaller, bilobed
Remarks: As detailed in the genus section, Nu aakhu gen. nov., sp. nov. is unique in not having notochaetae and in having very short notoacicular lobes, very small elytrophores and neurochaetae with prominent spines along both margins.

Etymology: Again, in the ancient Egyptian religion, 'āakhu' is one of the elements that compose the human soul. An 'āakhu' is the glorified spirit or a blessed soul which has passed the final judgement (the Weighing of the Heart). The term refers to the translucent character of the body of this worm.

Genetic data: DNA sequencing was successful only for 18S but not for COI or 16S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in GSR license area (type locality).

**Polaruschakov Pettibone, 1976**

Polaruschakov Pettibone, 1976: 55. – Uschakov, 1982: 124 (translated version). – Jirkov, 2001: 133. – Barnich & Fiege, 2003: 92.

Type species: Macellicephala polaris Uschakov, 1957.

Diagnosis (emended): Short body, dorsoventrally flattened, up to 25 segments. Frontal filaments absent. Eyes absent. Median and lateral antennae absent. Facial tubercle absent. Reduced palpophores. Tentacular segment fused with prostomium, tentaculophores without acicula or chaetae. Pharynx with seven pairs of distal papillae; two pairs of jaws with smooth margins or with a secondary small tooth (Polaruschakov lamellae sp. nov. and Polaruschakov omnesae sp. nov.). Dorsal tubercles present (Polaruschakov lamellae sp. nov. and Polaruschakov polaris) or absent (Polaruschakov reyssi, Polaruschakov limaeae sp. nov. and Polaruschakov omnesae sp. nov.). Elytrophores prominent, up to ten pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroacicular not penetrating epidermis. Notochaetae distally with spinous rows; notochaetae more slender than neurochaetae. Neurochaetae numerous, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae small. Pygidium small, with terminal anus.

Remarks: The diagnosis of genus Polaruschakov is emended to include the following characters observed in the new species described below: jaws with small secondary tooth on margin and absence of flattened scale-like structures on segment 6. As highlighted for Hodor gen. nov., this feature, occasionally present on anterior segments, is likely to be a reproductive character, as suggested by its presence or absence without pattern among the taxa belonging to the Anantennata clade (i.e. without median and lateral antennae).

**Polaruschakov lamellae sp. nov.**

(Fig. 18A–G; Tables 1, 2, 5)

Polychaeta sp. EBS12o-Po143 (GenBank KJ736547) Janssen et al. (2015).

Type material: Holotype, MNHN-IA-TYPE 1837 (IFR151), complete, length 8.41 mm, width 1.40 mm, 22 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR license area, station 59, collected 28 March 2015, epibenthic sledge supra-net, start 11°48.201′ N, 117°30.500′ W, end 11°48.442′ N, 117°29.395′ W, 4384–4307 m depth, 2469 m trawling distance. Paratype 1, MNHN-IA-TYPE 1838 (IFR659-1-1), complete, length 3.40 mm, width 0.58 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′ N, 128°21.874′ W, end 18°45.338′ N, 128°20.418′ W, 3307–4307 m depth, 2799–4821 m trawling distance.
m trawling distance. Paratype 2, MNHN-IA-TYPE 1839 (IFR607), incomplete, length 2.06 mm, width 0.67 mm, ten segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge supra-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description (based on holotype): Holotype complete, 8.42 mm long and 1.40 mm wide for 22 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; live specimen slightly translucent, bluish (Fig. 18A); ethanol-preserved specimen pale white; chaetae golden.

Prostomium bilobed, wider than long, lobes not developed anteriorly, short, rounded anteriorly, with an abrupt depression connecting to superior lip (Fig. 18A, B); frontal filaments absent; median notch between prostomial lobes narrow and shallow; eyes absent; a pair of internal white ganglia visible through translucent epidermis (difficult to see). Median and lateral antennae absent. Palps smooth, tapering, thin, short (reaching to segment 3; Fig. 18A, B).

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly ventral to prostomium; without acicula or chaetae; tentaculophores prominent, cylindrical, dorsal longer than ventral; dorsal tentacular style smooth, tapering, thin, short (reaching segment 4; Fig. 18B); ventral tentacular style missing. Pharynx not everted on holotype; dissected in paratype (MNHN-IA-TYPE 1838), with pharyngeal papillae not possible to count, two pairs of jaws, each one with one main fang, outer margin with a small, secondary tooth (small elevation; Fig. 18C). Second segment with eutyphores, subbiramous parapodia, with chaetae and ventral cirri.

Ten pairs of large (largest in anterior segments), spherical eutyphores, present on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19 (all elytra missing).

Cirrigerous segments with prominent dorsal cirrophores (largest in anterior segments); styles smooth, tapering, long (longer than tip of neuroacicula lobe; Fig. 18D); on segment 3 longer than on subsequent segments; dorsal tubercles present, rounded on segment 2, lamelliform on subsequent segments (Fig. 18D), decreasing in size posteriorly, largest on segment 8, inconspicuous on segment 18 (in paratypes, dorsal tubercles not seen).

Segment 6 with a pair of flattened scale-like structures present (Fig. 18B); inserted before cirrophore, basally inflated, rounded; distally lamelliform, small, not reaching mid-dorsal line.

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (much longer than tip of neuroacicula lobe); in subsequent segments inserted medially on neuropodia (Fig. 18D), style short (shorter than tip of neuroacicula lobe).

Parapodia subbiramous, notopodia reduced, much shorter than neuropodia (Fig. 18D). Notopodia reduced, narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis; post-chaetal lobe oval, slightly enlarged. Notochaetae very few (three observed), short, slender, slightly curved, with distinct spinous rows on convex side, with blunt tips (Fig. 18E); nexecostaetae more slender than neurochaetae. Neurochaetae moderate in number (26 observed), long, distally flattened to concave, serrated along both margins, with blunt tips (Fig. 18F); lower neurochaetae shorter, with pointed tips (Fig. 18G), shorter than upper or middle groups.

