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Taxonomy, distribution and ecology of the order Phyllodocida (Annelida, Polychaeta) in deep-sea habitats around the Iberian margin

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ABSTRACT

The polychaetes of the order Phyllodocida (excluding Nereidiformia and Phyllodociformia *incertae sedis*) collected from deep-sea habitats of the Iberian margin (Bay of Biscay, Horseshoe continental rise, Gulf of Cadiz and Alboran Sea), and Atlantic seamounts (Gorringe Bank, Atlantis and Nameless) are reported herein. Thirty-six species belonging to seven families – Acoetidae, Pholoidae, Polynoidea, Sigalionidae, Glyceridae, Goniadidae and Phyllodocidae, were identified. Amended descriptions and/or new illustrations are given for the species *Allmaniella setubalensis*, *Anotochaetonoe michelbhaudi*, *Lepidasthenia brunnea* and *Polynoë* sp. Relevant taxonomical notes are provided for other seventeen species. *Allmaniella setubalensis*, *Anotochaetonoe michelbhaudi*, *Harmothoe evei*, *Eumida longicirrata* and *Glycera noelae*, previously known only from their type localities were found in different deep-water places of the studied areas and constitute new records for the Iberian margin. The geographic distributions and the bathymetric range of thirteen and fifteen species, respectively, are extended. The morphology-based biodiversity inventory was complemented with DNA sequences of the mitochondrial barcode region (COI barcodes) providing a molecular tag for future reference. Twenty new sequences were obtained for nine species in the families Acoetidae, Glyceridae and Polynoidea and for three lineages within the *Phyllococe madeirensis* complex (Phyllodocidae). A brief analysis of the newly obtained sequences and publicly available COI barcode data for the genera herein reported, highlighted several cases of unclear taxonomic assignments, which need further study.

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1. Introduction

Phyllodocida Dales, 1962 is one of the larger polychaete orders, including at present four suborders (Aphroditiformia, Glyceriformia, Nereidiformia and Phyllodociformia) plus several unplaced taxa (Phyllodociformia *incertae sedis*). More than 3500 species names are treated as valid within this order (Read, 2014). The majority of the Phyllodocida are marine benthic species although some may also occur in brackish, freshwater and even terrestrial habitats. A few taxa within the suborder Phyllodociformia are holopelagic. Except for the members of the family Acoetidae, which occur mainly in warm water temperate and tropical seas, the Phyllodocida are distributed worldwide and live as in- or epifauna in a variety of substrata (muddy and sandy

bottoms, mixed sediments or under rocks and in crevices in hard surfaces) from the littoral to great depths (Rouse and Pleijel, 2001). There are records of scale-worms (suborder Aphroditiformia) and phyllodociforms (suborder Phyllodociformia) also living in deep-sea extreme habitats such as hydrothermal vents (e.g. Blake, 1985; Chevaldonné et al., 1998; Pettibone, 1985, 1989a, 1989b; Schander et al., 2010). Most Phyllodocida are free living (especially the Nereidiformia and Phyllodociformia) or live in association with other benthic species of echinoderms, cnidarians, polychaetes and decapods (Aphroditiformia), some are burrowers in muddy or sandy sediments (Glyceriformia) and other are tubiculous (family Acoetidae, of Aphroditiformia). They usually prey actively on other invertebrates, but some are 'sit-and-wait' predators (Acoetidae). Relevant taxonomic studies on the North Atlantic deep-sea Phyllodocida include Budaeva et al. (2014), Fiege and Barnich (2009), Kirkegaard (1980, 2001a, 2001b) and Kongsrud et al. (2013).

Although the study of the deep-sea benthic diversity in southern Europe has been increasing in recent years (e.g. Cunha et al., 2011, 2013a, 2013b; Hilário et al., 2015; Paterson et al., 2011;

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Ravara et al., 2015), the deep-sea polychaete fauna of the Iberian margin is still poorly known when compared to the north European. Most deep-sea polychaetes documented for this region were collected during early oceanographic cruises on board of the 'Challenger' (McIntosh, 1885), 'Hirondelle' and 'Princess Alice' (Fauvel, 1914a), 'Hirondelle II' (Fauvel, 1932), 'Thalassa', (Amouroux, 1972, 1974) and 'Meteor' (Hartmann-Schröder, 1975, 1977). More recently, several studies on the polychaete fauna of the Cap Breton canyon resulted from four oceanographic cruises on board the RV 'Côte d'Aquitaine' within the framework of a Franco-Spanish research project (e.g. Aguirrezabalaga and Ceberio, 2005; Aguirrezabalaga and Parapar, 2014; Bonifácio et al., 2015; Núñez et al., 2000; San Martín et al., 1996). However, none of these latter studies concern the polychaete families included herein. Several other studies in the NW and SW Iberian margin focused mainly on shelf and upper slope polychaete assemblages (e.g. Gil and Sardá, 1999; López-Jamar and González, 1987; Martins et al., 2013; Parapar and Moreira, 2009a; Ravara and Moreira, 2013; Viéitez et al., 2004).

Over the past 15 years, several cruises took place around the Iberian margin, from the Bay of Biscay (NE Atlantic) to the Alboran Sea (W Mediterranean Sea), under the framework of several international deep-sea research programmes (e.g. UNESCO-IOC Training Through Research, HERMES, HERMIONE, CHEMECO). Within these projects several submarine canyons and seamounts, mud volcanoes and other deep-sea habitats were sampled yielding over one thousand invertebrate species, the majority of which are polychaetes. This material, not yet fully studied, includes many putative novel species (e.g. Ravara and Cunha, 2016).

Here, we report on the phyllodocid polychaetes of the sub-orders Aphroditiformia, Glyceriformia and Phyllodociformia from deep-sea habitats of the Iberian margin and Atlantic seamounts, covering a depth range from 214 to 4864 m. The aim of this paper is to extend the knowledge on the biodiversity and distribution of the phyllodocid polychaetes around the Iberian margin. The morphology-based biodiversity inventory is complemented whenever possible with DNA sequences of the mitochondrial

barcode region (COI) with the purpose of providing a molecular tag for future reference.

2. Material and methods

2.1. Study areas

The biological material studied herein was obtained from five NE Atlantic regions: Bay of Biscay, West Iberian margin, Horseshoe continental rise, Gulf of Cadiz and Alboran Sea as well as from three Atlantic seamounts (Fig. 1). In the Bay of Biscay the sampled stations were located at the Saint Nazaire canyon (depths of 537–1105 m), the head of a Cap Breton canyon tributary (214–221 m), and at the Pagès escarpment area (594–813 m). These areas are characterised by the presence of cold-water corals that are known to enhance habitat complexity and faunal diversity: the scleratinians *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* (Linnaeus, 1758) in Saint Nazaire canyon and *Dendrophyllia cornigera* (Lamarck, 1816) in the Cap Breton tributary, and the alcyonacean *Callogorgia verticillata* (Pallas, 1766) in Pagès escarpment. In the W Iberian margin only one location was studied, Fontanelas ridge, covering a depth range of 1110 to 1340 m and characterised by the presence of fossilised corals and carbonates. The NE Atlantic seamounts studied herein include the Gorringe Bank in the SW Iberian margin, the Atlantis in Azores Exclusive Economic Zone (EEZ) and Nameless in Madeira EEZ. The samples were taken from the flanks of these seamounts at depths of 111–2285 m, 375–614 m and 1853 m, respectively. The Gulf of Cadiz is an extensive cold-seepage area located west of the Strait of Gibraltar, characterised by the presence of over 40 known mud volcanoes that pierce a thick accretionary wedge in a complex geological and oceanographic setting. The SW Iberian seepage area further extends westwards into the Horseshoe continental rise and eastwards into the Alboran Sea (W Mediterranean). In the Gulf of Cadiz and the Alboran Sea, samples were taken at depths ranging from 227–3890 m and 365–1022 m, respectively, from several mud

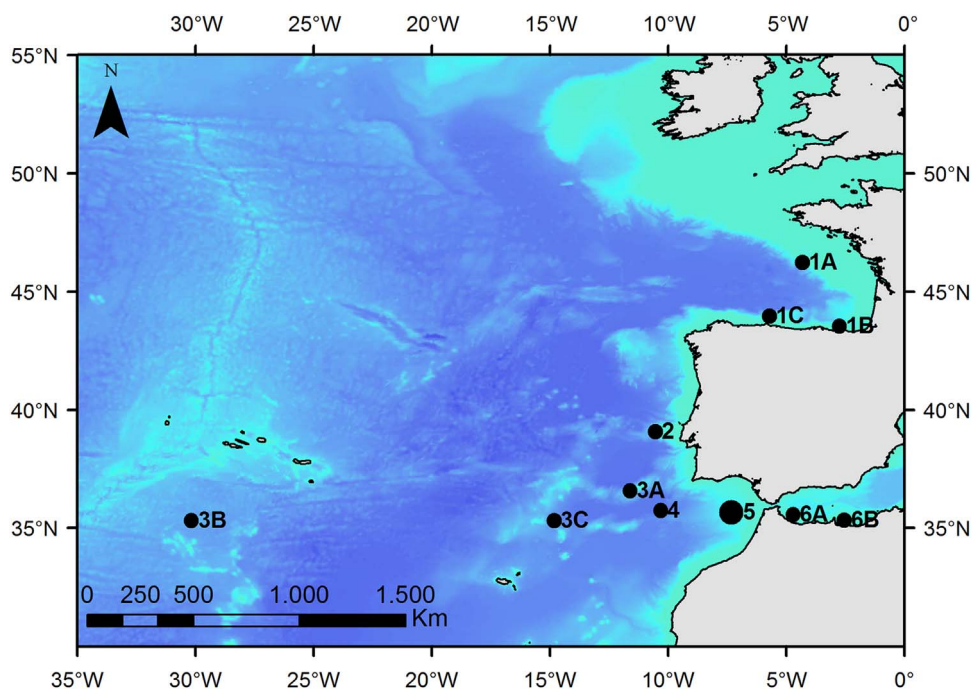


Fig. 1. Map with the location of the studied areas. 1 – Bay of Biscay: (1A) Saint Nazaire Canyon (1B) tributary of Cap Breton Canyon (1C) Pagès Escarpment Area; 2 – West Iberian margin; 3 – Atlantic seamounts: (3A) Gorringe Bank, (3B) Atlantis seamount, (3C) Nameless seamount; 4 – Horseshoe continental rise; 5 – Gulf of Cadiz; 6 – Alboran Sea: (6A) Melilla coral mound field, (6B) cold seeps.

volcanoes and adjacent deep-sea habitats such as coral and carbonate mounds, pockmarks and mud volcanoes. The samples from the Horseshoe continental rise were taken from three recently discovered mud volcanoes (4497–4864 m) siting along deep-reaching strike-slip faults. Further details on some of these study areas can be found in Cunha et al. (2013a, Gulf of Cadiz), Hilário et al. (2011, Alboran Sea), Hensen et al. (2015, Horseshoe continental rise) and Vieira et al. (2015, Gorringe Bank).

2.2. Sampling and laboratory processing

A total of 197 stations were sampled, the majority of which located in the Gulf of Cadiz (150 stations: 84 from mud volcanoes and 66 from carbonate crust and fossil cold-water coral settings). The remaining stations are distributed as follow: 16 from four coral facies in the Bay of Biscay, 5 in W Iberian margin, 11 in the Atlantic seamounts (Gorringe Bank, Madeira and Azores), 6 from mud volcanoes in Horseshoe Continental Rise and 9 in the Alboran Sea (6 from cold seeps and 3 from carbonate crusts and cold-water corals). The samples were taken using a range of different sampling gears during 17 oceanographic cruises carried out from 2002 to 2012 under the framework of several international research programmes (Table 1). Metadata of the sampling sites including geographical coordinates, sampling date and gear as well as some observations on the substrate are provided in Table S1 (supplementary material). Whenever possible the specimens were sorted on board and preserved in 96% ethanol.

Taxonomic re-descriptions and drawings are given for poorly known species. Drawings were prepared from preserved specimens with a camera lucida. Measurements of body width were recorded from the widest part of the body and exclude chaetae. Body length excludes prostomium appendages and anal cirrus. Unless stated otherwise, the material was deposited in the Biological Research Collection of the Department of Biology, University of Aveiro.

2.2.1. Abbreviations used in this work

AS: Alboran Sea; ASM: Atlantic seamounts; BB: Bay of Biscay; CC: carbonate crusts and/or fossil cold-water corals; cf.: *confer*; CS: cold seeps; CWC: cold water corals; DBUA: Department of Biology, University of Aveiro (Biological Research Collection); GB: Gorringe Bank; GC: Gulf of Cadiz; HCR: Horseshoe continental rise; MV:

Table 1

Main target areas and oceanographic cruises. AS: Alboran Sea; ASM: Atlantic seamounts; BB: Bay of Biscay; GB: Gorringe Bank; GC: Gulf of Cadiz; HCR: Horseshoe continental rise; OET: Ocean Exploration Trust; TTR: Training Through Research; WIM: West Iberian Margin.

Region	Cruise	Ship	Date	Programme
GC/ASM	TTR11	RV Prof. Logachev	Aug–Sep 2001	TTR
GC/ASM	TTR12	RV Prof. Logachev	Jul–Aug 2002	TTR
GC	TTR14	RV Prof. Logachev	Aug–Sep 2004	TTR
GC	64PE237	RV Pelagia	May–Jun 2005	Moundforce
GC	TTR15	RV Prof. Logachev	Jul–Aug 2005	TTR
GC	MSM 01/03	RV Maria S. Merian	Apr–May 2006	HERMES
GC	TTR16	RV Prof. Logachev	May–Jul 2006	TTR
GC	64PE253	RV Pelagia	Sep–Oct 2006	Microsystems
GC	64PE268	RV Pelagia	Apr–May 2007	Microsystems
GC	JC10	RRS James Cook	May–Jul 2007	HERMES
GC	64PE284	RV Pelagia	Feb–Mar 2008	HERMES
AS	TTR17-1	RV Prof. Logachev	Jun 2008	TTR
GC/WIM	TTR17-2	RV Prof. Logachev	Jun–Jul 2008	TTR
GC	B09/14b	RV Belgica	May 2009	CHEMECO
BB	M84-5	RV Meteor	May–Jun 2011	HERMIONE
GB	NA017	EV Nautilus	Oct 2011	OET
HCR	M86-5	RV Meteor	Feb–Mar 2012	SWIMGLO

Table 2
PCR and sequencing primers.

Primer	Sequence (5'–3')	References
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
COI-E	TACTACTCTGGGTGTCCGAAGAATCA	Bely and Wray (2004)
Pol LCO	GAYTATWTTCAACAAATCATAAAGATATTGG	Carr et al. (2011)
Pol HCO	TAMACTTCWGGGTGACCAARAATCA	Carr et al. (2011)

mud volcanoes; NHM: The Natural History Museum (London, UK); spm(s): specimen(s); WIM: West Iberian Margin.

2.3. Molecular analyses

2.3.1. DNA extraction, amplification and sequencing

DNA sequences from the mitochondrial gene of the cytochrome oxidase subunit I (COI) were obtained depending on successful amplification of the target region from representatives of each species. Genomic DNA was isolated using either the DNeasy Blood & Tissue kit or the QIAamp[®] DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA), following the protocol supplied by the manufacturer. Fragments of c. 500 to 700 bp of the COI barcode region were amplified using a range of primers (Table 2). Polymerase chain reaction (PCR) mixtures contained ddH₂O, 1 µL of each primer (10 µM), 2 µL template DNA and puReTaq Ready-To-Go PCR Beads (Amersham Biosciences) in a mixture of total 25 µL. The temperature profile was as follows: 96 °C/ 120 s - (94 °C/ 30 s - 48 °C/ 30 s - 72 °C/ 60 s)*45 cycles - 72 °C/ 480 s. PCR products were purified with the QIAquick-PCR purification kit (Qiagen Inc., Valencia, CA) following the protocol supplied by the manufacturer. Bidirectional sequencing was performed by Macrogen on an ABI 3730XL DNA Analyser (Applied Biosystems). The primers used for sequencing are listed in Table 2. Part of the sequences was generated at the Biodiversity Institute of Ontario (BIO), following the protocol described by Lobo et al. (2016). Forward and reverse sequence trace files were individually inspected and edited for ambiguities, and merged into consensus sequences using MEGA v. 6.06 (Tamura et al., 2013). DNA sequences were deposited in Barcode of Life Data System (BOLD; Ratnasingham and Hebert, 2007) and submitted to GenBank.

2.3.2. Molecular data analyses

A dataset was created in BOLD (DS-POLYGEN) by merging our original DNA barcode sequences with published sequences of the same genera (except for a set of four sequences from NE Atlantic Spain and seven from Pacific USA, which were available through BOLD but lacked GenBank Accession numbers). All available sequences from Atlantic locations were used, but some sequences from other locations were also included for representativeness. Sequences from specimens that were not identified to species level were excluded. Only one to three sequences per species were used (except for species represented by different lineages). BOLD automatically assigns deposited sequences into molecular operational taxonomic units (MOTUs) by means of an internally implemented algorithm, the Barcode Index Number (BIN) (Ratnasingham and Hebert, 2013). In cases where a species was assigned to more than one BIN (i.e. more than one MOTU), we selected at least one representative of each BIN to retain the information on within-species molecular diversity. Multiple alignments with all compiled sequences were created using the Clustal W and Muscle implemented in MEGA v. 6.06 (Tamura et al., 2013). The alignments were consensual, and the final alignment was translated to amino acid and checked for stop codons or unusual amino acid sequence patterns. Best-fit models were determined in MEGA as GTR+G+I for nucleotide and Jones-

Taylor-Thornton (Jones et al., 1992) for protein. Phylogenetic reconstruction was conducted using maximum likelihood (ML) methods implemented in MEGA v. 6.06, both for nucleotide and protein data. Node support was determined through 5000 bootstrap replicates in both cases, and sequences of the eunicid *Marpysa sanguinea* (Montagu, 1813) were introduced as outgroup. Genetic distances within and between species, were calculated for selected cases using the Kimura-2-parameter model (Kimura, 1980) to facilitate comparisons with other studies.

3. Results and discussion

3.1. Systematics

Class Polychaeta Grube, 1850.

Order Phyllodocida Dales, 1962.

Suborder Aphroditiformia Levensen, 1883.

Family Acoetidae Kinberg, 1856.

Genus *Panthalis* Kinberg, 1856.

Panthalis oerstedii Kinberg, 1856.

Panthalis oerstedii Kinberg, 1856: 387.

Material examined. Atlantic Ocean. Gulf of Cadiz: Captain Arutyunov, St MSM01-3_180, 1323 m, 1 spm (DBUA0001730.01.v01).

