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Polychaetes (Annelida) of the abyssal SE Atlantic

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Abstract

The DIVA-1 (2000), DIVA-2 (2005) and BIOZAIRE (2001, 2003) expeditions to abyssal zones of three ocean basins (Angola, Cape and Guinea) in the SE Atlantic have yielded more than 23,000 specimens or fragments of Polychaeta. Most of the thirteen collecting areas were sampled with an Agassiz trawl, an epibenthic sledge and repeated box corer and multicorer hauls at depths between 3945 and 5672 m. Among the 47 families found, the best-represented were Acrocirridae, Ampharetidae, Chrysopetalidae, Cirratulidae, Hesionidae, Paraonidae, Spionidae and Sabellidae, whereas Alciopidae, Aphroditidae, Cossuridae, Pholoidae, Sternaspidae, Tomopteridae and Typhloscolecidae were rarely found. The present work generally deals with the taxa in Phyllodocida; the remaining groups are planned to be treated in future publications. The material was examined for morphological and partially for molecular characters (18S rDNA, 16S rDNA, COI, ITS1, ITS2); phylogenetic reconstructions were performed using maximum likelihood and parsimony.

The following new taxa and names and other changes to nomenclature are proposed. Family Amphinomidae: *Bathychloeia balloniformis* sp. nov.; Chrysopetalidae: *Dysponetus hesionides* sp. nov., *Dysponetus profundus* sp. nov., *Pseudodysponetus fragmentosus* gen. et sp. nov.; Glyceridae: *Glycera diva* sp. nov., *Glycera southeastatlantica* sp. nov.; Hesionidae: *Gyptis incisa* sp. nov., *Nereimyra auripalpa* sp. nov., *Sirsoe hessleri* (Blake, 1991) comb. nov.; Lacydoniidae: *Lacydonia elongata* Hartmann-Schröder & Rosenfeldt, 1992 syn. nov. of *L. papillata* Uschakov, 1958; Nereididae: *Profundilycastis* Hartmann-Schröder, 1977 syn. nov. of *Rullierinereis* Pettibone, 1971, *Ruillerinereis profundus* (Hartman, 1965) comb. nov.; Phyllodocidae: *Eulalia meteorensis* sp. nov., *Eumida angolensis* sp. nov., *Pseudomystides bathysiphonicola* (Hartmann-Schröder, 1983) comb. nov., *Pseudomystides brevicirra* sp. nov., *Pseudomystides rarica* (Uschakov, 1958) comb. nov., *Pterocirrus remus* sp. nov.; Sphaerodoridae: *Sphaerephesia regularis* sp. nov., *Sphaerodoropsis longianalpapilla* sp. nov., *Sphaerodoropsis macrotubercula* sp. nov., *Sphaerodoropsis protuberanca* sp. nov. and *Sphaerodoropsis rosehipiformis* sp. nov.; Syllidae: *Guillermogonita abyssicola* gen. et sp. nov.

Identification keys to the encountered families of Polychaeta as well as to the species within each family are presented, where applicable. For the new and many previously established species, detailed morphological descriptions are given and the respective geographic distribution is discussed.

Keywords: Deep sea; Atlantic Ocean; Phyllodocida; Molecular data; Biodiversity; Phylogeny

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Introduction

> "*For below all is fearful, of moment sad;*
> *let not man to tempt the immortals e'er try,*
> *Let him never desire the thing to see*
> *that with terror and night they veil graciously.*"
> (F. Schiller 1797, "The Diver")

Fortunately, mankind ignores this advice. However, even today one of the largest ecosystems on earth – the deep sea – is still one of the least explored. Due to darkness, low temperature, high pressure and food shortage, this region was long considered as an azoic desert. Therefore, the discoveries of hydrothermal vents (1977), cold seeps (1984) and their associated faunas were real sensations, especially because these rich communities are based only on chemolithoautotrophic bacteria and not on sunlight energy (e.g. Corliss et al. 1979; Southward 1982; Paull et al. 1984; Jannasch 1985; Jannasch and Mottl 1985; Jones 1985; Grassle 1987; Desbruyères et al. 2006). Since then, the deep sea is no longer assumed to be a completely monotonous, stable and very sparsely populated habitat. Furthermore, chemosynthetic ecosystems are also associated with whale skeletons on the sea floor (e.g. Smith et al. 2002; Baco and Smith 2003; Smith and Baco 2003; Dahlgren et al. 2004; Rouse et al. 2004; Pleijel et al. 2008; Wiklund et al. 2009). However, little is known about the biodiversity of the vast realms between these spectacular environments, which are only locally and temporally restricted oases of life.

The multinational Census of the Diversity of Abyssal Marine Life (CeDAMar) programme (a component of the Census of Marine Life) was conceived to overcome this lack of information concerning the abyssal plains of the world oceans. These basins seem to be homogeneous over hundreds or thousands of kilometres and have great potential significance as a reservoir of biodiversity (Martínez Arbizu and Schminke 2005). The programme concentrates on the endo-, epi-, and hyperbenthic organisms, i.e., those that live in, on or directly above the sea floor. CeDAMar also promotes the testing of hypotheses regarding potential barriers to, and mechanisms of, dispersal of species by morphological and molecular methods. Within CeDAMar various projects complement each other to obtain a global picture of the diversity of the abyssal areas of the world, and how it changes in space and time. One of these projects is named DIVA (Latitudinal gradients of deep sea bio**DIV**ersity in the **A**tlantic Ocean); it explores the fauna inhabiting sediments in Atlantic deep-sea basins from pole to pole (Martínez Arbizu and Schminke 2005).

Polychaetes are one of the dominant groups in marine environments worldwide and form an important food base for many other animals such as fish and crabs (Hartmann-Schröder 1996; Beesley et al. 2000; Rouse and Pleijel 2001). This is also the case in the deep-sea benthic communities of the southeast Atlantic Ocean (Kröncke and Türkay 2003; Türkay 2006). However, only a few species found during the DIVA-1 expedition have been described to date (Böggemann 2005; Böggemann and Purschke 2005; Hilbig 2005). On the other hand, a number of publications have dealt with crustaceans (e.g. Brandt 2001, 2002, 2004; Malyutina et al. 2001; Guerrero-Kommritz et al. 2002; Schmid et al. 2002; Guerrero-Kommritz 2003a, 2003b, 2005; Guerrero-Kommritz and Heard 2003; Mühlenhardt-Siegel 2003; Brökeland and Wägele 2004; Guerrero-Kommritz and Błażewicz-Paskowycz 2004; Brandt et al. 2005; Brenke et al. 2005; Bröhldick 2005; Leese and Brenke 2005; Mühlenhardt-Siegel 2005a, 2005b, 2005c; Veit-Köhler 2005; Willen 2005), Loricifera (Gad 2005a, 2005b), sponges (Cristobo et al. 2005), cephalopods (Piatkowski and Diekmann 2005), and even holothurians (Bohn 2005). A series of papers dealing especially with taxa within the Phyllodocida (see Appendix 1) will fill this knowledge gap. In addition to morphological descriptions, some of the groups are studied with molecular methods to clarify phylogenetic relationships and to elucidate whether some of the so-called cosmopolitan or otherwise widely distributed species are in fact cosmopolites or only complexes of cryptic or sibling species.

According to relevant references (e.g. Westheide and Hass-Cordes 2001; Westheide et al. 2003), non-coding regions of the nuclear DNA, such as the internal transcribed spacers of the nuclear rDNA (ITS1 and ITS2), are variable areas in the genome and allow species differentiation. They can be used for the analysis of phenotypically identical, widespread populations of a given taxon, to clarify whether the latter constitutes a cosmopolitan species or a complex of cryptic or sibling species. On the other hand, the more conservative coding regions from the nuclear ribosomal subunit 18S rDNA, the mitochondrial ribosomal subunit 16S rDNA and the mitochondrial cytochrome *c* oxidase subunit I genes (COI), are supposed to be good markers to analyse various phylogenetic questions concerning the systematization of Annelida (e.g. Struck et al. 2002; Jördens et al. 2004; Bleidorn et al. 2005; Worsaae et al. 2005; Halanych and Janosik 2006; Aguado et al. 2007; Eklöf et al. 2007; Rousset et al. 2007; Ruta et al. 2007; Pleijel et al. 2008; Wiklund et al. 2008, 2009).

Methods and material

Field work

The DIVA-1 expedition on board the German research vessel METEOR (cruise 48 leg 1) took place in July–August 2000 (Türkay 2006). It was one of the pioneering projects embedded in the DIVERSITAS programme as a German contribution to the International Biodiversity Observation Year (IBOY). During the expedition, sampling was done with various types of gear to assess corresponding sections of the benthos (nano- to megafauna). The transect of about 700 km in the southern Angola Basin comprised six working areas separated by approximately equal distances, with depths between 5148 and 5500 m (Fig. 1, Table 1).

The DIVA-2 expedition (R/V METEOR cruise 63 leg 2; February–March 2005) examined the Cape Basin (one area), the northern Angola Basin (one area), and the Guinea Basin (three areas), using the same types of gear as before at depths between 5022 and 5672 m (Fig. 1, Table 1). The Walvis Ridge and the Guinea Rise (Fig. 1) are underwater ridges between the sampled basins, which might influence the composition and distribution of the species. The Walvis Ridge is 455 m deep and about 3000 km long, whereas the Guinea Rise is at least 1280 m deep.

The equatorial West African margins were studied by the BIOZAIRE project, which was initiated by IFREMER and cofinanced by the French oil company Total. The project focused on benthic communities at six selected sites ranging from 400 m to 4000 m in depth. These areas are under pelagic and continental input, under the influence of the Zaire Canyon, or in the vicinity of cold seeps. The box corer material from two of the deep-sea stations of the BIOZAIRE 1–3 expeditions (R/V L'ATALANTE; January and November 2001, December 2003) is also included in this study (Fig. 1, Table 1).

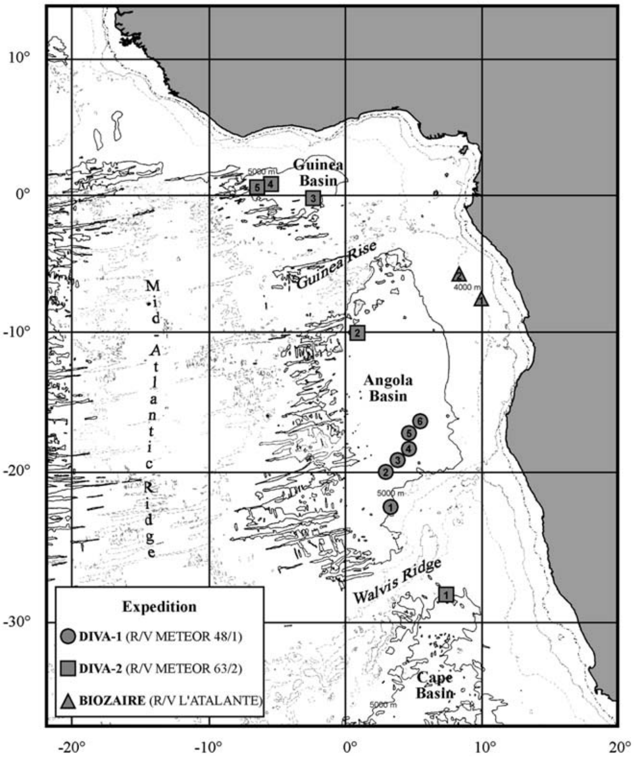

Fig. 1. Map of areas sampled during the three expeditions.

The deep-sea benthos was examined (Fig. 1, Table 1) with reference to all size classes (nano-, meio-, macro-, and megafauna) using various types of gear as outlined below (Fig. 2). For additional and more detailed information concerning the gear, see Türkay (2006).

Agassiz trawl (AT)

A modified Agassiz trawl (Fig. 2A) of 3.5 m width with a cod end mesh size of 1 cm was used during the DIVA-1 and DIVA-2 expeditions for benthic epi- and infaunal megafauna (Kröncke and Türkay 2003). The ocean floor was trawled for 1.5–3.5 h at 2 knots, which resulted in a sampling area of at least 26,300–45,500 m^2. Specimens were fixed in 4% formaldehyde-seawater solution and preserved in 70% ethanol.

Box corer (BC)

A 50 cm × 50 cm (0.25 m^2) USNEL box corer (Fig. 2B) was used for macrofaunal organisms that live on or just below the sediment surface. Specimens were sieved from the sediment (minimum mesh size 300 μm), fixed in 4% formaldehyde-seawater solution, and later preserved or directly fixed in 70% ethanol.

Epibenthic sledge (ES)

Meio- and macrofaunal organisms were sampled with an epibenthic sledge (Fig. 2C) slightly modified according to the model described by Brandt and Barthel (1995). The ocean floor was trawled for 0.25–3 h. The lower epinet and the upper supranet were both used, with a mesh size of 500 μm in the front and 300 μm in the tail. Specimens were usually fixed in cold 70% (DIVA-1) or 100% ethanol (DIVA-2) for morphologic and genetic analyses, respectively. However, a few samples from DIVA-1 were also fixed in a 4% formaldehyde-seawater solution and later preserved in 70% ethanol.

Multicorer (MC)

Nano- and meiofaunal organisms were sampled using a multicorer (Fig. 2D; Barnett et al. 1984) with 12 cores of 10 cm diameter. Each core was fixed in 4% formaldehyde-seawater solution on board, and later sieved at 40 μm mesh size. Specimens and organic material were extracted from the remaining sand particles by the differential-flotation method using the colloidal silica gel Levasil and centrifugation at 4000 rpm (McIntyre and Warwick 1984), then preserved in 70% ethanol. Sorting of the DIVA-1 material was done with the aid of Rose Bengal staining.

Table 1. Details on samples including studied polychaetes.

Sample[a]	Coordinates	Date	Depth [m]	Fixative
GUINEA BASIN				
DIVA-2 Area 5				
M 63/2 st. 93 AT	0°30.3′N 6°30.8′W – 0°30.8′N 6°25′W	22.iii.2005	5168–5217	formalin
M 63/2 st. 94 ES	0°37.7′N 6°25.9′W – 0°37.6′N 6°26.4′W	23.iii.2005	5159–5163	ethanol
M 63/2 st. 95 MC	0°37.4′N 6°28.1′W	23.iii.2005	5170	formalin
M 63/2 st. 96 MC	0°37.2′N 6°28′W	23.iii.2005	5165	formalin
M 63/2 st. 97 MC	0°37.2′N 6°28.1′W	23.iii.2005	5170	formalin
M 63/2 st. 98 MC	0°37.2′N 6°28.1′W	23.iii.2005	5170	formalin
M 63/2 st. 99 MC	0°37.2′N 6°28.1′W	23.iii.2005	5168	formalin
M 63/2 st. 100 MC	0°37.2′N 6°28.1′W	23.iii.2005	5167	formalin
M 63/2 st. 101 BC	0°37.2′N 6°28.1′W	24.iii.2005	5171	formalin
M 63/2 st. 102 BC	0°37.3′N 6°28.1′W	24.iii.2005	5169	formalin
M 63/2 st. 103 BC	0°37.2′N 6°28.1′W	24.iii.2005	5167	formalin
M 63/2 st. 104 BC	0°37.3′N 6°28.1′W	24.iii.2005	5168	formalin
M 63/2 st. 105 BC	0°37.3′N 6°28.1′W	24.iii.2005	5173	formalin
M 63/2 st. 106 BC	0°37.2′N 6°28.1′W	24.iii.2005	5170	formalin
DIVA-2 Area 4				
M 63/2 st. 74 MC	0°50′N 5°35.1′W	19.iii.2005	5144	formalin
M 63/2 st. 75 MC	0°50′N 5°35′W	19.iii.2005	5139	formalin
M 63/2 st. 76 MC	0°50′N 5°35′W	19.iii.2005	5136	formalin
M 63/2 st. 77 MC	0°50′N 5°35′W	19.iii.2005	5142	formalin
M 63/2 st. 78 MC	0°50′N 5°35.1′W	19.iii.2005	5138	formalin
M 63/2 st. 79 MC	0°50′N 5°35′W	19.iii.2005	5139	formalin
M 63/2 st. 80 MC	0°50′N 5°35′W	19.iii.2005	5139	formalin
M 63/2 st. 81 BC	0°50′N 5°35′W	19.iii.2005	5136	formalin
M 63/2 st. 82 BC	0°50.1′N 5°35′W	19.iii.2005	5144	formalin
M 63/2 st. 83 BC	0°50′N 5°35′W	19.iii.2005	5140	formalin
M 63/2 st. 84 BC	0°50′N 5°35′W	20.iii.2005	5138	formalin
M 63/2 st. 85 BC	0°50′N 5°35′W	20.iii.2005	5138	formalin
M 63/2 st. 87 BC	0°50′N 5°35.1′W	20.iii.2005	5142	formalin
M 63/2 st. 88 BC	0°50′N 5°35.1′W	20.iii.2005	5137	formalin
M 63/2 st. 89 ES	0°43′N 5°31.3′W – 0°43′N 5°31.2′W	20.iii.2005	5137–5141	ethanol
M 63/2 st. 90 ES	0°40.5′N 5°29.7′W – 0°40.4′N 5°29.7′W	21.iii.2005	5143–5144	ethanol
M 63/2 st. 91 AT	0°50.9′N 5°38.3′W – 0°54.6′N 5°43.2′W	21.iii.2005	5139–5141	formalin
M 63/2 st. 92 AT	0°53.4′N 5°38.4′W – 0°49.1′N 5°32.9′W	22.iii.2005	5142–5144	formalin
DIVA-2 Area 3				
M 63/2 st. 56 MC	0°0′S 2°25′W	14.iii.2005	5064	formalin
M 63/2 st. 57 MC	0°0′N 2°25′W	14.iii.2005	5064	formalin
M 63/2 st. 58 MC	0°0′S 2°25′W	14.iii.2005	5065	formalin
M 63/2 st. 59 MC	0°0.1′S 2°24.8′W	15.iii.2005	5063	formalin
M 63/2 st. 60 MC	0°0′S 2°25′W	15.iii.2005	5064	formalin
M 63/2 st. 61 MC	0°0′S 2°24.9′W	15.iii.2005	5062	formalin
M 63/2 st. 62 MC	0°0′S 2°25′W	15.iii.2005	5062	formalin
M 63/2 st. 63 ES	0°8.8′S 2°28.8′W – 0°8.2′S 2°28.7′W	15.iii.2005	5048–5051	ethanol
M 63/2 st. 64 ES	0°13.3′S 2°29.9′W – 0°13.2′S 2°29.5′W	16.iii.2005	5053–5055	ethanol
M 63/2 st. 65 AT	0°18.1′S 2°27.1′W – 0°24.3′S 2°25′W	16.iii.2005	5051–5076	formalin
M 63/2 st. 66 AT	0°24.1′S 2°21.6′W – 0°30.3′S 2°19.2′W	17.iii.2005	5052–5054	formalin
M 63/2 st. 69 BC	0°26.8′S 2°20.5′W	17.iii.2005	5058	formalin
M 63/2 st. 70 BC	0°26.7′S 2°20.6′W	17.iii.2005	5061	formalin
M 63/2 st. 71 BC	0°26.8′S 2°20.5′W	17.iii.2005	5062	formalin
M 63/2 st. 72 BC	0°26.8′S 2°20.5′W	18.iii.2005	5059	formalin
M 63/2 st. 73 BC	0°26.8′S 2°20.6′W	18.iii.2005	5059	formalin

Table 1. (*continued*)

Sample[a]	Coordinates	Date	Depth [m]	Fixative
ANGOLA BASIN				
BIOZAIRE Area 2				
A st. 25 BC	5°51′S 8°20.5′E	9.i.2001	3952	formalin
A st. 26 BC	5°51′S 8°20.5′E	9.i.2001	3950	formalin
A st. 27 BC	5°49.9′S 8°21.6′E	10.i.2001	3945	formalin
A st. 39 BC	5°51′S 8°21.8′E	25.xi.2001	3950	formalin
A st. 41 BC	5°51′S 8°20′E	26.xi.2001	3970	formalin
A st. 48 BC	5°50.8′S 8°20.8′E	18.xii.2003	3962	formalin
A st. 50 BC	5°50.8′S 8°20.8′E	19.xii.2003	3961	formalin
A st. 51 BC	5°50.8′S 8°20.8′E	19.xii.2003	3964	formalin
BIOZAIRE Area 1				
A st. 22 BC	7°40′S 9°59.9′E	7.i.2001	3982	formalin
A st. 23 BC	7°40.5′S 9°59.7′E	8.i.2001	3993	formalin
A st. 24 BC	7°40.2′S 9°59.7′E	8.i.2001	3988	formalin
A st. 36 BC	7°39.9′S 10°0.4′E	23.xi.2001	3993	formalin
A st. 37 BC	7°39.9′S 10°0.4′E	24.xi.2001	3991	formalin
A st. 52 BC	7°39.9′S 10°0.4′E	23.xii.2003	3993	formalin
A st. 53 BC	7°39.9′S 10°0.4′E	23.xii.2003	3994	formalin
A st. 54 BC	7°39.9′S 10°0.4′E	23.xii.2003	3993	formalin
DIVA-2 Area 2				
M 63/2 st. 44 AT	9°53.4′S 0°52.5′E – 9°59.3′S 0°54.4′E	10.iii.2005	5646–5672	formalin
M 63/2 st. 45 ES	9°53.1′S 0°52.6′E – 9°53.8′S 0°53.6′E	11.iii.2005	5647–5655	ethanol
M 63/2 st. 46 MC	9°56′S 0°53.8′E	11.iii.2005	5648	formalin
M 63/2 st. 48 MC	9°56.2′S 0°54.1′E	11.iii.2005	5647	formalin
M 63/2 st. 49 MC	9°56′S 0°54′E	11.iii.2005	5649	formalin
M 63/2 st. 50 MC	9°56′S 0°54.2′E	11.iii.2005	5653	formalin
M 63/2 st. 51 MC	9°56.1′S 0°54.2′E	12.iii.2005	5649	formalin
DIVA-1 Area 6				
M 48/1 st. 345 BC 2	16°17′S 5°27′E	26.vii.2000	5424	formalin
M 48/1 st. 345 BC 3	16°17′S 5°27.1′E	26.vii.2000	5434	formalin
M 48/1 st. 345 BC 4	16°17′S 5°27.1′E	26.vii.2000	5433	formalin
M 48/1 st. 345 BC 5	16°17′S 5°27′E	26.vii.2000	5434	ethanol
M 48/1 st. 345 BC 6	16°17′S 5°27′E	26.vii.2000	5433	formalin
M 48/1 st. 345 BC 7	16°17′S 5°27′E	26.vii.2000	5433	formalin
M 48/1 st. 345 BC 8	16°16.9′S 5°27.1′E	26.vii.2000	5432	ethanol
M 48/1 st. 346-1 MC	16°17′S 5°27′E	27.vii.2000	5432	formalin
M 48/1 st. 346-2 MC	16°17′S 5°27′E	27.vii.2000	5433	formalin
M 48/1 st. 346-3 MC	16°17′S 5°27′E	27.vii.2000	5436	formalin
M 48/1 st. 346-4 MC	16°16.9′S 5°27′E	27.vii.2000	5433	formalin
M 48/1 st. 346-5 MC	16°16.9′S 5°27′E	27.vii.2000	5433	formalin
M 48/1 st. 346-6 MC	16°17′S 5°27′E	27.vii.2000	5433	formalin
M 48/1 st. 346-7 MC	16°17′S 5°27′E	27.vii.2000	5433	formalin
M 48/1 st. 346-8 MC	16°17′S 5°27′E	27.vii.2000	5432	formalin
M 48/1 st. 348 ES	16°17′S 5°27.3′E – 16°19.3′S 5°27.2′E	28.vii.2000	5430–5433	ethanol
M 48/1 st. 350 ES	16°13.3′S 5°26.8′E – 16°14.8′S 5°26.7′E	29.vii.2000	5433–5434	ethanol
DIVA-1 Area 5				
M 48/1 st. 341 BC 1	17°8′S 4°42′E	23.vii.2000	5466	formalin
M 48/1 st. 341 BC 4	17°7.9′S 4°42′E	23.vii.2000	5463	ethanol
M 48/1 st. 341 BC 6	17°8′S 4°42′E	24.vii.2000	5465	formalin
M 48/1 st. 341 BC 8	17°8.1′S 4°41.9′E	24.vii.2000	5464	formalin
M 48/1 st. 341 BC 9	17°8′S 4°42′E	24.vii.2000	5460	formalin

Table 1. (*continued*)

Sample[a]	Coordinates	Date	Depth [m]	Fixative
M 48/1 st. 342-1 MC	17°8′S 4°42′E	24.vii.2000	5460	formalin
M 48/1 st. 342-2 MC	17°8′S 4°42′E	24.vii.2000	5460	formalin
M 48/1 st. 344 ES	17°4.9′S 4°40.8′E – 17°7.5′S 4°42.3′E	25.vii.2000	5460–5460	ethanol
DIVA-1 Area 4				
M 48/1 st. 336 BC 1	18°16.7′S 4°44.4′E	20.vii.2000	5437	formalin
M 48/1 st. 336 BC 2	18°17.1′S 4°44.8′E	21.vii.2000	5461	formalin
M 48/1 st. 338 ES	18°18′S 4°39.9′E – 18°20.9′S 4°38.7′E	22.vii.2000	5439–5443	ethanol
M 48/1 st. 340 ES	18°17.3′S 4°41.2′E – 18°19.3′S 4°41.8′E	23.vii.2000	5419–5443	ethanol
DIVA-1 Area 3				
M 48/1 st. 330 BC 1	19°7′S 3°52′E	17.vii.2000	5468	ethanol
M 48/1 st. 330 BC 2	19°7.1′S 3°51.9′E	17.vii.2000	5468	formalin
M 48/1 st. 330 BC 3	19°8.3′S 3°51′E	17.vii.2000	5469	ethanol
M 48/1 st. 330 BC 4	19°7′S 3°51.9′E	17.vii.2000	5473	ethanol
M 48/1 st. 330 BC 5	19°7′S 3°52′E	17.vii.2000	5468	formalin
M 48/1 st. 330 BC 6	19°7′S 3°52′E	17.vii.2000	5467	formalin
M 48/1 st. 330 BC 7	19°7′S 3°52′E	17.vii.2000	5468	formalin
M 48/1 st. 330 BC 8	19°7′S 3°52′E	18.vii.2000	5469	formalin
M 48/1 st. 331-1 MC	19°7′S 3°52′E	18.vii.2000	5470	formalin
M 48/1 st. 331-2 MC	19°6.9′S 3°52′E	18.vii.2000	5468	formalin
DIVA-1 Area 2				
M 48/1 st. 324 BC 3	19°58.2′S 2°59.8′E	13.vii.2000	5494	ethanol
M 48/1 st. 324 BC 4	19°58.3′S 2°59.7′E	13.vii.2000	5494	ethanol
M 48/1 st. 324 BC 6	19°58.3′S 2°59.7′E	13.vii.2000	5495	formalin
M 48/1 st. 324 BC 7	19°58.3′S 2°59.8′E	13.vii.2000	5494	formalin
M 48/1 st. 324 BC 8	19°58.3′S 2°59.8′E	13.vii.2000	5493	formalin
M 48/1 st. 324 BC 9	19°58.3′S 2°59.7′E	13.vii.2000	5494	formalin
M 48/1 st. 325-2 MC	19°58.2′S 2°59.7′E	14.vii.2000	5494	formalin
M 48/1 st. 325-3 MC	19°58.2′S 2°59.8′E	14.vii.2000	5494	formalin
M 48/1 st. 325-4 MC	19°58.2′S 2°59.8′E	14.vii.2000	5494	formalin
M 48/1 st. 325-5 MC	19°58.2′S 2°59.6′E	14.vii.2000	5497	formalin
M 48/1 st. 325-6 MC	19°58.3′S 2°59.7′E	14.vii.2000	5496	formalin
M 48/1 st. 325-7 MC	19°58.4′S 2°59.8′E	14.vii.2000	5493	formalin
M 48/1 st. 325-8 MC	19°58.2′S 2°59.7′E	14.vii.2000	5493	formalin
DIVA-1 Area 1				
M 48/1 st. 318 ES	22°20′S 3°18.3′E – 22°20.2′S 3°18.4′E	9.vii.2000	5179–5180	ethanol/formalin
M 48/1 st. 320 ES	22°19.9′S 3°18′E – 22°20′S 3°18′E	10.vii.2000	5161–5162	formalin
CAPE BASIN				
DIVA-2 Area 1				
M 63/2 st. 30 BC	28°6.7′S 7°20.8′E	3.iii.2005	5042	formalin
M 63/2 st. 33 MC	28°6.7′S 7°20.8′E	3.iii.2005	5050	formalin
M 63/2 st. 34 MC	28°6.7′S 7°20.8′E	3.iii.2005	5030	formalin
M 63/2 st. 35 MC	28°6.8′S 7°20.7′E	3.iii.2005	5022	formalin
M 63/2 st. 36 MC	28°6.7′S 7°20.9′E	4.iii.2005	5040	formalin
M 63/2 st. 37 MC	28°6.7′S 7°20.8′E	4.iii.2005	5030	formalin
M 63/2 st. 38 MC	28°6.8′S 7°20.8′E	4.iii.2005	5037	formalin
M 63/2 st. 40 ES	28°3.1′S 7°19.8′E – 28°3.2′S 7°19.8′E	4.iii.2005	5052–5062	ethanol
M 63/2 st. 41 ES	28°4.1′S 7°20.5′E – 28°4.2′S 7°20.7′E	5.iii.2005	5058–5060	ethanol
M 63/2 st. 42 AT	28°0.2′S 7°16.9′E – 28°4′S 7°20.8′E	5.iii.2005	5082–5089	formalin
M 63/2 st. 43 AT	28°1.2′S 7°17.9′E – 28°4.9′S 7°21.6′E	6.iii.2005	5076–5077	formalin

[a] A = R/V L′ATALANTE; M = R/V METEOR; st. = station.

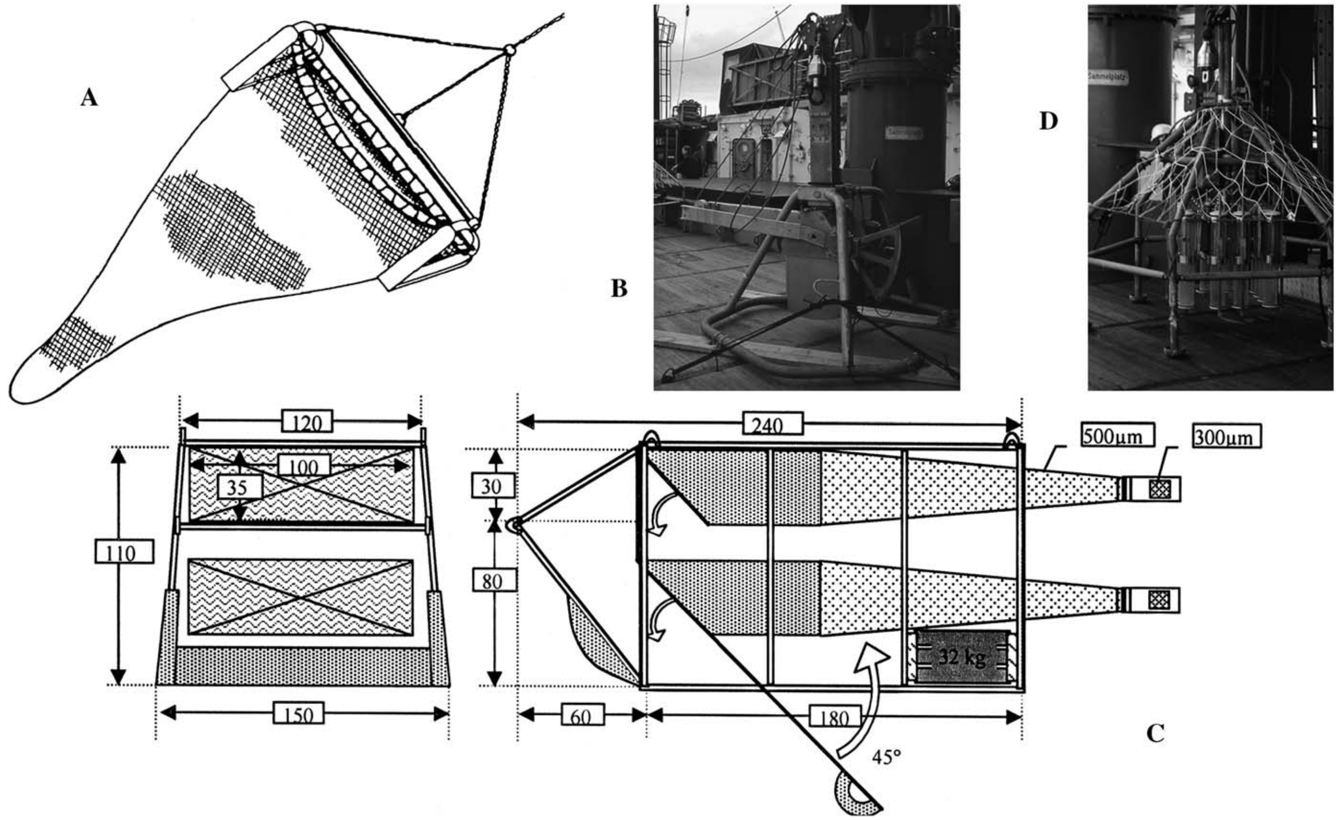

Fig. 2. Sampling gear used during the expeditions. (A) Modified Agassiz trawl. (B) USNEL box corer. (C) Epibenthic sledge. (D) Multicorer. (A, C: from Türkay 2006; B, D: courtesy of G. Purschke).

Laboratory work

Observations, measurements and figures were made using a Leica Wild M 3 stereo microscope, a Zeiss compound microscope, and a Leitz Laborlux S compound microscope, each equipped with a camera lucida.

For SEM investigation specimens or fragments were dehydrated in a graded ethanol series, critical point-dried using CO_2, mounted on aluminium stubs, coated with gold, and examined with a Zeiss DSM 962.

Genomic DNA was extracted from ethanol-preserved material (Table 2) using the DNeasy Blood & Tissue Kit (Qiagen). Amplification and sequencing of the genes (nuclear ribosomal subunit 18S rDNA, mitochondrial 16S rDNA, mitochondrial cytochrome *c* oxidase subunit I (COI), and the internal transcribed spacers (ITS1 and 2) of the nuclear rDNA) were done with primers as given in Table 1.

HotStart-PCR was performed in 25 µl reaction volumes including 2.5 µl 10 × PCR buffer (BioTherm) with 15 mM $MgCl_2$, 0.5 µl 50 mM $MgCl_2$, 0.5 µl 0.1 M dNTPs, 0.5 µl of each primer (10 pmol/µl), 15.5 µl ddH_2O, 3 µl DNA template, and 2 µl Taq-polymerase solution (GeneCraft, 5 U/µl). Biometra Personal Cycler protocol: Prerun: 5 min at 94 °C; application of polymerase; 1 cycle: 1 min 94 °C; 40 cycles: 1 min 94 °C, 1 min 45–53 °C, 2 min 72 °C; 1 cycle: 7 min 72 °C. PCR products were verified on a 1% agarose gel and purified with the QIAquick PCR Purification Kit (Qiagen). Sequencing was performed with ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit in an ABI PRISM 377 DNA Sequencer (both PE Biosystems) (Table 3).

Sequences were assembled and edited using Chromas 1.5 (© 1998 by Technelysium Pty Ltd.). For all genes investigated, the preliminary alignment was done with Clustal X 1.81 (Thompson et al. 1997) and subsequently corrected by hand using GeneDoc 2.6.002 (Nicholas et al. 1997), whereas COI sequences were sometimes translated into amino acid sequences based on the invertebrate mitochondrial codon table in GeneDoc. Alignments are available at TreeBASE (www.treebase.org).

Phylogenetic reconstructions were carried out by maximum-parsimony (MP) and maximum-likelihood (ML) methods using PAUP* 4.0b10 (Swofford 2002). The most adequate substitution model for ML analyses was selected for each alignment by ModelTest 3.04 (Posada and Crandall 1998). Further methodological specifics are given in each corresponding text section, i.e.

Table 2. Taxa and sequences used for phylogenetic analyses, with source and voucher data.

Taxon	Geographic origin	Voucher	GenBank accession numbers		
			18S rDNA	16S rDNA	COI (3–6W)
CHRYSOPETALIDAE					
Dysponetus caecus (Langerhans, 1880)	DIVA-2 st. 63 ES-E	ZMH P24951 A	–	GQ426603	GQ426647
Dysponetus hesionides sp. nov.	DIVA-2 st. 40 ES-S	ZMH P24960 B	–	GQ426604	GQ426648
	DIVA-2 st. 41 ES-S	ZMH P24961 C	GQ426554	–	–
	DIVA-2 st. 89 ES-E	ZMH P24965	–	–	GQ426649
Dysponetus profundus sp. nov.	DIVA-2 st. 45 ES-S	ZMH P24979	–	–	GQ426650
	DIVA-2 st. 89 ES	ZMH P25003 + 25005	–	–	GQ426652, GQ426653
Pseudodysponetus fragmentosus sp. nov.	DIVA-2 st. 89 ES-S	ZMH P25057	–	–	GQ426657
GLYCERIDAE					
Glycera capitata Ørsted, 1842	DIVA-2 st. 45 ES-S	ZMH P25080	–	–	GQ426658
	DIVA-2 st. 90 ES-E	ZMH P25099	GQ426559	GQ426607	–
Glycera lapidum Quatrefages, 1866	France, Roscoff		GQ426560	GQ426608	GQ426661
Glycera southeastatlantica sp. nov.	DIVA-2 st. 89 ES	ZMH P25128 A + P25128 B	–	–	GQ426662, GQ426663
	DIVA-2 st. 90 ES-E	ZMH P25129	–	GQ426609	GQ426664
Glycera tridactyla Schmarda, 1861	France, Roscoff		GQ426564	GQ426610	GQ426665
GONIADIDAE					
Bathyglycinde profunda (Hartman & Fauchald, 1971)	DIVA-2 st. 40 ES-S	ZMH P25142	–	GQ426611	GQ426666
	DIVA-2 st. 89 ES-E	ZMH P25143	GQ426567	–	GQ426667
Bathyglycinde sibogana (Augener & Pettibone in Pettibone, 1970)	DIVA-2 st. 41 ES-S	ZMH P25147	GQ426568	–	GQ426669
Glycinde multidens F. Müller, 1858	Brazil, Pontal do Sul		GQ426569	GQ426612	GQ426670
Goniada vorax (Kinberg, 1865)	France, Banyuls-s.-M.		GQ426570	GQ426613	GQ426671
Goniadella bobrezkii (Annenkova, 1929)	France, St. Efflam		GQ426571	GQ426614	–
Progoniada regularis Hartman, 1965	DIVA-2 st. 41 ES-S	ZMH P25156	–	GQ426615	–
	DIVA-2 st. 45 ES-S	ZMH P25157 B	GQ426573	GQ426616	GQ426673
	DIVA-2 st. 89 ES-E	ZMH P25161	–	–	GQ426674
HESIONIDAE					
Hesiospina cf. *aurantiaca* (Sars, 1862)	DIVA-2 st. 89 ES-S +	ZMH P25221 B	GQ426577	–	–
	DIVA-2 st. 90 ES-S	ZMH P25222 B	GQ426578	–	GQ426676
Hesiospina aurantiaca (Sars, 1862)	Papua New Guinea, Madang		–	AY340464[E]	–
LACYDONIIDAE					
Lacydonia laureci Laubier, 1975	DIVA-2 st. 40 ES-E	ZMH P25262 A	GQ426579	–	GQ426677
Lacydonia sp.	DIVA-2 st. 90 ES-E	ZMH P25287 A	GQ426580	GQ426617	GQ426678
LOPADORHYNCHIDAE					
Pelagobia longicirrata Greeff, 1879	DIVA-2 st. 89 ES-S	ZMH P25294	GQ426582	–	–
LUMBRINERIDAE					
Lumbrineris inflata Moore, 1911	Germany, Osnabrück, aquarium population		–	–	AY366520[D]
NEPHTYIDAE					
Aglaophamus groenlandiae Hartman, 1967	DIVA-2 st. 89 ES-S	ZMH P25323 B	–	–	GQ426681
	DIVA-2 st. 90 ES-S	ZMH P25324 B	GQ426583	–	–
Aglaophamus malmgreni Théel, 1879	Spitsbergen		–	AY996070[C]	–

Table 2. (*continued*)

Taxon	Geographic origin	Voucher	GenBank accession numbers		
			18S rDNA	16S rDNA	COI (3–6W)
Nephtys kersivalensis McIntosh, 1908	Germany, Helgoland		GQ426584	–	GQ426682
NEREIDIDAE					
Ceratocephale abyssorum (Hartman & Fauchald, 1971)	DIVA-2 st. 89 ES-E	ZMH P25363 B	GQ426585	GQ426618	GQ426683
Nereididae sp.	Germany, Helgoland		GQ426586	–	–
PARALACYDONIIDAE					
Paralacydonia paradoxa Fauvel, 1913	France, Banyuls-s.-M.		GQ426587	GQ426619	GQ426684
PHYLLODOCIDAE					
Eumida nuchala (Uschakov, 1972)	DIVA-2 st. 41 ES-E	ZMH P25389 B	GQ426588	–	GQ426685
Phyllodocidae sp.	DIVA-2 st. 40 ES-E	ZMH P25397	GQ426589	–	–
Pseudomystides bathysiphonicola (Hartmann-Schröder, 1983)	DIVA-2 st. 41 ES-S	ZMH P25415 B	GQ426590	GQ426620	GQ426686
PILARGIDAE					
Sigambra magnuncus Paterson & Glover, 2000	DIVA-2 st. 63 ES-S	ZMH P25478 B	–	GQ426621	–
	DIVA-2 st. 89 ES-E	ZMH P25487 A	–	GQ426622	GQ426688
	DIVA-2 st. 89 ES-S	ZMH P25487 C	GQ426593	–	–
	DIVA-2 st. 90 ES-E	ZMH P25488 A	–	GQ426624	GQ426690
POECILOCHAETIDAE					
Poecilochaetus serpens Allen, 1904	France, Arcachon		–	AY569680[B]	–
Poecilochaetus serpens Allen, 1904	France, Banyuls-s.-M.		GQ426595	–	–
SPHAERODORIDAE					
Sphaerephesia regularis sp. nov.	DIVA-2 st. 63 ES-S	ZMH P25499	GQ426596	–	–
Sphaerodoropsis anae Aguado & Rouse, 2006	Easter Island		–	EF123798[A]	–
Sphaerodoropsis protuberanca sp. nov.	DIVA-2 st. 63 ES-E	ZMH P25555 A	–	–	GQ426691
SYLLIDAE					
Anguillosyllis capensis Day, 1963	DIVA-2 st. 41 ES-S	ZMH P25587	GQ426597	–	GQ426692
	DIVA-2 st. 45 ES-E	ZMH P25588 A	GQ426598	GQ426627	–
	DIVA-2 st. 63 ES-E	ZMH P25593 A	–	GQ426628	GQ426694
	DIVA-2 st. 64 ES-S	ZMH P25594	GQ426600	GQ426629	–
	DIVA-2 st. 89 ES-E	ZMH P25611 A	GQ426601	–	–

Sequences obtained from GenBank are identified by superscript letters following the accession number; corresponding literature references are: [A]Aguado et al. (2007); [B]Bleidorn et al. (2005); [C]Eklöf et al. (2007); [D]Jördens et al. (2004); [E]Rousset et al. (2007).

in "Molecular phylogeny of abyssal Phyllodocida" below, and under "Molecular data" in each family chapter. Except where mentioned otherwise, the outgroup chosen for phylogenetic analysis was *Paralacydonia paradoxa* Fauvel (Paralacydoniidae; Fauvel 1913).

Species descriptions are based solely on specimens newly reported in this study, unless otherwise stated. This also applies to the distribution data provided, whereas the diagnoses list more general information about the respective taxon.

Abbreviations used in the "Material examined" section for each species: af = anterior fragment, cs = complete specimen, mf = middle fragment, pf = posterior fragment. Those data are followed by: length of specimen (in mm); number of chaetigers; maximum width of specimen including and excluding parapodia (in mm).

Table 3. Primers used for amplification and sequencing.

Target	Primer	Sequence (5′ → 3′)	Positions	Direction	Reference
18S rDNA	18e	AAC-CTG-GTT-GAT-CCT-GCC-AGT	1–21	forward	Hillis and Dixon (1991
	18F35	TCT-CAA-AGA-TTA-AGC-CAT-GCA	35–55	forward	Struck et al. (2002)
	18F509	CCC-CGT-AAT-TGG-AAT-GAG-TAC-A	548–569	forward	Struck et al. (2002)
	18F997	TTC-GAA-GAC-GAT-CAG-ATA-CCG	1044–1065	forward	Struck et al. (2002)
	18R925	GAT-CCA-AGA-ATT-TCA-CCT-CT	955–974	reverse	Struck et al. (2002)
	18R1256	AGC-TCT-CAA-TCT-GTC-AAT-CCT	1236–1256	reverse	Struck et al. (2002)
	18R3+	GAA-TCA-AGA-AAG-AGC-TCT-C	1250–1268	reverse	present study
	18R1779	TGT-TAC-GAC-TTT-TAC-TTC-CTC-TA	1811–1834	reverse	Struck et al. (2002)
16S rDNA	16SArL	CGC-CTG-TTT-ATC-AAA-AAC-AT	571–588	forward	Palumbi et al. (1991)
	16SBrH	CCG-GTC-TGA-ACT-CAG-ATC-ACG-T	1055–1076	reverse	Palumbi et al. (1991)
COI	LCO 1490	GGT-CAA-CAA-ATC-ATA-AAG-ATA-TTG-G	14–38	forward	Folmer et al. (1994)
	HCO 2198	TAA-ACT-TCA-GGG-TGA-CCA-AAA-AAT-CA	697–722	reverse	Folmer et al. (1994)
	COI 3	GTN-TGR-GCN-CAY-CAY-ATR-TTY-ACN-GT	850–875	forward	Kojima et al. (1997)
	COI 6W	GCR-TCN-GGR-TAR-TCN-GAR-TAY-CGY-CGN-GGY-AT	999–1030	reverse	Jördens et al. (2004)
ITS1	18Sf	GGA-AGT-AAA-AGT-CGT-AAC-AAG	–	forward	Haß-Cordes, unpublished
	5,8Sr	GCT-GCG-CTC-TTC-ATC-GAC	–	reverse	Haß-Cordes, unpublished
ITS2	5,8SF	CAT-CGA-CTT-CTT-GAA-CGC-A	–	forward	Westheide et al. (2003)
	5,8Sv2	ACT-CTA-AGC-GGT-GGA-TCA	–	forward	present study
	28SR	AAT-GCT-TAA-ATT-CAG-CGG-GTA	–	reverse	Westheide et al. (2003)

The following abbreviations are used for institutions: BMNH = Natural History Museum, London; MNHN = Muséum national d'Histoire naturelle, Paris; SMF = Senckenberg Museum, Frankfurt am Main; UUZM = Museum of Evolution, Uppsala University; ZMA = Instituut voor taxonomische Zoölogie (Zoölogisch Museum), Amsterdam; ZMH = Zoologisches Museum, Hamburg).

General results

Abundance

The studied material consists of polychaetes from 136 samples (DIVA-1: 54; DIVA-2: 66, BIOZAIRE: 16) from the abyssal zones of the southeast Atlantic Ocean (Table 1). The altogether more than 23,000 specimens or fragments (DIVA-1: >9400; DIVA-2: >9700, BIOZAIRE: >4000) were found in all investigated areas and represented 47 (DIVA-1: 39; DIVA-2: 42; BIOZAIRE: 35) different families (Table 4). Most of the latter (36) were present in all three basins, sometimes in high abundance (e.g. Acrocirridae, Ampharetidae, Chrysopetalidae, Cirratulidae, Hesionidae, Paraonidae, Spionidae, Sabellidae). Three families (Pilargidae, Poecilochaetidae, Serpulidae) were restricted to the Angola Basin and the Guinea Basin, some others to only one of the examined regions (Angola Basin: Cossuridae, Pholoidae, Sternaspidae, Tomopteridae, Trichobranchidae; Cape Basin: Aphroditidae; Guinea Basin: Alciopidae, Typhloscolecidae). Cossuridae, Pholoidae and Sternaspidae were exclusively present in the box corer samples of the BIOZAIRE expeditions and might be limited by lower depths (around 4000 m). The other rarely found taxa were either larger megafauna forms like the Aphroditidae or uncommon by-catch from pelagic groups.

Overall, the three different ocean basins are more or less similar in family-level diversity, although some of the thirteen areas are represented with lower abundances (Fig. 3). This may be an artefact of sampling, however, as the number of samples taken varied among sites (Table 1) and different types of gear may have had different collecting efficiencies (Bett et al. 1994). Therefore, the two large underwater ridges (Walvis Ridge and Guinea Rise) between the basins do not seem

Table 4. Distribution of the polychaete taxa among geographic areas and types of sampling gear.

Taxon Basin	Cape Basin				Angola Basin																		Guinea Basin											
Expedition	D2				D1	D1		D1		D1		D1			D1			D2			BZ	BZ	D2				D2				D2			
Station	A1				A1	A2		A3		A4		A5			A6			A2			1	2	A3				A4				A5			
Gear	AT	BC	ES	MC	ES	*BC*	MC	*BC*	MC	*BC*	ES	*BC*	ES	MC	*BC*	ES	MC	AT	ES	MC	BC	BC	AT	BC	ES	MC	AT	BC	ES	MC	AT	BC	ES	MC
Acrocirridae		x	x	x	x		x		x		x	x	x	x		x	x		x	x	x	x		x	x	x		x	x	x		x		x
Alciopidae																							x											
Ampharetidae	x	x	x	x	x		x		x		x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x		x	x	x
Amphinomidae			x																		x	x			x				x					
Aphroditidae	x																																	
Capitellidae	x	x	x	x	x	x	x	x	x			x	x		x	x	x				x	x			x	x			x	x				x
Chaetopteridae	x																	x	x								x		x		x			
Chrysopetalidae			x	x			x		x				x	x		x	x		x	x	x	x		x	x	x		x	x	x		x	x	x
Cirratulidae		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x	x		x	x	x		x	x	x
Cossuridae																					x	x												
Ctenodrilidae				x	x		x							x		x	x			x						x		x		x				x
Dorvilleidae			x	x	x		x				x			x		x	x				x				x				x	x				
Fauveliopsidae			x		x		x	x	x	x	x	x	x		x	x	x				x	x			x	x			x					x
Flabelligeridae			x		x	x	x	x	x	x	x	x	x	x	x	x	x				x	x			x				x	x			x	x
Glyceridae	x				x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x	x		x	x	x		x		x
Goniadidae			x	x	x	x	x	x			x	x	x		x	x	x		x	x	x	x			x	x		x	x			x		
Hesionidae			x	x	x		x		x		x		x	x		x	x		x	x	x	x			x	x			x	x				x
Lacydoniidae			x				x				x		x	x		x	x			x	x	x				x			x	x				x
Lopadorhynchidae			x										x			x									x				x					x
Lumbrineridae			x		x		x	x	x	x	x		x	x	x	x	x		x	x	x	x			x	x		x	x	x			x	x
Magelonidae			x								x								x		x				x				x					
Maldanidae	x		x		x			x			x	x		x	x	x	x				x	x			x	x			x				x	x
Nephtyidae			x													x	x		x		x	x	x	x	x			x	x	x				x
Nereididae			x		x		x	x	x				x		x	x	x				x	x		x	x	x		x	x	x		x		x
Nerillidae				x			x		x					x			x			x	x	x				x				x				x
Onuphidae	x		x	x									x			x									x									
Opheliidae			x	x	x	x	x	x		x	x		x	x	x	x	x		x	x	x	x			x	x			x	x				
Orbiniidae			x		x	x	x		x		x		x		x	x	x		x	x	x	x			x	x		x	x	x		x		x
Oweniidae	x		x	x			x		x		x		x	x		x	x	x					x		x	x	x		x		x		x	x
Paraonidae		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x	x		x	x	x		x	x	x
Pholoidae																					x	x												
Phyllodocidae			x	x	x	x	x	x			x	x	x	x	x	x	x				x	x		x	x	x		x	x	x		x		x
Pilargidae					x	x	x	x			x	x	x	x	x	x	x				x	x		x	x	x		x	x	x		x		x
Poecilochaetidae					x										x		x								x				x			x		
Polynoidae			x	x	x		x				x		x	x		x	x		x						x				x					

Sabellidae		x	x	x	x		x		x		x		x	x		x	x		x	x	x	x		x	x	x		x	x	x			x	x
Scalibregmatidae			x		x		x	x	x		x	x	x			x	x				x	x		x	x	x		x	x		x			
Serpulidae													x			x				x			x				x							
Sigalionidae	x		x	x	x		x				x		x			x	x				x	x			x	x		x	x	x		x		
Sphaerodoridae			x				x		x		x		x			x	x				x	x		x	x	x		x	x	x		x		x
Spionidae		x	x	x	x		x		x		x		x	x		x	x		x	x	x	x		x	x	x		x	x	x		x	x	x
Sternaspidae																					x	x												
Syllidae			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x	x	x		x	x	x		x		x
Terebellidae	x		x	x							x		x			x					x						x		x					
Tomopteridae					x																													
Trichobranchidae					x								x								x	x												
Typhloscolecidae																												x						

Material not available for present study: Most of DIVA-1 BC (corresponding column heading in italics: "*BC*"); some DIVA-2 BC; all DIVA-1 AT.
Abbreviations: A = Area; AT = Agassiz trawl; BC = box corer; BZ = BIOZAIRE; D1 = DIVA-1; D2 = DIVA-2; ES = epibenthic sledge; MC = multicorer.

to have exerted major influence on the biodiversity of the polychaete families, whose species were often distributed by planktonic larval stages.

So far, only very small areas of the large abyssal basins have been explored. For this reason it is not surprising that about one third of the examined species are new for science. Another large part are taxa previously known from the deep sea in the northern Atlantic Ocean, the Pacific Ocean and the Antarctic region, whereas the remaining species belong to abyssal or sometimes also eurybathic taxa, which probably have a cosmopolitan or widespread distribution. The latter morphologically uniform taxa are the more interesting ones with regard to cosmopolitan versus cryptic species and were partially studied during this project using molecular data. However, this was only possible and useful for material fixed directly in ethanol, as had been done with most of the epibenthic sledge samples.

The Agassiz trawl, with a mesh size of 1 cm, seems to be the least effective gear to capture abyssal polychaetes, because only about 700 specimens or fragments representing 14 different families were found in the eight available samples from DIVA-2 (Table 4, Fig. 3). However, two of these taxa were only collected with this equipment. The first, specimens of Aphroditidae, were really gigantic epibenthic megafauna organisms with lengths around 5 cm, whereas most of the other investigated polychaetes ranged in length between 1 mm and 1 cm. The second of those taxa, the pelagic Alciopidae, are represented by a single anterior fragment that might have been picked up during the vertical haul of the gear, which was not provided with a closing mechanism. The remaining groups also included larger specimens (e.g. Capitellidae, Glyceridae, Nephtyidae) or tube-building forms which are often colony-forming (e.g. Chaetopteridae, Onuphidae, Terebellidae) or attached to hard substrates (e.g. Serpulidae).

Much more and more diverse material was present in the 63 box-corer (>5500 fragments; 38 families), 15 epibenthic-sledge (>8300 frag.; 40 fam.) and 50 multicorer samples (>8600 frag.; 36 fam.). The latter gear was included to obtain smaller individuals or especially meiofauna organisms such as Nerillidae. However, the subsequent sieving of the multicorer as well as the box-corer samples more or less damaged many of the DIVA polychaetes or at least their mostly very fragile appendages (e.g. antennae, palps, cirri, elytra, etc.), whereas the usually ethanol-fixed epibenthic-sledge material was often conserved in acceptable condition and was also valuable for molecular analysis. Furthermore, the epibenthic-sledge samples included some pelagic groups (e.g. Tomopteridae), in addition to the benthic taxa, that were caught with the box corer (Typhloscolecidae) or multicorer (Lopadorhynchidae) only by chance.

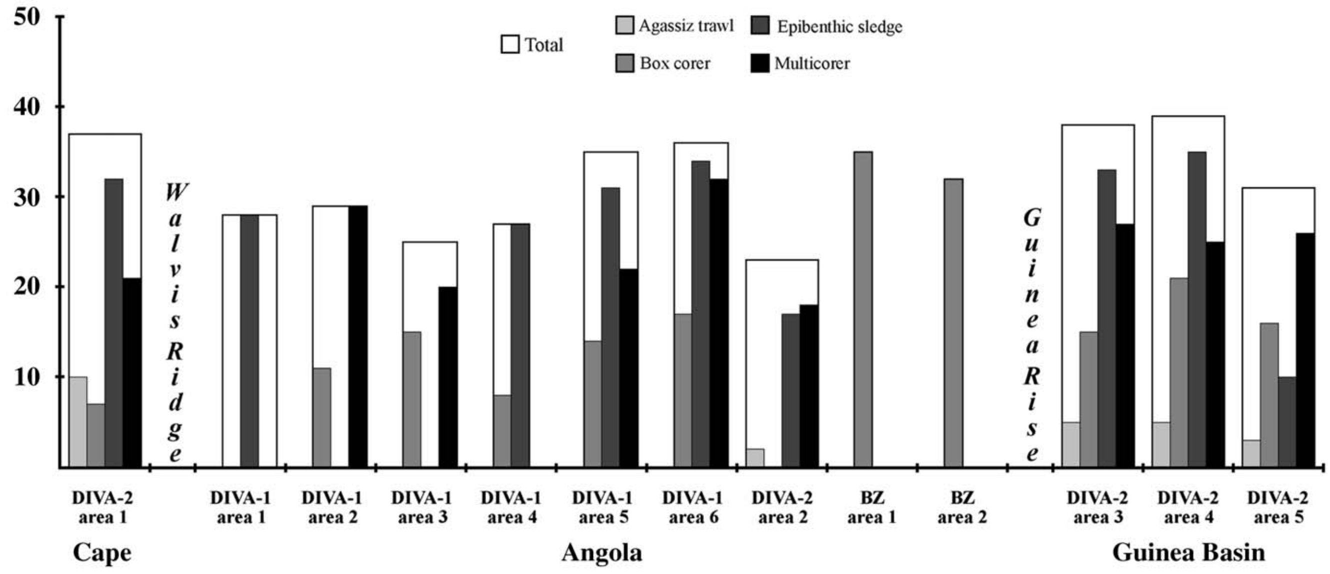

Fig. 3. Number of polychaete families collected per geographic area and type of sampling gear.

Key to families of Polychaeta from the abyssal SE Atlantic

This key is limited to taxa present in the examined material.

1\. Dorsum more or less covered with series of elytra (scales) 2
– Dorsum without elytra or elytral scars 5
2\. Prostomium with 1–3 antennae; harpoon-shaped notochaetae absent 3
– Prostomium with one median antenna; some notochaetae harpoon-shaped .... Aphroditidae
3\. Dorsal cirri usually absent; neurochaetae compound 4
– Dorsal cirri on non-elytra-bearing segments; all chaetae simple .... Polynoidae
4\. Elytra alternate with dorsal cirri along whole length of body; prostomium usually with one median antenna; neurochaetae with short blades; parapodia without branchiae .... Pholoidae
– From 25th or 27th segment backwards only elytra present; prostomium with two lateral and mostly one median antenna; neurochaetae with short and long blades; parapodia usually with branchiae.......... Sigalionidae
5\. Posterior end without cuticularised shield 6
– Posterior end ventrally covered by cuticularised shield .... Sternaspidae
6\. Anterior end (prostomium and/or some anterior segments) with at least two appendages in form of often paired or tuft-like antennae/palps, cirri, tentacles, etc.; or terminating in collar or frilled membrane 7
– Anterior end without such appendages, but prostomium can be laterally pointed, with one median antenna and sometimes additional pairs of branchiae on some anterior segments, or with single median branchia (tentacle) arising dorsally on one anterior segment 38
7\. Anterior end without collar or frilled membrane 8
– Anterior end usually terminating in frilled membrane or more or less developed collar; notochaetae simple capillaries and neurochaetae bidentate hooks arranged in low ridges (tori); body enclosed in tube of distinctly overlapping sediment particles .... Oweniidae
8\. Anterior end with numerous tentacles arranged in a tuft or feathery in two halves around mouth (radiolar crown) 9
– Prostomium and/or some anterior segments with mostly paired appendages (e.g. antennae, palps, cirri); often with eversible pharynx (proboscis) 13
9\. Anterior end with crown of bipinnate radioles; thorax region with notopodial simple capillaries and neuropodial uncini, abdominal region with chaetal inversion 10
– Anterior end with soft tentacles for deposit feeding; notochaetae simple capillaries and neurochaetae uncini, without chaetal inversion 11
10\. Usually one (rarely two or zero) modified radiole forms an operculum; tube calcareous .... Serpulidae
– Operculum not present; tube leathery or of mucus, sand or mud .... Sabellidae

11\. Tentacles not retractile into mouth; 1–4 pairs of simple to branched branchiae, or one single branchial trunk or branchiae absent 12

– Tentacles retractile into mouth; 2–4 pairs of usually simple branchiae .... Ampharetidae

12\. Thoracic and abdominal uncini usually short-handled .... Terebellidae

– Thoracic uncini long-handled, abdominal ones short-handled .... Trichobranchidae

13\. Prostomium conical, more or less annulated, distally terminating in four appendages 14

– Prostomium not as above 15

14\. Proboscis with four jaws arranged in a cross, each basally supported by an aileron; prostomial appendages not articulated .... Glyceridae

– Proboscis generally with ring of two macrognaths and variable number of micrognaths, sometimes with additional chevrons; prostomial appendages usually biarticulated .... Goniadidae

15\. Chaetae of first parapodium elongated, forming a cephalic cage 16

– Cephalic cage absent 17

16\. Body papillated, often with thick covering of sediment or gelatinous sheath; parapodial lobes generally reduced; anterior end retractable, usually with branchiae; capillary and compound chaetae mostly with distinctive cross-barring .... Flabelligeridae

– Body surface usually smooth; parapodial lobes well developed, sometimes flask- or spindle shaped; anterior end not retractable; branchiae, if present, only in middle or posterior part of body; various forms of capillary chaetae and spines, without cross-barring .... Poecilochaetidae

17\. Body with numerous pairs of filiform branchiae or only some pairs on a few anterior segments 18

– Branchiae, if present, not filiform and arranged in various ways 19

18\. Body covered with epidermal papillae; anterior end with two palps; notochaetae capillary, neuropodia with compound falcate chaetae .... Acrocirridae

– Body surface smooth; one pair of palps or groups of palps (tentacular filaments) arise in front of first chaetiger; all chaetae simple .... Cirratulidae

19\. Acicula and/or chaetae present in most segments 20

– Second segment with one pair of prolonged parapodial lobes with internal aciculae, other acicula and/or chaetae absent; biramous parapodia with paddle-like pinnules .... Tomopteridae

20\. Body surface usually smooth, only with some papillae of various sizes 21

– Body surface more or less densely covered with symmetrically or randomly arranged large spherical tubercles and papillae; prostomium indistinct, with three antennae and two palps .... Sphaerodoridae

21\. Fourth chaetiger without large spines, other chaetigers can have modified chaetae 22

– Anterior end with one pair of short or long palps; fourth chaetiger with large spines; some median parapodia can be modified, sometimes fan-shaped; posterior part with biramous parapodia .... Chaetopteridae

22\. Prostomium without appendages (dorsal median or ‘occipital’ antenna can be present), sometimes expanded to form ‘horns’; one pair of elongated peristomial palps (often broken off) 23

– Prostomium with at least two appendages and/or 1–4 anterior segments with modified cirri 24

23\. Prostomium flattened and spatulate; palps papillose; branchiae always absent .... Magelonidae

– Prostomium not flattened; palps usually grooved; branchiae often present .... Spionidae

24\. Proboscis usually with distinct, complex jaw apparatus comprising mandibles and variable number of maxillary elements 25

– Pharyngeal region with much simpler jaws, stylets or teeth or without such structures 26

25\. First two segments without chaetae or cirri; prostomium with up to four antennae/palps .... Dorvilleidae

– First segment without chaetae, sometimes with one pair of cirri; prostomium with seven appendages (three antennae, two palps, and two short frontal lips) .... Onuphidae

26\. Parapodia well developed, usually with noto- and/or neuropodial lobes, chaetae and generally additional appendages (e.g. cirri, branchiae) 27

– Parapodial lobes absent or only indistinctly developed, with two chaetal bundles separated by 1–2 interramal cirri; prostomium with 0–3 antennae and/or two palps (or lateral horns); minute interstitial forms .... Nerillidae

27\. First segment with biramous parapodia and chaetae 28

– First segment achaetous, only with 0–2 pairs of cirri 29

28\. Prostomium with three antennae and two palps, usually continuing posteriorly into conspicuous caruncle; branchiae, if present, inserted behind dorsal cirri or above notopodia; body circular or oval in cross section .... Amphinomidae

– Prostomium with 0–2 antennae and two palps, caruncle absent; interramal cirri (branchiae) inserted together with dorsal cirri on lower side of notopodia, rarely absent; body rectangular in cross section .... Nephtyidae

29\. Dorsal cirri usually flattened, foliose or more or less globular; parapodia generally uniramous 30

– Dorsal cirri not foliose or globular; parapodia uni-, bi- or subbiramous 32

30\. Prostomium with 2–3 antennae and two palps (note: palps antenna-shaped) 31

– Prostomium without appendages or ending with one median antenna/papilla .... Typhloscolecidae

31\. Prostomium laterally with two large, complex spherical eyes with internal globular lenses; pelagic forms .... Alciopidae

– Eyes, if present, usually much smaller pigmented spots; benthic forms .... Phyllodocidae

32\. Compound chaetae present, especially in neuropodia 33

– All chaetae simple, reduced notopodia sometimes with few hooks or spines; prostomium with 2–3 antennae and two palps; first segment usually with two pairs of cirri .... Pilargidae

33\. Notochaetae, if present, simple and neurochaetae mostly compound 34

– All noto- and neurochaetae generally compound; proboscis with large pair of jaws and sometimes additional paragnaths or papillae; prostomium usually with two antennae (rarely zero or three) and two biarticulated palps; first segments with four (rarely two) pairs of cirri .... Nereididae

34\. First (rarely also second) segment achaetous, with 0–2 pairs of cirri 35

– Anterior 2–4 segments achaetous, with 4–8 pairs of usually elongated cirri; prostomium with 2–3 antennae and mostly two biarticulated palps; proboscis sometimes with jaws or teeth; parapodia uni-, bi- or subbiramous .... Hesionidae

35\. Parapodia biramous, only some anterior ones can be uniramous 36

– Parapodia uniramous, only in reproductive stages sometimes subbiramous 37

36\. Dorsal cirri inserted behind fan-like tufts of notochaetae, which are stout or flattened and more or less cover the dorsum; first segment with two pairs of cirri, or anterior two segments each with one pair of cirri; proboscis often with one pair of stylet-like jaws; prostomium with three antennae and two palps .... Chrysopetalidae

– Dorsal cirri inserted above bundle of notochaetae, which are laterally arranged capillaries; first segment with one pair of cirri; proboscis unarmed; prostomium with three antennae and two palps .... Lacydoniidae

37\. Prostomium with two antennae and two palps of similar shape; proboscis unarmed and proventricle absent; first segment with 1–2 pairs of cirri; pelagic forms .... Lopadorhynchidae

– Prostomium with 0–3 antennae and two palps differing in shape, palps can be partially or completely fused; proboscis sometimes with teeth, muscular proventricle present, often visible through body wall; first segment with 0–2 pairs of cirri; benthic forms .... Syllidae

38\. Parapodia usually biramous, only some anterior ones might be uniramous; proboscis without jaws 39

– All parapodia uniramous, dorsal and/or ventral cirri absent; proboscis with distinct complex jaw apparatus comprising mandibles and variable number of maxillary elements .... Lumbrineridae

39\. At least abdominal segments with neurochaetal hooks arranged in low ridges (tori) 40

– Chaetae not arranged in tori 41

40\. Prostomium conical; median segments not elongated; thoracic segments with capillaries and sometimes hooded hooks, abdominal noto- and neuropodial tori generally with hooded hooks .... Capitellidae

– Prostomium often narrow, keel- or ridge-shaped; some median segments more than twice as long as wide; notopodia with capillaries and neuropodial tori usually with hooks with subdistal beard .... Maldanidae

41\. Parapodia low ridges or completely absent, with noto- and neurochaetae emerging directly from body wall, one papilla might be present between bundles of chaetae 42

– Parapodia more or less developed, with cirri and/or parapodial lobes and often branchiae 44

42\. Interramal papilla absent; prostomium not retractable 43

– Interramal papilla present; prostomium retractable within some anterior segments; chaetae capillary and stout spines; branchiae absent .... Fauveliopsidae

43\. Single filiform branchia (tentacle) arising dorsally from chaetigers 2–5; chaetae all capillary or additional thick spines present .... Cossuridae

– Branchiae, if present, paired and on variable number of anterior to middle segments; chaetae vary from simple capillaries to serrated pectinate or dentate forms .... Ctenodrilidae

44\. Parapodia lateral in all parts of body; without aciculae; capillary chaetae smooth or faintly striated 45

– Thorax with lateral parapodia, mostly shifted dorsally in abdominal part; at least abdominal notopodia usually with aciculae; chaetae including crenulated or camerated capillaries; branchiae, if present, oval to cylindrical and continuing to posterior region .... Orbiniidae

45. Prostomium conical or rounded, in some taxa with terminal palpode or one median antenna; body not swollen anteriorly 46

– Prostomium usually T- or V-shaped, without antenna or palpode; body often swollen anteriorly; branchiae, if present, usually branched and limited to first few segments .... Scalibregmatidae

46. Prostomium without median antenna; body usually grooved ventrally; branchiae, if present, cirriform or branched and present on most segments, or restricted to special regions .... Opheliidae

– Median prostomial antenna can be present; body never grooved ventrally; branchiae, if present, flattened and limited to some anterior segments .... Paraonidae

Molecular phylogeny of abyssal Phyllodocida

All analyses were conducted using the branch-swapping heuristic algorithm tree bisection-reconnection (TBR) with random addition of taxa (COI: 10,000 replicates; 16S and 18S: 100,000 replicates). Gaps were treated as missing; characters were unordered and unweighted. Clade support values were calculated with nonparametric bootstrapping (replicate numbers as above), heuristic searches, TBR swapping, and 10 random addition sequences.

18S rDNA data set

Twenty-nine newly acquired sequences (Table 2) were included; analyses were rooted using *Poecilochaetus serpens* Allen (Spionida) as outgroup. The ML analysis was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set as follows: base frequencies ($A = 0.2323$, $C = 0.2420$, $G = 0.2863$, $T = 0.2394$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 1.1564$, $A \leftrightarrow G = 2.5506$, $A \leftrightarrow T = 1.4259$, $C \leftrightarrow G = 1.2161$, $C \leftrightarrow T = 4.0424$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0.3915; and gamma distribution shape parameter = 0.6024.

After exclusion of the primer sites, the alignment (TreeBASE Acc. Nr. SN4591–23654) for the 29 sequences contained 1762 characters, of which 583 were variable and 360 parsimony informative. The MP analysis yielded eight most parsimonious trees, which are 1184 steps long with CI = 0.6934 (0.6084), RI = 0.7692, and RC = 0.5334. The topologies of the strict consensus tree and the ML tree ($-\ln L = 8376.02549$) are very similar (Fig. 4A, B). Both methods confirmed the monophyly of Glyceridae, Goniadidae, Lacydoniidae, Nephtyidae, Nereididae, Phyllodocidae and Syllidae by bootstrap values greater than 50. Other well supported groups are Chrysopetalidae+Hesionidae, Lacydoniidae + Paralacydoniidae, Lopadorhynchidae + Phyllodocidae, and Nephtyidae + Pilargidae. Furthermore, a major clade consisting of Chrysopetalidae, Glyceridae, Hesionidae, Lacydoniidae, Lopadorhynchidae, Nephtyidae, Paralacydoniidae, Phyllodocidae, Pilargidae and Syllidae is delineated from the Goniadidae, Nereididae, Sphaerodoridae group.

16S rDNA data set

Twenty-six sequences (22 new, 4 from GenBank; Table 2) were included; analyses were rooted using *Poecilochaetus serpens* Allen (Spionida) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the hierarchical Likelihood Ratio Tests (hLRT) and the AIC. Accordingly, the priors were set as follows: base frequencies ($A = 0.3738$, $C = 0.1295$, $G = 0.1558$, $T = 0.3409$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 2.7266$, $A \leftrightarrow G = 9.6314$, $A \leftrightarrow T = 5.8936$, $C \leftrightarrow G = 0.5279$, $C \leftrightarrow T = 17.6258$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0.1976; and gamma distribution shape parameter = 0.8204.

After exclusion of the primer sites, the alignment (TreeBASE Acc. Nr. SN4591–23653) for the 26 sequences contained 539 characters, of which 383 were variable and 328 parsimony informative. The MP (tree length = 1721, CI = 0.6934 (0.6084), RI = 0.7692, RC = 0.5334) and the ML analysis ($-\ln L = 7123.07585$) found single trees with only slightly different general topologies (Fig. 5A, B). However, two distinctly incongruent positions are present, though neither is well supported: (a) the phyllodocid *Pseudomystides bathysiphonicola* (Hartmann-Schröder) is either sister to a Glyceriformia clade (MP) or more closely related to Lacydoniidae, Paralacydoniidae and Sphaerodoridae (ML); and (b) the hesionid *Hesiospina* cf. *aurantiaca* (Sars) appears as sister either to Pilargidae (MP) or to a major clade consisting of Chrysopetalidae (part), Glyceridae, Goniadidae, Lacydoniidae, Paralacydoniidae, Phyllodocidae and Sphaerodoridae (ML). Pilargidae and Syllidae are the only well defined monophyletic clades (bootstrap: 100). Other closely related groups are Lacydoniidae + Paralacydoniidae + Sphaerodoridae; Nephtyidae + Nereididae; and Glyceridae + Goniadidae (Glyceriformia). However, these clades are often not

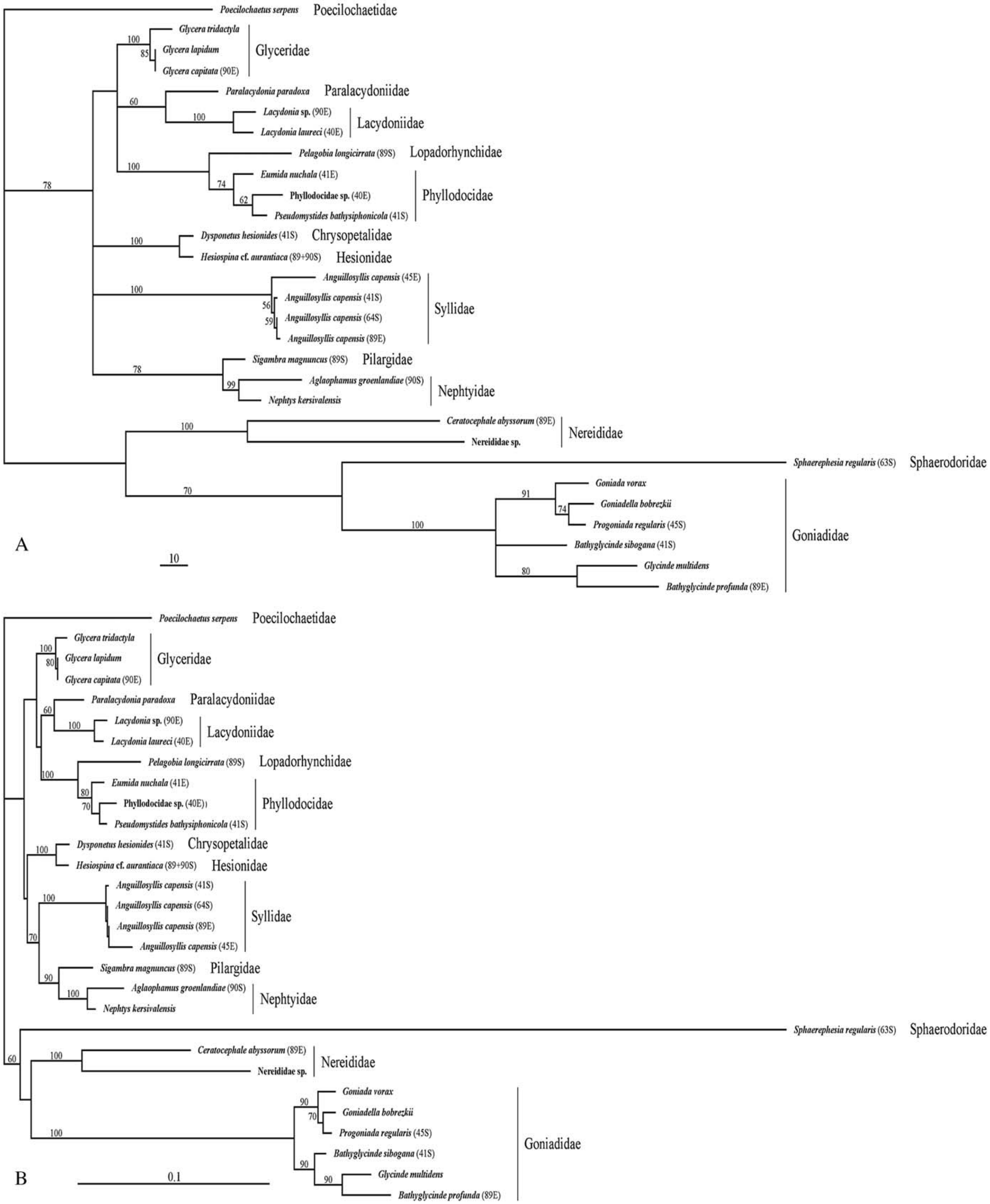

Fig. 4. Phylogeny of Phyllodocida reconstructed from 18S rDNA sequences. (A) Strict consensus phylogram of eight trees obtained from MP analysis; tree length: 1184, CI: 0.6934 (0.6084), RI: 0.7692, RC: 0.5334. (B) ML phylogram based on GTR + I + G ($-\ln L = 8376.02549$). Bootstrap values >50 shown above branches; scale represents evolutionary distance in substitutions per position.