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with terminal anus (Fig. 18A). Anal cirri lost, scars not seen.

Morphological variation: All specimens shared the following morphological characters: short palps, chaetae, insertion and length of ventral cirri, slightly enlarged post-chaetal lobe. Although the paratypes are in poor condition, they do not seem to present the lamelliform dorsal tubercles. The tubercles might have been lost or this character could be age dependent, because the holotype has 22 segments whereas the paratypes have 18 segments.

Remarks: The notoaciculae and neuroaciculae are closer to those present in Polaruschakov species. However, as described above, the lamelliform dorsal tubercles and the very reduced prostomium are unique characters, which allow differentiation of Polaruschakov lamellae sp. nov. from the other species belonging to Polaruschakov (Table 5).

Etymology: The species name came from Latin ‘lamellae’ meaning lamella in plural. It refers to lamelliform dorsal tubercles.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S. The specimens shared 100% of genetic material in COI and 18S, and ≥ 99.5% in 16S. The average K2P distance for intraspecific variation was 0.0% for COI and 0.2% for 16S.

Distribution: Based on the material examined (three specimens), this species has a wide distribution within the Clarion-Clipperton Fracture Zone, being sampled in BGR (type locality) and APEI#3 areas.
Figure 18. Polaruschakov lamellae gen. nov., sp. nov., holotype MNHN-IA-TYPE 1837 (A, B, D–G) and paratype 1 MNHN-IA-TYPE 1838 (C). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, inner view of half side of dissected jaws. D, left parapodia, posterior view, segment 8. E, notochaeta with distinct faint spinous rows, segment 3. F, upper neurochaeta, lateral view, segment 11. G, lower neurochaeta, segment 11. Abbreviations: dt, dorsal tubercle; el, elytrophore; sc, scale-like structure; st, secondary tooth.
**Polaruschakov limaee sp. nov.**

*(Fig. 19A–G; Table 1, 2, 5)*

**Type material:** Holotype, MNHN-IA-TYPE 1840 (IFR639-1), complete, length 3.98 mm, width 0.60 mm, 18 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge epi-net, start 14°3.411′ N, 130°6.481′ W, end 14°3.813′ N, 130°7.989′ W, 4946–4978 m depth, 3789 m trawling distance.

**Description (based on holotype):** Holotype complete, 3.98 mm long and 0.60 mm wide for 18 segments (including tentacular segment), dorsoventrally flattened, posteriorly slightly tapering; colour of live animal not known; ethanol-preserved specimen pale white, slightly translucent.

Prostomium bilobed, wider than long, anteriorly lobes not developed, conical; frontal filaments absent; median notch between prostomial lobes moderately wide and deep (Fig. 19A); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching segment 3); palpophores not enlarged. Facial tubercle absent.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching segment 4), dorsal tentacular style slightly longer than ventral tentacular style (Fig. 19A). Pharynx not everted.

Second segment with elytrophores, subbibramous parapodia, chaetae and ventral cirri; lower lip and ventral tentacular style (Fig. 19A). Pharynx not everted. Second segment with elytrophores, subbibramous parapodia, chaetae and ventral cirri; lower lip and ventral tentacular segment ventrally lower in relationship to segment 3, which is inflated (Fig. 19B).

Nine pairs of distinct, bulbous to knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segments with distinct, small dorsal cirrophores, inserted subdistally on notopodia; styles smooth, tapering into thin tips, long (slightly longer than tip of neuroacicula lobe); dorsal tubercles absent. Segment 6 with very large (covering half of neuropodia in length), swollen dorsal structure (Fig. 19A), located between the dorsum and the base of cirrophores, interiorly whitish, of similar size.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (about as long as tip of neuroacicula lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicula lobe).

Parapodia subbibramous; notopodia reduced, much shorter than neuropodia (Fig. 19C). Neurochaetae of two types: (1) moderate in number (24 observed), short to long, distally flattened to concave, coarsely serrated along both margins, with abrupt pointed tips (Fig. 19E); (2) middle group on segments 3–7 modified, few (four to six observed), slightly stouter, long, distally flattened to concave, serrated along both margins, with blunt tips (Fig. 19G).

Nephridial papillae present on segments 10–14, small, bulbous; internally whitish, subtriangular, originating from anterior margin of segment, extending onto posterior margin. Ventrally, on last segment, a pointed structure is present (Fig. 19D). Pygidium rounded, slightly enclosed by last segment; with terminal anus. Anal cirri lost, scars not seen.

**Remarks:** Only two species of *Polaruschakov* have been described until now: *Polaruschakov polaris* from the Polar Basin and north of the Canadian arctic islands (730–2245 m depth); and *Polaruschakov reyssi* Pettibone, 1976 from the Mediterranean Sea (750 m depth). *Polaruschakov reyssi* is the only species having notochaetae with capillary tips. *Polaruschakov limaee* sp. nov. is very close to *Polaruschakov omnesae* sp. nov. and *Polaruschakov polaris* in having notochaetae with blunt tips (Table 5). However, in *Polaruschakov limaee* sp. nov. there are two types of neurochaetae having abrupt pointed tips and blunt tips, whereas *Polaruschakov omnesae* sp. nov. has one type of neurochaetae with pointed tips, and *Polaruschakov polaris* has one type of neurochaetae with rounded tips. Moreover, the the average K2P distance among *Polaruschakov lamellae* sp. nov., *Polaruschakov limaee* sp. nov. and *Polaruschakov omnesae* sp. nov. was high (24.4–24.8% for 16S). The pointed structure on the last segment resembles a minute keel, but it is not clear whether this is an artefact of fixation or a natural structure.

**Etymology:** This species is dedicated to Dr Maria Lima for her friendship and for initiating P.B. into the systematics of polychaetes.