Distribution and habitat. NE Atlantic (from Skagerrak to Northwest Africa), Mediterranean Sea; from the sublittoral to 1470 m depth; in mud, sand, shell and shell sand bottoms (Ben-Eliahu and Fiege, 1994; Chambers and Muir, 1997; Palmero et al., 2008; Pettibone, 1989c).

Remarks. Although this species is known to occur from Norway to the Mediterranean Sea, only a few records are known for the Atlantic European margin south of the North Sea (Campoy, 1982 – Iberian Peninsula from Galiza to Gibraltar; Palmero et al., 2008 – Cap Breton). The single specimen examined herein was found in an active cold seepage site.

Family Polynoidae Kinberg, 1856.

Genus *Acanthicolepis* Norman in McIntosh, 1900.

Acanthicolepis asperrima (M. Sars, 1861).

Polynoe asperrima Sars, 1861: 59; *Dasylepis asperrima* - Malmgren, 1867a: 132; *Acanthicolepis asperrima* - McIntosh, 1900: 311; *Acanthicolepis cousteaui* Laubier, 1961: 1, Figs. 1–3a and c.

Material examined. Atlantic Ocean. Bay of Biscay: Cap Breton Area, St M84-5_633, 221 m, 1 spm (DBUA0001731).

Distribution and habitat. NE Atlantic (from Norway to Azores), W Mediterranean (from the Catalan margin to Monaco), from 15 to 1360 m depth, on hard substrata, including the coral *Madrepora oculata* Linnaeus, 1758 (Barnich et al., 2000; Fiege and Barnich, 2009).

Remarks. The genus *Acanthicolepis* includes at present two species, *A. asperrima* (M. Sars, 1861) and *A. zibrowii* Barnich and Fiege, 2010, both occurring in the NE Atlantic, at similar shallow depths and on the cold-water coral *Madrepora oculata* Linnaeus, 1758. According to Barnich and Fiege (2010), the two species can be easily differentiated by the ornamentation of the elytra. In *A. asperrima*, elytra are covered by conspicuous spines with simple, bifid, or multifid tips, while in *A. zibrowii* elytra have rounded, bifid, or branched multifid microtubercles and cylindrical to club-shaped, distally nodular to spiny macro-tubercles. The specimen examined herein has undoubtedly conspicuous spine-shaped tubercles.

Genus *Allmaniella* McIntosh, 1885.

Allmaniella setubalensis McIntosh, 1885.

(Fig. 2A–H).

Allmaniella setubalensis McIntosh, 1885: 102, pl. XIV Fig. 2, pl. XA Figs. 3 and 4.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_644, 820 m, 3 spms; St M84-5_653, 753 m, 4 spms; St M84-5_689, 752 m, 5 spms; St M84-5_690, 755 m, 2 spms (DBUA0001732.01-04).

Description (amended). Examined specimens incomplete, only one specimen with two elytra. Larger fragment with 14 chaetigers, 3.19 mm long and 1.36/2.14 mm wide without and with parapodia, respectively (measures taken on the widest part of the body, excluding chaetae). Body whitish with pale brown pigmentation dorsally on the first segments. Dorsal tubercles absent. Elytral scars on segments 2, 4, 5, 7, alternating to the end of fragment. Elytra large, overlapping, covering the dorsum, with conical mammiliform tubercles on anterior part and cirriform tubercles near posterior and lateral borders, fringing papillae present (Fig. 2C and D). Prostomium subsphaerical to hexagonal, bilobed anteriorly, without cephalic peaks; anterior pair of eyes slightly larger than posterior ones, situated dorsolaterally at the widest part of prostomium, posterior pair near hind margin of prostomium, each eye with a central white speck (Fig. 2A and B). Median antenna long, gradually tapering, with disperse clavate papillae; ceratophore inserted in median notch of prostomium (Fig. 2B). Lateral antennae very short (about six times shorter than median antennae) with bulbous bases abruptly tapering to filiform tips; ceratophores large, inserted terminally on anterior extensions of prostomium (Fig. 2A and B). Palps stout, gradually tapering, slightly smaller than median antenna, smooth. First segment not visible dorsally; tentaculophores long, bearing chaetae; two pairs of tentacular cirri similar in length to palps, with clavate papillae. Buccal cirri of the second segment shorter than tentacular cirri and substantially longer than ventral cirri of subsequent segments, gradually tapering. Pharynx with nine dorsal and nine ventral large terminal papillae and two pairs of brown jaws. Parapodia biramous; both rami with acutely pointed acicular lobes (Fig. 2E and F). Notopodia shorter, inserted on anterodorsal sides of neuropodia. Dorsal cirri much longer than parapodia including chaetae, with short, cylindrical cirrophores and long, ciliated styles, tapering gradually to filiform tips, present on segments without elytra. Ventral cirri shorter than neuropodia, gradually tapering, with few disperse clavate papillae. Notochaetae with rows of spinules and blunt tips (Fig. 2H). Neurochaetae slender, with long spinulose region ending distally on a small cusp and prolonged by a shorter smooth region with slightly bidentate tips (Fig. 2G). Pygidium not observed.

Distribution and habitat. NE Atlantic (from St. Nazaire canyon, Bay of Biscay to off Setúbal, Portugal), from 753 to 859.5 m depth, in mud and CWC (McIntosh, 1885; present study).

Remarks. McIntosh (1885) described this species upon a small anterior fragment of about 3 mm long, lacking elytra, collected around 860 m depth off Setúbal (W Portugal). The specimens examined herein were found in association with scleractinian corals and are the first record of the species since its original description. They are all very small and also incomplete, but unlike McIntosh's specimen, two elytra were found attached to one of our specimens. The description of the species is here amended to include elytral morphology and new drawings are provided. The genus includes at present two species, *A. setubalensis* and *A. arafurensis* Horst, 1915, the latter originally described from Indonesia.

Genus *Anotochaetonoe* Britayev and Martin, 2005.

Anotochaetonoe michelbaudi Britayev and Martin, 2005.

(Fig. 3A–H).

Anotochaetonoe michelbaudi Britayev and Martin, 2005: 4084, Figs. 1–5.

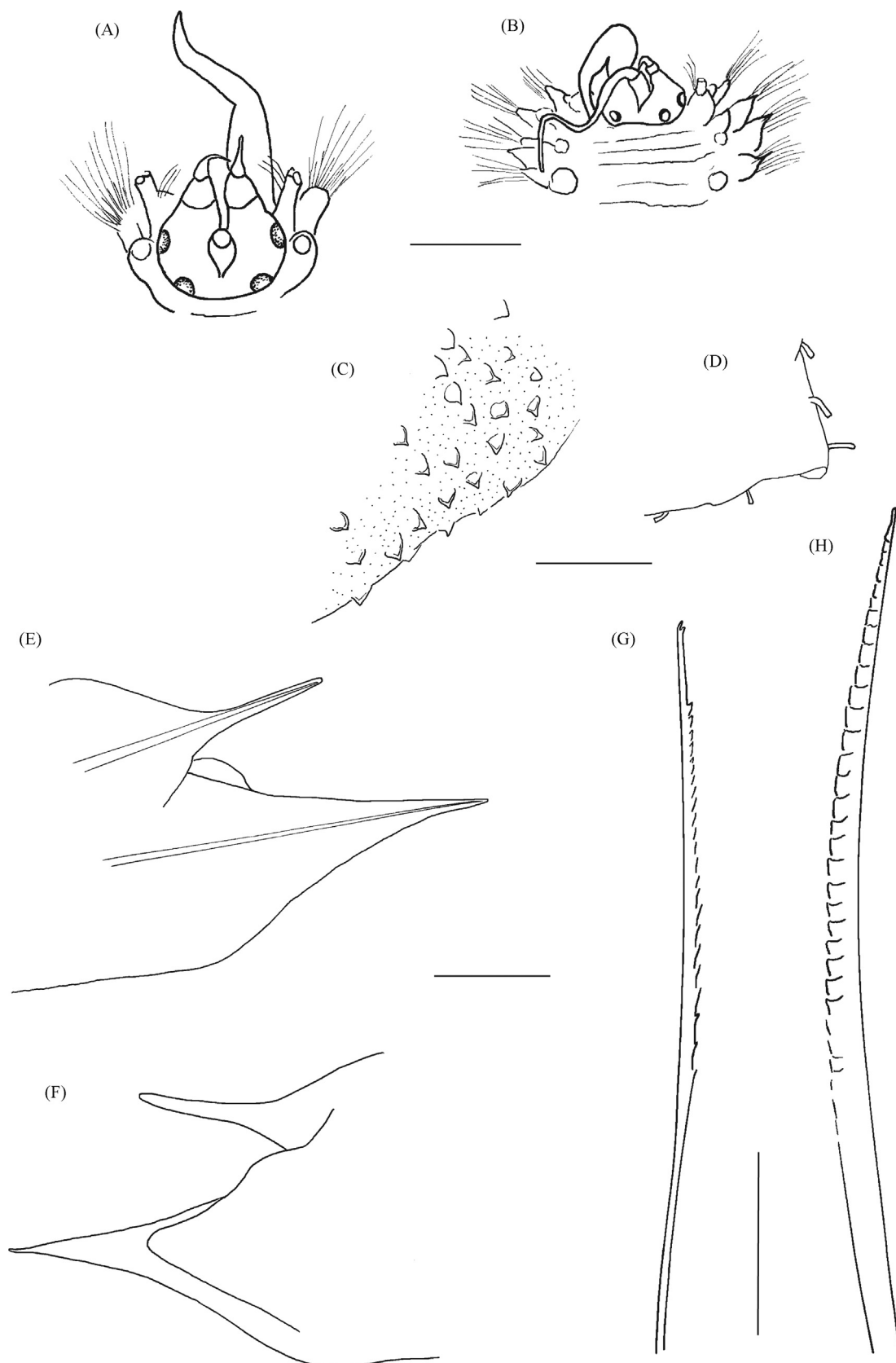


Fig. 2. *Allmaniella setubalensis*. A – Prostomium, dorsal view; B – Anterior end of a different specimen from the same site, dorsal view; C – Papillae from elytra surface; D – Fringing papillae from elytra margin; E – Parapodium 9, anterior view; F – Parapodium 9, posterior view; G – Neurochaetae; H – Notochaetae. Scale bars (μm): A – B=500, C – H=100. Illustrated specimens were collected from St. Nazaire Canyon, St M84-5_689, DBUA0001732.03.

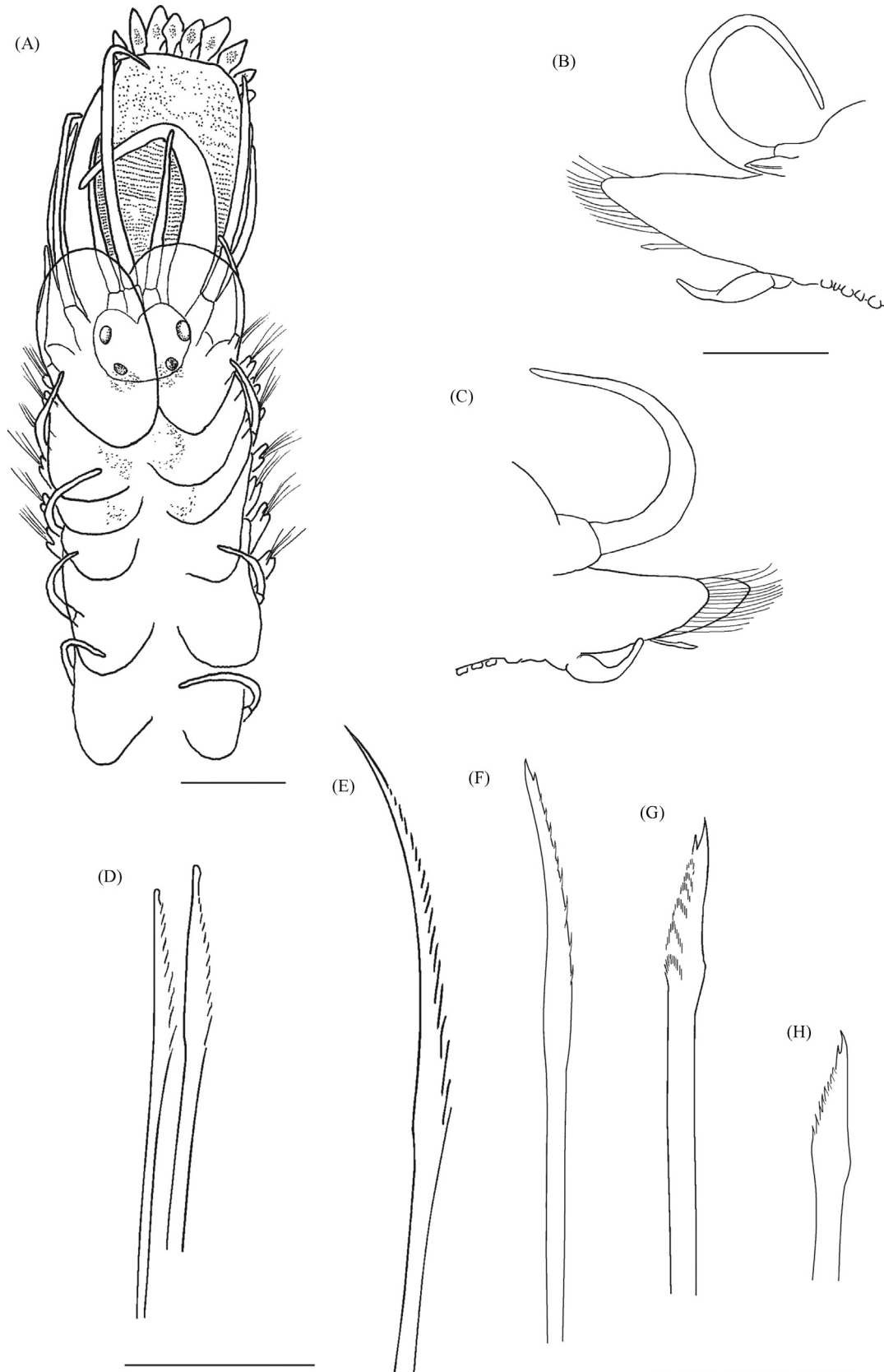


Fig. 3. *Anotochaetonoe michelbaudi*. A – Anterior end, dorsal view; B – Parapodium 14, anterior view; C – Same, posterior view; D – Neurochaetae of anterior parapodia; E–H – Neurochaetae, from dorsalmost (left) to ventralmost (right). Scale bars (μm): A=500, B–H=50. Illustrated specimen was collected from Gulf of Cadiz, St 64PE253_46A, DBUA0001733.

Material examined. Atlantic Ocean. Gulf of Cadiz: Al Idrisi MV, St 64PE253_46 A, 228 m, 1 spm (DBUA0001733).

Additional material. Atlantic Ocean. Republic of Congo: N'Kossa oil field, St. 13(3), 5°16.52'S, 11°33.87'E, sandy silt, 180 m depth, 11 April 2003, 1 spm (MNCN 16.01/10388 - holotype); Emeraude oil field: St 1, 4°59.41'S, 11°45.01'E, 70 m depth, silt, 15 November 1999, 1 spm (MNCN 16.01/10389 - paratype).

Description. Examined specimen with 32 chaetigers, 5.60 mm long and 0.72/1.06 mm wide without and with parapodia, respectively (measures taken on the widest part of the body, excluding chaetae). Body whitish, without pigmentation patterns or dorsal tubercles, compressed dorsoventrally, truncate anteriorly and gradually tapering posteriorly. Fourteen pairs of elytra on segments 2, 4, 5, 7, alternating to 23, then on every third segment until the posterior end. All elytra oval, slightly folded along the external margin, delicate, smooth except for some scarce, irregularly distributed micro-papillae, transparent, with light brown pigmentation in median part of the anterior-most elytra. Prostomium wider than long, bilobed anteriorly, without cephalic peaks; anterior pair of eyes larger than posterior ones, situated dorsolaterally at widest part of prostomium, posterior pair near hind margin of prostomium (Fig. 3A). All antennae gradually tapering, smooth; ceratophore of median antenna inserted in median notch, lateral antennae inserted laterally and with about half the length of median antenna. Palps stout, gradually tapering, about the same length of median antenna, smooth. First segment not visible dorsally; tentaculophores long, achaetous; two pairs of tentacular cirri, similar in length or dorsal ones slightly longer than ventral, slightly shorter than median antenna, smooth. Ventral buccal cirri of the segment shorter than ventral tentacular cirri and substantially longer than ventral cirri of subsequent segments, gradually tapering, smooth. Pharynx brownish, with nine dorsal and nine ventral large terminal papillae and two pairs of brown jaws; pharyngeal papillae with prominent dark spots at the basis. Parapodia relatively long, sub-biramous (Fig. 3B and C). Notopodia achaetous, reduced, located on the anterodorsal side of larger neuropodia, with acicular tips confined inside lobes. Dorsal cirri with short, cylindrical cirrophores and long, smooth styles, tapering gradually to filiform tips, present on segments without elytra, attached to basal dorsal side of neuropodia. Dorsal cirri much longer than parapodia including chaetae, gradually decreasing in size posteriorly. Neuropodia deeply incised dorsally and ventrally, with longer subtriangular prechaetal lobes, and shorter, distally rounded postchaetal lobes. Ventral cirri shorter than neuropodia, gradually tapering, smooth. A single row of five to six globular ciliated papillae extends from the ventral cirri to the ventral basis of parapodia (Fig. 3B–C). Neurochaetae relatively short (comparing to parapodia), around 14 in median parapodia; upper and middle chaetae all similar in length, serrated, gradually tapering to an entire, knob-like tip with a minute distal spherical swelling (Fig. 3D) in anterior parapodia, or entire spinigerous (uppermost) or bifid tips (Fig. 3E) in median and posterior parapodia; ventralmost chaetae (up to two) shorter and stouter, with a shorter serrated section and bidentate tips (Fig. 3H). Pygidium with terminal anus; pygidial cirri not present.

Distribution and habitat. E Atlantic (from the Gulf of Cadiz to the shelf off the Republic of Congo), from 70 to 228 m depth, symbionts of chaetopterid genera *Spiochaetopterus* M. Sars, 1856 and *Phyllochaetopterus* Grube, 1863, on silt and silty sand (Britayev and Martin, 2005; present study).