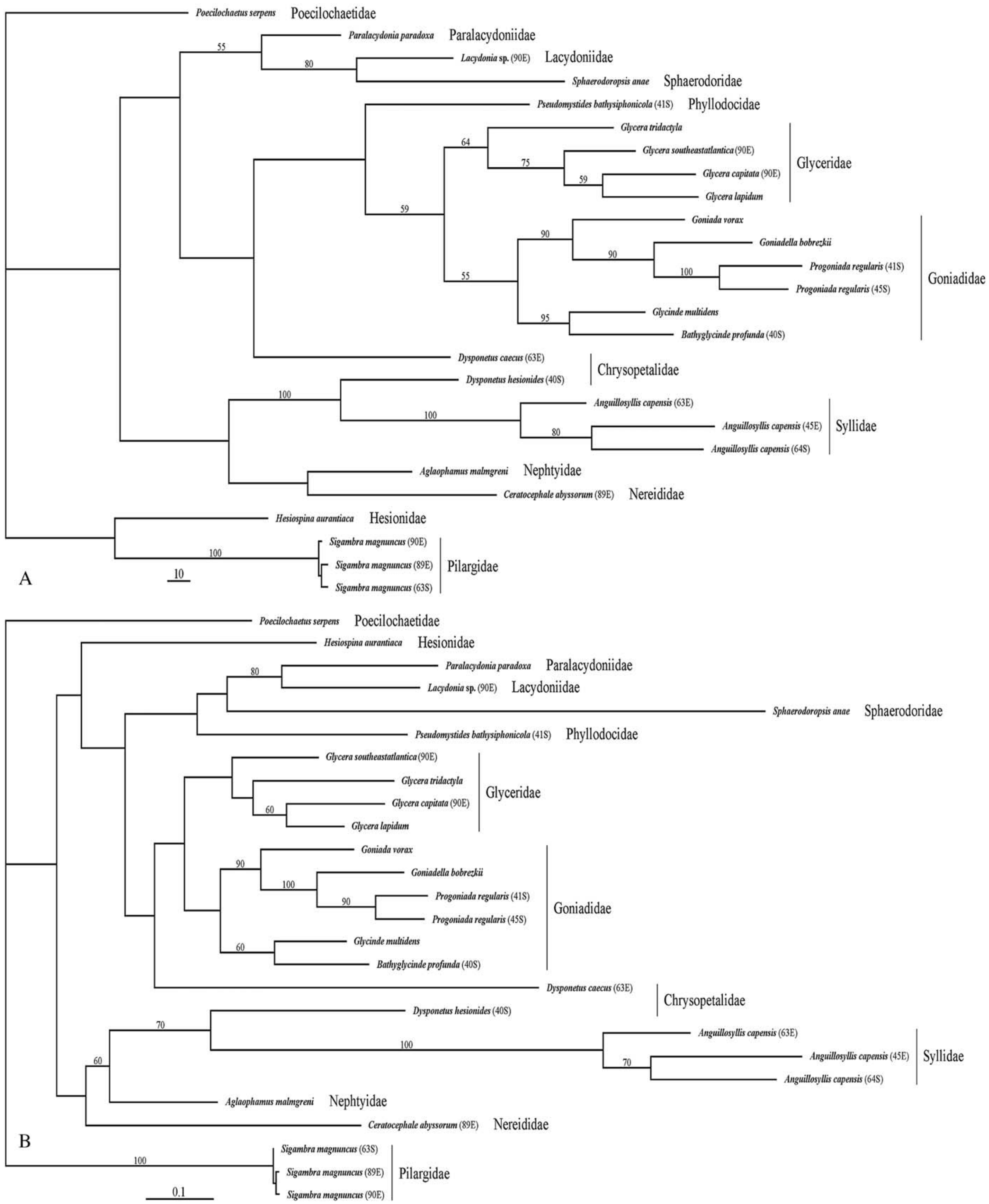

Fig. 5. Phylogeny of Phyllodocida reconstructed from 16S rDNA sequences. (A) MP phylogram; tree length: 1721, CI: 0.4126 (0.3880), RI: 0.4813, RC: 0.1985. (B) ML phylogram based on GTR + I + G ($-\ln L = 7123.07585$). Bootstrap values > 50 shown above branches; scale represents evolutionary distance in substitutions per position.

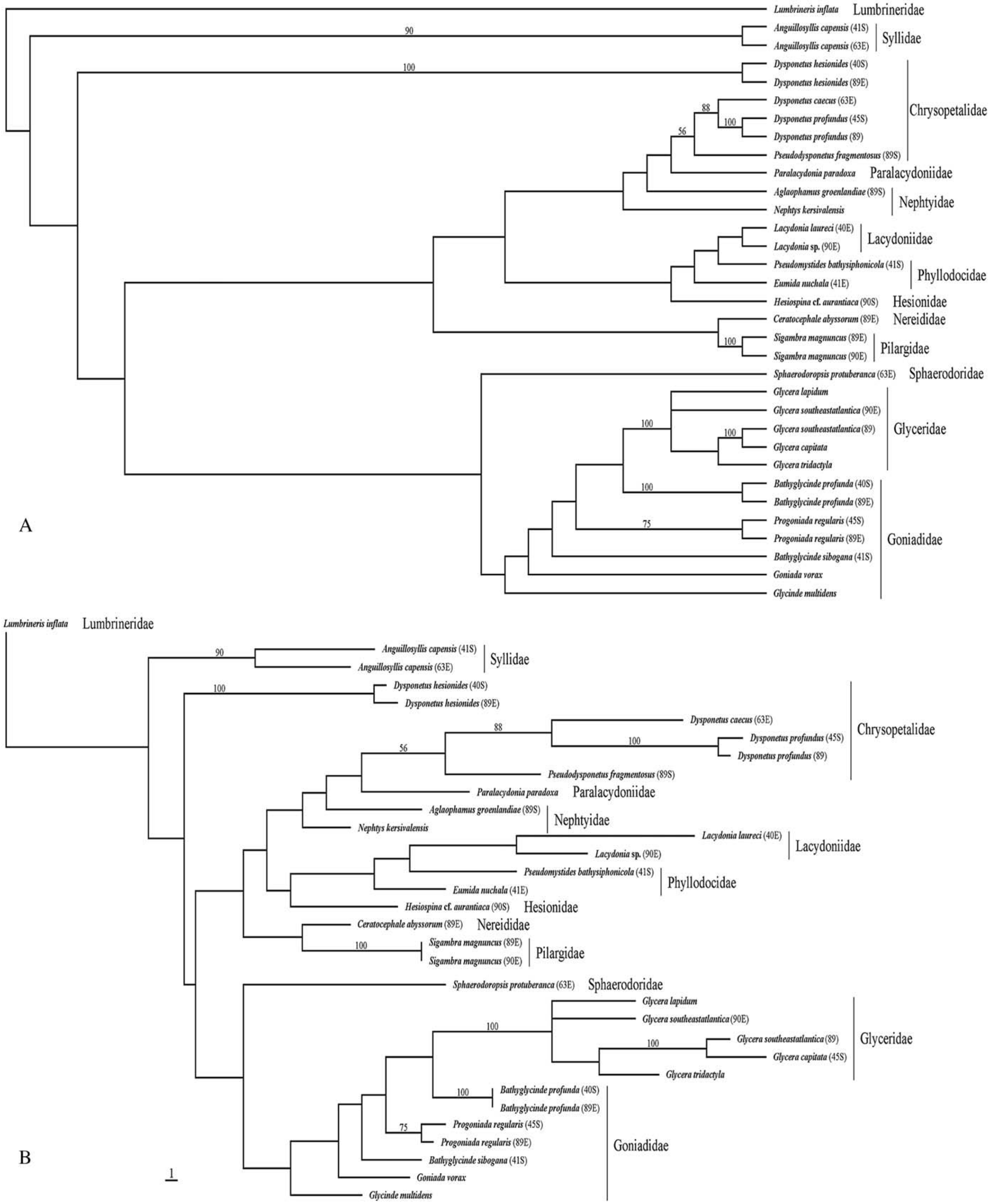

Fig. 6. Phylogeny of Phyllodocida reconstructed from COI (3-6W) sequences. Strict consensus cladogram (A) and phylogram (B) of two trees obtained from MP analysis; tree length: 343, CI: 0.5219 (0.5000), RI: 0.6029, RC: 0.3146. Bootstrap values > 50 shown above branches; scale in (B) represents evolutionary distance in substitutions per position.

strongly supported. Furthermore, both analyses agree on the non-monophyly of chrysopetalids, because *Dysponetus hesionides* sp. nov. is sister to Syllidae and not grouped with *Dysponetus caecus* (Langerhans).

COI (3-6W) data set

Preliminary analyses with the complete COI (3-6W) sequence produced consensus trees in which the relationships of most taxa were unresolved and formed polytomies even when the third codon position was excluded. Therefore, the more conservative amino acid sequences were chosen for the analysis.

Thirty-three amino acid sequences (32 new, 1 from GenBank; Table 2) were included; analyses were rooted using *Lumbrineris inflata* Moore (Eunicida) as outgroup. ML was not possible, because there is no established test to determine the appropriate substitution model for amino acid sequences.

After exclusion of the primer sites, the alignment (TreeBASE Acc. Nr. SN4591–23655) for the 33 included amino acid sequences contained 141 characters, of which 69 were variable and 58 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 343 steps long with CI = 0.5219 (0.5000), RI = 0.6029, and RC = 0.3146. The strict consensus tree (Fig. 6A, B) shows monophyly of Glyceridae, Pilargidae and Syllidae strongly supported by bootstrap values of 100, whereas the Chrysopetalidae are not recovered as monophyletic. All other clades are only weakly supported, sometimes forming paraphyletic groups (e.g. Goniadidae).

Discussion of molecular results

The results of the analyses based on sequence data of the nuclear ribosomal subunit 18S rDNA, mitochondrial 16S rDNA and mitochondrial cytochrome *c* oxidase subunit I gene showed little overall congruence and could not resolve the phylogenetic relationships within Phyllodocida (Figs. 4–6). The main disagreements are the position of the probably chrysopetalid *Dysponetus hesionides* sp. nov., which is either sister to the Hesionidae (18S) or more closely related to the Syllidae (16S and COI), and the relationship between Glyceridae and Goniadidae. The latter two taxa alternatively resulted as distinctly separated (18S), as monophyletic clades with a sister-group relationship (16S), or with a monophyletic Glyceridae nested within a paraphyletic Goniadidae (COI). With regard to previous morphological studies (Pleijel 2001d; Böggemann 2002, 2005, 2006) they are combined as Glyceriformia, which is also indicated by the 16S rDNA data (Fig. 5). However, the investigations of Worsaae et al. (2005), using 18S rDNA and morphological data, suggested a close relationship between the two taxa but no monophyly of Glyceriformia. On the other hand, in the exclusively molecular study of Rousset et al. (2007), the glycerids come out as well supported sister to Dorvilleidae/Lumbrineridae (Eunicida), and the goniadids as sister to Acrocirridae/Flabelligeridae (Cirratuliformia). This indicates that the great morphological similarities might be the result of convergent evolution due to similar selection pressures. The question now is: Which of these phylogenetic hypotheses reflects evolutionary relationships? In other words, how much weight should be placed on characters derived from molecular methods compared to the more traditional morphological analyses? Given the morphologically undoubtedly close relationships between Glyceridae and Goniadidae, some of the results seem somewhat anomalous, and especially the application of 18S rDNA data to evaluate relatively high-level phylogenetic relationships might be problematic.

General conclusions

The abyssal basins seem to be homogeneous over hundreds or thousands of kilometres, but hardly anything is known about their significance as a reservoir of biodiversity. In spite of this, they are or possibly will be misused in the near future as final disposal sites (for, e.g., nuclear waste or fluid carbon dioxide) or their supplies of raw materials (e.g. manganese nodules, methane hydrate) will be exploited if that becomes more profitable, because these basins are far away from mankind, thus hardly anyone cares about conservation measures.

The examined abyssal plains of the southeast Atlantic Ocean really can be considered as a homogeneous environment, with a temperature of 2.48 ± 0.02 °C, salinity of 34.81 ± 0.03‰, pH of 7.5–7.8, and atmospheric pressure of 395–567 atm (Kröncke and Türkay 2003; Balzer et al. 2006; Türkay 2006). However, they definitely are not azoic deserts, as evidenced by the capture of more than 23,000 polychaetes belonging to 47 different families. Most of these specimens were very small (< 1 cm) and might have been overlooked or washed out in previous deep-sea studies. In any case, even 'monotonous mud deserts' in the deep sea are densely populated and worthy of protection.

Some of the abyssal species were new to science, but others were widely distributed; some of the benthic species even seem to be real cosmopolitans as expected by Kirkegaard (1994). The molecular data make it obvious that the enormous rises and ridges between the basins often are no barriers for the usually planktonic larvae. These results might become of great worldwide interest, because any radioactive waste, fluid carbon dioxide or other anthropogenic waste deposited in those basins could be subject to the current systems and be spread on a global scale, as has happened with the

"Friendly Floatees" (plastic bath toys) after a container spill in 1992 (e.g. Ebbesmeyer and Ingraham 1994).

Alciopidae Ehlers, 1864

The pelagic Alciopidae are an easily recognizable group of polychaetes which clearly belong to the Phyllodocida, but sometimes are treated only as a part of the benthic Phyllodocidae (Pleijel 2001k; Halanych et al. 2007). The two family-level taxa are closely related; possibly, the alciopids are derived from a subgroup of the phyllodocids (Dales 1955), in which case the latter would be paraphyletic unless the former are included (Fauchald and Rouse 1997). However, the Alciopidae are clearly distinguished from the Phyllodocidae by their large, complex spherical eyes with an internal lens (Wu and Hua 1994; Fauchald and Rouse 1997). Furthermore, they have an eversible pharynx with at least one pair of papillae or lateral horns for grasping prey (Wilson 2000a).

The Alciopidae are active swimmers that are generally common in tropical and warm temperate oceans from surface waters to a depth of at least 300 m (Rice 1987), but the genus *Vanadis* Claparède, 1870 is also known from deep water (Eliason 1951). They are considered holopelagic carnivores, capturing prey with the eversible proboscis, feeding on crustaceans (copepods and euphausiaceans) and pelagic tunicates (thaliaceans), and probably hunting by sight (Fauchald and Jumars 1979). In most taxa the animals are transparent or semi-transparent, but this is not the case in the species examined here.

The only alciopid collected in the present study is an incomplete single specimen of *Alciopa reynaudii* Audouin & Milne Edwards. This species was previously reported as a cosmopolitan living holopelagically in surface waters (e.g. Audouin and Milne Edwards 1833; Greeff 1876; Levinsen 1885; McIntosh 1885; Apstein 1900; Reibisch 1905; Monro 1930, 1936; Støp-Bowitz 1948, 1992; Dales 1957a; Tebble 1960; Pettibone 1963; Day 1967; Dales and Peter 1972; Uschakov 1972). The specimen reported here was collected with an Agassiz trawl not provided with a closing mechanism; see the "Remarks" below.

Alciopa Audouin & Milne Edwards, 1833

Alciopa reynaudii Audouin & Milne Edwards, 1833

(Figs. 7, 8)

Alciopa "Reynaudii" [nomen nudum]—Audouin and Milne Edwards (1830, p. 202)

Alciopa Reynaudii Audouin & Milne Edwards, 1833—Audouin and Milne Edwards (1833, p. 238; pl. 15, figs. 6–11)

Greeffia oahuensis McIntosh, 1885—McIntosh (1885, p. 182; pl. 28, figs. 5–7; pl. 32, fig. 11; pl. 15A, fig. 4)

Nauphanta celox Greeff, 1876—Greeff (1876, p. 69; pl. 3, figs. 40–42; pl. 4, figs. 43–55)

Nauphanta "spectabilis" [incorrect (alternative) original spelling for *Nauphanta celox*]—Greeff (1876, p. 56)

Material examined

See Appendix 1.

Diagnosis

Prostomium with reduced median antenna; three pairs of cirri on anterior three segments (1 + 1 + 1); parapodia of segment four reduced and without chaetae; each parapodium with two cirriform appendages distally; dorsal and ventral cirri foliaceous; dorsal segmental glands and additional swollen vesicles present; chaetae compound spinigers; proboscis with one pair of lateral horns.

Description

Body at least 11 mm long with at least 25 chaetigers; pale brownish with distinct dorsal and ventral ridges and significant musculature. Darker pigmented regions on posterior border of prostomium, segmental ridges and segmental glands, which occur at parapodial bases (Fig. 7A, B, D).

Prostomium small rectangular and not projecting in front of eyes, with three antennae and two palps (Fig. 7A). Frontal pair of antennae and the two palps all short, conical, and of about same length; antennae inserted latero-dorsally and palps latero-ventrally; median antenna is reduced to a swollen ridge in dorsal groove between eyes (Fig. 7A). Large complex spherical eyes with internal globular lenses, directed laterally (Fig. 7A, D). Nuchal organs might be present, but are not conspicuous.

Proboscis eversible, without jaws but with one pair of distally located grasping fleshy lateral horns and a membraneous margin between them (Fig. 7A, D).

Anterior three segments each with one pair of tentacular cirri, of which the second is the longest; anterior two pairs of cirrophores inserted more dorsally and third one more ventrally (Fig. 7A).

All parapodia uniramous, but first pair reduced and lack chaetae (Figs. 7A). Parapodia well developed from segment five onwards, with a conical lobe terminating distally in two small cirriform appendages; upper one slightly longer than lower one (Fig. 7B). Dorsal and ventral cirri massive, foliaceous, covering parapodia almost completely; dorsal ones slightly larger and more

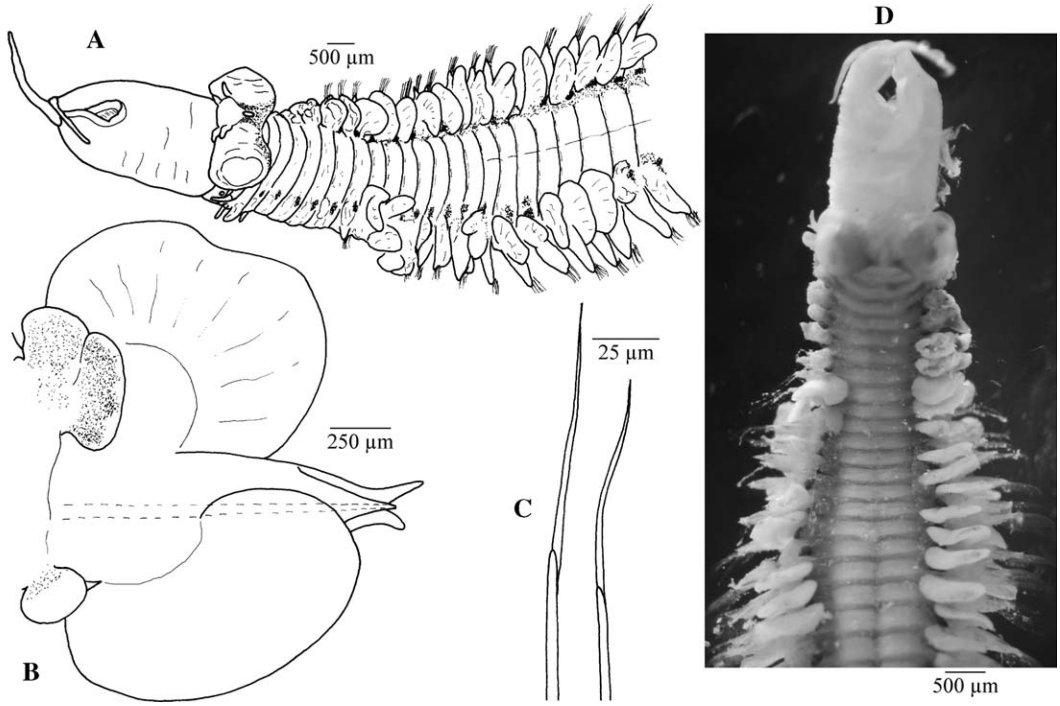

Fig. 7. *Alciopa reynaudii* Audouin & Milne Edwards. (A) Anterior end with everted proboscis; dorso-lateral view. (B) Right parapodium of mid-body; posterior view, chaetae omitted. (C) Chaetae. (D) Light micrograph of anterior end with everted proboscis; dorsal view. (A–D: ZMH 24926).

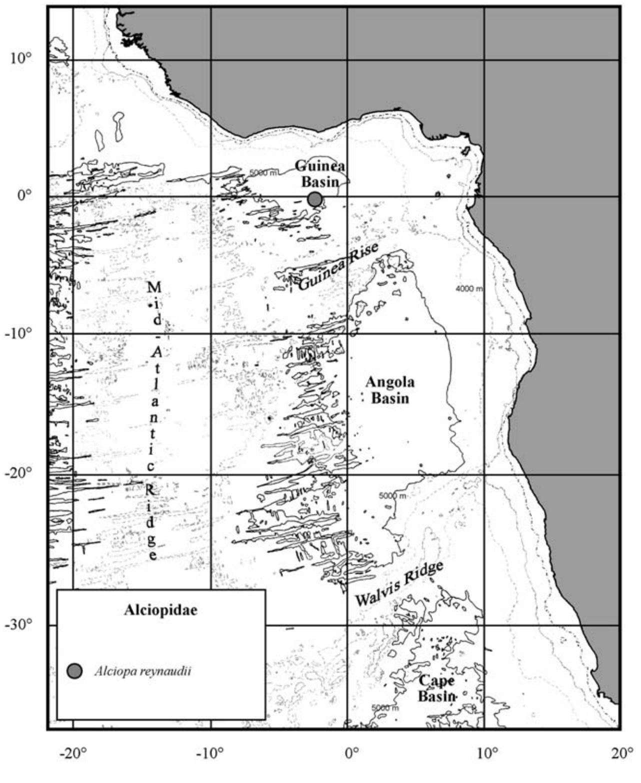

Fig. 8. Distribution of *Alciopa reynaudii* in the studied region.

oval than ventral ones; both inserted near noto- or neuropodial base (Fig. 7B). Dark cushion-shaped dorsal segmental glands are present behind dorsal cirri from segment four (Fig. 7A, D); additional swollen vesicles above and below the parapodium starting from about chaetigers 10–12; upper ones are slightly pigmented and lower ones colourless (Fig. 7C).

With exception of reduced first pair of parapodia, all other ones with one straight acicula, which barely extending beyond tip of lobe (Fig. 7B), and numerous smooth, translucent compound spinigers with very long shafts and shorter blades (Fig. 7C), which are arranged in a dense, fan-shaped fascicle.

Posterior end and pygidium not preserved.

Distribution

Guinea Basin; 5052–5054 m (Fig. 8); but see "Remarks".

Remarks

As the corresponding sample was taken using an Agassiz trawl not provided with a closing mechanism, it is unclear whether the specimen of this presumably pelagic species was captured near the bottom or during the vertical haul of the gear.

Amphinomidae Lamarck, 1818

The Amphinomidae and the closely related Euphrosinidae Williams, 1851 together constitute a monophyletic clade which occupies an 'isolated' position within the Annelida (Pleijel 2001a). Typical apomorphies are calcareous chaetae, rasp-like eversible proboscis, and caruncle (Hutchings 2000a; Pleijel 2001a). Nevertheless, the two groups can be separated by the structure of the notopodia, which are circular compact lateral lobes in amphinomids but elliptical transverse dorsal lobes in euphrosinids (Fauchald 1977a). Furthermore, molecular data strongly support their sister-group relationship (Wiklund et al. 2008).

The Amphinomidae are generally common in shallow tropical and subtropical areas, but a few species are also represented in polar habitats and deep water (Kudenov 1995). They are usually considered to be active predators feeding on soft-skinned sessile animals such as sponges, hydroids and ascidians, rasping and possibly squeezing food material with their muscular eversible proboscis (Day 1967). However, sand and mud-associated species might be carrion-feeders (Fauchald and Jumars 1979), and some are parasites of echinoids or cirripeds (Emson et al. 1993; Kudenov 1995). Most of these animals are strongly coloured, but this is not the case for the abyssal species examined in this study.

Paramphinome australis Monro is a well known taxon from Antarctic and Subantarctic regions recorded from subtidal to abyssal depths (e.g. Hartman 1964, 1967, 1978; Averincev 1972; Orensanz 1972; Kudenov 1993; Knox and Cameron 1998). *Bathychloeia sibogae* Horst is known only through its original description from deep water in the Banda Sea (Horst 1910, 1912) and from abyssal regions in the Tasman Sea and off Kenya (Kirkegaard 1995). In addition to the above two taxa, a new species of *Bathychloeia* Horst is described below.

Key to amphinomid species from the abyssal SE Atlantic

1. Body short and ovate, maggot-like (Figs. 9A; 10A, B; 12A, 13B); well developed caruncle present, extending from posterior margin of prostomium (Figs. 9A, 10C, 12A, 13C); branchiae pinnate (Figs. 9A, C; 12A); chaetae usually all bifurcate (Figs. 9D; 10D; 12D, E; 13D–F) 2

– Body elongate (Fig. 15A); caruncle reduced and partially covered by first chaetigerous segment (Fig. 15A, B); branchiae arborescent (Fig. 15C); chaetae of various types, including special curved hooks in notopodia of 1st chaetiger (Fig. 14F, G) .... *Paramphinome australis* Monro

2. Anterior five notopodia with two cirri per ramus (Figs. 9A, 10A); branchiae confined to chaetigers 6–10 (Fig. 9A); caruncle with folded margins (Figs. 9A, 10C); parapodia with only a few chaetae (Fig. 10A) .... *Bathychloeia balloniformis* sp. nov.

– All notopodia with two cirri per ramus (12A); branchiae from chaetiger 5 (Fig. 12A); caruncle wedge-shaped, laterally with more or less distinct undulating margins (Fig. 12A); parapodia with numerous chaetae (Fig. 13A) .... *Bathychloeia sibogae* Horst

Bathychloeia Horst, 1910

Bathychloeia balloniformis sp. nov.

(Figs. 9–11, 16)

Etymology

The species epithet refers to the shape of the body resembling a zeppelin airship. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 89 ES-S, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii.2005, 5137–5141 m; holotype: cs/7.0/12/1.9/1.5 (ZMH P24929); paratypes: cs/5.8/12/1.2/1.0, cs/4.1/11/1.0/0.9, cs/1.4/9/0.5/0.4 (ZMH P24930 A); cs/1.7/9/0.6/0.5 (ZMH P24930 B, on SEM stub).

Additional material. See Appendix 1.

Diagnosis

Body short and ovate, maggot-like; well developed caruncle, extending to 3rd chaetiger; anterior five notopodia with two cirri per ramus; branchiae pinnate, confined to chaetigers 6–10; a few bifurcate chaetae with serrated long prongs.

Description

Body up to 7.0 mm long with up to 12 chaetigers; oval and broadly elliptical in cross section; slightly tapering

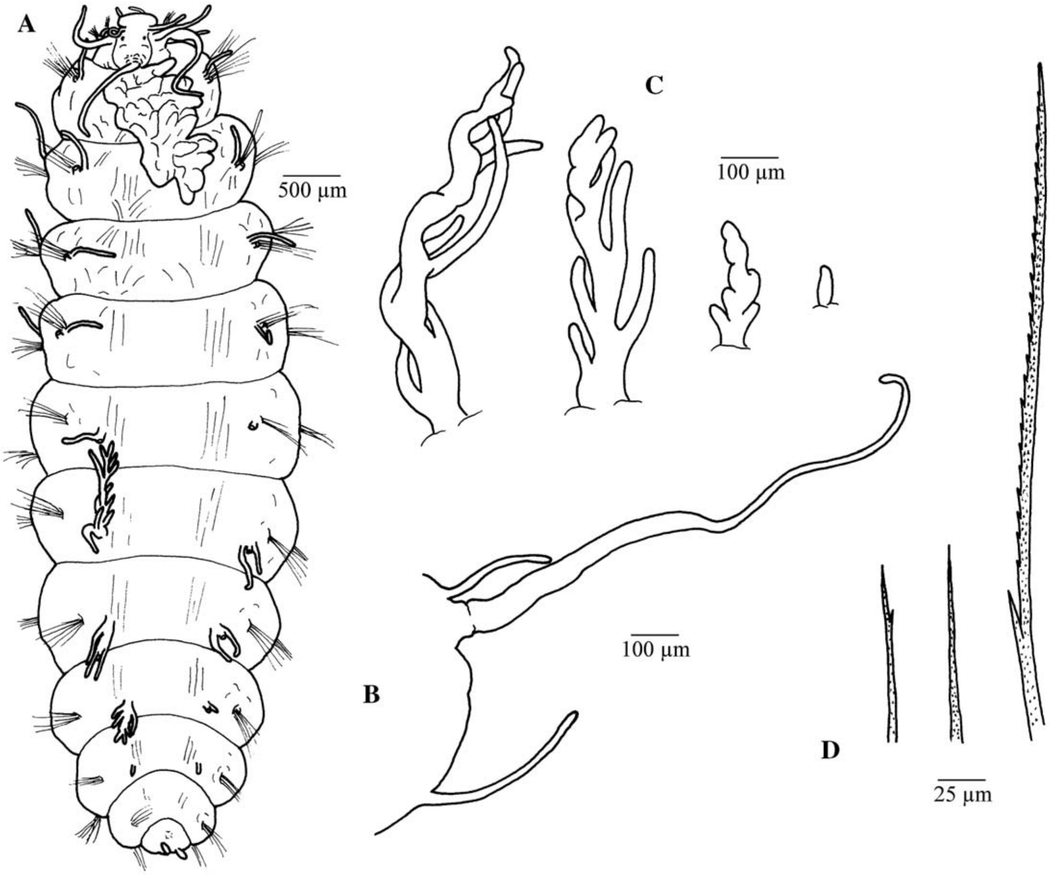

Fig. 9. *Bathychloeia balloniformis* sp. nov. (A) Complete specimen; dorsal view. (B) Left parapodium of chaetiger 3; anterior view, chaetae omitted. (C) Branchiae. (D) Chaetae. (A: ZMH P24929; B, D: ZMH P24927 A; C: ZMH P24930 A).

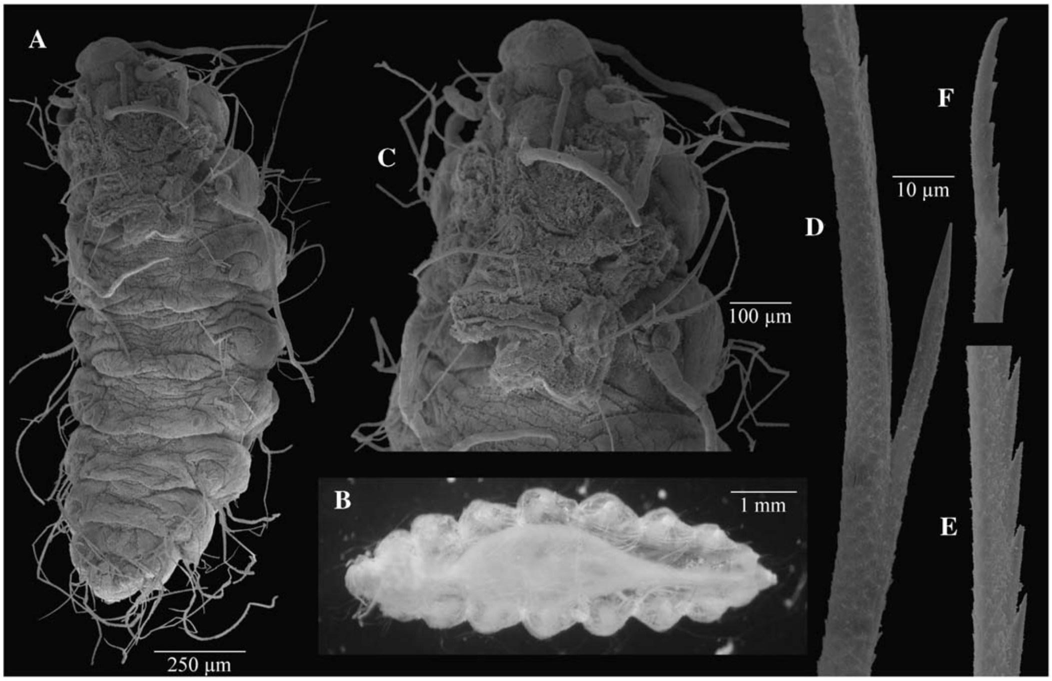

Fig. 10. *Bathychloeia balloniformis* sp. nov. (A) Complete specimen; dorsal view. (B) Light micrograph of complete specimen; dorsal view. (C) Anterior end; dorsal view. (D) Basal part of chaeta. (E) Middle part of chaeta. (F) Distal part of chaeta. (A, C–F: ZMH P24930 B; B: ZMH P24929).

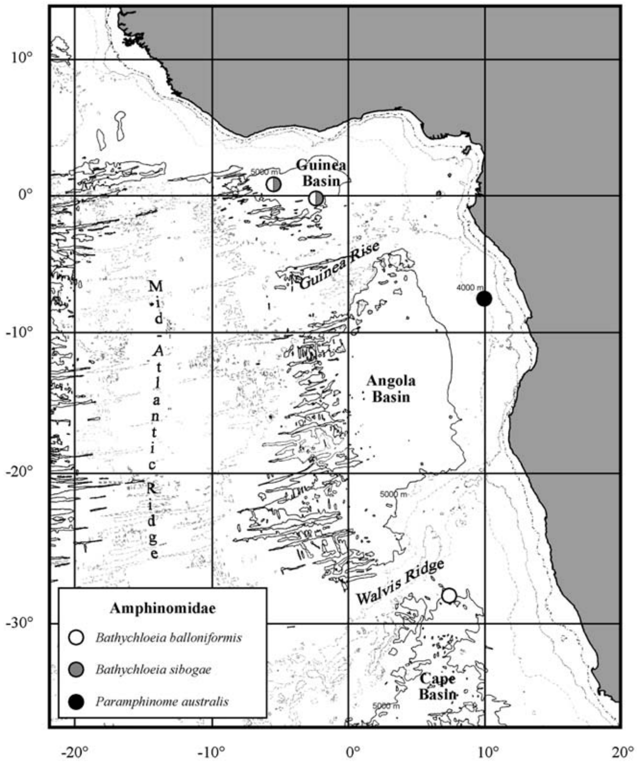

Fig. 11. Distribution of amphinomid species in the studied region.

anteriorly and posteriorly (Figs. 9A; 10A, B). Segments deeply cut along body, with transverse ridge patterns. Colourless except anterior part of prostomium, which is sometimes darkly pigmented dorsally and ventrally.

Prostomium indistinctly divided into an anterior and posterior lobe; tightly surrounded by reduced first chaetigerous segment (Figs. 9A, 10A). Anterior lobe broadly rounded, bearing a mediodorsal pair of digitiform antennae plus a pair of subequal or slightly shorter ventrolateral palps (Fig. 9A). Posterior lobe about as long as wide, with a much longer median antenna, inserted on the posterior part (Figs. 9A; 10A, C); a few specimens with two pairs of small eyes, anterior pair larger than posterior one, latter often completely absent (Fig. 9A); usually an additional pair of brownish, eye-resembling spots at the base of the palps. Prostomium posteriorly extended into a conspicuous caruncle, reaching end of 3rd chaetiger; large, ramified and with folded margins (Figs. 9A, 10C).

Proboscis eversible, sac-like, unarmed.

All parapodia biramous with distinctly separated rami, but without noto- or neuropodial lobes (Fig. 9A–C). Anterior five chaetigers with two cirri (dorsal and lateral) per notopodium which are both lacking afterwards (Fig. 9A, B), although dorsal cirrus present on 6th chaetiger in a few specimens; dorsal cirrus enlarged and more filiform in first chaetiger, about two times longer than more slender and digitiform following ones; inserted above notochaetae (Fig. 9A); lateral cirrus with short cirrophore and slender filiform cirrostyle, which is very long in chaetigers 1–3 (Figs. 9B; 10A, C); always distinctly thicker and longer than dorsal cirrus; inserted medially behind notopodial chaetae (Fig. 9B). Ventral cirri of first two chaetigers enlarged and filiform, second one the largest; following five to seven decreasing in size and more digitiform (Fig. 9A, B) to conical or oval; absent in a few posterior parapodia; about as long as upper dorsal cirri or slightly longer; inserted near neuropodial base (Fig. 9B). Bipinnate branchiae numbering five pairs, starting from 6th chaetiger and extending back to chaetiger 10 (Fig. 9A, C); depending on body size, therefore, juveniles may lack or have only a few pairs of simple or slightly ramified branchiae (Fig. 10A); first pair usually larger than following ones, with a large primary axis and up to seven lateral branches; inserted posteriorly above dorsal cirri (Fig. 9A).

Aciculae not observed, possibly lacking. Some large simple, bifurcate noto- and neurochaetae arising directly from body wall, with serrated long prongs (Figs. 9D, 10D–F); often broken or not completely everted; whole surface of chaetae with small file-like teeth or asperites (Fig. 10D–F); a few additional smaller spinous chaetae, sometimes with small subdistal spur (Fig. 9D).

Pygidium with dorsal anus and a pair of subterminal conical papillae (Fig. 9A).

Distribution

Cape and Guinea Basins; 5048–5144 m (Fig. 11).

Discussion

Bathychloeia balloniformis sp. nov. is the only member of the genus with dorsal and lateral cirri limited to the anterior part of the body and with bipinnate branchiae starting from chaetiger six.

Bathychloeia sibogae Horst, 1910

(Figs. 11–13, 16)

?*Chloenea atlantica* McIntosh, 1885—McIntosh (1885, p. 15; pl. 1, fig. 4; pl. 1A, figs. 10–13)

Bathychloeia sibogae Horst, 1910—Horst (1910, p. 175); Horst (1912, p. 25; pl. 8, figs. 12–17)

?*Chloenopsis atlantica* (McIntosh)—Fauchald (1977a, p. 102)

Material examined

Type material. Bathychloeia sibogae: H.M. SIBOGA St. 211, Banda-Sea, 5°40.7′S 120°45.5′E, 1158 m; holotype: cs/7.5/16/3.2/2.7 (ZMA V.Pol. 124). *Chloenea atlantica*: HMS Challenger St. 3, S of Canaries, 25°45′N 20°14′W, 18.ii.1873, 1525 fms, hard ground;

syntypes: cs/14/19/4.7/4.0, af/4.5/7/4.0/3.5, pf/6.0/10/4.2/3.8 (BMNH 1885.12.1.11).

Additional material. See Appendix 1.

Diagnosis

Body short and ovate, maggot-like; well developed caruncle, extending to chaetigers 3–4; all notopodia with two cirri per ramus; branchiae pinnate, present from 5th chaetiger, first pair enlarged; numerous bifurcate chaetae with long prongs serrated to sometimes smooth.

Description

Body up to 4.0 mm long with up to 12 chaetigers; oval and broadly elliptical in cross section; tapering anteriorly and posteriorly (Figs. 12A, 13B). Segments slightly cut along body, without distinct transverse ridge patterns. Colourless except anterior part of prostomium, which is sometimes darkly pigmented dorsally and ventrally.

Prostomium indistinctly divided into an anterior and a posterior lobe; tightly surrounded by reduced first chaetigerous segment (Fig. 13C). Anterior lobe rounded, bearing a pair of mediodorsal digitiform antennae plus a pair of slightly shorter ventrolateral palps (Figs. 12A; 13A, C). Posterior lobe about as long as wide, with a distinctly longer median antenna, inserted on the posterior part (Figs. 12A; 13A, C); a few specimens with two pairs of small eyes, anterior pair slightly larger than posterior one (Figs. 12A, 13B); sometimes an additional pair of brownish, eye-resembling spots at the base of the palps. Prostomium posteriorly extended into a conspicuous caruncle, reaching chaetigers 3–4; wedge-shaped with undulated lateral margins on upper plate and smooth margins on lower one (Fig. 12A), thinner with smooth margins in smaller specimens (Fig. 13C).

Proboscis retracted in all specimens, not examined.

All parapodia biramous with distinctly separated rami, but without noto- or neuropodial lobes (Fig. 12A–C). Dorsal and lateral cirri slender and filiform, present on all notopodia; dorsal cirrus inserted above notochaetae, always distinctly shorter than lateral cirrus, which is inserted medially behind notopodial chaetae (Fig. 12B, C), and often coiled especially in posterior parapodia (Fig. 12A). Ventral cirri of first two chaetigers enlarged and filiform, second one the largest; both distinctly longer than dorsal and lateral cirri (Fig. 12B); following five to eight ventral cirri (depending on body size) much shorter and more digitiform (Fig. 12C); absent from last few posterior neuropodia; inserted near neuropodial base (Fig. 12B, C). One pair of bipinnate branchiae on 5th chaetiger, with a large primary axis and up to seven lateral branches; absent in juveniles or present as simple (Fig. 13A) to slightly ramified processes; inserted posteriorly and medial to notopodial dorsal cirri (Fig. 12A, C).

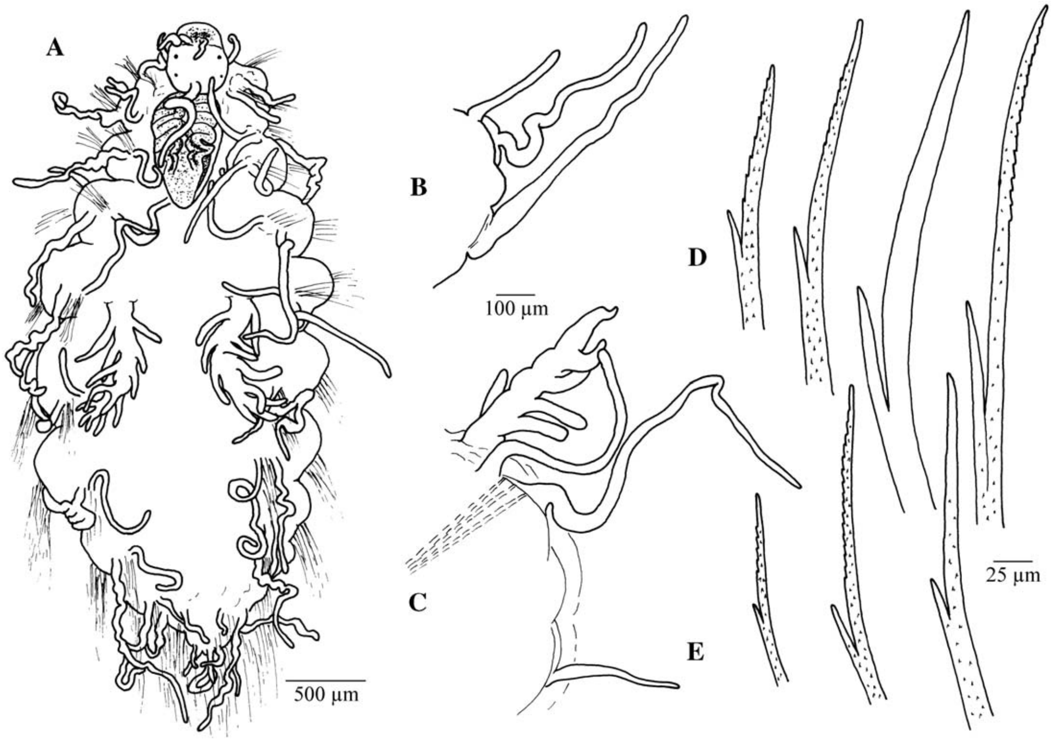

Fig. 12. *Bathychloeia sibogae* Horst. (A) Complete specimen; dorsal view, chaetae partly omitted. (B) Left parapodium of chaetiger 2; anterior view, chaetae omitted. (C) Left parapodium of chaetiger 5; anterior view, chaetae omitted. (D) Notochaetae. (E) Neurochaetae. (A: SMF 18801; B–E: ZMH P24932 C).

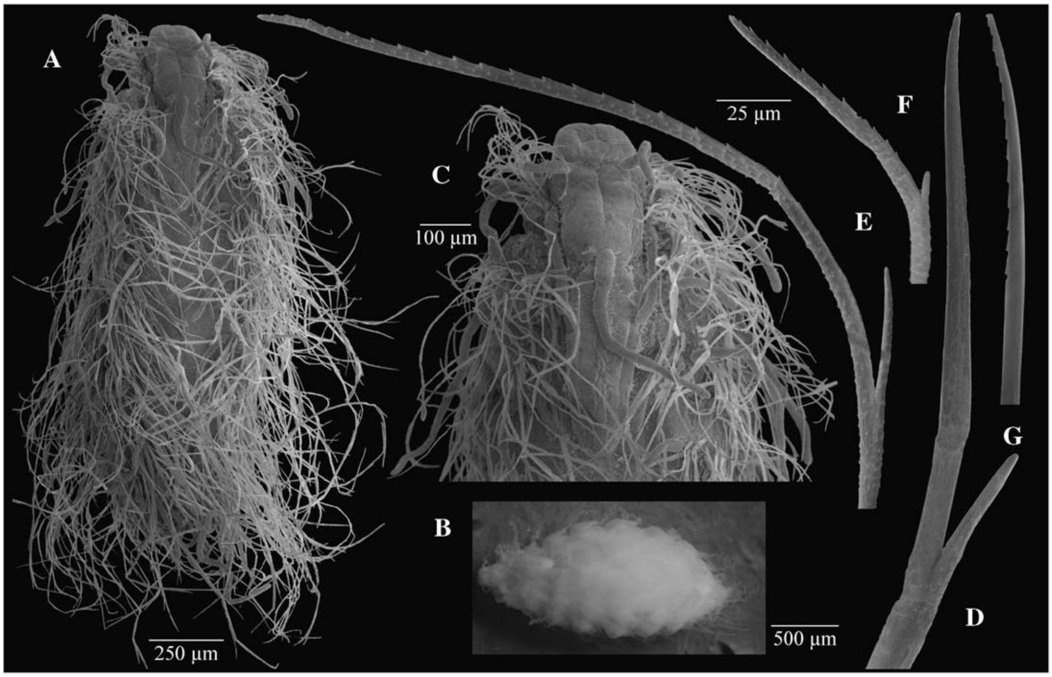

Fig. 13. *Bathychloeia sibogae* Horst. (A) Complete specimen; dorsal view. (B) Light micrograph of complete specimen; dorsal view. (C) Anterior end; dorsal view. (D) Smooth notochaeta. (E, F) Chaetae with serration along inner border. (G) Long prong of notochaeta with serration along outer border. (A, C–F: ZMH P24932 B; B: SMF 18801).

Notopodia in mid-body with up to three pointed aciculae (Fig. 12C), other noto- and all neuropodia probably without aciculae or aciculae inconspicuous. Numerous simple, bifurcate chaetae (Figs. 12D, E; 13D–G), with long prongs typically serrated along normal cutting surface (Figs. 12D, E; 13E, F) or sometimes smooth (Figs. 12D, 13D); a few notochaetae of posterior parapodia with long prongs serrated along outer border (Figs. 12D, 13G); except for largest bristles (Fig. 13D), whole surface of chaetae with small file-like teeth or asperites (Fig. 13E, F); notopodia with chaetae much larger and usually thicker than those of neuropodia (Fig. 12D, E); chaetae directly arise from body wall and more or less covering posterior part of dorsum (Fig. 13A).

Pygidium with dorsal anus and a pair of terminal conical to digitiform papillae (Fig. 12A).

Distribution

Guinea Basin; 5048–5144 m (Fig. 11).

Discussion

The examined specimens generally agree well with the holotype (ZMA V.Pol. 124) of *Bathychloeia sibogae* Horst from the Banda Sea and with the material reported by Kirkegaard (1995) from the Tasman Sea and off Kenya. However, the SE Atlantic material consists of smaller individuals which are lacking even the one pair of enlarged branchiae of the 5th chaetiger that is characteristic on larger individuals. The syntypes (BMNH 1885.12.1.11) of *Chloenopsis atlantica* (McIntosh) from the NE Atlantic, with similar branchiae and also two notopodial cirri, possibly are larger individuals belonging to the same species. However, pending confirmation from additional material, the corresponding synonymy is not enacted here.

Paramphinome M. Sars in G.O. Sars, 1872

Paramphinome australis Monro, 1930

(Figs. 11, 14–16)

Paramphinome australis Monro, 1930—Monro (1930, p. 32, fig. 3a–g)

Material examined

See Appendix 1.

Diagnosis

Body elongated; eyes absent; caruncle reduced and partially covered by first chaetigerous segment; branchiae arborescent, beginning on chaetiger four, numbering 4–15 pairs; chaetae of various types, including special curved hooks in notopodia of chaetiger one.

Description

Body up to 7.4 mm long with up to 31 chaetigers; elongate and subrectangular in cross section. Segments

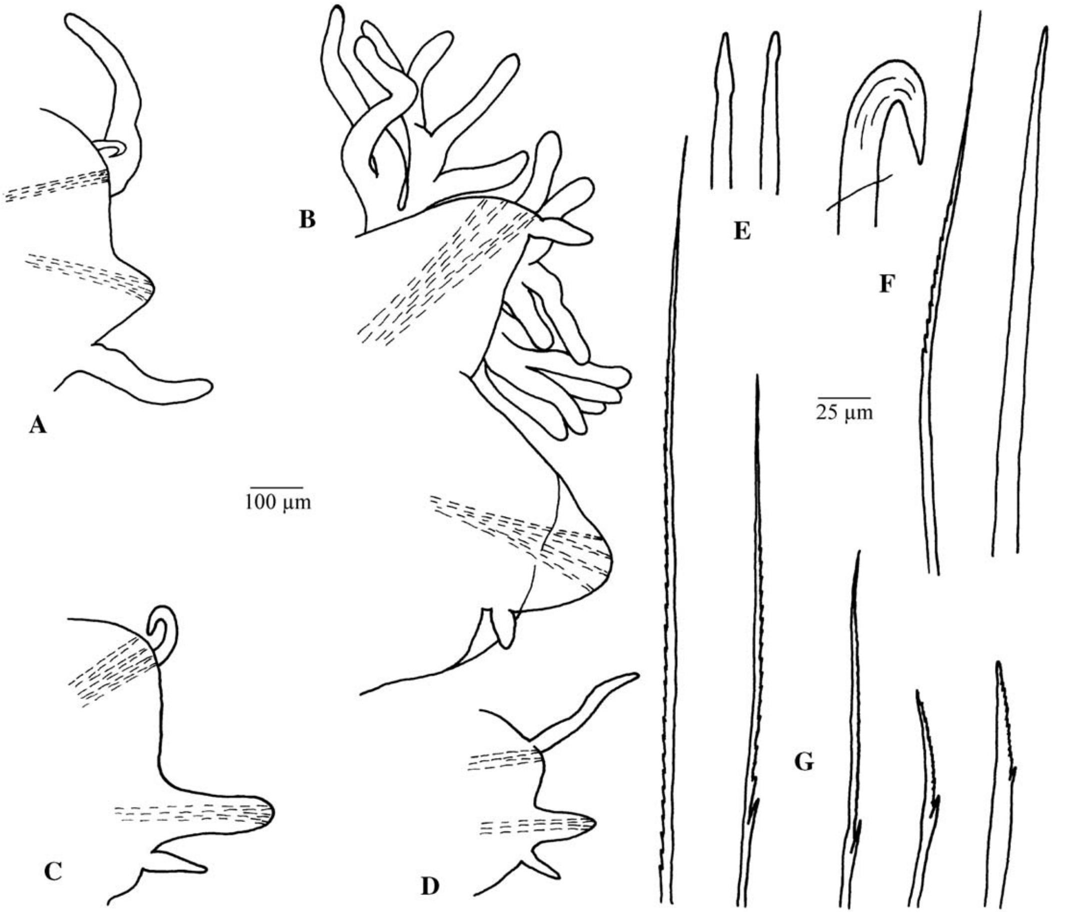

Fig. 14. *Paramphinome australis* Monro. (A–D) Anterior to posterior parapodia; anterior view, chaetae omitted. (E) Noto- and neuropodial acicula. (F) Notopodial chaetae. (G) Neuropodial chaetae. (A–G: ZMH P24947 B).

deeply cut along body, with distinct transverse ridge patterns and small median ciliary bands located dorsally and between noto- and neuropodia (Fig. 15A, C).

Prostomium divided into an anterior and a posterior lobe, both with short ciliary bands; tightly surrounded by reduced first chaetigerous segment. Anterior lobe broadly rounded, bearing a pair of digitiform antennae and a pair of subequal lateral palps, all indistinctly articulated and arranged approximately on the same level (Fig. 15A, B). Posterior lobe wider than long, with median antenna of same size as other appendages, inserted on its posterior part; eyes absent; posteriorly extended into an inconspicuous caruncle (Fig. 15A, B). Caruncle resembling a small low-lying lobe, which is densely ciliated and divided into a median keel and two lower lateral lobes; partially covered by first chaetigerous segment (Fig. 15B).

Proboscis eversible, sac-like, unarmed, with series of transverse ridges (Fig. 15A).

All parapodia biramous with distinctly separated rami (Figs. 14A–D, 15A). Notopodia short rounded and neuropodia with longer conical lobes (Fig. 14A–D). Dorsal cirri of 1st chaetiger elongate and digitiform (Fig. 14A), thereafter becoming much shorter and more conical in shape (Fig. 14B, C) until the last few posterior notopodia, where cirri again become elongate and digitiform (Fig. 14D); inserted behind notopodial chaetae (Fig. 15C) and in mid-body below aciculae (Fig. 14B, C). Ventral cirri of 1st chaetiger enlarged and digitiform, absent from 2nd chaetiger, following ones distinctly shorter and more conical; always slightly shorter than corresponding dorsal cirrus; inserted near neuropodial base (Fig. 14A–D). Depending on body size, up to seven pairs of tuft-like branchiae each with up to 15 ciliated rami, present from 4th chaetiger up to chaetiger 10, juveniles with only a few pairs of simple or slightly ramified branchiae; inserted posterior to dorsal cirri (Figs. 14B; 15A, C).

Noto- and neuropodia with up to four subdistally inflated aciculae (Fig. 14E) and numerous simple chaetae. Notochaetae are arranged in dorsal radiating circular whorls (Fig. 15C) and include three kinds of chaetae per fascicle (Fig. 14F): 1. up to three (usually two) strongly curved hooks, which are only present in 1st chaetiger;

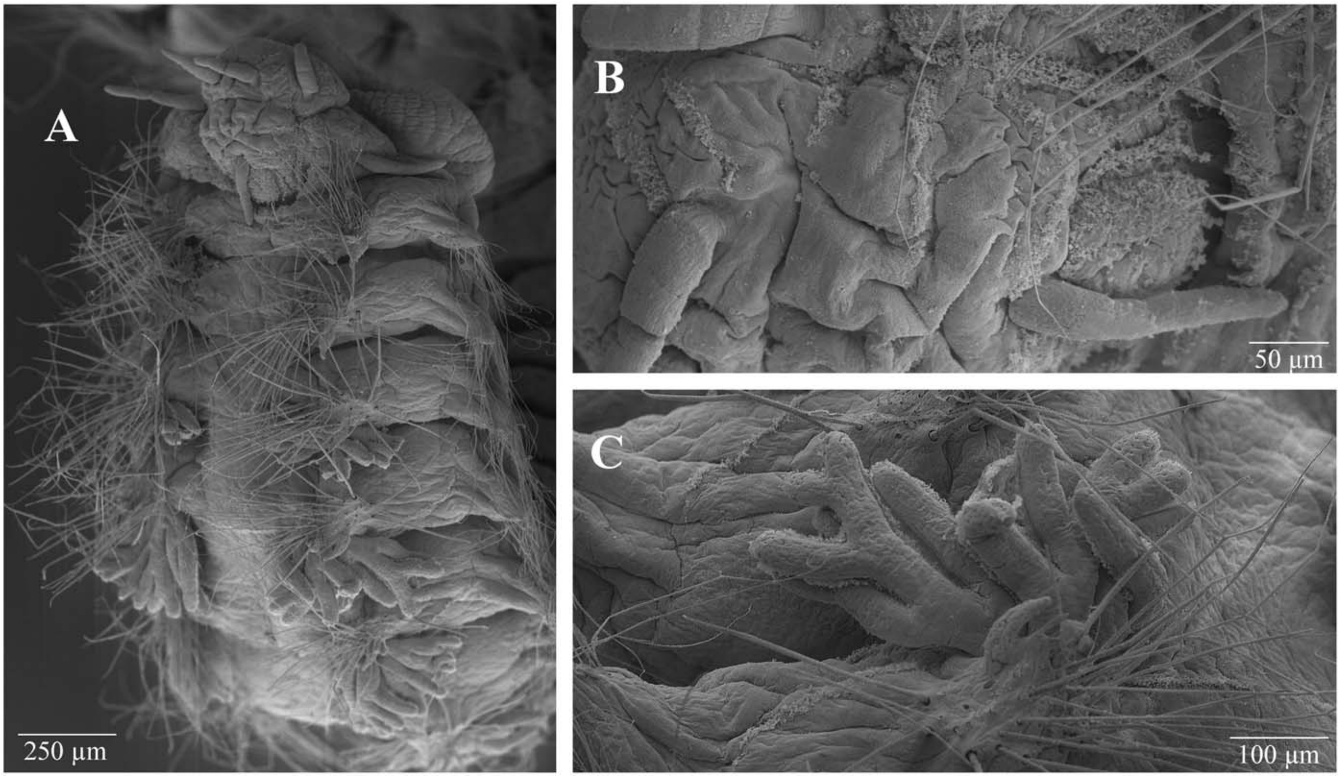

Fig. 15. *Paramphinome australis* Monro. (A) Anterior end; dorsal view. (B) Prostomium with caruncle; dorso-lateral view. (C) Right branchia of chaetiger 5; anterior view. (A–C: ZMH P24935 A).

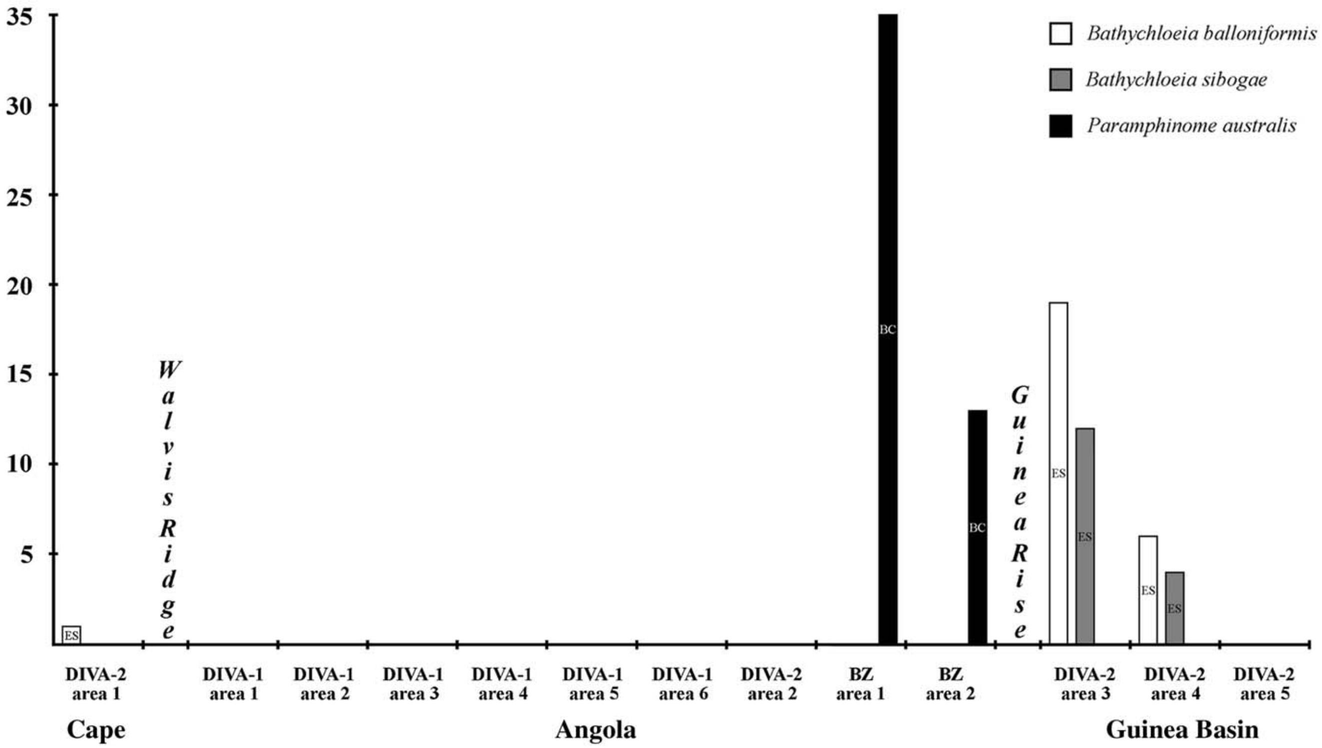

Fig. 16. Abundance of the three amphinomid species in the sampling areas; only complete specimens or anterior fragments counted. BC = box corer; ES = epibenthic sledge.

2. slender capillaries, which are finely serrated; 3. smooth spines, with thicker ones in outer and thinner ones in inner positions. Neurochaetae extend laterally from the body (Fig. 15A) and include three kinds of chaetae per fascicle (Fig. 14G): 1. slender capillaries, which are finely serrated; 2. similar but slightly shorter capillaries, with long basal spurs; 3. a few small and subdistally inflated bifurcate chaetae, with long prongs distinctly serrated.

Pygidium with dorsal anus and a single terminal oval papilla.

Distribution

Angola Basin; 3945–3993 m (Fig. 11).

Abundance of Amphinomidae

A total of 90 specimens and 2 fragments of amphinomids were found in the investigated basins. Most of them (49) belong to *Paramphinome australis*. This species was only present in the BIOZAIRE box corer material (Fig. 16), with the highest abundance in area 1. *Bathychloeia balloniformis* sp. nov. and *B. sibogae* were sampled only with the epibenthic sledge. Most of the 27 *B. balloniformis* sp. nov. and 16 *B. sibogae* specimens and fragments were from the Guinea Basin, especially from DIVA-2 area 3, although one additional individual of the former was taken in the Cape Basin.

Aphroditidae Kinberg, 1856

The Aphroditidae are easily recognized polychaetes which clearly belong to the Phyllodocida. No apomorphies for the group are known (Pleijel 2001b), but its members are characterized by the presence of elytra, which in some species are covered by a highly iridescent mat of felt-like chaetae, hence the common name 'sea mice' (Hutchings 2000b; Pleijel 2001b).

The Aphroditidae are slow-moving polychaetes which are distributed worldwide and inhabit especially soft muddy bottoms, from the intertidal to abyssal depths (Day 1967; Hutchings 2000b; Pleijel 2001b). They are usually considered carnivores, feeding on large active polychaetes (Mettam 1980) as well as on sedentary invertebrates (Fauchald and Jumars 1979), but some taxa seem to be deposit-feeders (Day 1967). In *Laetmonice* Kinberg, the gut is often distended by foraminiferans (Day 1967), but this has not been confirmed for the species examined here.

The only member of Aphroditidae collected in the present study, *Laetmonice benthaliana* McIntosh, is a widely distributed taxon which is very common in abyssal regions. It was previously reported from abyssal depth of the Antarctic Ocean, Indian Ocean, E and S of Africa, and from the Pacific Ocean (e.g. McIntosh 1885; Uschakov 1962; Day 1963a, 1967; Hartman 1964, 1967; Averincev 1972; Levenstein 1975; Kirkegaard 1994, 1995).

Laetmonice Kinberg, 1856

Laetmonice benthaliana McIntosh, 1885

(Figs. 17–19)

Lætmonice producta var. *benthaliana* McIntosh, 1885—McIntosh (1885, p. 45; pl. 8, figs. 4, 5; pl. 4A, fig. 12; pl. 5A, figs. 1, 2)

Laetmonice benthaliana McIntosh—Uschakov (1962, p. 147; pl. 1, fig. 3)

Material examined

See Appendix 1.

Diagnosis

Dorsum without felt, covered by 15 pairs of elytra; venter with minute papillae; ventral cirri of mid-body short, not reaching base of neurochaetae; harpoon-shaped notochaetae with tuberculated shaft; neurochaetae with gap between basal spur and fringe of distal hairs.

Description

Body up to 53 mm long with up to 34 chaetigers; elongate oval. Dorsum not covered by felt (Fig. 18A). Venter and parapodia with irregularly arranged minute conical to globular papillae; appendages like median antenna, palps, dorsal and ventral cirri with tiny conical papillae (Fig. 17H).

Prostomium rounded with slightly rectangular unpigmented ommatophores reaching to about half the length of the prostomium (Fig. 17A). Median antenna with ceratophore of about same length as ommatophores and long, slender ceratostyle, which is about three times longer than prostomium (Fig. 17A). Palps very long and slender, extending ventrally to chaetiger 15 (Fig. 18B). Facial tubercle well developed; located below ceratophore and covered with numerous small cylindrical papillae (Fig. 17A).

Everted proboscis not observed, but ventrally located mouth opening with longitudinally grooved area and numerous small papillae.

15 pairs of elytra attached on elytrophores of chaetigers 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25, 28 and 31; overlapping each other and covering whole dorsum (Fig. 18A). Elytra smooth, thin, semitransparent; with some inconspicuous brownish spots in the middle (Fig. 17C, E). First pair heart-shaped with centrally attached elytrophores (Fig. 17C); following

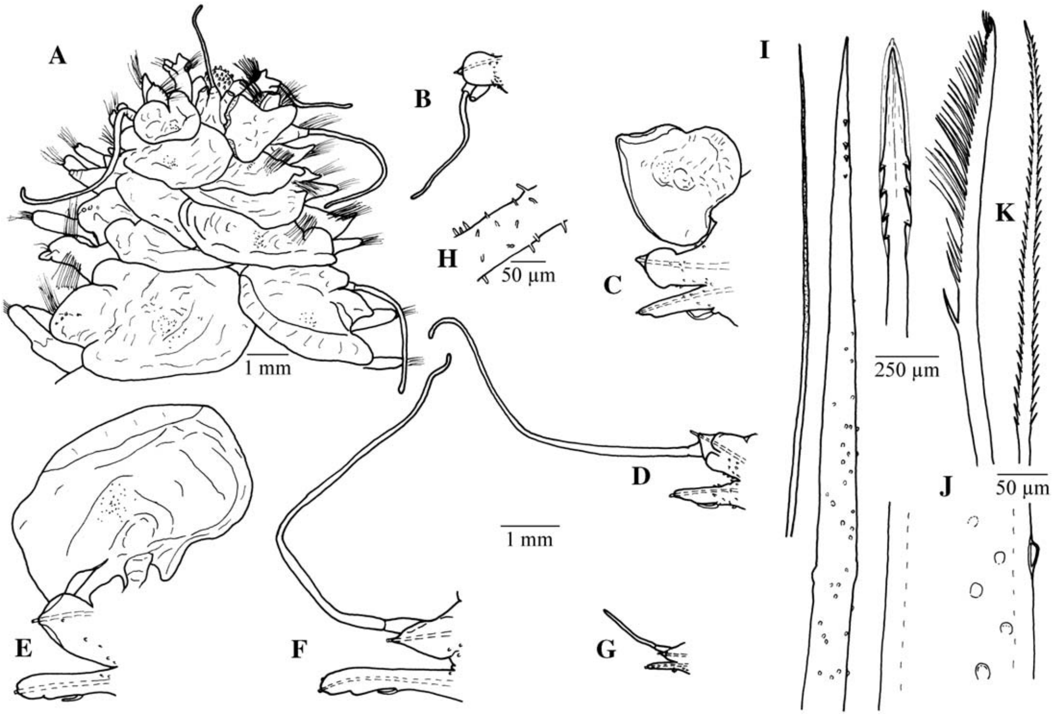

Fig. 17. *Laetmonice benthaliana* McIntosh. (A) Anterior end; dorsal view. (B–G) Respective right parapodia of chaetigers 1–3, 7, 8, 33; anterior views, chaetae omitted. (H) Papillae on cirrus from chaetiger 1. (I) Notochaetae. (J) Tubercles on harpoon-shaped chaetae. (K) Neurochaetae. (A–K: ZMH P24948 B).

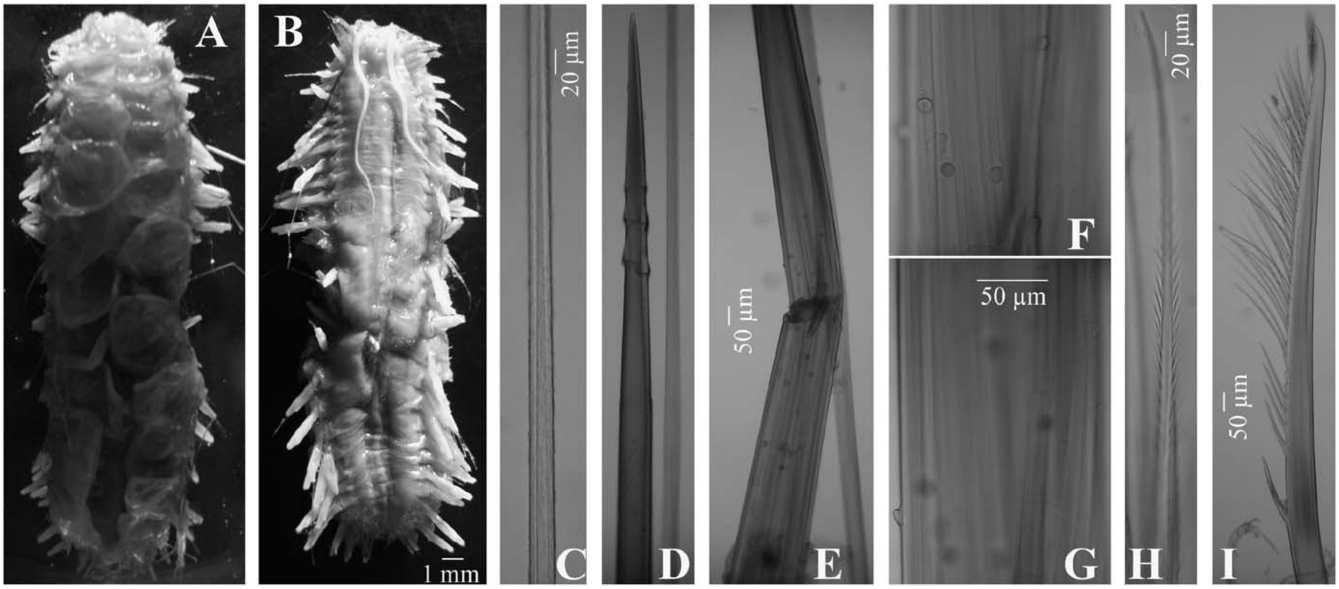

Fig. 18. *Laetmonice benthaliana* McIntosh. (A) Complete specimen; dorsal view. (B) Complete specimen; ventral view. (C) Acicular-like notochaeta. (D) Distal part of harpoon-shaped chaeta. (E) Basal part of harpoon-shaped chaeta. (F, G) Tubercles on harpoon-shaped chaeta. (H) Bipinnate neurochaeta. (I) Neurochaeta with basal spur and fringe of subdistal hairs. (A, B: SMF 18799; C–I: ZMH P24948 B).

ones much larger and more oval to leaf-shaped with elytrophores attached antero-laterally (Fig. 17E); last pair distinctly smaller.

First segment reduced and uniramous; projecting anteriorly and laterally to prostomium (Fig. 17A). Anterior lobe rounded, with small median notch and tufts of capillary chaetae emerging anteriorly and posteriorly; acicular lobe slightly longer and pointed (Fig. 17B). Posteriorly two pairs of cirri with large rectangular cirrophores and subequal long, slender

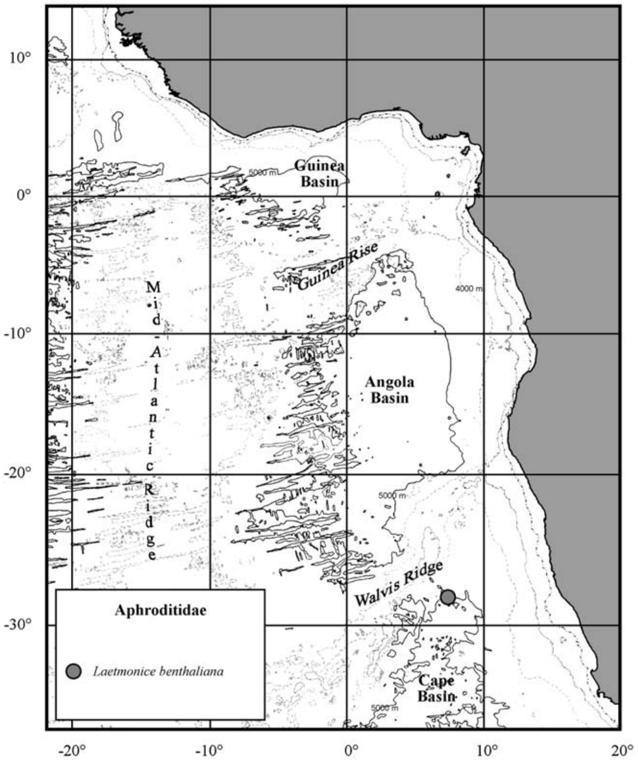

Fig. 19. Distribution of *Laetmonice benthaliana* in the studied region.

cirrostyles, which are about as long as the median antenna, but with a slightly swollen tip (Fig. 17A, B).

Following parapodia biramous, with distinctly separated rami (Figs. 17C–G). Notopodia broadly conical; shorter than more cylindrical neuropodia. Dorsal cirri present on segments lacking elytra (Fig. 17D, F, G); with large rectangular cirrophores and very long, slender cirrostyles, ending in slightly swollen tips; distinctly shorter in last parapodia (Fig. 17G); inserted posteriorly on upper side of notopodia. Ventral cirri present on all segments (Fig. 17C–G); with short cirrophores and digitiform cirrostyles, ending in tapering tips; never reaching base of inferior neurochaetae; inserted near neuropodial base of 2nd chaetiger (Fig. 17C); but more medially located on following chaetigers (Fig. 17D–G).

Each noto- and neuropodium with one acicula; extending well beyond tip of parapodia (Fig. 17B–G). Notopodia with tufts of numerous golden chaetae, which are acicular-like or fine capillary with unidentate tips and inconspicuous hairs subdistally (Figs. 17I, 18C), sometimes dorsally directed, but not forming a felt-like covering over dorsum; elytrigerous parapodia with some additional stout reddish-brown harpoon-shaped chaetae (Figs. 17I; 18D, E), with about 3–5 recurved fangs on lateral margins and tuberculated shaft (Fig. 17J; 18F, G); occasionally tips of probably regenerated chaetae covered with sheaths (Fig. 17I). Neuropodia with 3–4 brownish chaetae, with a gap between basal spur and fringe of subdistal hairs, and a slightly curved tip (Figs. 17K, 18I); 2nd, 3rd and 4th chaetigers with additional tufts of numerous small golden yellow, bipinnate chaetae (Figs. 17K, 18H).

Pygidium with dorsal anus; cirri not observed.

Distribution

Cape Basin; 5076–5089 m (Fig. 19).

Discussion

Laetmonice benthaliana McIntosh and the closely related *L. filicornis* Kinberg, 1856 from the northern hemisphere can be separated by the presence of large ventral cirri and distinct papillae on the venter of the latter species, whereas *L. benthaliana* has only minute papillae and small ventral cirri, which are not reaching the base of the neurochaetae (Day 1963a, 1967).

Chrysopetalidae Ehlers, 1864

The Chrysopetalidae are considered part of the Phyllodocida (Pleijel 2001c), but their phylogenetic position is still problematic (e.g. Pleijel and Dahlgren 1998). A possible autapomorphy is the presence of characteristic, often flattened notochaetae (= paleae), which cover the dorsum (Watson Russell 2000). However, these paleae are usually absent in some genera (*Acanthopale* San Martín, 1986; *Dysponetus* Levinsen, 1879; *Vigtorniella* Kiseleva, 1996 [replacement name for *Victoriella* Kiseleva, 1992; see Kiseleva 1996]), and a phylogenetic analysis of *Dysponetus* indicates that non-flattened chaetae represent the plesiomorphic state for the group (Dahlgren and Pleijel 1995; Dahlgren 1996; Pleijel 2001c).