**Genetic data:** DNA sequencing for this species was successful for 16S and 18S but not for COI.

**Distribution:** Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).
**Polaruschakov omnesae sp. nov.**

*(Fig. 20A–G; Tables 1, 2, 5)*

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**Type material:** Holotype, MNHN-IA-TYPE 1841 (IFR424), complete, length 4.43 mm, width 0.83 mm, 19 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, IOM license area, station 99, collected 4 April 2015, epibenthic sledge epi-net, start 11°2.296′ N, 119°40.825′ W, end 11°2.612′ N, 119°39.512′ W, 4398–4402 m depth, 2529 m trawling distance. Paratype, MNHN-IA-TYPE 1842 (IFR530-1), complete, length 4.16 mm, width 0.81 mm, 20 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, GSR license area, station 117, collected 7 April 2015, epibenthic sledge epi-net, start 13°52.317′ N, 123°15.442′ W, end 13°52.622′ N, 123°14.263′ W, 4498–4521 m depth, 3129 m trawling distance.

**Description (based on holotype and paratype):**

Holotype complete, 4.43 mm long and 0.83 mm wide for 19 segments (including tentacular segment), dorsoventrally flattened, posteriorly tapering; colour of live animal not known; ethanol-preserved specimen pale white, slightly translucent.

Prostomium bilobed, wider than long, anterior lobes not developed, conical; frontal filaments absent; median notch between prostomial lobes moderately narrow and moderately deep (Fig. 20A); eyes absent. Median and lateral antennae absent. Palps smooth, tapering into thin tips, short (reaching segment 3); palpophores not enlarged (Fig. 20A). Facial tubercle absent. Upper lip with multiple minute folds.

Tentacular segment fused to prostomium, with a pair of short lobes, inserted laterally and slightly below prostomium; without acicula or chaetae; tentaculophores distinct, bulbous, equal sized; styles smooth, tapering into thin tips, short (reaching...
segment 3), dorsal tentacular style slightly shorter than ventral tentacular style (Fig. 20A); ventrally to the tentaculophores is a distinct globular pad, located laterally to the mouth. Pharynx not everted in holotype; dissected in paratype (MNHN-IA-TYPE 1842), with seven pairs of distal papillae, subtriangular, equal sized; two pairs of jaws, each one with one main fang, outer margin with a very small, secondary tooth (small elevation; Fig. 20B). Second segment with elytrophores, subbiramous parapodia, chaetae and ventral cirri.

Nine pairs of distinct, knob-like elytrophores present on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17 (all elytra missing).

Cirrigerous segments with distinct, small dorsal cirrophores (Fig. 20C), inserted subdistally on notopodia; styles smooth, tapering into thin tips, long (slightly longer than tip of neuroacicula lobe); dorsal tubercles absent.

Segment 6 without modification.

Ventral cirri smooth, tapering into thin tips, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style short (shorter than tip of neuroacicula lobe); in subsequent segments inserted medially on neuropodia (Fig. 20C), style short (shorter than tip of neuroacicula lobe).

Parapodia subbiramous; notopodia much shorter than neuropodia (Fig. 20C). Notopodia narrow, subtriangular, tapering into very short acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, subtriangular, tapering into long acicular lobe, tip of neuroacicula not penetrating epidermis. Notochaetae very few (one to three observed), short, slender, slightly curved, with distinct spinous rows on convex side, with blunt tips (Fig. 20D); notochaetae more slender than neurochaetae. Neurochaetae moderate in number (ten to 15 observed), long, distally flattened to concave, serrated along both margins, with pointed tips (Fig. 20E, F); slightly stouter in middle of fascicle.

Figure 20. *Polaruschakov omnesae* sp. nov., holotype MNHN-IA-TYPE 1841 (A, C–G) and paratype MNHN-IA-TYPE 1842 (B). A, anterior end, dorsolateral view, with chaetae omitted. B, inner view of half side of dissected pharynx with few papillae. C, right parapodia, anterior view, segment 10. D, notochaeta with faint spinous rows, segment 10. E, upper neurochaeta, frontolateral view, segment 3. F, middle neurochaeta, frontal view, segment 10. G, last two segments with pygidial papilla, ventrolateral view. Abbreviations: mf, minute folds; pa, papilla.
Phylogenetics of deep-sea polynoids

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with terminal anus; with ventral papilla, rounded to ovoid (Fig. 20G). Anal cirri lost, scars not seen.

Morphological variation: Specimens with 19 and 20 segments were found, which share most of the morphological characters given in the species description. However, the holotype shows a minute prostomial peak and a minute ventral papilla on the pygidium, whereas the paratype does not show those peaks but presents a more rounded, small, ventral papilla.

Remarks: Polaruschakov omnesae sp. nov. is more similar to Polaruschakov polaris, with both having notochaetae with blunt tips, a wide notch and fewer chaetae than Polaruschakov reyssi. However, in Polaruschakov omnesae sp. nov. the neurochaetae tips are pointed and the palps are short (reaching segment 3), whereas in Polaruschakov polaris the neurochaetae tips are rounded and the palps are longer (Table 5). The presence of minute prostomial peaks could be an artefact of preservation, because its presence cannot be observed in the paratype.

Etymology: This species is dedicated to Emmanuelle Omnes (Ifremer) for her help with laboratory work.

Genetic data: DNA sequencing for this species was successful for COI, 16S and 18S. Both specimens shared 100% of genetic material in COI and 16S. 18S was not successfully sequenced for the paratype. The average K2P distance for intraspecific variation was 0.0% for both COI and 16S.

Distribution: Based on the material examined (two specimens), this species has a restricted distribution within the Clarion-Clipperton Fracture Zone, being sampled in IOM (type locality) and GSR license areas.

Yodanoe gen. nov.

Type species: Yodanoe desbruyeresi gen. nov., sp. nov.

Gender: Masculine.