Remarks. The genus *Anotochaetonoe* includes at present only one species, *A. michelbhaudi* Britayev and Martin, 2005, described from Republic of Congo (tropical E Atlantic), at 70–180 m depth, on silt and silty sand. This species is reported as a symbiont of chaetopterid species of the genera *Spiochaetopterus* and *Phyllochaetopterus*, living inside the host tube with the dorsum in contact with the body of the

host (Britayev and Martin, 2005). The only specimen examined herein was found inside an empty chaetopterid tube, both inside a larger tube hosted by a specimen of *Hyalinoecia tubicola* (O. F. Müller, 1776) (family Onuphidae). However, this probably does not reflect a particular behaviour of the species involved as both tubes were also partially filled with silty sediment. This specimen agrees overall with the original description of *A. michelbhaudi*, except for the unidentate neurochaetae that have a very small knob-like tip on the type material while in our specimen the neurochaetae of the anterior parapodia have a knob-like tip but the ones from median and posterior parapodia are more acutely pointed. Furthermore, the original description of *A. michelbhaudi* mentions a “marked alternation in length” of the dorsal cirri and the presence of 2–4 globular ciliated papillae between ventral cirri and the base of neuropodia. However, by examining the type material, we could not find such clear alternation. Also, while the paratype has only a few indistinct globular ciliated papillae on the ventral side of neuropodia, the holotype has up to eight very distinct papillae. In our specimen the dorsal cirri seem to be slightly larger and there are 5–6 globular ciliated papillae on the ventral side of neuropodia. Therefore, despite the distance from the type locality, we ascribed our specimen to the same species.

Genus *Australaugeneria* Pettibone, 1969.

***Australaugeneria iberica* Ravara and Cunha, 2016.**

***Australaugeneria iberica* Ravara and Cunha, 2016:** 445, Fig. 2, Table 1.

Material examined. Atlantic Ocean. Gulf of Cadiz: Carlos Ribeiro MV, St JC10_051, 2230 m, 3 incompl. spms (NHMUK2016.347, holotype; DBUA0001726.01, paratypes).

Distribution and habitat. NE Atlantic (Gulf of Cadiz), at 2230 m depth, in association with alcyonarian colonies (cf. *Acanella* sp.) (Ravara and Cunha, 2016).

Remarks. For further information on this recently described species check Ravara and Cunha (2016).

Genus *Bathyfauvelia* Pettibone, 1976.

cf. ***Bathyfauvelia affinis* (Fauvel, 1914).**

***Macellicephala affinis* Fauvel, 1914b:** 6, Figs. 3, 4; ***Macellicephala annae* Reys, 1971:** 248, Fig. 3A–E.

Material examined. Atlantic Ocean. Gorrington Bank: Ormonde Seamount, NA017_H1204, 116–1655 m (exact depth unknown), 2 spms (DBUA0001734).

Distribution and habitat. Arctic (Jan Mayen, Franz Josef Land, Wrangel Island), NE Atlantic (off Madeira), Mediterranean Sea, N Pacific (Kurile-Kamchatka Trench), from 0 to 5495 m depth, possibly bathypelagic (Fiege and Barnich, 2009; Pettibone, 1976).

Remarks. The two specimens examined herein are incomplete and much damaged hindering an accurate determination. However, the general characteristics of the species seem to be present.

Genus *Gorgoniapolynoe* Pettibone, 1991.

***Gorgoniapolynoe caeciliae* (Fauvel, 1913).**

***Polynoe caeciliae* Fauvel, 1913:** 24, Fig. 7A–D; ***Gorgoniapolynoe caeciliae* Pettibone, 1991** p. 704, Fig. 12.

Material examined. Atlantic Ocean. Gorrington Bank: Gettysburg Seamount, St NA017_H1202, 1926–2003 m, 1 spm; St NA017_H1203, 1490 m, 1 spm (DBUA0001735).

Distribution and habitat. NE Atlantic (from Bay of Biscay to Cape Verde islands), NW Atlantic (from off Georgia to Caribbean Sea), from 400 to ca. 2000 m depth, associated with octocorals of the families Acanthogorgiidae, Coralliidae and Primnoidae (Barnich et al., 2013; Britayev et al., 2014; Pettibone, 1991; this study).

Remarks. This species was initially described from the Bay of Biscay and later also found off Portugal and around Madeira, Canary and Cape Verde Islands, always associated with gorgonians (Fauvel, 1913; Hartmann-Schröder, 1985). Pettibone (1991) further

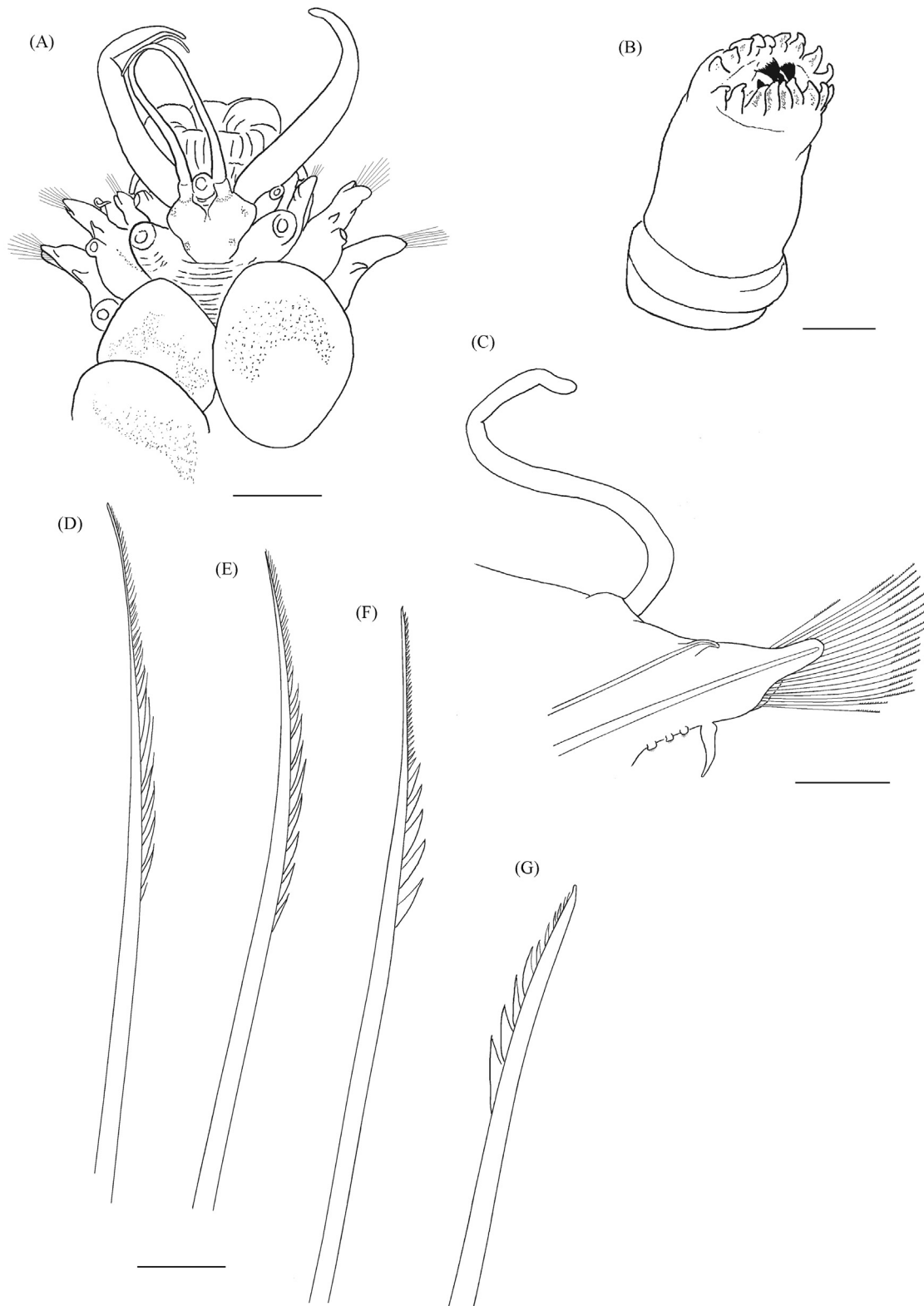


Fig. 4. *Lepidasthenia brunnea*. A – Anterior end, dorsal view (DBUA 0001749.02); B – Everted pharynx, ventral view; C – Parapodium 19, anterior view; D–G – Neurochaetae, from dorsalmost (left) to ventralmost (right). Scale bars (μm): A–B=1000, C–G=50. Illustrated specimens were collected from the Cap Breton area, St M84-5_678, DBUA0001749.02 (A), Alboran Sea, St TTR17-1_MS392, DBUA 0001750.01 (B–G).

extended its distribution to the western Atlantic and recognised its association with octocorals of the families Acanthogorgiidae and Primnoidae (also confirmed by Barnich et al., 2013). The specimens examined herein were taken from a sample also containing acanthogorgiid and primnoid gorgonians and extend the

bathymetric distribution of the species from 1543 to ca. 2000 m depth. The two examined specimens are entire but lack elytra and dorsal cirri. However, all other characteristics of the species are present. Recently, Britayev et al. (2014) examined specimens from Galicia Bank (NW Iberian Peninsula) and Avilés Canyon System

(Bay of Biscay) and amended the species description by Fauvel (1913) and by Pettibone (1991) to include the presence of clavate papillae on dorsal cirri. The lack of dorsal cirri in our specimens impeded the confirmation of this characteristic.

Genus *Harmothoe* Kinberg, 1856.

***Harmothoe aspera* (Hansen, 1879).**

Polynoë aspera Hansen, 1879: 1, pl. I; *Harmothoë aspera* Levinsen, 1883: 36.

Material examined. Mediterranean Sea. Alboran Sea: Mulhacen MV, St TTR17-1_MS416, 365 m, 1 spm (DBUA0001736).

Distribution and habitat. Arctic, NE Atlantic (from Kattegat to North Sea), W Mediterranean, N Pacific (Hartmann-Schröder, 1996), from 200 to 1000 m depth on a wide range of substrata, may be associated with corals (Amoureux, 1972; Barnich and Fiege, 2000, 2009).

***Harmothoe evei* Kirkegaard, 1980.**

Harmothoe evei Kirkegaard, 1980: 82, Fig. 1.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 1 spm; St M84-5_644, 820 m, 6 spms (2 cf.); St M84-5_653, 753 m, 1 spm; St M84-5_687, 537 m, 7 spms

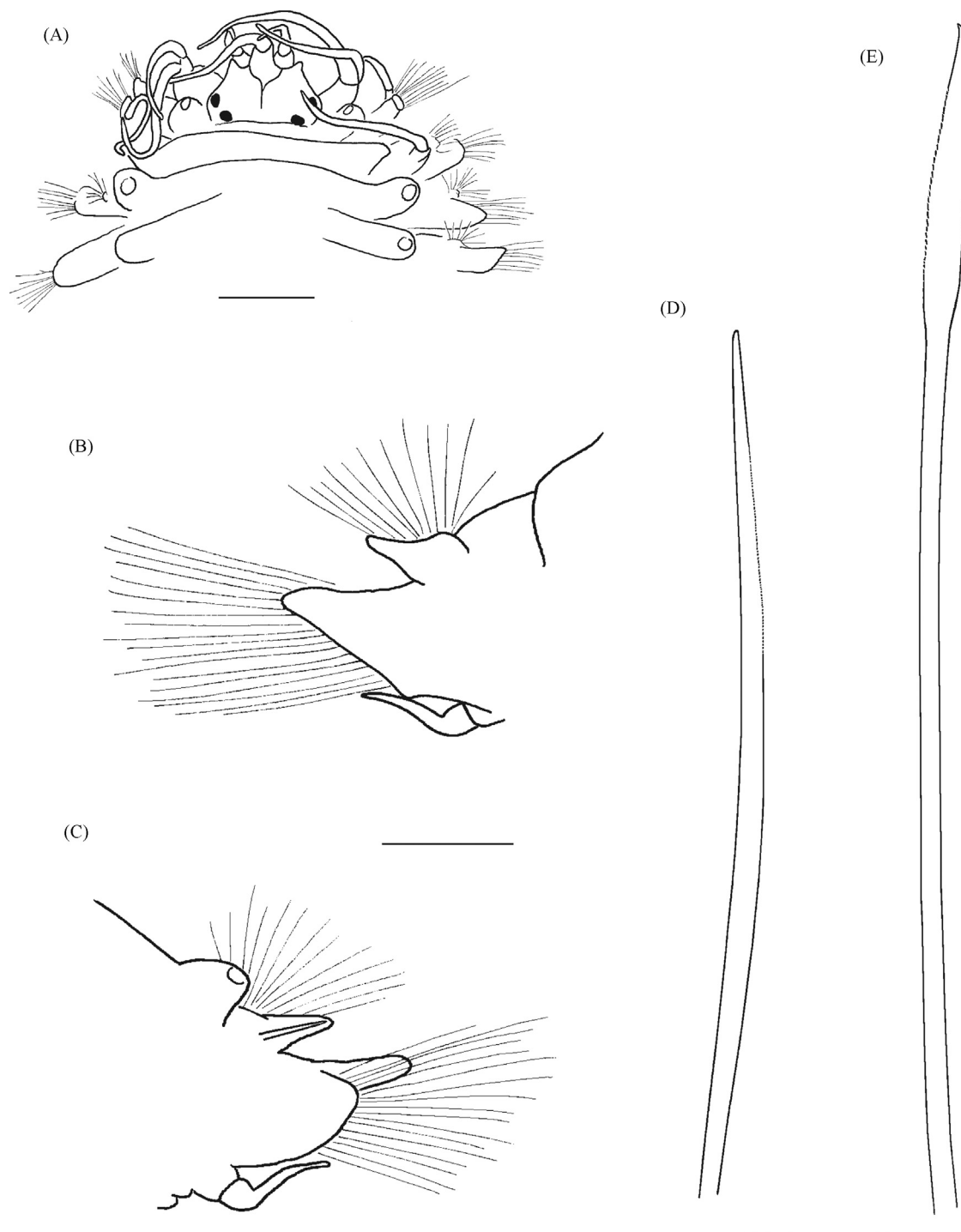


Fig. 5. *Polynoë* sp. A – Anterior end, dorsal view; B – Parapodium 36, anterior view; C – Same, posterior view; D – Notochaeta; E – Neurochaetae. Scale bars (μm): A – 1000 B–C=500, D–E=100. Illustrated specimen was collected from the Ormonde Seamount, St NA017_H1204, DBUA0001756.

(1 cf.); St M84-5_688, 667 m, 8 spms; St M84-5_689, 752 m, 4 spms; St M84-5_690, 755 m, 12 spms; Cap Breton Area, St M84-5_633, 221 m, 7 spms; St M84-5_679, 216 m, 1 spm (DBUA0001737). **Azores:** Atlantis Seamount, St TTR12_AT422, 375 m, 1 spm (DBUA0000697). **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 116-2003 m (exact depth unknown), 1 spm (cf.); St NA017_H1203, 116-1490 m (exact depth unknown), 1 spm; St NA017_046, 385 m, 3 spms (DBUA0001739). **Gulf of Cadiz:** Guadalquivir Ridge, St TTR11_AT339, 1021-1086 m, 1 spm (DBUA0001738); Formosa Ridge, St TTR12_AT388, 1079 m, 13 spm (1 cf.) (DBUA0001553.01); W of Gibraltar Strait, St TTR14_AT551, 393-445 m, 3 spms (1 cf.); St TTR14_AT552, 428 m, 1 spm (cf.) (DBUA0001740); Moroccan Margin, St TTR17-2_AT650, 326 m, 1 spm (cf.) (DBUA0001741); Pen Duick Escarpment, St TTR12_AT406, 550 m, 3 spms (1 cf.) (DBUA0001553.02); St TTR12_AT407, 560 m, 2 spms (1 cf.) (DBUA0001553.03); St 64PE237_07, 570 m, 1 spm (cf.) (DBUA0001742.01); St 64PE253_33, 542 m, 1 spm (cf.) (DBUA0001743.01); Mound B, St 64PE268_13B, 493 m, 1 spm; St 64PE268_16, 473 m, 1 spm (cf.); St 64PE268_23 A, 496 m, 1 spm (cf.); St 64PE268_27, 471 m, 1 spm (cf.) (DBUA0001744); Al Idrisi MV, St 64PE253_46B, 227 m, 1 spm (cf.) (DBUA0001743.02); Mercator MV, St JC10_018-Rock2, 432 m, 2 spms; St JC10_018-Rock5, 373 m, 3 spms; St JC10_018-Rock6, 35°18.827'N, 6°37.058'W, 376 m, 1 spm (DBUA0001745); St 64PE284_12750 W, 354 m, 6 spms (DBUA0001619.01); St B09-14b_01, 354 m, 22 spms (DBUA0001626.02); Lazarillo MV, St 64PE237_21, 498 m, 1 spm (cf.) (DBUA0001742.02); TTR MV, St TTR12_AT416, unknown depth, 4 spms (1 cf.) (DBUA0001553.04); Meknès MV, St MSM01-3_321, 732 m, 1 spm (cf.) (DBUA0001746.01); St B09-14b_03 W, 698 m, 1 spm (DBUA0001626.03). Captain Arutyunov MV, St MSM01-3_180, 1323 m, 1 spm (cf.) (DBUA0001746.02). **Mediterranean Sea. Alboran Sea:** Crow's Foot Pockmark, St TTR17-1_MS423, 572 m, 1 spm (cf.); St TTR17-1_MS425, 570 m, 1 spm (cf.); Melilla Coral Mound Field, St TTR17-1_MS395, 300 m, 10 spms (cf.) (DBUA0001747).

Distribution and habitat. NE Atlantic (from SW of the British Isles to the Gulf of Cadiz, including the Atlantis seamount), W Mediterranean (Alboran Sea), from 217 to 4250 m depth (Kirkegaard, 1980; present study).

Remarks. A total of 137 specimens of *Harmothoe evei* were examined within this study, 32 of which are incomplete or damaged and thus impossible to be fully confirmed. This species was originally described by Kirkegaard (1980) from abyssal depths (4250 m) southwest of British Isles. Barnich and Fiege (2009) present a redescription of the species based on the holotype but add no further records. The records herein are therefore the first since the original description, establishes its shallower occurrence at 217 m depth and extends its geographic distribution to the Bay of Biscay, the Atlantis seamount, the Gorringe Bank, the Gulf of Cadiz and the Alboran Sea (W Mediterranean).

***Harmothoe fraserthomsoni* McIntosh, 1897.**

Harmothoe fraserthomsoni McIntosh, 1897a: 401.

Material examined. Atlantic Ocean. Bay of Biscay: Cap Breton Area, St M84-5_633, 221 m, 1 spm (DBUA 1,748).