The Chrysopetalidae are recorded worldwide from intertidal to sometimes abyssal depths in rocky and sandy environments, but taxa with paleae are generally restricted to temperate and tropical regions (Watson Russell 2000; Pleijel 2001c). They are usually considered as active scavengers and carnivores, but might also be semi-parasitic feeding, for example, on other invertebrates or algae, possibly piercing and sucking food material with their muscular eversible proboscis and the terminal stylet-like pair of jaws (Watson Russell 1986, 1991, 2000). Furthermore, *Vigtorniella* species are known to graze on bacterial mats covering whale bones (Dahlgren et al. 2004; Wiklund et al. 2009).

In the four species of Chrysopetalidae collected in the present study, *Dysponetus caecus* (Langerhans), *D. hesionides* sp. nov., *D. profundus* sp. nov., and

Pseudodysponetus fragmentosus gen. et sp. nov., the spines are more circular rather than typical flattened notochaetae. Previously, *Dysponetus caecus* had been reported from intertidal to subtidal depths of the NE Atlantic (e.g. Langerhans 1880; Dahlgren and Pleijel 1995; Brito et al. 1996). However, in all four species the animals are very small and fragile, thus could easily have been missed by earlier deep-water expeditions.

Key to chrysopetalid species from the abyssal SE Atlantic

1. First segment achaetous, with two pairs of cirri (Figs. 20A, B; 23A, B; 25A; 26B); numerous notopodial chaetae on all chaetigers (Figs. 20A; 23A; 24A; 25A; 26A), usually carrying two alternating rows of spines (Figs. 20D; 21C; 23D; 24B; 25D; 26C); antennae and palps uni- or biarticulated (Figs. 20A, B; 23A, B; 24A; 25A, B; 26B) 2
– First two segments achaetous, each one with one pair of cirri (Figs. 27A; 28A); up to six notopodial chaetae starting from chaetigers 5–6 (Figs. 27A; 28A), which are smooth and acicular-like (Figs. 27D; 28C); antennae and palps all biarticulated (Figs. 27A, B; 28A) .... *Pseudodysponetus fragmentosus* sp. nov.
2. Antennae and palps more or less distinctly biarticulated (Figs. 20A, B; 23A, B; 24A) 3
– Antennae and palps simple and globular (Figs. 25A, B; 26B) .... *Dysponetus profundus* sp. nov.
3. Mouth smooth, without conical appendages (Fig. 23B); dorsal cirri with short cirrophores (Fig. 23C); notopodial chaetae with two longitudinal rows of alternating spines (Figs. 23E; 24B) .... *Dysponetus hesionides* sp. nov.
– Single mouth appendage on lower lip (Fig. 20B); dorsal cirri with elongated cirrophores (Fig. 20A, C); notopodial chaetae with two longitudinal rows of large alternating spines which are integrated into one row in distal part of tip (Figs. 20D; 21C, E) .... *Dysponetus caecus* (Langerhans)

***Dysponetus* Levinsen, 1879**

***Dysponetus caecus* (Langerhans, 1880)**
(Figs. 20–22, 29)

Chrysopetalum caecum Langerhans, 1880—Langerhans (1880, p. 278; pl. 14, fig. 9a–c); Brito et al. (1996, p. 159, fig. 1E–H)

Dysponetus caecus (Langerhans)—Dahlgren and Pleijel (1995, p. 167, figs. 2–4)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae, the median one inserted antero-dorsally, and two elongated palps, all biarticulated; eyes and caruncle absent; single mouth appendage on lower lip; anterior segments formula: 1/1 + Ch1/1 + ChN/ChN; dorsal cirri with elongated cirrophores and filiform cirrostyles; ventral cirri on all chaetigers; numerous notochaetae on all chaetigers with two and distally one row of large spines, D-shaped in cross-section, paleae absent.

Description

If specimen ZMH P24950 B is really complete then body up to 4.1 mm long with up to 16 chaetigers, with indistinct dorsal ridges. Material not in good shape, with most of the appendages broken off.

Prostomium rectangular with rounded corners, slightly longer than wide, bearing three antennae and two palps; tightly surrounded by first segments (Fig. 20A, B). Two lateral antennae inserted anteriorly and one median antenna with antero-dorsal insertion; with small inconspicuous ceratophores and missing ceratostyles (Fig. 20A). Latero-ventrally palps with large palpophores and missing palpostyles (Fig. 20A, B). Eyes absent. Nuchal organs might be present, but are not conspicuous.

Pronounced conical mouth appendage on lower lip; inserted medially and directed anteriorly (Fig. 20B). Retracted proboscis extending to chaetigers 3–4, with one terminal pair of stylet-like jaws; more or less visible through body wall between chaetigers one and two.

First segment reduced and achaetous; with two pairs of large cirrophores inserted ventro-laterally and missing cirrostyles (Fig. 20A, B). Parapodia of second segment (= 1st chaetiger) uniramous with notopodial lobes, dorsal cirrophores and a few notopodial chaetae, but neuropodia only presented by ventral cirrophores of same size as in first segment (Fig. 20A, B).

Parapodia of third segment and following ones biramous, with dorsal and ventral cirri and more or less developed lobes (Figs. 20A–C, 21A). Notopodia reduced; broadly rounded with large conical to rectangular dorsal cirrophores, which are inserted posteriorly on lower side of notopodia (Figs. 20C, 21A); cirrostyles are all missing. Neuropodial lobes conical and much longer than notopodial ones, each with a biarticulated ventral cirrus (Figs. 20C, 21A). Complete ventral cirri only present in a few anterior and posterior parapodia of largest specimen

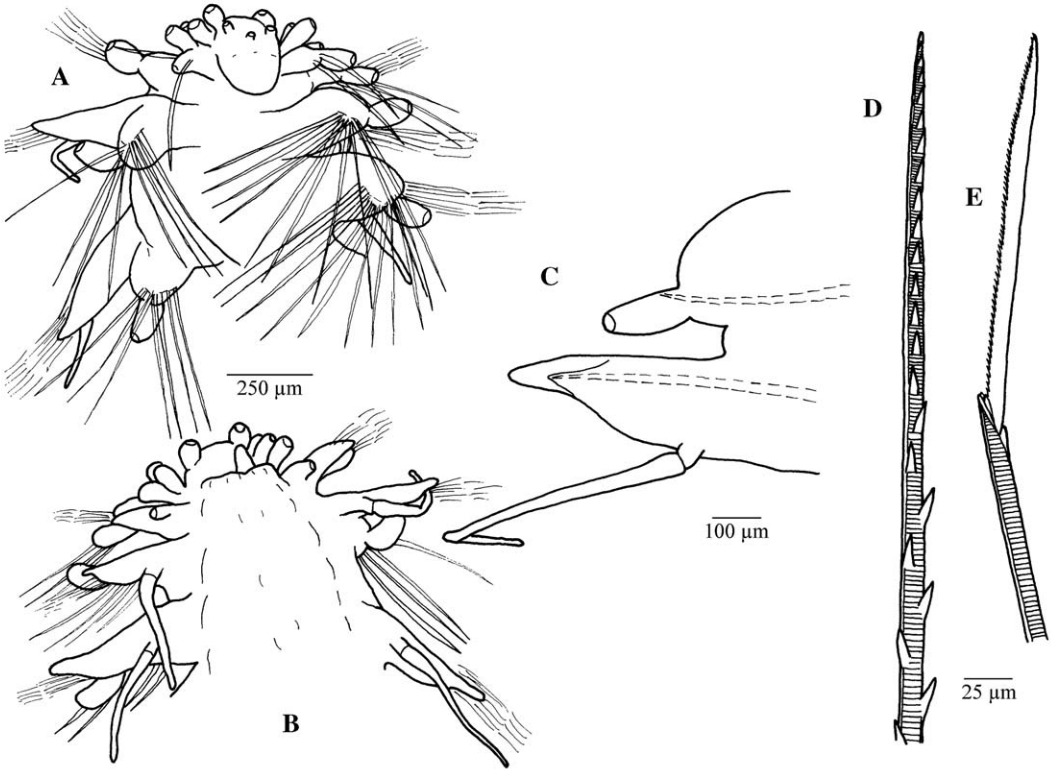

Fig. 20. *Dysponetus caecus* (Langerhans). (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Left parapodium of chaetiger 8; posterior view, chaetae omitted. (D) Notopodial chaeta; frontal view. (E) Neuropodial chaeta. (A–E: ZMH P24950 B).

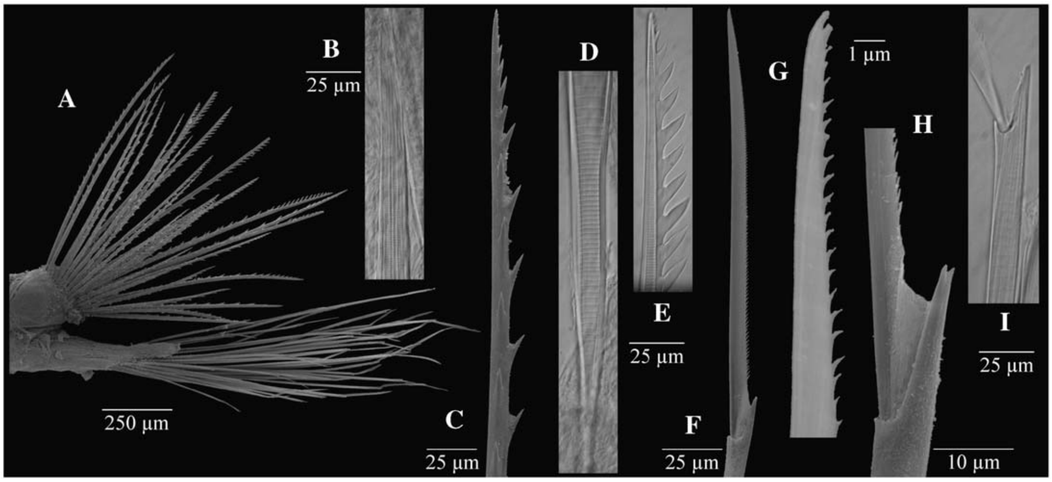

Fig. 21. *Dysponetus caecus* (Langerhans). (A) Parapodium of mid-body; anterior view. (B) Light micrograph of acicula. (C) Notopodial chaeta. (D) Light micrograph of basal part of notochaeta. (E) Light micrograph of distal part of notochaeta; lateral view. (F) Neuropodial chaeta. (G) Distal part of neurochaeta. (H) Shaft of neurochaeta. (I) Light micrograph of neurochaetal shaft. (A, C, F–H: ZMH P24950 A; B, D, E, I: ZMH P24950 B).

(Fig. 20B); with medially inserted short cirrophores and usually very long, slender cirrostyles, which are distinctly longer than neuropodial lobes; decreased in length and more conical in last chaetiger.

Each noto- and neuropodial lobe with one pointed acicula; with internal longitudinal ribs and more or less distinct internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Figs. 20C, 21B). Numerous simple notochaetae arranged in dense, irregularly fan-shaped fascicles, which more or less cover dorsum (Figs. 20A, 21A); notochaetae internally chambered, D-shaped in cross-section, with two

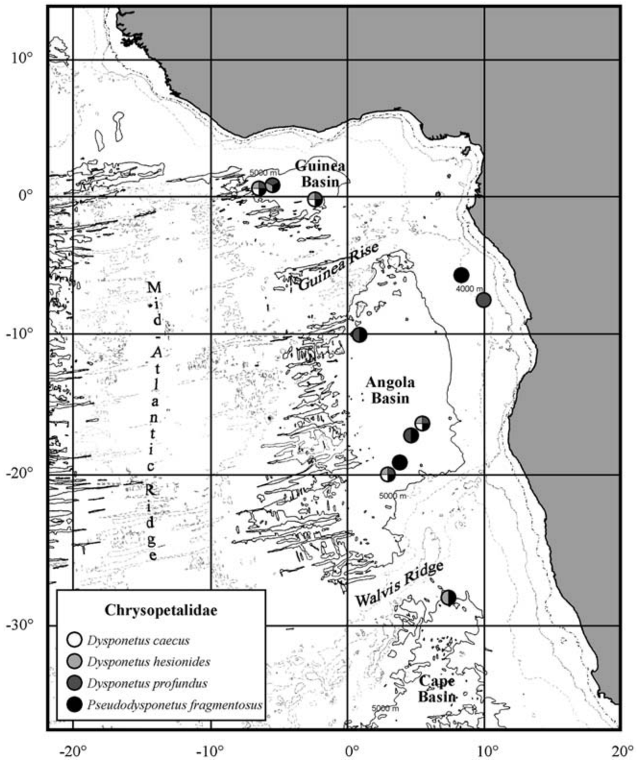

Fig. 22. Distribution of chrysopetalid species in the studied region.

longitudinal rows of large alternating spines which are integrated into one row at distal part of tip (Figs. 20D, 21C–E). Neuropodia with falcigerous compound chaetae having bidentate, long pseudospinigerous blades of slightly different length, with fine serration over entire length of margin; internally chambered shafts strongly heterogomph with two apical teeth (Figs. 20E, 21F–I).

Pygidium with an anus; cirri not observed.

Remarks

In smaller specimens the mouth appendage and sometimes also the cirri on the first segment are inconspicuous or not yet developed.

Distribution

Angola and Guinea Basins; 5048–5494 m (Fig. 22).

Dysponetus hesionides sp. nov.

(Figs. 22–24, 29)

Etymology

The epithet is intended to reflect the great similarity of this species to members of the Hesionidae (see the "Discussion of molecular results" for Chrysopetalidae below). It is to be treated as a noun in apposition, therefore as indeclinable, for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 34 MC 9, 28°6.7′S 7°20.8′E, 3.iii.2005, 5030 m; holotype: cs/2.0/16/0.6/0.3 (ZMH P24955); paratypes: cs/0.9/11/0.3/0.2, af/0.4/6/0.2/0.1 (ZMH P24956).

Additional material. See Appendix 1.

Diagnosis

Prostomium with three antennae, the median one inserted antero-dorsally, and two elongated palps, all biarticulated; distinct eyes and caruncle absent; mouth smooth, without appendages; anterior segments formula: 1/1 + Ch1/Ch1 + ChN/Ch0; dorsal cirri with short cirrophores and bottle-shaped to filiform cirrostyles; ventral cirri absent on third segment (= 2nd chaetiger); numerous notochaetae on all chaetigers with two rows of spines, D-shaped in cross-section, paleae absent.

Description

Body up to 2.0 mm long with up to 16 chaetigers; widest in proboscidial region, tapering both anteriorly and posteriorly. Segments with numerous indistinct dorsal ridges (Fig. 24A).

Prostomium rectangular with rounded corners, wider than long, bearing three antennae and two palps (Figs. 23A, B; 24A). Two lateral antennae inserted anteriorly and one shorter median antenna with antero-dorsal insertion; lateral antennae with globular to conical ceratophores and more digitiform ceratostyles; median antenna with inconspicuous ceratophores and often missing conical ceratostyles (Figs. 23A, B; 24A). Latero-ventrally palps with globular palpophores and longer conical palpostyles (Figs. 23B, 24A). Distinct eyes absent, but some specimens with remaining pigmented eye-like spots. Nuchal organs might be present, but are not conspicuous.

Retracted proboscis extending to about chaetiger six; distinct jaws not observed, terminal papillae absent and mouth opening not covered by appendage.

First segment reduced and achaetous; with two pairs of short cirrophores inserted ventro-laterally and bottle-shaped cirrostyles; dorsal pair slightly longer than ventral one (Fig. 23A, B). Parapodia of second segment (= 1st chaetiger) biramous with noto- and neuropodial lobes, both with chaetae and cirri of same shape as in first segment (Fig. 23A, B). Parapodia of third segment biramous; dorsal cirri present, ventral cirri absent (Fig. 23A, B).

Parapodia of fourth segment and following ones biramous, with dorsal and ventral cirri and more or less developed lobes (Fig. 23A–C). Parapodial lobes more or less triangular; neuropodial lobes much longer than notopodial ones (Fig. 23C). Dorsal cirri with long, slender cirrostyles; inserted posteriorly on upper side of notopodia (Fig. 23C). Ventral cirri similar in shape but

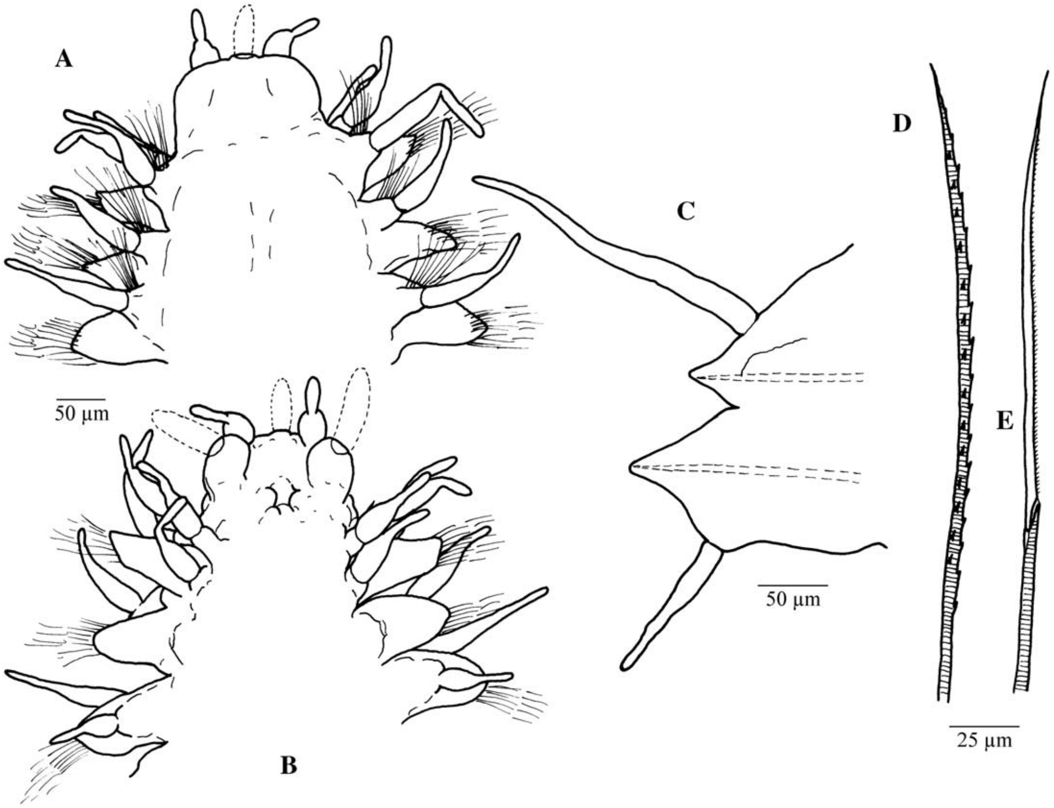

Fig. 23. *Dysponetus hesionides* sp. nov. (A) Anterior end; dorsal view; missing median antenna suggested by dashed line. (B) Anterior end; ventral view; missing median antenna and palpostyles suggested by dashed lines. (C) Right parapodium of midbody; posterior view, chaetae omitted. (D) Notopodial chaeta. (E) Neuropodial chaeta. (A–E: ZMH P24955).

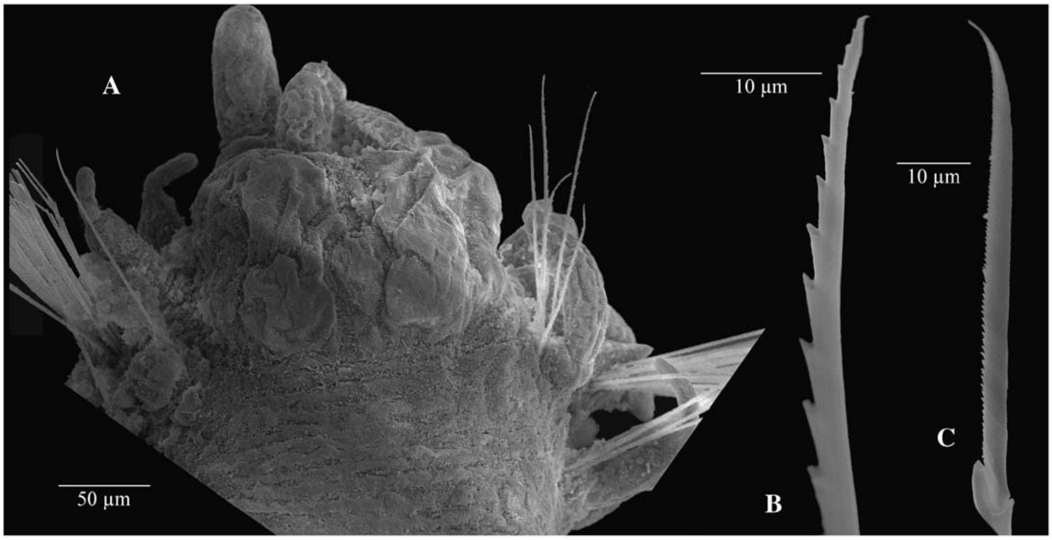

Fig. 24. *Dysponetus hesionides* sp. nov. (A) Anterior end; dorsal view. (B) Notopodial chaeta. (C) Neuropodial chaeta. (A–C: ZMH P24961 B).

distinctly shorter than dorsal ones; inserted near middle of parapodia (Fig. 23B, C).

Each noto- and neuropodial lobe with one pointed acicula; with internal longitudinal ribs and more or less distinct internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 23C). Numerous simple notochaetae arranged in dense, irregularly fan-shaped fascicles, which partly cover dorsum (Fig. 23A); notochaetae internally chambered, D-shaped in cross-section, with two longitudinal rows of alternating spines (Figs. 23D, 24B). Neuropodia with spinigerous compound chaetae having unidentate blades of slightly different length, with fine serration over entire length of margin; internally chambered shafts strongly heterogomph (Figs. 23E, 24C).

Pygidium with an anus; cirri not observed.

Remarks

In smaller specimens the cirri on the first segment and the ventral cirri on the second segment are sometimes inconspicuous or not yet developed.

Distribution

Angola, Cape and Guinea Basins; 5022–5494 m (Fig. 22).

Discussion

Dysponetus hesionides sp. nov. belongs to a group of *Dysponetus* species (*D. bidentatus* Day, 1954; *D. bipapillatus* Dahlgren, 1996; *D. macroculatus* Dahlgren, 1996) characterised by elongated palps and the absence of ventral cirri on the third segment (= 2nd chaetiger). However, all those previously described species show a single mouth appendage, more or less distinct bidentate neuropodial chaetae, four eyes, and no neurochaetae on the second segment (Dahlgren 1996). *Dysponetus bulbosus* Hartmann-Schröder, 1982 and *D. caecus* (Langerhans) also have elongated palps, but clearly differ from the new species in the presence of ventral cirri on the third segment.

Dysponetus profundus sp. nov.

(Figs. 22, 25, 26, 30)

Etymology

The species epithet refers to the deep-sea habitats. It is to be treated as a Latin adjective for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 89 ES-S, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii.2005, 5137–5141 m;

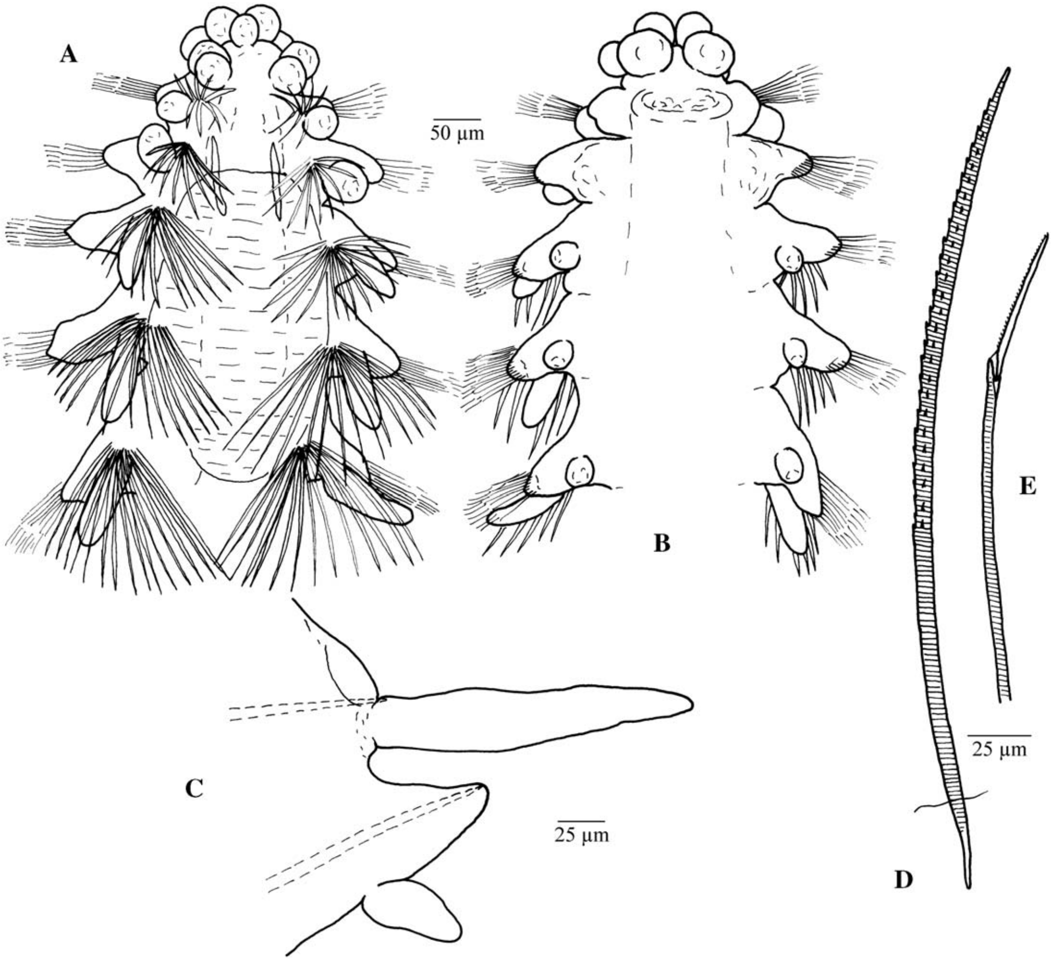

Fig. 25. *Dysponetus profundus* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Right parapodium of midbody; posterior view, chaetae omitted. (D) Notopodial chaeta. (E) Neuropodial chaeta. (A–E: ZMH P25008).

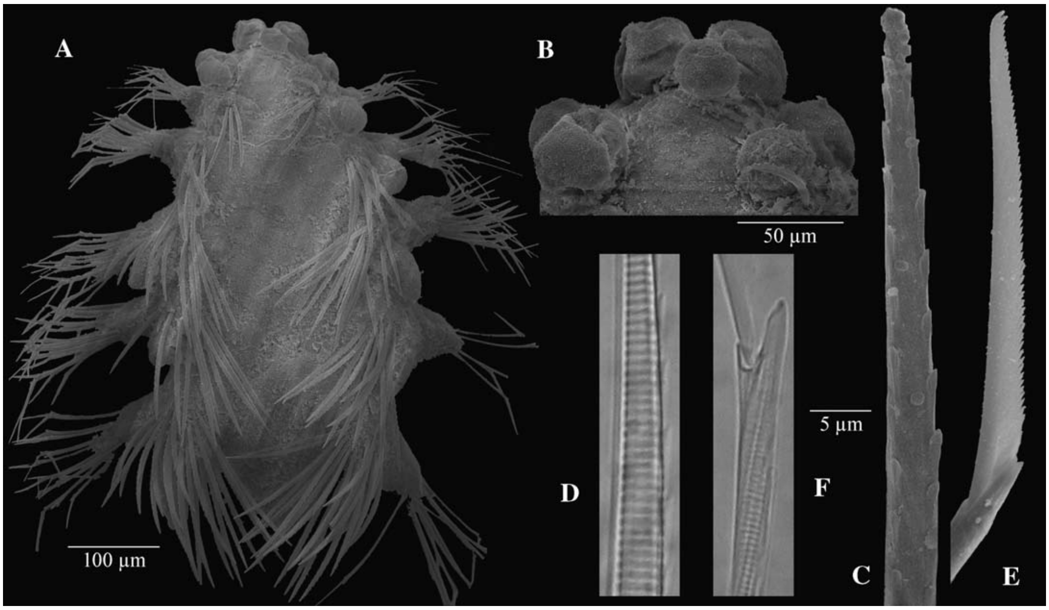

Fig. 26. *Dysponetus profundus* sp. nov. (A) Anterior end; dorsal view. (B) Prostomium and first segment; dorsal view. (C) Notopodial chaeta with damaged tip. (D) Light micrograph of subdistal part of notochaeta. (E) Neuropodial chaeta. (F) Light micrograph of neurochaetal shaft. (A–C, E: ZMH P24988 C; D, F: ZMH P24988 B).

holotype: af/2.0/14/0.4/0.2 (ZMH P25004); paratypes: af/0.8/7/0.5/0.3, af/0.8/7/0.5/0.3, af/0.8/6/0.5/0.3, af/0.8/6/0.5/0.3, af/0.8/6/0.4/0.2, af/0.8/6/0.4/0.2, af/0.8/6/0.4/0.2, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.4/0.2, af/0.6/6/0.4/0.2, af/0.6/6/0.4/0.2, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.4/0.2, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.4/5/0.4/0.2, af/0.4/5/0.4/0.2, af/0.4/5/0.4/0.2, 44 mf with 1–6 chaetigers (ZMH P25005, 1 mf for DNA).—R/V METEOR 63/2 st. 89 ES-E, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii. 2005, 5137–5141 m; paratypes: af/1.2/9/0.5/0.3, af/0.8/7/0.5/0.3, af/0.8/6/0.4/0.2, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.5/0.3, af/0.7/6/0.4/0.2, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.5/0.3, af/0.6/5/0.4/0.2, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.5/5/0.5/0.3, af/0.4/5/0.4/0.2, af/0.4/5/0.4/0.2, 54 mf with 1–9 chaetigers (ZMH P25003, 1 mf for DNA).

Additional material. See Appendix 1.

Diagnosis

Prostomium with three antennae, the median one inserted antero-dorsally, and two palps, all simple and globular; eyes and caruncle absent; mouth smooth, without appendages; anterior segments formula: 1/1 + Ch1/Ch0 + Ch1/Ch0 + ChN/ChN; dorsal cirri globular to digitiform, without pronounced cirrophores; ventral cirri starting from fourth segment (= 3rd chaetiger); numerous notochaetae on all chaetigers with two rows of spines, D-shaped in cross-section, paleae absent.

Description

Body at least 2.0 mm long with at least 14 chaetigers; dorso-ventrally flattened, widest in proboscidial region, tapering both anteriorly and posteriorly. Segments deeply cut along body, but without distinct transverse ridges; often fragmented, especially after chaetiger five (Figs. 25A, B; 26A).

Prostomium short and inconspicous, bearing three antennae and two palps, which are all simple and globular (Figs. 25A, B; 26B). Two antennae inserted termino-laterally and one distinctly smaller median antenna with antero-dorsal insertion (Figs. 25A, 26B). Two larger palps inserted latero-ventrally (Fig. 25A, B). Eyes absent. Nuchal organs might be present, but are not conspicuous.

Retracted proboscis extending to chaetiger five, with one terminal pair of stylet-like jaws (Fig. 25A); more or less visible through body wall between chaetigers one and two. Everted proboscis without terminal papillae and mouth opening not covered by appendage.

First segment reduced and achaetous, only indistinctly separated from prostomium; with two pairs of simple and globular cirri, which are inserted dorso-laterally; dorsal pair slightly smaller than ventral one

(Figs. 25A, 26B). Parapodia of second segment (= 1st chaetiger) biramous with noto- and neuropodial chaetae and dorsal cirri of same shape as in first segment; ventral cirri absent (Figs. 25A, B; 26A). Parapodia of third segment biramous; dorsal cirri slightly larger than before; ventral cirri absent (Figs. 25A, B; 26A).

Parapodia of fourth segment and following ones biramous, with dorsal and ventral cirri and more or less developed lobes (Fig. 25C). Notopodia reduced; broadly rounded with conical to digitiform dorsal cirri; which are inserted posteriorly on lower side of notopodia (Fig. 25C). Neuropodial lobes blunt conical and longer than notopodia (Fig. 25C). Ventral cirri starting from 3rd chaetiger (Fig. 25B); a few anterior pairs globular and following ones slightly enlarged and more conical; always shorter than dorsal cirri and neuropodial lobes; inserted near parapodial base (Fig. 25C).

Each noto- and neuropodial lobe with one pointed acicula; with internal longitudinal ribs and more or less distinct internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 25C). Notopodia with about 3–30 simple chaetae arranged in dense, irregularly fan-shaped fascicles, which more or less cover dorsum (Figs. 25A, 26A); notochaetae internally chambered (Fig. 26D), D-shaped in cross-section, with two longitudinal rows of alternating spines (Figs. 25D, 26C). Neuropodia with about 4–25 falcigerous compound chaetae having bidentate, long bread-knife-shaped blades of slightly different length, with fine serration over entire length of margin (Figs. 25E, 26E); internally chambered shafts strongly heterogomph (Fig. 26F).

Pygidium with an anus and one digitiform cirrus.

Distribution

Angola and Guinea Basins; 3991–5655 m (Fig. 22).

Discussion

Dysponetus profundus sp. nov. belongs to a group of *Dysponetus* species (*D. pygmaeus* Levinsen, 1879; *D. hebes* (Webster & Benedict, 1887); *D. gracilis* Hartman, 1965; *D. paleophorus* Hartmann-Schröder, 1974) characterized by globular antennae and palps. However, all those previously described species have unidentate instead of bidentate neuropodial chaetae and only one rather than two pairs of cirri on the first segment. Furthermore, the NW Atlantic deep-sea species *Dysponetus gracilis* has more flattened notopodial chaetae (Hartman 1965; Aguirrezabalaga et al. 1999). A few of these more paleae-like notochaetae are also present in the mid-body of *D. paleophorus* (Hartmann-Schröder 1974). The two very similar taxa *Dysponetus pygmaeus* and *D. hebes* have doubled mouth appendages (Levinsen 1879; Dahlgren 1996), a structure which is absent in *Dysponetus profundus* sp. nov.

Pseudodysponetus gen. nov.

Etymology

The name is intended to reflect the similarity between the new genus and *Dysponetus* Levinsen.

Type species

Pseudodysponetus fragmentosus sp. nov.

Diagnosis

Body dorso-ventrally flattened with tapered anterior and posterior ends; mid-body segments behind chaetiger four easily fragmented. Prostomium with three antennae and two palps, which are all biarticulated; mouth opening without appendages; proboscis with one terminal pair of stylet-like jaws. First two segments achaetous, each with one pair of cirri. Four (in juveniles: five) anterior pairs of parapodia uniramous, with neuropodia only; notopodia reduced to a few chaetae, starting from chaetiger five (juveniles: six). First dorsal cirri from chaetiger one and ventral cirri from chaetiger two (juveniles: three). A few acicular-like notochaetae; without lateral rows of spines; circular in cross-section; paleae absent. Numerous falcigerous compound neuropodial chaetae with blades of varying length and bidentate tips. Pygidium with one anal cirrus.

Pseudodysponetus fragmentosus sp. nov.

(Figs. 22, 27, 28, 30)

Etymology

The species epithet refers to the fragmented state of the specimens. It is to be treated as a Latin adjective for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 89 ES-E, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii.2005, 5137–5141 m; holotype: af/1.3/7/0.5/0.3 (ZMH P25055); paratypes: af/1.7/9/0.6/0.3, af/1.0/6/0.5/0.3, af/1.0/6/0.5/0.3, af/0.9/4/0.4/0.2, af/0.8/5/0.5/0.3, af/0.8/5/0.5/0.3, af/0.7/4/0.5/0.3, af/0.7/4/0.4/0.2, af/0.6/5/0.3/0.1, af/0.6/5/0.2/0.05, af/0.6/4/0.3/0.1, af/0.6/4/0.3/0.1, af/0.5/4/0.4/0.2, af/0.5/4/0.4/0.2, af/0.5/4/0.4/0.2, af/0.5/4/0.3/0.1, af/0.5/4/0.3/0.1, af/0.5/4/0.3/0.1, af/0.4/4/0.3/0.1, 13 mf with 1–7 chaetigers (ZMH P25056 A); af/0.7/5/0.4/0.2, 1 mf with 4 chaetigers (ZMH P25056 B, on SEM stub).—R/V METEOR 63/2 st. 89 ES-S, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii.2005, 5137–5141 m; paratypes: af/1.4/3/0.6/0.3, af/0.9/5/0.4/0.2, af/0.9/4/0.5/0.2, af/0.8/5/0.4/0.2, af/0.8/5/0.4/0.2, af/0.8/4/0.4/0.2, af/0.8/4/0.4/0.2, af/0.8/4/0.4/0.2, af/0.8/4/0.4/0.2, af/0.8/4/0.3/0.1, af/0.7/4/0.4/0.2, af/0.7/4/0.4/0.2, af/0.6/4/0.4/0.2, af/0.6/4/0.4/0.2, af/0.6/4/0.3/0.1, af/0.5/4/0.3/0.1, af/0.5/4/0.3/

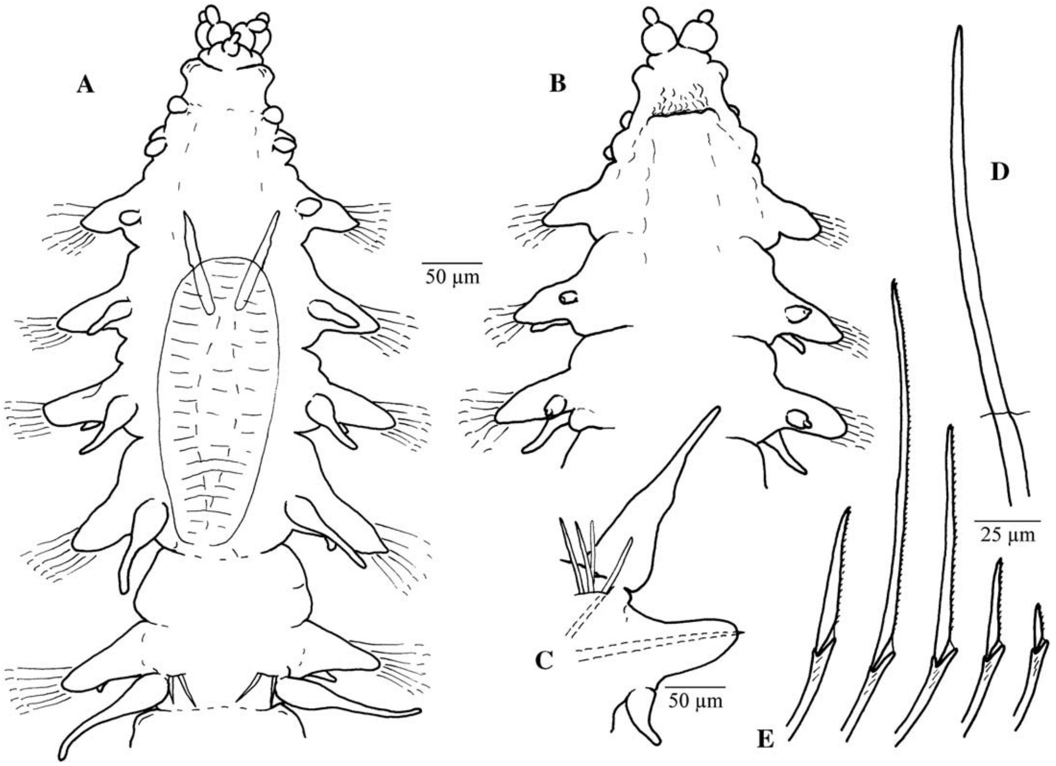

Fig. 27. *Pseudodysponetus fragmentosus* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Left parapodium of mid-body; anterior view, neurochaetae omitted. (D) Notopodial chaeta. (E) Neuropodial chaetae from upper to lower part of fascicle (left to right in figure). (A, B: ZMH P25042 A; C–E: ZMH P25032 D).

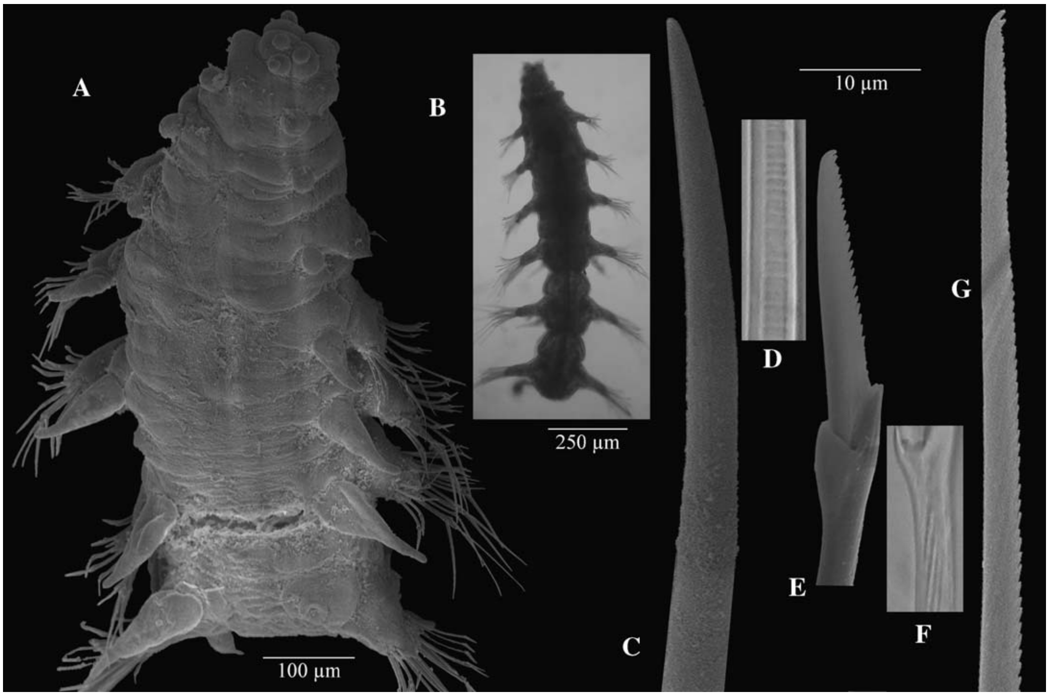

Fig. 28. *Pseudodysponetus fragmentosus* sp. nov. (A) Anterior end; dorsal view. (B) Light micrograph of anterior end; ventral view. (C) Notopodial chaeta. (D) Light micrograph of subdistal part of notochaeta. (E) Neuropodial paring knife-shaped falciger. (F) Light micrograph of neurochaetal shaft. (G) Distal part of neuropodial pseudospinigerous blade. (A, C, E, G: ZMH P25056 B; B, D, F: ZMH P25032 D).

0.1, af/0.5/4/0.3/0.1, af/0.5/4/0.3/0.1, af/0.5/4/0.3/0.1, af/0.5/4/0.3/0.1, 43 mf with 1–4 chaetigers (ZMH P25057, 2 mf for DNA).

Additional material. See Appendix 1.

Diagnosis

Prostomium with three antennae, the median one inserted antero-dorsally, and two palps, all biarticulated; eyes and caruncle absent; mouth smooth, without appendages; anterior segments formula: 1/0 + 1/0 + 1/Ch0 + N/ChN + N/ChN + N/ChN + ChN/ChN; dorsal cirri globular to digitiform, without pronounced cirrophores; ventral cirri usually starting from segment four (= 2nd chaetiger); up to six smooth and acicular-like notochaetae usually starting from segment seven (= 5th chaetiger), paleae absent.

Description

Body at least 2.0 mm long with at least 11 chaetigers; dorso-ventrally flattened, widest in proboscidial region, tapering both anteriorly and posteriorly. Anterior segments slightly narrower and without clear division between them, but after 4th chaetiger more deeply cut and with distinct transverse ridges (Figs. 27A; 28A, B), therefore, mid-body of specimens usually fragmented.

Prostomium short and inconspicous, bearing three antennae and two palps, which are all biarticulated and consist of large, globular ceratophores or palpophores and smaller oval ceratostyles or palpostyles (Figs. 27A, B; 28A). Two antennae inserted termino-laterally and one distinctly smaller median antenna with antero-dorsal insertion. Two larger palps inserted latero-ventrally (Figs. 27A, 28A). Eyes absent. One pair of furrow-like dorso-lateral nuchal organs situated between prostomium and first segment (Fig. 28A).

Retracted proboscis extending to chaetiger four, with one terminal pair of stylet-like jaws (Fig. 27A); more or less visible through body wall between chaetigers one and two. Everted proboscis not observed, but mouth opening not covered by appendage.

First segment with collar-like structure surrounding posterior part of prostomium (Figs. 27A, 28A). First and second segment achaetous; each one with one pair of simple and globular to oval cirri, which are inserted dorso-laterally (Figs. 27A, 28A). Parapodia of third segment (= 1st chaetiger) uniramous with neuropodial chaetae and dorsal cirri of same shape as in anterior two segments; ventral cirri absent (Figs. 27A, B; 28A). Parapodia of fourth to sixth segment uniramous with neuropodial chaetae; dorsal cirri increasing in length and more conical with an elongated digitiform distal part; ventral cirri oval to conical (Figs. 27A, B; 28A).

Parapodia of seventh segment and following ones biramous, with dorsal and ventral cirri and more or less developed lobes (Fig. 27A, C). Notopodia reduced, without pronounced lobes (Fig. 27C). Dorsal cirri conical with an elongated digitiform distal part, which are longest in mid-body (Figs. 27A, C; 28A); decreasing in length in posterior part of body; inserted near parapodial base, slightly behind notochaetae (Fig. 27C). Neuropodial lobes bluntly conical and longer than notopodia (Fig. 27C). Ventral cirri more or less conical in shape, longest in mid-body; always shorter than dorsal cirri and neuropodial lobes; inserted near parapodial base (Fig. 27C).

Each noto- and neuropodium with one pointed acicula; with internal longitudinal ribs and more or less distinct internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 27C). Notopodia with up to six smooth and acicular-like notochaetae (Figs. 27D, 28C), usually starting from chaetiger five; arranged in irregularly fan-shaped fascicles, which extend over dorsum; notochaetae internally chambered (Fig. 28D) and circular in cross-section. Neuropodia with numerous falcigerous compound chaetae having bidentate blades of different length, their lengths decreasing superiorly and especially inferiorly within each fascicle, and their shape changing from pseudospiniger to paring-knife-shaped falciger (Fig. 27E); subdistally blades with fine serration over entire length of margin (Fig. 28E, G); internally inconspicuous chambered shafts strongly heterogomph (Fig. 28E, F).

Pygidium with an anus and one digitiform cirrus.

Remarks

In smaller specimens the cirri on the first two segments, the ventral cirri on the fourth segment (= 2nd chaetiger), and the notochaetae on the seventh segment (= 5th chaetiger) are sometimes inconspicuous or not yet developed, and the dorsal cirri of the fourth segment (= 2nd chaetiger) still globular to oval.

The fragmentation might be a strategy of the species in situ, though probably not for reproduction, because no regenerating mid-body segments were found.

Distribution

Angola, Cape and Guinea Basins; 3964–5655 m (Fig. 22).

Discussion

The two anterior achaetous segments with dorsal cirri only and the acicular notochaetae starting from segment seven or eight (= chaetiger five or six) are unique among Chrysopetalidae and prevent any misidentification. However, anterior fragments of *Pseudodysponetus fragmentosus* sp. nov. with only four chaetigers, and therefore without notochaetae, might be erroneously referred to other families of polychaetes (e.g. Syllidae).

Abundance of Chrysopetalidae

A total of 1316 specimens or fragments were found in all investigated areas. Most of them (726) belong to *Pseudodysponetus fragmentosus* sp. nov. This species was present in the Angola, Cape and Guinea basins (Fig. 30), with the highest abundance in the Guinea Basin (DIVA-2 areas 3 and 4). The 469 specimens or fragments of *Dysponetus profundus* sp. nov. show a similar pattern, but none were present in the Cape Basin. *Dysponetus caecus* (48) and *D. hesionides* sp. nov. (73) were found in much lower numbers in a few epibenthic sledge and multicorer samples (Fig. 29). However, *Dysponetus caecus* was absent in the Cape Basin, a region in which most of the *D. hesionides* sp. nov. specimens were found (DIVA-2 area 1). The most effective gear for collecting chrysopetalids was the epibenthic sledge. The box corer and multicorer were also useful, but these samples were usually fixed in formalin; therefore, the specimens were not useful for molecular analyses.

Molecular data

COI (3-6W) data set

Twelve newly acquired sequences (Table 5) were included; analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. The MP analyses were conducted with the branch-and-bound algorithm, ML analyses using the branch-swapping heuristic algorithm tree bisection-reconnection (TBR) with random addition of taxa (1,000 replicates). For the ML analyses the General Time Reversible model with invariant gamma distribution (GTR + I + G) was selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies ($A = 0.2763$, $C = 0.1333$, $G = 0.1700$, $T = 0.4204$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 1.1785$, $A \leftrightarrow G = 12.0903$, $A \leftrightarrow T = 1.3465$, $C \leftrightarrow G = 4.7129$, $C \leftrightarrow T = 10.6099$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0.3729; and gamma distribution shape parameter = 0.7778. Clade support values were calculated with nonparametric bootstrapping with 100,000 replicates and branch-and bound searches

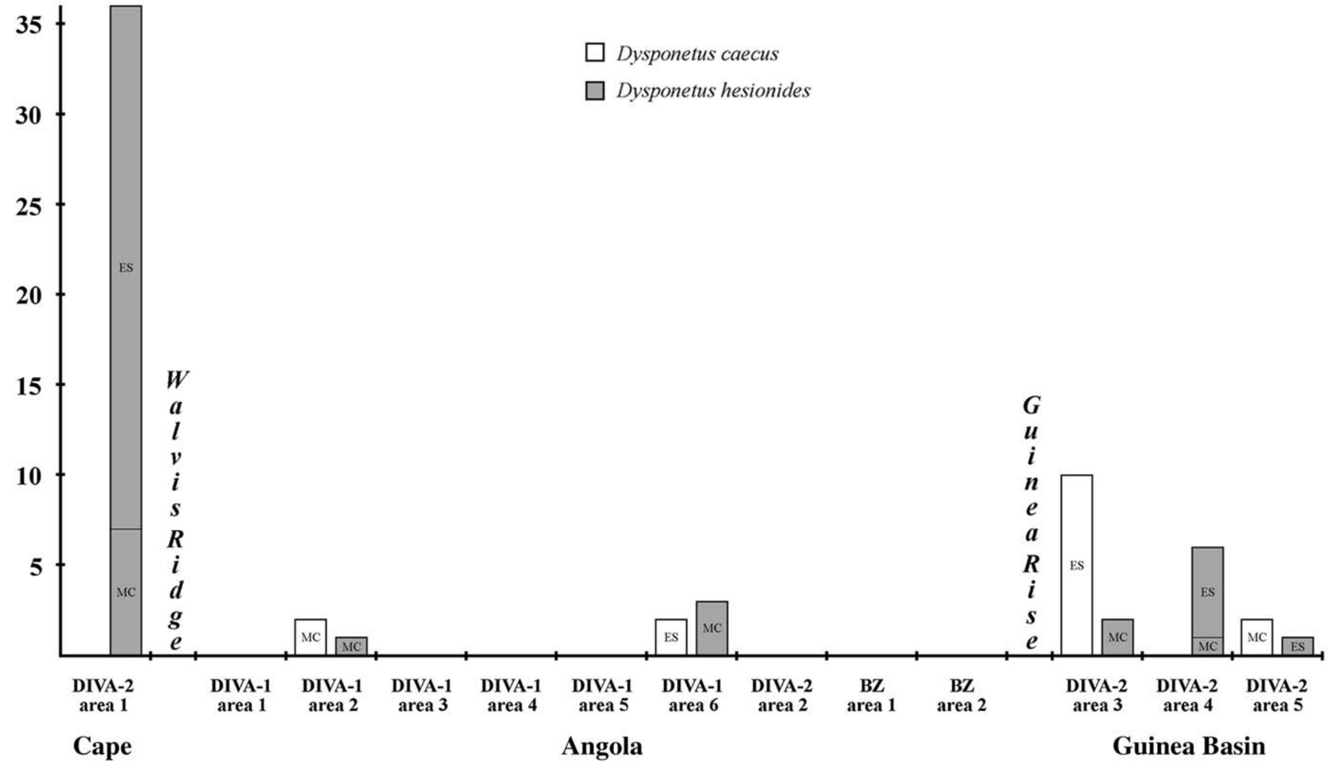

Fig. 29. Abundance of the chrysopetalids *Dysponetus caecus* and *D. hesionides* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

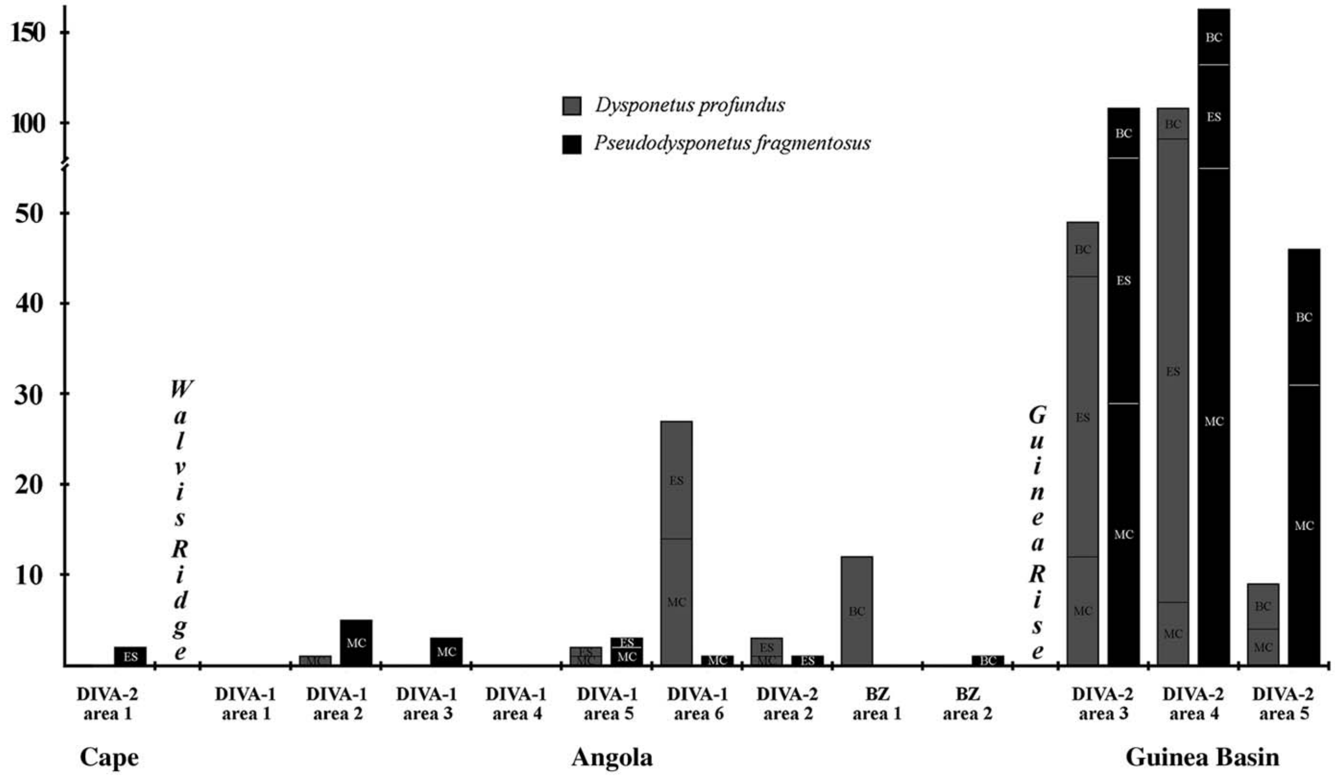

Fig. 30. Abundance of the chrysopetalids *Dysponetus profundus* and *Pseudodysponetus fragmentosus* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

(MP), or with 1,000 replicates, heuristic searches, TBR swapping and 10 random addition sequences (ML).

After exclusion of the primer sites, the alignment for the twelve sequences contained 421 characters, of which 202 were variable and 156 parsimony informative. The MP analysis yielded eighteen most parsimonious trees, which are 407 steps long with CI = 0.7543 (0.7101), RI = 0.7619, and RC = 0.5747. The topologies of the strict consensus tree and the ML tree (−ln L = 2142.69914) are very similar (Fig. 31). Only *Dysponetus caecus* resulted either as sister to *Pseudodysponetus fragmentosus* sp. nov. (MP) or as more closely related to *Dysponetus profundus* sp. nov. (ML). However, both methods confirmed the monophyly of three of the four chrysopetalid species by bootstrap values of 100 and suggested *Dysponetus hesionides* sp. nov. as sister group to a clade including the other three species.

ITS2 data set

Six newly acquired sequences (Table 5) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. All analyses were conducted with the branch-and-bound algorithm. The ML analysis was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1809, C = 0.3102, G = 0.2838, T = 0.2251); number of substitution types = 6; substitution rate matrix (A↔C = 0.8487, A↔G = 1.8180, A↔T = 1.2575, C↔G = 0.9381, C↔T = 3.1573, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and gamma distribution shape parameter = 1.8042. Clade support values were calculated with nonparametric bootstrapping with 1,000 (ML) or 100,000 replicates (MP) and branch-and bound searches.

After exclusion of the primer sites, the alignment for the six sequences contained 440 characters, of which 175 were variable and 73 parsimony informative. The MP (tree length = 189, CI = 1.0000, RI = 1.0000, RC = 1.0000) and the ML analysis (−ln L = 1200.32581) found single trees with slightly different topologies (Fig. 31). The MP analysis showed *Dysponetus hesionides* sp. nov. and *Dysponetus profundus* sp. nov. as well defined clades (bootstrap: 100), whereas in the ML analysis only the *Dysponetus profundus* sp. nov. group is strongly supported.

Discussion of molecular results

Based on the molecular data *Dysponetus hesionides* sp. nov. seems more or less separated from the other three chrysopetalid species – which either resulted as sister to Glyceriformia (16S) or grouped together with paralacydoniids and nephtyids (COI) – and might be more

Table 5. List of taxa and corresponding sequences in Chrysopetalidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession numbers				
			18S rDNA	16S rDNA	COI (3-6W)	ITS1	ITS2
CHRYSOPETALIDAE							
Dysponetus caecus (Langerhans)	Guinea Basin						
	D-2 st. 63 ES-E	ZMH P24951 A	–	GQ426603	GQ426647	GQ426704	–
Dysponetus hesionides sp. nov.	Cape Basin						
	D-2 st. 40 ES-S	ZMH P24960 B	GQ426553	GQ426604	GQ426648	–	GQ426718
	D-2 st. 41 ES-S	ZMH P24961 C	GQ426554	–	–	–	–
	Walvis Ridge and Guinea Rise						
	Guinea Basin						
	D-2 st. 89 ES-E	ZMH P24965	–	–	GQ426649	–	GQ426719
Dysponetus profundus sp. nov.	Angola Basin						
	D-2 st. 45 ES-S	ZMH P24979	–	–	GQ426650	–	GQ426720
	Guinea Rise						
	Guinea Basin						
	D-2 st. 63 ES-S	ZMH P24988 B	–	–	GQ426651	–	GQ426721
	D-2 st. 89 ES-E	ZMH P25003	–	–	GQ426652	–	–
	D-2 st. 89 ES-S	ZMH P25005	–	–	GQ426653	–	–
	D-2 st. 90 ES-E	ZMH P25006 A	–	–	GQ426654	–	GQ426722
Pseudodysponetus fragmentosus sp. nov.	Cape Basin						
	D-2 st. 40 ES-S	ZMH P25025	–	–	GQ426655	–	–
	D-2 st. 41 ES-S	ZMH P25026	–	–	GQ426656	–	–
	Walvis Ridge and Guinea Rise						
	Guinea Basin						
	D-2 st. 89 ES-S	ZMH P25057	–	–	GQ426657	–	–
PARALACYDONIIDAE							
Paralacydonia paradoxa Fauvel	France		–	–	GQ426684	–	GQ426700
	Banyuls-s.-M.						

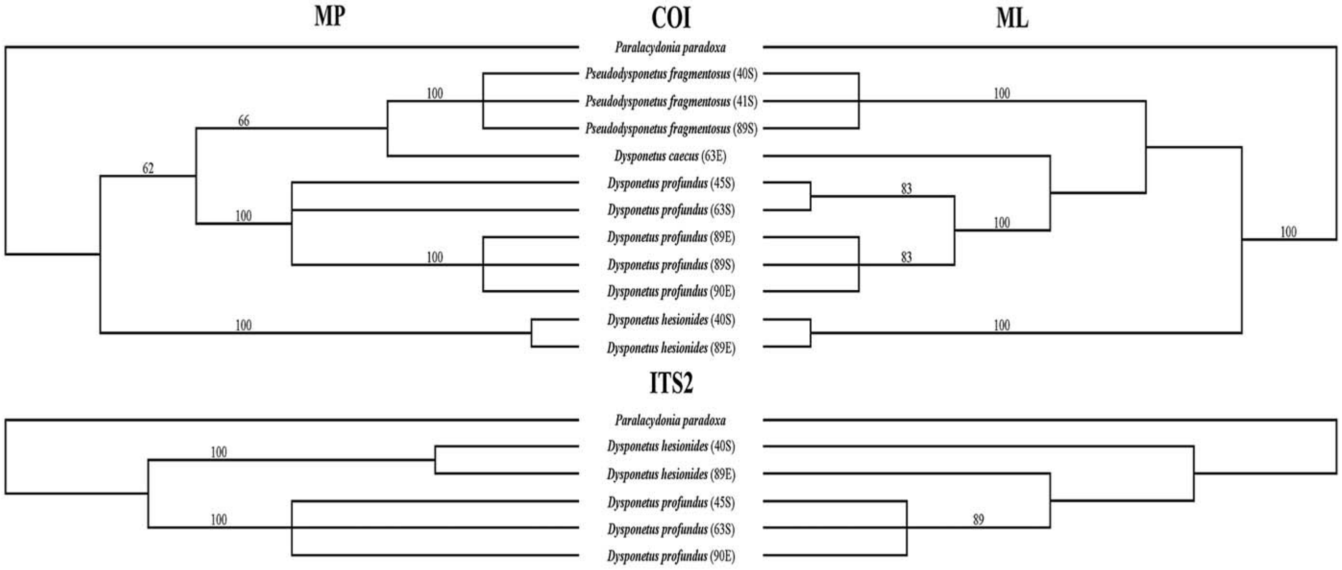

Fig. 31. Cladograms obtained from MP and ML analysis of the COI (3-6W) and ITS2 sequences, respectively. Bootstrap values > 50 shown above branches.

closely related to hesionids (18S) or syllids (16S and COI); see "Discussion of molecular analyses" in the "General results" chapter. On the other hand, the morphological features suggest that *D. hesionides* belongs to the Chrysopetalidae. The two sequences of the 18S rDNA gene of specimens from the Cape Basin are completely congruent, whereas the COI and ITS2 regions of specimens from the Cape Basin and the Guinea Basin are slightly variable. However, the corresponding COI amino acid sequences completely agree with each other.

Specimens of *Dysponetus profundus* sp. nov. from the Angola Basin and the Guinea Basin and of *Pseudodysponetus fragmentosus* sp. nov. from the Cape Basin and the Guinea Basin, respectively, also show slightly different COI sequences. However, no patterns possibly caused by the underwater ridges are observed, because three of the sequences of *Dysponetus profundus* sp. nov. from the Guinea Basin are identical (st. 89E/S and 90E) and the remaining fourth (st. 63S) shares more similarities with the sequence from the Angola Basin (st. 45S). Furthermore, the data for the non-coding internal transcribed spacer ITS2 completely agree with each other and show no restriction in gene flow between the two geographically separated populations.

Glyceridae Grube, 1850

The Glyceridae and the very similar Goniadidae Kinberg, 1865 (see the following chapter) are monophyletic clades within the Phyllodocida (Pleijel 2001d). Their pointed, usually annulated prostomium with two pairs of terminal appendages, and their long, muscular, eversible axial proboscis, which is densely covered with papillae and provided with terminal jaws, are unique characters among polychaetes (Böggemann 2006). However, the two groups can be clearly separated from each other, especially by the proboscidial armature. The four similar jaws of the glycerids are hook-shaped with an accessory lateral aileron, whereas goniadids usually have two macrognaths and a variable number of dorsal and ventral micrognaths, and sometimes additional longitudinally arranged rows of V-shaped chevrons on each side of the proboscis (Böggemann 2002, 2005).

The Glyceridae have a worldwide distribution from intertidal to abyssal depths (Böggemann 2002). They are generally considered to be carnivorous, capturing prey with their jaws and killing it by the injection of venom (Ockelmann and Vahl 1970; Fauchald and Jumars 1979; Manaranche et al. 1980). In most species the animals form semi-permanent burrow systems in sandy or muddy sediments (Ockelmann and Vahl 1970), which seems to be the typical substrate in deep sea basins. Therefore, it is no wonder that some species of *Glycera* Lamarck, 1818 and the single species of *Glycerella* Arwidsson, 1899 are known even from the abyssal zone.

In the present study, three species of Glyceridae were collected. *Glycera capitata* Ørsted, 1842 represents one of the well known, widely distributed taxa (e.g. Averincev 1972; Hartman 1978; Böggemann 2002), whereas *Glycera diva* sp. nov. and *G. southeastatlantica* sp. nov. are newly described below.

Key to glycerid species from the abyssal SE Atlantic

1. Parapodia with two short postchaetal lobes, notopodial prechaetal lobes about as long as or slightly shorter than neuropodial lobes (Figs. 35D–K, 37D–K); main type of proboscidial papillae conical with three indistinct transverse ridges (Figs. 35B, 36A–C) or with a straight median longitudinal ridge on one side (Figs. 37B; 38A, B) 2

– All parapodia with one postchaetal lobe, notopodial prechaetal lobes much shorter than neuropodial lobes (Fig. 32D–K); main type of proboscidial papillae digitiform with a straight median longitudinal ridge on one side (Figs. 32B, 33D) .... *Glycera capitata* Ørsted

2. Notopodial prechaetal lobes slightly shorter than neuropodial lobes, dorsal cirri inserted on body wall far above parapodial base (Fig. 35D–K); main type of proboscidial papillae conical with three indistinct transverse ridges (Figs. 35B, 36A–C) .... *Glycera diva* sp. nov.

– Prechaetal lobes of about same length, dorsal cirri inserted near parapodial base (Fig. 37D–K); main type of proboscidial papillae conical with a straight median longitudinal ridge on one side (Figs. 37B; 38A, B) .... *Glycera southeastatlantica* sp. nov.

Glycera Lamarck, 1818

Glycera capitata Ørsted, 1842

(Figs. 32–34, 39)

Glycera capitata Ørsted, 1842—Ørsted (1842, p. 123); Böggemann (2002, p. 34, figs. 16–18)

Glycera setosa Ørsted, 1842—Ørsted (1842, p. 124)

Glycera Mulleri Quatrefages, 1866 [partim]—Quatrefages (1866, p. 172)

Glycera kerguelensis McIntosh, 1885—McIntosh (1885, p. 344; pl. 35A, figs. 3, 4)

?*Glycera* "longipes" [nomen nudum]—M. Sars in Arwidsson (1899, p. 9)

Glycera nana Johnson, 1901—Johnson (1901, p. 411; pl. 10, figs. 103, 103a)

Hemipodia canadensis Treadwell, 1937—Treadwell (1937, p. 348, figs. 1–3)

Glycera mimica Hartman, 1965—Hartman (1965, p. 97, pl. 15a–e)

Glycera capitata antarctica Averincev, 1972—Averincev (1972, p. 136; pl. 16, figs. 1–6, 11, 12)

Glycera capitata abyssicola Averincev, 1972—Averincev (1972, p. 138; pl. 16, figs. 7–10; pl. 17, figs. 4–6)

Material examined

See Appendix 1.

Diagnosis

Proboscidial papillae mainly digitiform with straight median longitudinal ridge; ailerons with pointed triangular bases; parapodia of mid-body with slightly longer neuropodial than notopodial prechaetal lobes and one rounded postchaetal lobe; branchiae absent.

Description

Body up to 20 mm long with up to 43 chaetigers. Mid-body segments more or less distinctly triannulate.

Conical prostomium consisting of about 8–10 rings; terminal ring with four appendages and basal one with pair of nuchal organs (Figs. 32A; 33A, B).

Proboscis with two types of papillae with subapical tufts of cilia, arranged in more or less distinct longitudinal rows: 1. numerous digitiform papillae with straight, median, longitudinal ridge on posterior surface (Figs. 32B, 33D, E); 2. isolated, shorter and broader, oval to globular papillae without ridges (Figs. 32B, 33F). Terminal part of proboscis with four hook-shaped jaws arranged in a cross (Fig. 33A, C) and accessory ailerons with pointed triangular base (Fig. 32C).

First two pairs of parapodia uniramous, following parapodia biramous (Fig. 32D–K). Two slender triangular to digitiform prechaetal lobes; neuropodial lobe always distinctly longer than notopodial lobe; both lobes becoming slightly slimmer in posterior parapodia; in last parapodia notopodial lobe much shorter than neuropodial one. One shorter, rounded postchaetal lobe. Dorsal cirri from 3rd parapodium, oval to globular; inserted – most clearly in anterior part of body – on body wall far above parapodial base. Ventral cirri slender triangular to digitiform, shorter than postchaetal lobes; in posterior parapodia slender and elongated; situated near parapodial base. Branchiae absent.

Noto- and neuropodia each with a single acicula. Notochaetae slender, straight or weakly recurved capillary with one side covered with spines or hairs. Neurochaetae

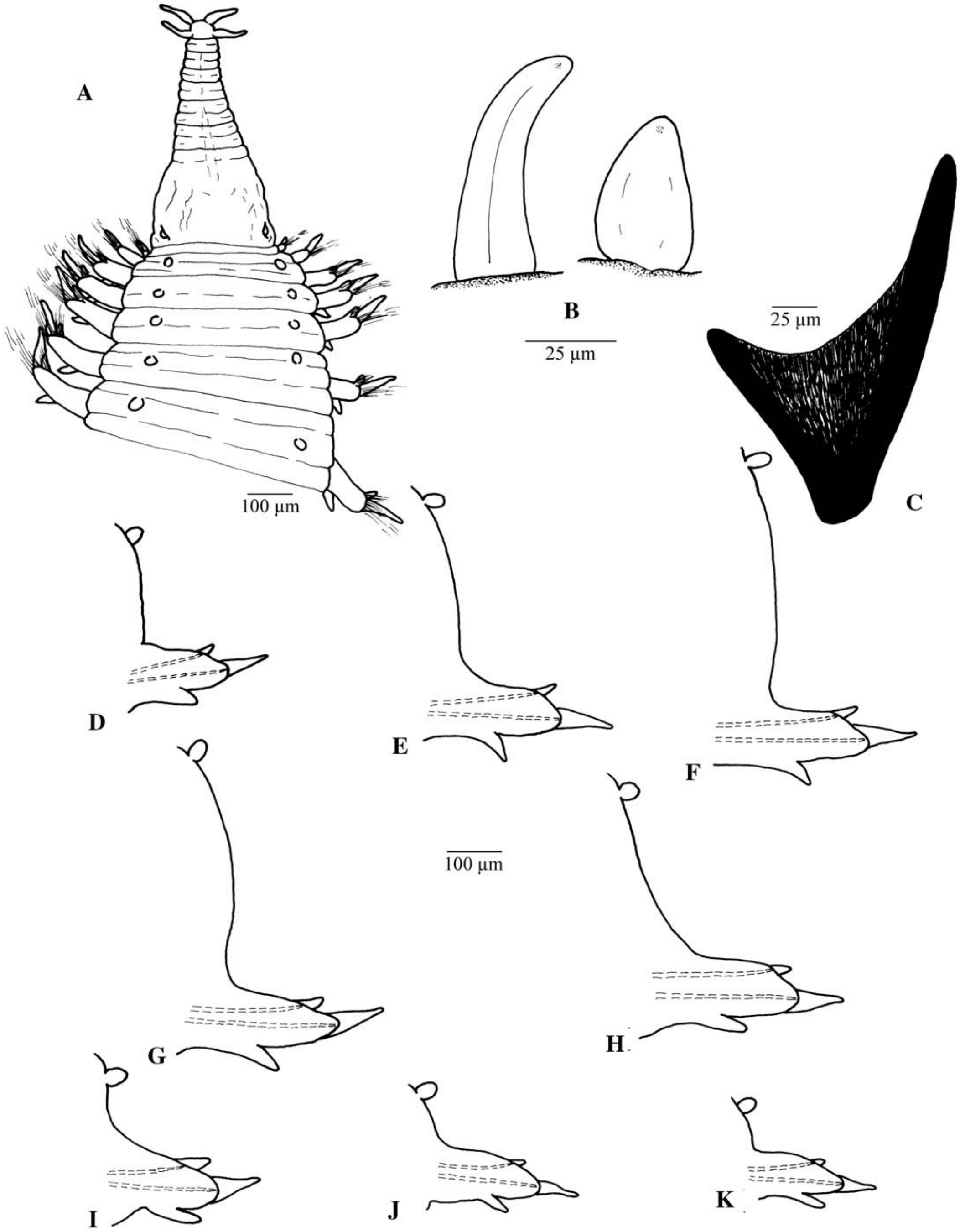

Fig. 32. *Glycera capitata* Ørsted. (A) Anterior end. (B) Proboscidial papillae. (C) Aileron. (D–K) Anterior to posterior parapodia; posterior views, chaetae omitted. (A: ZMH P25069 A; B–K: ZMH P25075 A).

compound spinigers with blades of different lengths, covered on one side with spines or hairs.

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Remarks

The deep-sea specimens of this study are usually very small; therefore, their notopodial prechaetal lobes are much shorter than in larger animals, which are up to 182 mm long (Böggemann 2002). Some of the proboscidial papillae have additional laterally located groups of cilia (Fig. 33D, right side), which are also described for other glycerid species (Böggemann et al. 2000).

Distribution

Angola and Guinea Basins; 3945–5655 m (Fig. 34).

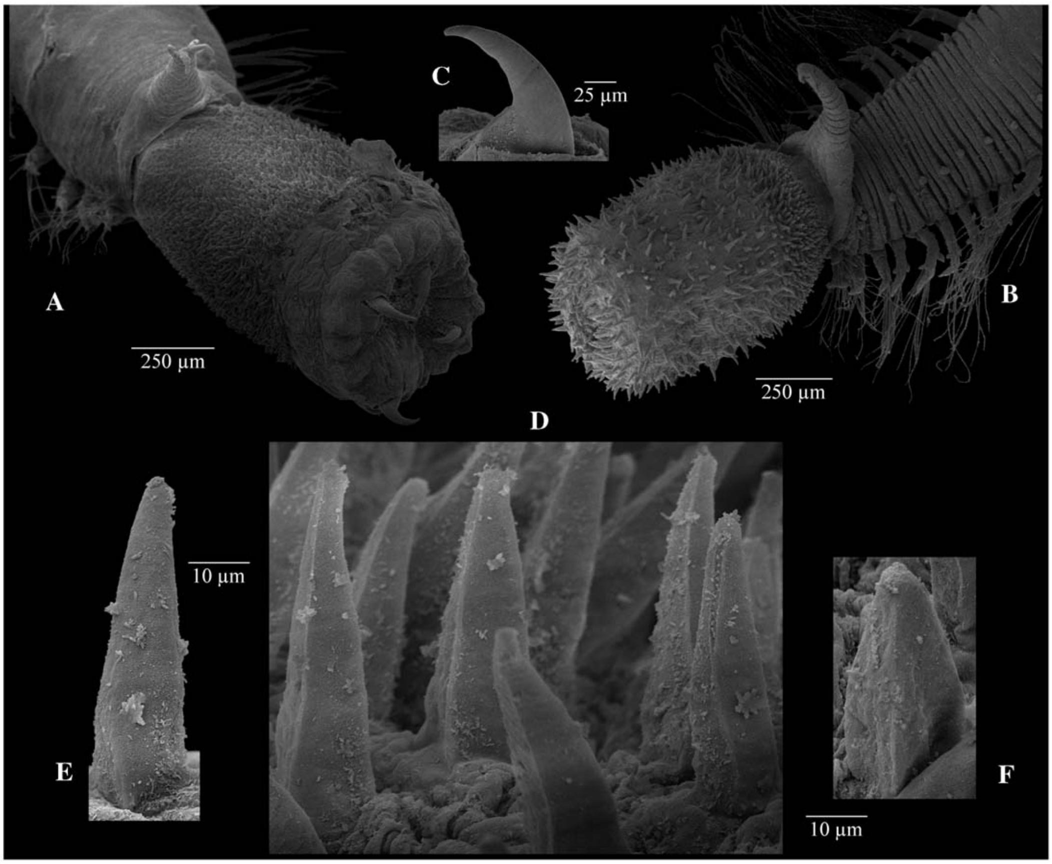

Fig. 33. *Glycera capitata* Ørsted. (A) Anterior end with totally everted proboscis. (B) Anterior end with partly everted proboscis. (C) Jaw. (D) Main type of proboscidial papillae; posterior view. (E) Main type of proboscidial papilla; anterior view. (F) Additional type of proboscidial papillae; posterior view. (A, C: ZMH P25098 A; B, D–F: ZMH P25077 A).