Diagnosis: Short body, dorsoventrally flattened, up to 17 segments. Prostomium bilobed anteriorly, tapering to triangular peaks. Frontal filaments absent. Eyes absent. Median antenna present, lateral antennae absent. Facial tubercle absent. Tentaculophores with acicula, without chaetae. Pharynx with two pairs of jaws, with a secondary small tooth; with nine pairs of pharyngeal papillae. Dorsal tubercles forming cirriform to lamelliform branchial-like processes. Elytrophores large, up to eight pairs, on segments 2, 4, 5, 7, 9, 11, 13 and 15. Parapodia subbiramous, notopodia shorter than neuropodia; noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroacicular not penetrating epidermis. Notochaetae stout, distally with spinous rows; notochaeatae stouter than neuropodia. Neurochaetae distally flattened to concave, serrated along both margins. From segment 3, ventral cirri inserted medially on neuropodia. Nephridial papillae absent. Pygidium rounded, with dorsal anus.

Remarks: Among polynoids of the Macellicephalinae subfamily, the presence of a cirriform dorsal tubercle can be observed in the following genera: Bathyfauvelia, Bathycatalina Pettibone, 1976, Bathybahamas Pettibone, 1985d and Vampiropolynoe Marcus & Hourdez, 2002. However, these genera differ by the number of segments, the development of notopodia relative to neuropodia and the prostomium (Pettibone 1976, 1985d).

Yodanoe gen. nov. presents many similarities with Bathyfauvelia, such as a reduced number of segments, nine pairs of pharyngeal papillae, and notopodia shorter than neuropodia. However, the new genus presents genetic and morphological differences (Fig. 2). The K2P distance between these two genera was high (29.5% for COI and 37.8% for 16S). Furthermore, Yodanoe gen. nov. shows a triangular and tapering prostomial shape, only one type of notochaetae, an achaetous tentacular segment and jaws with a small secondary tooth, whereas Bathyfauvelia shows a short conical prostomial shape, two types of notochaetae, a tentacular segment with chaetae and serrated jaws.

Etymology: This genus is dedicated to Yoda, the Grand Master of the Jedi Order. The name is composed by Yoda and ‘noe’ from Polynoe, the ancient Greek nymph.

Yodanoe desbruyeresi sp. nov. (Fig. 21A–G; Tables 1, 2)

Type material: Holotype, MNHN-IA-TYPE 1843 (IFR448b), complete, length 3.86 mm, width 0.64 mm, 17 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone.
Zone, Ifremer license area, station 158, collected 15 April 2015, epibenthic sledge supra-net, start 14°3.411′ N, 130°7.989′ W, end 14°3.813′ N, 130°6.481′ W, 4946–4978 m depth, 3789 m trawling distance.

Description (based on holotype): Holotype complete, 3.86 mm long and 0.64 mm wide for 17 segments (including tentacular segment), dorsoventrally flattened, tapering posteriorly; live specimen slightly translucent, bluish (Fig. 21A); ethanol-preserved specimen pale white, prostomium whitish.

Prostomium bilobed, about as wide as long, lobes pronounced, anteriorly tapering to triangular peaks, located close to the notch; frontal filaments absent; median notch between pro stomal lobes wide and moderately deep (Fig. 21B); eyes absent. Median antenna present, lateral antennae absent; ceratophore of segment 9; Fig. 21D). Segment 3, longest on segment 10 (as long as elytra forming cirriform branchial-like processes, small on notopodia; styles missing; dorsal tubercles present, dorsal cirrophores (Fig. 21C), inserted subdistally on segments 2, 4, 5, 7, 9, 11, 13 and 15 (all elytra missing).

Cirrigerous segments with two thickened ridges; notopodia subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neurochaetae moderate in number (23–30 observed), short to long, distally flattened to conical, serrated along both margins, with pointed tips (Fig. 21F); lower group very short, leaf-like (Fig. 21G).

Nephridial papillae absent. Pygidium rounded, not enclosed by last segment; with dorsal anus (Fig. 21A). Anal cirri lost, scars not seen.

Etymology: This species is dedicated to Dr Daniel Desbruyères (Laboratoire Environnement Profond, Ifremer, Brest, France) for his many contributions to the taxonomy and ecology of polychaetes mainly from extreme environments.

Remarks: This species shares many similarities with Yodanoe sp. 659-3 but the palps are shorter in Yodanoe desbruyeresi gen. nov., sp. nov. (reaching segment 5) than in Yodanoe sp. 659-3 (reaching segment 7). Moreover, the R2P distance between these species was high (24.0% for COI and 19.3% for 16S).

Genetic data: DNA sequencing for this species was successful for COI and 16S but not for 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in Ifremer license area (type locality).

YODANOE SP. 659-3
(Fig. 22; Tables 1, 2)

Material examined: MNHN-IA-PNT 73 (IFR659-3), complete, length 3.27 mm, width 0.50 mm, 15 segments (including tentacular segment), Equatorial Eastern Pacific Ocean, Clarion-Clipperton Fracture Zone, APEI#3, station 192, collected 21 April 2015, epibenthic sledge epi-net, start 18°44.807′N, 128°21.874′W, end 18°45.338′N, 128°20.418′W, 4821–4820 m depth, 2799 m trawling distance.

Description: Complete, 3.27 mm long and 0.50 mm wide for 15 segments (including tentacular segment), dorsoventrally flattened, tapering posteriorly; colour of live animal not known; ethanol-preserved specimen pale white, prostomium white; most of chaetae lost.

Prostomium bilobed, about as wide as long, lobes pronounced, anteriorly tapering to triangular peaks, located close to the notch; frontal filaments absent; median notch between pro stomal lobes wide and moderately deep (Fig. 22); eyes absent. Median antenna present, lateral antennae absent; ceratophore of median...
Figure 21. *Yodano desbruyeresi* gen. nov, sp. nov., holotype MNHN-IA-TYPE 1843 (A–G). A, dorsal view of a live complete specimen. B, anterior end, dorsal view, chaetae omitted. C, left parapodia, posterior view, segment 7. D, dorsal view of segments 9 and 10 with elytrophore and dorsal tubercles and with parapodia omitted. E, notochaeta with developed spinous rows, segment 4. F, middle neurochaeta, segment 9. G, lower neurochaetae, segment 9. Abbreviations: dt, dorsal tubercle; el, elytrophore.
antenna large, cylindrical, as long as prostomium lobes), inserted anteromedially on prostomium, in the notch; style missing. Palps smooth, tapering, very long (reaching around segment 7; Fig. 22). Facial tubercle absent; upper lip with bilobed folds.