Distribution and habitat. From NE to SE Atlantic, Mediterranean Sea (from the W basin to the Aegean Sea), from 50 to 927 m depth, on hard and detritic substrata, or associated with corals, (Barnich and Fiege, 2000, 2009).

Genus *Lepidasthenia* Malmgren, 1867.

***Lepidasthenia brunnea* Day, 1960.**

(Fig. 4A-H).

Lepidasthenia brunnea Day, 1960: 285, Fig. 3a-d.

Material examined. Atlantic Ocean. Bay of Biscay: Cap Breton Area, St M84-5_633, 221 m, 1 spm; St M84-5_678, 215 m, 1 spm (cf.); St M84-5_679, 216 m, 1 posterior fragment (DBUA 0001749.01-03).

Mediterranean Sea. Alboran Sea: Melilla Coral Mound Field, St TTR17-1_MS392, 246 m, 2 spms (DBUA 0001750.01.v01 and v02).

Distribution and habitat. E Atlantic (from the Bay of Biscay to South Africa, including the Azores), Mediterranean Sea (Barnich and Fiege, 2003; Britayev and Martin, 2005; Hartmann-Schröder, 1977; this study), from 80 to 246 m depth, free-living on muddy bottoms or inside chaetopterid tubes (Barnich and Fiege, 2003; Britayev and Martin, 2005; Day, 1960; this study).

Remarks. *Lepidasthenia brunnea* was originally described from False Bay (S Africa), at 88 m depth, and later recorded from the same area both as free-living and in association with *Phyllochaetopterus* sp. (family Chaetopteridae) (Day, 1967). However, this species was previously found in Azores, but reported as *L. maculata* Potts, 1910 (Fauvel, 1923). Later, Hartmann-Schröder (1977) extended its distribution to the west margin of Portugal (off Setúbal). More recently, Barnich and Fiege (2003) and Britayev and Martin (2005) found the same species in the Mediterranean Sea, living freely on muddy bottoms and also inside *Phyllochaetopterus* sp. tubes. The specimens examined by Britayev and Martin (2005) agreed in general with the previous descriptions except by having nearly invisible eyes deeply hidden inside the prostomium tissue. In the present study, five complete specimens (with 75-80 chaetigers) from the Bay of Biscay (NE Atlantic) and the Alboran Sea (W Mediterranean) were examined. These specimens agree with the description by Britayev and Martin (2005) for the Mediterranean specimens. Molecular analyses (see Section 3.2.) confirmed that the specimens from the Bay of Biscay and the Alboran Sea form a single MOTU (Molecular Operational Taxonomic Unit). The presently known wide geographical range of *L. brunnea* (from NE Atlantic to S Africa) should however be considered with caution and the occurrence of putative cryptic species must be further investigated. The northern limit of the geographic distribution of this species is herein extended to the Bay of Biscay, and its deepest occurrence is established at 246 m.

Genus *Leucia* Malmgren, 1867.

***Leucia nivea* (Sars, 1863).**

Polynoe nivea Sars, 1863: 291; *Leucia nivea* Malmgren, 1867: 13; *Polynoe zonata* Langerhans, 1880: 275; *Harmothoe echinopustulata* Fauvel, 1913: 19.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 820 m, 8 spms; St M84-5_687, 537 m, 6 spms; St M84-5_688, 667 m, 1 spm; St M84-5_689, 752 m, 4 spms; St M84-5_690, 755 m, 8 spms; Cap Breton Area, St M84-5_633, 221 m, 3 spms; St M84-5_678, 215 m, 1 spm (DBUA0001751.01-07).

Distribution and habitat. NE Atlantic (from Norwegian margin to Morocco, including W Azores and Madeira), sublittoral, from 8 to 820 m depth, on sandy and shell substrates and associated with the sponge genus *Desmacidon* Bowerbank, 1861 and cold-water corals (Barnich and Fiege, 2010; Chambers and Muir, 1997; this study).

Remarks. Only a few elytra were retrieved with the examined specimens. The elytra ornamentation and other characteristics of the Bay of Biscay specimens agree with the previous descriptions (Barnich and Fiege, 2010; Chambers and Muir, 1997) except for the well-defined pigmentation pattern observed in their posterior region. This study extends the bathymetric distribution of the species from 400 to 820 m.

***Leucia violacea* (Storm, 1879).**

Laenilla violacea Storm, 1879: 32; *Harmothoe violacea* Bidentkap, 1895: 47; *Evarne normani* McIntosh, 1897b: 168, 169, 178, pl. III, Fig. 13; *Leucia violacea* Fiege and Barnich, 2009: 157, Fig. 4a-j.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 1 spm; St M84-5_644, 820 m, 1 spm; St M84-5_653, 753 m, 4 spms; St M84-5_688, 667 m, 2 spms; St M84-5_690, 755 m, 1 spm (DBUA0001752). **Gulf of Cadiz:** Central Coral Mound Province, St 64PE284_12729, 754 m, 2 spms (DBUA0001753.01.v01). **Mediterranean Sea. Alboran Sea:** Crow's Foot Pockmark, St TTR17-1_MS423, 572 m, 1 spm (DBUA0001754.01.v01).

Distribution and habitat. NE Atlantic (from the Norwegian margin to the Gulf of Cadiz), W Mediterranean Sea (Alboran Sea), from 30 to 1262 m depth, on hard substrata, often associated with cold-water corals like *Lophelia pertusa* (Linnaeus, 1758), or *Madrepora oculata* Linnaeus, 1758 (Fiege and Barnich, 2009; this study).

Remarks. The specimens studied herein are in accordance to the species description given by Fiege and Barnich (2009), including the pigmentation pattern. These records extend the southern geographic limit of the species from the Bay of Biscay to the Gulf of Cadiz and the Alboran Sea (W Mediterranean).

Genus *Macellicephal* McIntosh, 1885.

Macellicephal *laubieri* Reyss, 1971.

Macellicephal *laubieri* Reyss, 1971: 244, Figs. 1 and 2.

Material examined. Atlantic Ocean. Gulf of Cadiz: Mercator MV, St MSM01-3_241, 353 m, 1 spm (DBUA0001755).

Distribution and habitat. NE Atlantic (Gulf of Cadiz), Mediterranean Sea, from 353 to 2699 m depth (Barnich and Fiege, 2003; Pettibone, 1976; this study).

Remarks. The single complete specimen without elytra examined herein was found in sediments influenced by mild seepage. This record extends the geographic distribution to the Gulf of Cadiz and the shallower bathymetric limit from 2447 to 353 m depth.

Genus *Polynoe* Savigny in Lamarck, 1818.

Polynoe sp.

(Fig. 5A–E).

Material examined. Atlantic Ocean. Gorrington Bank: Ormonde Seamount, St NA017_H1204, 116–1655 m, 3 spms (DBUA0001756).

Description. Largest complete specimen with 104 segments, 3.80 cm long and 2.90/4.36 mm wide without and with parapodia, respectively (measures taken on the widest part of the body, excluding chaetae). Body whitish, without pigmentation patterns or dorsal tubercles, compressed dorsoventrally, truncate anteriorly and gradually tapering posteriorly. Fifteen pairs of elytra on segments 2, 4, 5, 7, alternating to 23, 26, 29 and 32. Posterior part of the body without elytra. Elytra large, smooth except for some scarce, irregularly distributed micro-papillae. Prostomium wider than long, bilobed anteriorly, with cephalic peaks; anterior pair of eyes situated dorsolaterally at widest part of prostomium, posterior pair near hind margin of prostomium (Fig. 5A). Median antenna gradually tapering, smooth, ceratophore inserted in median notch. Lateral antenna tapering into filiform tips, smooth, with about half the length of median antenna, inserted ventrally. Palps not observed. First segment not visible dorsally; tentaculophores long, achaetous; two pairs of tentacular cirri, ventral ones similar in length to median antennae, dorsal ones longer, smooth. Ventral buccal cirri of the second segment not much longer than ventral cirri of subsequent segments, gradually tapering, smooth. Pharynx with terminal papillae and two pairs of brown jaws. Parapodia short, sub-biramous (Fig. 5B–C). Notopodia conical, with acicular tips confined inside lobes. Dorsal cirri with smooth styles, gradually tapering, much longer than parapodia including chaetae, present on segments without elytra. Neuropodia with longer subtriangular prechaetal lobes, and shorter, distally rounded postchaetal lobes. Ventral cirri shorter than neuropodia, gradually tapering, smooth. Notochaetae slender (similar to neurochaetae),

spine-like, with inconspicuous spinulation (Fig. 5D). Neurochaetae faintly spinulated, unidentate with slightly falcate tips (Fig. 5E). Pygidium with terminal anus; pygidial cirri not observed.

Remarks. Many of the species previously referred to *Polynoe* were posteriorly moved to several other genera, while others have not been recorded since their original descriptions, which are frequently incomplete. At present, this genus includes circa 50 species but a revision is required in order to validate their status. Only three specimens and a few loose elytra of *Polynoe* were examined herein. Owing to the lack of a comprehensive recent revision of the genus, we opted not to pursue with the determination to a species level.

Genus *Robertianella* McIntosh, 1885.

Robertianella *synophthalma* McIntosh, 1885.

Polynoe (*Robertianella*) *synophthalmica* McIntosh, 1885: 122, pl. 14, Fig. 4, pl. 20, Fig. 5, pl. 12A, Figs. 12, 13; *Harmothoe lunulata fauveli* Bellan, 1960: 277, Figs. 1–4; *Harmothoe hyalonemae* Martin, Rosell and Uriz, 1992: 169, Figs. 2–6.

Material examined. Atlantic Ocean. Gulf of Cadiz: Pen Duick Escarpment, St TTR16_AT600, 610 m (DBUA0001757), 1 spm; St 64PE253_19, 908 m, 1 spm (DBUA0001758.01); Gemini MV, St 64PE253_13, 516 m, 1 spm (DBUA0001758.02).

Distribution and habitat. NE Atlantic and Mediterranean Sea, from 516 to 2912 m depth, free-living on muddy substrata or in association with sponges and crinoids (Barnich and Fiege, 2000).

Remarks. The genus *Robertianella* includes two species, both for the NE Atlantic, *R. synophthalma* McIntosh, 1885 and *R. platychaeta* Detinova, 1985. However, based on the absence of significant differences between the descriptions and figures of these two species and the lack of type material for *R. platychaeta*, Barnich and Fiege (2000) considered this latter species as a possible junior synonym of *R. synophthalma*. Only three specimens lacking elytra were examined herein. The morphology of the prostomium, parapodia and neurochaeta is in accordance with *R. synophthalma* description.

Genus *Subadyte* Pettibone, 1969.

Subadyte *pellucida* (Ehlers, 1864).

Polynoe *pellucida* Ehlers, 1864: 105, pl. 2 Fig. 10, pl. 3, Figs. 5, 7–13, pl. 4, Figs. 1–3; *Adyte* *pellucida* Tebbin and Chambers, 1982: 63, Fig. 5a, 20c, d, 56b; *Scalissetosus communis* McIntosh, 1900: 372, pl. 26, Fig. 6, pl. 27, Fig. 12, pl. 30, Fig. 9, pl. 33, Fig. 7, pl. 34, Fig. 1, pl. 40, Figs. 17–19; *Scalissetosus fragilis* Day, 1967: 59, Fig. 1.7, g–k; *Scalissetosus pellucidus* Fauvel, 1914a: 47; *Subadyte* *pellucida* Pettibone, 1969: 8, Fig. 4.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_644, 820 m, 5 spms; St M84-5_653, 753 m, 4 spms; St M84-5_688, 667 m, 1 spm; St M84-5_689, 752 m, 2 spms; Cap Breton Area, St M84-5_633, 221 m, 1 spm (DBUA0001869.01-05). **W Iberian Margin:** Fontanelas, St TTR17-2_AT691, 1308–1460 m, 1 spm (cf.) (DBUA0001762.01); **Gulf of Cadiz:** Formosa Ridge, St TTR12_AT388, 1079 m, 1 spm (cf.) (DBUA0000672.01); W of Gibraltar, St TTR14_AT551, 393–445 m, 1 spm (DBUA0001759.01); St TTR14_AT552, 428 m, 1 spm (DBUA0001759.02); Pen Duick Escarpment, St TTR12_AT406, 550 m, 1 spm (DBUA0000672.02); St TTR12_AT407, 560 m, 1 spm (DBUA0000672.03); St TTR16_AT600, 610 m, 1 spm (DBUA0001760.01); St 64PE268_41, 461 m, 1 spm (DBUA0001764.01); Mound B, St 64PE268_16, 473 m, 1 spm (DBUA0001764.02); Central Carbonate Mound Province, St 64PE284_12729, 754 m, 1 spm (DBUA0001765.01); Meknès Carbonate Mound Province, St 64PE284_12739, 736 m, 1 spm (DBUA0001765.02); **Mercator MV,** St TTR15_AT575_355 m, 1 spm (DBUA0001763.01); St 64PE284_12750 W, 354 m, 4 spms (DBUA0001765.03); St B09-14b_01, 354 m, 9 spms (DBUA0001668.02.v01); TTR MV, St TTR12_AT416, unknown depth, 1 spm

(DBUA0000672.04); Meknès MV, St B09-14b_03 W, 698 m, 5 spms (DBUA0001668.04); Darwin MV, St TTR16_AT608, 1115 m, 2 spms (cf.) (DBUA0001760.02); St TTR17-2_AT664, 1128 m, 1 spm (DBUA0001762.02); St B09-14b_02 W, 1100 m, 4 spms (cf.) (DBUA0001668.03).

Mediterranean Sea. Alboran Sea: Melilla Coral Mound Field, St TTR17-1_MS395, 300 m, 5 spms (DBUA0001761.01).

Distribution and habitat. E Atlantic (from North Sea to South Africa), Mediterranean Sea (Adriatic Sea), Indian Ocean (Bay of Bengal), Pacific (New South Wales) (Chambers and Muir, 1997; Pettibone, 1969), littoral and sub-littoral from 300 to 820 m depth, on various sediment types or among algae, often associated with echinoderms, crinoids and corals (Brito et al., 1991; Chambers and Muir, 1997; Pettibone, 1969; this study).

Remarks. Most of the 55 specimens examined herein were collected at depths from 300 to 825 m, and were in accordance with the species description. However, nine specimens that occurred at deeper locations (1079–1460 m), mainly on Darwin MV, are much smaller or incomplete, without elytra and overall in poor condition. The cusps on neurochaetae are clearly present but all other characteristics were difficult to confirm. Therefore, and considering the different depth range, the identification of these specimens should be considered with caution.

Family Pholoidae Kinberg, 1858.

Genus Pholoe Johnston, 1839.

Pholoe fauveli Kirkegaard, 1983.

Pholoe fauveli Kirkegaard, 1983: 599, Fig. 1.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St. M84-5_644, 820 m, 1 spm (cf.); St M84-5_649, 1105 m, 8 spms; St M84-5_651, 982 m, 4 spms (1 cf.) (DBUA0001766.01-03).

Distribution and habitat. NE Atlantic (Bay of Biscay, Azores), from 800 to 1350 m depth (Kirkegaard, 1983).

Pholoe petersenae Ravara and Cunha, 2016.

Pholoe petersenae Ravara and Cunha, 2016, Fig. 3.

Material examined. Atlantic Ocean. Gulf of Cadiz (MV): Darwin MV, St B09-14b_02, 1100 m, 1 spm (DBUA0001729.01); Captain Arutynov MV, St TTR14_AT546, 1345 m, 3 spms (DBUA0001728.01); St MSM01-3_190.1, 1322 m, 3 spms (DBUA0001727.03); St MSM01-3_218, 1318 m, 13 spms (DBUA0001727.04); St. MSM01-3_225, 1320 m, 1 spm (DBUA0001727.05); St MSM01-3_180, 1323 m, 3 spms (NHMUK2016.349-351); St MSM01-3_274, 1321 m, 1 spm (NHMUK2016.348, holotype); Carlos Ribeiro MV, St MSM01-3_184, 2204 m, 1 spm (DBUA0001727.06).

Distribution and habitat. NE Atlantic (Gulf of Cadiz), from 1100 to 2204 m depth in sediments influenced by active seepage (Ravara and Cunha, 2016).

Family Sigalionidae Malmgren, 1867.

Genus Fimbriosthenelais Pettibone, 1971.

Fimbriosthenelais zetlandica (McIntosh, 1876a).

Sthenelais? zetlandica McIntosh, 1876a: 390, pl. LXX, Figs. 15-17; *Sthenelais atlantica* McIntosh, 1876b: 405, pl. LXII, Figs. 16, 17; *Sthenelais sarsi* McIntosh, 1897b: 174, pl. III, Figs. 1-5; *Sthenelais papillosa* Day, 1960: 289, Fig. 3e-j; *Sthenelais vachoni* Rullier, 1964: 139, Fig. 6a-l; *Fimbriosthenelais zetlandica* Pettibone, 1971: 32, Figs. 21, 22.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 3 spms; St M84-5_644, 820 m, 1 spm (cf.); St M84-5_688, 667 m, 1 spm (cf.) (DBUA0001773.01-03). **Gulf of Cadiz:** Vernadsky Ridge, St 64PE284_12759, 524 m, 1 spm (DBUA0001772.01); Pen Duick Escarpment, St TTR16_AT600, 610 m, 1 spm (DBUA0001766.01); St 64PE253_23, 557 m, 1 spm (DBUA0001771.01); Meknès MV, TTR14_AT541, 703 m, 1 spm (DBUA0001767.01.v01); St MSM01-3_321, 732 m, 1 spm (DBUA0001770.01.v01); St B09-14b_03 W, 698 m, 1 spm

(DBUA0001667.01); Ginsburg MV, St TTR16_AT607, 983 m, 1 spm (DBUA0001768.02); Jesus Baraza MV, St TTR12_AT391, 1105 m, 1 spm (DBUA0000671.01); Darwin MV, St TTR16_AT608, 1115 m, 1 spm (DBUA0001768.03); St TTR17-2_AT664, 1128 m, 1 spm (DBUA0001769.01).

Distribution and habitat. NE Atlantic (from off Norway to Cape Verde Islands), SE Atlantic (False Bay), from 33 to 1128 m depth (Chambers, 1985; Chambers and Muir, 1997; Pettibone, 1971; this study).