Glycera diva sp. nov.

(Figs. 34–36, 39)

Etymology

The species epithet represents the standard abbreviation of the project name, 'Latitudinal gradients of deep sea bio**DIV**ersity in the **A**tlantic Ocean'. It is to be treated as indeclinable for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 48/1 st. 350 ES-S, 16°13.3′S 5°26.8′E–16°14.8′S 5°26.7′E, 29.vii.2000, 5433–5434 m; holotype: af/30/77/3.3/2.0 (ZMH P25103 B, 3 parapodia for DNA), part of proboscis (ZMH P25103 A, on SEM stub).—R/V METEOR 48/1 st. 350 ES-E, 16°13.3′S 5°26.8′E–16°14.8′S 5°26.7′E, 29.vii.2000, 5433–5434 m; paratype: af/4.8/19/0.9/0.4 (ZMH P25102).

Additional material. See Appendix 1.

Diagnosis

Proboscidial papillae mainly conical with three indistinct transverse ridges; ailerons with pointed triangular bases; parapodia of mid-body with slightly longer neuropodial than notopodial prechaetal lobes and two short postchaetal lobes; branchiae absent.

Description

Body at least 54 mm long with at least 128 chaetigers. Mid-body segments more or less distinctly triannulate.

Conical prostomium consisting of about eight rings; terminal ring with four appendages and basal one with pair of nuchal organs (Fig. 35A).

Proboscis with two types of papillae with subapical tufts of cilia, arranged in more or less distinct longitudinal rows: 1. numerous conical papillae with three indistinct V-shaped ridges on posterior surface (Figs. 35B, 36A–D); 2. isolated, broader, oval to globular papillae probably without ridges (Figs. 35B; 36B, C). Terminal part of proboscis with four hook-shaped jaws arranged in a cross and accessory ailerons with pointed triangular base (Fig. 35C).

First two pairs of parapodia uniramous, following parapodia biramous (Fig. 35D–K). Two slender triangular to digitiform prechaetal lobes; neuropodial lobe usually slightly longer and wider than notopodial lobe; both lobes becoming slightly slimmer in posterior

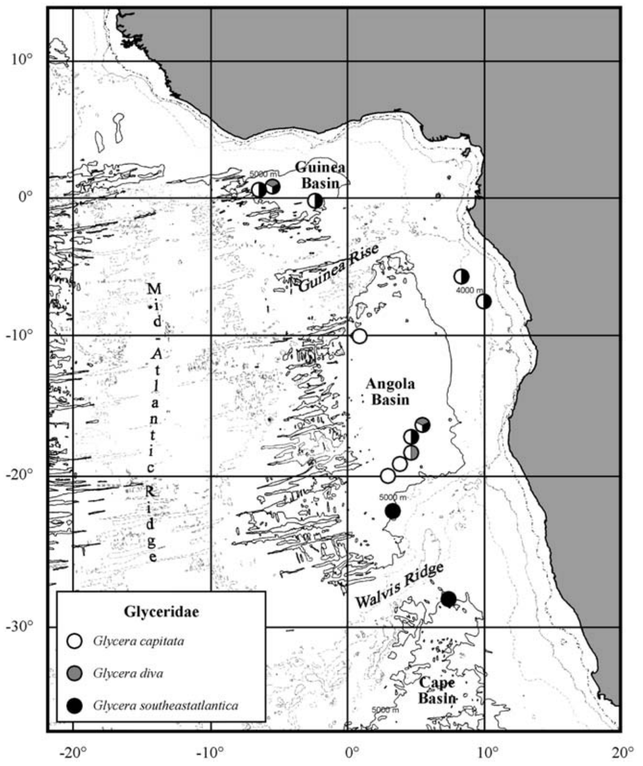

Fig. 34. Distribution of glycerid species in the studied region.

parapodia; in last parapodia notopodial lobe distinctly shorter than neuropodial one. Two shorter, rounded or blunt triangular postchaetal lobes; notopodial lobe always slightly shorter than neuropodial one. Dorsal cirri from 1st or 2nd parapodium, conical to oval; inserted – most clearly in anterior part of body – on body wall far above parapodial base. Ventral cirri slender triangular to digitiform, slightly longer than postchaetal lobes; in posterior parapodia slender and elongated; in last parapodia about as long as neuropodial prechaetal lobe; situated medio-ventrally on parapodia, subterminally on posterior segments. Branchiae absent.

Noto- and neuropodia each with a single acicula. Notochaetae slender, straight or weakly recurved capillary with one side covered with spines or hairs. Neurochaetae compound spinigers with blades of different lengths, covered on one side with spines or hairs.

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Remarks

The proboscidial papillae are not well preserved; therefore, the structure of their posterior sides described above is not absolutely certain.

Distribution

Angola and Guinea Basins; 5143–5443 m (Fig. 34).

Discussion

Glycera diva sp. nov. shows some similarities with *G. tesselata* Grube, 1863 in the structure of the parapodia. However, the latter species has ailerons with deeply incised bases, and mainly digitiform proboscidial papillae with a straight median longitudinal ridge on one side. Concerning the proboscidial papillae, *G. diva* sp. nov. belongs to a group of eight congeners characterised by conical papillae with three transverse ridges. However, the shape of the ailerons and the parapodial lobes are totally different, and most of the other species are provided with branchiae.

Glycera southeastatlantica sp. nov.

(Figs. 34, 37–39)

Etymology

The species epithet refers to the study area. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V L'ATALANTE st. 54 BC, 7°39.9′S 10°0.4′E, 23.xii.2003, 3993 m; holotype: cs/65/132/3.7/2.5 (MNHN Type 1498), part of proboscis (MNHN Type 1499, on SEM stub).—R/V L'ATALANTE st. 36 BC, 7°39.9′S 10°0.4′E, 23.xi.2001, 3993 m; paratype: cs/11.5/64/1.0/0.6 (MNHN Type 1500 spec. 1).—R/V L'ATALANTE st. 36 BC, 7°39.9′S 10°0.4′E, 23.xi.2001, 3993 m; paratype: af/35/104/2.5/1.2 (MNHN Type 1500 spec. 2), part of proboscis (MNHN Type 1501, on SEM stub).

Additional material. See Appendix 1.

Diagnosis

Proboscidial papillae mainly conical with straight median longitudinal ridge; ailerons with triangular bases; parapodia of mid-body with prechaetal lobes of about same length and two short postchaetal lobes; branchiae absent.

Description

Body up to 65 mm long with up to 132 chaetigers. Mid-body segments more or less distinctly triannulate.

Conical prostomium consisting of about 7–8 rings; terminal ring with four appendages and basal one with pair of nuchal organs (Fig. 37A).

Proboscis with two types of papillae with subapical tufts of cilia, arranged in more or less distinct longitudinal rows: 1. numerous conical papillae with straight, median, longitudinal ridge on posterior surface

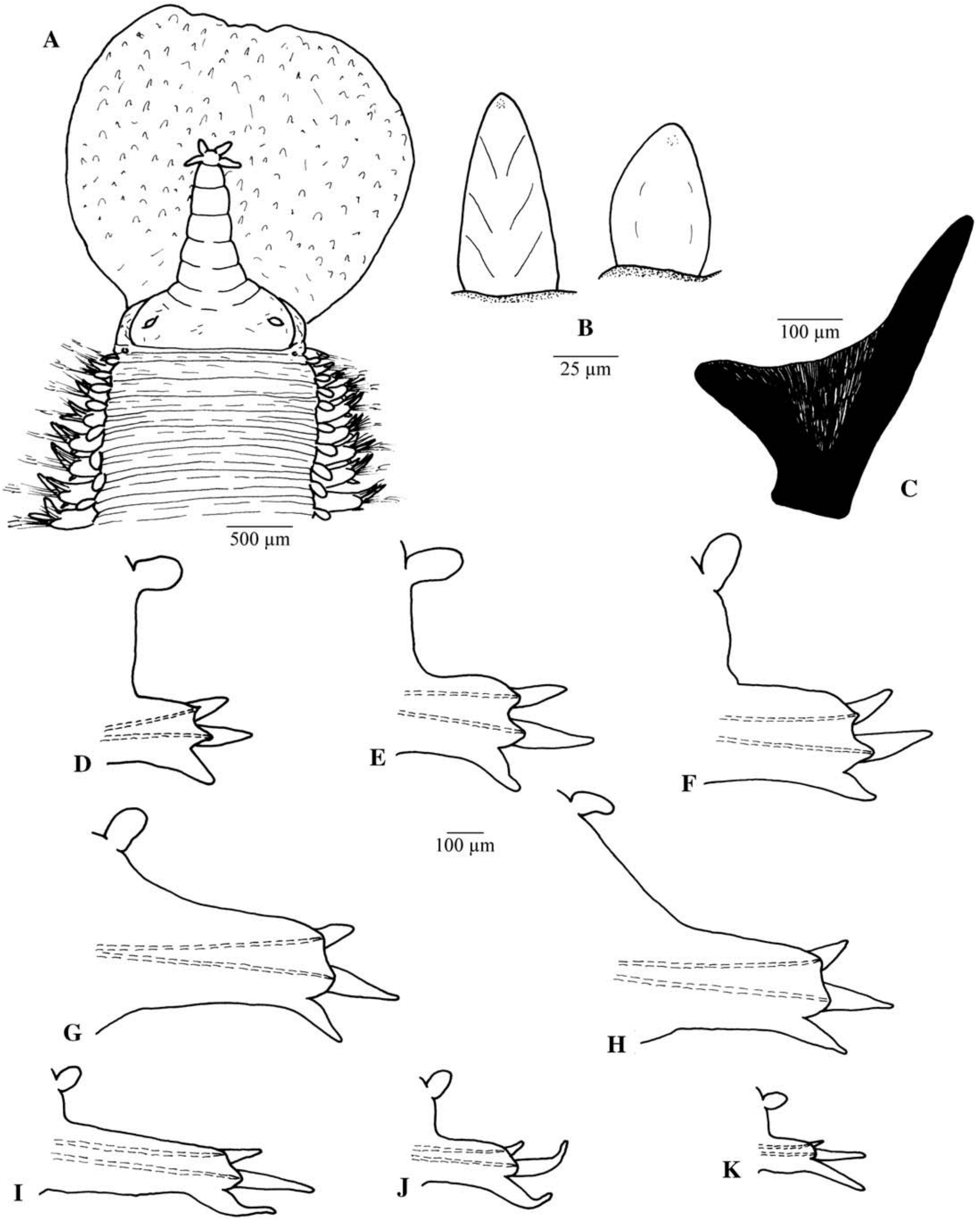

Fig. 35. *Glycera diva* sp. nov. (A) Anterior end. (B) Proboscidial papillae. (C) Aileron. (D–K) Anterior to posterior parapodia; posterior views, chaetae omitted. (A–H: ZMH P25103 B; I–K: SMF 18796).

(Figs. 37B; 38A, B, D); 2. isolated, slightly shorter and broader, oval to globular papillae without ridges (Figs. 37B, 38C). Terminal part of proboscis with four hook-shaped jaws arranged in a cross and accessory ailerons with triangular base (Fig. 37C).

First two pairs of parapodia uniramous, following parapodia biramous (Fig. 37D–K). Two slender triangular to digitiform prechaetal lobes of about same length; both lobes becoming slightly slimmer in posterior parapodia; in last parapodia notopodial lobe slightly shorter than neuropodial one. Two shorter, rounded or blunt triangular postchaetal lobes; notopodial lobe usually slightly shorter than neuropodial one. Dorsal cirri from 1st parapodium, oval to globular; inserted near parapodial base. Ventral cirri slender triangular to digitiform, about as long as postchaetal lobes; in posterior parapodia slender and elongated; in last parapodia about as long as neuropodial prechaetal

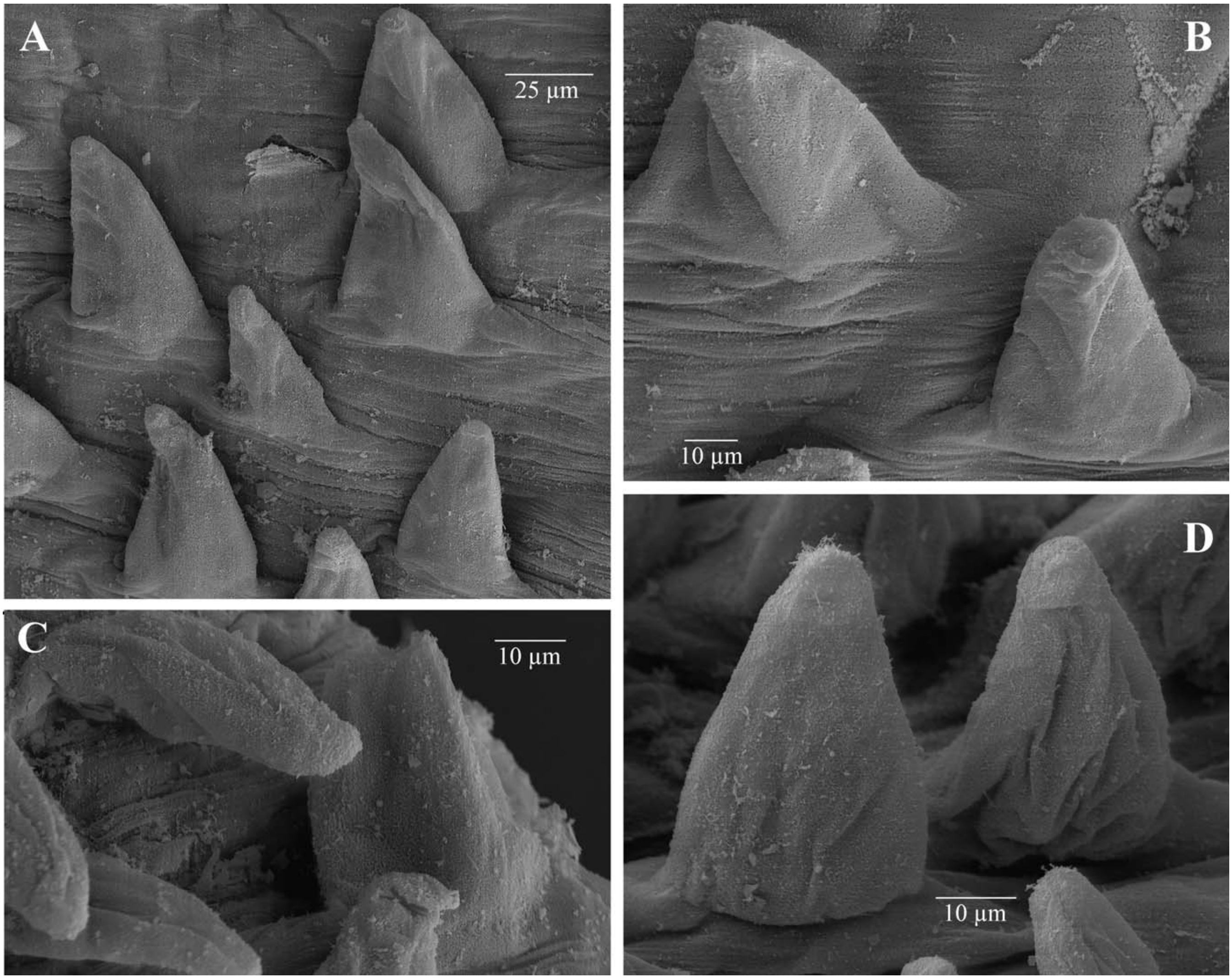

Fig. 36. *Glycera diva* sp. nov. (A) Main type of proboscidial papillae; posterior view. (B) Main and additional type of proboscidial papillae; posterior view. (C) Main and additional type of proboscidial papillae; lateral view. (D) Main type of proboscidial papillae; anterior view. (A–D: ZMH P25103 A).

lobe; situated medio-ventrally on parapodia, subterminally on posterior segments. Branchiae absent.

Noto- and neuropodia each with a single acicula. Notochaetae slender, straight or weakly recurved capillary with one side covered with spines or hairs. Neurochaetae compound spinigers with blades of different lengths, covered on one side with spines or hairs.

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Remarks

Some of the proboscidial papillae have additional laterally located groups of cilia (Fig. 38A, right side), which are also described for other glycerid species (Böggemann et al. 2000).

Distribution

Angola, Cape and Guinea Basins; 3945–5460 m (Fig. 34).

Discussion

Glycera southeastatlantica sp. nov. shows some similarities with *G. guatemalensis* Böggemann & Fiege, 2001 in the structure of the proboscidial papillae. However, the latter species has ailerons with deeply incised bases, and distinctly longer notopodial prechaetal lobes and ventral cirri in the mid-body region.

Abundance of Glyceridae

A total of 239 specimens or fragments were found in all investigated areas. Most of them (173) belong to *Glycera capitata*. This species was present in the Angola

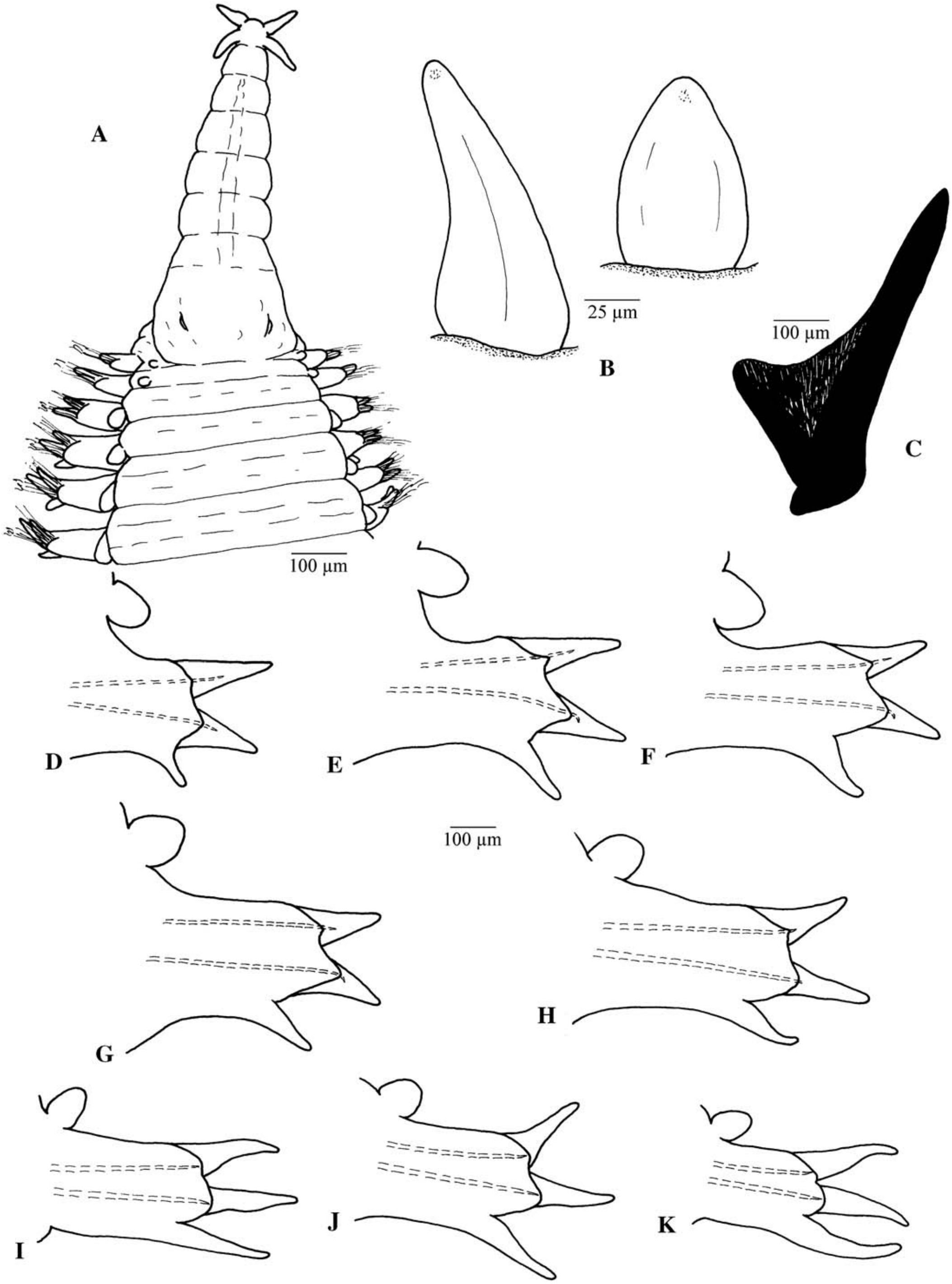

Fig. 37. *Glycera southeastatlantica* sp. nov. (A) Anterior end. (B) Proboscidial papillae. (C) Aileron. (D–K) Anterior to posterior parapodia; posterior views, chaetae omitted. (A: MNHN Type 1500 spec. 1; B–K: MNHN Type 1498).

and Guinea Basins (Fig. 39), sometimes in high abundance (DIVA-1 areas 5–6 and DIVA-2 areas 3–4). This is in contrast to *Glycera diva* sp. nov., which was found in the same basins, but only in the epibenthic sledge samples and in very low numbers (8 specimens or fragments). The 48 specimens or fragments of *Glycera southeastatlantica* sp. nov. were widely distributed through all basins, with the highest abundance in the Angola Basin (DIVA-1 area 6 and BIOZAIRE areas 1–2). The most effective gear for collecting glycerids was the epibenthic sledge. Box corer and multicorer were also very useful, but the corresponding samples were usually fixed in formalin; therefore, the specimens were not valuable for molecular analyses.

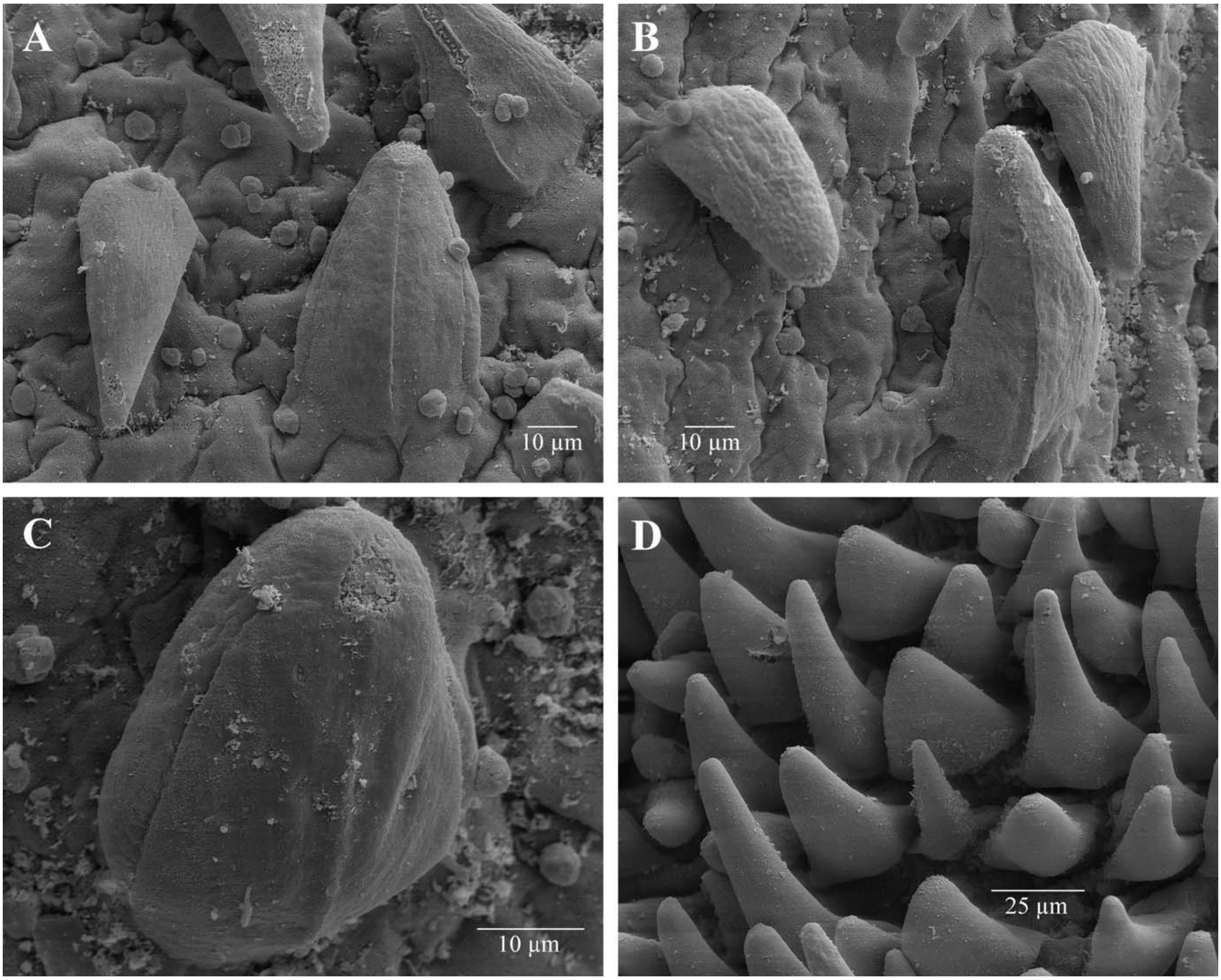

Fig. 38. *Glycera southeastatlantica* sp. nov. (A) Main type of proboscidial papillae; anterior and posterior views. (B) Main type of proboscidial papillae; anterior and posterior views. (C) Additional type of proboscidial papilla; posterior view. (D) Main and additional type of proboscidial papillae; anterior view. (A–C: MNHN Type 1499; D: MNHN Type 1501).

Molecular data

All analyses were conducted using the branch-and bound algorithm. Gaps were treated as missing and characters were unordered and unweighted. Clade support values were calculated with nonparametric bootstrapping with 100 (ML: 18S rDNA, ITS1), 1,000 (ML: 16S rDNA, COI (3-6W), ITS2) or 100,000 replicates (MP).

18S rDNA data set

Nine newly acquired sequences (Table 6) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. The ML analysis was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies ($A = 0.2462$, $C = 0.2254$, $G = 0.2723$, $T = 0.2561$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 0.6889$, $A \leftrightarrow G = 1.0398$, $A \leftrightarrow T = 1.1194$, $C \leftrightarrow G = 0.7478$, $C \leftrightarrow T = 3.4458$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the nine sequences contained 1,704 characters, of which 63 were variable and 4 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 63 steps long with CI = 1.0000, RI = 1.0000 and RC = 1.0000. The topologies of the strict consensus tree and the ML tree ($-\ln L = 2700.98544$) agree completely (Fig. 40).

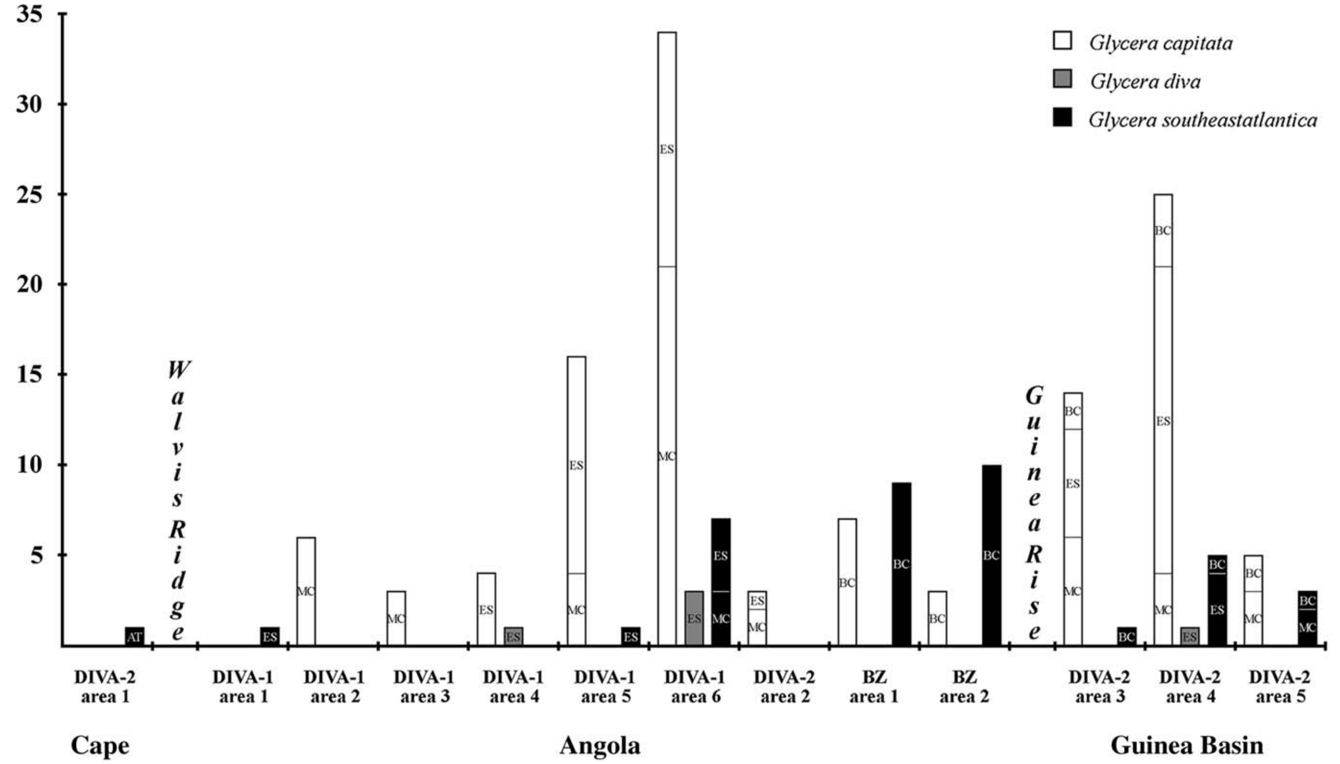

Fig. 39. Abundance of the three glycerid species in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. AT = Agassiz trawl, BC = box corer, ES = epibenthic sledge, MC = multicorer.

16S rDNA data set

Five newly acquired sequences (Table 6) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.3863, C = 0.1473, G = 0.1687, T = 0.2977); number of substitution types = 6; substitution rate matrix (A ↔ C = 3.9556, A ↔ G = 9.1715, A ↔ T = 8.6265, C ↔ G = 2.6271, C ↔ T = 27.6896, G ↔ T = 1.0000); among-site rate variation with proportion of invariable sites = 0.5004; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the five sequences contained 500 characters, of which 150 were variable and 29 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 167 steps long with CI = 1.0000, RI = 1.0000 and RC = 1.0000. The topologies of the strict consensus tree and the ML tree (–ln L = 1262.51225) agree completely (Fig. 40).

COI (3-6W) data set

Six newly acquired sequences (Table 6) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2663, C = 0.1709, G = 0.1828, T = 0.3800); number of substitution types = 6; substitution rate matrix (A ↔ C = 1118.6729, A ↔ G = 2327.0088, A ↔ T = 1358.4171, C ↔ G = 1172.8712, C ↔ T = 4660.6045, G ↔ T = 1.0000); among-site rate variation with proportion of invariable sites = 0.3241; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the six sequences contained 421 characters, of which 142 were variable and 20 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 149 steps long with CI = 1.0000, RI = 1.0000, and RC = 1.0000. The topologies of the strict consensus tree and the ML tree (−ln L = 1048.16887) agree completely (Fig. 40).

ITS1 data set

Nine newly acquired sequences (Table 6) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1577, C = 0.2962, G = 0.2904, T = 0.2557); number of substitution types = 6; substitution rate matrix (A ↔ C = 1.3083, A ↔ G = 4.7375, A ↔ T = 1.0845, C ↔ G = 0.4457, C ↔ T = 4.0601, G ↔ T = 1.0000); among-site rate variation with

Table 6. List of taxa and corresponding sequences in Glyceridae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank acession numbers					
			18S rDNA	16S rDNA	COI		ITS1	ITS2
					(LCO-HCO)	(3-6W)		
GLYCERIDAE								
Glycera capitata Ørsted	Angola Basin							
	D-2 st. 45 ES-S	ZMH P25080	GQ426555	–	–	GQ426658	GQ426705	GQ426723
	Guinea Rise							
	Guinea Basin							
	D-2 st. 63 ES-S	ZMH P25087 B	GQ426556	–	–	GQ426659	GQ426696	GQ426696
	D-2 st. 64 ES-S	ZMH P25088	GQ426557	GQ426605	–	–	GQ426706	–
	D-2 st. 89 ES-E	ZMH P25098 B	GQ426558	GQ426606	–	–	GQ426697	GQ426697
	D-2 st. 90 ES-E	ZMH P25099	GQ426559	GQ426607	–	GQ426660	GQ426707	GQ426724
Glycera southeastatlantica sp. nov.	Guinea Basin							
	D-2 st. 89 ES-E	ZMH P25128 A	GQ426561	–	GQ426630	GQ426662	GQ426708	–
	D-2 st. 89 ES-S	ZMH P25128 B	GQ426562	–	GQ426631	GQ426663	GQ426709	GQ426725
	D-2 st. 90 ES-E	ZMH P25129	GQ426563	GQ426609	GQ426632	–	GQ426710	GQ426726
PARALACYDONIIDAE								
Paralacydonia paradoxa Fauvel	France,							
	Banyuls-s.-M.		GQ426587	GQ426619	–	GQ426684	GQ426700	GQ426700

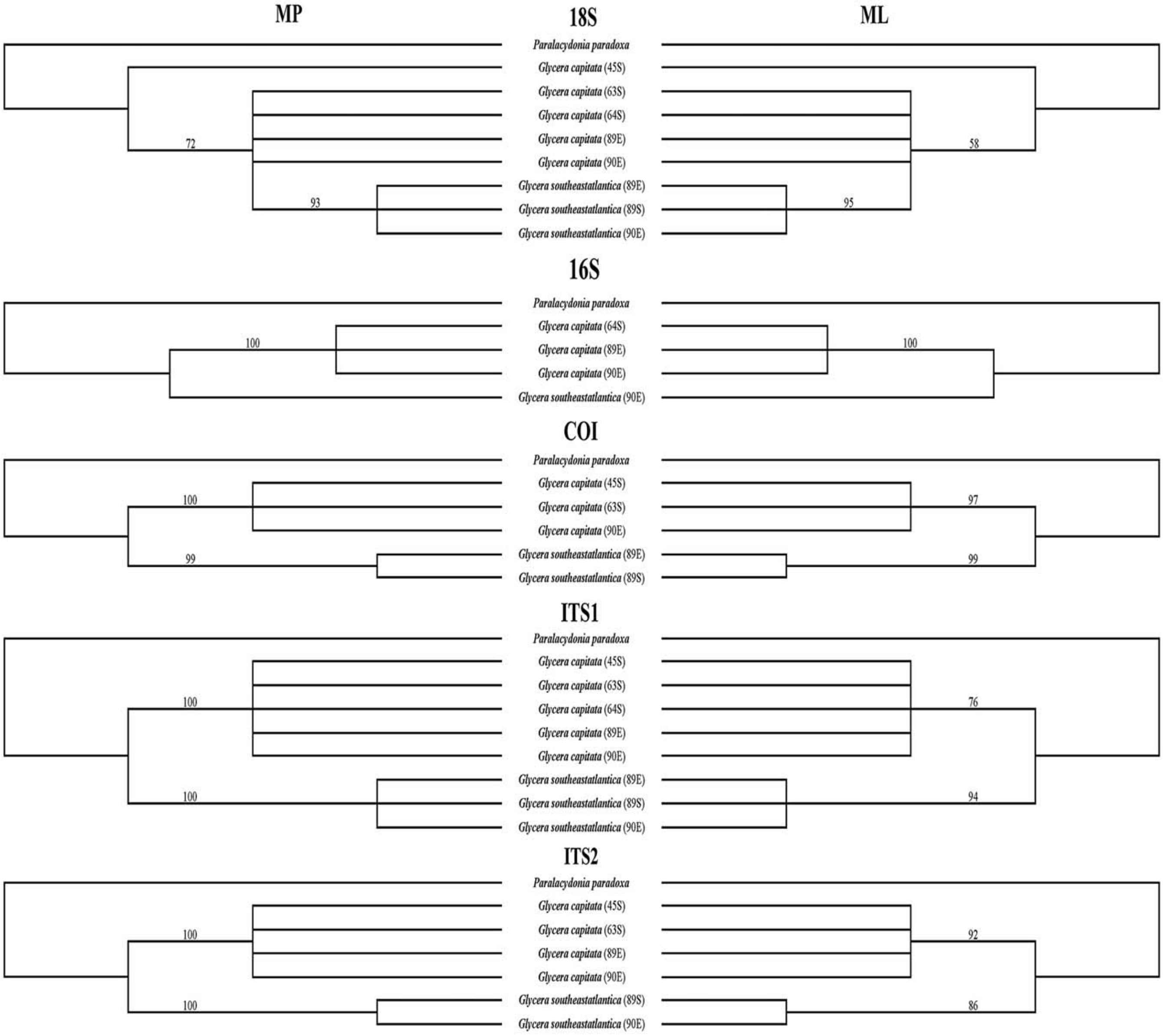

Fig. 40. Cladograms obtained from MP and ML analysis of the 18S, 16S, COI (3-6W), ITS1 and ITS2 sequences, respectively. Bootstrap values > 50 shown above branches.

proportion of invariable sites = 0.3312; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the nine sequences contained 725 characters, of which 323 were variable and 139 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 357 steps long with CI = 1.0000, RI = 1.0000, and RC = 1.0000. The topologies of the strict consensus tree and the ML tree ($-\ln L = 2103.93589$) agree completely (Fig. 40).

ITS2 data set

Seven newly acquired sequences (Table 6) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1702, C = 0.2993, G = 0.2894, T = 0.2411); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 4.1295$, $A \leftrightarrow G = 8.9602$, $A \leftrightarrow T = 8.4175$, $C \leftrightarrow G = 2.9805$, $C \leftrightarrow T = 17.7523$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0.5304; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the seven sequences contained 483 characters, of which 129 were variable and 42 parsimony informative. The MP (tree length = 136, CI = 1.0000, RI = 1.0000, RC = 1.0000) and the ML analysis (−ln L = 1171.14014) found single trees with identical topologies (Fig. 40).

Discussion of molecular results

The monophyly of Glyceridae has been supported, usually strongly, by all phylogenetic analyses so far (see "Molecular phylogeny of abyssal Phyllodocida"). However, the group's placement variously resulted as closely related to lacydoniids, lopadorhynchids, paralacydoniids and phyllodocids (18S), as sister to goniadids (16S), or as nested within the latter, which thereby was rendered paraphyletic (COI). The first of these three alternatives suggested convergent evolution of Glyceridae and Goniadidae, the latter two alternatives implied at least shared ancestry and led to the morphology-based Glyceriformia clade (Pleijel 2001d; Böggemann 2002, 2005, 2006). Much more material and data need to be studied to elucidate the true phylogenetic relationship of the two groups.

The respective members of *Glycera capitata* and *G. southeastatlantica* sp. nov. formed well defined and strongly supported clades in all analyses (Fig. 40). Furthermore, the individual sequences per species and gene differed in one position at the most, which demonstrates that there was no restriction in gene flow between the populations. Consequently, the Guinea Rise does not seem to constitute a barrier for the cold water-adapted and probably cosmopolitan *Glycera capitata*, the larvae of which are known to be planktonic, and the adults possibly active swimmers like other glycerids (see Böggemann 2002).

Goniadidae Kinberg, 1865

The Goniadidae are very similar to the Glyceridae; for details, see the first paragraph of the preceding chapter on the latter family.

Goniadids are generally considered to be endopsammal benthic predators that occur from intertidal to abyssal depths (Fauchald and Jumars 1979; Mattson 1981). Although they constitute a significant component of soft-bottom benthic communities worldwide, their diversity and distribution are still poorly documented in many regions, especially in the deep sea. However, species of the genera *Bathyglycinde* Fauchald and *Progoniada* Hartman are known from abyssal zones and seem to be widely distributed or cosmopolitan (e.g. Hartman 1965, 1967; Hartman and Fauchald 1971; Averincev 1972; Fauchald 1972; Levenstein 1975; Fauchald and Hancock 1981; Amoureux 1986; Kirkegaard 1995; Buzhinskaja 2001, 2004; Böggemann 2005).

The collection of goniadids from the present study contains 96 specimens and fragments belonging to three species: *Bathyglycinde profunda* (Hartman & Fauchald), *Bathyglycinde sibogana* (Augener & Pettibone), and *Progoniada regularis* Hartman.

Key to goniadid species from the abyssal SE Atlantic

1. Anterior uniramous and posterior biramous parapodia (Figs. 41D–K, 44D–K) with capillary notochaetae (Fig. 42E) and spinigerous compound neurochaetae (Fig. 42F); proboscis without chevrons; proboscidial papillae of several different types (Figs. 41B, 42A–D, 44B), arranged in distinct longitudinal rows 2
– All parapodia uniramous (Fig. 45E–L) with falcigerous and spinigerous compound neurochaetae (Fig. 46D); proboscis with chevrons (Figs. 45D, 46A); proboscidial papillae of slightly differing types (Figs. 45B, 46A–C), more irregularly arranged .... *Progoniada regularis* Hartman
2. All parapodia with only one neuropodial prechaetal lobe (Fig. 41D–K); proboscidial area II with six rows of papillae (Figs. 41B, 42B) .... *Bathyglycinde profunda* (Hartman & Fauchald)
– Posterior parapodia with two neuropodial prechaetal lobes (Fig. 44H–K); proboscidial area II with five rows of papillae (Fig. 44B) .... *Bathyglycinde sibogana* (Augener & Pettibone)

Bathyglycinde Fauchald, 1972

Bathyglycinde profunda (Hartman & Fauchald, 1971)
(Figs. 41–43, 47)

Glycinde profunda Hartman & Fauchald, 1971—Hartman and Fauchald (1971, p. 74; pl. 4, figs. c–e)

Bathyglycinde profunda (Hartman & Fauchald)—Böggemann (2005, p. 189, figs. 111, 112)

Material examined

See Appendix 1.

Diagnosis

Proboscis with several different types of papillae, area II with six rows of papillae; four dorsal and no ventral micrognaths; chevrons absent; chaetigers with only one neuropodial prechaetal lobe; 32–39 uniramous parapodia,

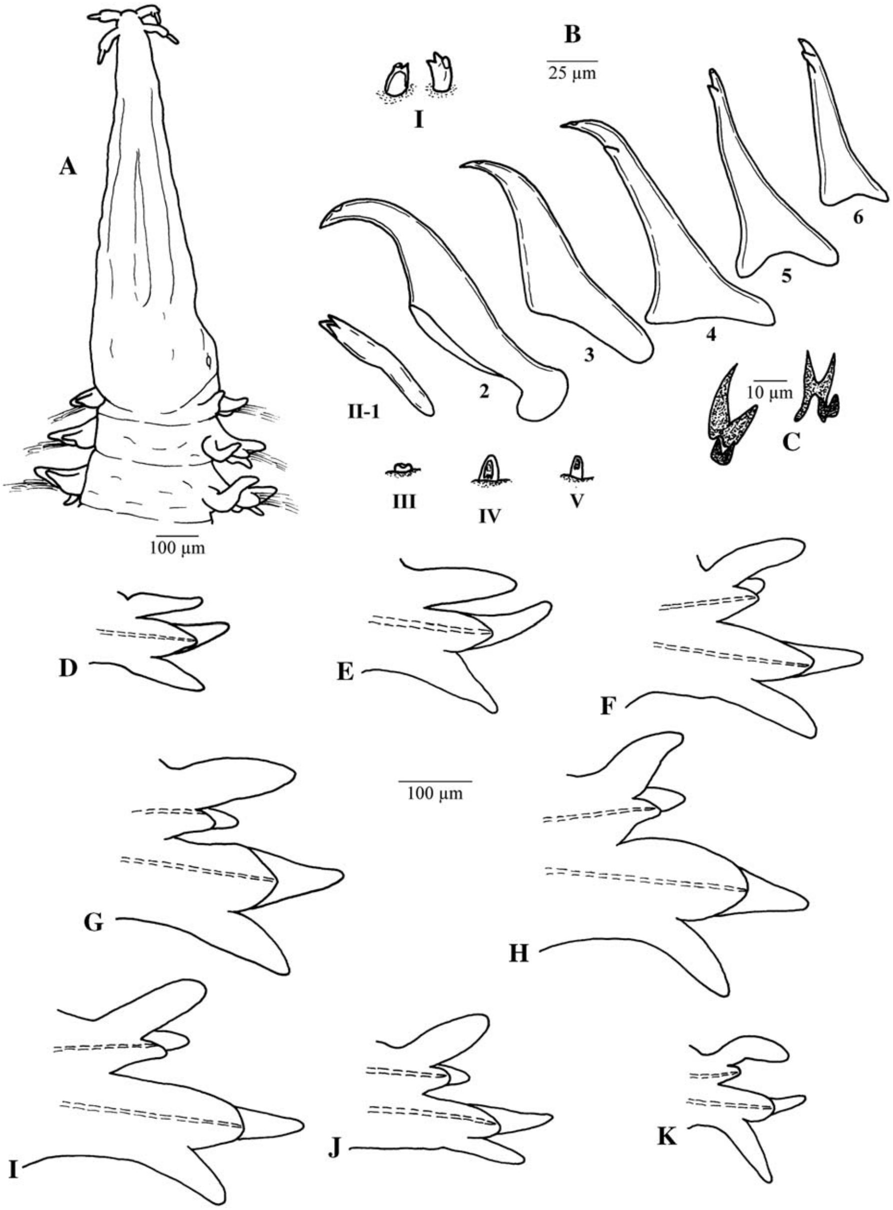

Fig. 41. *Bathyglycinde profunda* (Hartman & Fauchald). (A) Anterior end. (B) Proboscidial papillae. (C) Macro- and micrognaths. (D–K) Anterior to posterior parapodia; posterior views, chaetae omitted. (A, C–K: ZMH P25135; B: ZMH P25142).

the following biramous; notochaetae capillary, neurochaetae compound spinigers.

Description

Body up to 23.5 mm long with up to 64 chaetigers. Segments uniannulate, but median part of dorsum sometimes appears to be bi- or indistinctly triannulate.

Conical prostomium smooth or indistinctly annulated; terminal end with four biarticulate appendages and basal with pair of nuchal organs (Fig. 41A). Eyes absent.

Proboscis with several different types of papillae, arranged in distinct longitudinal rows and best developed in median proboscidial part; papillae usually with a subapical, cuplike depression containing tufts of short cilia; area I: one row of small teapot-shaped papillae with laterally pointed beak, which are sometimes bidentate (Figs. 41B, 42A); area II-1: short, tridentate papillae with broad base (Figs. 41B, 42B); longer fang-shaped papillae of areas II-2 to II-6 decreasing in length, bases becoming slender and tips less curved, areas II-2 and II-3: unidentate, areas II-4 to II-6: bidentate, with decreasing distance between distal and subdistal tooth (Figs. 41B, 42B); area III: one row of very small, rectangular more canoe-shaped papillae (Figs. 41B, 42C); area IV: one row of small, conical papillae with duckfoot-shaped structure on posterior side, which ends in three tiny tips (Figs. 41B, 42D); area V: one row of slightly smaller, conical papillae

Fig. 42. *Bathyglycinde profunda* (Hartman & Fauchald). (A–D) Proboscidial papillae of areas I, II, III, and IV–V, respectively. (E) Notopodial chaetae. (F) Neuropodial chaeta. (A–F: ZMH P25144 A).

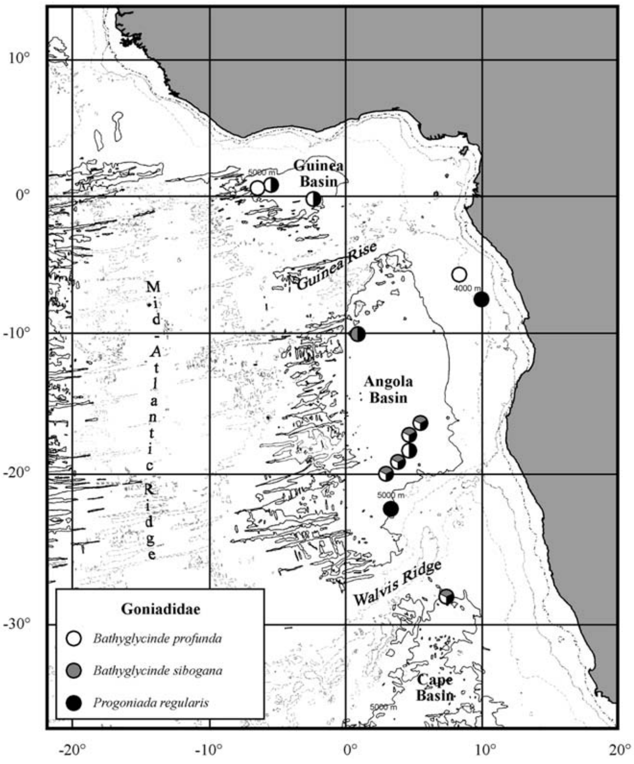

Fig. 43. Distribution of goniadid species in the studied region.

with duckfoot-shaped structure on posterior side, which ends in two tiny tips (Figs. 41B, 42D); area VI: without papillae. Macrognaths indistinctly bi- to quadridentate, compound and only slightly different from micrognaths; 4 H + v-shaped dorsal and no ventral compound micrognaths (Fig. 41C). Chevrons absent.

Anterior chaetigers with one conical to digitiform neuropodial prechaetal lobe and one short, rounded to slightly conical postchaetal lobe (Fig. 41D, E). 34–38 uniramous chaetigers, following parapodia biramous with conical to digitiform notopodial prechaetal lobes and distinctly shorter rounded to conical postchaetal lobes (Fig. 41F). From 39th to 42nd chaetiger (17–19 in juvenile specimens) parapodia slightly enlarged and with noto- and neuropodia clearly separated (Fig. 41G–I); lobes of about same shape as before; in posterior parapodia notopodial prechaetal lobes shorter and neuropodial prechaetal lobes slightly more slender (Fig. 41J, K). Dorsal cirri on anterior chaetigers digitiform, about as long as neuropodial postchaetal lobes or slightly shorter (Fig. 41D, E); in biramous parapodia more conical and about as long as notopodial prechaetal lobes or slightly longer (Fig. 41F–J); in posterior parapodia slender, elongated and more digitiform (Fig. 41K). Ventral cirri on anterior chaetigers digitiform, about as long as neuropodial postchaetal lobes or slightly longer (Fig. 41D–G); in enlarged biramous parapodia more conical and slightly shorter than neuropodial postchaetal lobes (Fig. 41H, I); in posterior parapodia slender digitiform and about as long as neuropodial prechaetal lobes (Fig. 41J, K).

Noto- and neuropodia each with a single acicula. Notochaetae slender, straight or weakly recurved capillary with one side covered with spines or hairs (Fig. 42E). Neurochaetae compound spinigers with blades of different lengths, covered on one side with spines or hairs (Fig. 42F).

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Remarks

Posterior enlarged body part of one specimen (ZMH P25142) filled with large eggs. One specimen (SMF 14117) with additional long natatory chaetae in middle part of body.

Distribution

Angola, Cape and Guinea Basins; 3961–5494 m (Fig. 43).

Bathyglycinde sibogana (Augener & Pettibone in Pettibone, 1970)

(Figs. 43, 44, 47)

Glycinde sibogana Augener & Pettibone in Pettibone, 1970—Pettibone (1970, p. 244, figs. 40, 41)

Bathyglycinde sibogana (Augener & Pettibone)—Böggemann (2005, p. 196, figs. 115, 116)

Material examined

See Appendix 1.

Diagnosis

Proboscis with several different types of papillae, area I with only small conical papillae, area II with five rows of papillae; 2–8 dorsal and no ventral micrognaths; chevrons absent; posterior chaetigers with two neuropodial prechaetal lobes, lower lobe developed from parapodium 26–41; 28–39 uniramous parapodia, the following biramous; notochaetae capillary, neurochaetae compound spinigers.

Description

Body up to 18 mm long with up to 75 chaetigers. Segments uniannulate, but median part of dorsum sometimes appears to be biannulate.

Conical prostomium consisting of about four irregular, indistinct rings, with a lateral longitudinal groove on each side; terminal annulus with four biarticulate appendages and basal one with pair of nuchal organs (Fig. 44A). Eyes absent.

Proboscis with several different types of papillae, arranged in distinct longitudinal rows and best developed in median proboscidial part; papillae usually with a subapical, cuplike depression containing tufts of short cilia; area I: one row of small conical to cylindrical papillae with terminal plate (Fig. 44B); area II-1: short, globular papillae with lateral beak (Fig. 44B); longer unidentate, fang-shaped papillae of areas II-2 to II-5 decreasing in length, bases becoming slender and tips less curved, papillae of area II-3 sometimes with broader more hammer-shaped tip (Fig. 44B); area III: probably with one row of very small, rectangular more canoe-shaped papillae (Fig. 44B); areas IV, V: both with one row of small, conical papillae probably with duckfoot-shaped structure on posterior side (Fig. 44B); area VI: without papillae. Macrognaths bi- to tridentate; 2–8 H + v-shaped dorsal and no ventral compound micrognaths (Fig. 44C). Chevrons absent.

First segment apodous and achaetous, only with a pair of small lateral cirri (Fig. 44A). Anterior chaetigers with only one neuropodial pre- and one postchaetal lobe (Fig. 44D); from 25th to 32nd chaetiger parapodia slightly enlarged (Fig. 44E); second, lower prechaetal lobe developed from chaetigers 33–41; both prechaetal lobes conical to digitiform, upper one distinctly longer and broader than lower one; rounded to slightly conical postchaetal lobe always distinctly shorter (Fig. 44G–J). 35–38 uniramous chaetigers, following parapodia biramous with conical to digitiform notopodial prechaetal lobes and distinctly shorter rounded to conical postchaetal lobes (Fig. 44F). From mid-body with noto- and neuropodia clearly separated (Fig. 44G–I); lobes of about same shape as before; in posterior parapodia notopodial and lower neuropodial prechaetal lobes shorter and upper neuropodial prechaetal lobes slightly more slender (Fig. 44J, K). Dorsal cirri on anterior chaetigers digitiform, about as long as neuropodial postchaetal lobes or slightly shorter (Fig. 44D, E); in biramous parapodia more conical and about as long as notopodial prechaetal lobes or longer (Fig. 44F–I); in posterior parapodia slender, elongated and more digitiform (Fig. 44J, K). Ventral cirri digitiform; in anterior parapodia about as long as neuropodial postchaetal lobes or slightly longer (Fig. 44D–F); in enlarged biramous parapodia about as long as neuropodial postchaetal lobes or slightly shorter (Fig. 44G–I); in posterior parapodia slender, elongated and about as long as upper neuropodial prechaetal lobes (Fig. 44J, K).

Noto- and neuropodia each with a single acicula. Notochaetae slender, straight or weakly recurved capillary with one side covered with spines or hairs. Neurochaetae compound spinigers with blades of different lengths, covered on one side with spines or hairs.

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Distribution

Angola and Cape Basins; 5058–5648 m (Fig. 43).

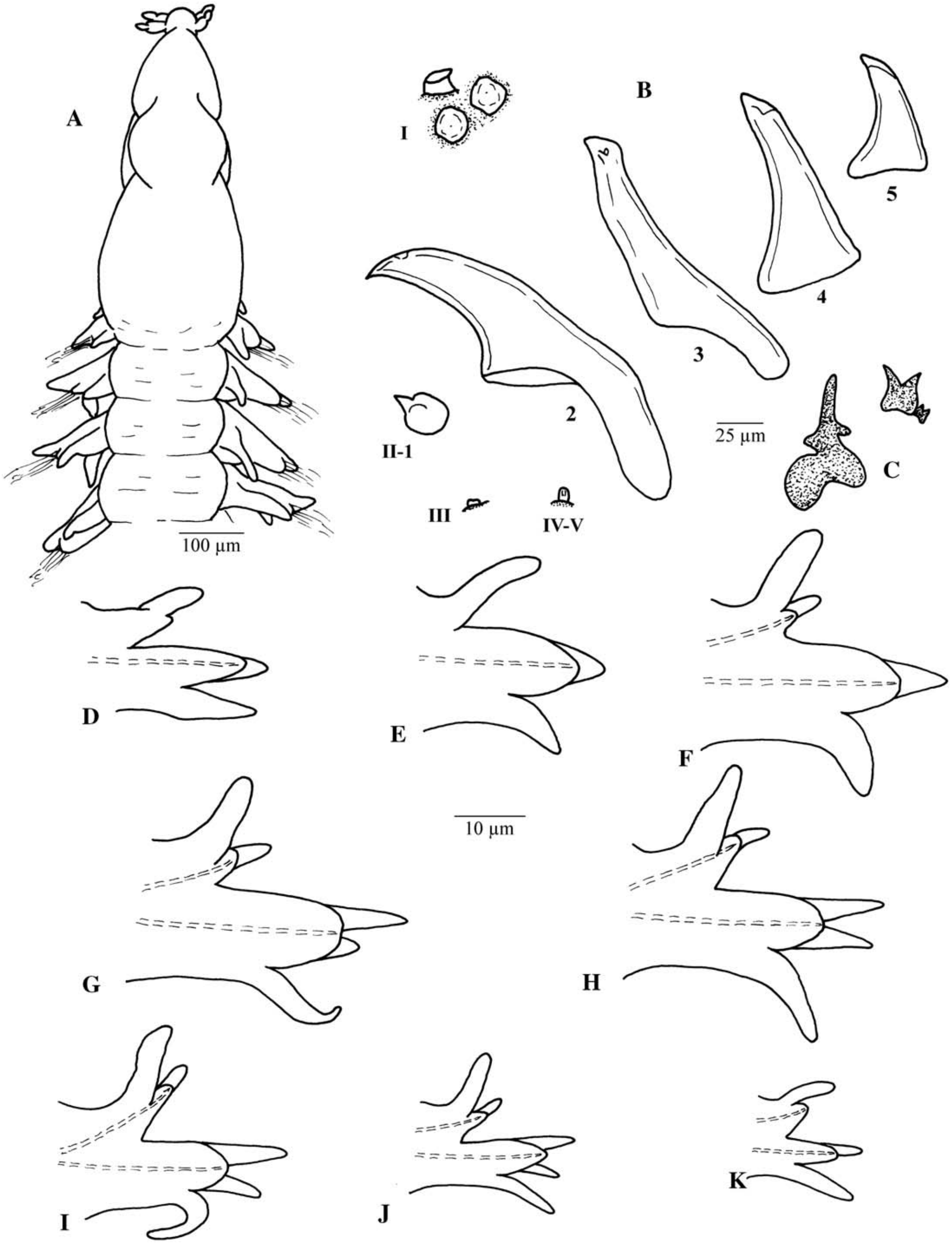

Fig. 44. *Bathyglycinde sibogana* (Augener & Pettibone). (A) Anterior end. (B) Proboscidial papillae. (C) Macro- and micrognaths. (D–K) Anterior to posterior parapodia; posterior view, chaetae omitted. (A: ZMH P25146; B–K: SMF 14110).

Progoniada Hartman, 1965

Progoniada regularis Hartman, 1965
(Figs. 43, 45–47)

Progoniada regularis Hartman, 1965—Hartman (1965, p. 100, pl. 16a–f); Böggemann (2005, p. 155, figs. 86–88)

Progoniada simplex Hartman, 1971—Hartman (1971, p. 1408, fig. 1a–d)

Material examined

See Appendix 1.

Diagnosis

Proboscidial papillae of slightly differing types; chevrons present; parapodia all uniramous; neurochaetae compound falcigers and/or spinigers.

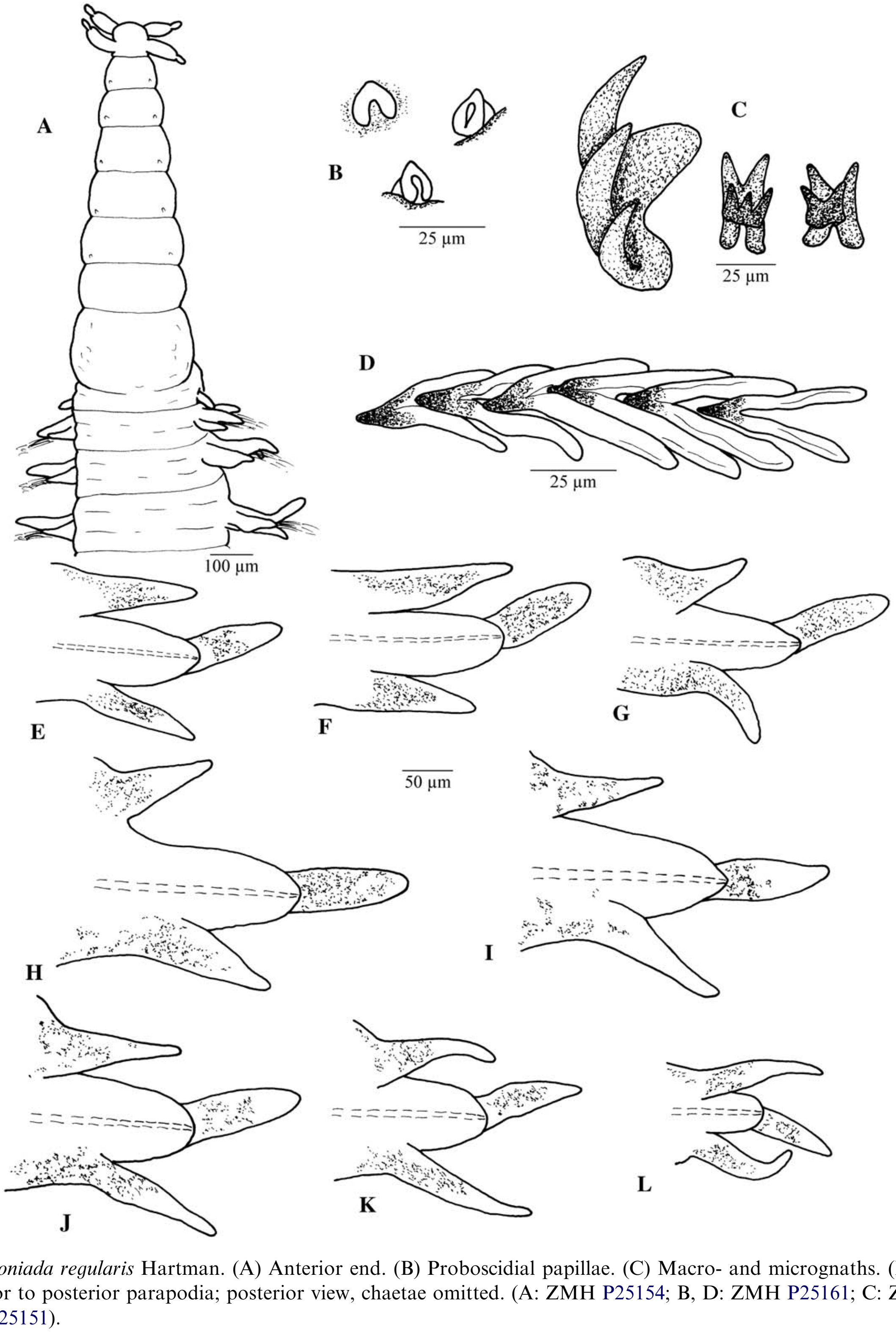

Fig. 45. *Progoniada regularis* Hartman. (A) Anterior end. (B) Proboscidial papillae. (C) Macro- and micrognaths. (D) Chevrons. (E–L) Anterior to posterior parapodia; posterior view, chaetae omitted. (A: ZMH P25154; B, D: ZMH P25161; C: ZMH P24687; E–L: ZMH P25151).

Description

Body up to 25 mm long with up to 107 chaetigers. Anterior segments biannulate, following segments triannulate.

Conical prostomium consisting of eight rings; terminal annulus with four biarticulate appendages and basal one with pair of nuchal organs (Figs. 45A). Eyes absent.

Proboscis with more or less distinct longitudinal rows of papillae (Fig. 46A), dorsally with high density and fewer in lateral and ventral parts; papillae usually with a

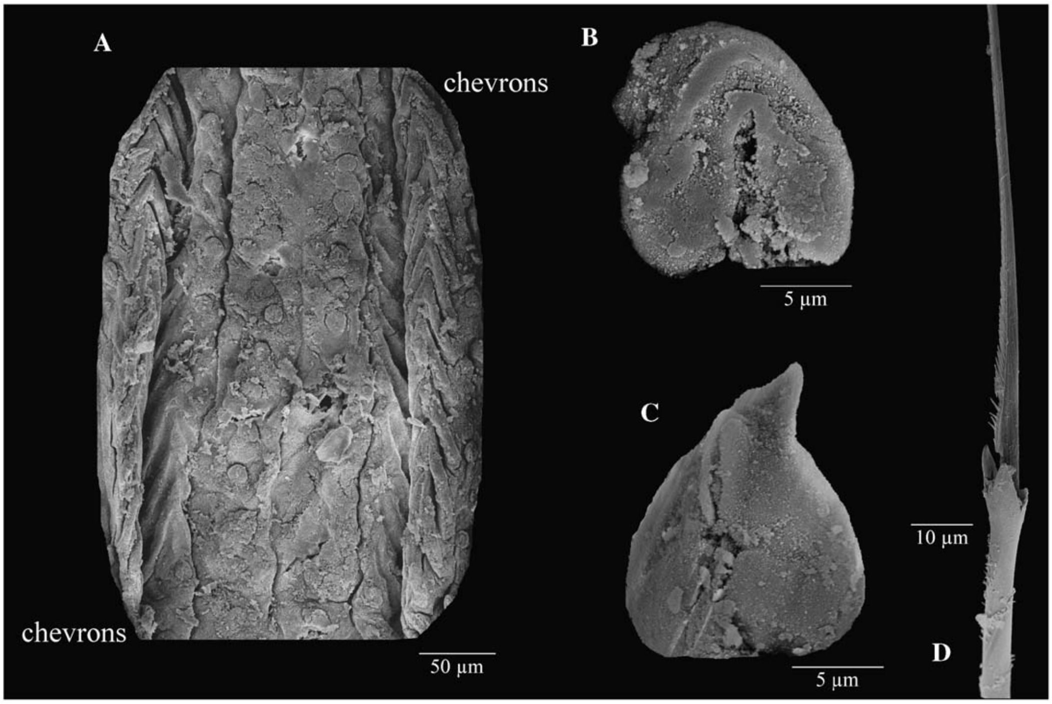

Fig. 46. *Progoniada regularis* Hartman. (A) Part of proboscis with papillae and chevrons. (B, C) Proboscidial papillae. (D) Neuropodial chaeta. (A–C: ZMH P25159 C; D: ZMH P25157 A).

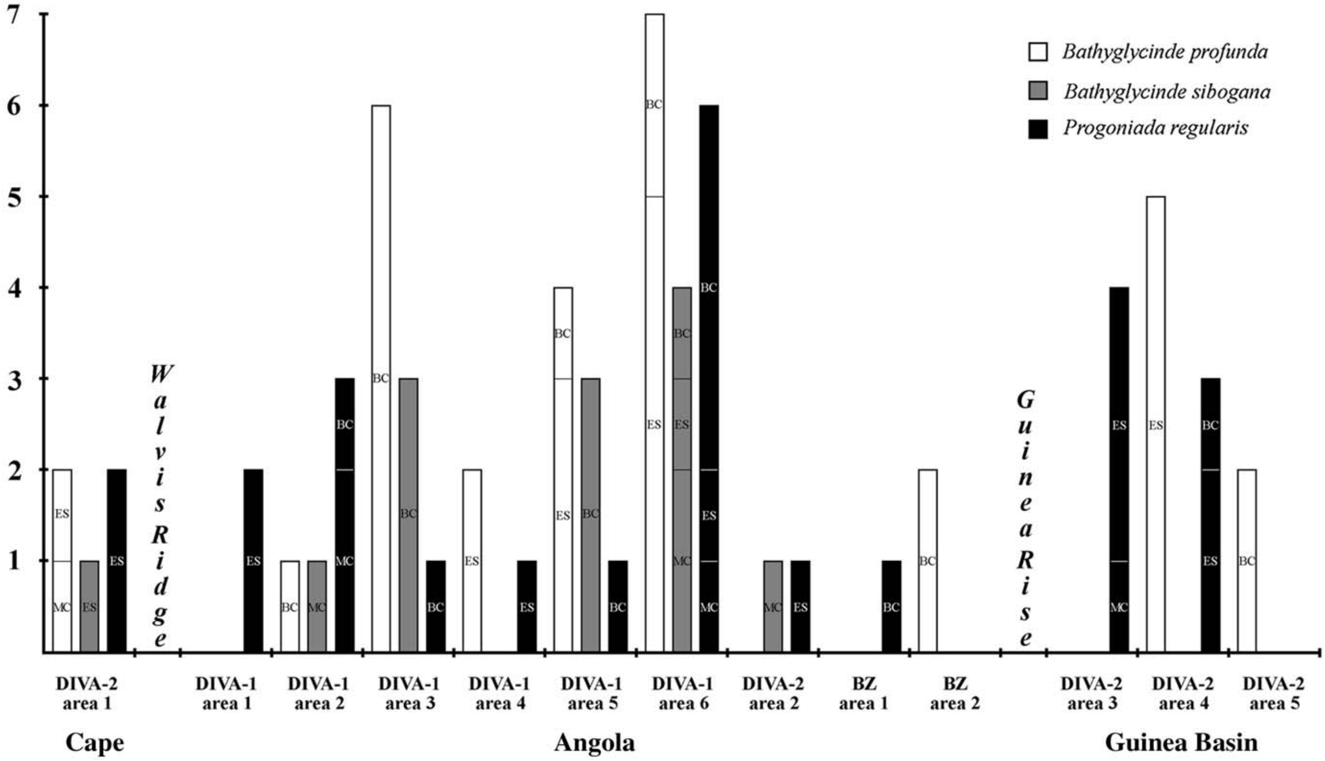

Fig. 47. Abundance of the three goniadid species in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

subapical, cuplike depression containing tufts of short cilia; dorsal rows with heart-shaped papillae on short stalks (Fig. 45B), lateral ones smaller, heart-shaped with slightly laterally bent tip on shorter stalks (Figs. 45B, 46C) and ventral rows with small bi- or trifid rectangular papillae without stalks; some small, distally rounded papillae especially around chevrons and in basal and terminal proboscidial parts (Figs. 45B, 46B). Macrognaths bi- to quinquedentate (Fig. 45C); 4–11 H + v-shaped dorsal and 0–3 H + v/w-shaped slightly larger ventral compound micrognaths, micrognaths in dorsal arc of different sizes usually arranged in the following manner: M-h-(0-3)H-h-(0-3)H-h-(0-3)H-h-M. 4–12 chevrons on each side of proboscis; each one with slender arms and mostly pointed tip (Figs. 45D, 46A).

First segment apodous and achaetous, only with a pair of small lateral cirri (Fig. 45A). Parapodia all uniramous, with one conical to digitiform neuropodial prechaetal lobe and one short, rounded postchaetal lobe (Fig. 45E–L); notopodial lobes absent; parapodia size increasing towards mid-body. Dorsal and ventral cirri pointed conical to digitiform; of about same length, both about as long as neuropodial postchaetal lobes or slightly shorter (Fig. 45E–H); in posterior parapodia both slender and elongated (Fig. 45I–K); in last parapodia about as long as neuropodial prechaetal lobes (Fig. 45L).

Notochaetae absent. Neuropodia with a single acicula. Neurochaetae compound with blades of different lengths, covered on one side with spines or hairs (Fig. 46D), uppermost and lowermost ones falcigers with short blades and middle ones spinigers with longer blades; length of blades increasing towards mid-body and also in larger specimens.

Pygidium with a dorsal anus and a terminal pair of slender, elongated cirri.

Distribution

Angola, Cape and Guinea Basins; 3993–5655 m (Fig. 43).

Abundance of Goniadidae

A total of 94 specimens or fragments of goniadids were found in all investigated areas. Most of them (43) belong to *Bathyglycinde profunda*. This species was present in all basins (Fig. 47), with the highest abundance in the Angola Basin (DIVA-1 areas 3, 5, 6) and the Guinea Basin (DIVA-2 area 4). *Bathyglycinde sibogana* was not found in the Guinea Basin. However, the majority of the fifteen specimens or fragments are from the Angola Basin (DIVA-1 areas 3, 5, 6). The 36 specimens or fragments of *Progoniada regularis* were widely distributed through all basins, with the highest abundance in the Angola Basin (DIVA-1 area 6) and the Guinea Basin (DIVA-2 areas 3, 4). The most effective types of gear for collecting goniadids were the box corer and the epibenthic sledge, while only a few specimens were collected with the multicorer (Fig. 47). The epibenthic sledge samples have the added advantage of generally being rapidly fixed in ethanol; therefore, the material was more or less useful for molecular analyses.

Molecular data

All analyses were conducted using the branch-and bound algorithm. Gaps were treated as missing and characters were unordered and unweighted. Clade support values were calculated with nonparametric bootstrapping with 100 (ML: 18S rDNA, COI), 1,000 (ML: ITS1 + 2) or 100,000 replicates (MP).

18S rDNA data set

Ten newly acquired sequences (Table 7) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. The ML analysis was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies (A = 0.2445, C = 0.2320, G = 0.2795, T = 0.2440); number of substitution types = 6; substitution rate matrix (A ↔ C = 0.8058, A ↔ G = 1.2729, A ↔ T = 1.1497, C ↔ G = 0.9394, C ↔ T = 2.8814, G ↔ T = 1.0000); among-site rate variation with proportion of invariable sites = 0.6650; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the ten sequences contained 1,746 characters, of which 305 were variable and 112 parsimony informative. The MP analysis yielded eight most parsimonious trees, which are 362 steps long with CI = 0.9448 (0.8734), RI = 0.8864, and RC = 0.8374. The topologies of the strict consensus tree and the ML tree (–ln L = 4120.58400) are congruent (Fig. 48).

COI (L-HCO) data set

Eight sequences (7 new, 1 from GenBank; Table 7) were included and analyses were rooted using *Parandalia* sp. (Pilargidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2570, C = 0.1817, G = 0.1763, T = 0.3850); number of substitution types = 6; substitution rate matrix (A ↔ C = 6.9032, A ↔ G = 20.1033, A ↔ T = 7.7481, C ↔ G = 5.9980, C ↔ T = 35.9687, G ↔ T = 1.0000); among-site rate variation with proportion of invariable sites = 0.4785; and gamma distribution shape parameter = 2.6554.

Table 7. List of taxa and corresponding sequences in Goniadidae, Paralacydoniidae and Pelargidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank acession numbers					
			18S rDNA	16S rDNA	COI		ITS1	ITS2
					(LCO-HCO)	(3-6W)		
GONIADIDAE								
Bathyglycinde profunda	Cape Basin							
(Hartman & Fauchald)	D-2 st. 40 ES-S	ZMH P25142	GQ426565	GQ426611	GQ426633	GQ426666	–	–
	Walvis Ridge							
	Angola Basin							
	D-1 st. 338 ES-S	ZMH P25134	GQ426566	–	–	–	–	–
	Guinea Rise							
	Guinea Basin							
	D-2 st. 89 ES-E	ZMH P25143	GQ426567	–	GQ426634	GQ426667	–	–
	D-2 st. 90 ES-E	ZMH P25144 B	–	–	GQ426635	GQ426668	GQ426711	–
Bathyglycinde sibogana	Cape Basin							
(Augener & Pettibone)	D-2 st. 41 ES-S	ZMH P25147	GQ426568	–	GQ426636	GQ426669	GQ426712	–
Progoniada regularis	Cape Basin							
Hartman	D-2 st. 41 ES-S	ZMH P25156	GQ426572	GQ426615	GQ426637	GQ426672	–	GQ426727
	Walvis Ridge							
	Angola Basin							
	D-2 st. 45 ES-S	ZMH P25157 B	GQ426573	GQ426616	GQ426638	GQ426673	–	GQ426728
	Guinea Rise							
	Guinea Basin							
	D-2 st. 63 ES-S	ZMH P25159 B	GQ426574	–	–	–	–	GQ426729
	D-2 st. 89 ES-E	ZMH P25161	GQ426575	–	GQ426639	GQ426674	–	–
	D-2 st. 90 ES-S	ZMH P25162	GQ426576	–	–	–	GQ426698	GQ426698
PARALACYDONIIDAE								
Paralacydonia paradoxa	France,							
Fauvel	Banyuls-s.-M.		GQ426587	–	–	GQ426684	GQ426700	GQ426700
PILARGIDAE								
Parandalia sp.	Australia, Darwin		–	–	EU835664*	–	–	–

*Sequence obtained from GenBank.