Tentacular segment with elongate acicular lobe, inserted laterally and slightly ventral to prostomium; with acicula not penetrating epidermis, without chaetae; tentaculophores distinct, large; dorsal tentacular style missing; ventral tentacular style thin, tapering into thin tip, smooth, long (reaching segment 5). Pharynx not everted, dissected with nine pairs of distal equal-sized, subtriangular papillae; two pairs of jaws, each with main fang with a small elevation as secondary tooth. Second segment with elytrophores, subbiramous parapodia, with chaetae and ventral cirri.

Probably eight pairs of bulbous to massive, cylindrical elytrophores, present on segments 2, 4, 5, 7, 9, 11, 13 and 15; elytra still attached on segment 2, translucent, rounded, almost entire margin papillated, microtubercles not seen. Dorsal ridges pronounced (V shape).

Cirrigerous segments with distinct, cylindrical dorsal cirrophores, inserted subdistally on notopodia; style missing; dorsal tubercles present, forming cirriform branchial-like processes, small on segment 3, becoming longer from segment 6 (as long as elytrophores; Fig. 22).

Ventral cirri smooth, tapering, present from segment 2 to last segment; inserted basally on neuropodia of segment 2, style long (reaching tip of neuroacicular lobe); in subsequent segments inserted medially on neuropodia, style short (shorter than tip of neuroacicular lobe).

Parapodia subbiramous; notopodia shorter than neuropodia. Notopodia arising from dorsum as two thickened ridges; notopodia narrow, subtriangular, tapering into long acicular lobe, tip of notoacicula not penetrating epidermis. Neuropodia large, rectangular to subtriangular, tapering into long acicular lobe, tip of neuroacicular not penetrating epidermis. Notochaetae short to long, slender, slightly curved, with developed spinous rows on convex side, with blunt tips; notochaetae as stout as neurochaetae. Neurochaetae distally flattened to concave, serrated along both margins, with pointed tips.

Nephridial papillae absent. Pygidium rounded, not enclosed by last parapodia; with dorsal anys. Anal cirri lost, scars not seen.

Remarks: The present specimen is in too poor condition to be described as a new species, but it was used to describe the pharynx for this genus. See Remarks on Yodane desbruyeresi gen. nov., sp. nov. for more details.

Genetic data: DNA sequencing for this species was successful for COI and 16S but not for 18S.

Distribution: Only one specimen was sampled at a single station within the Clarion-Clipperton Fracture Zone in APEI#3 area.
The following key contains the 37 genera currently considered valid (including the newly described ones); six genera for which the presence/absence of antennae is doubtful are further discussed below the key. An asterisk indicates monotypic genera.

1 Median antenna present ................................................................................................................................2
Median antenna absent ...............................................................................................................................30

2 Body with segmental branchiae ....................................................................................................................3
Body without segmental branchiae ...............................................................................................................7

3 Branchiae formed by flattened elongated sacs, deeply folded .............. Branchiplicatus Pettibone, 1985b*
Branchiae arborescent ...................................................................................................................................4
Branchiopodites Desbruyères & Laubier, 1988

4 Ceratophore of median antenna absent ................................................................. Branchipolynoe Pettibone, 1984a
Ceratophore of median antenna present ......................................................................................................5

5 Branchiae from segment 2 ............................................................................................................. Peinaleopolynoe
Branchiae from segment 3 ...........................................................................................................................6

6 Twenty-seven segments, 11 pairs of elytrophores ........................................ Thermopolynoe Miura, 1994*
Twenty-one segments, ten pairs of elytrophores .............. Branchiopodites Pettibone, 1985a

7 Bracts well developed (lobe encircling notopodia anteriorly and dorsally) .......... Lepidonotopodium
Bracts absent ..................................................................................................................................................8

8 Notochaetae absent .................................................................................................................................9
Notochaetae present .....................................................................................................................................10

Table 5. Diagnostic characters for all valid species in the genus Polaruschakov

| Species                  | P. lamellae sp. nov. | P. limae sp. nov. | P. omnesae sp. nov. | P. polaris | P. reyssi |
|--------------------------|----------------------|-------------------|---------------------|------------|-----------|
| Prostomium shape         | Short, rounded anteriorly | Short, conical anteriorly | Short, conical anteriorly | Globular, rounded anteriorly | Subcordiform, rounded anteriorly |
| Notch between prostomial lobes | Narrow and shallow | Moderately narrow and deep | Moderately narrow and Wide and deep | Narrow and shallow |
| Dorsal tubercles on non-elytrigerous segments | Lamelliform | Absent | Absent | Subconical | Absent |
| Notopodial development relative to neuropodia | Notopodia shorter than neuropodia | Notopodia shorter than neuropodia | Notopodia shorter than neuropodia | Notopodia shorter than neuropodia |
| First segment with nephridial papillae | ? | Segment 10 | Not seen | After segment 10 |
| Notochaetae              | Three in number, distinct spinous rows, with blunt tips | One or two in number, distinct but faint spinous rows with blunt tips | One to three in number, Two to six in number, with blunt tips | About ten in number, with capillary tips |
| Neurochaetae             | Two types, with blunt and pointed tips | Two types, with abrupt pointed and blunt tips | One type, with pointed tips | One type, with rounded and blunt tips |
| Number of segments       | 22 segments | 18 segments | 19–20 segments | 25 segments | 23 segments |