Remarks. Pettibone (1971) erected the genus *Fimbriosthenelais* to accommodate species previously referred to the genus *Sthenelais* (including *S. zetlandica*) that have papillate parapodial stylodes. Chambers (1985) considered that this single difference does not warrant generic separation and thus re-ascribed the species to the genus *Sthenelais*. The latter classification was maintained by Chambers and Muir (1997) and Jirkov (2001). Recently, Aungtonya (2002) and Barnich and Fiege (2003) recognised the genus *Fimbriosthenelais* as valid. In the present study, this genus is also maintained (see Section 3.2). However, further studies should be addressing this issue, in order to clearly establish the relation between these two genera. All the 15 specimens examined herein are incomplete; the majority is of small size and/or lack elytra. However, the diagnostic characteristics of the species were overall verified, namely, the morphology of the prostomium and its appendages, the papillate stylodes, the neurochaetae and the elytra (when present). The bathymetric distribution of the species is here extended from 558 m (Chambers, 1985; Chambers and Muir, 1997; Pettibone, 1971) to 1128 m depth.

Genus Labioleanira Pettibone, 1992.

Labioleanira yhleni (Malmgren, 1867).

Leanira yhleni Malmgren, 1867: 17; *Sthenolepis yhleni* Hartman, 1965: 14; *Labioleanira yhleni* Pettibone, 1992b: 621, Figs. 5, 6.

Material examined. Mediterranean Sea. Alboran Sea: Melilla Coral Mound Field, St TTR17-1_MS393, 245 m, 1 incomplete spm (DBUA0001774).

Distribution and habitat. E Atlantic (France, Spain, SW Iberian Peninsula, W Africa), Mediterranean Sea, from 1 to 1900 m depth (Pettibone, 1992b; Gil and Sardá, 1999).

Genus Leanira Kinberg, 1856.

Leanira hystricis Ehlers, 1874.

Leanira hystricis Ehlers, 1874: 292; *Leanira laevis* McIntosh, 1874: 268 (*nomen nudum*).

Material examined. Atlantic Ocean. Gulf of Cadiz: Bonjardim MV, St TTR15_AT597, 3061 m, 1 spm (DBUA0001775); Porto MV, St TTR16_AT622, 3902 m, 1 spm (DBUA0001776); St MSM01-3_161, 3864 m, 1 spm (DBUA0001777).

Distribution and habitat. N Atlantic (SE Canada, S Iceland, off Great Britain, off Azores, Gulf of Cadiz), from 957 to 3902 m depth (Pettibone, 1970; this study).

Remarks. The three specimens examined herein are incomplete and lack elytra. However the general morphological characteristics, in particular the spinigerous neurochaetae and the absence of eyes and auricles on prostomium, point out to the species *Leanira hystricis*. This is a deep-sea species occurring from off S Iceland to Azores, and here reported also from the Gulf of Cadiz. The bathymetric distribution is also extended from 2640 m (Pettibone, 1970) to 3902 m depth.

Genus Pholoides Pruvot, 1895.

Pholoides dorsipapillatus (Marenzeller, 1893).

Pholoe dorsipapillata Marenzeller, 1893: 30, pl. I, Fig. 3a-d; *Pholoides dorsipapillatus* Pettibone, 1992a: 16, Figs. 8, 9; *Psammolyce fjensis* McIntosh, 1885: 146; *Peisidice bermudensis* Hartman and Fauchald, 1971: 30, pl. II, Figs. a-e; *Peisidice dorsipapillata* Katzmann,

1973: 111; *Pholoides bermudensis* Uebelacker, 1984: 23.1, Figs. 23.1, 23.2; *Peisidice aspera* Rosenfeldt, 1989: 217 [not Johnson, 1897].

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 1 spm; St M84-5_644, 820 m, 1 spm; St M84-5_649, 1105 m, 3 spms; St M84-5_651, 982 m, 3 spm; St M84-5_653, 753 m, 2 spms; St M84-5_688, 667 m, 4 spms; St M84-5_689, 752 m, 2 spms; St M84-5_690, 755 m, 1 spm (DBUA0001778.01-08). **W Iberian Margin:** Fontanelas, St TTR17-2_AT689, 1194-1250 m, 4 spms; St TTR17-2_AT690, 1340-1498 m, 1 spm; St TTR17-2_AT691, 1308-1460 m, 3 spms (DBUA0001784.01-03); **Azores:** Atlantis Seamount, St TTR12_AT421, 555-614 m, 1 spm (DBUA0001779.01). **Madeira:** Nameless Seamount, St TTR11_AT353, 1853 m, 1 spm (DBUA0000571.03). **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 116-2003 m (exact depth unknown), 1 spm (DBUA0001791.01); St NA017_045, 614 m, 1 spm (DBUA0001791.03); Ormonde Seamount, St NA017_H1204, 116-1655 m (exact depth unknown), 2 spms (DBUA0001791.02). **Gulf of Cadiz:** Cadiz Channel, St TTR15_AT599, 1275-1418 m, 3 spms (DBUA0001781.01); Guadalquivir Ridge, St TTR11_AT339, 1086 m, 44 spm (DBUA0000571.02); Formosa Ridge, St TTR12_AT388, 1079 m, 113 spms (DBUA0001779.02); Ibérico Mound, St TTR11_AT335, 905-1037 m, 26 spm (DBUA0000571.01); W of Gibraltar Strait, St TTR14_AT550, 368-392 m, 5 spms; St TTR14_AT551, 393-445 m, 4 spms; St TTR14_AT552, 428 m, 2 spms (DBUA0001780.01-03); Vernadsky Ridge, St TTR15_AT574, 508-512 m, 4 spms (DBUA0001781.02); St 64PE284_12759, 524 m, 3 spms (DBUA0001789.01). Pen Duick Escarpment, St TTR12_AT406, 550 m, 3 spms (DBUA0001779.03); St TTR12_AT407, 560 m, 2 spms (DBUA0001779.04); St 64PE237_16 A, 660 m, 1 spm (DBUA0001786.01); St TTR16_AT600, 610 m, 3 spms (DBUA0001782.01); St 64PE253_23, 557 m, 1 spm (DBUA0001787.01); St 64PE253_24, 571 m, 1 spm (DBUA0001787.02); St 64PE253_25, 648 m, 1 spm (DBUA0001787.03); St 64PE253_40 A, 560 m, 1 spm (DBUA0001787.04); St 64PE253_53, 651 m, 1 spm (DBUA0001787.05); St 64PE253_54, 634 m, 1 spm (DBUA0001787.06); St 64PE268_20, 765 m, 1 spm (DBUA0001788.01); St 64PE268_40, 473 m, 2 spms (DBUA0001788.02); St 64PE268_46, ~720 m, 6 spms (DBUA0001788.03); Mound B, St 64PE268_11, 493 m, 1 spm; St 64PE268_11 A, 489 m, 1 spm; St 64PE268_12, 500 m, 1 spm; St 64PE268_13 A, 475 m, 1 spm; St 64PE268_13B, 493 m, 1 spm; St 64PE268_16, 473 m, 3 spms; St 64PE268_27, 471 m, 1 spm (DBUA0001788.04-10); SE of Yuma Carbonate Mound Province, St 64PE284_12721, 868 m, 4 spms; St 64PE284_12722, 907 m, 5 spms (DBUA0001789.02-03); Mekkès Carbonate Mound Province, St 64PE284_12739, 736 m, 4 spms (DBUA0001789.04); Mercator MV, St MSM01-3_241, 353 m, 1 spm (DBUA0001785.01); St JC10_018-Rock2, 432 m, 1 spm (DBUA0001790.01); Fiúza MV, St TTR14_AT566, 414 m, 3 spms (DBUA0001780.04); Gemini MV, St 64PE253_08, 444 m, 1 spm (DBUA0001787.07); St 64PE253_09, 451 m, 3 spms (DBUA0001787.08); St 64PE253_10, 432 m, 4 spms (DBUA0001787.09); St 64PE268_19, 430 m, 6 spms (DBUA0001788.11); Kidd MV, St TTR14_AT528, 489 m, 17 spms; St TTR14_AT560, 498 m, 6 spms; St TTR14_AT561, 526 m, 5 spms (DBUA0001780.05-07); Lazarillo MV, 64PE237_21, 498 m, 9 spms (DBUA0001786.02); St 64PE253_38B, 497 m, 5 spms (DBUA0001787.10); TTR MV, St TTR12_AT413, 695 m, 1 spm (DBUA0001779.05); St TTR12_AT416, unknown depth, 6 spms (DBUA0001779.06); Mekkès MV, St TTR14_AT541, 703 m, 2 spms (DBUA0001780.08); St MSM01-3_321, 732 m, 1 spm (DBUA0001785.02); St 64PE284_12748, 722 m, 1 spm (DBUA0001789.05); Yuma MV, St TTR14_AT524, 960 m, 3 spms (DBUA0001780.09); St TTR16_AT604, 1030 m, 1 spm (DBUA0001782.02); Jesus Baraza MV, St TTR12_AT391, 1105 m,

2 spms (DBUA0001779.07); Darwin MV, St TTR16_AT608, 1115 m, 2 spms (DBUA0001782.03); St JC10_028-Rock5, 1119 m, 1 spm (DBUA0001790.02); Captain Arutyunov MV, St TTR12_AT399, 1339 m, 1 spm (DBUA0001779.08); St MSM01-3_180, 1323 m, 2 spms (DBUA0001785.03); Carlos Ribeiro MV, St MSM01-3_184, 2204 m, 1 spm (DBUA0001785.04). **Mediterranean Sea. Alboran Sea:** Melilla Coral Mound Field, St TTR17-1_MS395, 300 m, 1 spm (DBUA0001783).

Distribution and habitat. Atlantic ocean (Gulf of Mexico, Cuba, Bermuda, Azores; from Bay of Biscay to South Africa), Mediterranean Sea, Adriatic Sea, Red Sea, from 37 to 2285 m depth, on coarse sand, pumice stone and muddy substrata (Pettibone, 1992a; this study).

Remarks. A total of 366 specimens were examined mostly in association with carbonate crusts and fossil cold-water corals but also in sediments influenced by mild seepage. The geographic distribution of this species is here extended for the NE Atlantic (from the Cape Verde Islands to the Bay of Biscay) and its deepest limit is established at 2204 m (instead of 1153 m, Pettibone, 1992a).

Genus *Sthenelais* Kinberg, 1856.

Sthenelais jeffreysi McIntosh, 1876a.

Sthenelais jeffreysi McIntosh, 1876b: 406, pl. LXXII Fig. 18-19, pl. LXXIII Figs. 1-2.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 1 spm (DBUA0001792.01). **Gulf of Cadiz:** Pen Duick Escarpment, St TTR12_AT407, 560 m, 1 spm (DBUA0000670); St TTR16_AT600, 610 m, 1 spm (DBUA0001793.01); Mekkès MV, St MSM01-3_321, 732 m, 1 spm (cf.) (DBUA0001794.01).

Distribution and habitat. N Atlantic (Davis Strait; from Skagerrak to the Gulf of Cadiz), from 271 to 820 m depth (Ditlevsen, 1917; Eliason, 1962; McIntosh, 1876b; this study).

Remarks. The four specimens examined herein verify the diagnostic characteristics of *Sthenelais jeffreysi*. This species can be distinguished from other *Sthenelais* species known from the NE Atlantic, *S. boa* and *S. limicola*, mainly by the larger fringing papillae of the elytra (shorter on *S. boa* and absent or only a few bifurcate papillae on *S. limicola*) and the presence of spinigerous neurochaetae (absent in the other two species) (McIntosh, 1876b). *Sthenelais boa* occurs mainly in shallower coastal waters, while *S. limicola* is referred to occur offshore down to continental slope depths. A possible synonymy between *S. jeffreysi* and *Eusthenelais hibernica* McIntosh, 1876a, both species originally described from off Ireland, with *E. hibernica* being based also on syntypes collected off Cape Sagres, was suggested by Eliason (1962) and Hartman (1965). The latter species has been found in Iberian waters ranging from 327 to 480 m depth (e.g. Amoureux, 1972 as *Parasthenelais hibernica*; Gil and Sardá, 1999; Nuñez et al., 2015). Apparently the two species differ only by the presence of a long dorsal cirri on the third chaetiger in *E. hibernica*, while *S. jeffreysi* presents a tubercle, as it happens with the specimens examined in this study. According to Chambers (1985) and Aungtonya and Eibye-Jacobsen (2014) the holotypes of both species are unidentifiable due to their poor condition and thus the species are considered to be of uncertain status. This issue should be further addressed in the future, preferably with the inclusion of material from the type localities of both species.

The geographic and bathymetric distribution of *S. jeffreysi*, previously known only from Skagerrak and West Ireland down to ca. 300 m depth, is here extended to the Bay of Biscay and the Gulf of Cadiz at depths down to 820 m.

Suborder Glyceriformia Fauchald, 1977.

Family Glyceridae Grube, 1850.

Genus *Glycera* Savigny in Lamarck, 1818.

***Glycera lapidum* Quatrefages, 1866.**

Glycera lapidum Quatrefages, 1866: 187.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 2 spms; St M84-5_649, 1105 m, 10 spms; St M84-5_651, 982 m, 3 spms; St M84-5_653, 753 m, 2 spms; St M84-5_688, 667 m, 2 spms (DBUA0001807.01-05); Cap Breton Area, St M84-5_633, 221 m, 2 spms; St M84-5_677, 214 m, 13 spms; St M84-5_678, 215 m, 7 spms (DBUA0001807.06-08). **Gulf of Cadiz:** Moroccan Margin, St TTR17-2_AT650, 326 m, 1 spm; St TTR17-2_AT654, 395 m, 1 spm (DBUA0001801.01-02); Vernadsky Ridge, St 64PE284_12758#01, 527 m, 1 spm (DBUA0001802.01); Pen Duick Escarpment, St 64PE237_05 C, 533 m, 3 spms (DBUA0001803.01); St 64PE237_07, 570 m, 1 spm (DBUA0001803.02); St 64PE237_31, 559 m, 1 spm (DBUA0001803.03); St TTR16_AT602, 556 m, 1 spm (DBUA0001798.01); St 64PE253_23, 557 m, 1 spm; St 64PE253_26, 628 m, 1 spm; St 64PE253_40 A, 560 m, 1 spm; St 64PE253_41, 568 m, 3 spms; St 64PE253_42, 637 m, 3 spms; St 64PE253_52, 622 m, 1 spm; St 64PE253_53, 651 m, 1 spm; St 64PE253_59, 637 m, 2 spms (DBUA0001804.01-08); St 64PE268_04, 597 m, 1 spm; St 64PE268_05, 581 m, 1 spm; St 64PE268_09, 428 m, 1 spm; St 64PE268_36, 465 m, 2 spms; St 64PE268_39, 441 m, 2 spms; St 64PE268_42, 451 m, 1 spm; St 64PE268_45, ~800 m, 1 spm; St 64PE268_46, ~720 m, 3 spms; St 64PE268_51, ~740 m, 2 spms; St 64PE268_53B, 750 m, 1 spm; St 64PE268_54 A, 750 m, 1 spm (DBUA0001805.01-11); Mound B, St 64PE268_11 A, 489 m, 1 spm; St 64PE268_13 A, 475 m, 2 spms; St 64PE268_13B, 493 m, 2 spms; St 64PE268_23 A, 496 m, 1 spm; St 64PE268_24, 495 m, 1 spm; St 64PE268_25, 490 m, 2 spms; St 64PE268_27, 471 m, 3 spms (DBUA0001805.12-18); Al Idrisi MV, St 64PE253_46B, 227 m, 1 spm (cf.) (DBUA0001804.09); Mercator MV, St TTR15_AT575, 355 m, 2 spms (DBUA0001797.01); St MSM01-3_237.2, 353 m, 2 spms (DBUA0001799.01); St MSM01-3_241, 353 m, 8 spms (DBUA0001799.02); St MSM01-3_242, 350 m, 6 spms (DBUA0001799.03); St 64PE253_48, 376 m, 4 spms; St 64PE253_49, 360 m, 2 spms (DBUA0001799.10-11); Gemini MV, St 64PE253_10, 432 m, 1 spm; St 64PE253_11, 438 m, 1 spm; St 64PE253_13, 516 m, 2 spms; St 64PE253_15, 600 m, 2 spms; St 64PE253_17, 612 m, 1 spm; St 64PE253_18, 608 m, 2 spms (DBUA0001804.12-17); St 64PE268_19, 430 m, 1 spm (DBUA0001805.19); Kidd MV, St TTR14_AT528, 489 m, 1 spm (cf.) (DBUA0001796.01); Anastasia Area, St 64PE284_12706, 702 m, 1 spm (DBUA0001802.02); Lazarillo MV, St 64PE237_20, 516 m, 1 spm (DBUA0001803.04); St 64PE237_22, 518 m, 1 spm (DBUA0001803.05); St 64PE253_38 A, 494 m, 2 spms; St 64PE253_38B, 497 m, 1 spm (DBUA0001804.18-19); Meknès MV, St TTR14_AT541, 703 m, 1 spm (DBUA0001796.02); St TTR15_AT586, 701 m, 1 spm (DBUA0001797.02); St MSM01-3_319, 695 m, 11 spms (DBUA0001799.04); St MSM01-3_321, 732 m, 3 spms (DBUA0001799.05); St MSM01-3_335, 703 m, 4 spms (DBUA0001799.06); St 64PE284_12748, 722 m, 3 spms (DBUA0001802.03); Yuma MV, St TTR16_AT604, 1030 m, 6 spms; St TTR16_AT605, 975 m, 2 spms (DBUA0001798.02-03); Ginsburg MV, St TTR16_AT607, 983 m, 7 spms (DBUA0001798.04); Darwin MV, St TTR16_AT608, 1115 m, 5 spms (DBUA0001798.05); St TTR17-2_AT664, 1128 m, 4 spms (DBUA0001801.03); Chechaouen MV, St TTR16_AT610, 1177 m, 2 spms (DBUA0001798.06); Captain Arutynov MV, St TTR12_AT393, 1327 m, 1 spm (DBUA0001795.01); St TTR14_AT546, 1345 m, 1 spm (DBUA0001796.03); St MSM01-3_180, 1323 m, 21 spms (DBUA0001799.07); St MSM01-3_212, 1317 m, 5 spms (DBUA0001799.08); St MSM01-3_218, 1318 m, 3 spms (DBUA0001799.09); St MSM01-3_225, 1320 m, 8 spms (DBUA0001799.10); St MSM01-3_274, 1321 m, 9 spms (DBUA0001799.11); St MSM01-3_344, 1320 m, 1 spm (DBUA0001799.12); Sagres MV, St TTR17-2_AT667, 1562 m, 13

spms (DBUA0001801.04); Carlos Ribeiro MV, St MSM01-3_157, 2200 m, 1 spm (DBUA0001799.13); St MSM01-3_184, 2204 m, 2 spms (DBUA0001799.14); St JC10_054, 2179 m, 1 spm (DBUA0001806.01); Unnamed Mound, St TTR17-2_AT673, 2368 m, 1 spm (DBUA0001801.05); Bonjardim MV, St MSM01-3_149, 3089 m, 1 spm (DBUA0001799.15); Semenovich MV, TTR17-2_AT679, 3265 m, 2 spms (DBUA0001801.06); Porto MV, St MSM01-3_167, 3862 m, 1 spm (cf.) (DBUA0001799.16); Porto MV, St TTR17-2_AT683, 3890 m, 1 spm (DBUA0001801.07). **Mediterranean Sea. Alboran Sea:** Mulhacen MV, St TTR17-1_MS416, 365 m, 1 spm (DBUA0001800.01); Dakha MV, St TTR17-1_MS413, 377 m, 2 spm (DBUA0001800.02); Crow's Foot Pockmark, St TTR17-1_MS425, 570 m, 1 spm (DBUA0001800.03); Pockmark, St TTR17-1_MS427, 657 m, 3 spm (DBUA0001800.04); Reference Site, St TTR17-1_MS384, 1022 m, 1 spm (DBUA0001800.05); Melilla Coral Mound Field, St TTR17-1_MS393, 245 m, 1 spm (DBUA0001800.06).