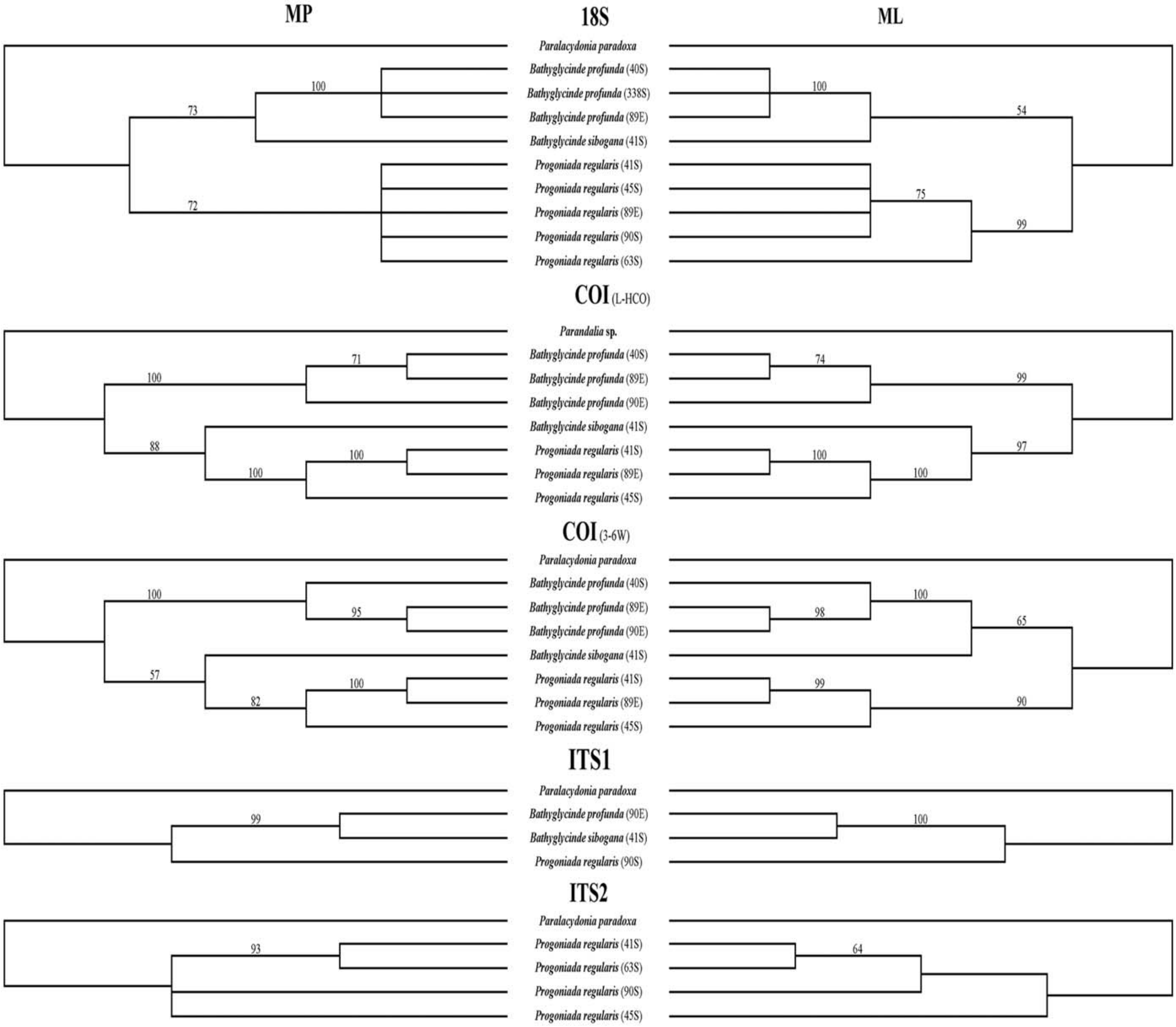

Fig. 48. Cladograms obtained from MP and ML analysis of the 18S, COI, ITS1 and ITS2 sequences, respectively. Bootstrap values > 50 shown above branches.

After exclusion of the primer sites, the alignment for the eight sequences contained 658 characters, of which 272 were variable and 202 parsimony informative. The MP (tree length = 428, CI = 0.8738 (0.8457), RI = 0.8586, RC = 0.7503) and the ML analysis (–ln L = 2532.46921) found single trees with identical topologies (Fig. 48).

COI (3-6W) data set

Eight newly acquired sequences (Table 7) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2680, C = 0.1871, G = 0.1592, T = 0.3857); number of substitution types = 6; substitution rate matrix (A ↔ C = 9.5883, A ↔ G = 12.5388, A ↔ T = 5.1255, C ↔ G = 2.3875, C ↔ T = 26.6068, G ↔ T = 1.0000); among-site rate variation with proportion of invariable sites = 0.4977; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the eight sequences contained 421 characters, of which 165 were variable and 110 parsimony informative. The MP (tree length = 262, CI = 0.8244 (0.7677), RI = 0.7937, RC = 0.6544) and the ML analysis (–ln L = 1591.99724) found single trees differing with regard to the position of *Bathyglycinde sibogana* (Fig. 48).

ITS1 data set

Four newly acquired sequences (Table 7) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1842, C = 0.2961, G = 0.3242, T = 0.1955); number of substitution types = 6; substitution rate matrix (A↔C = 0.7664, A↔G = 2.0927, A↔T = 1.1663, C↔G = 1.3450, C↔T = 2.0331, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and equal rates for all sites.

After exclusion of the primer sites, the alignment for the four sequences contained 590 characters, of which 378 were variable and 30 parsimony informative. The MP (tree length = 491, CI = 0.9756 (0. 7143), RI = 0.6000, RC = 0.5853) and the ML analysis (–ln L = 2164.17290) found single trees with identical topologies (Fig. 48).

ITS2 data set

Five newly acquired sequences (Table 7) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1885, C = 0.3033, G = 0.2870, T = 0.2212); number of substitution types = 6; substitution rate matrix (A↔C = 3.6453, A↔G = 6.9970, A↔T = 2.1399, C↔G = 0.4207, C↔T = 6.0843, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.0798; and gamma distribution shape parameter = 0.4763.

After exclusion of the primer sites, the alignment for the five sequences contained 461 characters, of which 179 were variable and 15 parsimony informative. The MP analysis yielded two most parsimonious trees, which are 198 steps long with CI = 0.9697 (0.7500), RI = 0.6000, and RC = 0.5818. The topologies of the strict consensus tree and the ML tree (–ln L = 1303.52156) are congruent (Fig. 48).

Discussion of molecular results

Analyses of 18S and 16S rDNA sequences have usually provided strong support for monophyly of the Goniadidae, which resulted as either closely related to nereidids and sphaerodorids (18S) or as sister to glycerids (16S), whereas the COI amino acid sequences weakly supported their paraphyly with Glyceridae as a monophyletic group within Goniadidae (see "Molecular phylogeny of abyssal Phyllodocida"). In contrast to these inconsistent molecular results the morphological features clearly indicate common ancestry of the monophyletic Goniadidae and Glyceridae (Pleijel 2001d; Böggemann 2002, 2005, 2006). However, more taxa and characters need to be studied to assess the true phylogenetic relationships of the two groups.

The clade topologies of the different molecular analyses more or less agree, except concerning the position of *Bathyglycinde sibogana* (Fig. 48). This species resulted as more closely related either to *B. profunda* (18S, COI 3-6W ML, ITS1) or to *Progoniada regularis* (COI L-HCO, COI 3-6W MP), with both hypotheses supported by high bootstrap values. However, the latter relationship made the morphologically clearly delineated genus *Bathyglycinde* paraphyletic.

The analyzed data of *Bathyglycinde profunda* and *Progoniada regularis* strongly supported both groups as monophyletic. In contrast to the former taxon, in which the genes or their translated amino acid sequences were homogeneous among individuals, the latter species seems to be divided in slightly different populations. However, the patterns is obviously not directly influenced by the underwater ridges, because the specimens from the Cape Basin and the Guinea Basin, separated by the Walvis Ridge and the Guinea Rise, were more closely related to each other than to the one from the intermediate Angola Basin. These molecular data suggest that *Bathyglycinde profunda* might be regarded as cosmopolitan, whereas *Progoniada regularis* is more likely to be a complex of cryptic or sibling species. Further studies will be needed to assess their transmission and dispersion patterns, because in contrast to glycerids with their active planktotrophic larvae, some goniadid larvae have been described as lecithotropic and not very mobile (see Böggemann 2005). Nevertheless, sometimes natatory chaetae have been observed in adult specimens (see above for *Bathyglycinde profunda*), which might be used by epitokes for spawning or by atokes for migration.

Hesionidae Grube, 1850

The Hesionidae are a rather heterogeneous part of Nereidiformia, which clearly belongs to the Phyllodocida (Pleijel 2001e). However, no apomorphies for the group are known, because cephalisation of anterior segments with pairs of elongated cirri is also present in the Nereididae Lamarck, 1818 (Fauchald and Rouse 1997). Nevertheless, according to Pleijel and Dahlgren (1998) the Hesionidae seem to be most closely related to the Chrysopetalidae, whereas some previously included interstitial genera (e.g. *Hesionides* Friedrich, 1937 and *Microphthalmus* Mecznikow, 1865) have been removed and are currently considered as Nereidiformia incertae sedis (Pleijel 2001e).

The Hesionidae have a worldwide distribution from the intertidal to abyssal depths; however, most of the taxa occur in subtidal to slope depths but usually in low abundance (Pleijel 2001e). They are found on hard substrates as well as on soft sediments (Uebelacker 1984; Wilson 2000b); a few taxa are also known from hydrothermal vents (Blake 1991; Desbruyères et al. 2006), cold seeps (Desbruyères and Toulmond 1998) or whale carcasses (Pleijel et al. 2008). Fauchald and Jumars (1979) suggested that larger hesionids are carnivores feeding on a varity of small invertebrates, which was corroborated by Shaffer (1979) and Oug (1980). Otherwise, some species are known to live in commensalism with polychaetes or other invertebrates such as echinoderms, crustaceans and molluscs (Martin and Britayev 1998). Hesionids are usually extremely fragile and mostly fragmented; especially antennae, cirri and palps readily break during collecting. Therefore, descriptions are often inadequate (Fauchald and Rouse 1997; Hilbig 1997a; Wilson 2000b; Pleijel 2001e), which might be the case also for the six abyssal species examined here, the material of which often was poorly preserved or incompletely developed.

Hesiospina aurantiaca (Sars) has been reported as widely distributed in cold- and warm-temperate and tropical regions from depths of 1–545 m (e.g. Sars 1862; Hessle 1925; Wesenberg-Lund 1951; Eliason 1962; Imajima and Hartman 1964; O'Connor and Shin 1983; Pleijel 2004). *Sirsoe hessleri* (Blake) comb. nov., on the other hand, was known only from hydrothermal vents in the western central Pacific Mariana back-arc basin at 3640 m depth (Blake 1991). Two of the four remaining taxa (*Gyptis incisa* sp. nov. and *Nereimyra auripalpa* sp. nov.) are new to science, while *Gyptis* sp. B seems to be a juvenile form.

Key to hesionid species from the abyssal SE Atlantic

1\. Parapodia uniramous or subbiramous without distinct notopodial lobes (Figs. 56C, 59C, 61C); shafts of neurochaetae indistinctly chambered (Figs. 56F, 59E, 61D) 2
– Parapodia biramous with conspicuous notopodial lobes (Figs. 49B, 52B, 54B); notochaetae and shafts of neurochaetae distinctly chambered (Figs. 49D, 52D, 54D) 4
2\. Prostomium with straight or slightly rounded anterior border (Figs. 56A, 57A, 61A) 3
– Prostomium with slightly notched anterior border (Figs. 59A, B; 60B); reduced notopodia with one acicula and a few capillary chaetae, especially in posterior part of body (Fig. 59C) .... *Nereimyra auripalpa* sp. nov.
3\. Frontal antennae and palps of subequal length (Fig. 61A, B); anterior two segments reduced and achaetous, each with two pairs of enlarged cirri (Fig. 61A, B); parapodia usually uniramous (Fig. 61C) but posteriorly a few with one notoacicula .... *Sirsoe hessleri* (Blake)
– Palps distinctly broader and longer than antennae (Figs. 56A, 57A); anterior three segments reduced and achaetous, each with two pairs of enlarged cirri (Fig. 56A); parapodia usually uniramous but some median ones with one notoacicula and one internal or partly protruding notopodial hook (Fig. 56C) .... *Hesiospina* cf. *aurantiaca* (Sars)
4\. Posterior border of prostomium more or less rounded (Figs. 52A, 53A, 54A, 55A); anterior two or four segments reduced and achaetous, each with two pairs of enlarged cirri (Figs. 52A, 54A) 5
– Prostomium with distinct posterior incision (Figs. 49A, 50A); anterior three segments reduced and achaetous, each with two pairs of enlarged cirri (Figs. 49A) .... *Gyptis incisa* sp. nov.
5\. Prostomium rectangular (Figs. 52A, 53A); anterior four segments reduced and achaetous (Figs. 52A) .... *Gyptis* sp. A
– Prostomium oval to rounded (Figs. 54A, 55A); anterior two segments reduced and achaetous (Figs. 54A) .... *Gyptis* sp. B

Gyptis Marion & Bobretzky in Marion, 1874

Gyptis incisa sp. nov.

(Figs. 49–51, 62)

Etymology

The species epithet is derived from the Latin verb incidere (to cut into), and refers to the incision in the prostomial posterior border. It is to be treated as a Latin participle for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 40 ES-E, 28°3.1′S 7°19.8′E–28°3.2′S 7°19.8′E, 4.iii.2005, 5052–5062 m; holotype: af/1.9/8/0.9/0.4, pf/1.9/8/1.0/0.3 (ZMH P25173).—R/V METEOR 63/2 st. 40 ES-S, 28°3.1′S 7°19.8′E–28°3.2′S 7°19.8′E, 4.iii.2005, 5052–5062 m; paratypes: af/2.2/8/1.3/0.6, af/2.0/7/0.9/0.4 (ZMH P25174 B); af/1.5/6/0.9/0.4 (ZMH P25174 A, on SEM stub).

Additional material. See Appendix 1.

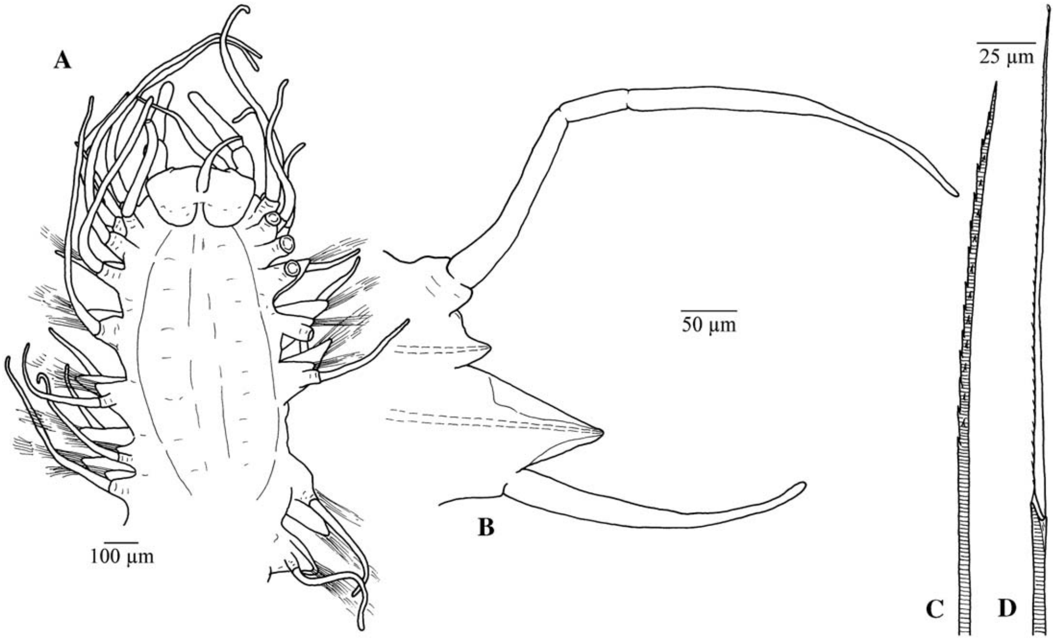

Fig. 49. *Gyptis incisa* sp. nov. (A) Anterior end; dorsal view. (B) Parapodium of mid-body; posterior view, chaetae omitted. (C) Notopodial chaeta. (D) Neuropodial chaeta. (A–D: ZMH P25173).

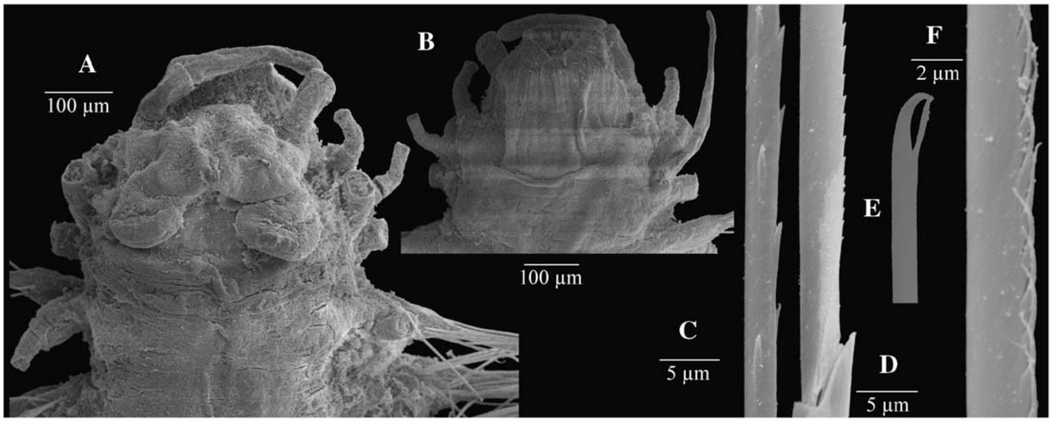

Fig. 50. *Gyptis incisa* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Detail of notopodial chaeta. (D) Detail of neuropodial chaeta. (E) Tip of neuropodial blade. (F) Detail of neuropodial blade. (A–F: ZMH P25174 A).

Diagnosis

Prostomium with three antennae, the median one inserted dorsally, and with distinct posterior incision; eyes absent; lip glands absent; anterior three segments reduced and achaetous; enlarged dorsal cirri on segments 1–5, enlarged ventral cirri on segments 1–3; biramous parapodia with conspicuous notopodial lobes from segment five; dorsal and ventral cirri smooth; notochaetae and shafts of neurochaetae distinctly chambered, notochaetae capillaries with two rows of alternating spines, neurochaetae falcigers with bidentate pseudospinigerous blades.

Description

Body at least 3.1 mm long with at least 17 chaetigers; anteriorly slightly truncate (Figs. 49A; 50A, B), posteriorly tapered. Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens whitish to yellowish, without pigmented patterns.

Prostomium rectangular, wider than long; with slightly curved anterior border and distinct posterior incision; facial tubercle not observed; bearing three antennae and two palps (Figs. 49A, 50A). Two lateral antennae inserted anteriorly and one median antenna more dorsally

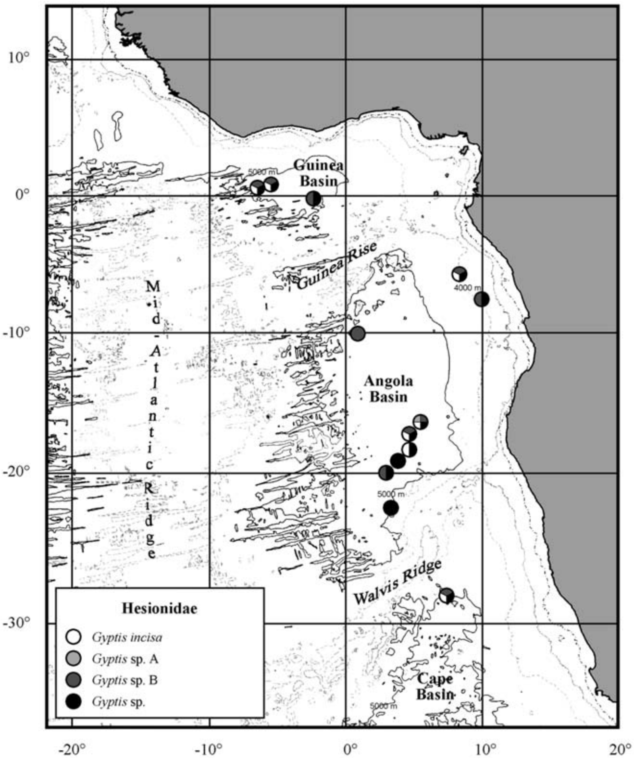

Fig. 51. Distribution of some hesionid species in the studied region.

(Fig. 49A); without conspicuous ceratophores but with digitiform ceratostyles; lateral antennae longer than median one. Latero-ventrally palps with cylindrical palpophores and longer, slightly thinner conical to digitiform palpostyles; palps about as long as frontal antennae (Figs. 49A, 50A). Eyes absent. Nuchal organs might be present as a more or less coalescing ciliated groove between posterior margin and first segment.

Proboscis divided into proximal and distal parts by indistinct concentric groove; terminal ring with numerous cylindrical papillae (Fig. 50B); jaws not observed; retracted proboscis extending to chaetiger 4–5 (Fig. 49A). Lip glands not observed.

Three anterior segments reduced and achaetous; each one with two pairs of short cirrophores inserted laterally and enlarged cirrostyles (Figs. 49A; 50A, B). Cirrostyles smooth, slender and filiform; upper pairs always distinctly longer (about two times) than corresponding lower ones, with second upper pair the longest. Parapodia of fourth segment (= 1st chaetiger) uniramous with enlarged dorsal cirri, distinct neuropodial lobes with chaetae and ventral cirri similar to remaining ones; dorsal cirrophores of about same shape as before but slightly shorter (Fig. 49A). Parapodia of fifth segment biramous with enlarged dorsal cirri, noto- and neuropodial lobes with chaetae and ventral cirri (Fig. 49A).

Parapodia of sixth segment and following ones with dorsal and ventral cirri and parapodial lobes (Fig. 49B). Parapodial lobes conical to triangular; neuropodial lobes much longer than notopodial ones (Fig. 49B). Dorsal cirri with short cirrophores and filiform cirrostyles; inserted near base of parapodia (Fig. 49B). Ventral cirri with inconspicuous cirrophores and slender digitiform cirrostyles; about half as long as dorsal cirri; inserted near terminal end of parapodia (Fig. 49B).

Each noto- and neuropodial lobe with one transparent and distally pointed acicula; with longitudinal ribs and internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 49B). Noto- and neuropodia with numerous chaetae arranged in dense, fan-shaped fascicles. Notochaetae simple and distinctly internally chambered, with two longitudinal rows of alternating spines (Figs. 49C, 50C). Neuropodia with falcigerous compound chaetae having bidentate, pseudospinigerous blades of different lengths, with fine serration over entire length of margin (Figs. 49D; 50D, E) or rarely prolonged teeth (Fig. 50F); shafts internally distinctly chambered (Fig. 49D).

Pygidium with an anus, a pair of slender cirri and a small digitiform medio-ventral papilla.

Distribution

Angola, Cape and Guinea Basins; 3952–5460 m (Fig. 51).

Discussion

Gyptis incisa sp. nov. belongs to a group of *Gyptis* species – *G. brunnea* (Hartman, 1961); *G. hians* Fauchald & Hancock, 1981; *G. incompta* Ehlers, 1912; *G. lobata* (Hessle, 1925); *G. paucilineata* Pleijel et al., 2009; *G. polymorpha* Pleijel et al., 2009; *G. propinqua* Marion & Bobretzky, 1875; *G. simpsonorum* Pleijel et al., 2009; *G. vittata* Webster & Benedict, 1887 – characterized by a more or less distinct posterior incision of the prostomium. Within this group, *Gyptis incisa* sp. nov. most closely resembles *G. hians*, another deep-water form, in the absence of eyes and the shape of the chaetae. However, it differs from the latter species by having a much longer median antenna, shorter noto- and neuropodial lobes, longer dorsal and ventral cirri, only three rather than four reduced and achaetous anterior segments, and by absence of notopodial spines (Hilbig 1997a). In contrast, all other species in this group possess eyes and have four reduced and achaetous anterior segments. Furthermore, distinct lip glands are reported for *Gyptis brunnea*, *G. paucilineata*, *G. polymorpha*, *G. propinqua*, *G. simpsonorum* and *G. vittata* (Pleijel 1993b, 1993c, 1998; Pleijel et al. 2009).

Within the genus *Gyptis*, *G. comata* (Ehlers, 1913) and *G. mackiei* Pleijel, 1993(b) were also described with only three reduced and achaetous anterior segments. However, these two species have a rounded prostomium with eyes and articulated cirri. In *Gyptis crypta* Pleijel, 1993(c) segment five is also equipped with noto- and neuropodial lobes and chaetae, but this taxon is separated from *Gyptis incisa* sp. nov., among other features, by having four reduced and achaetous anterior segments, eyes, and only ten terminal papillae on the proboscis.

Gyptis sp. A

(Figs. 51–53, 62)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae, the short median one inserted dorsally, and with more or less rounded posterior border; eyes absent; lip glands absent; anterior four segments reduced and achaetous; enlarged dorsal cirri on segments 1–5, enlarged ventral cirri on segments 1–4; biramous parapodia with conspicuous notopodial lobes from segment six; dorsal and ventral cirri smooth; notochaetae and shafts of neurochaetae distinctly chambered, notochaetae capillaries with two rows of alternating spines or with fine serration on one margin, neurochaetae falcigers with bidentate pseudospinigerous and paring knife-shaped blades.

Description

Body at least 9.0 mm long with at least 12 chaetigers; anteriorly slightly truncate (Figs. 52A, 53A), posteriorly tapered. Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens whitish to yellowish, without pigmented patterns.

Prostomium rectangular, wider than long; with slightly curved anterior and posterior borders; facial tubercle not observed; bearing three antennae and two palps (Figs. 52A, 53A). Two lateral antennae inserted anteriorly and one median antenna more dorsally (Figs. 52A, 53A); without conspicuous ceratophores but with digitiform ceratostyles; median antenna distinctly shorter and more conical or partly missing. Latero-ventrally palps with cylindrical palpophores and subequal conical palpostyles; palps about as long as frontal antennae or slightly longer (Figs. 52A, 53A). Eyes absent. Nuchal organs might be present, but are not conspicuous.

Proboscis divided into proximal and distal parts by indistinct concentric groove; terminal ring with numerous cylindrical papillae; jaws not observed; retracted proboscis extending to chaetiger 5–6. Lip glands not observed.

Four anterior segments reduced and achaetous; each one with two pairs of short cirrophores inserted laterally and enlarged cirrostyles (Figs. 52A, 53A). Cirrostyles smooth, slender and filiform; usually completely or partly missing. Parapodia of fifth segment (= 1st chaetiger) uniramous with enlarged dorsal cirri, distinct neuropodial lobes with chaetae and ventral cirri similar to remaining ones; dorsal cirrophores of about same shape as before (Fig. 52A).

Parapodia of sixth segment and following ones biramous with dorsal and ventral cirri and noto- and neuropodial lobes with chaetae (Fig. 52B). Parapodial lobes conical to triangular; neuropodial lobes slightly larger than notopodial ones (Fig. 52B). Dorsal and ventral cirri with short or inconspicuous cirrophores and filiform or slender digitiform cirrostyles; dorsal cirri about two times longer than ventral ones; both inserted near terminal end of parapodial lobes (Fig. 52B).

Each noto- and neuropodial lobe with one transparent and distally pointed acicula; with longitudinal ribs and internal horizontal striae (Fig. 52B). Noto- and neuropodia with numerous chaetae arranged in dense, fan-shaped fascicles. Notochaetae simple and distinctly internally chambered, with two longitudinal rows of alternating spines (Figs. 52C, 53B) or with fine serration on one margin (Fig. 52C). Neuropodia with falcigerous

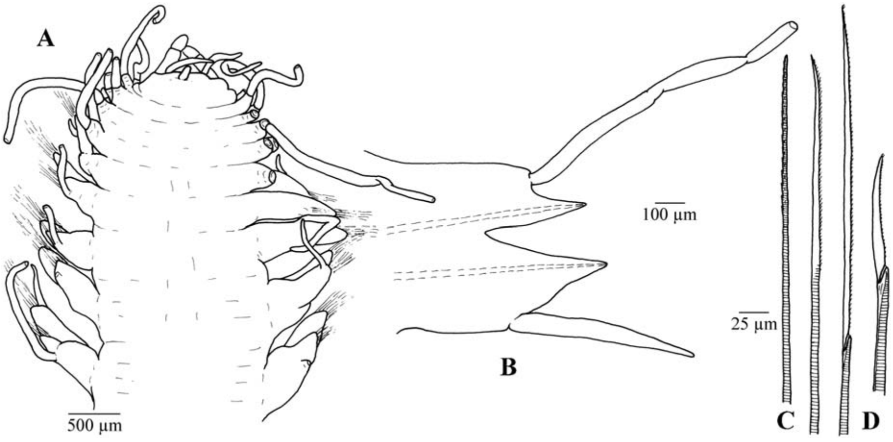

Fig. 52. *Gyptis* sp. A. (A) Anterior end; dorsal view. (B) Parapodium of mid-body; posterior view, chaetae omitted. (C) Notopodial chaetae. (D) Neuropodial chaetae. (A–D: SMF 18789).

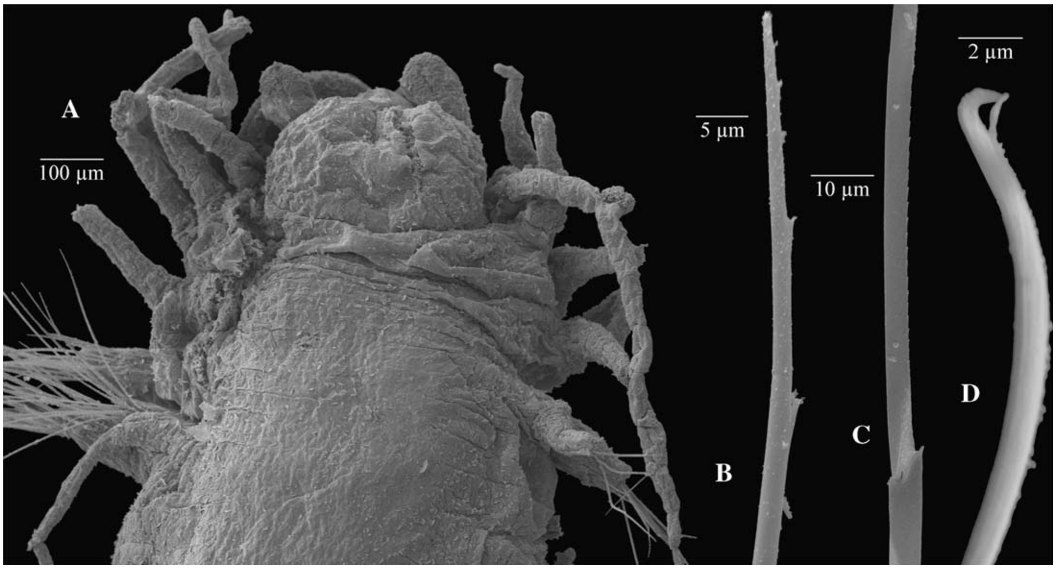

Fig. 53. *Gyptis* sp. A. (A) Anterior end; dorsal view. (B) Detail of notopodial chaeta. (C) Detail of neuropodial chaeta. (D) Tip of neuropodial blade. (A–D: ZMH P25163 B).

compound chaetae having bidentate blades of different length, superior blades pseudospinigerous and inferior ones more paring-knife-shaped, with fine serration over entire length of margin (Figs. 52D; 53C, D); shafts internally distinctly chambered (Fig. 52D).

Pygidium with an anus; cirri not observed.

Distribution

Angola Basin; 5430–5434 m (Fig. 51).

Discussion

The rather poorly preserved specimens show great similarity to *Gyptis hians* Fauchald & Hancock, a species known from abyssal depths off Oregon to central California (Hilbig 1997a). Both taxa are characterized by the absence of eyes, a short median prostomial antenna and four reduced and achaetous anterior segments. However, the posterior prostomial incision of *G. hians* is not observed in the specimens examined here, and the respective sizes of the parapodial lobes and ventral cirri are slightly different.

Gyptis sp. B

(Figs. 51, 54, 55, 62)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae, the median one inserted dorsally, and with rounded posterior border; eyes absent; lip glands absent; anterior two segments reduced and achaetous; enlarged dorsal cirri on segments 1–3, enlarged ventral cirri on segments 1–2; biramous parapodia with conspicuous notopodial lobes from segment four; dorsal and ventral cirri smooth; notochaetae and shafts of neurochaetae distinctly chambered, notochaetae capillaries with two rows of alternating spines, neurochaetae falcigers with bidentate pseudospinigerous blades.

Description

If fragments of ZMH P25203 E really include one complete specimen then body up to 5.9 mm long with up to 24 chaetigers; anteriorly slightly truncate (Figs. 54A, 55A), posteriorly tapered. Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens whitish to yellowish, with a few pigmented spots on posterior part of prostomium and nuchal organs (Fig. 54A).

Prostomium oval to rounded, about as long as wide; facial tubercle not observed; bearing three antennae and two palps (Figs. 54A, 55A). Two lateral antennae inserted anteriorly and one median antenna more dorsally (Fig. 54A); without conspicuous ceratophores but with digitiform ceratostyles; of about equal length but lateral antennae slightly broader than median one. Latero-ventrally palps with cylindrical palpophores and slightly longer and thinner conical palpostyles; palps about as long as antennae (Figs. 54A; 55A, B). Eyes absent. One pair of furrow-like dorso-lateral nuchal organs situated between prostomium and first segment (Fig. 54A).

Proboscis divided into proximal and distal parts by indistinct concentric groove; terminal ring with numerous cylindrical papillae and basal part with numerous minute

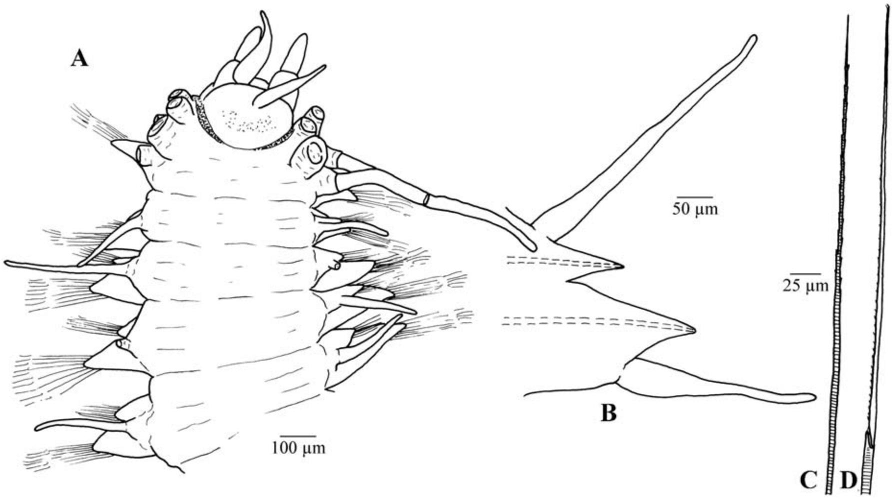

Fig. 54. *Gyptis* sp. B. (A) Anterior end; dorsal view. (B) Parapodium of mid-body; posterior view, chaetae omitted. (C) Notopodial chaeta. (D) Neuropodial chaeta. (A–D: ZMH P25210 A).

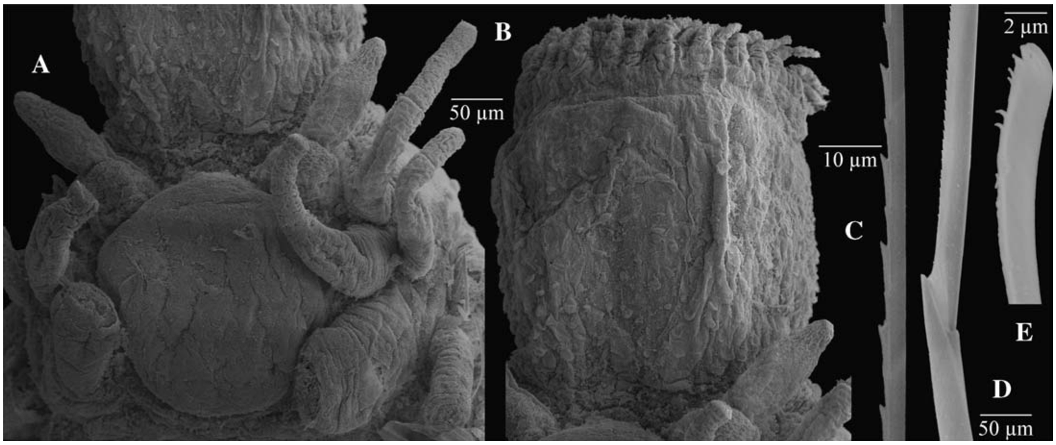

Fig. 55. *Gyptis* sp. B. (A) Anterior end; dorsal view. (B) Probocis. (C) Detail of notopodial chaeta. (D) Detail of neuropodial chaeta. (E) Tip of neuropodial blade. (A–E: ZMH P25213 C).

papillae (Fig. 55B); jaws not observed; retracted proboscis extending to chaetiger 4–5. Lip glands not observed.

Two anterior segments reduced and achaetous; each one with two pairs of cirrophores inserted laterally and mostly missing enlarged cirrostyles (Figs. 54A, 55A). Upper cirrophores of second segment much larger than other ones. Cirrostyles smooth, slender and filiform; upper pairs probably distinctly longer than corresponding lower ones, with second upper pair might be the longest. Parapodia of third segment (= 1st chaetiger) uniramous with enlarged dorsal cirri, distinct neuropodial lobes with chaetae and ventral cirri similar to remaining ones; dorsal cirrophores of about same shape as before (Fig. 54A).

Parapodia of fourth segment and following ones biramous with dorsal and ventral cirri and noto- and neuropodial lobes with chaetae (Fig. 54B). Parapodial lobes conical to triangular; neuropodial lobes much longer than notopodial ones (Fig. 54B). Dorsal cirri with short cirrophores and filiform cirrostyles; inserted near base of parapodia (Fig. 54B). Ventral cirri with inconspicuous cirrophores and slender digitiform cirrostyles; about $\frac{1}{3}$ shorter than dorsal cirri; inserted near terminal end of parapodia (Fig. 54B).

Each noto- and neuropodial lobe with one transparent and distally pointed acicula; with longitudinal ribs and internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 54B). Noto- and neuropodia with numerous chaetae arranged in dense, fan-shaped fascicles. Notochaetae simple and distinctly internally chambered, with two longitudinal rows of alternating spines (Figs. 54C, 55C). Neuropodia with falcigerous compound chaetae having bidentate, long pseudospinigerous blades of slightly different length, with fine serration over entire length of margin (Figs. 54D;

55D, E), apparently subdistal teeth longer than basal ones; shafts internally distinctly chambered (Fig. 54D).

Pygidium with an anus; cirri not observed.

Distribution

Angola, Cape and Guinea Basins; 3962–5655 m (Fig. 51).

Discussion

The examined specimens are probably juveniles and therefore incompletely developed, because only two achaetous anterior segments and five pairs of enlarged cirri are present. They resemble *Gyptis hians*, *G. incisa* sp. nov. and *G.* sp. A in lacking eyes and having smooth dorsal and ventral cirri. However, the first and the third of those species show a much shorter median prostomial antenna, more elongated parapodial lobes, additional types of chaetae, and four reduced and achaetous anterior segments. *Gyptis incisa* sp. nov. has a median prostomial antenna similar in shape and size to that of *G.* sp. B, and also only one type of noto- and neuropodial chaetae; it is separated, however, by a distinct posterior prostomial incision and three reduced and achaetous anterior segments.

Gyptis sp.

(Fig. 51)

Material examined

See Appendix 1.

Remarks

Indeterminable specimens or fragments which might belong to *Gyptis incisa* sp. nov., *G.* sp. A or *G.* sp. B, or to another member of the genus.

Hesiospina Imajima & Hartman, 1964

Hesiospina cf. *aurantiaca* (Sars, 1862)

(Figs. 56–58, 63)

Castalia aurantiaca Sars, 1862—Sars (1862, p. 90)

Castalia longicornis Sars, 1862—Sars (1862, p. 90)

Kefersteinia similis Hessle, 1925—Hessle (1925, p. 29, fig. 10)

Hesiospina aurantiaca (Sars)—Pleijel (2004, p. 2550, figs. 1–5)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and straight or slightly rounded anterior border; eyes absent; lip glands absent; basal part of proboscis smooth; jaws absent; anterior three segments reduced and achaetous; enlarged dorsal cirri on segments 1–5, enlarged ventral cirri on segments 1–3; parapodia usually uniramous but some median ones subbiramous with one notoacicula and one notopodial hook; dorsal and ventral cirri smooth; notochaetae and shafts of neurochaetae indistinctly chambered, notopodial hooks only in a few median parapodia, neurochaetae falcigers with bidentate bread knife-shaped to pseudospinigerous blades.

Description

Body up to 7.8 mm long with up to 26 chaetigers; anteriorly slightly truncate (Fig. 56A), posteriorly tapered. Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens yellowish; venter of a few specimens with indistinctly pigmented longitudinal midline.

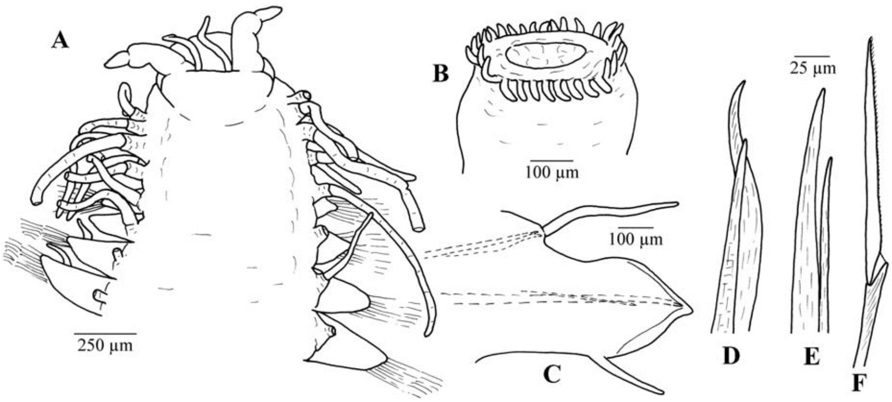

Fig. 56. *Hesiospina* cf. *aurantiaca* (Sars). (A) Anterior end; dorsal view. (B) Terminal part of proboscis. (C) Parapodium of midbody; posterior view, chaetae omitted. (D) Notopodial acicula and chaeta. (E) Neuropodial aciculae. (F) Neuropodial chaeta. (A–F: ZMH P25221 B).

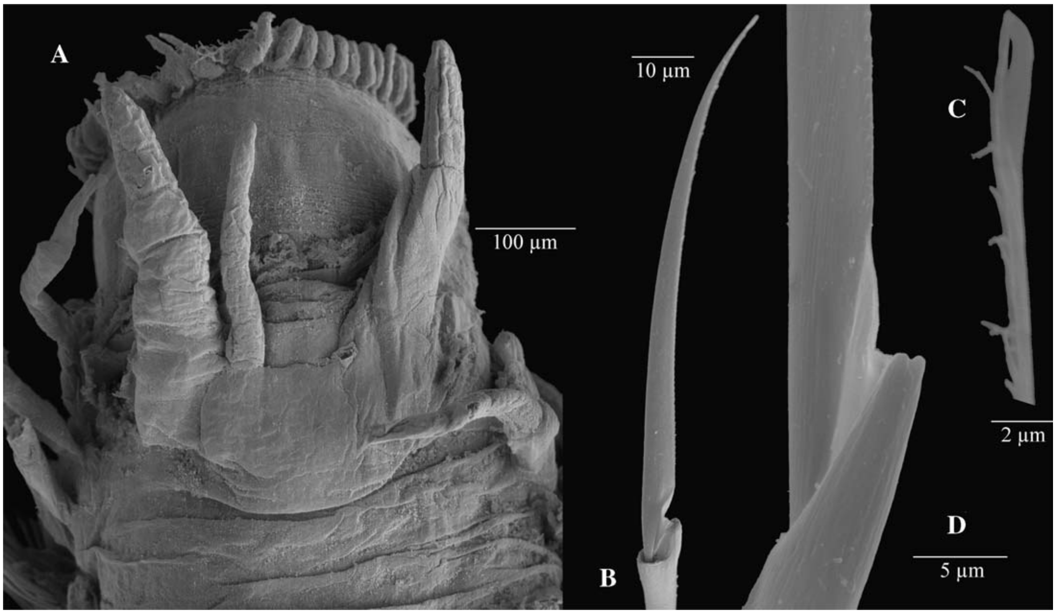

Fig. 57. *Hesiospina* cf. *aurantiaca* (Sars). (A) Anterior end with everted proboscis; dorsal view. (B) Neuropodial chaeta. (C) Tip of blade. (D) Detail of shaft. (A–D: ZMH P25221 A).

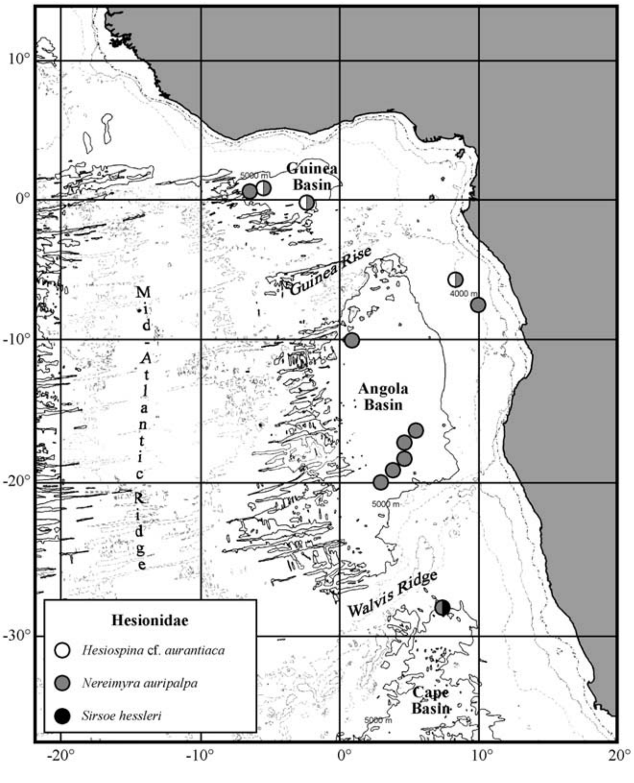

Fig. 58. Distribution of some hesionid species in the studied region.

Prostomium rectangular, wider than long; with straight anterior border and more rounded posterior one; facial tubercle not observed; bearing two antennae and two longer palps (Figs. 56A, 57A). Antennae inserted anteriorly; without conspicuous ceratophores but with slender and digitiform ceratostyles (Figs. 56A, 57A). Lateroventrally palps with broadly cylindrical palpophores and distinctly shorter, thinner, more conical palpostyles (Figs. 56A, 57A). Eyes absent. Nuchal organs might be present, but are not conspicuous.

Proboscis divided into proximal and distal parts by indistinct concentric groove; terminal ring with up to 50 cylindrical papillae; basal part smooth (Figs. 56B, 57A); jaws not observed; retracted proboscis extending to chaetiger 8–9. Lip glands not observed.

Three anterior segments reduced and achaetous; each one with two pairs of cirrophores inserted laterally and enlarged cirrostyles (Figs. 56A, 57A). Cirrostyles indistinctly annulated, slender and filiform; upper pairs longer than corresponding lower ones, but usually partly or completely missing. Parapodia of fourth (= 1st chaetiger) and fifth segment uniramous with enlarged dorsal cirri, distinct neuropodial lobes with chaetae and ventral cirri similar to remaining ones; dorsal cirrophores of about same shape as before and also indistinctly annulated (Fig. 56A).

Parapodia of sixth segment and following ones mainly uniramous but some median ones subbiramous; notopodial lobes completely reduced and neuropodial lobes broadly conical to triangular (Fig. 56C). Dorsal and ventral cirri with short or inconspicuous cirrophores and smooth, slender digitiform cirrostyles; both more or less reaching tip of neuropodial lobes, but dorsal cirri distinctly longer than ventral ones; dorsal cirri inserted above base and ventral ones near middle of parapodia (Fig. 56C).

Neuropodial lobes with one large and one minute transparent and distally pointed acicula; with longitudinal ribs and indistinct internal horizontal striae (Fig. 56C, E). Some median parapodia with one additional notopodial acicula and single stout, distally curved internal or partly protruding notopodial hook (Fig. 56C, D). Neuropodia with numerous falcigerous compound chaetae arranged in dense, fan-shaped fascicles; having bidendate bread-knife-shaped to pseudospinigerous blades of slightly different length, with fine serration over entire length of margin (Figs. 56F, 57B–D), apparently subdistal teeth longer than basal ones; shafts internally not distinctly chambered (Figs. 56F).

Pygidium with an anus and a pair of slender cirri.

Distribution

Angola and Guinea Basins; 3961–5144 m (Fig. 58).

Discussion

The genus *Hesiospina* includes two species: *H. aurantiaca* and *H. vestimentifera* Blake, 1985 (Pleijel 1998, 2004). The latter deep-sea taxon from the Pacific Ocean is identified by rows of papillae on the basal part of the proboscis, by the jaws and reduced eyes, whereas the former lacks basal proboscidial papillae and jaws and has two pairs of eyes (Blake 1985; Pleijel 2004). Consequently, the specimens examined here are referred to *H. aurantiaca*, even though no eyes are present. The latter might be a fixation artefact or, more likely, an adaptation to the deep sea, because previously decribed populations are only known from 1–545 m depth (Pleijel 2004). Nevertheless, the studied material includes only juveniles with three reduced and achaetous anterior segments, instead of the four segments described for adults.

Nereimyra Blainville, 1828

Nereimyra auripalpa sp. nov.

(Figs. 58–60, 63)

Etymology

The species epithet is intended to refer to the ear-like (Latin auris = ear) enlarged palpostyles. It is to be treated as a compound word with a Latin final component that is adjectival for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 41 ES-S, 28°4.1′S 7°20.5′E–28°4.2′S 7°20.7′E, 5.iii.2005, 5058–5060 m; holotype: af/1.4/11/0.8/0.4 (ZMH P25242); paratypes: af/1.0/10/0.5/0.2, af/1.0/9/0.5/0.2, af/1.0/6/0.7/0.3, 5 mf with 2–9 chaetigers (ZMH P25243).—R/V METEOR 63/2 st. 41 ES-E, 28°4.1′S 7°20.5′E–28°4.2′S 7°20.7′E, 5.iii.2005, 5058–5060 m; paratypes: cs/3.0/23/1.0/0.5, cs/2.9/22/0.9/0.4, af/1.8/13/0.9/0.4, 1 pf with 9 chaetigers (ZMH P25241 B); cs/2.9/22/1.0/0.5 (ZMH P25241 B, on SEM stub).

Additional material. See Appendix 1.

Diagnosis

Prostomium with two (in juveniles: three) antennae and slightly notched anterior border; eyes present; lip glands absent; anterior three segments reduced and achaetous; enlarged dorsal cirri on segments 1–5, enlarged ventral cirri on segments 1–3; parapodia uni- or subbiramous with one acicula and a few capillary chaetae, especially in posterior part of body; dorsal and ventral cirri smooth; notochaetae and shafts of neurochaetae indistinctly chambered, notochaetae smooth capillaries, neurochaetae spinigers with unidentate blades.

Description

Body up to 3.7 mm long with at least 28 chaetigers; anteriorly slightly truncate, posteriorly tapered (Fig. 60A). Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens yellowish, without pigmented patterns.

Prostomium rectangular, wider than long; with slightly notched anterior border and indistinctly posterior one; facial tubercle not observed; bearing two or three antennae and two shorter palps (Figs. 59A, B; 60A, B). Two lateral antennae inserted anteriorly (Figs. 59A, 60B), and one median antenna more dorsally (Fig. 60D), only observed in a few smaller specimens; without conspicuous ceratophores but with digitiform ceratostyles; lateral antennae slightly broader and longer than median one, which is distally slightly swollen (Fig. 60D). Latero-ventrally palps with oval to quadrangular palpophores and longer, broadly conical, ear-like palpostyles, which are mostly posteriorly directed (Figs. 59A, B; 60B). Usually with two pairs of small eye-like spots; dorsal pair closely together near base of median antenna and latero-ventral pair beside palpophores (Figs. 59A, B; 60C, D). Nuchal organs might be present, but are not conspicuous.

Proboscis divided into proximal and distal parts by concentric groove; terminal ring with ten ciliated conical papillae (Fig. 60C); jaws not observed; retracted proboscis extending to chaetiger 5–8 (Fig. 59A). Lip glands not observed.

Three anterior segments reduced and achaetous, but aciculae might be present; each one with two pairs of short cirrophores inserted laterally and enlarged cirrostyles (Figs. 59A, B; 60B, C). Cirrostyles smooth, slender and filiform; upper pairs always distinctly longer (about two times) than corresponding lower ones, with second upper pair the longest. Parapodia of fourth (= 1st chaetiger) and fifth segment uniramous with enlarged dorsal cirri, distinct neuropodial lobes with chaetae and ventral cirri similar to remaining ones; dorsal cirrophores of about same shape as before but distinctly shorter (Fig. 59A, B).

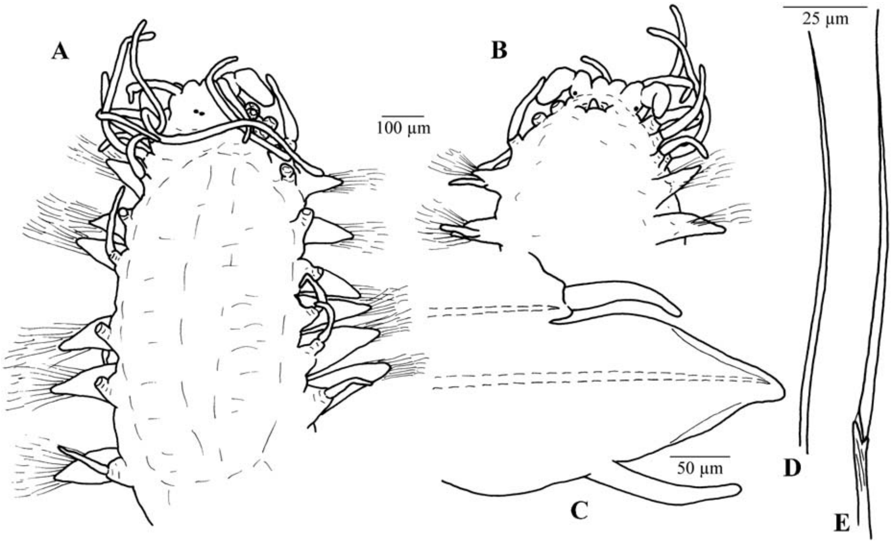

Fig. 59. *Nereimyra auripalpa* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Parapodium of mid-body; posterior view, chaetae omitted. (D) Notopodial chaeta. (E) Neuropodial chaeta. (A–E: ZMH P25242).

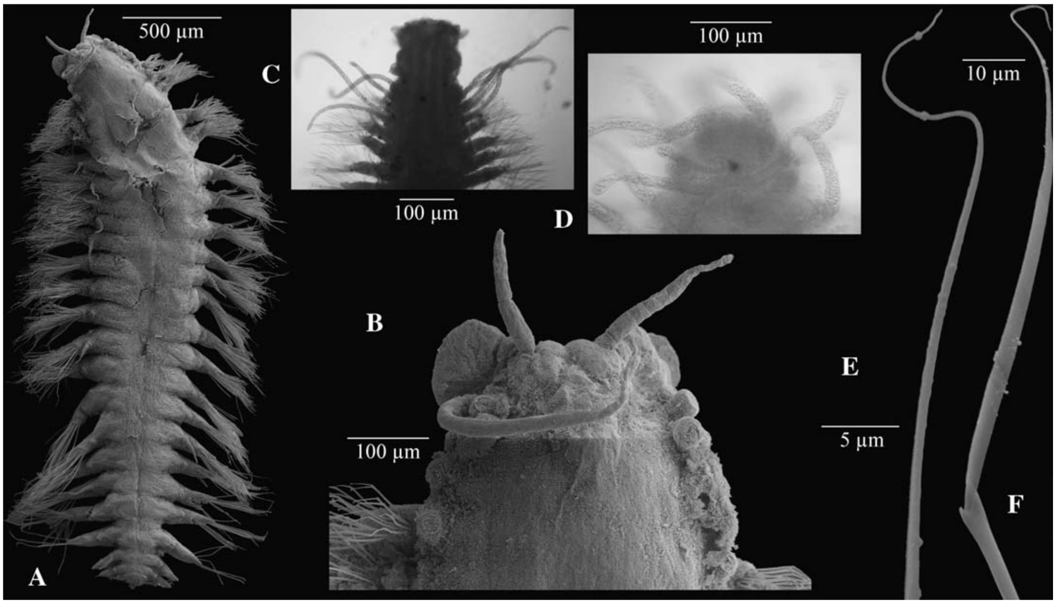

Fig. 60. *Nereimyra auripalpa* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of anterior end with everted proboscis; dorsal view. (D) Light micrograph of anterior end; dorsal view. (E) Notopodial chaeta. (F) Neuropodial chaeta. (A, B: ZMH P25241 A; C: ZMH P25230 C; D: ZMH P25236 B; E, F: ZMH P25246 B).

Parapodia of sixth segment and following ones more or less distinctly subbiramous with dorsal and ventral cirri and neuropodial lobes; notopodial lobes completely reduced and neuropodial lobes broadly conical to triangular (Fig. 59C). Dorsal and ventral cirri with short or inconspicuous cirrophores and smooth digitiform cirrostyles of about equal length; both shorter than neuropodial lobes; dorsal cirri inserted near base and ventral ones near middle of parapodia (Fig. 59C).

Reduced notopodia and each neuropodial lobe with one transparent and distally pointed acicula; all with longitudinal ribs and indistinct internal horizontal striae; neuropodial aciculae slightly larger than notopodial ones (Fig. 59C). In small juveniles all parapodia and in larger specimens only a few remaining posterior ones with up to three notopodial capillaries, which are smooth and internally very indistinctly chambered (Figs. 59D, 60E). Neuropodia with numerous spinigerous compound chaetae arranged in dense, fan-shaped fascicles; having unidendate blades of slightly different length, with indistinct serration over entire length of margin, apparently subdistal teeth much longer than basal ones; shafts internally very indistinctly chambered (Figs. 59E, 60F).

Pygidium with an anus; cirri not observed.

Remarks

The presence of the notopodial chaetae is clearly size-related, and the median antenna seems to be present in juveniles only, which is also reported for other species of hesionids (Schram and Haaland 1984; Pleijel 1998).

Distribution

Angola, Cape and Guinea Basins; 3961–5655 m (Fig. 58).

Discussion

Jaw plates and neuropodia with three lobes are not observed in the herein examined specimens, which might be incompletely developed. However, a prostomium with notched anterior border and the typical shape of the palps is not reported for any other *Nereimyra* species. The prostomial shape of *Hesiodeira glabra* Blake & Hilbig, 1990 is slightly similar, but this taxon from hydrothermal vents of the northeastern Pacific is provided with short fingerlike palps, distinct notopodial lobes, and four reduced and achaetous anterior segments.

Sirsoe Pleijel, 1998

Sirsoe hessleri (Blake, 1991) comb. nov.

(Figs. 58, 61, 63)

Hesiocaeca hessleri Blake, 1991—Blake (1991, p. 175, fig. 1)

Material examined

See Appendix 1.

Diagnosis

Prostomium with at least two, probably three antennae and straight or slightly rounded anterior border; eyes probably present; lip glands absent; anterior two segments reduced and achaetous; enlarged dorsal and ventral cirri on segments 1–2; with four pairs of enlarged cirri; parapodia usually uniramous but posteriorly a few subbiramous with one notoacicula; anterior dorsal cirri indistinctly annulated, posterior ones and ventral cirri smooth; notochaetae and shafts of neurochaetae indistinctly chambered, notochaetae absent, neurochaetae falcigers with bidentate bread knife-shaped to paring knife-shaped blades.

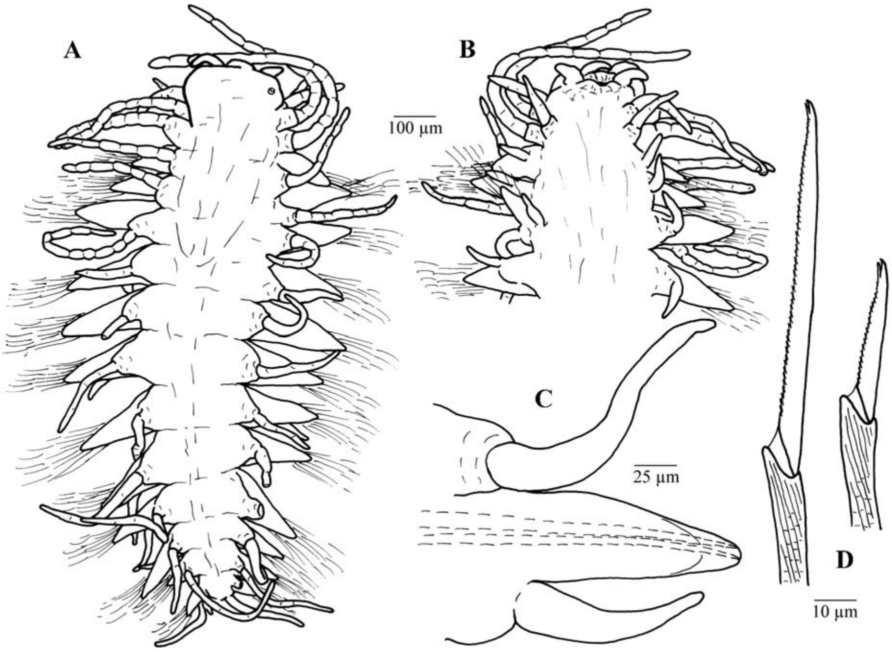

Fig. 61. *Sirsoe hessleri* (Blake) comb. nov. (A) Complete specimen; dorsal view. (B) Anterior end; ventral view. (C) Right parapodium of 7th chaetiger; posterior view, chaetae omitted. (D) Neuropodial chaetae. (A–D: ZMH P25258).

Description

Body 1.3 mm long with 12 chaetigers; anteriorly slightly truncate, posteriorly tapered (Fig. 61A). Segments uniannulate; indistinctly separated from each other in anterior part of body. Preserved specimens whitish, without pigmented patterns.

Prostomium rectangular, wider than long; with straight or slightly rounded anterior border and indistinctly posterior one; facial tubercle not observed; bearing two antennae and two palps of subequal length (Fig. 61A, B, but see "Remarks"). Antennae inserted anteriorly; without conspicuous ceratophores but with conical to digitiform ceratostyles (Fig. 61A). Lateroventrally palps with short palpophores and indistinctly separated conical palpostyles (Fig. 61B). One remaining small eye-like spot, probably with lens; laterally located on right side (Fig. 61A). Nuchal organs might be present, but are not conspicuous.

Retracted proboscis extending to about 5th chaetiger (Fig. 61A). Jaws, terminal ring and lip glands not observed.

Two anterior segments reduced and achaetous; each one with two pairs of short cirrophores inserted laterally and enlarged cirrostyles (Fig. 61A, B). Cirrostyles indistinctly annulated, slender and filiform; upper pairs distinctly longer (about four times) than corresponding lower ones, with second upper pair the longest.

Parapodia of third segment (= 1st chaetiger) and following ones mostly uniramous but posteriorly a few subbiramous; notopodial lobes completely reduced and neuropodial lobes conical (Fig. 61C). Dorsal cirri with short cirrophores and slender digitiform cirrostyles of different length; about as long as neuropodial lobes or distinctly longer; indistinctly annulated in anterior part of body; inserted near base of parapodia (Fig. 61A, C). Ventral cirri with inconspicuous cirrophores and smooth digitiform cirrostyles; slightly shorter than neuropodial lobes, but elongated in last chaetiger; inserted near base of parapodia (Fig. 61A–C).

Neuropodial lobes with up to two transparent and distally pointed aciculae; with longitudinal ribs and indistinct internal horizontal striae; upper one slightly larger than lower one (Fig. 61C). Additional notopodial acicula seems to be present from chaetiger eight backwards; notopodial chaetae absent. Neuropodia with numerous falcigerous compound chaetae arranged in dense, fan-shaped fascicles; having bidendate, different long bread-knife-shaped to paring-knife-shaped blades, with fine serration over entire length of margin; shafts internally very indistinctly chambered (Fig. 61D).

Pygidium with an anus and a pair of slender cirri (Fig. 61A).

Remarks

A dorsally located, small median antenna is described for all species of the genus and was possibly also present in the examined animal before the latter was collected, but seems to be completely lost from the specimen. However, according to Blake (1991) "a closely related undescribed species, lacking a medial antenna, has been discovered at the cold-seep site on the Florida Escarpment."

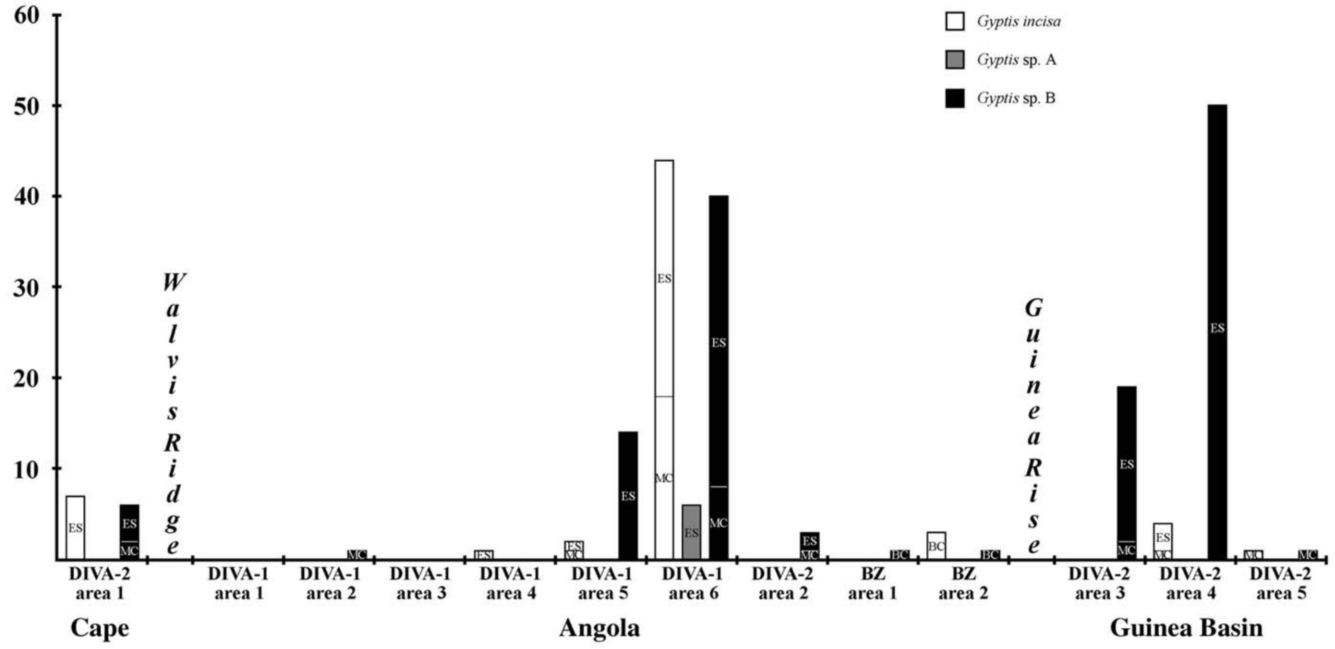

Fig. 62. Abundance of the hesionids *Gyptis incisa*, *G.* sp. A and *G.* sp. B in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

Distribution

Cape Basin; 5052–5062 m (Fig. 58).

Discussion

The genus *Sirsoe* originally included only two species, *S. grasslei* (Blake, 1985) and the 'iceworm', *S. methanicola* (Desbruyères & Toulmond, 1998), whereas *Hesiocaeca hessleri* Blake was considered as a juvenile form "possible near *Psamathe*" (Pleijel 1998). However, *H. hessleri* shows all characteristics of *Sirsoe* and is therefore transferred to the latter genus.

The herein examined small and obviously not mature specimen is referred to this taxon, reported from the hydrothermal vents at the Marianas Islands, even though only a few posterior parapodia have a notoacicula and one remaining eye-like spot is present, which both might be juvenile features. Furthermore, the tips of the neurochaetae are interpreted to be bidentate, not unidentate with a hoodlike membrane as mentioned by Blake (1991).

Abundance of Hesionidae

A total of 988 specimens or fragments were found in all investigated areas. Most of them belong to *Nereimyra auripalpa* sp. nov. (209), *Gyptis incisa* sp. nov. (86) and *G.* sp. B (331) or were indeterminable fragments of *Gyptis* sp. (322). The first of these species was more regularly distributed (Fig. 63), whereas the other two were found especially in a few areas (*G. incisa*: DIVA-1 area 6, *G.* sp. B: DIVA-1 areas 5–6 and DIVA-2 areas 3–4) in a higher abundance (Fig. 62). Only a few specimens belong to the three remaining taxa. *Hesiospina* cf. *aurantiaca* (28) was present in two of the investigated basins, with the highest abundance in the Guinea Basin, whereas *Gyptis* sp. A (11) and *Sirsoe hessleri* (1) were found at only one station each in the Angola and Cape Basins, respectively (Figs. 62, 63). The epibenthic sledge was the most effective gear for quantitative and qualitative sampling of hesionids, whereas lower numbers of indivudals and only three or four of the six taxa were present in the multicorer or box corer samples (Figs. 62, 63).

Molecular data

ITS2 data set

Four newly acquired sequences (Table 8) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. All analyses were conducted with the branch-and-bound algorithm. ML was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies ($A = 0.2075$, $C = 0.2982$, $G = 0.2655$, $T = 0.2288$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 2.0822$,

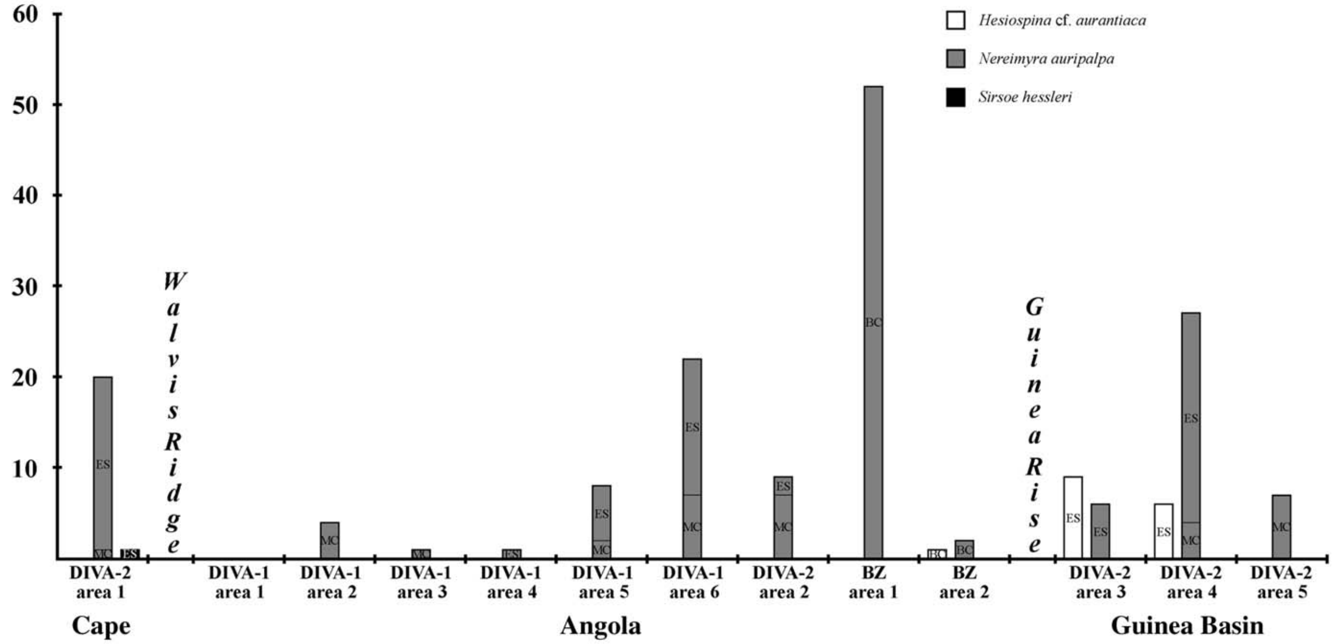

Fig. 63. Abundance of the hesionids *Hesiospina* cf. *aurantiaca*, *Nereimyra auripalpa* and *Sirsoe hessleri* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

Table 8. List of taxa and corresponding sequences in Hesionidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession numbers			
			18S rDNA	COI (3-6W)	ITS1	ITS2
HESIONIDAE						
Hesiospina cf. *aurantiaca* (Sars)	Guinea Basin					
	D-2 st. 89 ES-S	ZMH P25221 B	GQ426577	GQ426675	GQ426713	GQ426730
	D-2 st. 90 ES-E	ZMH P25222 A	–	–	GQ426714	GQ426731
	D-2 st. 90 ES-S	ZMH P25222 B	GQ426578	GQ426676	–	GQ426732
PARALACYDONIIDAE						
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		–	–	–	GQ426700

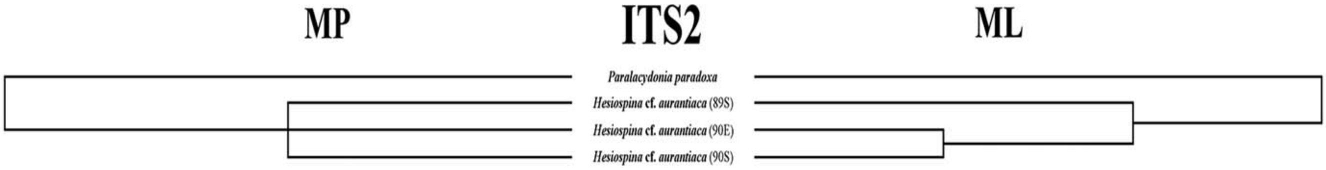

Fig. 64. Cladograms obtained from MP and ML analysis of the ITS2 sequences.

A↔G = 3.4012, A↔T = 3.8995, C↔G = 1.3586, C↔T = 4.8077, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and equal rates for all sites. Clade support values were calculated with nonparametric bootstrapping with 1,000 (ML) or 100,000 replicates (MP) and branch-and bound searches.

After exclusion of the primer sites, the alignment for the four sequences contained 532 characters, of which 101 were variable but none was parsimony informative. The MP analysis yielded two most parsimonious trees, which are 101 steps long with CI = 1.0000, RI = 0, and RC = 0. The topologies of the strict consensus tree and the ML tree (−ln L = 1083.77493) are slightly different (Fig. 64).

Discussion of molecular results

The 18S rDNA data strongly supported a sister-group relationships between hesionids and chrysopetalids, which is more or less in agreement with analyses based on morphological (Pleijel and Dahlgren 1998) or combined characters (Ruta et al. 2007). In contrast, the COI amino acid analysis proposed a closer relationship to lacydoniids and phyllodocids (see "Molecular phylogeny of abyssal Phyllodocida"). However, the latter hypothesis was not confirmed by high bootstrap values.

The analyzed sequences of *Hesiospina* cf. *aurantiaca* specimens from the Guinea Basin completely agree with each other in the 18S rDNA data and the translated amino acid sequences of the COI (3-6W) gene. Furthermore, the sequences of COI (3-6W) and the non-coding regions (ITS1 + 2, Fig. 64) were also only slightly different from each other, which demonstrates that gene flow exists between the populations. However, there were distinct differences from previous 18S rDNA data reported under the same species name from Papua New Guinea (Rousset et al. 2007; Ruta et al. 2007), which suggests a complex of cryptic or sibling species around the world.

Lacydoniidae Bergström, 1914

The Lacydoniidae are a homogeneous but not well known part of the Phyllodocida, although closer affinities are uncertain (Pleijel 2001f), and no apomorphies for the probably monophyletic group are known (Fauchald and Rouse 1997). The family is now monotypic for *Lacydonia* Marion & Bobretzky in Marion, 1874, because the other two previously included monotypic genera, *Paralacydonia* Fauvel, 1913 and *Pseudolacydonia* Rullier, 1964 have been referred to Paralacydoniidae (Pettibone 1963) or synonymized with the glycerid *Glycerella* Arwidsson (Böggemann 2002), respectively. Furthermore, *Lacydonia incognita* Rullier, 1965 from W Africa, of which no specimen with complete anterior body parts is known, has been tentatively referred to the goniadid *Goniada congoensis* Grube, 1877 (Böggemann 2005). The remaining eleven species – *Lacydonia miranda* Marion & Bobretzky in Marion, 1874; *L. mikrops* Ehlers, 1913; *L. papillata* Uschakov, 1958; *L. oculata* (Hartman, 1967); *L. cirrata* (Hartman & Fauchald, 1971); *L. laureci* Laubier, 1975;

L. antarctica Hartmann-Schröder & Rosenfeldt, 1988; *L. elongata* Hartmann-Schröder & Rosenfeldt, 1992; *L. gordia* Hartmann-Schröder, 1993; *L. hampsoni* Blake, 1994; *L. eliasoni* Hartmann-Schröder, 1996 [= *L.* "near *miranda*" of Eliason (1962)] – are more or less homogeneous morphologically, even though their original descriptions vary in presence/absence of the median antenna. This fragile and easily lost or presumably overlooked structure was noted for the first time by Eliason (1962), but may be present in all *Lacydonia* species (Pleijel and Fauchald 1993; Blake 1994; Pleijel 2001f).