References for species are provided in Table 2. '?' indicates uncertain information.
|   | Description                                                                                                                                                                                                 | Reference   |
|---|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------|
| 9 | Notoacica very short, neuropodia very long, neuropodia with spinous rows, pharynx with two pairs of narrow denticed plates (jaw-plates)................................. Macelloides Uschakov, 1957*                                                                 |             |
| 10| Posterior end with ventral keel.                                                                                                                                                                             |             |
| 11| Nine pairs of elytrophores, 20 segments................................................................. Austropolaria Neal, Barnich, Wiklund & Glover, 2012*                                                                                   |             |
| 12| Wing-like structure present on lower lip of mouth ................................................................................................................................. Bruinilla Hartman, 1971             |             |
| 13| Prostomial palps anteriorly directed, neuropodia without well-developed pre-chaetal lobes .......................................................................................... Bathylevensteiniella Pettibone, 1976*                       |             |
| 14| Ten pairs of elytrophores, 19 segments, nine pairs of pharyngeal papillae ................................................................................................................ Bathytasmania McIntosh, 1885    |             |
| 15| Accessory filamentous sensory organs absent, attached to dorsal cirrophores from segment 8 ................................................................. Gesiella Pettibone, 1976*                                      |             |
| 16| Prostomium lobes medially with processes (not frontal filaments) ......................................................... Bathylevensteiniella Pettibone, 1976*                                           |             |
| 17| Prostomial palps anteriorly directed, neuropodia without well-developed pre-chaetal lobes .................................................................................. Abyssarya gen. nov.*                                             |             |
| 18| Posterior four segments modified and compressed ......................................................... Bathykermadeca Pettibone, 1976*                                                  |             |
| 19| Accessory filamentous sensory organs absent .................................................................................................................................................................................  |             |
| 20| Seven pairs of elytrophores .......................................................................................... Bathyrakis Pettibone, 1976*                                               |             |
| 21| Eight pairs of elytrophores ..................................................................................... Bathytasmania Levenstein, 1982a*                                       |             |
| 22| More than seven pairs of elytrophores.                                                                                                                                                                      |             |
| 23| More than eight pairs of elytrophores.                                                                                                                                                                      |             |
| 24| Nine pairs of elytrophores ..................................................................................... Bathytasmania Levenstein, 1982a*                                       |             |
| 25| More than nine pairs of elytrophores.                                                                                                                                                                      |             |
| 26| Eighteen segments, pharyngeal papillae of similar size ........................................ Macelloides Uschakov, 1957*                                                                                           |             |
| 27| Eleven pairs of elytrophores, up to 28 segments, seven pairs of pharyngeal papillae .......... Levensteiniella Pettibone, 1985c                                                     |             |
| 28| Prostomial palps with rounded, large palpophores, jaws with serrated margin ..........  |             |
BATHYLEVENSTEINA Pettibone, 1976

*Type species:* Bathylevensteina bicornis (Levenstein, 1962).

The genus is monotypic. The type species was originally described as Macellicephalo by Levenstein (1962), who described a particular shape of the prostomium, ending with ‘bifurcate frontal horns’. Pettibone (1976) incorrectly considered these frontal horns as lateral antennae inserted medially. Later, Pettibone (1994) corrected this interpretation and placed Bathylevensteina within the subfamily Macellicephalinae.

BATHYMIRANDA Levenstein, 1981

*Type species:* Bathymiranda microcephala Levenstein, 1981.

The genus is monotypic. Although Levenstein (1981) considered the presence of a median antenna uncertain, Pettibone (1985d, 1989c) classified it in the subfamily Polaruschakovinae. We followed Pettibone and coded the species as lacking a median antenna.

BATHYNOTALIA Levenstein, 1982a

*Type species:* Bathynotalia perplexa Levenstein, 1982a.

The genus is monotypic. Bathynotalia perplexa was originally classified as Macellicephalo, Macellicephaloides and Macelloides as having no lateral antennae (Averincev, 1972; Hartmann-Schröder, 1974). Later, Pettibone (1976) revised the genus considering that the lateral prostomial horns described by Averincev (1972) were, in fact, lateral antennae. There are some misunderstandings and confusions between frontal filaments, frontal horns, cephalic peaks or lateral antennae in descriptions of polynoids. Further investigation of polynoid anatomy is required to gain a better understanding of these structures and their differences. In the present study, this species has been coded as having a median antenna and no lateral antennae.

GESIELLA Pettibone, 1976

*Type species:* Gesiella jamensis (Hartmann-Schröder, 1974).

The genus is monotypic. The type species was originally described as Macellicephalo by Hartmann-Schröder (1974). Pettibone (1976) incorrectly considered the presence of small spherical lobes with distal filaments as lateral antennae. Later, Muir (1982)
erected the subfamily Gesiellinae Muir, 1982 for this species based on the unique diagnostic character, presence of filamentous sensory organs on the cirrophores of the dorsal cirri. However, Pettibone (1994) did not agree and finally placed this genus within the subfamily Macellicephalinae.

**SINANTENNA** HARTMANN-SCHRÖDER, 1974

*Type species:* Macellicephalha (Sinantenna) macrophalhma Fauvel, 1913.

Fauvel (1913, 1914b) erected Macellicephalha (?) macrophalhma for a single specimen in poor condition having enlarged eyes, lacking lateral antennae, and with parapodia, jaws and neurochaetae similar to Macellicephalha species. According to Fauvel, the protostomium was too damaged to ascertain the presence of a median antenna. Later, Hartmann-Schröder (1974) erected a new subgenus for species lacking a median antenna. She designated Macellicephalha (Sinantenna) macrophalhma as type species and included two additional species: Macellicephalha (Sinantenna) arctica Knox, 1959 and Macellicephalha (Sinantenna) paucidentata Eliason, 1962. Pettibone (1976) did not have access to the holotype of Macellicephalha (Sinantenna) macrophalhma and considered it as doubtful, despite all the similarities highlighted by Fauvel. We believe the specimen should be re-examined in order to confirm Fauvel's observations, and species validity. The other two species that once belonged to Sinantenna were assigned to new genera by Pettibone (1976): Macellicephalha paucidentata appearing to have ceratophores on the median and lateral antennae, is no longer considered as a member of Macellicephalinae; and Macellicephalha (Sinantenna) arctica Hartmann-Schröder, 1974 (part) were synonymized with Polaruschakov polaris; and Macellicephalha (Sinantenna) arctica Hartmann-Schröder, 1974 (part) was re-described as Polaruschakov reyssi.