Distribution and habitat. Barents Sea, Atlantic (from Norway to W Africa including Iceland and Azores; from the eastern margin of North America to Argentina), Mediterranean Sea, Indian Ocean, Pacific (Australia, New Zealand and the western margin of North and South America), mainly in temperate regions from 1 to 4400 m depth (Böggemann, 2002; Kirkegaard, 1998; Rizzo et al., 2007), in various habitat settings including cold-water corals and sediments influenced by mild to active seepage (this study).

Remarks. A total of 263 specimens were examined from the Bay of Biscay to the Alboran Sea, from 214 to 3890 m depths. Some morphological variability was observed among those specimens (including specimens within the same locality), concerning the shape of the ailerons and the proportional length of the parapodial prechaetal lobes. Variability in these same features was already noticed by Støp-Bowitz (1941) and O'Connor (1987) for N Atlantic and Mediterranean specimens. Consequently, O'Connor (1987) considered *G. lapidum* as a species complex and described four different varieties. This species is also morphologically very similar to *G. capitata* Örsted, 1843b, originally described from Greenland, with which it has been often confused. Fauvel (1923) suggested *G. lapidum* to be a variety of *G. capitata* and was followed by many subsequent authors. The distinction between the two species was later confirmed by O'Connor (1987) and Böggemann (2002). *Glycera lapidum* differs from *G. capitata* by having two digitiform prechaetal lobes of which the dorsal one is much smaller than the ventral, and by having triannulate instead of biannulate segments. According to O'Connor (1987), *G. capitata sensu Fauvel (1923)*, Støp-Bowitz (1941) and Hartmann-Schröder (1971) should be referred to variety C of *G. lapidum*. Böggemann (2002) however did not recognise these varieties.

Glycera lapidum was originally described for the Mediterranean Sea at depths shallower than 200 m, and is commonly found in the Lusitanian region. However, it has also been recorded much further north (e.g. Wesenberg-Lund, 1951; Kirkegaard, 1998, 2001), deeper than 200 m and both in warm Atlantic (SW Iceland) and cold Arctic waters (N Iceland). The variability within the species and its wide geographic distribution (including Indian and Pacific Oceans) should be investigated more carefully with the inclusion of molecular tools.

***Glycera noelae* Böggemann, Bienhold and Gaudron, 2012.**

Glycera noelae Böggemann, Bienhold and Gaudron, 2012: 50, Fig. 3.

Material examined. Atlantic Ocean. Horseshoe Continental Rise: M Ivanov MV, St M86-5_348, 4497 m, 1 spm; St M86-5_407, 4507 m, 2 spms (DBUA0001808.01-02); Tiamat MV, St M86-5_339, 4551 m, 1 spm (cf.) (DBUA0001808.03); Site 2, St M86-5_366, 4864 m, 1 spm (cf.) (DBUA0001808.04); **Gulf of Cadiz:** Porto MV, St TTR17-2_AT683, 3890 m, 1 spm (DBUA0001809.01).

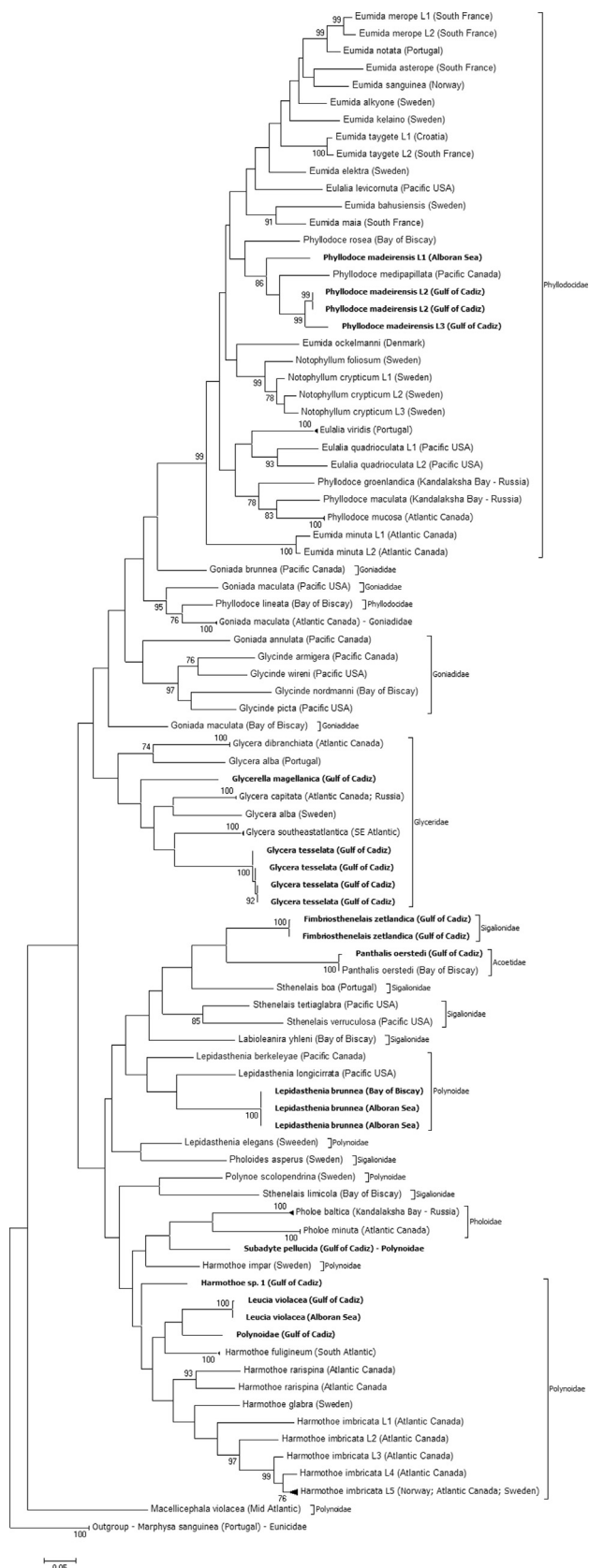


Fig. 6. Maximum likelihood tree inferred from partial COI nucleotide sequences from 62 species of Phyllococida (BOLD dataset: PHYLOGEN), based on the GTR+G+I substitution model. Collapsed branches represent specimens with a genetic distance below 4%. New sequences generated in the scope of this study are highlighted in bold. Bootstrap values > 70, obtained from 5000 iterations, are shown near the respective node. Scale bar represents 0.05 substitutions per site.

Distribution and habitat. NE Atlantic (Gulf of Cadiz), E Mediterranean, from 1694 to 4864 m depth, near cold seeps (Böttgeman et al., 2012; this study).

Remarks. *Glycera noelae* was recently described by Böttgeman et al. (2012) from cold seeps of the eastern Mediterranean, at 1694 m depth. This study extends the geographic and bathymetric distribution of the species to the Gulf of Cadiz and 4864 m depth, respectively. The specimens studied herein were also found on cold seep areas. *Glycera noelae* is morphologically similar to *G. capitata* Örsted, 1843 and *G. lapidum* Quatrefages 1866, differing mainly by the presence of transversal ridges on the pharynx papillae.

***Glycera tessellata* Grube, 1863.**

Glycera tessellata Grube, 1863: 41, pl. 4, Fig. 4A.

Material examined. **Atlantic Ocean. Bay of Biscay:** Cap Breton Area, M84-5_633, 221 m, 6 spms; St M84-5_678, 215 m, 2 spms; St M84-5_679, 216 m, 1 spm (cf.) (DBUA0001810.01-03). **W Iberian Margin:** Fontanelas, St TTR17-2_AT691, 1308-1460 m, 1 spm (DBUA0001811.01); **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 116-2003 m (exact depth unknown), 2 spms (DBUA0001812.01); **Gulf of Cadiz:** Ginsburg MV, St TTR16_AT607, 983 m, 4 spms (DBUA0001813.01); Darwin MV, St TTR16_AT608, 1115 m, 1 spm (DBUA0001813.02); St TTR17-2_AT664, 1128 m, 3 spms (DBUA0001811.02); St B09-14b_02, 1100 m, 1 spm (DBUA0001814.01.v01); Captain Arutyunov MV, St MSM01-3_225, 1320 m, 2 spms; St MSM01-3_274, 1321 m, 1 spm (DBUA0001815.01-02); Sagres MV, St TTR17-2_AT667, 1562 m, 1 spm (DBUA0001811.03); Semenovich MV, St TTR17-2_AT679, 3265 m, 1 spm (DBUA0001811.04).

Distribution and habitat. Atlantic (from Faroes to West Africa; from North Carolina to Brazil), Mediterranean Sea, Red Sea, Indian (Madagascar), Pacific (Hawaiian, Mariana and Marshall Islands; from Japan to Lizard Island), from 0.5 to 4476 m depth (Böttgeman, 2002, 2015, 2016; Kirkegaard, 1998; Magalhães and Rizzo, 2012), in various habitat settings including fossil cold-water corals and sediments influenced by mild to active seepage (this study).

Remarks. *Glycera tessellata* was originally described from the Mediterranean Sea at waters deeper than 300 m, where it was considered to be more common than in the Atlantic Ocean (O'Connor, 1987). Although its distribution extends to the Faroes, this species is considered to be typical of warmer waters (Kirkegaard, 1998). In the present study, *G. tessellata* was only found in Atlantic waters from the Bay of Biscay to the Gulf of Cadiz. This species has also been recorded from the West Atlantic and the Indian and Pacific Oceans. However, this wide distribution should be considered with caution. In a recent record from South Brazil Rizzo et al. (2007) denoted a small morphological difference at the insertion of the dorsal cirri on their specimens (at the base of the parapodia instead of far from it). Such differences may be found in other specimens from localities far from the type and should be carefully investigated.

***Glycera unicornis* Savigny in Lamarck, 1818.**

Glycera unicornis Savigny in Lamarck, 1818: 315, pl. 14, Figs. 1-4; *Glycera rouxii* Audouin and Milne Edwards, 1833: 264.

Material examined. **Atlantic Ocean. Gulf of Cadiz:** Al Idrisi MV, St 64PE253_46B, 227 m, 1 spm (cf.) (DBUA0001816.01); Mercator MV, St TTR12_AT409, 375 m, 1 spm (DBUA0000666.01); St TTR12_AT410, 392 m, 1 spm (DBUA0000666.01); St TTR15_AT575, 355 m, 1 spm (DBUA0001817.01).

Distribution and habitat. E Atlantic (from Norway to South Africa), Mediterranean Sea, W Indian, E Pacific (Peru), from 10 to 4380 m depth (Böttgeman, 2002; Kirkegaard, 1998).

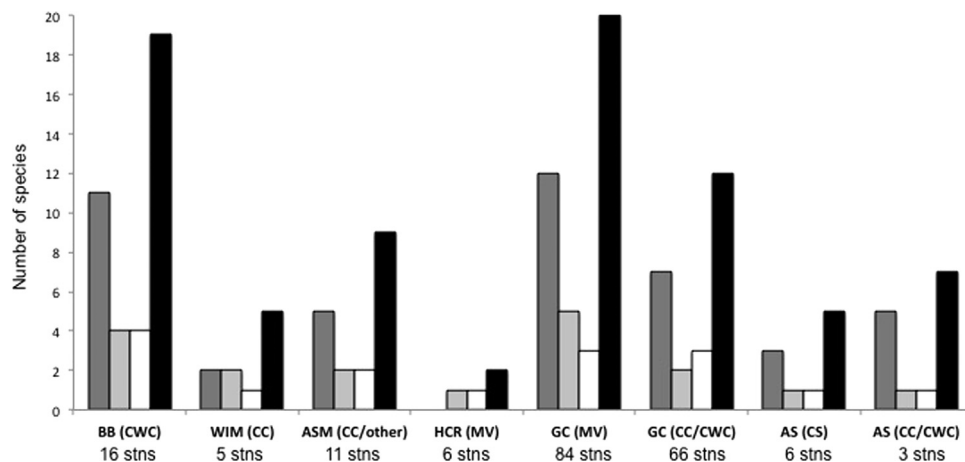


Fig. 7. Species richness for each suborder within the studied areas. Bars: dark grey – Aphroditiformia, light grey – Glyceriformia, white – Phyllodociformia, black – total. Areas: BB – Bay of Biscay, WIM – W Iberian Margin, ASM – Atlantic Seamounts, HCR – Horseshoe Continental Rise, GC – Gulf of Cadiz, AS – Alboran Sea. Habitat: CC – carbonate crusts, CWC – cold-water corals, MV – mud volcanoes.

Remarks. The type locality of *Glycera unicornis* is not referred in the original description, but the species is known to have a large geographic distribution in the Atlantic Ocean, extending from Norway to South Africa (including the Mediterranean). Herein it is reported from sediments influenced by mild seepage in the Gulf of Cadiz. Its presence in the Indian and Pacific Oceans should be considered with caution and further investigated. *Glycera rouxii* Audouin and Milne Edwards, 1833, originally described from the Mediterranean at depths lower than 200 m, was recently considered as a synonym of *G. unicornis* (Böttgermann, 2002).

Genus *Glycerella* Arwidsson, 1899.

Glycerella magellanica (McIntosh, 1885).

Hemipodus magellanicus McIntosh, 1885: 349, pl. XLII, Figs. 11–15; pl. XXIIa, Figs. 12–15; pl. XXXVa, Figs. 5, 7; *Glycerella magellanica* Arwidsson, 1899: 26, pl. II, Fig. 22; pl. III, Fig. 52–53, pl. IV, Fig. 57; *Glycerella atlantica* Wesenberg-Lund, 1950: 24, pl. V, Fig. 22; pl. VI, Fig. 28.

Material examined. Atlantic Ocean. Azores: Atlantis Seamount, St TTR12_AT421, 555–614 m, 2 spms; St TTR12_AT422, 375 m, 1 spm (DBUA0001550.01–02); **W Iberian Margin:** Fontanelas, St TTR17-2_AT689, 1194–1250 m, 1 spm; St TTR17-2_AT693, 1110–1270 m, 1 spm (DBUA0001818.01–02); **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 116–2003 m (exact depth unknown), 1 spm; St NA017_034, 1140 m, 1 spm (DBUA0001819.01–02). **Coral Patch Seamount,** St 64PE284_12767#05, 666 m, 1 spm (DBUA0001820.01); **Gulf of Cadiz:** Formosa Ridge, St TTR12_AT388, 1079 m, 1 spm (DBUA0000665.01); Pen Duick Escarpment, St TTR12_AT406, 550 m, 1 spm (DBUA0000665.02); St 64PE268_51, ~740 m, 1 spm (DBUA0001821.01); Central Carbonate Mound Province, St 64PE284_12729, 754 m, 1 spm (DBUA0001820.02); Mercator MV, St JC10_018-Rock5, 373 m, 8 spms; St JC10_018-Rock7, 381 m, 1 spm (DBUA0001822.01–02); TTR MV, St TTR12_AT416, unknown depth, 2 spms (DBUA0000665.03).

Distribution and habitat. N Atlantic (Iceland, Ireland, Azores, W Iberian margin, Gorringe Bank, Gulf of Cadiz), Pacific (Chile; Japan, Lizard Island), Antarctic, sublittoral from 45 to 1960 m depth (Böttgermann, 2015; Parapar and Moreira, 2009b).

Remarks. *Glycerella magellanica* was originally described by McIntosh (1885) from the Strait of Magellan in the Chilean margin and was recorded for the first time in the N Atlantic by Fauvel (1913, 1914a), for the Azores Islands. Later, Wesenberg-Lund (1950) described a new species, *G. atlantica*, from Icelandic waters, that was also recorded by Amoureux (1982) from Irish

waters. Detinova (1985) recorded again *G. magellanica* in Icelandic waters and considered *G. atlantica sensu Amoureux (1982)* as a synonym of *G. magellanica*, but did not refer the original description by Wesenberg-Lund (1950). Böttgermann (2002) and Parapar and Moreira (2009a) examined the type material of both *G. magellanica* and *G. atlantica*, and found no significant morphological differences that could justify the distinction of the two species. However, considering its very wide distribution, we agree with Parapar and Moreira (2009b) that in the future, with the use of other morphological characters and molecular tools, this species may reveal to be a complex of species.

Family Goniadidae Kinberg, 1866.

Genus *Glycinde* Müller, 1858.

Glycinde nordmanni (Malmgren, 1866).

Eone Nordmanni Malmgren, 1866: 409; *Goniada oculata* Treadwell, 1901: 201, Figs. 50–53; *Eone longepapillata* Voit, 1911: 114, Figs. 11, 12; *Glycinde nordmanni* Helgason et al., 1990: 209.

Material examined. Atlantic Ocean. Bay of Biscay: Cap Breton Area, St M84-5_677, 214 m, 1 spm; St M84-5_678, 215 m, 1 spm; St M84-5_679, 216 m, 2 spms (DBUA0001823.01–03).

Distribution and habitat. Atlantic (from Iceland and Norway to NW Africa; from North Carolina to Brazil), Mediterranean Sea, from 9 to 470 m depth (Böttgermann, 2005).

Remarks. Up to date, *G. nordmanni* is the only *Glycinde* species recorded for the N Atlantic. The specimens studied herein match the description of this species with the possible exception of the pharynx papillae, which could not be observed. Amoureux (1982) recorded specimens from depths to 1400 m, although such deep records were never confirmed afterwards.

Genus *Goniada* Audouin and Milne Edwards, 1833.

Goniada vorax (Kinberg, 1866).