The Lacydoniidae are collected worldwide from intertidal to abyssal depths, but no information on feeding habits or population biology is available (Wilson 2000c; Pleijel 2001f). However, Gathof (1984) suggested that they are motile and carnivorous or omnivorous, capturing food with the eversible proboscis.

Both species collected in the present study, *Lacydonia laureci* and *L. papillata*, are uncommonly encountered. The former was known only from the Matapan trench, eastern Mediterranean Sea, at 4690 m depth (Laubier 1975). The latter was first reported from the Kuril-Kamchatka trench, 5070 m depth (Uschakov 1958), and subsequently mentioned from two abyssal stations around SE Honshu, at 3352 and 5690 m depth (Uschakov 1972), and from the Antarctic region, 634 m depth (Hartmann-Schröder and Rosenfeldt 1992; under the name *Lacydonia elongata*).

Key to lacydoniid species from the abyssal SE Atlantic

1\. Prostomium with two lateral lobes on posterior margin (Fig. 65A); antennae and palps filiform (Fig. 65A, B); lateral pair of anal cirri distinctly longer than median one (Fig. 65C) .... *Lacydonia laureci* Laubier

– Prostomium with nearly straight posterior margin (Figs. 67A; 68A, B); antennae and palps shorter and conical to digitiform (Figs. 67A, B; 68A, B); lateral pair of anal cirri of about same length as median one or only slightly longer (Fig. 67C) .... *Lacydonia papillata* Uschakov

Lacydonia Marion & Bobretzky in Marion, 1874

Lacydonia laureci Laubier, 1975

(Figs. 65, 66, 69)

Lacydonia laureci Laubier, 1975—Laubier (1975, p. 76, figs. A–E)

Material examined

Type material. Campagne Polymède II du N.O. JEAN CHARCOT dragage DS 05, Matapan trench, eastern Mediterranean, 35°49.8′N 22°20.7′E, v.1972, 4690 m; holotype: af/1.8/15–16/1.0/0.4, pf/2.1/21/1.0/0.4 (MNHN Type 1421).

Additional material. See Appendix 1.

Diagnosis

Prostomium with two lateral lobes on posterior margin; antennae and palps filiform; eyes absent; conical cirri on first segment; anterior three pairs of parapodia uniramous; dorsal and ventral cirri conical; lateral pair of filiform anal cirri distinctly longer than median one.

Description

Body up to 1.3 mm long with up to 16 chaetigers; dorso-ventrally slightly flattened, stout anteriorly and tapering posteriorly (Fig. 65A, C). Anterior segments uniannulate, following ones indistinctly biannulate. Preserved specimens yellowish, sometimes with diffusely distributed small red-brown pigmented spots, especially on prostomium and first segment.

Prostomium rectangular, wider than long, with two lateral lobes on posterior margin and three antennae and two palps (Fig. 65A, B). Antennae and palps all slender and filiform; frontal antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna about as long as frontal ones, inserted near posterior margin (Fig. 65A, B). Eyes absent. Nuchal organs present, forming ciliated slits laterally between prostomium and first segment.

Proboscis retracted in all specimens, not observed.

First segment achaetous, slightly shorter than following segments; with one pair of conical cirri, inserted latero-ventrally (Fig. 65A, B).

Anterior three pairs of parapodia uniramous, with neuropodial lobes and shorter conical dorsal and ventral cirri; both inserted near parapodial base (Fig. 65A, B). Following parapodia biramous, with widely separated noto- and neuropodial rami of about equal length (Fig. 65D); prechaetal lobes always larger than postchaetal ones; lower part of noto- and upper part of neuropodial prechaetal lobes elongated. Dorsal and ventral cirri conical and of about same size; both inserted near terminal ends of noto- or neuropodial lobes (Fig. 65D).

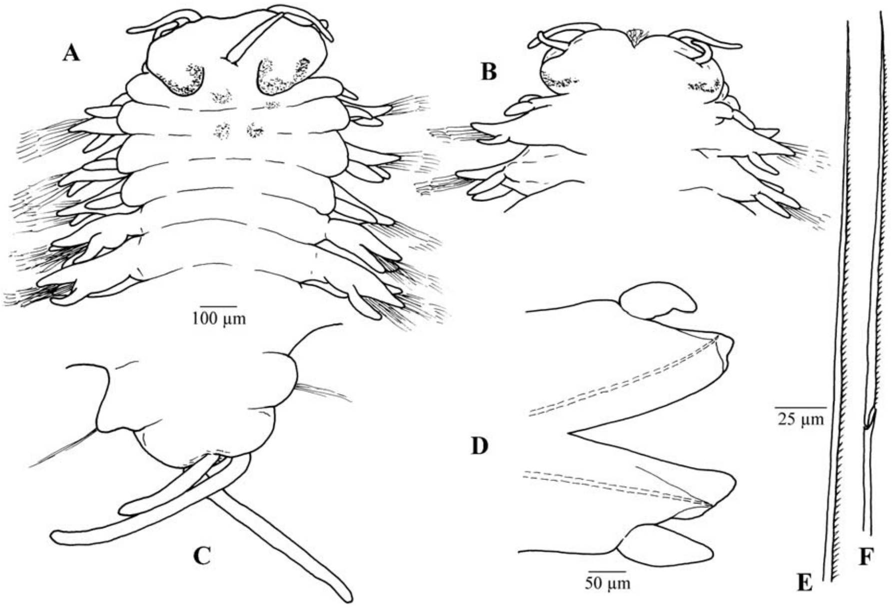

Fig. 65. *Lacydonia laureci* Laubier. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; ventral view. (D) Parapodium of mid-body; posterior view. (E) Notopodial chaeta. (F) Neuropodial chaeta. (A, B, D–F: ZMH P25262 A; C: ZMH P25287 A).

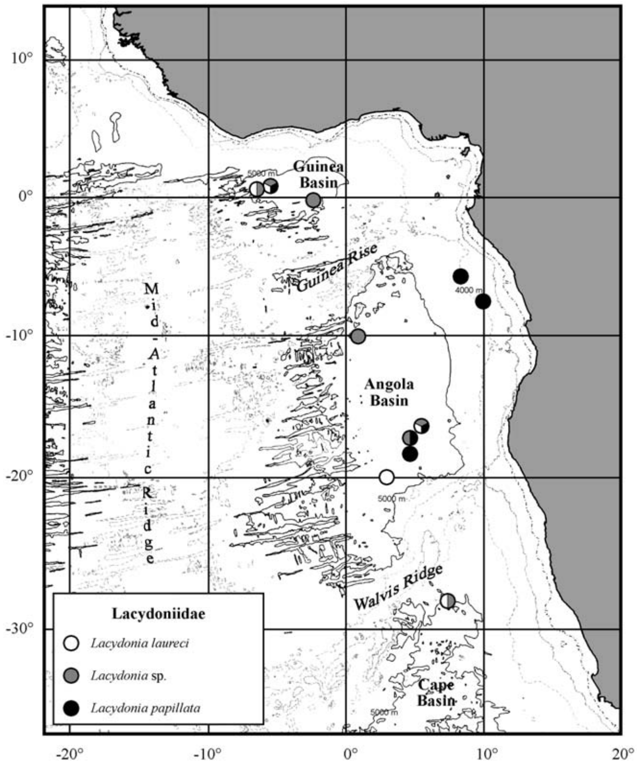

Fig. 66. Distribution of lacydoniid species and indeterminable material in the studied region.

All parapodial lobes with one straight or slightly curved acicula (Fig. 65D), and numerous internally diagonally striated notopodial capillaries and neuropodial spinigerous compound chaetae (Fig. 65E, F). Notopodial capillaries with fine serration over entire length of margin (Fig. 65E). Neuropodial spinigers with blades of slightly different length; subdistally blades with fine serration over entire length of margin; shafts with one large apical tooth and apparently an additional one on either side (Fig. 65F).

Pygidium with anus and a pair of termino-lateral slender, filiform cirri and a distinctly smaller medio-ventral cirrus (Fig. 65C).

Remarks

With the exception of ZMH P25262 A, all new specimens are very small in size and therefore only tentatively referred to this taxon.

Distribution

Angola, Cape and Guinea Basins; 5052–5497 m (Fig. 66).

Discussion

Lacydonia laureci Laubier is the only species of this taxon with two lateral lobes on the posterior margin of the prostomium. However, this structure is only developed distinctly in larger specimens, such as ZMH P25262 A or the holotype (MNHN Type 1421) from the abyssal eastern Mediterranean Sea.

Lacydonia papillata Uschakov, 1958

(Figs. 67–69)

Lacydonia papillata Uschakov, 1958—Uschakov (1958, p. 206, figs. Г, Д, Е)

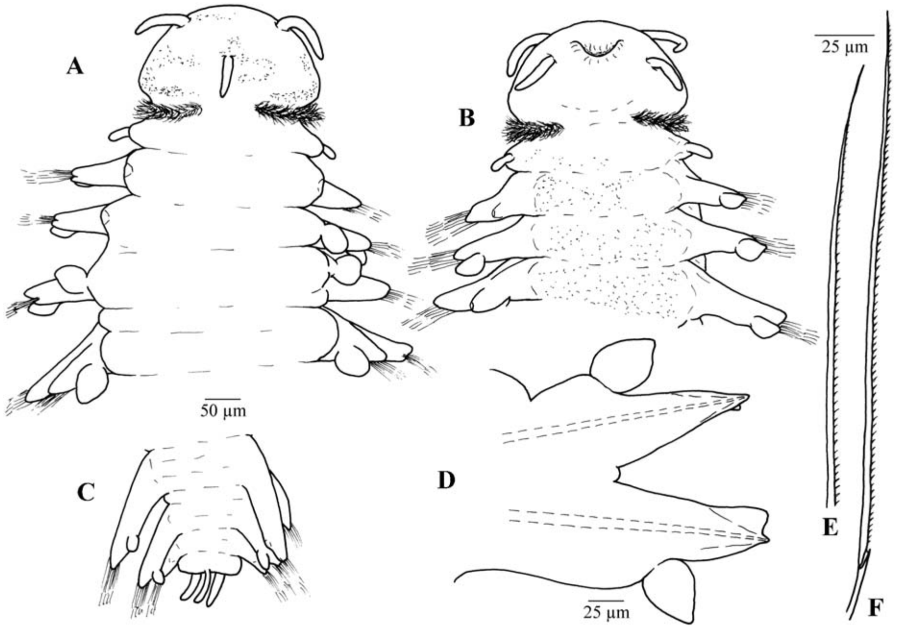

Fig. 67. *Lacydonia papillata* Uschakov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; ventral view. (D) Parapodium of mid-body; posterior view. (E) Notopodial chaeta. (F) Neuropodial chaeta. (A–F: ZMH P25273 F).

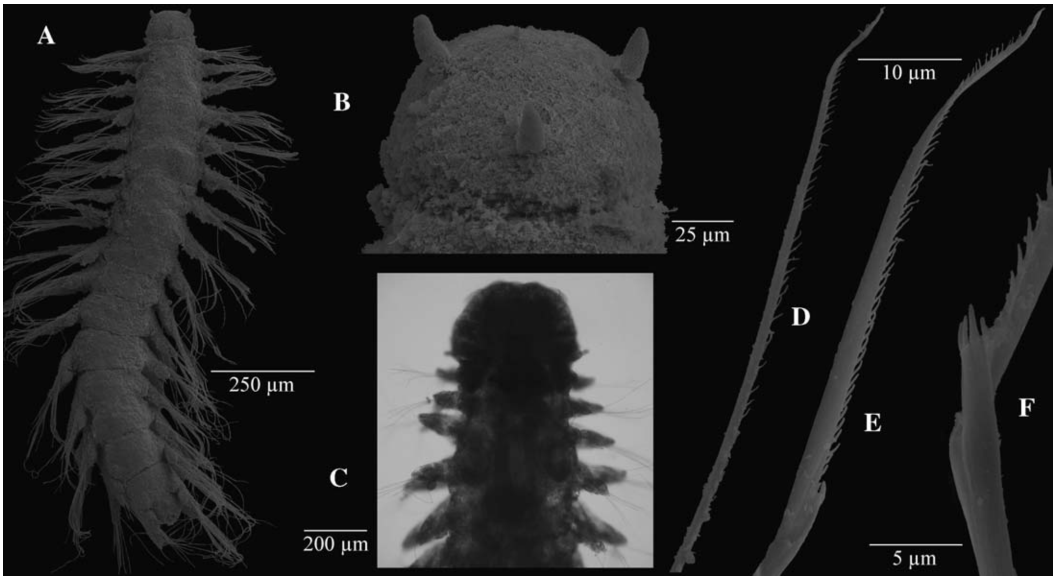

Fig. 68. *Lacydonia papillata* Uschakov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of anterior end; dorsal view. (D) Notopodial chaeta. (E) Neuropodial chaeta. (F) Detail of neuropodial chaeta. (A–F: ZMH P25268 B).

Lacydonia elongata Hartmann-Schröder & Rosenfeldt, 1992 [syn. nov.]—Hartmann-Schröder and Rosenfeldt (1992, p. 95, figs. 22–24)

Material examined

Type material. Lacydonia elongata: R/V POLARSTERN ANT V/1 st. 105, RMT 8, 64°38′S 62°64′W, 28.v.1986, 634 m; holotype: af/2.9/26/0.7/0.2 (ZMH P-20711).

Additional material. See Appendix 1.

Diagnosis

Prostomium with nearly straight posterior margin; antennae and palps conical to digitiform; eyes absent; conical cirri on first segment; anterior three pairs of parapodia uniramous; dorsal and ventral cirri globular to conical; lateral pair of conical to digitiform anal cirri

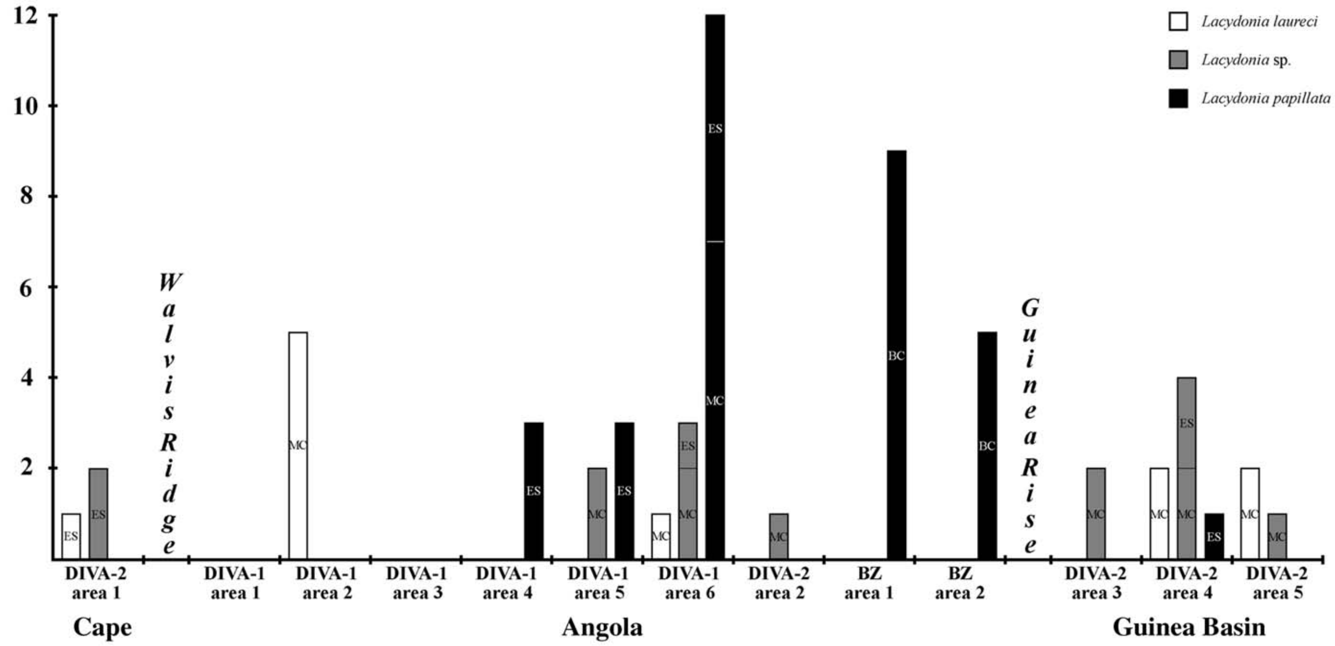

Fig. 69. Abundance of lacydoniids in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

of about same length as median one or only slightly longer.

Description

Body at least 3.9 mm long with up to 27 chaetigers; dorso-ventrally slightly flattened, stout anteriorly and tapering posteriorly (Fig. 68A). Anterior segments uniannulate, following ones indistinctly biannulate. Preserved specimens whitish to yellowish, often with diffusely distributed small red-brown pigmented spots, especially on prostomium, first segment and pygidium.

Prostomium anteriorly rounded, wider than long, with near straight posterior margin; three antennae and two palps (Figs. 67A, B; 68A–C). Antennae and palps all short and conical to digitiform; frontal antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna about as long as palps, inserted on posterior half of prostomium (Figs. 67A, B; 68A, B). Eyes absent. Nuchal organs present, forming ciliated slits laterally between prostomium and first segment (Fig. 67A, B).

Proboscis retracted in all specimens, not observed, but with a pair of large lateral glands (Fig. 68C).

First segment achaetous, slightly shorter than following segments; with one pair of conical cirri, inserted latero-ventrally (Figs. 67A, B; 68A).

Anterior three pairs of parapodia uniramous, with neuropodial lobes and shorter globular to conical dorsal and ventral cirri; dorsal ones inserted near parapodial base and ventral ones near middle of lobe (Fig. 67A, B). Following parapodia biramous, with widely separated noto- and neuropodial rami of about equal length (Fig. 67D); lower part of noto- and upper part of neuropodial prechaetal lobes slightly elongated. Dorsal and ventral cirri globular to conical and of about same size; both inserted near middle of noto- or neuropodial lobes (Fig. 67D).

All parapodial lobes with one straight or slightly curved acicula (Fig. 67D), and numerous internally diagonally striated notopodial capillaries and neuropodial spinigerous compound chaetae (Figs. 67E, F; 68D, E). Notopodial capillaries with fine serration over entire length of margin (Figs. 67E, 68D). Neuropodial spinigers with blades of slightly different length; subdistally blades with fine serration over entire length of margin (Figs. 67F, 68E); shafts with one large apical tooth and one or two additional ones on either side (Fig. 68F).

Pygidium with anus and a pair of termino-lateral conical to digitiform cirri and a thinner medio-ventral cirrus of subequal length (Fig. 67C).

Distribution

Angola and Guinea Basins; 3950–5460 m (Fig. 66).

Discussion

Lacydonia papillata Uschakov was originally described without the median antenna (Uschakov 1958, 1972). However, this antenna is probably always present in species of this genus but is easily lost or overlooked (Pleijel 2001f). Uschakov (1958) reported four dorsally located large, dark spots behind the prostomium of the holotype. This pigment pattern is present in some of the examined specimens (Fig. 68C).

The holotype (ZMH P-20711) of *Lacydonia elongata* Hartmann-Schröder & Rosenfeldt agrees with the studied specimens, except in few insignificant details. Therefore, the name is synonymized with *Lacydonia papillata* here.

***Lacydonia* sp.**

(Figs. 66, 69)

Material examined

See Appendix 1.

Remarks

This name is assigned to indeterminable juveniles or fragments that could belong to either *Lacydonia laureci* or *L. papillata*.

Abundance of Lacydoniidae

A total of 107 specimens or fragments were found in all investigated basins. They belong to *Lacydonia laureci* (35), to *L. papillata* (44), or were indeterminable (28). *Lacydonia laureci* can be found in all three examined basins, usually in low abundance, while *L. papillata* was present in the Guinea Basin and especially the Angola Basin (Fig. 69), with the highest abundance in DIVA-1 area 6 and BIOZAIRE areas 1–2. The most effective type of gear for collecting lacydoniids were the epibenthic sledge and particularly the multicorer, whereas a much lower number of specimens were collected with the box corer (Fig. 69).

Molecular data

ITS2 data set

Five newly acquired sequences (Table 9) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. All analyses were conducted with the branch-and-bound algorithm. ML was performed using the General Time Reversible model with invariant gamma distribution (GTR+I+G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies ($A=0.1834$, $C=0.2850$, $G=0.2756$, $T=0.2560$); number of substitution types=6; substitution rate matrix ($A\leftrightarrow C=1.5877$, $A\leftrightarrow G=9.6583$, $A\leftrightarrow T=6.9411$, $C\leftrightarrow G=0.8828$, $C\leftrightarrow T=7.8977$, $G\leftrightarrow T=1.0000$); among-site rate variation with proportion of invariable sites=0.4534; and gamma distribution shape parameter=1.2543. Clade support values were calculated with nonparametric bootstrapping with 1,000 (ML) or 100,000 replicates (MP) and branch-and bound searches.

After exclusion of the primer sites, the alignment for the five sequences contained 447 characters, of which 140 were variable and 17 parsimony informative. The MP (tree length=171, CI=0.9591 (0.7083), RI=0.5882, RC=0.5642) and the ML analysis (–ln L=1271.42516) found single trees with identical topologies (Fig. 70).

Discussion of molecular results

The phylogenetic position of the Lacydoniidae varied according to the analyzed sequences (see "Molecular phylogeny of abyssal Phyllodocida"). The 18S rDNA data strongly supported monophyly of the group and a close relationship to Paralacydoniidae. This was also shown by the 16S rDNA maximum-likelihood analysis,

Table 9. List of taxa and corresponding sequences in Lacydoniidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession numbers			
			18S rDNA	16S rDNA	COI (3-6W)	ITS2
LACYDONIIDAE						
Lacydonia laureci Laubier	Cape Basin					
	D-2 st. 40 ES-E	ZMH P25262 A	GQ426579	–	GQ426677	GQ426733
Lacydonia papillata Uschakov	Guinea Basin					
	D-2 st. 90 ES-S	ZMH P25276	–	–	–	GQ426734
Lacydonia sp.	Cape Basin					
	D-2 st. 40 ES-S	ZMH P25279	–	–	–	GQ426735
	Guinea Basin					
	D-2 st. 89 ES-S	ZMH P25287 A	GQ426580	GQ426617	GQ426678	GQ426736
PARALACYDONIIDAE						
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		–	–	–	GQ426700

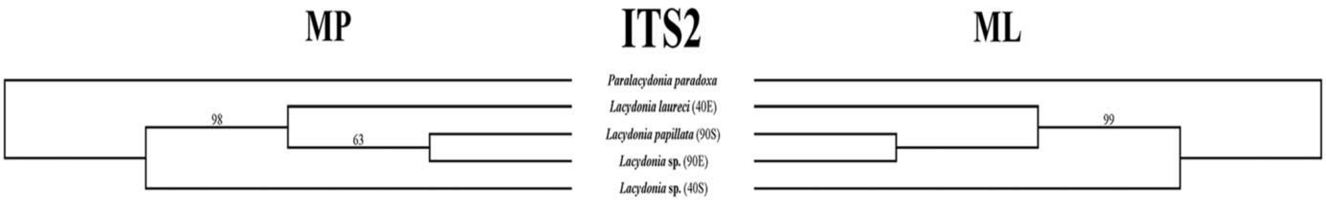

Fig. 70. Cladograms obtained from MP and ML analysis of the ITS2 sequences. Bootstrap values >50 shown above branches.

whereas the maximum-parsimony analysis gave a sister-group relationship to Sphaerodoridae, and the COI amino-acid data suggested placement within a paraphyletic Phyllodocidae. However, the latter hypothesis was only weakly supported.

The analyzed non-coding ITS2 sequences showed that the median fragment of *Lacydonia* sp. (st. 90E) might belong to *L. papillata*, whereas the sequence from the median fragment of *Lacydonia* sp. (st. 40S) was too short for a more accurate determination.

Lopadorhynchidae Claparède, 1868

The Lopadorhynchidae are a group of pelagic polychaetes that clearly belongs to the Phyllodocida (Pleijel 2001g) but is sometimes treated as a polyphyletic part of the benthic Phyllodocidae (Uschakov 1972). The family comprises two dissimilar clades (Fauchald and Rouse 1997; Wilson 2000d), which are considered as derived either from the *Chaetoparia* Malmgren, 1867 group or the *Eteone* Savigny, 1822 group within Phyllodocidae (Pleijel 2001g). However, most authors (e.g. Fauchald and Rouse 1997; Wilson 2000d) referred to Lopadorhynchidae as a separate taxon, even though no apomorphies defining it are known.

The Lopadorhynchidae are active swimmers; they are especially widely distributed in tropical and temperate oceans from surface to deep waters (Wilson 2000d) but also rather common in cold waters (Hartman 1964; Halanych et al. 2007). They are considered holopelagic carnivores, possibly capturing prey with their modified anterior segments bearing stout, hook-like chaetae (Dales 1955; Fauchald and Jumars 1979). However, these specialized chaetigers are present only in the genus *Lopadorhynchus* Grube, 1855, but missing in the taxon examined here.

The sole lopadorhynchid collected in the present study is *Pelagobia longicirrata* Greeff, 1879. This sometimes swarming species was previously reported to have a cosmopolitan distribution from the surface to depths of 3000 m, with larger representatives (6–12 mm with 24–30 segments) predominantly found in arctic or antarctic regions, smaller ones (2–7 mm with 14–20 segments) in between (e.g. Greeff 1879; Viguier 1886; Reibisch 1895, 1905; Vanhöffen 1897; Southern 1909; Gravier 1911; Ehlers 1913; Benham 1921; Monro 1936; Støp-Bowitz 1948, 1949, 1951, 1977, 1992; Friedrich 1950b; Dales 1957a; Tebble 1960, 1962; Hartman 1964; Day 1967; Dales and Peter 1972; Uschakov 1972; Hartmann-Schröder and Rosenfeldt 1992; Fernández-Álamo 2002, 2006).

Pelagobia Greeff, 1879

Pelagobia longicirrata Greeff, 1879

(Figs. 71–74)

Pelagobia longicirrata Greeff, 1879—Greeff (1879, p. 247; pl. 14, figs. 23–25)

Pelagobia Viguieri Gravier, 1911—Gravier (1911, p. 311)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps; two pairs of cirri on first chaetiger; second chaetiger without dorsal cirri; dorsal and ventral cirri digitiform, longer than parapodial lobes; compound spinigers with smooth shafts, hooked stout simple chaetae not present.

Description

Body up to 3.9 mm long with up to 12 chaetigers; small, compact, dorso-ventrally flattened with tapering anterior and posterior ends (Fig. 72A). Segments more or less distinctly bi- or triannulated (Fig. 72A, B). Preserved specimens whitish to yellowish, without pigment patterns.

Prostomium conical, truncated anteriorly; slightly longer than wide; with two antennae and two palps (Figs. 71A, B; 72A, B). Antennae and palps all digitiform, of about same length; slightly shorter than prostomium wide; inserted latero-dorsally and latero-ventrally; median antenna absent. One pair of inconspicuous eyes present in posterior half of prostomium (Fig. 71A); invisible in most specimens. Nuchal organs, forming two pairs of ciliated globular knobs laterally between prostomium and first segment (Fig. 71A, B).

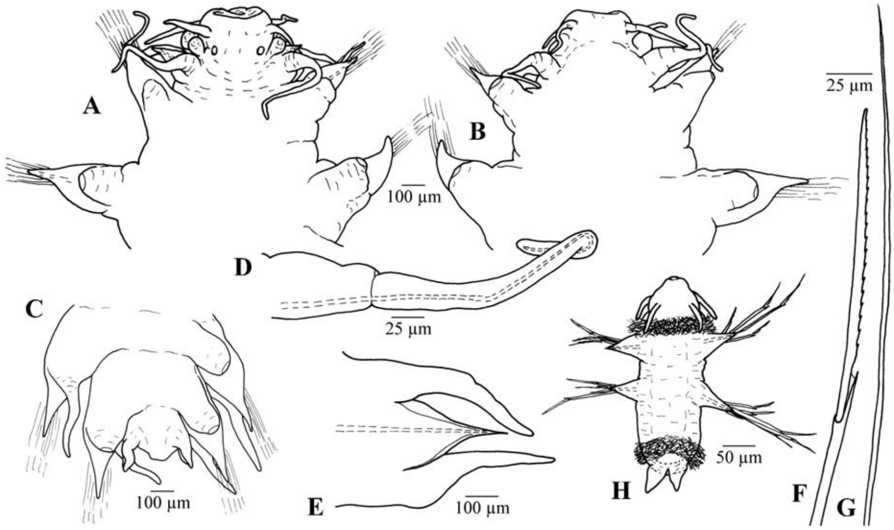

Fig. 71. *Pelagobia longicirrata* Greeff. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; ventral view. (D) Cirri of first segment with inner structure. (E) Right parapodium of mid-body; posterior view, chaetae omitted. (F) Compound spiniger. (G) Capillary chaeta. (H) Two-segmented larva. (A–C, E–G: ZMH P25292; D: SMF 18797; H: ZMH P25296).

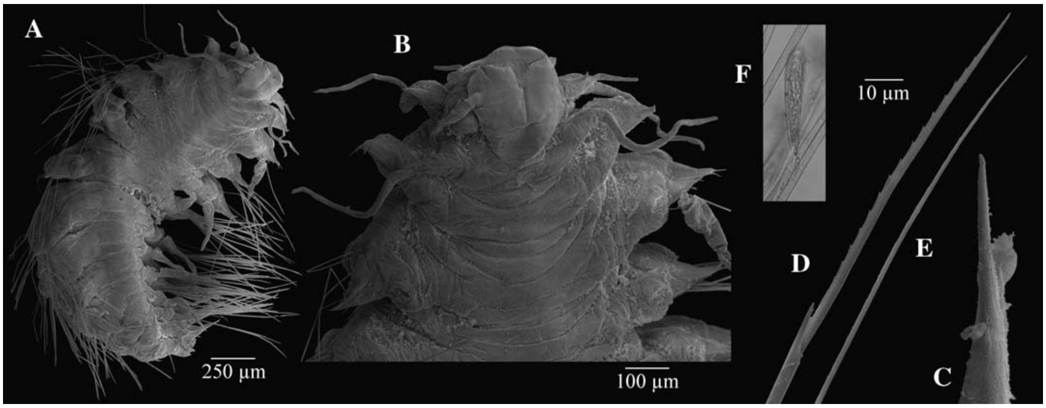

Fig. 72. *Pelagobia longicirrata* Greeff. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Acicula. (D) Compound spiniger. (E) Capillary chaeta. (F) Light micrograph of commensalist. (A–E: ZMH P25291 B; F: ZMH P25291 A).

Proboscis retracted in all specimens, not observed. However, jaws in form of stylet-like hooks, which are reported by Uschakov (1972), are not observed.

First segment dorsally reduced, partly covered by prostomium (Fig. 72A, B); dorsally and ventrally with pair of slender, cylindrical cirri, which are about two times longer than antennae or palps (Fig. 71A, B; 72A, B), and small aciculaerous lobes, which are partly fused to ventral cirrophores (Fig. 72B). Cirri of first segment are supported throughout their length by one or two more or less distinct acicular-like structures (Fig. 71D), which might be also present in antennae, palps and cirri of some larger specimens. These supporting structures are previously reported by Benham (1921) and Hartmann-Schröder and Rosenfeldt (1992). Second segment without dorsal cirri, but distinct chaetigerous lobes and normal ventral cirri. Following parapodia all uniramous with pointed parapodial lobes and distinctly longer digitiform dorsal and ventral cirri, which are of about equal length and inserted near parapodial bases (Fig. 71E).

All parapodia with one straight acicula, which barely extending beyond tip of lobe (Figs. 71E, 72C), and numerous spinigerous compound chaetae (Figs. 71F, 72D). Spinigers with blades of slightly different length, which are arranged in a dense, fan-shaped fascicle; blades with fine serration over entire length of margin; shafts smooth (Figs. 71F, 72D). Sometimes a few additional capillary chaetae with minute serration present (Figs. 71G, 72E), which are also mentioned by Tebble (1960). Chaetae occasionally with attached commensals (Fig. 72F).

Pygidium with a pair of small lateral conical to paddle-shaped cirri (Fig. 71C).

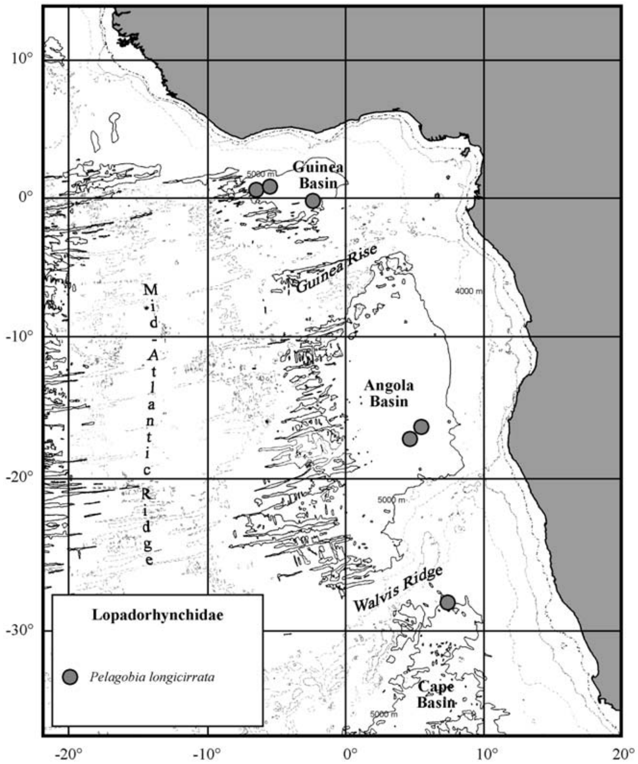

Fig. 73. Distribution of *Pelagobia longicirrata* in the studied region.

Remarks

Reibisch (1895, pl. 2, figs. 2–5, 7) described and illustrated various larval stages of this species which resemble juveniles of *Eteone* sp. (Phyllodocidae). He reported the typical ciliated bands as not present, but the two-segmented larva (ZMH P25296) examined here possesses a well-developed proto- and telotroch (Fig. 71H).

Distribution

Angola, Cape and Guinea Basins; 5048–5460 m.

Discussion

Pelagobia longicirrata Greeff and the closely related *P. serrata* Southern, 1909 from the N Atlantic can be separated by the presence of distinct serrated, spinigerous shafts in the latter, whereas in *P. longicirrata* these structures are smooth (Tebble 1960). However, Tebble also wrote that more material needed to be examined before it could be concluded whether or not that difference warrants division in two species.

Abundance of Lopadorhynchidae

Fourteen specimens and one median fragment of *Pelagobia longicirrata* were found in all investigated

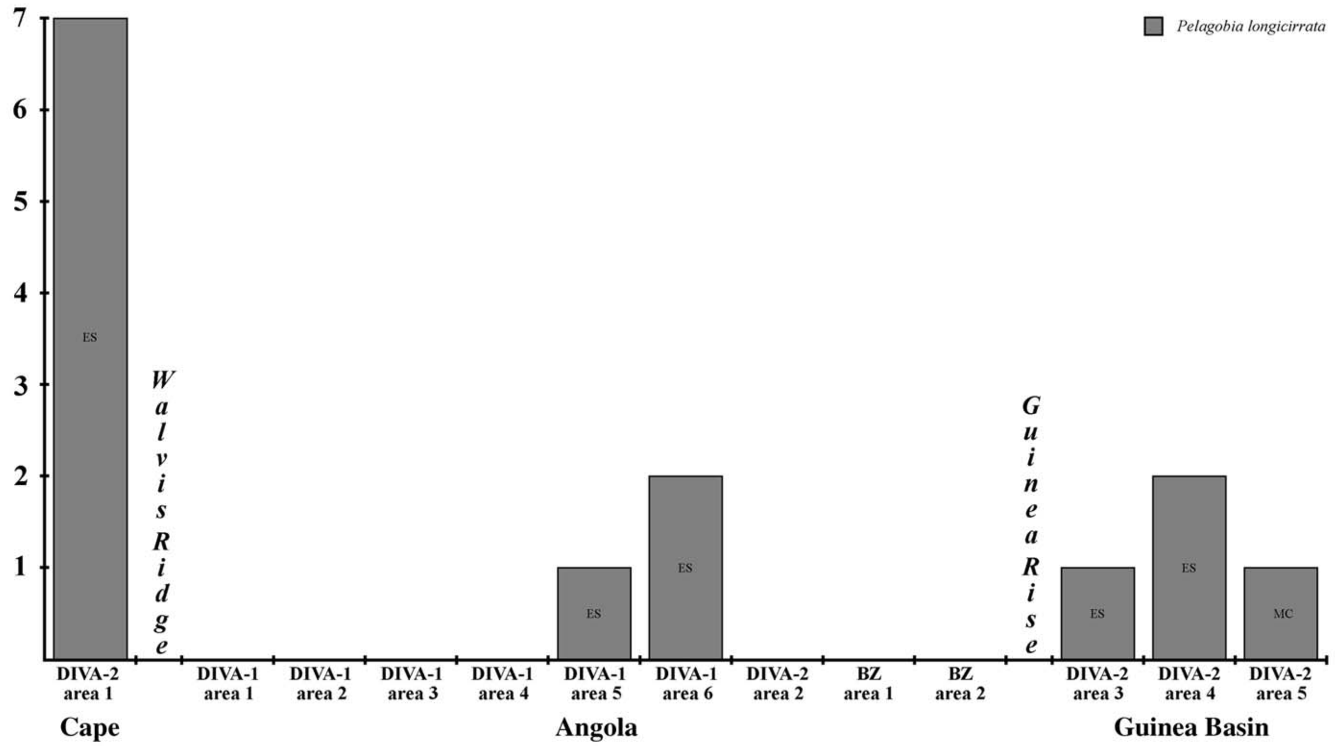

Fig. 74. Abundance of the lopadorhynchid *Pelagobia longicirrata* in the sampling areas; only complete specimens and anterior fragments counted. ES = epibenthic sledge, MC = multicorer.

basins (Fig. 74), with the highest abundance in the Cape Basin (DIVA-2 area 1). Only the two-segmented larva was collected with the multicorer, i.e. by chance, whereas all other specimens were present in the epibenthic sledge samples. The latter type of gear was provided with a closing mechanism, which clearly indicates that the herein-examined specimens of this holopelagic species were caught directly above the abyssal sea floor.

Molecular data

The 18S rDNA data strongly support a close relationship between the pelagic lopadorhynchids and the benthic phyllodocids, both of which might be monophyletic (see "Molecular phylogeny of abyssal Phyllodocida"). The two examined 18S rDNA sequences (Table 10) of *Pelagobia longicirrata* from the Cape and Guinea Basins were identical. Data on more variable regions (e.g. 16S, COI, ITS) would be needed to clarify distribution patterns, but all attempts at generating them during the present study were unsuccessful.

Nephtyidae Grube, 1850

The Nephtyidae are an easily recognizable group of polychaetes which clearly belong to the Phyllodocida, but their lower-level classification is less certain, and species identification especially of the smaller forms can be tricky (Pleijel 2001i). The body is characteristically rectangular in cross-section, and a possible autapomorphy for the group might be the interramal branchiae that are often present (Fauchald and Rouse 1997). Furthermore, nephtyids have an eversible pharynx with one pair of lateral jaws and, usually, accessory rows of soft papillae (Hilbig 1997c; Wilson 2000e), and the single anal cirrus is unique in Phyllodocida (Pleijel 2001i).

The Nephtyidae are motile burrowers in soft sediments and also active swimmers; they show worldwide distribution from intertidal to abyssal depths (Day 1967; Hilbig 1997c; Wilson 2000e; Pleijel 2001i). They are usually considered carnivores feeding on small invertebrates, but some species seem to be subsurface deposit-feeders (Fauchald and Jumars 1979).

In the single nephtyid collected in the present study, representing *Aglaophamus groenlandiae* Hartman, 1967, the excreted gut contents included spionid remains, which indicate predatory feeding. The species was previously reported from slope to abyssal depths in the northern Atlantic Ocean (Hartman 1967; Hartman and Fauchald 1971; Kirkegaard 1980; Detinova 1985).

Aglaophamus Kinberg, 1865

Aglaophamus groenlandiae Hartman, 1967

(Figs. 75–78)

Aglaophamus groenlandiae Hartman, 1967—Hartman (1967, p. 73; pl. 22, figs. A, B); Hartman and Fauchald (1971, p. 60)

Aglaophamus groenlandica Hartman [incorrect subsequent spelling]—Kirkegaard (1980, p. 85); Detinova (1985, p. 111)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps; eyes absent; noto- and neuropodial pre- and postchaetal lamellae nearly absent, much shorter than conical to triangular acicular lobes; interramal branchiae involute, starting from chaetiger 11–16, all large; lyrate chaetae absent; proboscis with 22 bifid papillae, subdistally with as many longitudinal rows of 6–10 papillae.

Description

Body up to 24 mm long with up to 53 chaetigers; nearly rectangular in cross section; with more or less distinct dorsal ridges. First parapodia anteriorly

Table 10. List of specimens and corresponding sequences in Lopadorhynchidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession number 18S rDNA
LOPADORHYNCHIDAE			
Pelagobia longicirrata Greeff	Cape Basin		
	D-2 st. 40 ES-S	ZMH P25291 C	GQ426581
	Walvis Ridge and Guinea Rise		
	Guinea Basin		
	D-2 st. 89 ES-S	ZMH P25294	GQ426582

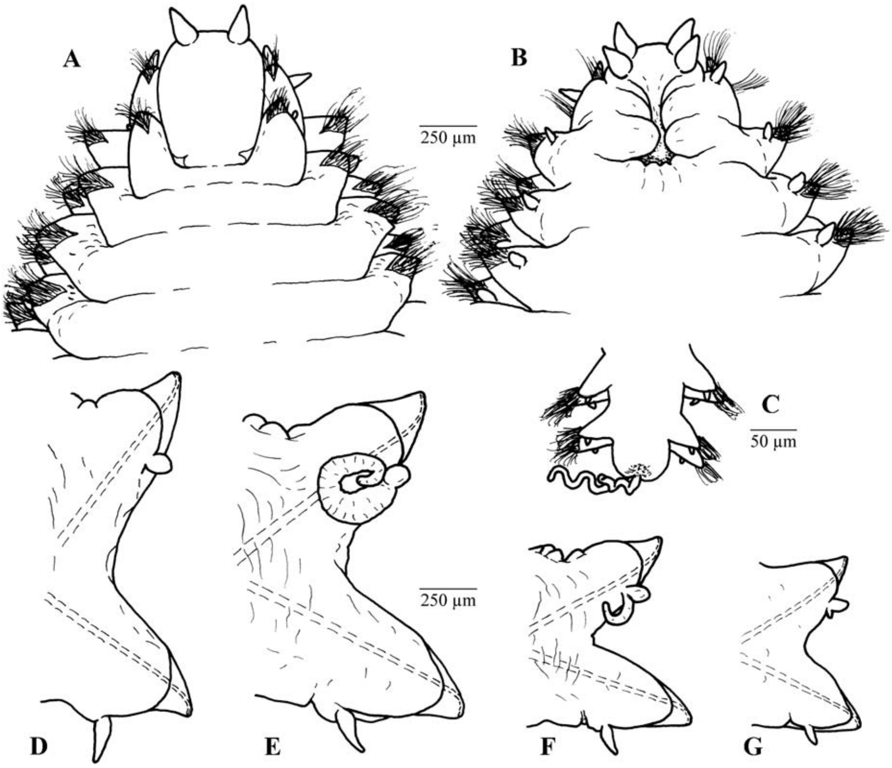

Fig. 75. *Aglaophamus groenlandiae* Hartman. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D–G) Anterior to posterior parapodia; posterior views, chaetae omitted. (A, B, D–G: ZMH P25311 B; C: ZMH P25304).

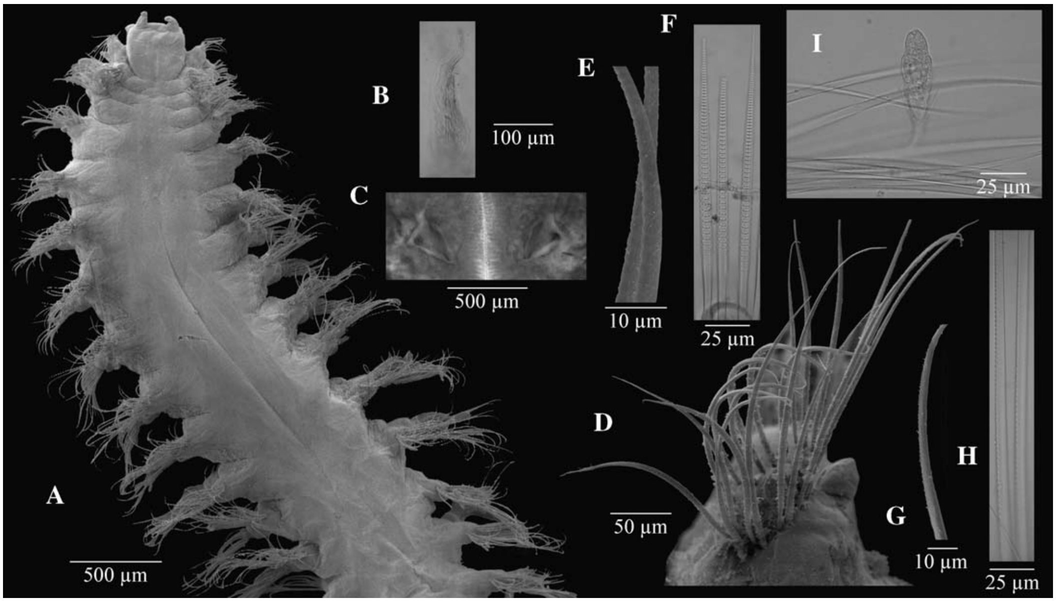

Fig. 76. *Aglaophamus groenlandiae* Hartman. (A) Anterior end; dorsal view. (B) Light micrograph of proboscidial papilla. (C) Light micrograph of jaws. (D) Notopodium of chaetiger 4; dorsal view. (E) Detail of preacicular chaetae. (F) Light micrograph of preacicular chaetae. (G) Detail of postacicular chaeta. (H) Light micrograph of postacicular chaetae. (I) Light micrograph of commensal. (A, D, E, G: ZMH P25317 B; B, C, F: ZMH P25323 B; H, I: ZMH P25311 B).

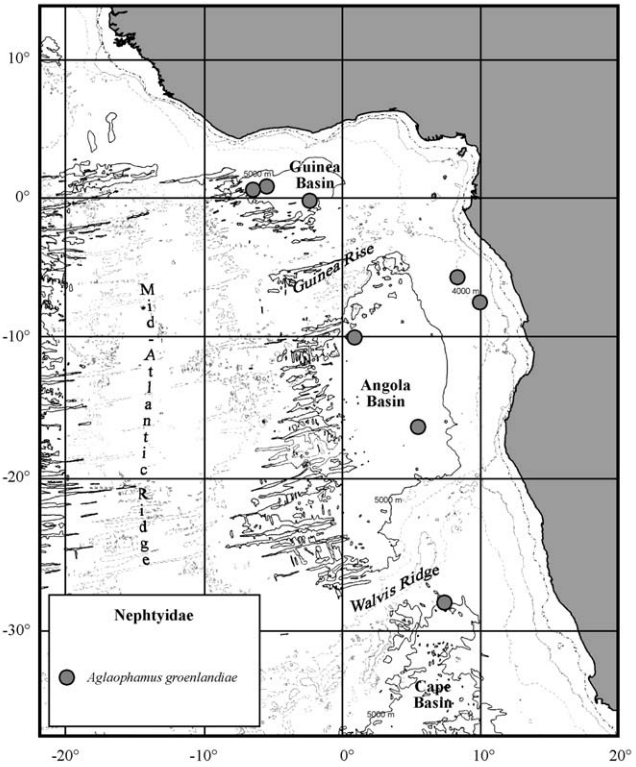

Fig. 77. Distribution of *Aglaophamus groenlandiae* in the studied region.

directed and following ones more laterally (Figs. 75A, 76A).

Prostomium about as long as wide or slightly longer, rectangular, with two antennae and two palps (Figs. 75A, B; 76A). Antennae and palps both short, conical, and of about same length; antennae inserted latero-dorsally and palps latero-ventrally. Eyes absent. Nuchal organs might be present, but are not conspicuous.

Proboscis laterally with one pair of pyramid-shaped jaws with a triangular base (Fig. 76C), only visible after dissection, and distally numerous soft papillae with internal glands. Anterior margin surrounded by a circlet of 22 long, proximally fused, bifid papillae and subdistally additional 22 longitudinal rows of six to ten cirriform to conical papillae (Fig. 76B), which decrease in size proximally.

All parapodia biramous, with distinctly separated rami (Figs. 75A–G, 76A). Noto- and neuropodia with short, rounded pre- and postchaetal lamellae and longer conical to triangular acicular lobes (Fig. 75D–G). Dorsal cirri of 1st chaetiger very small and papilla-like (Fig. 75A); following ones much larger and more oval to conical (Fig. 75D–G); inserted on lower side of notopodial postchaetal lamellae. Ventral cirri of 1st chaetiger enlarged; always slightly longer than corresponding dorsal ones and more conical to digitiform; inserted near neuropodial base (Fig. 75B, D–G).

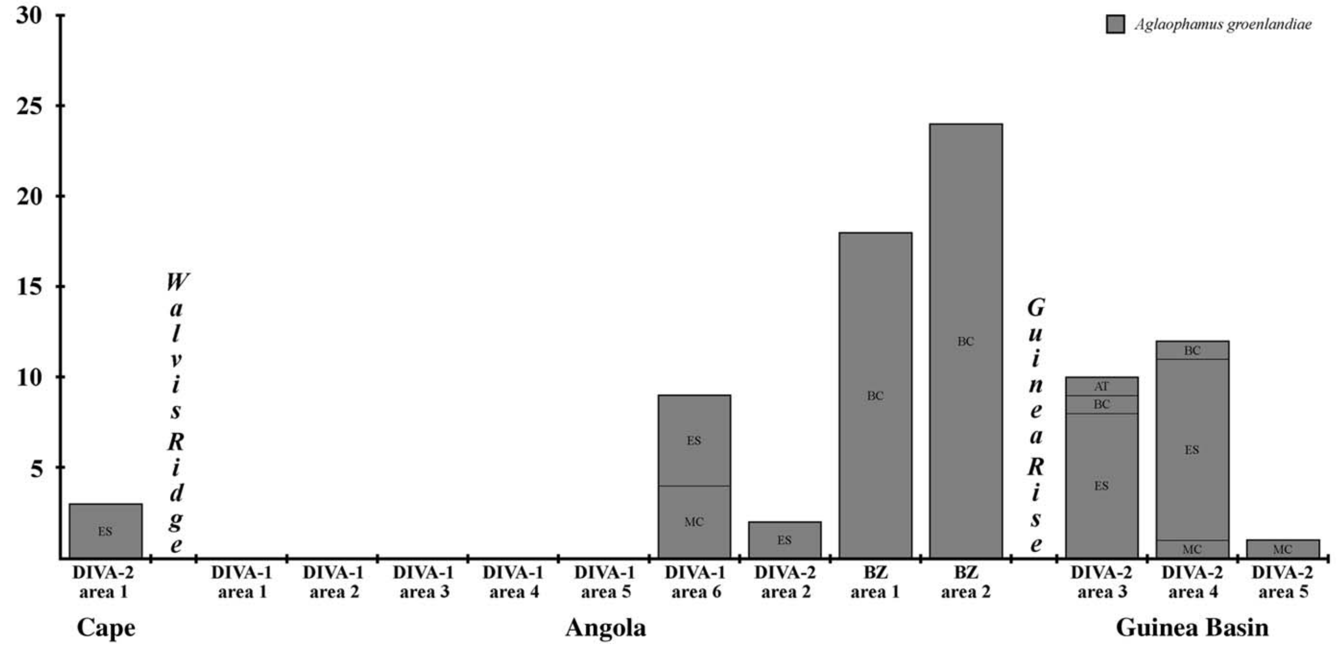

Fig. 78. Abundance of the nephtyid *Aglaophamus groenlandiae* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. AT = Agassiz trawl, BC = box corer, ES = epibenthic sledge, MC = multicorer.

Juveniles without interramal branchiae, but in the two largest specimens present, starting from chaetiger 12 (specimen ZMH P25319 is badly preserved and therefore only questionable referred to this species) and 16; slender digitiform in shape, coiled or curved inwards (involute) and inserted just underneath dorsal cirri (Fig. 75E); large from the first, but decreasing in size posteriorly (Fig. 75F, G) and lacking in a few posterior parapodia.

Each noto- and neuropodium have one distally curved acicula (Fig. 75D–G) and numerous simple capillary chaetae arranged in dense, fan-shaped fascicles. Preacicular chaetae usually smooth, curved and predominantly internally chambered which gives a barred or laddered appearance (Fig. 76D–F); all postacicular and also first neuropodial preacicular chaetae more straight, finely serrated capillaries (Fig. 76D, G, H); postacicular chaetae distinctly longer than preacicular ones and especially from about midbody in larger numbers. Lyrate chaetae not observed. Chaetae often with attached commensals (Fig. 76I).

Pygidium with anus and a single terminal slender cirrus (Fig. 75C).

Remarks

Hartman (1967) described a slight semicircular lobe, which was found in superior position on the upper edge of the notopodial base. In the material examined here such ‘lobes’ are present only in larger specimens (Fig. 75D–F), and seem to be no more than wrinkles.

The original description (Hartman 1967) gives no information concerning the number of proboscidial papillae. Hartman and Fauchald (1971) mention 20 bifid and 11 longitudinal rows of subdistal papillae, but this might be a mistake because, according to Hilbig (1997c, p. 322), “species with more than 14 terminal papillae also have more than 14 rows of subdistal papillae.”

Distribution

Angola, Cape and Guinea Basins; 3945–5655 m (Fig. 77).

Discussion

A few other *Aglaophamus* species from slope to abyssal depths are reported to have more or less completely reduced pre- and postchaetal lamellae and a relatively posterior onset of involute interramal branchiae, thus might be confused with *A. groenlandiae* Hartman. However, the two widespread taxa *A. elamellata* (Eliason, 1951) (Atlantic, Indian and Pacific Oceans; 990–7000 m) and *A. malmgreni* (Théel, 1879) (Atlantic and Pacific Oceans; 75–2300 m) both have 14 rows of bifid subterminal papillae, whereas in the two Antarctic species *A. paramalmgreni* Hartmann-Schröder & Rosenfeldt, 1992 (64°7.63′S 65°13.8′W; 546 m) and *A. posterobranchus* Hartman, 1967 (Antarctic seas; 400–4758 m) the posterior lamellae are more developed.

Abundance of Nephtyidae

A total of 92 specimens or fragments of *Aglaophamus groenlandiae* were found in all investigated basins (Figs. 78), with the highest abundance in BIOZAIRE areas 1 and 2. The most effective types of gear for collecting nephtyids were the box corer and the epibenthic sledge, whereas only a few specimens were collected with the multicorer and the Agassiz trawl (Fig. 78). The epibenthic sledge samples have the added advantage of being generally rapidly fixed in ethanol; therefore, the material was more or less useful for molecular analyses.

Molecular data

COI (3-6W) data set

Four newly acquired sequences (Table 11) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. All analyses were conducted with the branch-and-bound algorithm. The ML analysis was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies ($A = 0.2774$, $C = 0.1711$, $G = 0.1717$, $T = 0.3798$); number of substitution types = 6; substitution rate matrix ($A \leftrightarrow C = 15.2833$, $A \leftrightarrow G = 51.9244$, $A \leftrightarrow T = 39.1223$, $C \leftrightarrow G = 17.4280$, $C \leftrightarrow T = 128.5528$, $G \leftrightarrow T = 1.0000$); among-site rate variation with proportion of invariable sites = 0.2526; and equal rates for all sites. Clade support values were calculated with nonparametric bootstrapping with 1,000 (ML) or 100,000 replicates (MP) and branch-and-bound searches.

After exclusion of the primer sites, the alignment for the four sequences contained 421 characters, of which 113 were variable and four parsimony informative. The MP (tree length = 116, CI = 0.9828 (0.6667), RI = 0.5000, RC = 0.4914) and the ML analysis ($-\ln L = 927.45427$) found single trees with identical topologies (Fig. 79).

Discussion of molecular results

The 18S rDNA data strongly support monophyly of Nephtyidae and a sister-group relationship to pilargids, but the COI amino-acid analyses suggest paraphyly with

Table 11. List of taxa and corresponding sequences in Nephtyidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession numbers	
			18S rDNA	COI (3-6W)
NEPHTYIDAE				
Aglaophamus groenlandiae Hartman	Cape Basin			
	D-2 st. 41 ES-S	ZMH P25315	–	GQ426679
	Walvis Ridge and Guinea Rise			
	Guinea Basin			
	D-2 st. 63 ES-E	ZMH P25317 A	–	GQ426680
	D-2 st. 89 ES-S	ZMH P25323 B	–	GQ426681
	D-2 st. 90 ES-S	ZMH P25324 B	GQ426583	–
PARALACYDONIIDAE				
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		–	GQ426684

Fig. 79. Cladograms obtained from MP and ML analysis of the COI (3-6W) sequences. Bootstrap values > 50 shown above branches.

inclusion of chrysopetalids and paralacydoniids (see "Molecular phylogeny of abyssal Phyllodocida").

Each of the analyzed three COI (3-6W) sequences of *Aglaophamus groenlandiae* from the Cape and Guinea Basins differed from the others in only two positions, whereas the translated amino-acid sequences of the gene were identical. Therefore, the Walvis Ridge and the Guinea Rise probably represent no barrier to the distribution of the populations.

Nereididae Lamarck, 1818

The Nereididae are one of the most common groups of polychaetes and an extensively studied part of the Phyllodocida (Pleijel 2001j; Bakken and Wilson 2005). They are distinguished by an eversible pharynx with one pair of fang-shaped, often serrated terminal jaws and, usually, accessory soft papillae or hardened paragnaths (Wilson 2000f). Furthermore, usually large and biarticulated palps are present on the prostomium, and two to four pairs of tentacular cirri arising from the anterolateral corners of the first segment (Hilbig 1997b).

The Nereididae have a worldwide distribution from mainly intertidal to abyssal depths; a few taxa are also known from semiterrestrial environments and fresh water (Pleijel 2001j). Nereidids often live discretely motile in mucous tubes and generally appear to be omnivorous, capturing food with their jaws. However, some species are surface deposit-feeders, filter-feeders or live in commensalism with hermit crabs (Day 1967; Fauchald and Jumars 1979). Fauchald (1972, 1977b) mentioned that a few genera (e.g. *Ceratocephale* Malmgren, 1867) are better represented in deep water than others, and that these have prolonged appendages compared to shallow-water relatives, an observation confirmed in the species examined here.

Two species of Nereididae were collected in the present study. *Ceratocephale abyssorum* (Hartman & Fauchald, 1971) was originally described from the abyssal NW Atlantic (Hartman and Fauchald 1971), erroneously as a new pisionid. *Ruillerinereis profundus* (Hartman, 1965) comb. nov. was previously reported from slope depth (1000–1102 m) in the NW Atlantic (Hartman 1965; Hartman and Fauchald 1971; as *Profundilycastis profundus*). In the following morphological redescriptions of the two species, terminology and interpretation of the parapodial characters is based on Hylleberg and Nateewathana (1988).

Key to nereidid species from the abyssal SE Atlantic

1. Prostomium with tapering antennae and palps (Figs. 80A, 81A–C); ventral cirri double on some anterior parapodia (Fig. 80B, D–G); noto- and neuropodial chaetae predominantly homogomph spinigers (Fig. 81D–G) .... *Ceratocephale abyssorum* (Hartman & Fauchald)
– Prostomium with slender antennae and massive palps (Figs. 83A, B; 84A–C); all ventral cirri simple (Fig. 83B, D–G); notopodial chaetae homogomph spinigers and falcigers (Figs. 83I, 84D), neuropodial chaetae heterogomph falcigers and homogomph spinigers (Fig. 84E, F) .... *Rullierinereis profundus* (Hartman)

Ceratocephale Malmgren, 1867

Ceratocephale abyssorum (Hartman & Fauchald, 1971)

(Figs. 80–82, 85)

Pisionura abyssorum Hartman & Fauchald, 1971—Hartman and Fauchald (1971, p. 33; pl. 4, figs. a, b)

Ceratocephale abyssorum (Hartman & Fauchald) —Hartmann-Schröder (1977a, p. 146; pl. 1, figs. a–c)

Material examined

See Appendix 1.

Additional material examined (see "Discussion"). *Micronereides capensis* Day, 1963(b): South Africa, South Coast of Cape Provine, Agulhas Bank, st. SCD 233, 36°28.5′S 21°11′E, 4.xii.1960, 183 m, fine sand; holotype: cs/5.3/34/0.9/0.4 (BMNH 1963.1.60).

Diagnosis

Prostomium with two antennae and two biarticulate palps; eyes absent; four pairs of cirri on first segment; parapodia of first two chaetigers uniramous, the following biramous; conspicuous prechaetal neuropodial ligules present; branchiae absent; dorsal cirri simple throughout, with enlarged cirrophores in median body region; anterior and middle ventral cirri double, starting from first chaetiger; chaetae predominantly homogomph spinigers; soft proboscidial papillae present on oral ring; jaws with up to nine teeth.

Description

Body up to 10.3 mm long with up to 52 chaetigers; widest in pharyngeal region (up to chaetiger 4–5), much narrower in following segments (Fig. 81A). Anterior 8–10 parapodia crowded, with bushy fascicles of numerous chaetae. Larger specimens with more or less distinct dorsal ridges in anterior part of body.

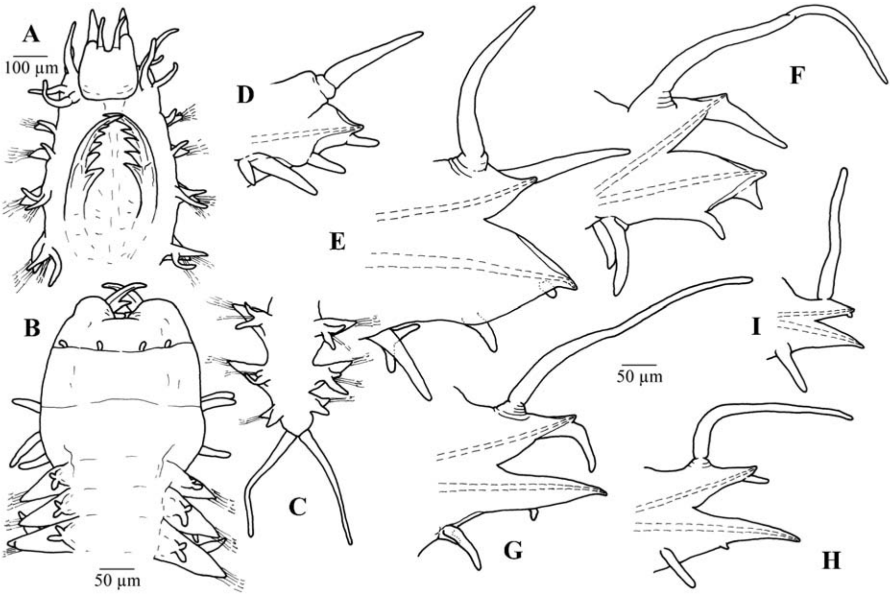

Fig. 80. *Ceratocephale abyssorum* (Hartman & Fauchald). (A) Anterior end; dorsal view. (B) Anterior end with everted proboscis; ventral view. (C) Posterior end; dorsal view. (D–I) Anterior to posterior parapodia; posterior views, chaetae omitted: D–G = 2nd, 5th, 14th, 24th parapodium; H, I = of posterior fragment. (A: ZMH P25358; B: ZMH P25348 A; C: ZMH P25348 D; D–I: ZMH P25343 A).

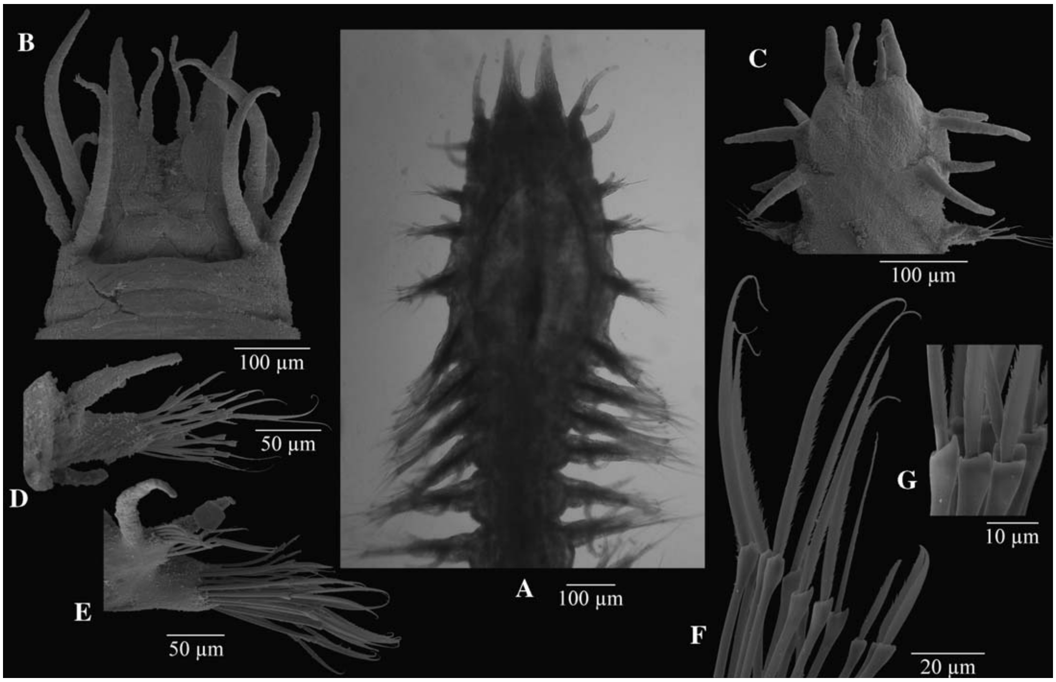

Fig. 81. *Ceratocephale abyssorum* (Hartman & Fauchald). (A) Light micrograph of anterior end; dorsal view. (B) Anterior end of large specimen; dorsal view. (C) Anterior end of juvenile; dorsal view. (D) Uniramous right parapodium of 1st chaetiger; posterior view. (E) Biramous right parapodium of 3rd chaetiger; posterior view. (F) Chaetae. (G) Details of chaetae. (A: ZMH P25342; B, D–G: ZMH P25326 A; C: ZMH P25363 A).

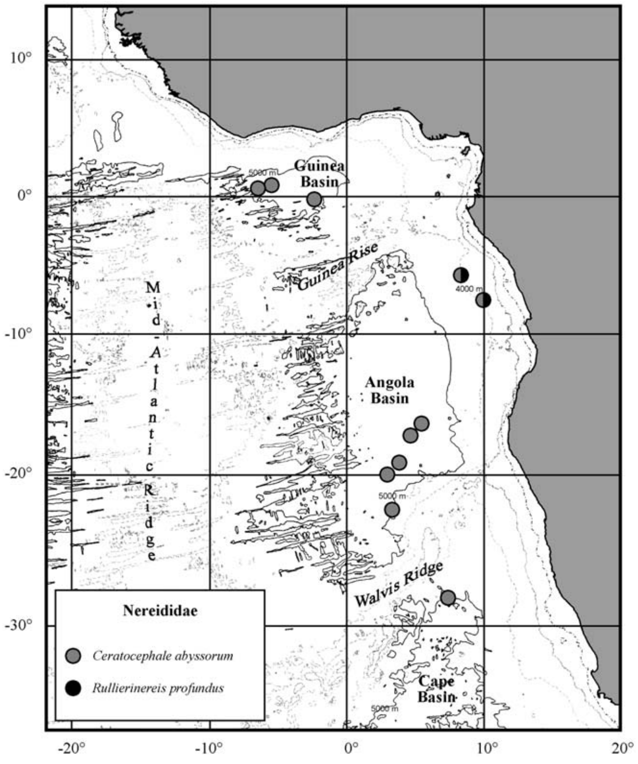

Fig. 82. Distribution of nereidid species in the studied region.

Prostomium wider than long, slightly incised anteriorly, with two antennae and two biarticulate palps (Figs. 80A, 81A–C). Antennae slender, digitiform, about as long as palps or slightly shorter; inserted medio-dorsally. Palps clearly broader than antennae, with short indistinct palpophores and tapering palpostyles; inserted latero-ventrally. Eyes absent. Nuchal organs inconspicuous.

Proboscis only everted in a few specimens; distally with amber-coloured jaws, each with up to nine teeth (Figs. 80A, 81A). Maxillary ring smooth but margin of oral ring with a few more or less obvious conical papillae arranged as follows: Area V = 0–2, Area VI = 0, Area VII–VIII = 0–6 (Fig. 80B). Paragnaths absent.

First segment achaetous, slightly longer than following segments; with four pairs of smooth and filiform cirri; extending to chaetigers 1–2 (Figs. 80A, 81A–C). Upper cirri subequal in length, about one third to one quarter longer than corresponding lower cirri; first pairs inserted laterally and second pairs more dorsally shifted. In juveniles these two double pairs of cirri have a greater distance to each other (Fig. 81C), whereas in larger specimens the originally two segments are more fused and a collar-like structure developed around the prostomium (Fig. 81B).

First two pairs of parapodia uniramous without notopodia, following parapodia biramous (Figs. 80A, D–I; 81D, E). Anterior notopodia with one slender digitiform prechaetal ligule and a much shorter, conical and pointed notoacicular papilla (Figs. 80E, 81E); in following parapodia prechaetal ligules becoming shorter and ventrally shifted (Fig. 80F–H); in posterior parapodia very short and more conical (Fig. 80I); in last parapodia absent. Conical to triangular neuroacicular papillae slightly broader than notoacicular papillae (Fig. 80D–I); usually with one conical subpodal ligule and in anterior parapodia (1–32) with one conical prechaetal ligule; both becoming shorter in posterior parapodia; in last parapodia even subpodal ligule absent. In juveniles subpodal and prechaetal ligules only present on a few anterior parapodia. Filiform dorsal cirri from 1st chaetiger (Fig. 80A); in anterior parapodia only slightly longer than noto- and neuropodial lobes (Fig. 80D, E), elongated on middle and early posterior parapodia (Fig. 80F–I); inserted on middle of parapodia; in mid-body region sometimes indistinctly separated into a large cirrophore and a digitiform style. Conical to digitiform ventral cirri double (triple, on a few parapodia of one specimen) from chaetiger one to about 34 (Fig. 80B); ventral ligule always distinctly shorter and sometimes minute in first chaetigers; both cirri much shorter than neuroacicular papilla (Fig. 80D–I); inserted near parapodial base.

Each noto- and neuropodium with one yellow to brownish acicula (Fig. 80D–I); 1–20 notopodial and 4–40 neuropodial chaetae. Chaetae predominantly compound homogomph spinigers (Fig. 81F); with blades of different length, decreasing superiorly and especially inferiorly; subdistally blades with fine hairs over entire length of margin; shafts internally camerated, with smooth tips but sometimes with a coarse tooth and subsequently a sesquigomph appearance (Fig. 81G). Notopodial chaetae in posterior part of body occasionally distinctly broader than neuropodial chaetae.

Pygidium with anus and terminal pair of slender cirri (Fig. 80C).

Distribution

Angola, Cape and Guinea Basins; 3945–5497 m (Fig. 82).

Discussion

The two previously described type specimens of *Pisionura abyssorum* Hartman & Fauchald, collected in the NW Atlantic (R/V ATLANTIS st. A 120, 34°43′N 66°32.8′W to 34°40.5′N 66°35′W, 5018–5023 m), are typical juveniles (0.9 and 2 mm long with 10 and 18 chaetigers, respectively) in which the first two segments are incompletely fused (as in Fig. 81C) and the prechaetal neuropodial ligules are not yet developed. However, in contrast to the original description, neuropodial subpodal ligules, jaws with four teeth and double ventral cirri were already reported for the type material examined by Hartmann-Schröder (1977a). This and the herein-examined additional specimens support that the species has to be placed in the genus *Ceratocephale*, rather than in the otherwise monotypic *Micronereides* Day, 1963(b) as recommended by Hylleberg and Nateewathana (1988). Quite to the opposite, examination of the only existing specimen of *Micronereides capensis* Day, 1963(b), from the Agulhas Bank (BMNH 1963.1.60), suggests that this species might have to be referred to the genus *Ceratocephale*. Banse (1977) regarded the holotype as a mature animal, and *Micronereides* as the most primitive genus within his Gymnonereidinae. However, the specimen's lack of prechaetal neuropodial ligules and large cirrophores are rather juvenile characters. Consequently, the relation of *Micronereides capensis* to *Ceratocephale* species, and the potential synonymy of the two genus names, cannot be evaluated until an indubitable adult specimen of *M. capensis* becomes available.

***Rullierinereis* Pettibone, 1971**

Rullierinereis Pettibone, 1971—Pettibone (1971, p. 31)

Profundilycastis Hartmann-Schröder, 1977 [syn. nov.]—Hartmann-Schröder (1977a, p. 149)

***Rullierinereis profundus* (Hartman, 1965) comb. nov.** (Figs. 82–85)

Namalycastis profundus Hartman, 1965—Hartman (1965, p. 84; pl. 11, figs. a, b); Hartman and Fauchald (1971, p. 58)

?*Nicon abyssalis* Hartman, 1967—Hartman (1967, p. 66; pl. 17, figs. A–D)

Profundilycastis profundus (Hartman)—Hartmann-Schröder (1977a, p. 149; 1977b, p. 45, figs. 1–6)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two biarticulate palps; eyes absent; four pairs of cirri on first segment; parapodia of first two chaetigers subbiramous, the following biramous; long and slender parapodial ligules; a few anterior notopodia with dorsal ligules; branchiae absent; all dorsal and ventral cirri simple; notopodial chaetae anteriorly homogomph spinigers, falcigerous thereafter, neuropodial chaetae heterogomph falcigers and homogomph spinigers; soft proboscidial papillae or paragnaths absent; jaws with up to eight teeth.

Description

Body up to 6 mm long with up to 35 chaetigers; widest in pharyngeal region (up to chaetiger 2–3), much narrower in following segments (Fig. 84A, B). Larger specimens with more or less distinct dorsal ridges.

Prostomium as long as wide or slightly longer, with two antennae and two biarticulate palps (Figs. 83A, B; 84A, B). Antennae slender, digitiform, about as long as palps or slightly longer; inserted medio-dorsally. Palps broader than antennae, with massive palpophores and conical to globular palpostyles; inserted latero-ventrally. Eyes usually absent, but one smaller specimen with three remaining red eye-like spots (Fig. 84C). Nuchal organs inconspicuous.

Proboscis retracted in all specimens; distally with amber-coloured jaws, each with up to eight teeth. Paragnaths and soft papillae absent.

First segment achaetous, slightly longer than following segments; with four pairs of smooth and digitiform to filiform cirri; extending to chaetigers 1–2 (Figs. 83A, B; 84A, B). Upper cirri of first pair about one third longer than corresponding lower cirri; upper cirri of second pair distinctly longer than first ones and about twice as long as corresponding lower cirri; first pairs inserted laterally and second pairs more dorsally shifted. In juveniles only two or three pairs of cirri present (Fig. 84A, B), whereas in larger specimens the second lower cirri and a collar-like structure around the prostomium developed (Fig. 83A, B).

First two pairs of parapodia usually subbiramous with notopodial lobes and aciculae but without chaetae, following parapodia biramous (Fig. 83A, D–H). Notopodia from 1st chaetiger, anteriorly with one digitiform prechaetal ligule and a much shorter, rounded to pointed notoacicular papilla (Fig. 83A, D); following parapodia of chaetiger 5–8 only in larger specimens with one slightly shorter dorsal ligule (Fig. 83E); in posterior parapodia prechaetal ligules becoming shorter and more conical (Fig. 83F–H); in last parapodia sometimes absent. Conical neuroacicular papillae slightly broader than notoacicular papillae; anteriorly with one longer digitiform subpodal ligule, becoming slender and more short, conical in posterior parapodia (Fig. 83D–H). Digitiform dorsal cirri from 1st chaetiger (Fig. 83A); in anterior parapodia slightly shorter than notopodial prechaetal ligules (Fig. 83D–F), elongated on posterior parapodia (Fig. 83H); inserted on middle of parapodia. Conical to digitiform ventral cirri from 1st chaetiger (Fig. 83B); in anterior parapodia distinctly shorter than neuroacicular papilla (Fig. 83D, E); elongated on posterior parapodia (Fig. 83F–H); inserted near parapodial base.