**DISCUSSION**

Historically, a large number of subfamilies has been erected within the family Polynoidae in order to accommodate the great morphological diversity among genera and species. Likewise, several genera have been erected for unique species, particularly from the deep sea. Based on molecular phylogenetic analysis and morphological observations, the present study stresses that the number of subfamilies cannot be justified because many of them are not monophyletic and they include very few genera. Nevertheless, much of deep-sea diversity remains undiscovered, therefore justifying the high number of monotypic genera. The 17 newly described species, with four new genera and 138 DNA sequences based on COI, 16S or 18S, represent a significant addition to the diversity of this deep-sea group. In total, 278 polynoids were sampled during the SO239 cruise; preliminary results classified them into 44 morphotypes, but they were subsequently split into ~80 MOTUs (Bonifácio et al., 2016). These large and mobile polychaetes are best sampled with an epibenthic sledge, because the area sampled by quantitative box-corers is too small [e.g. only one polynoid was reported by De Smet et al. (2017) from box-core samples collected in the CCFZ]. Using molecular criteria for the discrimination of species almost doubled the taxonomic richness of polynoids recorded compared with morphological criteria, suggesting a high level of cryptic species diversity within deep-sea polynoids. Subtle morphological variation, however, may still allow discrimination of cryptic species, for example between Bathyfauvelia glacigena sp. nov. and Bathyfauvelia ignigena sp. nov. Interestingly, these two species are sympatric, which raises questions about the mechanisms of speciation at abyssal depths.

Unfortunately, many described genera/species fitting in Macellicephalinae sensu Hartmann-Schröder, 1971 were not observed in the present study or included in the molecular analysis (i.e. only 32 species in 20 genera for which DNA sequences are available). However, 89 species fitting the concept of Macellicephalinae were coded morphologically. Taken together, the representatives of 65 (molecular data) and 127 (morphological data) polynoid species from shallow to deep water allowed us to infer their phylogenetic relationships.

**First steps in the deep sea for polynoids**

The polynoids present in our phylogenetic trees (Figs 2, 3) are clustered into two main groups: with lateral antennae and without lateral antennae. In the phylogenetic tree built from only molecular and combined with morphological data (MDS and CDS; Fig. 2), the polynoids with lateral antennae in clades a1 (mostly Lepidonotinae) and a3 are predominantly composed of shallow-water species, with only Polyeeuoa laevis (a facultative commensal) reaching ~1361 m depth (Serpetti et al., 2017). This well-supported shallow-water grouping of species with lateral antennae (clade a1 mostly with Lepidonotinae members and clade a3 mostly with Polynoinae members) agrees with Norlinder et al. (2012) and is partly supported by the morphological analysis. The clade a2, composed of Bathymoorea lucasi sp. nov. and Eulagisca gigantea, which both have lateral antennae, was supported by MDS, CDS and morphological analyses. Among the subfamily Eulagiscinae, the genus Bathymoorea is
the only known genus exclusively found in bathyal to abyssal depths, but congeneric members of the subfamily show a wide bathymetric distribution; some species of *Pareulagisca* and *Eulagisca* can be found from shallow depths down to bathyal depths (1000 m depth; Pettibone, 1997). The phylogenetic analyses (MDS, CDS and morphological only) suggest that *Bathymoorea lucasi* sp. nov. and *Eulagisca gigantea* are very close to the clade without lateral antennae (Figs 2, 3), although with poor support. Members of the subfamily *Eulagiscinae* may, thus, be among the first polynoids to colonize and radiate in the deep sea. The hypothesis would agree with Uschakov (1977, 1982), who already suggested that *Bathymoorea* can be considered as one of the ancestral forms of *Macellicephaliinae* owing to modifications of the placement of the median antenna and its short body.

**CONQUEST OF THE DEEP SEA BY MACELLICEPHALINAE**

The subfamily *Macellicephaliinae* was created by Hartmann-Schröder (1971) and amended by Hartmann-Schröder (1974) to include species with or without median antenna and without lateral antennae. Pettibone (1976) rearranged 37 such species into five subfamilies (*Bathyedithinae, Bathymacellinae, Macellicephaloidinae, Macelloidinae* and *Polaruschakovinae*), most of which contained few species or were monotypic. Although Pettibone’s revision is widely accepted, Uschakov (1982) did not agree with this classification and considered that those deep-sea taxa have ‘great many common distinctive morphological characters which unite them in a single natural group’. Our MDS, CDS and morphological analyses show that the following subfamilies are nested in the clade without lateral antennae (character 11: 0; Figs 2, 3): *Bathyedithinae*, *Bathymacellinae*, *Branchinotogluminae*, *Branchiplicatinae*, *Branchipolynoinae*, *Macellicephaliinae*, *Macelloidinae* and *Polaruschakovinae*). The presence of branchiae is an apomorphic character (branchiae character 41: 1), which is shared by the genera *Lepidonotopodium*, *Branchipolicatus*, *Gesiella*, *Levensteiniella*, *Thermopolynoe*, *Vampiropolynoe* and *Macellicephala aciculata*. However, no unique synapomorphy was identified for this clade. According to Norlinder et al. (2012), the presence of branchiae is likely to represent a synapomorphy of polynoids living at hydrothermal vents. Our morphological phylogenetic analysis, however, suggests that the presence of branchiae is an apomorphic character (branchiae character 41: 1), which is shared by the genera *Peinaleopolynoe, Branchinotogluma, Thermopolynoe, Branchipolicatus* and *Branchipolynoe* and has been lost in *Lepidonotopodium, Levensteiniella plicata* and *Vampiropolynoe embelyi*. Seventeen species in five genera (*Branchipolynoe, Peinaleopolynoe, Branchinotogluma, Branchipolicatus* and *Thermopolynoe*) sharing this character live in extreme environments, such as hydrothermal vents or cold seeps (Pettibone, 1984a, 1985a; Desbruyères & Aubier, 1988; Miura, 1994). Abramchiate polynoids belonging to the genera *Lepidonotopodium, Levensteiniella* and *Vampiropolynoe* can also be found in extreme habitats (Pettibone, 1983, 1985c; Desbruyères & Houdrez, 2000a, b; Marcus & Houdrez, 2002). Unfortunately, no sequence data are available to inform their phylogenetic relationships more accurately.