Leonnatus vorax Kinberg, 1866: 247; *Goniada pallida* Arwidsson, 1899: 43, pl. II, Figs. 35–39; *Goniada distorta* Moore, 1903: 461, pl. XXVI, Fig. 77; *Goniada maorica* Benham, 1932: 555, Figs. 1–5; *Goniada sagamiana* Imajima, 2003 p. 121, Figs. 72–74.

Material examined. Atlantic Ocean. Bay of Biscay: Cap Breton Area, St M84-5_678, 215 m, 1 spm (DBUA0001824.01).

Distribution and habitat. Atlantic (from Norway to SW Portugal; from North Carolina to Brazil), Mediterranean Sea, Indian Ocean, W Pacific (Indonesia, New Zealand), from 7 to 512 m depth (Böttgermann, 2005).

Family Phyllodocidae Örsted, 1843a.

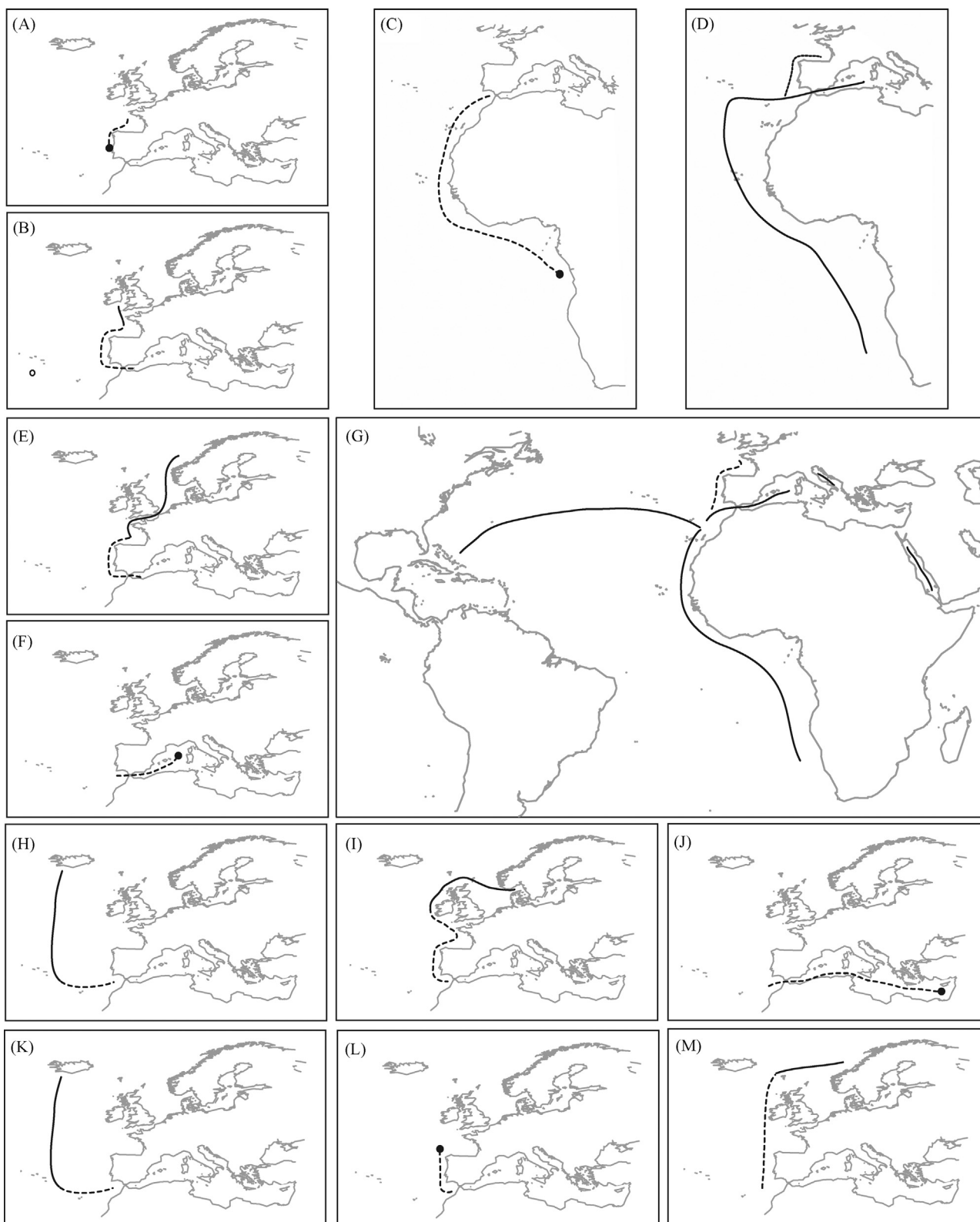


Fig. 8. Geographic distribution of the species: A - *Allmaniella setubalensis*, B - *Harmothoe evei*, C - *Anotochaetoneo michelbaudi*, D - *Lepidasthenia brunnea*, E - *Leucia violacea*, F - *Macelicephalla laubieri*, G - *Pholoides dorsipapillatus*, H - *Leanira hystericis*, I - *Sthenelais jeffreysi*, J - *Glycera noelae*, K - *Glycerella magellanica*, L - *Eumida longicirrata*, M - *Protomystides exigua*. Full line - previously known distribution, dash line - distribution extension.

Genus *Eulalia* Savigny in Lamarck, 1818.

***Eulalia* spp.**

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_649, 1105 m, 2 incompl. spms (DBUA0001825.01); Cap Breton Area, St M84-5_677, 214 m, 1 spm (DBUA0001825.

02); **Pagès**, St M84-5_602, 594 m, 1 spm (DBUA0001825.03). **W Iberian Margin:** Fontanelas, St TTR17-2_AT690, 1340–1498 m, 1 spm (DBUA0001826.01). **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 116–2003 m (exact depth unknown), 1 incompl. spm (DBUA0001827.01). **Gulf of Cadiz:** Mercator MV, St

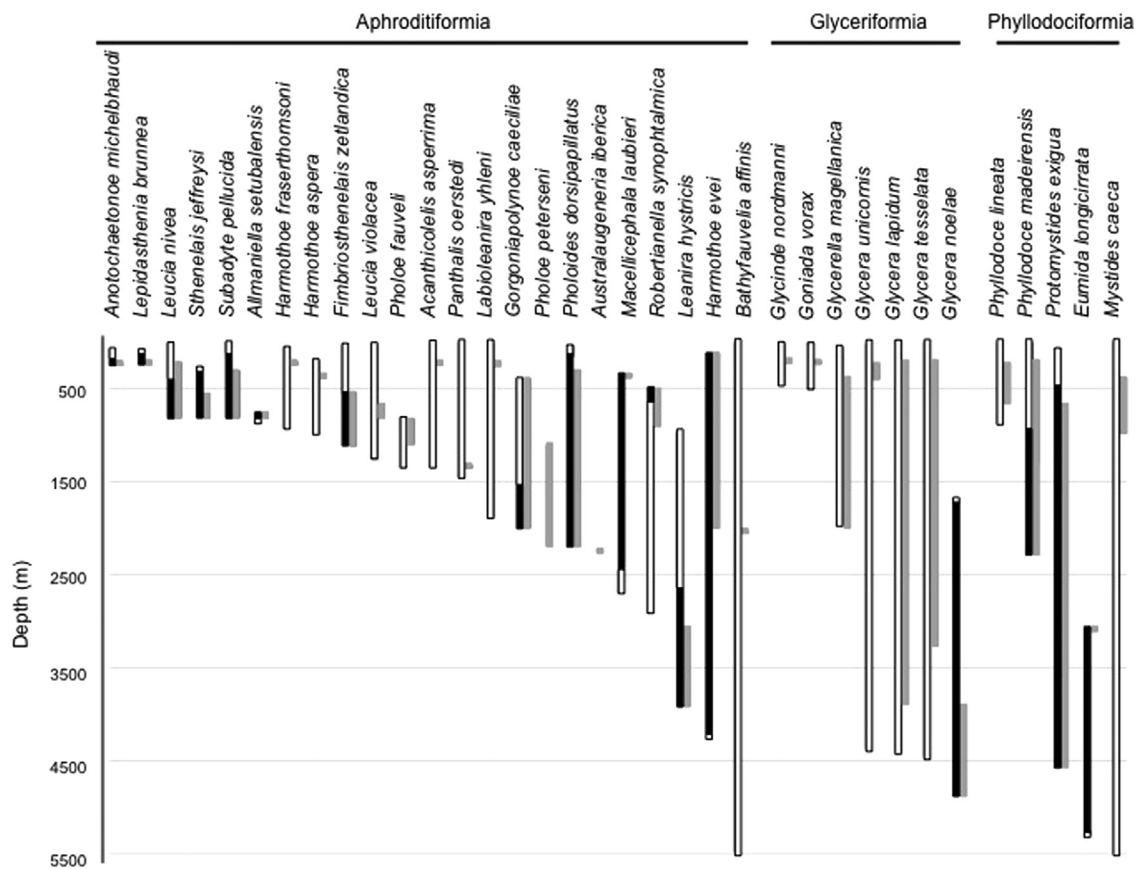


Fig. 9. Bathymetric distribution of the recorded species. White bar – previously known distribution, grey bar – distribution recorded in this studied, black bar – distribution extension.

TTR15_AT575, 355 m, 2 incompl. spm (cf.) (DBUA0001828.01); Captain Arutyunov MV, St MSM01-3_195, 1390 m, 1 incompl. Spm (DBUA0001829.01); Carlos Ribeiro MV, St TTR16_AT618, 2220 m, 1 incompl. spm (cf.) (DBUA0001830.01).

Remarks. The distinction between *Eulalia* species is frequently based on pigmentation patterns that are lost after fixation of the specimens. This factor together with the lack of relevant recent taxonomic studies on the group limited the identification of the specimens examined. However, its morphology denotes the presence of four potentially different species, one of which (from the Gulf of Cadiz) appears to be close to *E. meteorensis* Böggemann, 2009, described for the Gulf of Guinea at 5137–5141 m depth. There are several *Eulalia* species previously recorded in or nearby the studied region for which the descriptions could not be verified due to the animal conditions or because it was not possible to find bibliography.

Genus *Eumida* Malmgren, 1865.

Eumida longicirrata Hartmann-Schröder, 1975.

Eumida (*Eumida*) *longicirrata* Hartmann-Schröder, 1975: 55, Figs. 16–18.

Material examined. Atlantic Ocean. Gulf of Cadiz: Bonjardim MV, St TTR17-2_AT678, 3060 m, 1 compl. spm (DBUA0001831.01).

Distribution and habitat. NE Atlantic (Iberian basin, Gulf of Cadiz), from 3060 to 5260 m depth (Alós et al., 2004; Eibye-Jacobsen, 1991; this study).

Remarks. *Eumida longicirrata* differs from other species of the genus by the absence of eyes and the presence of slightly raised semi-circular structures near the posterior corners of the prostomium (Eibye-Jacobsen, 1991). The specimen examined herein also presents these characteristics along with all other features of the species, although the raised structures on the prostomium were

difficult to verify with certainty. Two other species, *E. alvini* Eibye-Jacobsen, 1991 from NW Atlantic (1830–3995 m depth) and *E. nuchala* (Uschakov, 1972) from NE Pacific (abyssal), lack eyes as well as the semicircular structures. However, both species differ from *E. longicirrata* and from the specimen examined herein, by the position of the median antennae, the shape of the dorsal cirri and the length of the chaetae. *Eumida longicirrata* is only known from its type locality, the NW Iberian margin (45°55.4'N, 14°07.9'W), at 5260 m depth. The present record extends the geographical distribution of this species to the Gulf of Cadiz and its shallower depth limit to 3060 m.

Genus *Mystides* Théel, 1879.

Mystides caeca Langerhans, 1880.

Mystides caeca Langerhans, 1880: 310, pl. 17, Fig. 42a–d; *Mystides* (*Mesomystides*) *borealis* Southern, 1914: 73, pl. VIII, Figs. 19A–D [not Théel, 1879].

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_651, 982 m, 2 spms (DBUA0001832.01). Azores: Atlantis Seamount, St TTR12_AT422, 375 m, 1 spm (DBUA0000696).

Distribution and habitat. E Atlantic (from Skagerrak to Cape Basin), in mud, sand, shell gravel and rocky bottoms (Böggemann, 2009; Pleijel and Dales, 1991). In the European margin the deepest record is 400 m (Pleijel and Dales, 1991) but in the African margin the bathymetric distribution extends to 5496 m (Böggemann, 2009).

Remarks. *Mystides caeca* was first described from Madeira. This species is morphologically very similar to *M. borealis* Théel, 1879, originally described from Novaya Zemlya, in the Arctic Ocean, and both have a close European geographical and bathymetrical distribution. The two species differ mainly by the presence of eyes on *M. borealis*, which are absent on *M. caeca*. The recent records of *M. caeca* for Guinea, Angola and Cape basins, at depths between

5048 and 5496 m (Böggemann, 2009), greatly extended the distribution of this species. However, this wide distribution should be considered with caution and be confirmed with further studies on the South African and North European specimens.

Genus *Notophyllum* Örsted, 1843a.

Notophyllum sp.

Material examined. Atlantic Ocean. Gulf of Cadiz: Formosa Ridge, St TTR12_AT388, 1079 m, 1 incompl. spm (DBUA0000668).

Remarks. The only specimen examined is incomplete and lacks all dorsal cirri. Nevertheless, the presence of very large rounded eyes, median antenna (broken) inserted between the eyes, nuchal epaulettes with two lobes at the tip, first segment reduced, parapodia biramous with clearly visible notoacacula and large dorsal cirrophores, unequivocally places this specimen within the genus *Notophyllum*. *Notophyllum foliosum*, originally described from Norway, has been the most commonly recorded *Notophyllum* for the NE Atlantic and Mediterranean Sea, from depths of 10–1280 m (Kato and Pleijel, 2002). However, Nygren et al. (2010) re-examined the type material of *N. foliosum*, along with new material from Norway and Sweden, and distinguish the shallower forms (20–125 m depth) from the deeper ones (101–350 m depth), based on different colour patterns and molecular evidence, describing the deeper form as *N. crypticum*. Furthermore, those authors considered as questionable the possible synonymy between those two species and *N. alatum* Langerhans, 1880 or *N. frontale* Langerhans, 1880, both originally described from Madeira Island, as previously established by Kato and Pleijel (2002). Therefore, all records of *N. foliosum* from S Europe need to be revised, along with the type material of *N. alatum* and *N. frontale*, if existing, or fresh topotype material. Since the morphologic distinction between phyllodocid congeneric species is frequently based exclusively on colour patterns (e.g. Nygren et al., 2009, 2010), molecular analyses of the specimens should be done whenever possible.

Genus *Phyllodoce* Savigny in Lamarck, 1818.

Phyllodoce lineata (Claparède, 1870).

Anaitides lineata Claparède, 1870: 94, pl. IX, Fig. 4; *Phyllodoce callirhynchus* Michaelsen, 1897: 33 pl. I, Figs. 14,15; *Phyllodoce papulosa* Saint-Joseph, 1898: 320, pl. XVIII, Figs. 117-121; *Phyllodoce lineata* Fauvel, 1923: 147, Fig. 51.

Material examined. Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_649, 1103 m, 1 incompl. spm (cf.); St M84-5_651, 982 m, 1 incompl. spm (cf.) (DBUA0001834.01-02); Pagès, St M84-5_600, 666 m, 1 spm; St M84-5_602, 594 m, 1 spm (DBUA0001834.03-04). **Gulf of Cadiz:** Pen Duick Escarpment, St 64PE268_46, ~720 m, 1 incompl. spm (cf.) (DBUA0001835.01); Mound B, St 64PE268_11 A, 489 m, 1 incompl. spm (cf.); St 64PE268_13B, 493 m, 1 incompl. spm (cf.) (DBUA0001835.02-03); Al Idrisi MV, St 64PE253_46B, 227 m, 1 incompl. spm (DBUA0001836.01); Gemini MV, St 64PE268_19, 430 m, 2 incompl. spms (cf.) (DBUA0001835.04); Anastasia Area, St 64PE284_12705, 525 m, 1 incompl. spm (cf.); St 64PE284_12706, 702 m, 1 incompl. spm (cf.) (DBUA0001837.01-02).

Distribution and habitat. NE Atlantic (from North Sea to Gibraltar Strait), Mediterranean Sea (Adriatic Sea), sublittoral to 900 m depth, in muddy sediments (Alós et al., 2004; Pleijel and Dales, 1991) and associated with fossil cold-water corals (this study).

Remarks. A total of 12 specimens were examined from Bay of Biscay and Gulf of Cadiz. The majority of the specimens is very small and lack dorsal cirri, and the pharynx is not everted. Therefore, the diagnostic characteristics of the species were only fully confirmed with certainty in a few specimens. The deepest location recorded herein was in the St. Nazaire canyon, at 1103 m

depth. However, the specimen could not be accurately identified and thus the known bathymetric distribution is maintained (900 m; Alós et al., 2004).

Phyllodoce madeirensis complex.