Anterior two notopodia with one yellow acicula, other noto- and all neuropodia with one brownish acicula (Fig. 83D–H); 1–3 (usually two) notopodial and 2–10 neuropodial chaetae. Notopodial chaetae usually from 3rd chaetiger, but in some juveniles occasionally from first chaetiger; anteriorly usually two in a few cases three compound homogomph spinigers (Fig. 83I); subdistally blades with fine hairs over entire length of margin; shafts internally camerated, with fine serrated tips; after first

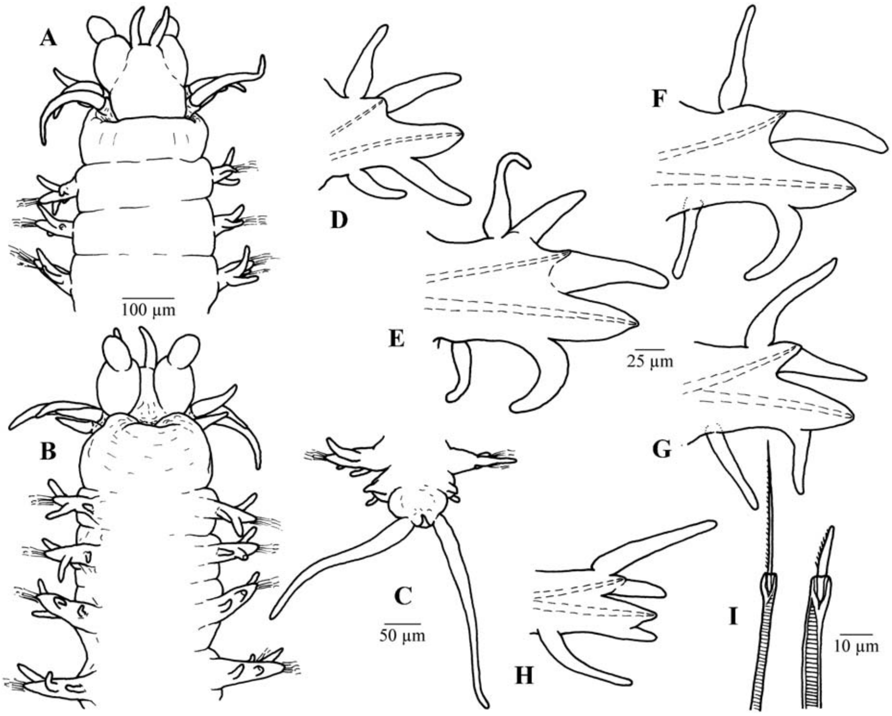

Fig. 83. *Rullierinereis profundus* (Hartman) comb. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D–H) Anterior to posterior parapodia; posterior views, chaetae omitted: D–H = 2nd, 6th, 12th, 23th, 34th parapodium. (I) Notopodial homogomph spiniger and falciger. (A, B: ZMH P25373 C; C: ZMH P25366; D–I: ZMH P25372 A).

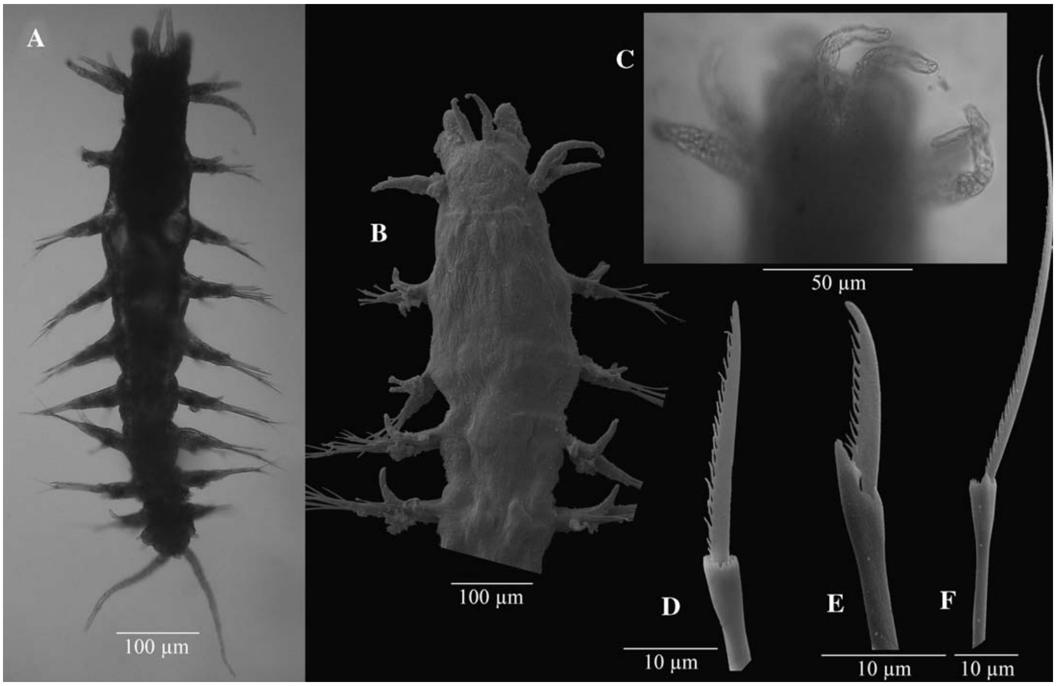

Fig. 84. *Rullierinereis profundus* (Hartman) comb. nov. (A) Light micrograph of complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of anterior end with eye-like spots. (D) Notopodial homogomph falciger. (E) Neuropodial heterogomph falciger. (F) Neuropodial homogomph spiniger. (A: ZMH P25366; B, D–F: ZMH P25371 A; C: ZMH P25372 B).

10–12 chaetigers notopodial chaetae slightly broader and with shorter falcigerous blades (Figs. 83I, 84D); posterior parapodia only with one homogomph falciger; in last parapodia absent. Upper fascicle of neuropodial chaetae with 0–2 heterogomph falcigers (Fig. 84E) and 1–5 homogomph spinigers (Fig. 84F) and lower fascicle with 1–6 heterogomph falcigers; subdistally all blades with fine hairs over entire length of margin; shafts internally camerated, smooth in hetergomph falcigers and with fine serrated tips in homogomph spinigers; blades of latter and of heterogomph falcigers from lower fascicles in anterior part of body with varying length.

Pygidium with anus and terminal pair of slender cirri (Fig. 83C).

Distribution

Angola Basin; 3945–3993 m (Fig. 82).

Discussion

The type material of *Namalycastis profundus*, from the NW Atlantic (off Bermuda, 32°21′18″N 64°33′W, 1000 m), was re-examined by Hartmann-Schröder (1977b), and the species transferred to *Profundilycastis* Hartmann-Schröder, 1977(a). According to Hartmann-Schröder (1977b), the latter genus is closely related to *Rullierinereis* but can be distinguished by: absence of notopodial dorsal ligules, absence of eyes, by the parapodia of the first two chaetigers being uniramous, and parapodial ligules long and slender. However, the anterior two uniramous chaetigers and especially the absence of the notopodial dorsal ligules are explainable by the small body size of *Namalycastis profundus* (3 mm long, 0.28 mm wide), and are also recognizable in the juveniles examined in the present study (see above). Furthermore, the absence of eyes and the long and slender parapodial ligules possibly are deep-water adaptations (Fauchald 1972). Consequently, *Profundilycastis* is synonymised with *Rullierinereis* here.

The original description of *Nicon abyssalis* Hartman, 1967 from the South Shetland Islands (1437 m depth) and the Antarctic Peninsula (4310–4328 m) shows great similarities with the examined material and might represent larger (25 mm long, 3.1 mm wide) and more developed specimens of *Rullierinereis profundus*. For example, Hartman (1967) mentioned the reduced notopodial dorsal ligules and the elongated prechaetal ligules in posterior parapodia. On the other hand, the notopodial homogomph falcigers, which are typical for species in the genus *Rullierinereis*, were not described by Hartman (1967), and it would be speculation to assume that she had overlooked them. Pettibone (1971) considered the generic affinities of *Nicon abyssalis* as doubtful. In light of these uncertainties, *N. abyssalis* is not treated as a synonym of *R. profundus* here.

Abundance of Nereididae

A total of 243 specimens or fragments were found. Most of them (229) belong to *Ceratocephale abyssorum*. This species was present in all investigated basins (Fig. 85), with the highest abundance in BIOZAIRE areas 1 and 2, while all 14 specimens or fragments of *Rullierinereis profundus* came from the BIOZAIRE material. The most effective type of gear for collecting nereidids was the box corer, whereas a much lower number of specimens were collected with the multicorer or the epibenthic sledge (Fig. 85). However, the latter samples have the advantage of being generally rapidly fixed in ethanol; therefore, the material was more or less useful for molecular analyses.

Molecular data

The phylogenetic position of Nereididae varied with the gene region analyzed. The group resulted as sister to Goniadidae (18S), closely related to Nephtyidae (16S), or as sister to Pilargidae (COI). However, the only result in this context that received strong support was the monophyly of Nereididae in the 18S rDNA analysis (see “Molecular phylogeny of abyssal Phyllodocida”). A nereidid-pilargid clade was also mentioned by Rousset et al. (2007).

The rather large differences between specimens of *Ceratocephale abyssorum* from the Cape Basin and the Guinea Basin in the two examined non-coding ITS2 sequences (Table 12) suggest restricted gene flow. The existence of a complex of cryptic or sibling species might be assumed, but much more well-preserved material is needed to test this hypothesis.

Phyllodocidae Örsted, 1843

The benthic Phyllodocidae are a very common group of often brightly coloured polychaetes that typifies Phyllodocida by definition, but might be paraphyletic if some taxa like the pelagic Alciopidae are not included (Pleijel 2001k). The two groups are closely related; possibly the alciopids, with their enlarged eyes, are derived from a subgroup of the phyllodocids (Dales 1955; Pleijel 1991). The phylogenetic relationships within the Phyllodocidae are also still problematical (e.g. Pleijel 1991; Eibye-Jacobsen 1993; Orrhage and Eibye-Jacobsen 1998), but an autapomorphy of the group might be the foliose dorsal cirri on reduced notopodia (Fauchald and Rouse 1997). Additionally, they have an eversible and usually papillated, large muscular axial proboscis, which is used to catch prey (Wilson 2000g).

The Phyllodocidae are found in all kinds of substrata, especially in crevices or under stones, and are most common in shallow-water habitats, but some taxa are also

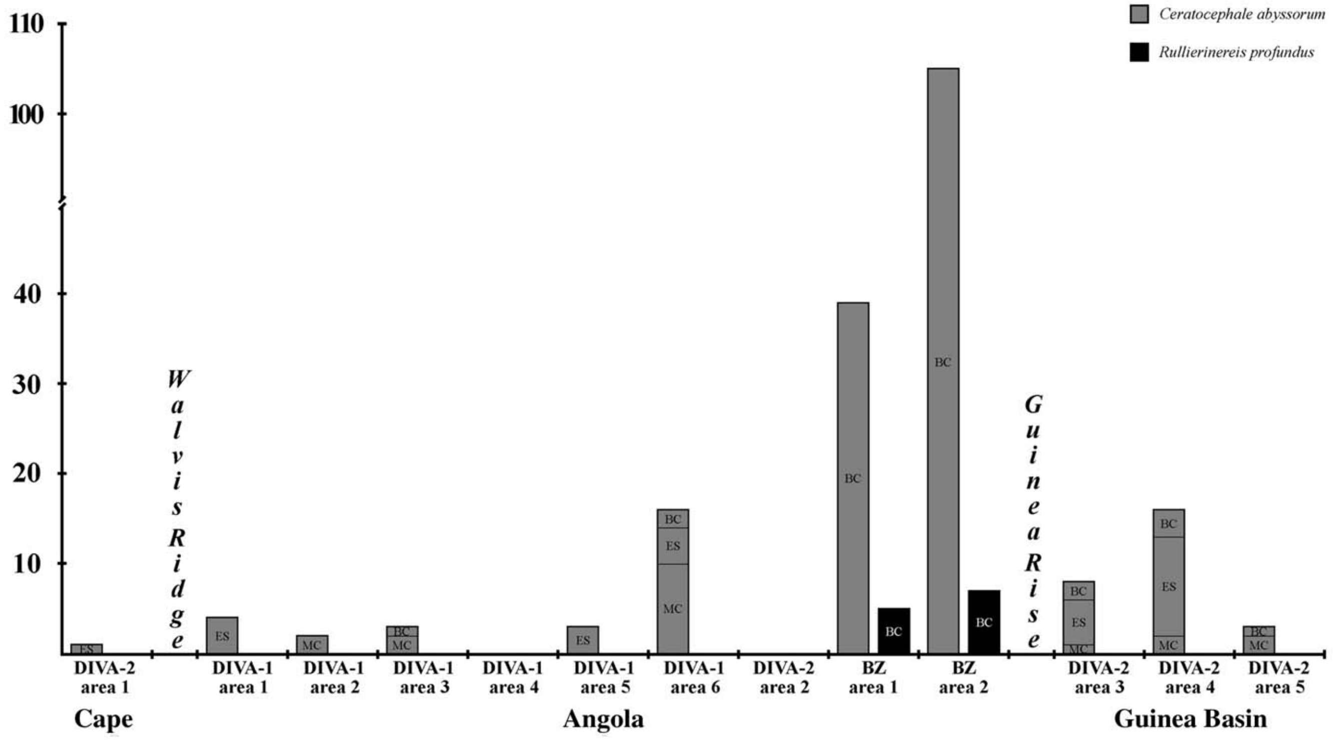

Fig. 85. Abundance of the two nereidid species in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

Table 12. List of specimens and corresponding sequences in Nereididae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank acession numbers				
			18S rDNA	16S rDNA	COI (3-6W)	ITS1	ITS2
NEREIDIDAE							
Ceratocephale abyssorum (Hartman & Fauchald)	Cape Basin D-2 st. 41 ES-E	ZMH P25352	–	–	–	–	GQ426737
	Walvis Ridge and Guinea Rise						
	Guinea Basin D-2 st. 89 ES-E	ZMH P25363 B	GQ426585	GQ426618	GQ426683	GQ426699	GQ426699

present in deep-water soft sediments (Blake 1997a). They are usually considered to be active predators or scavengers feeding either highly or non-selectively on various kinds of small invertebrates, e.g. on other polychaetes, with cannibalism is not uncommon (Fauchald and Jumars 1979). Their colouration is probably protective; pigment patterns are often useful to separate taxa, but unfortunately the pigments fade rapidly in preservatives (Blake 1997a). The latter might be the case in the soft-bottom species examined here, although they could also be more uniformly coloured by nature.

Most of the twelve species of Phyllodocidae collected in the present study had been reported earlier from deep waters in the N Atlantic (*Eulalia* cf. *anoculata* Hartman & Fauchald, 1971; *Mystides caeca* Langerhans, 1880; *Paranaitis abyssalis* (Hartmann-Schröder, 1975); *Pseudomystides bathysiphonicola* (Hartmann-Schröder, 1983) comb. nov.), or from the Pacific Ocean (*Eteone* cf. *vitiazi* Uschakov, 1972; *Eumida nuchala* (Uschakov, 1972); *Pseudomystides rarica* (Uschakov, 1958) comb. nov.). However, *Eulalia meteorensis* sp. nov., *Eumida angolensis* sp. nov., *Pseudomystides brevicirra* sp. nov. and *Pterocirrus remus* sp. nov. all are new to science, whereas the material recorded as *Phyllodoce* sp. below is lacking most appendages and therefore indeterminable.

Key to phyllodocid species from the abyssal SE Atlantic

1. One or two anterior segments with two (2 + 0) or three (1 + 2) pairs of specialized, usually elongated cirri (Figs. 86A; 95A; 99A, B; 100A, B; 102A; 103A) 2

– Three anterior segments with four (1 + 2 + 1) pairs of cirri (Figs. 88A; 89A, B; 90A, B; 91A, B; 92A; 96A; 98A; 104A, B) 6

2. Three pairs of cirri, one pair on first segment and two on second one (1 + 2); third segment without dorsal cirri (Figs. 95A; 99A, B; 100A, B; 102A; 103A) 3

– Two pairs of cirri on first segment (2 + 0), second segment without dorsal cirri (Fig. 86A) .... *Eteone* cf. *vitiazi* Uschakov

3. Antennae and palps conical to digitiform, distinctly shorter than prostomium; digitiform, conical or oval cirri on anterior two segments (Figs. 99A, B; 100A, B; 102A; 103A) 4

– Antennae and palps thin and filiform, about as long as prostomium; long, bottle-shaped cirri on anterior two segments (Fig. 95A, B, D) .... *Mystides caeca* Langerhans

4. Cirri of first segment digitiform; ventral cirri of second segment distinctly larger than following ones (Figs. 99A, B; 100A, B; 103A, C) 5

– Cirri of first segment very short and conical; ventral cirri of second segment about as large as following ones (Fig. 102A) .... *Pseudomystides brevicirra* sp. nov.

5. Prostomium without median antenna (Figs. 99A; 100A, B); ventral cirri of second segment oval (Fig. 99A, B) .... *Pseudomystides bathysiphonicola* (Hartmann-Schröder)

– Prostomium with minute median antenna (Fig. 103A) near posterior margin (can be difficult to detect); ventral cirri of second segment conical (Fig. 103A, C) .... *Pseudomystides rarica* (Uschakov)

6. First segment well developed and distinguishable from second segment (Figs. 88A; 89A) 7

– First segment partly or completely reduced or fused dorsally with second segment (Figs. 90A, B; 91A, B; 92A; 96A; 98A; 104A) 8

7. Third segment dorsally with pair of digitiform cirri, which are distinctly longer than the following, oval dorsal cirri; prostomium without eyes (Fig. 88A) .... *Eulalia* cf. *anoculata* Hartman & Fauchald
– Third segment dorsally with pair of more conical cirri, which are only slightly longer than the following, blunt conical dorsal cirri; prostomium with eye-like spots near posterior margin (Fig. 89A) .... *Eulalia meteorensis* sp. nov.
8. Prostomium with two palps, two frontal antennae and a distinct third median antenna (Figs. 90A; 91A, B; 92A; 104A) 9
– Prostomium with two palps and two antennae only, but small nuchal papilla can be present (Figs. 96A; 98A) 11
9. Ventral cirri of second segment cylindrical or slightly bottle-shaped (Figs. 90B; 92A) 10
– Ventral cirri of second segment extremely enlarged, flattened and paddle-like (Fig. 104A, B) .... *Pterocirrus remus* sp. nov.
10. Anterior three segments with slightly bottle-shaped cirri; nuchal organs inconspicuous (Figs. 90A, B; 91A, B) .... *Eumida angolensis* sp. nov.
– Anterior three segments with cylindrical cirri; nuchal organs enlarged (Fig. 92A) .... *Eumida nuchala* (Uschakov)
11. Anterior two segments dorsally fused, forming a collar partly covering prostomium (Fig. 96A); dorsal and ventral cirri shorter than parapodial lobes (Figs. 96B; 97A) .... *Paranaitis abyssalis* (Hartmann-Schröder)
– First segment reduced, partly covered by prostomium (Fig. 98A); dorsal and ventral cirri longer than parapodial lobes (Fig. 98C) .... *Phyllodoce* sp.

Eteone Savigny, 1822

Eteone cf. *vitiazi* Uschakov, 1972

(Figs. 86, 87, 106)

Eteone vitiazi Uschakov, 1972—Uschakov (1972, p. 178; pl. 18, figs. 8–10)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps, antennae slightly shorter and thinner than palps; eyes absent; nuchal papilla not observed; two pairs of cirri on first segment (2 + 0), upper pair shorter and thinner than lower one; second segment without dorsal cirri; dorsal cirri oval to conical, longer than wide; ventral cirri oval to conical; chaetae present from segment two.

Description

If fragments really include one complete specimen then body up to 3.4 mm long with up to 23 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 86A). Segments uniannulate. Preserved specimens whitish to yellowish.

Prostomium conical, slightly longer than wide, with two antennae and two palps (Fig. 86A, B). Frontal antennae and palps all conical to digitiform, but antennae slightly shorter and thinner than palps; inserted latero-dorsally and latero-ventrally; median antenna absent. Eyes absent. Nuchal papilla not observed.

Proboscis retracted, not observed.

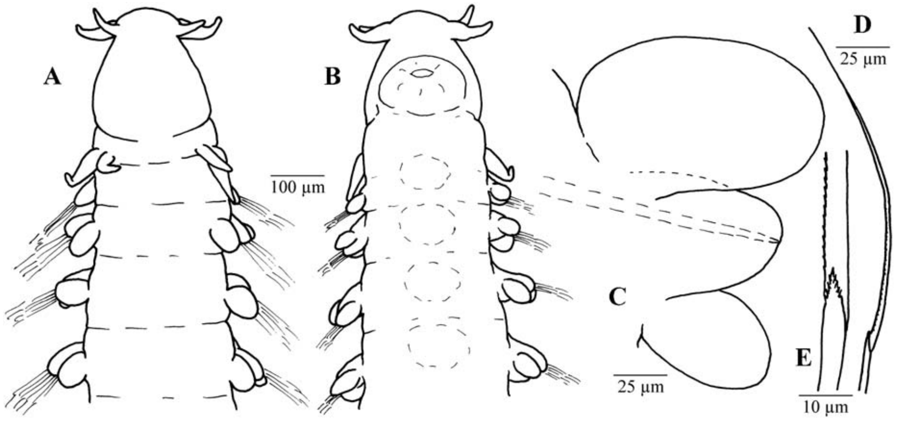

Fig. 86. *Eteone* cf. *vitiazi* Uschakov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Parapodium of mid-body; posterior view, chaetae omitted. (D) Chaeta. (E) Detail of chaeta. (A–E: ZMH P25374).

Anterior segments all well developed and separate (Fig. 86A, B), with two pairs of cirri (2 + 0). First segment achaetous, with two pairs of short, conical to digitiform cirri; upper pair shorter and thinner than lower one; reaching about segments 2–3; inserted dorsolaterally. Second segment without dorsal cirri, but with distinct chaetigerous lobes and ventrally with normal pair of cirri (= 1/1 + Ch0/N). Following parapodia all uniramous, with conical chaetigerous lobes and dorsal and ventral cirri (Fig. 86C). Dorsal cirri oval to conical, longer than wide; slightly longer than parapodial lobes; inserted slightly above parapodial base (Fig. 86C). Ventral cirri similar but much smaller than dorsal cirri; about as long as parapodial lobes; inserted near parapodial base (Fig. 86C).

All parapodia with one straight acicula (Fig. 86C) and up to about ten spinigerous compound chaetae (Fig. 86D). Spinigers with blades of different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 86D); shafts with one large apical tooth and some smaller ones subdistally (Fig. 86D).

Pygidium with dorsal anus and a pair of terminolateral cirri, which are broken off; median papilla not observed.

Distribution

Guinea Basin; 5137–5141 m (Fig. 87).

Discussion

The examined specimen is poorly preserved; many appendages are missing. Nevertheless, it shows great similarities with *Eteone vitiazi* Uschakov, 1972, originally described from the abyssal N Pacific.

Eulalia Savigny, 1822

Eulalia cf. *anoculata* Hartman & Fauchald, 1971 sensu Amoureux (1982)

(Figs. 87, 88, 106)

?*Eulalia* spp. [partim]—Hartman (1965, p. 60)

Eulalia anoculata Hartman & Fauchald, 1971—Hartman and Fauchald (1971, p. 41; pl. 6, figs. a–d); Amoureux (1982, p. 37, fig. 5)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps digitiform, much smaller median antenna near posterior margin; prostomium with terminal protuberance but without eyes; nuchal organs inconspicuous; four pairs of cirri on anterior three segments (1 + 2 + 1), segments well developed and separate; dorsal cirri of third segment digitiform, distinctly longer than following, oval dorsal cirri; ventral cirri more conical; chaetae present from segment two.

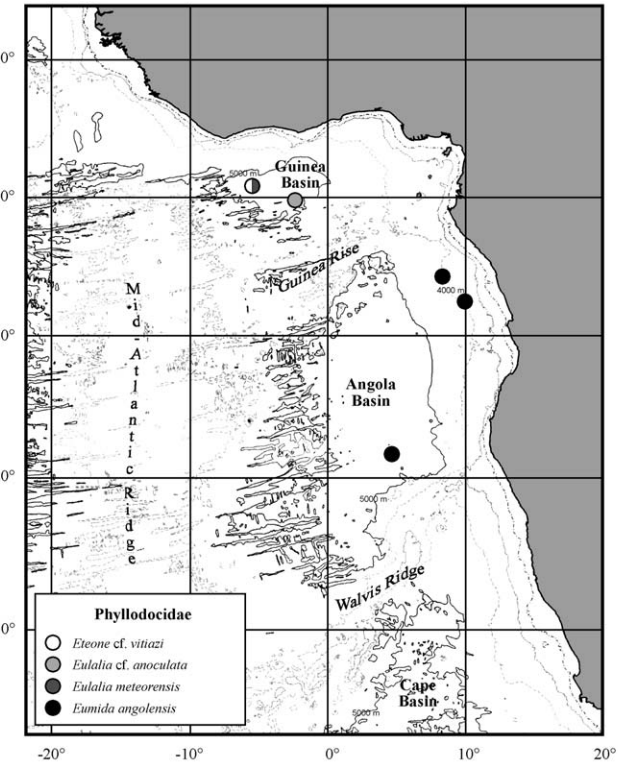

Fig. 87. Distribution of some phyllodocid species in the studied region.

Description

If fragments really include one complete specimen then body up to 12.5 mm long with up to 62 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 88A). Anterior segments uniannulate, following ones indistinctly biannulate with small anterior part and large posterior, parapodial part. Preserved specimen yellowish, sometimes with small brown pigmented spots on dorsum, venter and especially on bases of dorsal and ventral cirri.

Prostomium pentagonal, wider than long, with indistinct protuberance at insertion of two antennae and two palps (Fig. 88A). Frontal antennae and palps all digitiform and of about same length; slightly shorter than prostomial width; inserted latero-dorsally and latero-ventrally; median antenna conical to digitiform, much smaller and shorter than frontal ones; inserted near posterior margin of prostomium (Fig. 88A). Eyes absent. Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment.

Proboscis retracted, not observed.

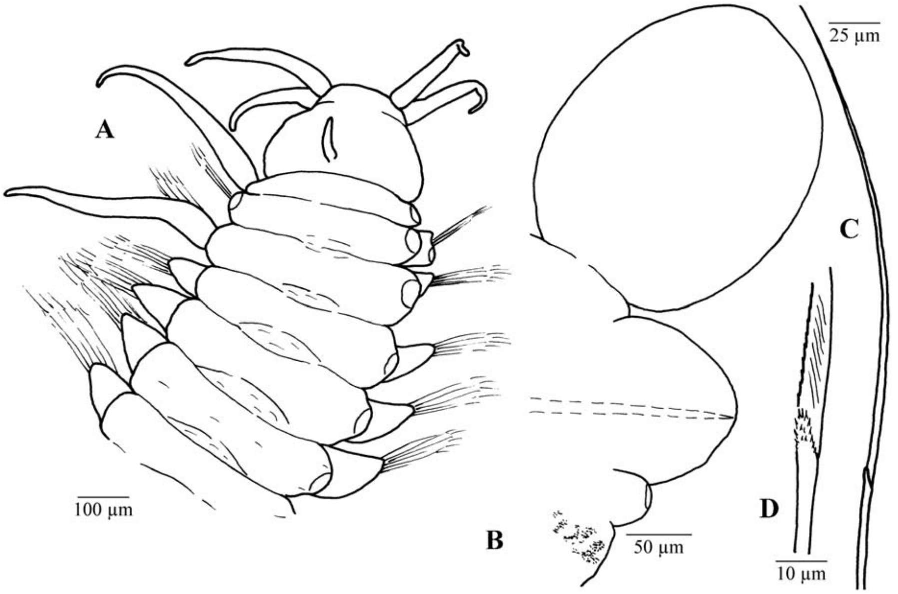

Fig. 88. *Eulalia* cf. *anoculata* Hartman & Fauchald. (A) Anterior end; dorsal view. (B) Parapodium of mid-body; anterior view, chaetae omitted. (C) Chaeta. (D) Detail of chaeta. (A–D: ZMH P25375).

Anterior segments all well developed and separate (Fig. 88A), with four pairs of cirri (1+2+1). First segment achaetous, with one pair of slender, cylindrical cirri; reaching about segments 5–6; inserted laterally. Second segment dorsally and ventrally only with short cirrophores, cirrostyles missing, and inconspicuous chaetigerous lobes, which are fused to ventral cirrophores. Third segment dorsally with pair of cirri, similar but slightly longer than those of first segment, distinct chaetigerous lobes and normal ventral cirri (= 1+ Ch1/1+Ch1/N). Following parapodia all uniramous, with broadly conical chaetigerous lobes and mainly missing dorsal and ventral cirri (Fig. 88B). Dorsal cirri with short cirrophores and oval cirrostyles, slightly longer than wide; much longer than parapodial lobes; inserted slightly above parapodial base (Fig. 88B). Only one ventral cirrus still present, from posterior part of body, much thinner and more conical than dorsal cirri; about as long as parapodial lobe; inserted near parapodial base.

All parapodia with one straight acicula (Fig. 88B), and up to about 15 spinigerous compound chaetae (Fig. 88C). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 88D); shafts with one large apical tooth on either side and numerous smaller ones, decreasing in size proximally (Fig. 88D).

Pygidium with dorsal anus and a pair of terminolateral cirri, which are broken off; median papilla not observed, but present on second posterior fragment which is questionably referred to this taxon.

Distribution

Guinea Basin; 5048–5051 m (Fig. 87).

Discussion

The examined specimen resembles *Eulalia anoculata* Hartman & Fauchald, 1971 (not *Eulalia anoculata* Fauchald, 1972, which has been replaced by *Eulalia lapsus* Pleijel, 1991). That abyssal species from the NW Atlantic was originally described without a median antenna, but following Hartman and Fauchald (1971) some of the earlier records of *Eulalia* sp., which had been described with the third antenna (Hartman 1965), were referred to *E. anoculata*. This was one reason for Amoureux (1982) to refer his very similar NE Atlantic specimens, some of which retain a small median antenna on the posterior margin of the prostomium, to *E. anoculata*, too. Furthermore, he suggested that *Pseudeulalia exigua* Eliason, 1962 from the Skagerrak might be transferred to the genus *Eulalia*. In contrast, Pleijel (1991) mentioned a questionable synonymy between *Pseudeulalia* and *Protomystides* Czerniavsky, 1882.

Eulalia meteorensis sp. nov.

(Figs. 87, 89, 106)

Etymology

The species epithet refers to the research vessel METEOR. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

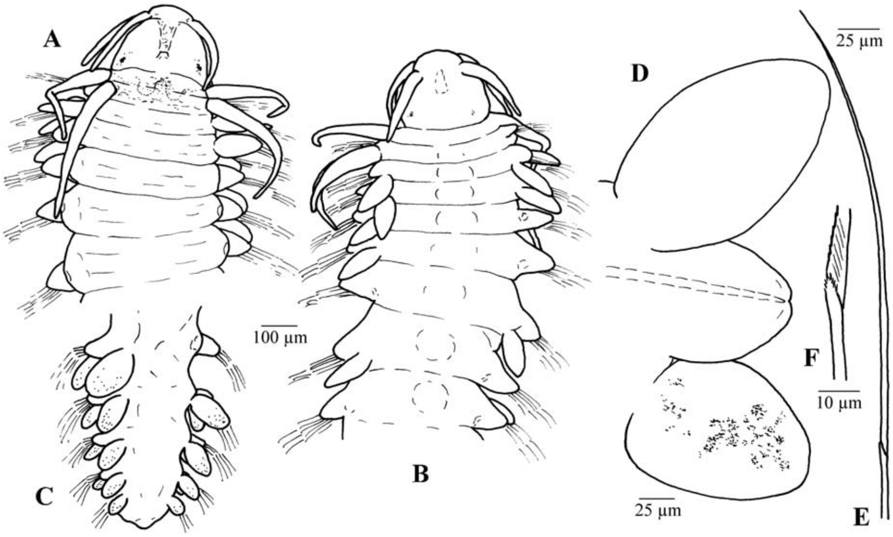

Fig. 89. *Eulalia meteorensis* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D) Parapodium of mid-body; posterior view, chaetae omitted. (E) Chaeta. (F) Detail of chaeta. (A–F: ZMH P25376).

Material examined

Type material. R/V METEOR 63/2 st. 89 ES-S, 0°43′N 5°31.3′W–0°43′N 5°31.2′W, 20.iii.2005, 5137–5141 m; holotype: af/2.4/15/0.7/0.3, 1 pf with 23 chaetigers (ZMH P25376).

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps digitiform, median antenna near posterior margin; prostomium with terminal protuberance and eye-like spots near posterior margin; nuchal organs inconspicuous; four pairs of cirri on three anterior segments (1 + 2 + 1), segments well developed and separate; dorsal cirri of third segment conical to digitiform, only slightly longer than following, oval to blunt conical dorsal cirri; ventral cirri oval to blunt conical; chaetae present from segment two.

Description

Body up to 6.4 mm long with up to 38 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 89A–C). Segments uniannulate. Preserved specimen yellowish, sometimes with small brown pigmented spots on dorsum, venter and especially on bases of ventral cirri.

Prostomium pentagonal, wider than long, with indistinct protuberance at insertion of two antennae and two palps (Fig. 89A, B). Frontal antennae and palps all digitiform and of about same length, but antennae slightly thinner than palps; slightly shorter than prostomial width; inserted latero-dorsally and latero-ventrally; median antenna broken off; inserted near posterior margin of prostomium (Fig. 89A). One pair of eye-like spots near posterior margin of prostomium (Fig. 89A). Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment.

Proboscis retracted, not observed.

Anterior segments all well developed and separate (Fig. 89A, B), with four pairs of cirri (1 + 2 + 1). First segment achaetous, with one pair of slender, cylindrical cirri; reaching about segments 5–6; inserted laterally. Second segment dorsally with similar but distinctly longer pair of cirri, reaching about segments 6–7, distinct chaetigerous lobes and ventrally with similiar but slightly shorter and broader pair of cirri, reaching about segments 5–6. Third segment dorsally with much shorter, more conical to digitiform cirri, reaching about segment five, chaetigerous lobes and normal ventral cirri (= 1 + Ch1/1 + Ch1/N). Following parapodia all uniramous, with conical chaetigerous lobes with inconspicuous terminal notch and often missing dorsal and ventral cirri (Fig. 89D). Dorsal cirri with short cirrophores and oval to blunt conical cirrostyles, distinctly longer than wide; much longer than parapodial lobes; inserted slightly above parapodial base (Fig. 89D). Ventral cirri similar but much smaller; slightly longer than parapodial lobe; inserted near parapodial base.

All parapodia with one straight acicula (Fig. 89B), and up to about 10–12 spinigerous compound chaetae (Fig. 89E). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 89E); shafts with one large apical tooth on either side and numerous smaller ones, decreasing in size proximally (Fig. 89E).

Pygidium with dorsal anus and a pair of termino-lateral cirri, which are broken off; median papilla not observed.

Distribution

Guinea Basin; 5137–5141 m (Fig. 87).

Discussion

Eulalia meteorensis sp. nov. can be distinguished clearly from all its congeners by the size of the dorsal cirri of segment three, which are significantly shorter than the cirri of segment two and only slightly longer than the following normal dorsal cirri. It resembles the deep-water species *Eulalia* cf. *anoculata* Hartman & Fauchald in some characters, but differs in having the dorsal pair of cirri on the third segment shorter and more conical than the long, digitiform ones of the latter species, the dorsal cirri blunt and conical instead of oval, and in carrying eye-like spots near the posterior margin of the prostomium.

Eumida Malmgren, 1865

Eumida angolensis sp. nov.

(Figs. 87, 90, 91, 107)

Etymology

The species epithet refers to the type locality in the Angola Basin. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V L'ATALANTE st. 54 BC, 7°39.9′S 10°0.4′E, 23.xii.2003, 3993 m; holotype: cs/2.0/22/0.7/0.4 (MNHN Type 1502); paratypes: cs/1.7/21/0.6/0.3 (MNHN Type 1503); cs/1.3/19/0.6/0.3 (MNHN Type 1504, on SEM stub).

Additional material. See Appendix 1.

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps conical to digitiform, digitiform median antenna near posterior margin; eyes absent; nuchal organs inconspicuous; four pairs of slightly bottle-shaped cirri on anterior three segments (1 + 2 + 1); first segment dorsally reduced; dorsal cirri conical to lanceolate; ventral cirri more digitiform; chaetae present from segment two.

Description

Body up to 4.6 mm long with up to 29 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 91A). Anterior segments uniannulate, following ones indistinctly biannulate with small anterior part and large posterior parapodial part (Fig. 91A). Preserved specimens whitish to yellowish, often with numerous small brown pigmented spots, denser on prostomium, anterior segments and cirri (Fig. 90A, B).

Prostomium oval, about as long as wide, with three antennae and two palps (Figs. 90A; 91A, B). Frontal antennae and palps all digitiform and of equal length, but antennae slightly thinner than palps; inserted latero-dorsally and latero-ventrally; median antenna also digitiform, but thinner than frontal ones; inserted near posterior margin of prostomium (Figs. 90A; 91A, B).

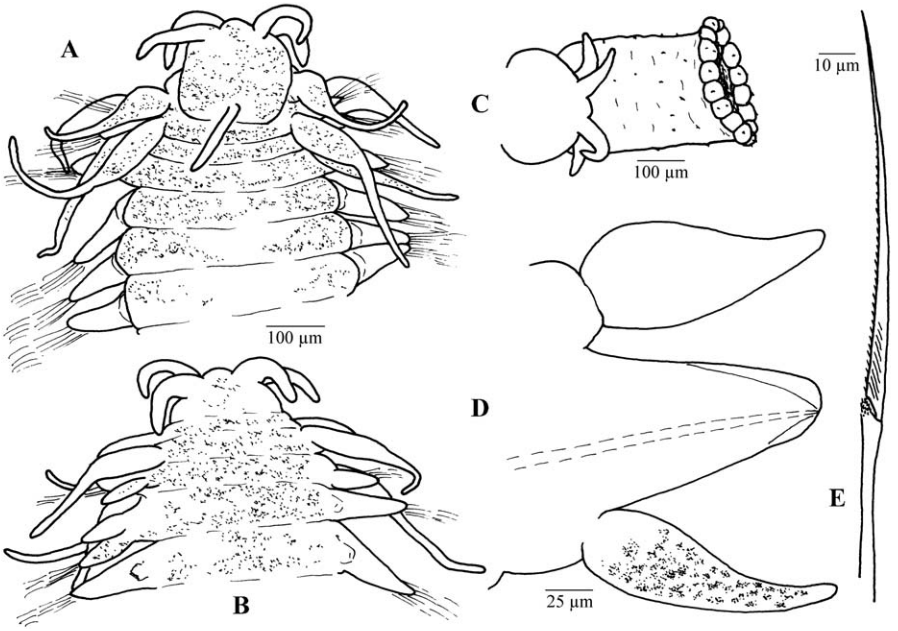

Fig. 90. *Eumida angolensis* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Anterior end with everted proboscis; dorsal view. (D) Parapodium of mid-body; anterior view, chaetae omitted. (E) Chaeta. (A, B, D, E: MNHN Type 1502; C: MNHN Type 1503).

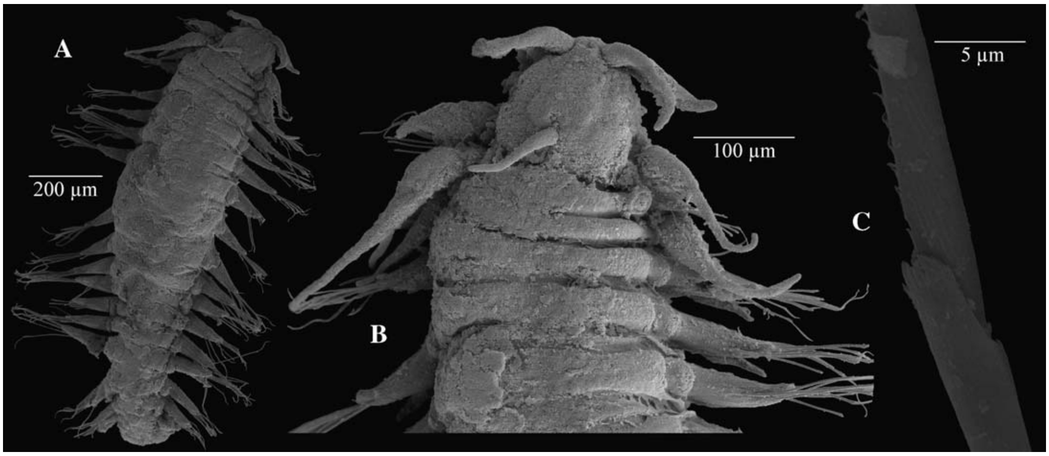

Fig. 91. *Eumida angolensis* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Detail of chaeta. (A–C: MNHN Type 1504).

Eyes absent. Nuchal organs inconspicuous, forming two ciliated lobes laterally between prostomium and first segment (Fig. 91B).

Terminal ring of proboscis with about 16 rounded larger papillae; these papillae and rest of proboscis with diffusely distributed micropapillae (Fig. 90C).

First segment dorsally reduced, second and third ones well developed and separate (Figs. 90A, B; 91A, B), with four pairs of slightly bottle-shaped cirri (1+2+1), which have short cirrophores and cirrostyles with enlarged bases and long drawn out tips. First segment achaetous, with one pair of cirri; reaching about segment five; inserted laterally. Second segment dorsally with similar but distinctly longer pair of cirri, reaching about segments 6–7, distinct chaetigerous lobes and ventrally with similiar but shorter pair of cirri, which are about as long as cirri from first segment or slightly longer, reaching about segments 5–6. Third segment dorsally with slightly shorter cirri, reaching about segments 6–7, chaetigerous lobes and normal ventral cirri (= 1+Ch1/1+Ch1/N). Following parapodia all uniramous, with conical lobes and often missing dorsal and ventral cirri (Fig. 90D). Dorsal cirri with short cirrophores and conical to lanceolate cirrostyles, about two times as long as wide; about as long as parapodial lobes; inserted slightly above parapodial base (Fig. 90D). Ventral cirri thinner and more digitiform; about as long as parapodial lobes; inserted near parapodial base (Fig. 90D).

All parapodia with one straight acicula (Fig. 90D), and up to about 10–12 spinigerous compound chaetae (Fig. 90E). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 91C); shafts with a few apical teeth (Fig. 91C).

Pygidium with dorsal anus and a pair of terminolateral cirri, which are all broken off, and a small medioventral papilla.

Distribution

Angola Basin; 3950–5443 m (Fig. 87).

Discussion

Eumida angolensis sp. nov. belongs to a group of abyssal species – *E. nuchala* (Uschakov, 1972); *E. longicirrata* (Hartmann-Schröder, 1975); *E. alvini* Eibye-Jacobsen, 1991 – which are characterised by the absence of eyes. However, all of these species have cylindrical rather than more bottle-shaped anterior cirri. Furthermore, the dorsal cirri in *E. alvini* and *E. longicirrata* are much longer than the parapodial lobes (Hartmann-Schröder 1975; Eibye-Jacobsen 1991), whereas in *E. nuchala* the nuchal organs are enlarged (Uschakov 1972).

Eumida nuchala (Uschakov, 1972)

(Figs. 92–94, 107)

Vitiaziphyllum nuchalum Uschakov, 1972—Uschakov (1972, p. 167; pl. 15, figs. 1–3)

Eumida nuchala (Uschakov)—Eibye-Jacobsen (1991, p. 114); Pleijel (1991, p. 256)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps conical to digitiform, digitiform median antenna near posterior margin; eyes absent; nuchal organs enlarged; four pairs of cylindrical cirri on anterior three segments (1+2+1); first segment dorsally reduced; dorsal cirri lanceolate; ventral cirri more digitiform; chaetae present from segment two.

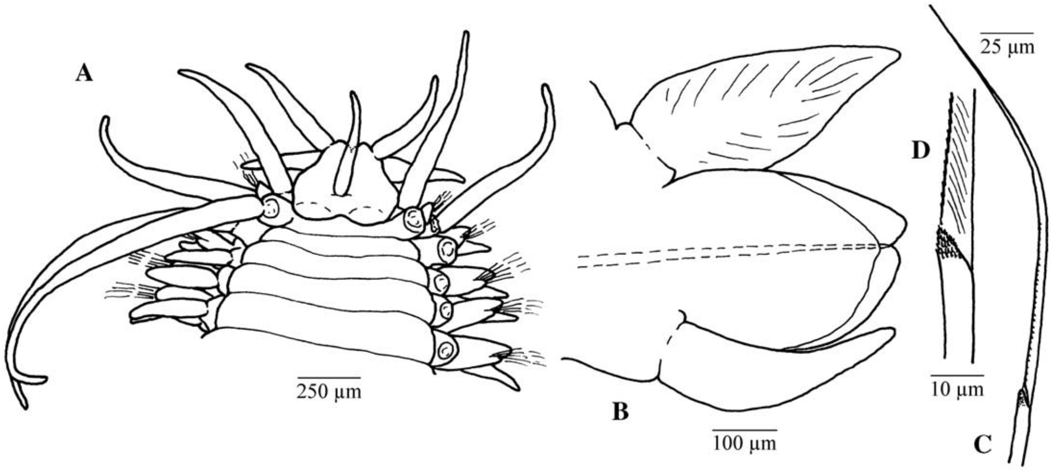

Fig. 92. *Eumida nuchala* (Uschakov). (A) Anterior end; dorsal view. (B) Parapodium of mid-body; posterior view, chaetae omitted. (C) Chaeta. (D) Detail of chaeta. (A–D: ZMH P25389 B).

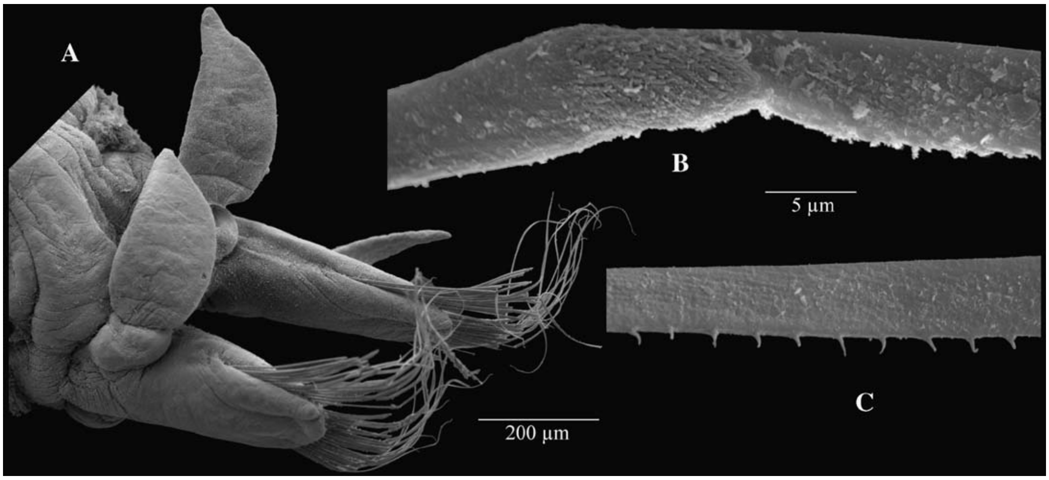

Fig. 93. *Eumida nuchala* (Uschakov). (A) Parapodia of mid-body; dorso-posterior view. (B) End of chaetal shaft and base of blade. (C) Chaetal blade. (A–C: ZMH P25389 A).

Description

If specimen ZMH P25389 is really complete then body up to 11.5 mm long with up to 46 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 92A). Anterior segments uniannulate, following ones indistinctly biannulate with small anterior part and large posterior parapodial part. Preserved specimens yellowish, sometimes with small brown pigmented spots on anterior part of prostomium, dorsum, dorsal and ventral cirri.

Prostomium pentagonal, wider than long, with a terminal notch and three antennae and two palps (Fig. 92A). Frontal antennae and palps all digitiform; about as long as prostomium, but antennae slightly longer and thinner than palps; inserted latero-dorsally and latero-ventrally; median antenna also digitiform, but thinner and slightly shorter than frontal ones; inserted near posterior margin of prostomium (Fig. 92A). Eyes absent. Nuchal organs well pronounced, forming two ciliated lobes laterally between prostomium and first segment (Fig. 92A).

Proboscis retracted in all specimens, not observed.

Anterior segment dorsally reduced, second and third ones well developed and separate (Fig. 92A), with four pairs of cirri (1 + 2 + 1). First segment achaetous, with one pair of slender, cylindrical cirri; reaching about segments 7–8; inserted laterally. Second segment dorsally with similar but distinctly longer pair of cirri, reaching about segment eleven, distinct chaetigerous lobes and ventrally with similiar pair of cirri, which are about as long as cirri from first segment. Third segment dorsally with cirri of length equal to that of dorsal cirri of second segment, chaetigerous lobes and normal ventral cirri (= 1 + Ch1/1 + Ch1/N). Following parapodia all uniramous, with conical to cylindrical lobes terminally indistinctly cleft; upper more conical part

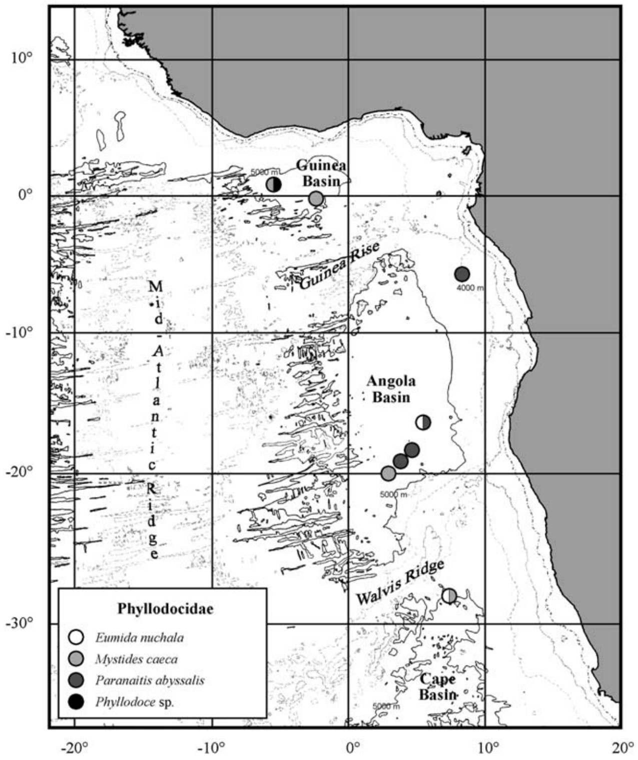

Fig. 94. Distribution of some phyllodocid species in the studied region.

slightly longer than rounded lower one (Figs. 92B, 93A). Dorsal cirri with conspicuous cirrophores and lanceolate cirrostyles, about two times longer than wide; slightly longer than parapodial lobes; inserted slightly above parapodial base (Figs. 92B, 93A). Ventral cirri thinner and more digitiform; about as long as parapodial lobes; inserted near parapodial base (Fig. 92B).

All parapodia with one straight acicula (Fig. 92B), and numerous spinigerous compound chaetae (Figs. 92C, 93A). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 93C); shafts with numerous small apical teeth (Fig. 93B).

Pygidium with dorsal anus and a pair of terminolateral cirri, which are all broken off; median papilla not observed.

Remarks

With the exception of (ZMH P25389), all specimens studied either were poorly preserved or consisted of median or posterior fragments, therefore are only tentatively referred to *Eumida nuchala* (Uschakov).

Distribution

Angola and Cape Basins; 5052–5433 m (Fig. 94).

Mystides Théel, 1879

Mystides caeca Langerhans, 1880

(Figs. 94, 95, 107)

Mystides caeca Langerhans, 1880—Langerhans (1880, p. 310; pl. 16, fig. 42a–d)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps, all thin and filiform; eyes absent; nuchal organs inconspicuous; three pairs of long, bottle-shaped cirri on anterior two segments (1 + 2); third segment without dorsal cirri; dorsal and ventral cirri oval; chaetae present from segment two.

Description

Body up to 5.5 mm long with up to 33 chaetigers; slender, slightly tapering anteriorly and posteriorly (Fig. 95A, C). Anterior segments uniannulate, following ones indistinctly biannulate with laterally rounded anterior part and slightly larger posterior parapodial part (Fig. 95C). Preserved specimens yellowish with some diffusely distributed small brown pigmented spots, especially on dorsal and ventral cirri.

Prostomium rounded, wider than long, with two antennae and two palps (Fig. 95A, B). Antennae and palps all thin and filiform; about as long as prostomium, but antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna absent (Fig. 95A, B). Eyes absent. Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment.

Proboscis retracted in all specimens, not observed.

Anterior two segments more or less developed, but partially fused dorsally (Fig. 95A, B), with three pairs of bottle-shaped cirri (1 + 2); which are mostly broken off. First segment achaetous, with one pair of cirri; all missing, but globular cirrophores still present; inserted laterally. Second segment dorsally with similar pair of cirrophores, distinct chaetigerous lobes and ventrally with bottle-shaped pair of cirri and very long drawn out tips (Fig. 95D), reaching about segment four, preserved on a few specimens. Third segment without dorsal cirri (= 1 + Ch1/1 + Ch0/N). Following parapodia all uniramous, with conical lobes and often missing dorsal and ventral cirri (Fig. 95E). Dorsal cirri oval, longer than wide; about as long as parapodial lobes; inserted slightly above parapodial base (Fig. 95E). Ventral cirri similar, but smaller than dorsal cirri; about as long as parapodial lobes or slightly shorter; inserted near parapodial base (Fig. 95E).

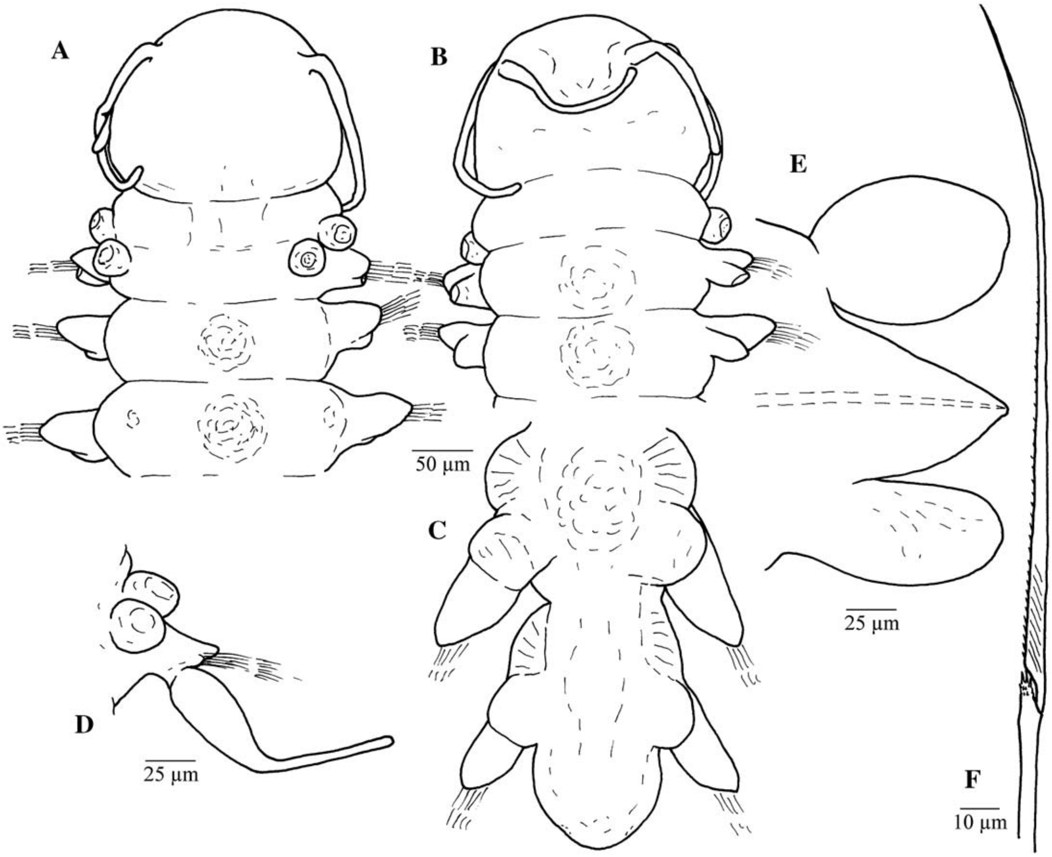

Fig. 95. *Mystides caeca* Langerhans. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; ventral view. (D) Right parapodium of 1st chaetiger (= second segment); dorsal view. (E) Parapodium of mid-body; posterior view, chaetae omitted. (F) Chaeta. (A–C: ZMH P25391 B; D–F: ZMH P25392).

All parapodia with one straight acicula (Fig. 95E), and up to about eight spinigerous compound chaetae (Fig. 95F). Spinigers with blades of different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 95F); shafts with one large apical tooth on either side and numerous smaller ones (Fig. 95F).

Pygidium with dorsal anus and a pair of termino-lateral cirri, which are all broken off, and a small medio-ventral papilla, preserved on a few specimens (Fig. 95C).

Distribution

Angola, Cape and Guinea Basins; 5048–5496 m (Fig. 94).

Discussion

Mystides borealis Théel, 1879 is a very similar species, which can be separated from *M. caeca* Langerhans, among other features, by the presence of two usually large red to black eyes (Blake, 1988).

Paranaitis Southern, 1914

Paranaitis abyssalis (Hartmann-Schröder, 1975)

(Figs. 94, 96, 97, 108)

Pareteone abyssalis Hartmann-Schröder, 1975—Hartmann-Schröder (1975, p. 58, figs. 19–21)

Paranaitis abyssalis (Hartmann-Schröder)—Pleijel (1991, p. 258); Kato and Pleijel (2003, p. 388, fig. 4)

Material examined

See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps, all conical to digitiform and antero-laterally orientated; eyes absent; nuchal papilla short and rounded, inserted near posterior margin in distinct, deep ligula; four pairs of cirri on anterior three segments (1 + 2 + 1); anterior two segments dorsally fused, forming a collar partly covering prostomium; dorsal cirri globular, ventral cirri

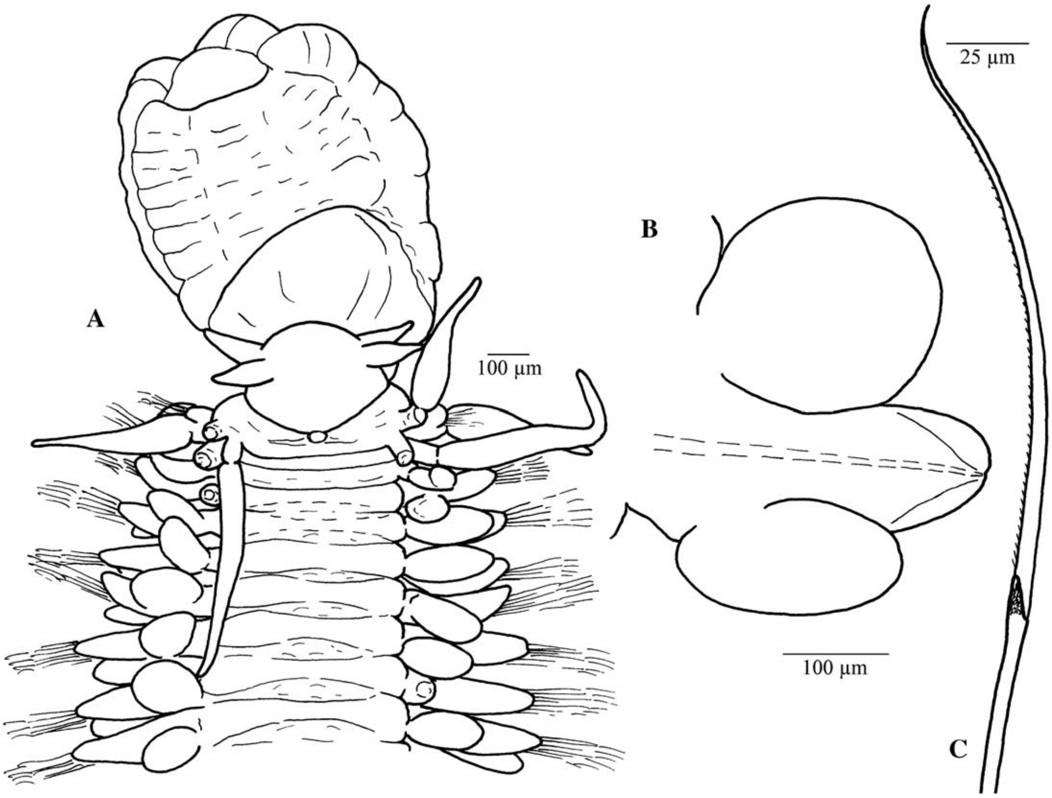

Fig. 96. *Paranaitis abyssalis* (Hartmann-Schröder). (A) Anterior end with everted proboscis; dorsal view. (B) Parapodium of mid-body; posterior view, chaetae omitted. (C) Chaeta. (A–C: ZMH P25395 A).

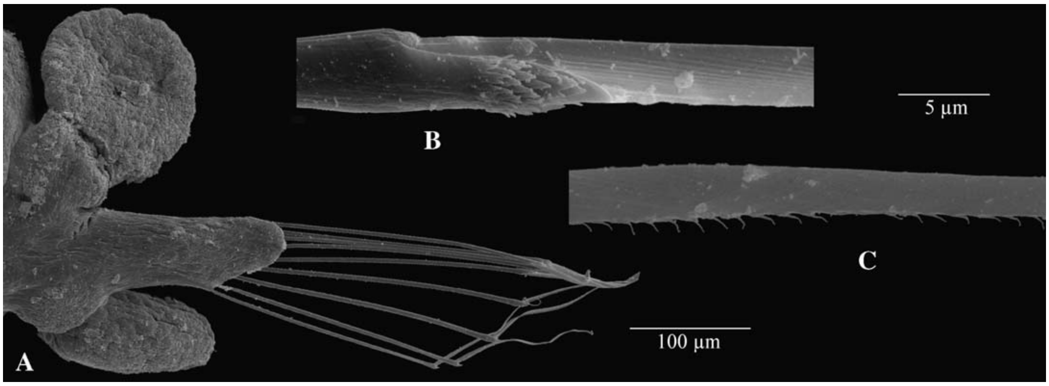

Fig. 97. *Paranaitis abyssalis* (Hartmann-Schröder). (A) Parapodium of mid-body; dorso-posterior view. (B) End of chaetal shaft and base of blade. (C) Chaetal blade. (A–C: ZMH P25395 B).

more oval, both shorter than parapodial lobes; chaetae present from segment two; proboscis subdivided, proximal part smooth, distal part with large tubercles.

Description

Body up to 23 mm long with up to 78 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 96A). Anterior segments uniannulate, following ones biannulate with small anterior part and large posterior parapodial part. Preserved specimens yellowish.

Prostomium anteriorly rounded, wider than long, with two antennae and two palps (Fig. 96A). Frontal antennae and palps all conical to digitiform and of subequal length; about half as long as prostomial width; inserted latero-dorsally and latero-ventrally; median antenna not present (Fig. 96A). Eyes absent. Single nuchal papilla short and rounded; inserted near posterior margin of prostomium in an incision (ligula) surrounded by first segment (Fig. 96A).

Proboscis indistinctly separated into proximal and distal part (Fig. 96A). Surface of proximal part smooth;

distal part with a longitudinal lateral row of about 8–10 large tubercles on each side; terminal ring with about six poorly delineated papillae. Numerous diffusely distributed minute rounded structures, especially under epithelium of proximal part, might be secretory glands.

Anterior two segments dorsally fused, forming a collar partly covering prostomium; third segment well developed and separate (Fig. 96A), with four pairs of cirri (1 + 2 + 1). First segment achaetous, with one pair of slightly bottle-shaped cirri, which have distinct cirrophores and cirrostyles with enlarged bases and drawn out tips, reaching about segments 6–7; inserted laterally. Second segment dorsally with cylindrical and distinctly longer pair of cirri, reaching about segment ten; small chaetigerous lobes, which are partly fused to ventral cirrophores and ventral bottle-shaped cirrostyles, slightly longer and broader than cirri from first segment, reaching about segments 7–8. Third segment dorsally with cirri of subequal size and length as dorsal cirri of second segment, chaetigerous lobes and normal ventral cirri (= 1 + Ch1/1 + Ch1/N). Following parapodia all uniramous, with conical to cylindrical lobes terminally indistinctly indented; upper part slightly longer than lower one (Figs. 96B, 97A). Dorsal cirri with conspicuous cirrophores and globular cirrostyles, about as long as wide; slightly shorter than parapodial lobes; inserted slightly above parapodial base (Figs. 96B, 97A). Ventral cirri thinner and more oval, about twice as long as wide; distinctly shorter than parapodial lobes; inserted near parapodial base (Fig. 96B, 97A).

All parapodia with one straight acicula (Fig. 96B), and up to about 15 spinigerous compound chaetae (Figs. 96C, 97A). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 97C); shafts with single main apical tooth and numerous smaller ones, decreasing in size proximally (Fig. 97B).

Pygidium with dorsal anus and a pair of terminolateral cirri, which are all broken off; and a small medioventral papilla.

Remarks

The possible secretory glands of the proximal proboscidial part may have been misinterpreted as papillae by Kato and Pleijel (2003), who examined the holotype.

Distribution

Angola Basin; 3952–5468 m (Fig. 94).

Phyllodoce Lamarck, 1818

Phyllodoce sp.

(Figs. 94, 98, 108)

Material examined

See Appendix 1.

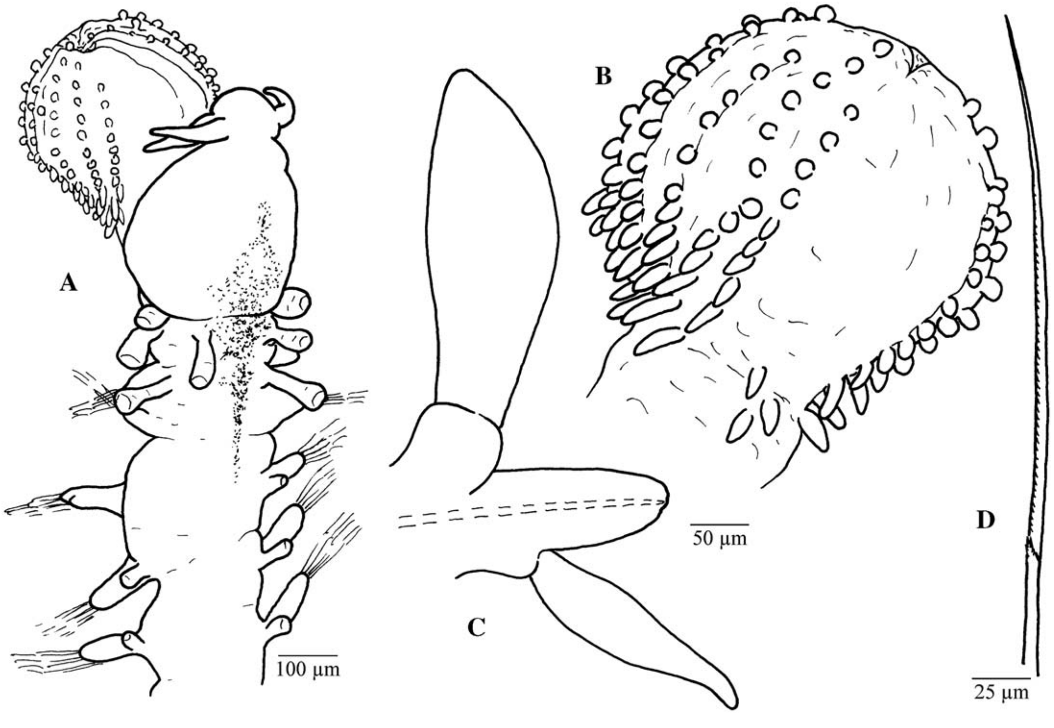

Fig. 98. *Phyllodoce* sp. (A) Anterior end with partly everted proboscis; latero-dorsal view. (B) Proboscis, latero-ventral view. (C) Parapodium of mid-body; posterior view, chaetae omitted. (D) Chaeta. (A, B, D: SMF 18776; C: ZMH P25396).

Diagnosis

Prostomium with two antennae and two palps, all conical to digitiform; eyes absent; nuchal papilla not observed; four pairs of cirri on anterior three segments (1 + 2 + 1); first segment reduced, partly covered by prostomium; dorsal cirri conical to lanceolate, ventral cirri more digitiform, both longer than parapodial lobes; chaetae present from segment three.

Description

Body at least 6.0 mm long with at least 30 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 98A). Segments uniannulate. Preserved specimen whitish, prostomium and first segments diffusely darkly pigmented and anterior part with indistinct mid-dorsal longitudinal line.

Prostomium pentagonal, wider than long, with indistinct protuberance at insertion of two antennae and two palps (Fig. 98A). Frontal antennae and palps all conical to digitiform and of about same length; slightly shorter than prostomial width; inserted latero-dorsally and latero-ventrally; median antenna absent. Eyes absent. Nuchal papilla not observed.

Proboscis partly everted (Fig. 98A, B); proximal part with 12 longitudinal rows of papillae, six on each side, separated by unpapillated middorsal and midventral areas; 9–14 papillae in each row, most proximal ones conical to digitiform, others shorter and globular (Fig. 98B); distal part and terminal ring not observed.

First segment dorsally reduced, second and third ones well developed and separate (Fig. 98A), with four pairs of cirri (1 + 2 + 1), which have large cirrophores but cirrostyles are all missing. First segment achaetous, with one pair of cirri; inserted laterally. Second segment dorsally and ventrally with pair of cirri; chaetigerous lobes not present. Third segment dorsally with one pair of cirri, chaetigerous lobes and probably normal ventral cirri (= 1 + 1/1 + Ch1/N). Following parapodia all uniramous, with conical to cylindrical lobes terminally indistinctly cleft; upper part slightly longer than lower one (Fig. 98C). Only one remaining dorsal cirrus present, which is in bad shape; with distinct cirrophore and probably conical to lanceolate cirrostyle, more than two times as long as wide; much longer than parapodial lobes; inserted slightly above parapodial base (Fig. 98C). Ventral cirri thinner and more digitiform; much longer than parapodial lobes; inserted near parapodial base (Fig. 98C).

All parapodia with one straight acicula (Fig. 98C), and a few spinigerous compound chaetae (Fig. 98D). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 98D); shafts with one large apical tooth on either side and some smaller ones (Fig. 98D).

Pygidium not observed.

Remarks

The specimens are poorly preserved, with most appendages broken off.

Distribution

Guinea Basin; 5137–5141 m (Fig. 94).

Discussion

Due to the lack of most appendages, species identification is impossible. The specimens resemble *Phyllodoce rosea* (McIntosh, 1877) in some points (e.g. shape of parapodia), but this species has two eyes and some of the proboscidial papillae are hard and tooth-like (Pleijel 1988).

Pseudomystides Bergström, 1914

Pseudomystides bathysiphonicola (Hartmann-Schröder, 1983) comb. nov.

(Figs. 99–101, 108)

Mystides bathysiphonicola Hartmann-Schröder, 1983—Hartmann-Schröder (1983, p. 169, figs. 1–7)

Material examined

Type material. R.R.S DISCOVERY st. 10112, haul 1, 50°25.2′N 13°20.3′W to 50°25.7′N 13°20.4′W, 9.ix.1979, 2640–2660 m; holotype: cs/10.4/87/0.4/0.2 (BMNH 1982.39).—R.R.S DISCOVERY st. 8532, haul 6, 13°48′N 18°8′W, 4.vii.1974, 2952–2958 m; paratype: af/5.0/31/0.5/0.2, mf/1.2/6-7/0.5/0.2, pf/2.0/14-13/0.4/0.2 (ZMH P-17383).—R.R.S DISCOVERY st. 10112, haul 3, 50°19.1′N 13°25.8′W to 50°19.9′N 13°26.9′W, 9.ix.1979, 2740–2755 m; paratypes: af/8.0/50/0.5/0.2, af/7.6/50/0.5/0.2, mf/2.7/19-22/0.4/0.2, pf/5.2/30/0.5/0.2, pf/4.2/36/0.5/0.2 (BMNH 1982.40–42).—R.R.S DISCOVERY st. 10113, haul 1, 50°16′N 13°32′W, 10.ix.1979, 2755–2760 m; paratypes: cs/12/91/0.5/0.2, cs/10/83/0.5/0.2, 4 cs or fragments in tubes, 1 af = syllid (ZMH P-17385).—R.R.S DISCOVERY st. 50605, haul 1, 50°11′N 13°30′W, 5.vii.1979, 2820–2930 m; paratype: af/2.7/23/0.5/0.2, mf/5.4/37/0.5/0.2 (ZMH P-17386).

Additional material. See Appendix 1.

Diagnosis

Prostomium with two antennae and two palps, all conical to digitiform; prostomium with terminal protuberance but without eyes; nuchal organs inconspicuous; three pairs of cirri on anterior two segments (1 + 2), first and second dorsal pairs digitiform, ventral pair oval, larger than following ones; third segment without dorsal cirri; dorsal and ventral cirri oval; chaetae present from segment two.

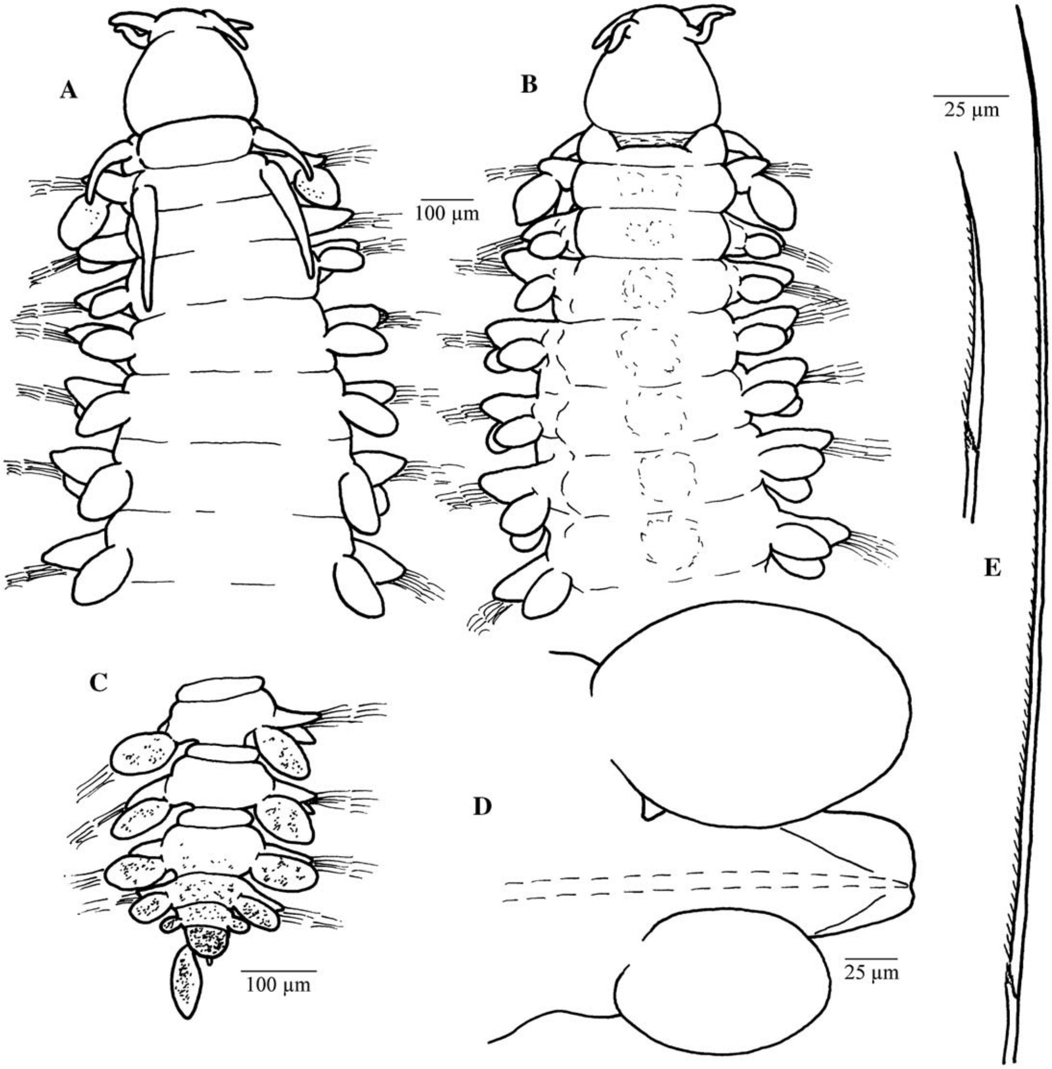

Fig. 99. *Pseudomystides bathysiphonicola* (Hartmann-Schröder) comb. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D) Parapodium of mid-body; posterior view, chaetae omitted. (E) Chaetae. (A, B, D, E: ZMH P25414; C: ZMH P25411).

Description

Body up to 7.5 mm long with at least 63 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 100A). Anterior segments uniannulate, following ones more or less distinct biannulate with small anterior part and larger posterior parapodial part (Fig. 99C). Preserved specimens whitish to yellowish, often with numerous diffusely distributed small brown pigmented spots, denser on pygidium and anal, dorsal and ventral cirri.