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The second main clade (clade b2 in Fig. 2) from the MDS and CDS analyses, which is well supported by BPP but not by MLB, included the genera Abyssarya gen. nov. and Macellicephala. The morphological analysis does not support this clade. In fact, Abyssarya gen. nov. presents two plesiomorphic characters: presence of notochaetae with serrulations/spinous rows (character 62: 1) and absence of crenulate/notochaetae (character 59: 0) in addition to the presence of three homoplastic characters not observed in Macellicephala genus: palps ventrally directed (character 5: 1), neurochaetal spines (character 55: 1) and neurochaeta distally recurved (character 56: 1). The genus Macellicephala, however, is not a monophyletic group. For instance, the type of notochaeta is not homogeneous within the genus: Macellicephala mirabilis (type species) have smooth notochaetae (character 51: 0); Macellicephala galapagensis, Macellicephala remigata, Macellicephala violacea, Macellicephala clarionensis sp. nov., Macellicephala parvafauces sp. nov., Macellicephala australis, Macellicephala laubieri and Macellicephala longipalpata have notochaetae with serrulations/spinous rows (character 51: 1); and Macellicephala aciculata and Macellicephala atlantica have notochaetae with spines along only one side (character 52: 1). Given that notochaetae with serrulations/spinous rows are observed in polynoids with lateral antennae, this character is likely to be plesiomorphic, whereas notochaetae with spines along only one side a derived character. This suggests the need for a complete revision within the genus, which is outside the scope of the present study.

The third clade from the MDS and CDS analyses (clade b3 in Fig. 2) is represented by the genera Bruunilla, Hodor gen. nov., Nu gen. nov., Polaruschakov and Bathyedithia. This clade is partly supported by the morphological analysis. Indeed, the results show that all members without median and lateral antennae (Hodor gen. nov., Nu gen. nov., Polaruschakov and Bathyedithia) are grouped into a well-supported clade in both analyses. This clade, called Anantennata (clade b3 in Fig. 2; clade d3 in Fig. 3), showed maximal support from Bayesian analysis (BPP = 1), low support from maximum likelihood (MLB = 53–73), and was supported by the unique synapomorphy, median antenna absent (character 7: 0). Pettibone (1976) erected two subfamilies for species lacking appendages on the prostomium: Bathyedithiinae and Polaruschakovinae. The main differences between these subfamilies were that Bathyedithiinae has large palpophores (character 4: 1), nine pharyngeal papillae (not coded) and serrated jaws (not coded), whereas Polaruschakovinae has reduced palpophores, seven pharyngeal papillae and smooth jaws. However, Hodor gen. nov. has characters of both subfamilies, presenting large palpophores, seven pharyngeal papillae and serrated jaws, which provides support for synonymizing the two subfamilies. According to Pettibone (1976), the genus Polaruschakov has a pair of scale-like structures on segment 6 as a generic character (not coded), absent in Polaruschakov limae sp. nov. and Polaruschakov omnesae sp. nov. as opposed to present in Polaruschakov lamellae sp. nov., suggesting that it is either a temporary character (maybe reproductive) or a specific character. Likewise, dorsal modifications between segments 5 and 8 (not coded) were observed in species belonging to the clade Anantennata without any clear pattern. For instance, the holotype of Hodor anduril gen. nov., sp. nov. showed swollen modifications on segments 6 and 8, whereas in the paratype no such modification was observed. More investigation is needed to evaluate whether these modifications are ontogenetic or reproductive and their patterns in the species. The MDS and CDS analyses suggest that the genus Bruunilla is a sister group of Anantennata, which seems consistent with the morphology considering the homoplastic characters, presence of spinous pockets or spines on notochaetae along both sides (character 53: 1), that species of the Bruunilla share with Bathyedithia berkeleyi (Anantennata) and Bathyeditidae pallida; in addition to the presence of neuropodial papillae (character 36: 1) shared with Diplaconotum paucidentatum (Anantennata).

In summary, the present study presents the largest dataset of molecular and morphological descriptors concerning deep-sea polynoids since Pettibone (1976) and is the first major contribution about abyssal polynoids from the Clarion-Clipperton Fracture Zone. Pettibone (1976) erected many genera to account for the diversity that she observed in 37 species around the world. We believe that Pettibone has established solid morphological bases with which to increase the knowledge about deep-sea polynoids. However, the present study points out a number of morphological characters useful for the description of genera and species. A re-examination of type specimens is needed in order to progress the phylogeny of Macellicephalinae. The association of morphological and molecular analyses allows new insights into the diversity and phylogeny of deep-sea polynoids. With our 17 newly described species, deep-sea polynoids now account for 95 species in the Macellicephalinae sensu Hartmann-Schröder, 1971. The diversity of deep-sea polynoids still remains at one-tenth of the diversity of their shallow-water counterparts, which may suggest either that a vast reservoir of undiscovered diversity in the deep sea is awaiting discovery or that deep-sea polynoids are relatively less diverse than shallow polynoids because of lower habitat diversity or relatively recent colonization of deep waters.
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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Detailed description of the 74 morphological characters and states analysed in the present study.

**Appendix S2.** Morphological data matrix listing all 128 taxa and the 74 characters included in the analysis. Characters doubtful or unknown were coded as '?'. Inapplicable characters were coded as '-'.

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