***Phyllodoce (Anaitis) madeirensis* Langerhans, 1880:** 307, pl. XVII, Figs. 44.

Material examined: Atlantic Ocean. Bay of Biscay: St. Nazaire Canyon, St M84-5_643, 825 m, 7 spms; St M84-5_644, 820 m, 4 spms; St M84-5_649, 1105 m, 1 spm; St M84-5_651, 982 m, 1 spm; St M84-5_653, 753 m, 1 spm; St M84-5_687, 537 m 3 spms; St M84-5_688, 667 m, 2 spms; St M84-5_689, 752 m, 1 spm; St M84-5_690, 755 m, 2 spms (DBUA0001854.01-09); Cap Breton Area, St M84-5_633, 221 m, 3 spms; St M84-5_677, 214 m, 5 incompl. spms (DBUA0001854.10-11); St M84-5_678, 215 m, 10 spms (DBUA0001854.12, 1 DNA voucher); St M84-5_679, 216 m, 1 spm (DBUA0001854.13); Pagès Area, St M84-5_619, 813 m, 1 compl. spm (DBUA0001854.14). **W Iberian Margin,** Fontanelas, St TTR17-2_AT692, 1230–1450 m, 1 spm (DBUA0001856.01); **Gorringe Bank:** Gettysburg Seamount, St NA017_H1202, 2285 m, 1 incompl. spm; St NA017_018, 1308 m, 1 incompl. spm; St NA017_H1203, 385 m, 1 incompl. spm (DBUA0001857.01-03). **Gulf of Cadiz:** Guadalquivir Ridge, St TTR11_AT339, 1021–1086 m, 1 spm (DBUA0000568); Formosa Ridge, St TTR12_AT388, 1079 m, 10 spms (DBUA0000669); W of Gibraltar Strait, St TTR14_AT550, 368–392 m, 5 incompl. spms (DBUA0001858.01, 2 DNA vouchers); St TTR14_AT552, 428 m, 2 incompl. spms (DBUA0001858.01.02); Moroccan Margin, St TTR17-2_AT654, 395 m, 1 incompl. spm (DBUA0001856.02); Pen Duick Escarpment, St 64PE237_16 A, 660 m, 1 incompl. spm; St 64PE237_30 A, 556 m, 1 spm; St 64PE237_31, 559 m, 1 spm (DBUA0001861.01-03); St 64PE268_39, 441 m, 1 incompl. spm; St 64PE268_40, 473 m, 1 spm; St 64PE268_46, ~720 m, 1 incompl. spm; St 64PE268_50, 740 m, 1 spm; St 64PE268_55, ~700 m, 1 incompl. spm (DBUA0001862.01-05); Mound B, St 64PE268_24, 495 m, 1 incompl. spm; St 64PE268_26, 485 m, 1 incompl. spm; St 64PE268_27, 471 m, 1 incompl. spm (DBUA0001862.06-08); Al Idrisi MV, St 64PE253_46B, 227 m, 1 incompl. spm (DBUA0001863.01); Mercator MV, St TTR15_AT569, 358 m, 1 incompl. spm; St TTR15_AT575, 355 m, 2 incompl. spms; St TTR15_AT576, 428 m, 1 incompl. spm (DBUA0001859.01-03); St MSM01-3_237.2, 353 m, 1 incompl. spm; St MSM01-3_241, 353 m, 2 spms (DBUA0001860.01-02); St 64PE253_48, 376 m, 1 incompl. spm (DBUA0001863.02); St JC10_018-Rock1, 428 m, 1 incompl. spm; St JC10_018-Rock5, 373 m, 1 incompl. spm (DBUA0001866.01-02); St 64PE284_12750, 354 m, 2 spms (DBUA0001864.01, 1 DNA voucher); Fiuza MV, St TTR14_AT566, 414 m, 3 incompl. spms (DBUA0001858.03); Gemini MV, St 64PE253_08, 444 m, 2 incompl. spms; St 64PE253_10, 432 m, 1 incompl. spm; St 64PE253_11, 438 m, 1 incompl. spm; St 64PE253_18, 608 m, 1 spm (DBUA0001863.03-06); Kidd MV, St TTR14_AT559, 552 m, 3 incompl. spms; St TTR14_AT561, 526 m, 1 incompl. spm (DBUA0001858.04-05); Anastasia Area, St 64PE284_12706, 702 m, 1 incompl. spm (DBUA0001864.02); Lazarillo MV, St 64PE237_20, 516 m, 1 spm; St 64PE237_21, 498 m, 1 incompl. spm (DBUA0001861.04-05); St 64PE253_38B, 497 m, 1 incompl. spm (DBUA0001863.07); Mekkès MV, St MSM01-3_319, 695 m, 1 incompl. spm; St MSM01-3_321, 732 m, 1 incompl. spm; St MSM01-3_335, 703 m, 4 incompl. spms (DBUA0001860.03-05); St B09-14b_03, 698 m, 1 spm (DBUA0001865.01). **Mediterranean Sea. Alboran Sea:** Dakha MV, St TTR17-1_MS413, 377 m, 1 spm (DBUA0001855.01); Melilla Coral Mound Field, St TTR17-1_MS392, 246 m, 1 compl. spm (DBUA0001855.02).

Remarks. A total of 113 specimens morphologically similar to *Phyllodoce madeirensis* Langerhans, 1880 were examined within this study, although for some of them the characteristics of the species could not be fully confirmed (approximately 40 specimens were small, incomplete or damaged). The single median row of

papillae in the proximal part of the pharynx, one of the diagnostic features of this species, could only be examined with certainty on the larger specimens. Despite a few subtle variations on body and dorsal cirri shape and proportions, all these specimens are morphologically very similar and no reasons were found to consider them as a different species. However, the molecular analysis performed in this study (see Section 3.2) indicates the presence of three different lineages, suggesting the existence of three putative cryptic species. Further research is needed in order to clarify this situation. *Phyllodoce madeirensis* was originally described from Madeira Island and has been recorded in temperate and tropical waters around the world, from sublittoral depths to 950 m, in various sediment types and hard substrata (Alós et al., 2004; Muir and Hossain, 2014). The records herein further extend the bathymetric distribution to 1308 m depth. This wide range of geographic and bathymetric distribution should be considered with caution and also need further investigation.

Genus *Protomystides* Czerniavsky, 1882.

Protomystides exigua (Eliason, 1962).

Pseudoeulalia exigua Eliason, 1962: 232, Fig. 7.

Material examined. Atlantic Ocean. Bay of Biscay: Pagès Area, St M84-5-600, 666 m, 1 incompl. spm (DBUA0001867.01).

Horseshoe Continental Rise: Abzu MV, St M86-5-349, 4560 m 1 spm; St M86-5-369, 4550 m, 1 spm (DBUA0001868.01-02).

Distribution and habitat. NE Atlantic (from Norway to Horseshoe Continental Rise), from 75 to 4560 m depth, in muddy sediments (Pleijel and Dales, 1991; this study).

Remarks. The specimens reported herein extend the geographic distribution of the species to the Horseshoe Continental Rise and its deeper limit to 4560 m (previously at 460 m, Pleijel and Dales, 1991).

3.2. Molecular analyses

Amplification and sequencing of the COI barcode region was possible for 20 specimens belonging to 10 of the phyllocid taxa studied herein (Table S2). In some cases, the lack of success in obtaining COI sequences prevented species-level determination (*Notophylum* sp.) or the distinction between multiple species within one genus (*Eulalia* spp.). The final molecular data set (BOLD DS-POLYGEN) including published data from other sources comprises 62 species and 108 sequences (Table S2). COI barcode sequences obtained in our study were, in general, taxonomically congruent with publicly available data (Fig. 6).

Each of the species for which we generated new sequences emerged in clearly separated branches of the ML tree (Fig. 6), and were assigned to exclusive BINs in BOLD (Table S2), including the species with specimens from different localities (*Lepidasthenia brunnea* from Bay of Biscay and Alboran Sea and *Leucia violacea* from Gulf of Cadiz and Alboran Sea). The only exceptions are the specimens ascribed to *Phyllodoce madeirensis*, which were distributed in three lineages with relatively high divergence (4.9–14.5%), and were assigned to three different BINs in BOLD. Notably, the two lineages with specimens from the Gulf of Cadiz (lineages L2 and L3 in Fig. 6) are closer to their congeneric *Phyllodoce medipapillata* than to their conspecifics from the Alboran Sea (lineage L1 in Fig. 6). These genetic distances between specimens of *P. madeirensis* are considerably higher than typical intraspecific distances reported for polychaetes (usually below 2%; Carr et al., 2011; Lobo et al., 2016), and similar to the average distances within the recently clarified species of the *Eumida sanguinea* complex (6.5–18.5%; Nygren and Pleijel, 2011) or within the *Harmotoe imbricata* complex (10–20%; Carr et al., 2011; Nygren et al., 2011). This result strongly suggests that *P. madeirensis* is in fact a complex of cryptic species, from which three are represented by the

sequences obtained herein. According to Fig. 6, *P. medipapillata* (Moore, 1909) may also be a part of this same complex. *Phyllodoce madeirensis* is known to have a very wide geographic and bathymetric distribution, occurring in all temperate waters around the world but the specimens examined herein, from two close localities in the Gulf of Cadiz and one in the Alboran Sea, suggest the existence of only subtle morphological variability (see Section 3.1). Some confusion has been reported between *P. madeirensis* and the closely related species *P. medipapillata*. However, published sequences of the latter species are very distinct from any of the *P. madeirensis* lineages included herein (13.1–15.1%).

Glycera lapidum is another taxon recurrently signalled as a putative species complex (see Section 3.1.). Regrettably, it was not possible to obtain sequences from our material and there are no published sequences of this taxon. Both *P. madeirensis* and *G. lapidum* must be further investigated preferably using integrated molecular and morphological approaches and covering a large set of specimens from various geographical and ecological contexts. Three other species included in this study, *Lepidasthenia brunnea*, *Glycerella magellanica* and *Mystides caeca*, have a wide geographic distribution and should also be further addressed (see Section 3.1.). New sequences for the two former species are included herein and may be used in future studies. Also some specimens of *Subadyte pellucida* and *Phyllodoce lineata* require further molecular analysis to confirm taxonomic identification.

From the comparison of our sequences with published ones, only one taxon (*Panthalis oerstedii*) had a species match with 99.5% similarity. Most of the remaining new sequences had nearest neighbours of the same genera (e.g. *Phyllodoce madeirensis*, *Glycera tessellata*, *Lepidasthenia brunnea*), or of the same family in the case of two species without matching genera in the dataset (*Leucia violacea*, *Glycerella magellanica*). However this was not the case for *Fimbriosthenelais zetlandica* (Sigalionidae) and *Subadyte pellucida* (Polynoidae), which appeared as nearest neighbours to members of the families Acoetidae and Pholoidae, respectively. These latter families are poorly represented in this dataset, with only 1 or 2 sequences from one genera each (*P. oerstedii* for Acoetidae, and *Pholoe baltica* and *Pholoe minuta* for Pholoidae). The poor taxonomic coverage of those families may help to explain, at least in part, the patterns observed. Nevertheless, addressing deeper phylogenetic relationships within Phyllocidida is beyond the scope of this study. It should also be noted that the species *F. zetlandica*, in particular, has been subjected to alternate re-assignments to the morphologically close genera *Fimbriosthenelais* and *Sthenelais* (see Section 3.1.). Further clarification of taxonomic and phylogenetic relationships in these taxa will likely require combined morphological and multi-locus molecular investigations and broader taxonomic coverage.

Among the sequences publicly available from BOLD and GenBank an obvious mismatch was observed in *Phyllodoce lineata* from north Atlantic Spain (reported by Aylagas et al., 2014; Table S2, Supplementary material), which appears embedded within two divergent lineages of *Goniada maculata* (Fig. 6). *Macellicephala violacea* (reported by Shields et al., 2013; Table S2, Supplementary material) also appears deeply divergent from all other Phyllocidida. In the absence of further information about these sequences, we may only conjecture that it may be due to possible specimen mislabeling or cross-contamination, without discarding other explanations.

Species-level discriminatory ability of COI sequences has been extensively demonstrated for polychaetes in general (Carr et al., 2011; Lobo et al., 2016) and is also patent in most phyllocid species in the analysed dataset. Indeed, COI sequences have been shown to perform well in species-level discrimination in most metazoans (Hebert et al., 2003; Radulovici et al., 2010; reviewed in Costa and Carvalho, 2010), but their ability for recovering higher

taxonomic ranks and deep phylogenetic relationships can be limited (Hajibabaei et al., 2006). In the dataset examined, few genera are fully resolved and the taxonomic recovery is particularly poor in some families (Polynoidae, Sigalionidae). The genetic distances within some genera are particularly high (*Glycera* 21%, *Sthenelais* 28%) compared to other genera in the dataset (e.g. *Eumida* 18%, *Eulalia* 17%), but they are within the average congeneric distances reported for other marine invertebrates (e.g. Borges et al., 2016; Costa et al., 2009; Matzen da Silva et al., 2011; Radulovici et al., 2010). The relatively high substitution rates in COI may mask deep phylogenies and preclude good resolution of taxonomic ranks higher than species. The fact that the amino-acid sequences (Fig. S1, Supplementary material) perform better at recovering monophyletic families supports this explanation. Other studies including combined morphological and multi-locus analyses of aphroditiform families have shown a better resolution, although suggesting a possible lack of monophyly in the family Sigalionidae, mainly because of the genera *Sthenelais* and *Sthenelanella* that cluster with the family Pholoidae (Wiklund et al., 2005; Norlinder et al., 2012). In our analysis, the spreading of four sequences by three different branches also points to a non-monophyletic condition of the genus *Sthenelais*. The high diversification and morphologic complexity of the aphroditiform taxa may also contribute for the poor resolution of genera and families. Several revisions of this group resulted in taxonomic re-assignments and erection of several new genera and species (e.g. Barnich and Fiege, 2000; Pettibone, 1970, 1971, 1976, 1989c). For a number of reasons, including inherent complexity of morphological characters and insufficient taxonomic work, polychaetes are much likely a group in which cryptic or hidden diversity will be increasingly revealed by molecular tools (Nygren, 2014), and even more among the poorly known deep-sea taxa.

4. Final remarks

A total of 1167 Phyllodocida specimens were examined and assigned to 36 species and one species complex, in 30 genera, and seven families, included in the suborders Aphroditiformia, Glyceriformia and Phyllodociformia. All the suborders were present in all the studied areas (except for the Aphroditiformia that were not found in the deeper mud volcanoes of the Horseshoe continental rise, Fig. 7). Although a comparison between the studied areas is impaired by differences in the sampling effort, the number of phyllodocid species recovered from the three locations in the Bay of Biscay (depth range 214–1105 m) is remarkable: 19 species in 16 stations, a number much higher than the 12 species in 66 stations from similar settings (cold-water corals) in the Gulf of Cadiz, and matching the value of the group with the highest sampling effort and depth range (20 species collected from 84 stations from mud volcanoes in the Gulf of Cadiz; 227–3890 m).

Aphroditiformia, the most speciose suborder, was represented by 24 species, mainly in the family Polynoidae (16 species). Many species in this family (e.g. *Acanthicolepis asperrima*, *Australaugeneria iberica*, *Gorgoniapolynoe caeciliae*, *Harmothoe aspera*, *H. fraserthomsoni*, *Leucia nivea*, *L. violacea*, *Robertianella synophthalmica*, *Subadyte pellucida*) typically occur as commensals, mainly with gorgonian or stylasterid corals, but also with sponges, echinoderms and crinoids. Not surprisingly, species of Aphroditiformia were commonly found in cold-water coral habitats (up to 11 species in the Bay of Biscay samples, Fig. 7) but many species were also collected from the mud volcanoes in the Gulf of Cadiz where some were very frequent and widespread (*Harmothoe evei*, *S. pellucida*, *Pholoides dorsipapillatus*). From a total of seven Glyceriformia species, four were assigned to the genus *Glycera*. This genus was particularly common in the mud volcanoes from the

Gulf of Cadiz, where all four species occurred, and some were often sympatric. The Phyllodociformia were represented by seven taxa from which four were determined to species level. From the other three taxa, *Eulalia* spp. includes potentially four different species not possible to determine within the frame of this study, and *Phyllodoce madeirensis* represents a complex of an undetermined number of species.

Relevant taxonomical remarks are provided for seventeen species. Also included are amended descriptions and new illustrations for *Allmaniella setubalensis* and *Anotochaetoneo michelbhaudi*, the description and illustrations of *Polynoe* specimens not ascribed to any species, and new illustrations for *Lepidasthenia brunnea*. Twenty new sequences were obtained for *Panthalis oerstedii* (Acoetidae), *Fimbriosthenelais zetlandica* (Sigalionidae), *Harmothoe* sp. 1, *Lepidasthenia brunnea*, *L. violacea*, Polynoidae undet. and *S. pellucida* (Polynoidae), *Glycera tessellata* and *Glycerella magellanica* (Glyceridae), and for three lineages within the *P. madeirensis* complex (Phyllodocidae). Although it would be desirable to obtain further molecular data for full comparison and cross-validation of the taxa examined herein, the new DNA barcodes, obtained from carefully identified specimens, constitute a robust molecular reference tag for future taxonomical studies.

Two species, *Australaugeneria iberica* and *Pholoe petersenae* (Ravara and Cunha, 2016), were recently described upon the material included in this study. The remaining examined species had been previously recorded in Europe or NW Africa with their northern limit at Bay of Biscay (7 species), British Isles (7), Norway (12) and the Arctic (3) and the southern limit at the Gulf of Cadiz or NW Africa. Five of the species are also reported for South Africa, although these records need confirmation and should therefore be considered with caution. Noteworthy are the record of species previously known only from their original description and type locality: *A. setubalensis*, known from the W Portuguese margin (McIntosh, 1885) is reported here from cold water corals in the Bay of Biscay; *A. michelbhaudi*, found inside chaetopterid tubes in oil fields (Britayev and Martin, 2005) is reported here in a similar ecological setting from a mud volcano in the Gulf of Cadiz; *H. evei*, known from abyssal depths southwest of British Isles is reported here from the Bay of Biscay, the Atlantis seamount, the Goringe Bank, the Gulf of Cadiz and the Alboran Sea; finally *Glycera noelae*, recently described from cold seeps in the E Mediterranean (Böggemann et al., 2012), and *Eumida longicirrata*, known from abyssal depths off the W Iberian margin (Hartmann-Schröder, 1975), were found in several deep-water mud volcanoes in the Gulf of Cadiz. Besides these new records, our study extends the known geographic distribution for nine other species (Fig. 8).

Fig. 9 summarises literature data on the bathymetric distribution of the examined species. Five species are restricted to depths shallower than 500 m (*A. michelbhaudi*, *L. brunnea*, *H. fraserthomsoni*, *Glycinde nordmanni*, *Goniada vorax*). The species *Allmaniella setubalensis*, *Robertianella synophthalmica*, *Pholoe fauveli*, *P. petersenae*, *Leanira hystricis*, *A. iberica*, *G. noelae*, *E. longicirrata* occur only deeper than 500 m and, from these eight species, the latter three are restricted to depths greater than 1500 m. With few exceptions, narrower distributions are from rare or poorly known species and, in fact, most examined species are known to occur over a wide bathymetric range from shelf to bathyal and abyssal depths. Nevertheless, our study extends the known depth range of fifteen species (Fig. 9), four to shallower limits and eleven to deeper limits. Noteworthy, are the cases of *Protomystides exigua*, *Pholoides dorsipapillatus* and *H. evei*, whose bathymetric range is greatly extended. Except for *P. exigua* and together with *Glycera lapidum* these are the three most common species in our dataset (over 100 specimens examined) and were found in different habitats and in all studied areas. In contrast, 18 out of the 36 species examined occurred at one locality only, and were usually

represented by less than five specimens. Overall, our results reveal the current poor knowledge on the deep-sea fauna, underpin the need for more comprehensive studies, and reinforce the importance of integrating morphological and molecular tools in modern taxonomy.

Author's contributions

MC was responsible for the collection of the biological material and the coordination of the work. AR examined the material, obtained part of the DNA sequences, and prepared descriptions and figures. DR compiled information on synonymies and ecology of the species recorded. MT and FC were responsible for the sequence compilation and molecular analysis. AR, FC and MC prepared the manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2016.08.008>.

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