Prostomium conical, slightly wider than long, with distinct protuberance at insertion of two antennae and two palps (Fig. 99A). Frontal antennae and palps all conical to digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna absent. Eyes absent. Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment (Fig. 100B).

Proboscis retracted in all specimens, not observed.

Anterior segments all well developed and separate (Figs. 99A, B; 100A, B), with three pairs of cirri (1 + 2). First segment achaetous, with one pair of short, digitiform cirri; reaching about segments 2–3; inserted laterally. Second segment dorsally with similar but longer and slightly stouter pair of cirri, reaching about segments 4–5, distinct chaetigerous lobes and ventrally with oval, flattened pair of cirri, which are much larger than following ones, reaching about segment three. Third segment without dorsal cirri (= 1 + Ch1/1 + Ch0/N). Following parapodia all uniramous, with conical to cylindrical lobes and dorsal

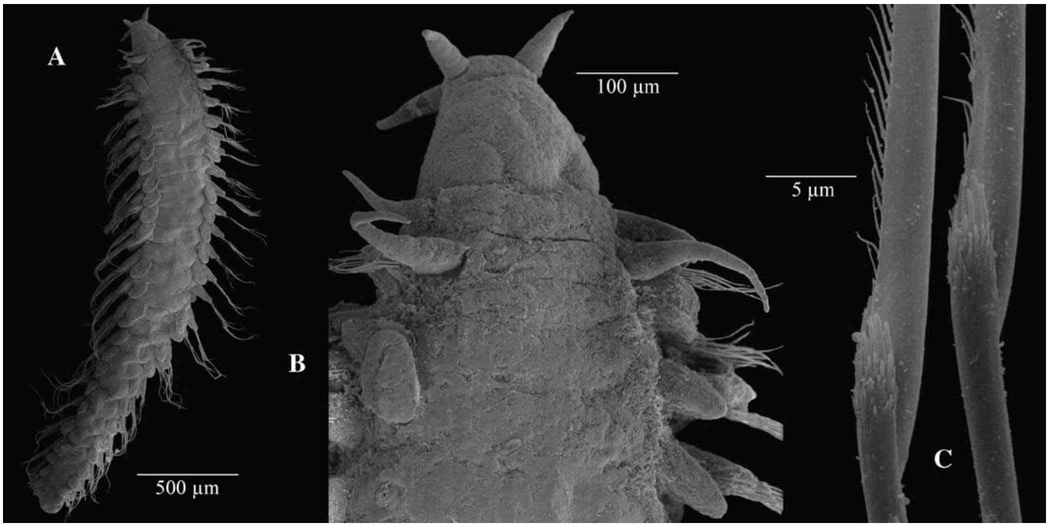

Fig. 100. *Pseudomystides bathysiphonicola* (Hartmann-Schröder) comb. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Detail of chaetae. (A–C: ZMH P25419 A).

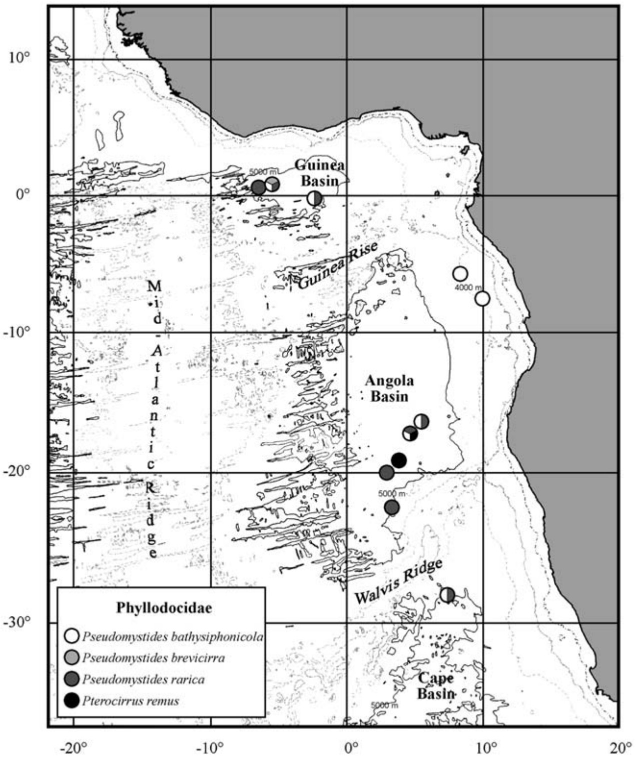

Fig. 101. Distribution of some phyllodocid species in the studied region.

and ventral cirri (Fig. 99D). Dorsal cirri oval, longer than wide; about as long as parapodial lobes; inserted slightly above parapodial base (Fig. 99D). Ventral cirri similar, but much smaller than dorsal cirri; distinctly shorter than parapodial lobes; inserted near parapodial base (Fig. 99D).

All parapodia with one straight acicula (Fig. 99D), and up to about ten spinigerous compound chaetae (Fig. 99E). Spinigers with blades of different length, decreasing in length superiorly and inferiorly (Fig. 99E); subdistally blades with hair-like serration (Fig. 100C); shafts with one large apical tooth on either side and numerous smaller ones, decreasing in size proximally (Fig. 100C).

Pygidium with dorsal anus and a pair of termino-lateral conical cirri and a small medio-ventral papilla (Fig. 99C).

Distribution

Angola, Cape and Guinea Basins; 3945–5460 m (Fig. 101).

Discussion

The examined specimens show clearly that this taxon shares more characters with the genus *Pseudomystides* Bergström than with *Mystides* Théel. For example, they have a well-defined protuberance with conical to digitiform antennae or palps, rather than a rounded prostomium with filiform appendages. Furthermore, anterior segments with bottle-shaped cirri, which are typical for *Mystides*, are not present. The median antenna is absent, but might be completely reduced; this structure is often very small and can be difficult to detect also in other species of *Pseudomystides*. Pleijel (1993a) already mentioned that "*Mystides bathysiphonicola* differs in several respects from other members of genus … and presumably does not belong within *Mystides*." Consequently, the species is transferred to *Pseudomystides* here.

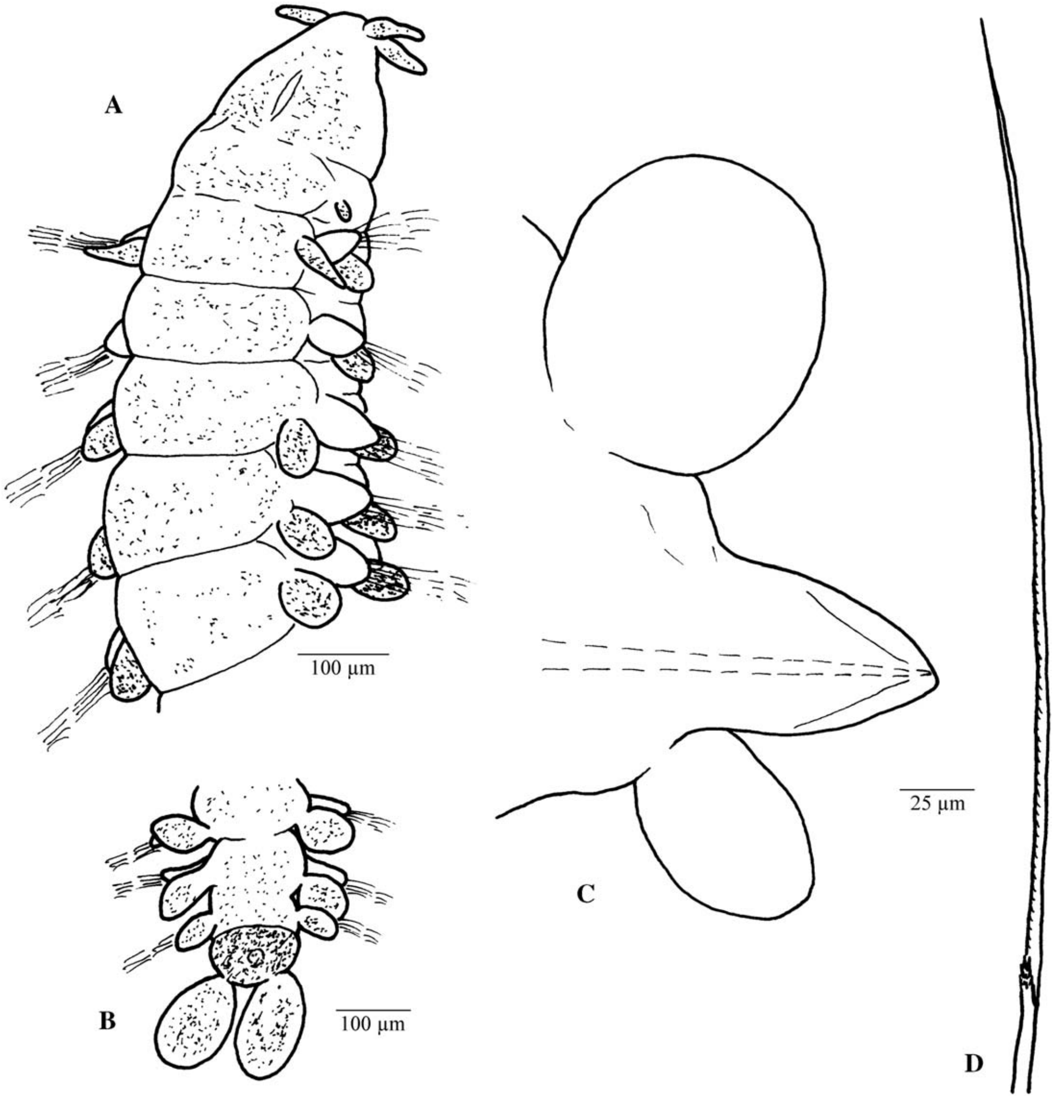

Fig. 102. *Pseudomystides brevicirra* sp. nov. (A) Anterior end; dorso-lateral view. (B) Posterior end; dorsal view. (C) Parapodium of mid-body; posterior view, chaetae omitted. (D) Chaeta. (A–D: ZMH P25420).

Pseudomystides brevicirra sp. nov.

(Figs. 101, 102, 109)

Etymology

The species epithet (Latin brevis = short) refers to the short cirri on the first segments. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 79 MC 6, 0°50′N 5°35′W, 19.iii.2005, 5139 m; holotype: cs/9.2/75/0.7/0.3 (ZMH P25420).

Diagnosis

Prostomium with two antennae and two palps, all conical to digitiform; prostomium with indistinct terminal protuberance but without eyes; nuchal organs inconspicuous; three pairs of cirri on anterior two segments (1 + 2), first pair very short conical, others dorsally more digitiform and ventrally oval, about as large as following ones; third segment without dorsal cirri; dorsal and ventral cirri oval; chaetae present from segment two.

Description

Body up to 9.2 mm long with up to 75 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 102A, B). Anterior segments uniannulate, following ones more or less distinct biannulate with small anterior part and larger posterior parapodial part. Preserved specimens yellowish, with numerous diffusely distributed small brown pigmented spots, denser on anterior end, pygidium and anal, dorsal and ventral cirri.

Prostomium conical, slightly wider than long, with indistinct protuberance at insertion of two antennae and two palps (Fig. 102A). Frontal antennae and palps all conical to digitiform and of about same length, but antennae slightly thinner than palps; inserted latero-dorsally and latero-ventrally; median antenna absent. Eyes absent. Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment.

Proboscis retracted, not observed.

Anterior segments all well developed and separate (Fig. 102A, B), with three pairs of cirri (1 + 2). First segment achaetous, with one pair of very short, conical cirri; inserted laterally. Second segment dorsally with distinctly stouter and longer, more digitiform pair of cirri, reaching anterior part of third segment, distinct chaetigerous lobes and ventrally with oval, flattened pair of cirri, which are about as large as following ones or slightly smaller. Third segment without dorsal cirri (= 1 + Ch1/N + Ch0/N). Following parapodia all uniramous, with conical lobes and dorsal and ventral cirri (Fig. 102C). Dorsal cirri oval, slightly longer than wide; about as long as parapodial lobes; inserted slightly above parapodial base (Fig. 102C). Ventral cirri similar, but much smaller than dorsal cirri; slightly shorter than parapodial lobes; inserted near parapodial base (Fig. 102C).

All parapodia with one straight acicula (Fig. 102C), and up to about ten spinigerous compound chaetae (Fig. 102D). Spinigers with blades of different length, decreasing in length superiorly and inferiorly; subdistally blades with fine serration (Fig. 102D); shafts with one large apical tooth on either side and numerous smaller ones, decreasing in size proximally (Fig. 102D).

Pygidium with dorsal anus and a pair of termino-lateral oval cirri; medio-ventral papilla not observed (Fig. 102B).

Remarks

Chaetae in middle and posterior parts of body with very long blades (natatory or swimming chaetae?); some median segments filled with numerous minute gametes (sperm?).

Distribution

Guinea Basin; 5139 m (Fig. 101).

Discussion

Pseudomystides brevicirra sp. nov. is remarkable for the very small size of the cirri on the first segment (seen on both sides of the body in the holotype) and for the fact that the ventral cirri of the second segment are unspecialized, not longer than those of following segments. The new species is closely related to the N Atlantic deep-sea species *P. bathysiphonicola* (Hartmann-Schröder) comb. nov. and *P. punctata* Hartman, 1965, which were both described without a median antenna (but see "Discussion" under *P. bathysiphonicola*). However, the latter two species have distinctly longer cirri on the first two segments; moreover, a pair of eyes is present in *P. punctata* (Hartman 1965; Hartmann-Schröder 1983).

Pseudomystides rarica (Uschakov, 1958) comb. nov. (Figs. 101, 103, 109)

Lugia rarica Uschakov, 1958—Uschakov (1958, p. 204, figs. A, Б, B)

?Pseudomystides limbata punctata Hartman, 1965—Hartman (1965, p. 63; pl. 5, figs. a–c)

?Mystides punctata (Hartman)—Hartmann-Schröder (1979, p. 74)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps conical to digitiform, minute median antenna near posterior margin; prostomium with terminal protuberance, eye-like spots near posterior margin might be present; nuchal organs inconspicuous; three pairs of cirri on anterior two segments (1 + 2), first and second dorsal pairs digitiform, ventral pair conical, larger than following ones; third segment without dorsal cirri; dorsal and ventral cirri conical to oval; chaetae present from segment two.

Description

Body at least 14.7 mm long with at least 81 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 103A, D). Segments uniannulate. Preserved specimens whitish to yellowish, often with numerous diffusely distributed small brown pigmented spots, denser on pygidium and anal, dorsal and ventral cirri; sometimes also ventrally on base of parapodia.

Prostomium conical, longer than wide, with distinct protuberance at insertion of two antennae and two palps (Fig. 103A). Frontal antennae and palps all conical to digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna minute, inserted near posterior margin of prostomium (Fig. 103A); often deeply sunken and difficult to detect. A few specimens with one pair of large eye-like spots near posterior margin of prostomium (Fig. 103B). Nuchal organs inconspicuous, forming ciliated pits laterally between prostomium and first segment.

Proboscis retracted in all specimens, not observed.

Anterior segments all well developed and separate (Fig. 103A), with three pairs of cirri (1 + 2). First segment achaetous, with one pair of short, digitiform cirri; reaching

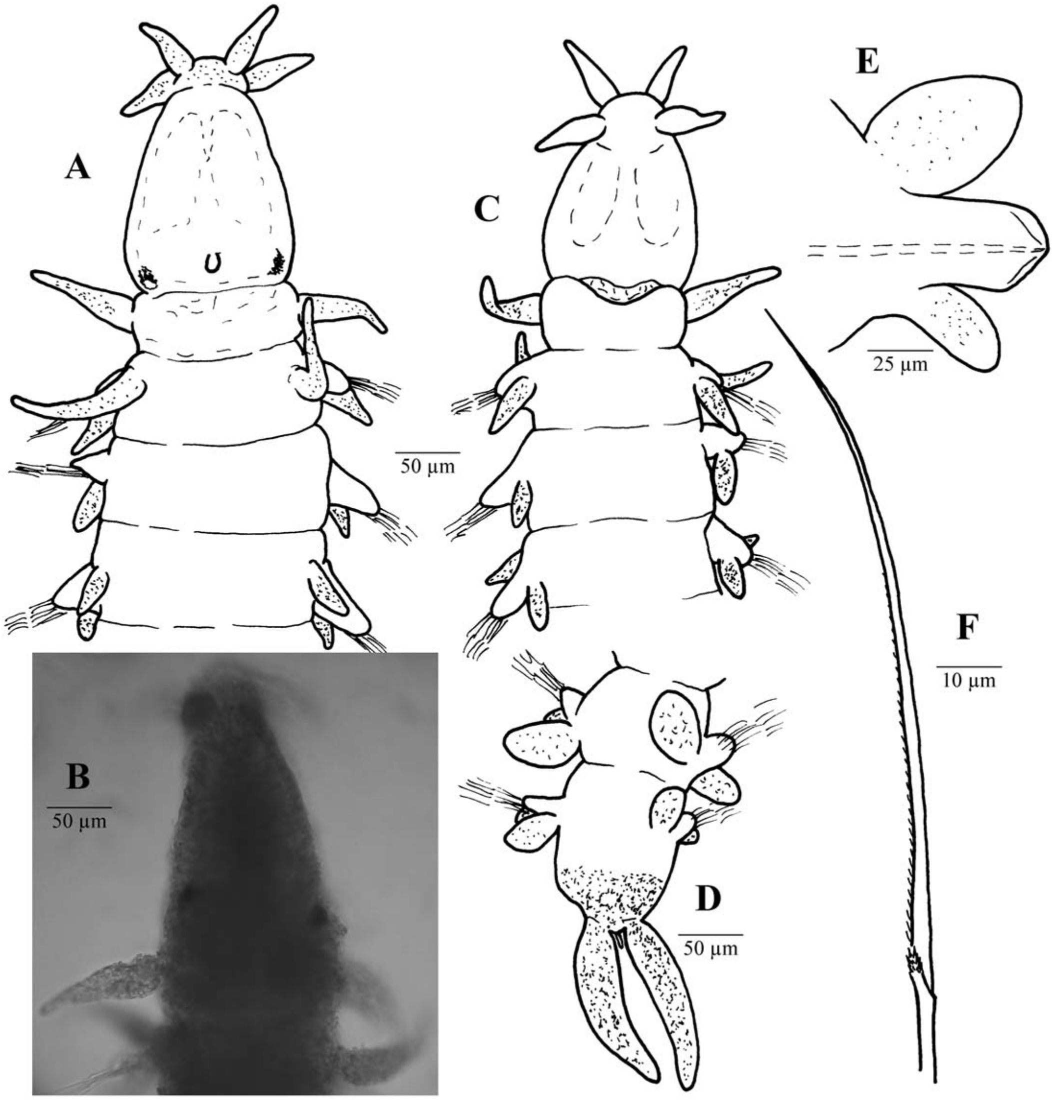

Fig. 103. *Pseudomystides rarica* (Uschakov) comb. nov. (A) Anterior end; dorsal view. (B) Light micrograph of anterior end; dorsal view. (C) Anterior end; ventral view. (D) Posterior end; dorsal view. (E) Parapodium of mid-body; posterior view, chaetae omitted. (F) Chaeta. (A, C–F: ZMH P25429 A; B: ZMH P25433).

about segments 2–3; inserted laterally. Second segment dorsally with similar but slightly longer pair of cirri, reaching about segment four, distinct chaetigerous lobes and ventrally with conical pair of cirri, which are slightly larger than following ones, reaching about segment three. Third segment without dorsal cirri (= 1+Ch1/1+Ch0/N). Following parapodia all uniramous, with conical to cylindrical lobes and dorsal and ventral cirri (Fig. 103E). Dorsal cirri conical to oval, longer than wide; about as long as parapodial lobes or slightly longer; inserted slightly above parapodial base (Fig. 103E). Ventral cirri similar, but much smaller than dorsal cirri; slightly shorter than parapodial lobes; inserted near parapodial base (Fig. 103E).

All parapodia with one straight acicula (Fig. 103E), and up to about 10–12 spinigerous compound chaetae (Fig. 103F). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with hair-like serration (Fig. 103F); shafts with one large apical tooth on either side and numerous smaller ones, decreasing in size proximally (Fig. 103F).

Pygidium with dorsal anus and a pair of terminolateral conical to digitiform cirri and a small medioventral papilla (Fig. 103D).

Distribution

Angola, Cape and Guinea Basins; 5058–5495 m (Fig. 101).

Discussion

The examined specimens are referred to *Pseudomystides rarica* (Uschakov) comb. nov., even though

Uschakov (1958, 1972, 1975) never mentioned the median antenna for his abyssal material from the Pacific Ocean. However, this structure is very small and usually difficult to detect, thus could have been overlooked. Unfortunately, verification is no longer possible, because the holotype lacks the anterior end, as reported by Pleijel (1993a). According to Hartmann-Schröder (1979) Pseudomystides *punctata* Hartman from slope and abyssal depths of the NW Atlantic Ocean (Hartman 1965; Hartman and Fauchald 1971) seems very similar and might even be conspecific.

Pseudomystides sp.

Material examined

See Appendix 1.

Remarks

Indeterminable fragments which could belong to *Pseudomystides bathysiphonicola*, *P. brevicirra* or *P. rarica*.

Pterocirrus Claparède, 1868

Pterocirrus remus sp. nov.

(Figs. 101, 104, 105, 109)

Etymology

The species epithet (Latin remus = paddle) refers to the enormously enlarged flattened cirri of the second segment. It is to be treated as a noun in apposition for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 48/1 st. 330 BC 8, 19°7′S 3°52′E, 18.vii.2000, 5469 m; holotype: cs/10/34/4.0/1.3 (ZMH P25440 A), 1 parapodium (ZMH P25440 B, on SEM stub); see "Remarks" below.

Additional material. See Appendix 1.

Diagnosis

Prostomium with three antennae and two palps, frontal antennae and palps conical to digitiform, median antenna centrally inserted; eyes absent; nuchal organs inconspicuous; four pairs of cirri on anterior three segments (1 + 2 + 1), ventral pair of second segment extremely enlarged, flattened and paddle-like; first segment dorsally reduced; dorsal and ventral cirri lanceolate; chaetae present from segment two.

Description

Body up to 10 mm long with up to 34 chaetigers; slender, tapering anteriorly and posteriorly (Fig. 104A). Anterior segments uniannulate, following ones indistinctly biannulate with small anterior part and large posterior parapodial part. Preserved specimens yellowish, some parts of the dorsum and a few dorsal cirri with small dark pigmented spots.

Prostomium anteriorly rounded, wider than long, with three antennae and two palps (Fig. 104A, B).

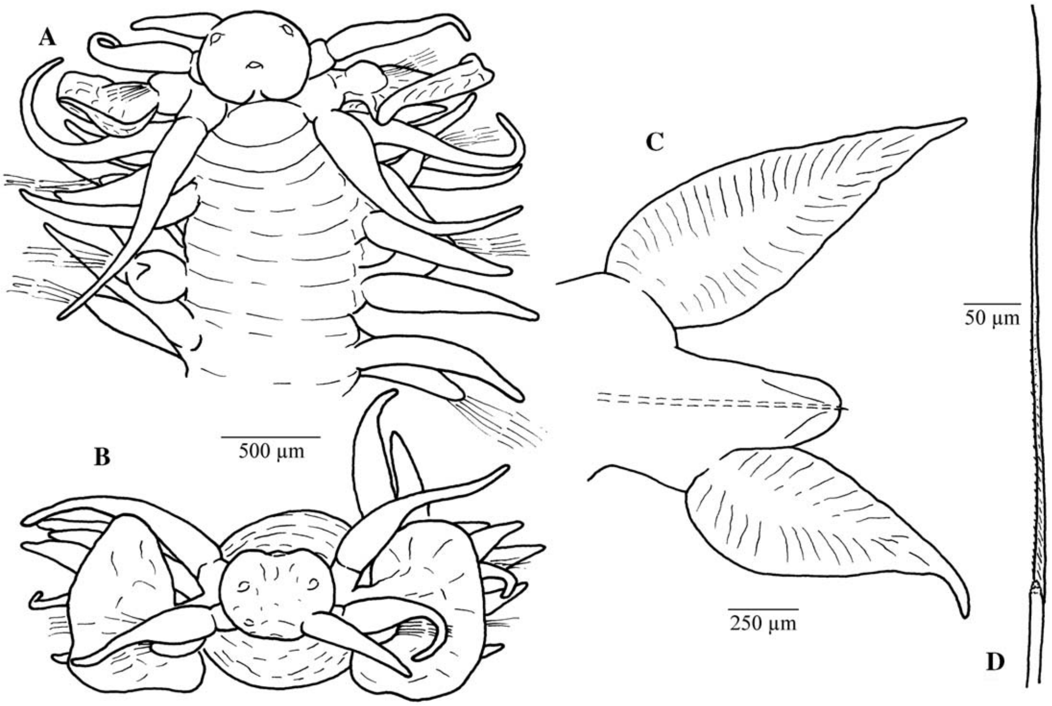

Fig. 104. *Pterocirrus remus* sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; anterior view. (C) Parapodium of mid-body; posterior view, chaetae omitted. (D) Chaeta. (A–D: ZMH P25440 A).

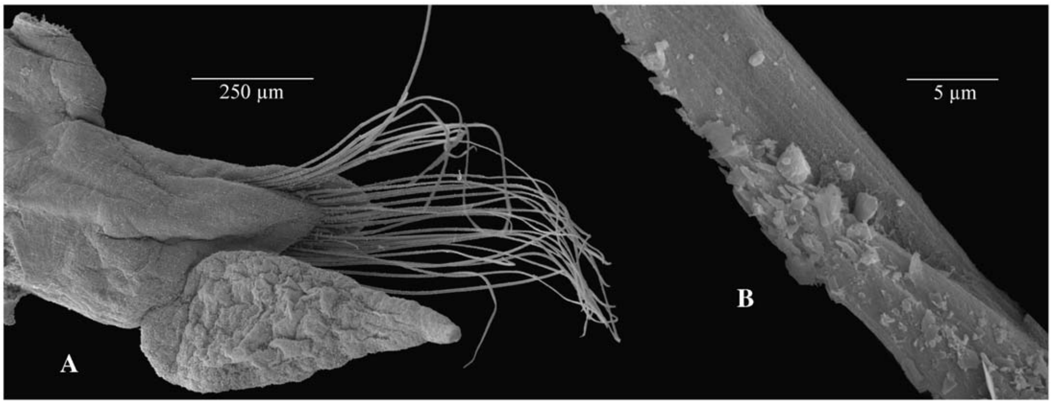

Fig. 105. *Pterocirrus remus* sp. nov. (A) Parapodium of mid-body; posterior view, dorsal cirrus missing. (B) Detail of chaeta. (A, B: ZMH P25440 B).

Antennae all missing and only left palp present, which is conical to digitiform; about as long as prostomial width; frontal antennae inserted latero-dorsally and palps latero-ventrally; median antenna centrally inserted (Fig. 104A). Eyes absent. Nuchal organs inconspicous, forming dorsal posterior outgrowths on prostomium.

Proboscis retracted in all specimens, not observed.

Anterior segment dorsally reduced, second and third ones well developed and separate (Figs. 104A), with four pairs of cirri (1 + 2 + 1). First segment achaetous, with one pair of slightly bottle-shaped cirri, which have distinct cirrophores and cirrostyles with enlarged bases and long drawn out tips, reaching about segments 4–5; inserted laterally. Second segment dorsally with similar but distinctly longer pair of cirri, reaching about segments 7–8; inconspicuous chaetigerous lobes, which are fused to ventral cirrophores and with enormously enlarged paddle-like ventral cirrostyles (Fig. 104B). Third segment dorsally with slightly shorter cirri than dorsal ones on second segment, reaching about segments 7–8; distinct chaetigerous lobes and normal ventral cirri, but both are smaller than following ones (= 1 + Ch1/1 + Ch1/N). Following parapodia all uniramous, with conical to cylindrical lobes and dorsal and ventral cirri (Figs. 104C, 105A). Dorsal cirri with short cirrophores and lanceolate cirrostyles, more than two times longer than wide; much longer than parapodial lobes; inserted above parapodial base (Figs. 104C, 105A). Ventral cirri of similar size but shorter and slightly thinner; much longer than parapodial lobes; inserted medially on parapodium (Figs. 104C, 105A).

All parapodia with one straight acicula (Fig. 104C), and numerous spinigerous compound chaetae (Fig. 104D). Spinigers with blades of slightly different length, decreasing in length superiorly and inferiorly; subdistally blades with serration (Fig. 105B); shafts with some small apical teeth (Fig. 105B).

Pygidium damaged and cirri all broken off; median papilla not observed (Fig. 106).

Remarks

The smaller specimen (ZMH P25441) is poorly preserved, therefore only questionably referred to this taxon.

Distribution

Angola Basin; 5460–5469 m (Fig. 101).

Discussion

Pterocirrus remus sp. nov. can be distinguished clearly from all other species of this genus by the enormously enlarged paddle-like cirri of the second segment. It resembles the deep-water species *Pterocirrus imajimai* Uschakov, 1972 from the N Pacific in some characters, but the latter species has distinctly shorter ventral cirri and chaetigerous lobes with a slightly prolonged upper lip. Moreover, the median antenna is inserted near the posterior margin (Uschakov 1972), rather than centrally on the prostomium.

Phyllodocidae sp.

Material examined

See Appendix 1.

Remarks

Small specimens or fragments which were indeterminable.

Abundance of Phyllodocidae

A total of 158 specimens or fragments were found in all investigated areas. Most of them belong to *Pseudomystides bathysiphonicola* comb. nov. (34) and *P. rarica* comb. nov. (44), or where indeterminable fragments

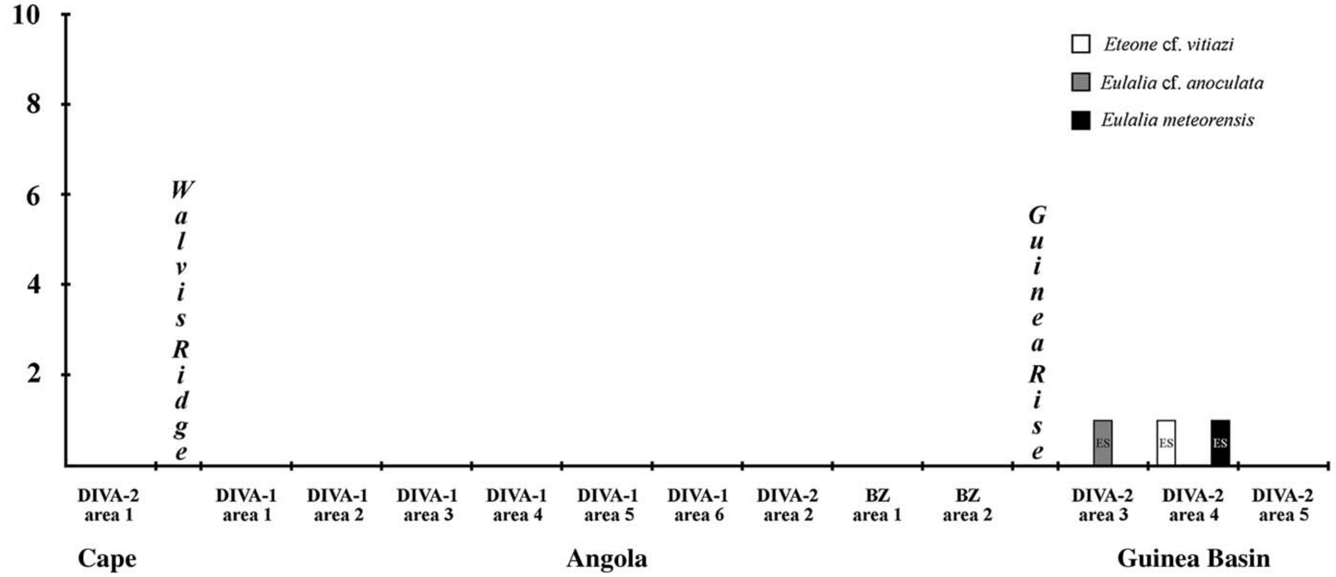

Fig. 106. Abundance of the phyllodocids *Eteone* cf. *vitiazi*, *Eulalia* cf. *anoculata* and *Eulalia meteorensis* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

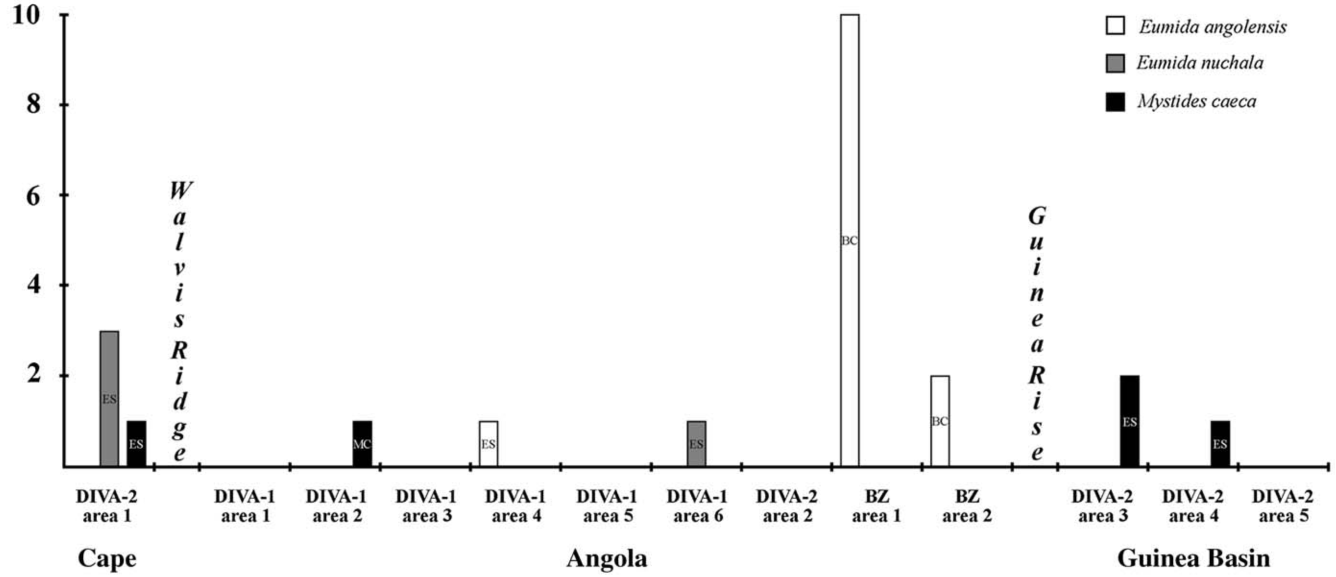

Fig. 107. Abundance of the phyllodocids *Eumida angolensis*, *E. nuchala* and *Mystides caeca* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

belonging to this genus (21). Both species were present in all three investigated basins (Figs. 108, 109), sometimes in slightly higher abundance (e.g. BIOZAIRE area 1). *Mystides caeca* was also widely distributed (Fig. 107), but in much lower numbers (6). *Eumida nuchala* (11) was found in the Cape and Angola Basins (Fig. 107), while all other species (Figs. 107–109) showed only scattered occurrence in the Angola Basin (*Eumida angolensis* sp. nov., *Paranaitis abyssalis*, *Pterocirrus remus* sp. nov.) or the Guinea Basin (*Eteone* cf. *vitiazi*, *Eulalia* cf. *anoculata*, *Eulalia meteorensis* sp. nov., *Phyllodoce* sp., *Pseudomystides brevicirra* sp. nov.). The most effective gear for collecting phyllodocids was the epibenthic sledge, taking ten of the twelve taxa in relatively high

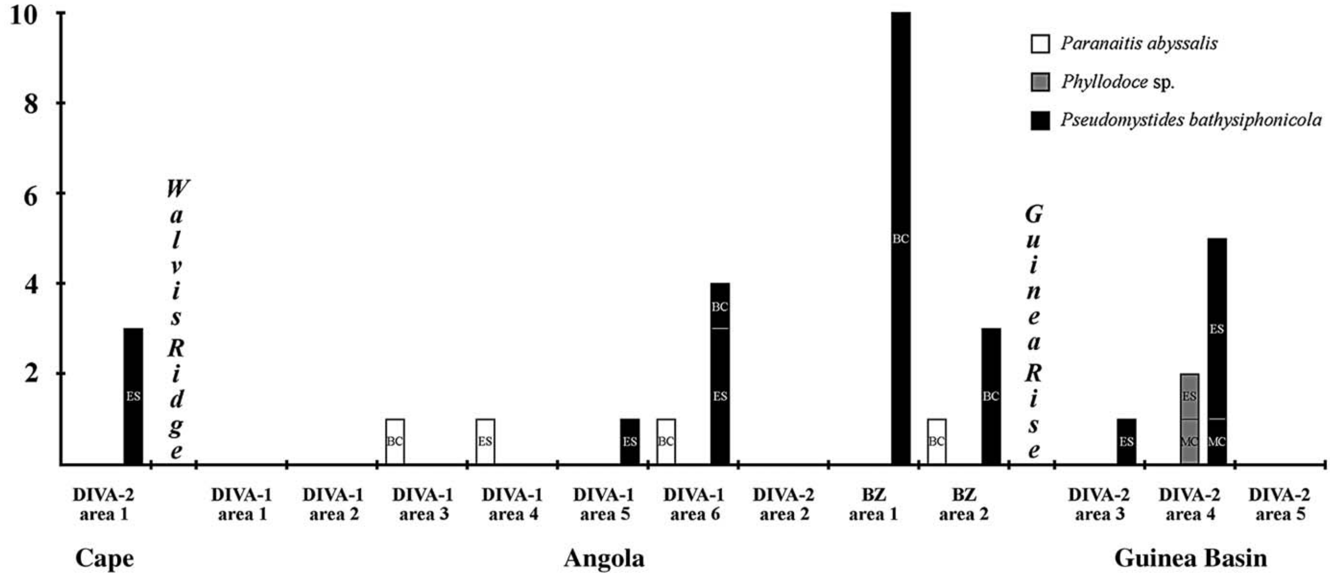

Fig. 108. Abundance of the phyllodocids *Paranaitis abyssalis*, *Phyllodoce* sp. and *Pseudomystides bathysiphonicola* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

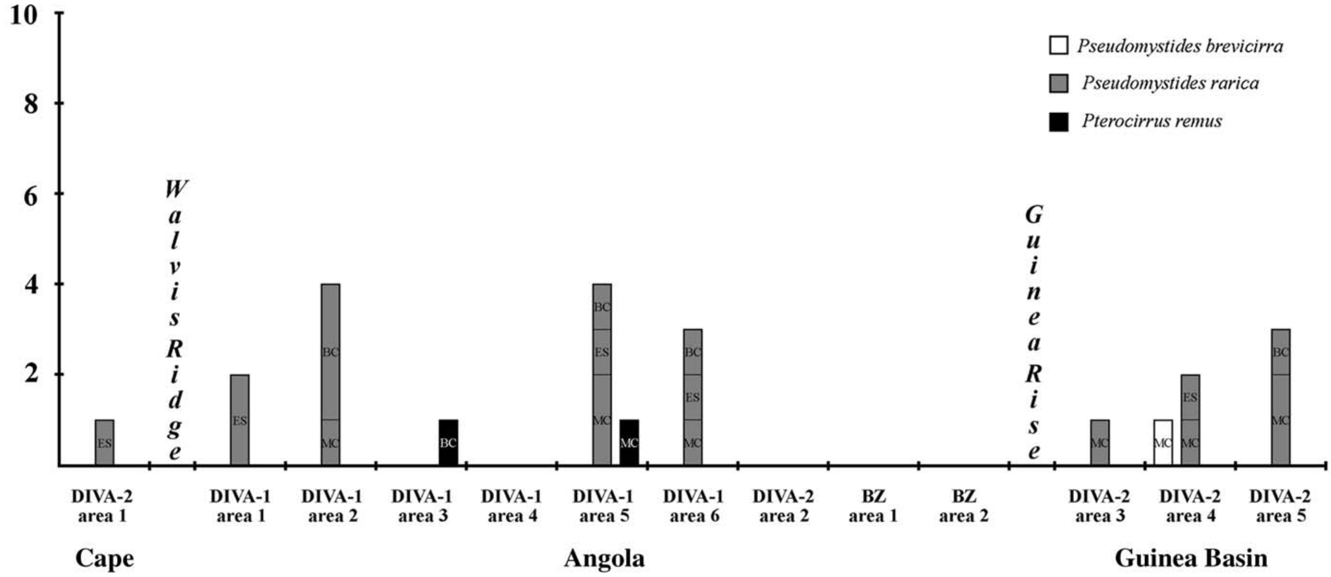

Fig. 109. Abundance of the phyllodocids *Pseudomystides brevicirra*, *P. rarica* and *Pterocirrus remus* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

abundance. However, the box corer was also very useful for quantitative sampling, whereas a lower number was present in the multicorer samples (Figs. 107–109).

Molecular data

ITS2 data set

Five newly acquired sequences (Table 13) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. Gaps were treated as missing and characters were unordered and unweighted. All analyses were conducted with the branch-and-bound algorithm. ML was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies (A = 0.1696, C = 0.3081, G = 0.2761, T = 0.2462); number of substitution types = 6;

Table 13. List of specimens and corresponding sequences in Phyllodocidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank acession numbers				
			18S rDNA	16S rDNA	COI (3-6W)	ITS1	ITS2
PHYLLODOCIDAE							
Eumida nuchala (Uschakov)	Cape Basin D-2 st. 41 ES-E	ZMH P25389 B	GQ426588	–	GQ426685	GQ426701	GQ426701
Mystides caeca Langerhans	Guinea Basin D-2 st. 90 ES-E	ZMH P25392	–	–	–	–	GQ426738
Phyllodocidae sp.	Cape Basin D-2 st. 40 ES-E	ZMH P25397	GQ426589	–	–	–	GQ426739
Pseudomystides bathysiphonicola (Hartmann-Schröder)	Cape Basin D-2 st. 41 ES-S	ZMH P25415 B	GQ426590	GQ426620	GQ426686	–	GQ426740
PARALACYDONIIDAE							
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		–	–	–	–	GQ426700

substitution rate matrix (A↔C = 2.0865, A↔G = 3.8410, A↔T = 2.0800, C↔G = 0.4940, C↔T = 3.0817, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.4253; and equal rates for all sites. Clade support values were calculated with nonparametric bootstrapping with 1,000 (ML) or 100,000 replicates (MP).

After exclusion of the primer sites, the alignment for the five sequences contained 566 characters, of which 254 were variable and 40 parsimony informative. The MP (tree length = 346, CI = 0.9538 (0.7333), RI = 0.6000, RC = 0.5723) and the ML analysis (–ln L = 2003.28435) found single trees with identical topologies (Fig. 110).

Discussion of molecular results

The 18S rDNA data strongly support monophyly of Phyllodocidae, and group them together with lopadorhynchids, lacydoniids, paralacydoniids and glycerids (see "Molecular phylogeny of abyssal Phyllodocida"). The 16S rDNA analyses placed *Pseudomystides bathysiphonicola* comb. nov. either as sister to a Glyceriformia clade (MP) or close to lacydoniids, paralacydoniids and sphaerodorids (ML). The COI amino acid data suggest paraphyly, because the lacydoniids were nested within Phyllodocidae, and both resulted as closely related to hesionids. However, the latter two hypotheses were only weakly supported (see "Molecular phylogeny of abyssal Phyllodocida").

Within Phyllodocidae, the ITS2 analyses strongly suggest a close relationship between *Mystides caeca* and *Pseudomystides bathysiphonicola* comb. nov. one the one hand, and between *Eumida nuchala* and an undeterminable Phyllodocidae on the other (Fig. 110). However, this is only partly in accordance with the 18S rDNA data (see "Molecular phylogeny of abyssal Phyllodocida") and with previous morphological and molecular-based studies (Eklöf et al. 2007).

Pilargidae Saint-Joseph, 1899

The Pilargidae are part of the Phyllodocida (Pleijel 2001l), but their lower-level classification is less certain: Licher and Westheide (1994) suggested that they belong to the Hesionidae, which was rejected by Pleijel and Dahlgren (1998). A possible autapomorphy of the Pilargidae is the presence of neuropodial capillaries, which distinguishes them from other nereidiforms with their compound chaetae (Glasby 2000a). Furthermore, several taxa show reduced notopodia with characteristic spines, which are mainly shaped like boat hooks (Blake 1997b).

The Pilargidae have a worldwide distribution from intertidal to abyssal depths and mainly prefer mud or muddy sands (Pleijel 2001l). They are generally considered

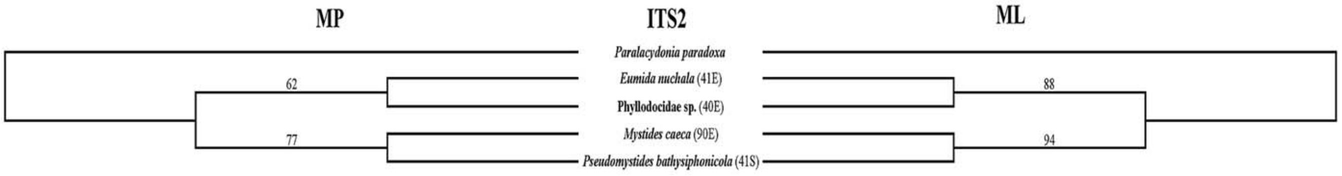

Fig. 110. Cladograms obtained from MP and ML analysis of the ITS2 sequences. Bootstrap values > 50 shown above branches.

to be carnivorous or omnivorous, capturing food with their eversible proboscis (Day 1967; Fauchald and Jumars 1979). The members of some species are probably free-living surface sediment dwellers; others might be active burrowers or live in commensalism with tube-building polychaetes (Day 1967; Gardiner 1976; Pleijel 20011).

In the present study two species of Pilargidae were collected, *Ancistrosyllis groenlandica* McIntosh, 1879 and *Sigambra magnuncus* Paterson & Glover, 2000. The former, like some other pilargids, appears to have a cosmopolitan distribution from subtidal to abyssal depths (e.g. Pettibone 1966; Katzmann et al. 1974; Kirkegaard 1983; Salazar-Vallejo 1986), whereas *Sigambra magnuncus* might be a typical deep-sea species from plains of the eastern Atlantic Ocean.

Key to pilargid species from the abyssal SE Atlantic

1. Prostomium small, inconspicuous, with short palps and antennae (Figs. 111A, B; 112A–C); hooked notochaetae present from chaetigers 5–6 (Fig. 111A, D, E; 112A, F); neurochaetae with bidentate tips (Figs. 111F; 112G, H) .... *Ancistrosyllis groenlandica* McIntosh

– Prostomium enlarged, with short palps and long antennae (Figs. 114A, B; 115A, B); hooked notochaetae and up to two addititional capillary chaetae present from chaetiger 3 (Fig. 114A, D, E; 115A, B, F–H); neurochaetae with pointed tips (Figs. 114F; 115I, J) .... *Sigambra magnuncus* Paterson & Glover

Ancistrosyllis McIntosh, 1879

Ancistrosyllis groenlandica McIntosh, 1879

(Figs. 111–113, 116)

Ancistrosyllis grœnlandica McIntosh, 1879—McIntosh (1879, p. 502; pl. 65, figs. 3, 20)

Material examined

See Appendix 1.

Diagnosis

Prostomium small, inconspicuous, with three short antennae and two biarticulate palps; eyes absent; dorsal cirri of first chaetiger about twice as long as on following segments; ventral cirri from chaetigers 1–3; notopodia with recurved hooks from chaetigers 4–6; neurochaetae serrated and with bidentate tips; integument distinctly papillated.

Description

Body up to 6.3 mm long with up to 36 chaetigers; dorso-ventrally flattened, widest in middle, tapering both anteriorly and posteriorly. Segments deeply cut along body, but without distinct transverse ridges (Figs. 111A–C, 112A). Integument and body appendages with numerous small conical to globular papillae (Fig. 112D). Irregular lateral darkly pigmented areas sometimes present throughout body; especially in smaller specimens.

Prostomium small and inconspicous, bearing three short conical antennae and two biarticulate palps (Fig. 111A, B). Two antennae inserted medio-laterally and one slightly shorter median antenna on the posterior end of the prostomium (Figs. 111A; 112B, C). Palps indistinctly set off from prostomium; palpophores large, basally slightly fused; palpostyles small conical, positioned antero-ventrally (Fig. 111A, B). Eyes absent. Nuchal organs might be present, but are not conspicuous.

Proboscis retracted in all specimens; extending through about 2–3 chaetigers (Fig. 111A, B).

First segment achaetous, about as long as following segments; with two pairs of conical to digitiform, subequal cirri inserted latero-ventrally, similar to antennae but slightly longer (Fig. 111A, B).

Parapodia subbiramous (Fig. 111D). Notopodia reduced; each with a single acicula; large curved hooks from chaetigers 5–6 (usually five) until the last one or two segments (Figs. 111A, C–E; 112A, F). Digitiform

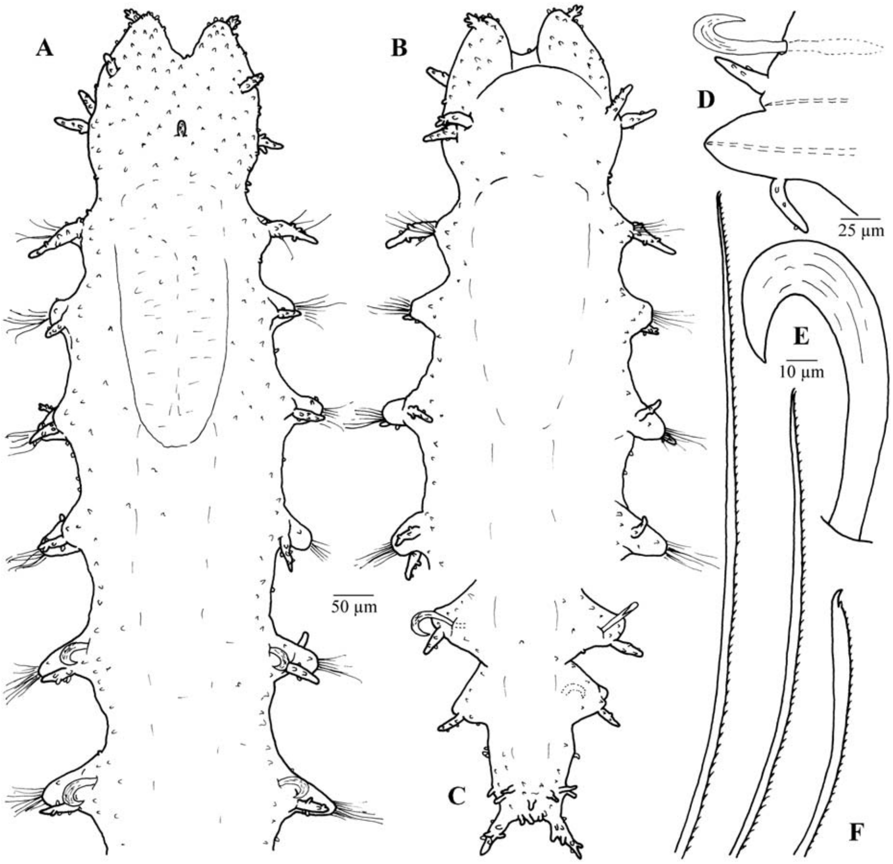

Fig. 111. *Ancistrosyllis groenlandica* McIntosh. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D) Right parapodium of chaetiger 15; anterior view, neurochaetae omitted. (E) Notopodial hook. (F) Neuropodial chaetae. (A–F: ZMH P25447).

dorsal cirri of first chaetiger about twice as long as on following segment, further cirri slightly longer than 2nd one (Fig. 111A). Neuropodial lobes conical; each with a single acicula; two types of laterally compressed and serrated simple neurochaetae with bidentate tips: 1. shorter and longer, slender upper chaetae with subequal long teeth at tip (Figs. 111D, F; 112G), 2. a few shorter, broader, sabre-like lower chaetae with distal tooth of tip distinctly longer than subdistal one (Figs. 111D, F; 112H). Distinct digitiform ventral cirri from 3rd chaetiger (Fig. 111B), but larger specimens possibly with very small cirri on first two chaetigers; slightly shorter than dorsal cirri.

Pygidium with an anus, a few scattered papillae and a terminal pair of conical to digitiform cirri (Figs. 111C, 112A, E).

Distribution

Angola Basin; 3945–3993 m (Fig. 113).

Discussion

Pettibone (1966) described two species, *Ancistrosyllis hartmanae* and *A. jonesi*, from the Chesapeake Bay which share some features with the herein-examined deep-sea specimens. In both taxa the ventral cirri are also absent on the first two chaetigers, but the notopodial hooks start on chaetiger three or six rather than on the 5th chaetiger as is typical in the present material. Furthermore, the deep-sea specimens are often very small; therefore, the ventral cirri on the first two chaetigers might be not yet developed or missing (see "Remarks" on the following species). However, all other characters are characteristic for *Ancistrosyllis groenlandica*, a species originally reported from the Davis Strait off West Greenland at 750 m depth (McIntosh 1879).

Sigambra Müller, 1858

Sigambra magnuncus Paterson & Glover, 2000
(Figs. 113–116)

Sigambra magnuncus Paterson & Glover, 2000—Paterson and Glover (2000, p. 167, figs. 1–3)

Material examined

See Appendix 1.

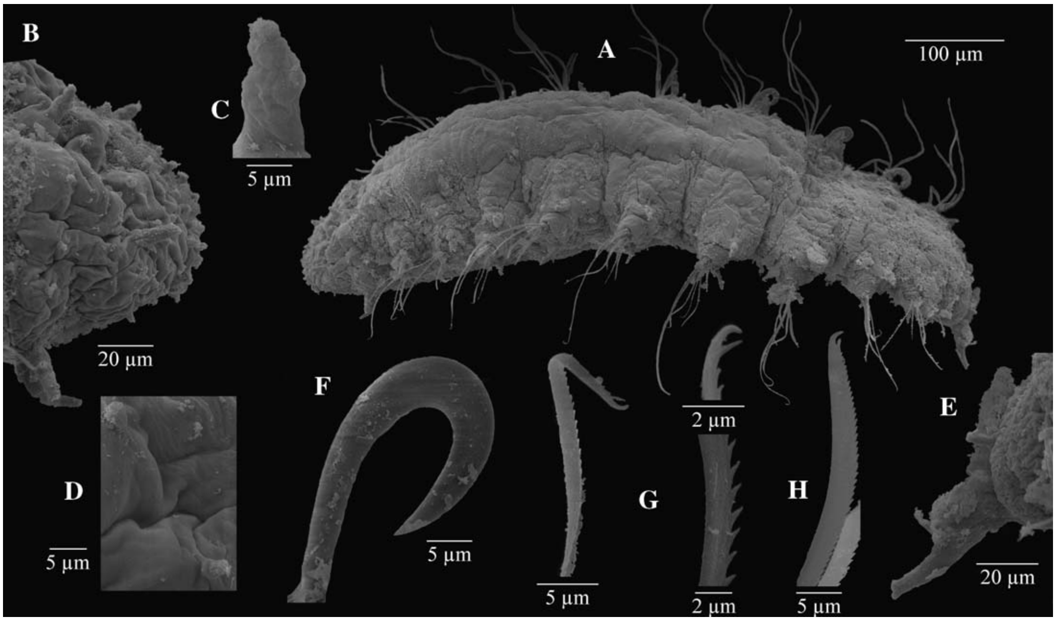

Fig. 112. *Ancistrosyllis groenlandica* McIntosh. (A) Complete specimen; latero-dorsal view. (B) Anterior end; latero-dorsal view. (C) Median antenna. (D) Prostomial papillae. (E) Pygidium; latero-dorsal view. (F) Notopodial hook. (G) Slender neuropodial chaetae with details. (H) Sabre-like neuropodial chaeta. (A–H: ZMH P25445 B).

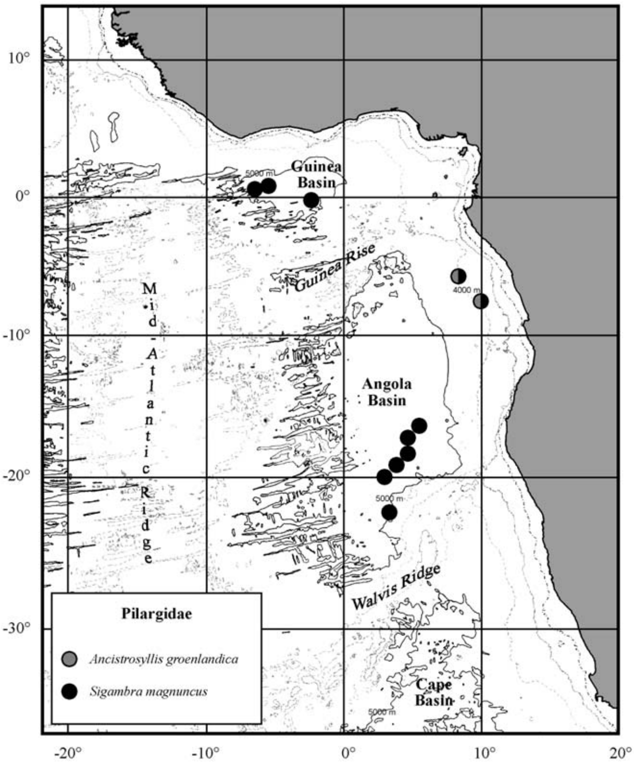

Fig. 113. Distribution of pilargid species in the studied region.

Diagnosis

Prostomium enlarged, with three long antennae and two biarticulate palps; proboscis with eight papillae; dorsal cirri of first chaetiger much longer than on following segments; ventral cirri from first chaetiger, but usually absent in chaetiger two; notopodia with recurved hooks and 1–2 additional capillary chaetae from chaetiger three; neurochaetae serrated and with pointed tips; integument predominantly smooth.

Description

Body at least 13 mm long with at least 65 chaetigers; dorso-ventrally flattened, anterior two segments in larger specimen elongated (Fig. 115A, B). Segments deeply cut along body, with two more or less distinct transverse ridges on dorsum (Fig. 115B). First achaetous segment dorsally with transverse line of small globular papillae (Fig. 115D) and following segments in posterior part with one row of conical to globular papillae (Fig. 115E); rest of integument smooth.

Prostomium trapezoidal, wider than long, bearing three long digitiform antennae and two biarticulate palps (Figs. 114A, B; 115A, B). Two antennae inserted medio-laterally and one distinctly longer median antenna on the posterior end of the prostomium (Figs. 114A; 115A, B). Palps indistinctly set off from prostomium; palpophores large, basally fused over half their length; palpostyles small conical, positioned antero-ventrally (Figs. 114A, B; 115C). Eyes absent. One pair of dorso-lateral nuchal organs situated between prostomium and first segment (Fig. 115B).

Proboscis with circlet of eight large, distally pointed conical papillae around opening and numerous much

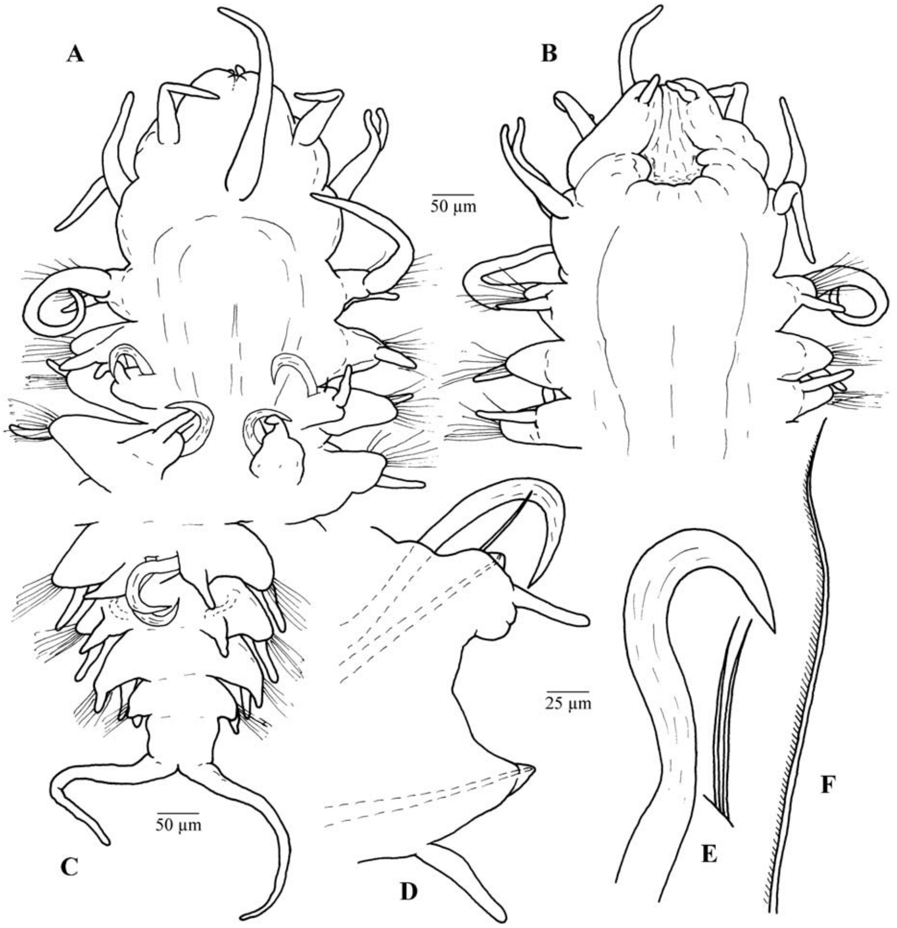

Fig. 114. *Sigambra magnuncus* Paterson & Glover. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D) Right parapodium of mid-body; posterior view, neurochaetae omitted. (E) Notopodial chaetae. (F) Neuropodial chaeta. (A–D: ZMH P25465 B; E, F: ZMH P25481).

smaller, conical to triangular papillae which are irregularly arranged (Fig. 115C); extending through about 3–4 chaetigers (Fig. 114A, B).

First segment achaetous; with two pairs of digitiform, subequal cirri inserted latero-ventrally, about same length as lateral antennae (Figs. 114A, B; 115A, B).

Parapodia subbiramous (Fig. 114D); which are dorsally shifted in middle or posterior part of body (Fig. 115A). Notopodia reduced; each with a single acicula; large curved hooks and 1–2 small additional capillary chaetae from chaetiger three until the last one to three segments (Figs. 114A, C–E; 115A, B, F–H). Digitiform dorsal cirri of first chaetiger about as long as median antenna; following cirri much shorter (Figs. 114A; 115A, B). Neuropodial lobes conical; each with a single acicula and a bundle of numerous slender, finely serrated capillary neurochaetae (Figs. 114D, F; 115I–K). Digitiform ventral cirri starting from 1st chaetiger; usually absent from 2nd chaetiger (Fig. 114B); about as long as dorsal cirri.

Pygidium with an anus and a terminal pair of long, slender cirri (Fig. 114C).

Remarks

Some of the juveniles carry distinct ventral cirri starting from the 3rd chaetiger; a very few of the larger specimens have an additional ventral cirrus on the left or right side of the 2nd parapodium.

Distribution

Angola and Guinea Basins; 3945–5497 m (Fig. 113).

Abundance of Pilargidae

A total of 341 specimens or fragments were found in two of the investigated basins. Most of them (331)

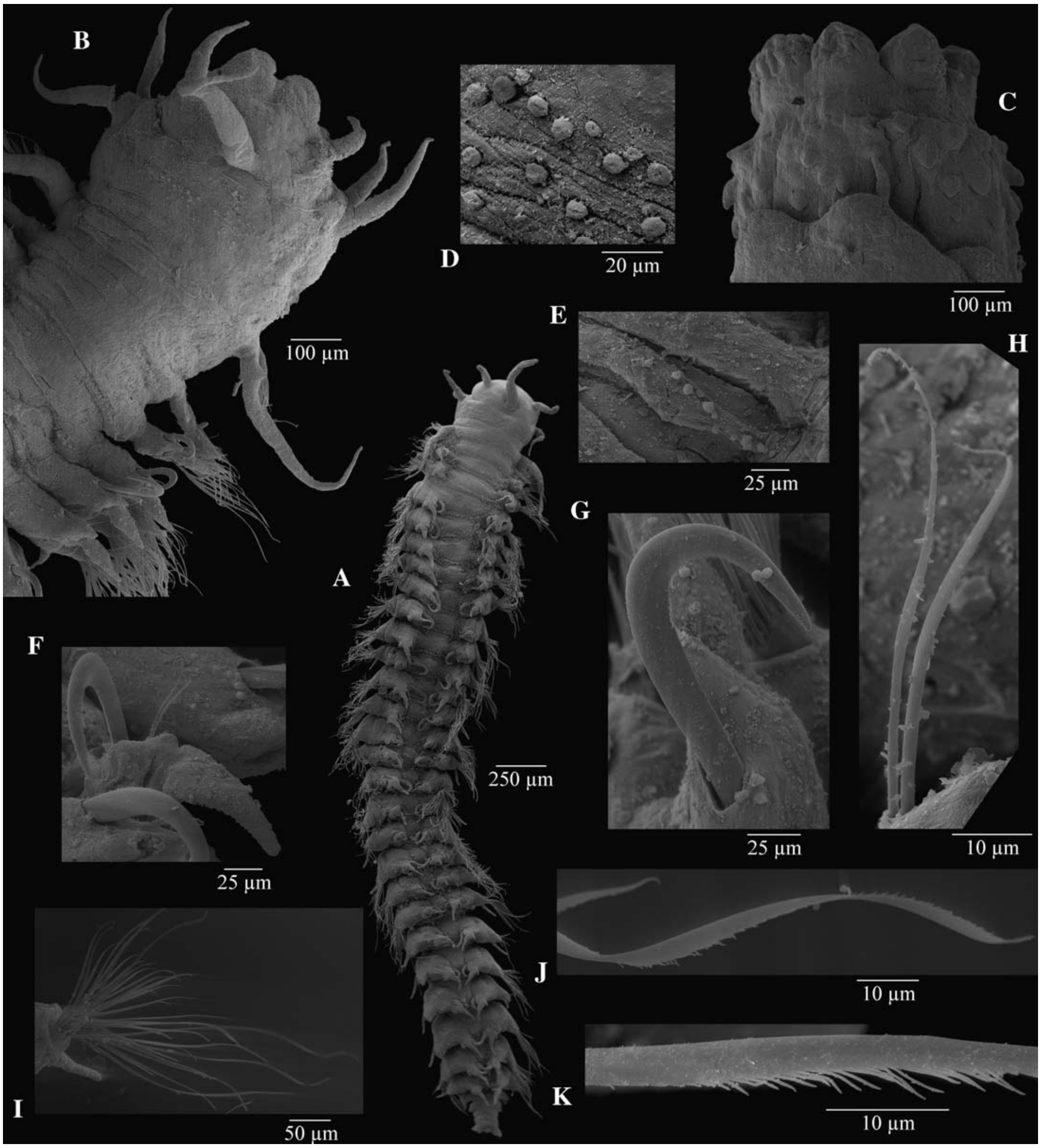

Fig. 115. *Sigambra magnuncus* Paterson & Glover. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end with everted proboscis. (D) Papillae on first segment. (E) Papillae on mid-body segment. (F) Notopodium. (G) Notopodial hook. (H) Notopodial capillary chaetae. (I) Neuropodium. (J) Neuropodial chaeta. (K) Serration of neuropodial chaeta. (A, D, K: ZMH P25487 B; B, E–J: ZMH P25460 B; C: ZMH P25469 B).

belong to *Sigambra magnuncus*. This species was present in the Angola and the Guinea Basins (Fig. 116), with the highest abundance in BIOZAIRE area 2 and DIVA-1 area 6. The 10 specimens of *Ancistrosyllis groenlandica* were only present in the BIOZAIRE material. The most effective type of gear for collecting pilargids were the box corer and the epibenthic sledge, whereas a much lower number of specimens were collected with the multicorer (Fig. 116). The epibenthic sledge samples have the added advantage of being generally rapidly fixed in ethanol; therefore, the material was more useful for molecular analyses.

Molecular data

All analyses were conducted using the branch-and bound algorithm. Gaps were treated as missing and characters were unordered and unweighted. Clade support values were calculated using nonparametric

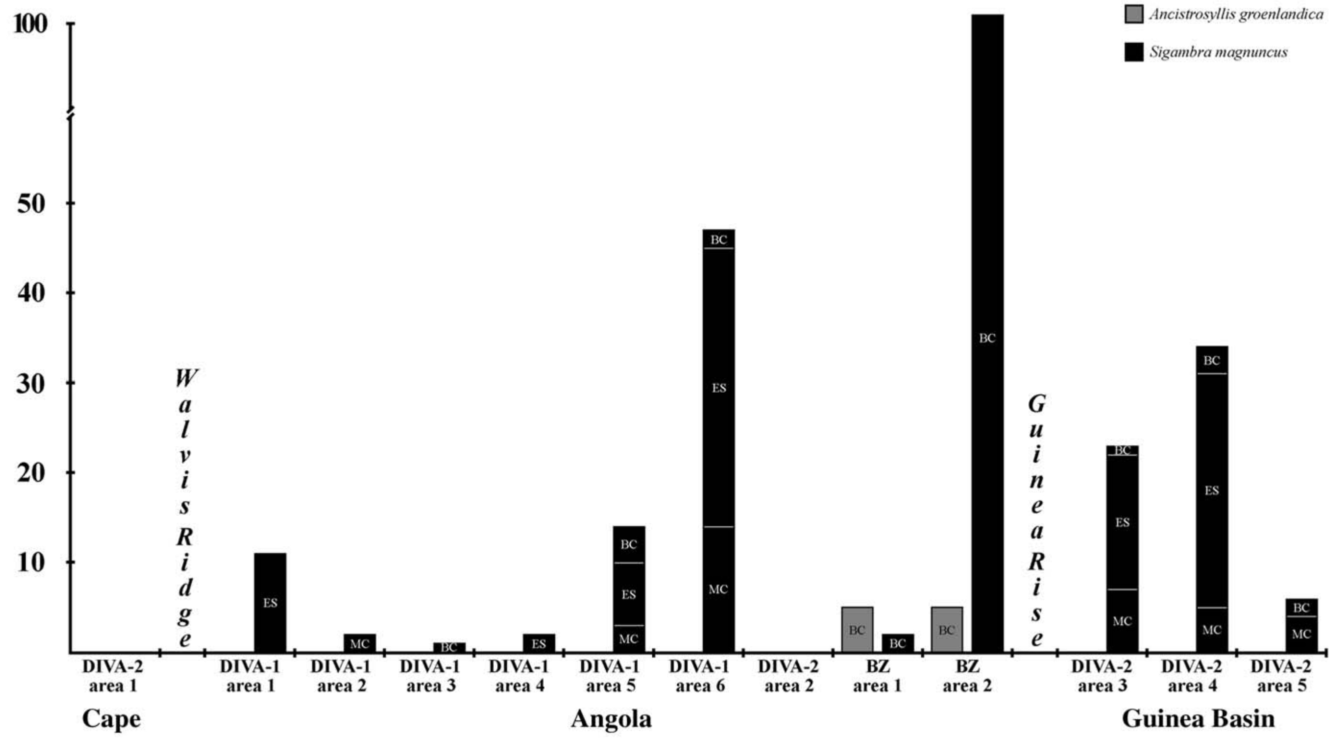

Fig. 116. Abundance of the two pilargid species in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

Table 14. List of specimens and corresponding sequences in Pilargidae and Paralacydoniidae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank acession numbers				
			18S rDNA	16S rDNA	COI		ITS2
					(LCO-HCO)	(3-6W)	
PILARGIDAE							
Sigambra magnuncus	Angola Basin						
Paterson & Glover	D-1 st. 344 ES-E	ZMH P25466 A	–	–	–	–	GQ426701
	Guinea Rise						
	Guinea Basin						
	D-2 st. 63 ES-S	ZMH P25478 B	GQ426591	GQ426621	GQ426640	GQ426687	GQ426742
	D-2 st. 89 ES-E	ZMH P25487 A	GQ426592	GQ426622	GQ426641	GQ426688	GQ426743
	D-2 st. 89 ES-S	ZMH P25487 C	GQ426593	GQ426623	GQ426642	GQ426689	GQ426744
	D-2 st. 90 ES-E	ZMH P25488 A	GQ426594	GQ426624	GQ426643	GQ426690	GQ426745
	D-2 st. 90 ES-S	ZMH P25488 B	–	GQ426625	–	–	GQ426746
Parandalia sp.	Australia, Darwin		–	–	EU835664*	–	–
PARALACYDONIIDAE							
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		–	GQ426619	–	GQ426684	GQ426700

*Sequence obtained from GenBank.

bootstrapping with 1,000 (ML) or 100,000 replicates (MP).

16S rDNA data set

Six newly acquired sequences (Table 14) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. The ML analysis was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies (A = 0.3742,

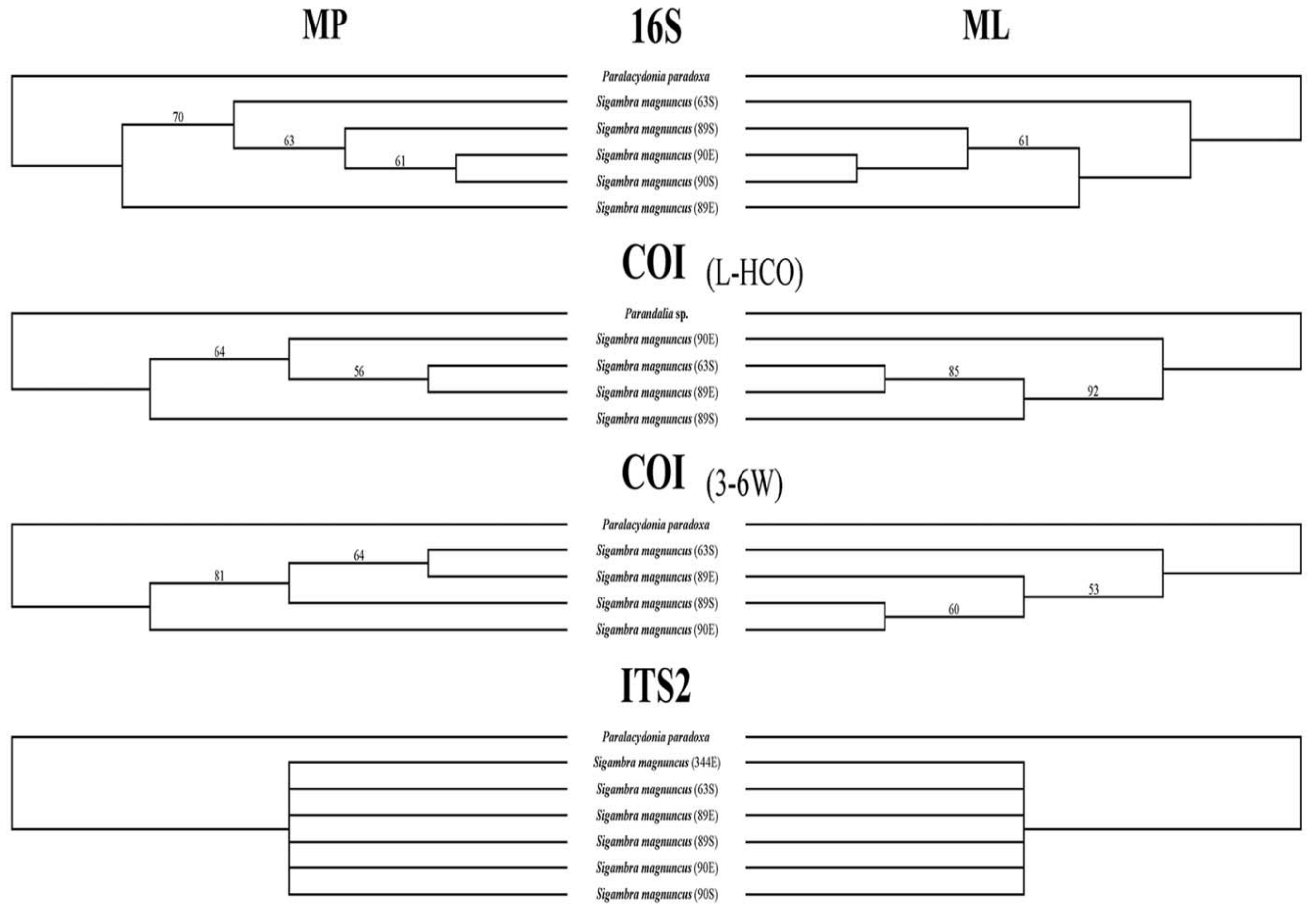

Fig. 117. Cladograms obtained from MP and ML analysis of the 16S, COI and ITS2 sequences. Bootstrap values > 50 shown above branches.

C = 0.1691, G = 0.1649, T = 0.2918); number of substitution types = 6; substitution rate matrix (A↔C = 5455.3633, A↔G = 15561.1738, A↔T = 7441.9106, C↔G = 3351.3784, C↔T = 21349.7070, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and gamma distribution shape parameter = 0.8596.

After exclusion of the primer sites, the alignment for the six sequences contained 507 characters, of which 133 were variable and three parsimony informative. The MP (tree length = 137, CI = 1.000, RI = 1.0000, RC = 1.0000) and the ML analysis (–ln L = 1129.49543) found single trees with slightly different topologies (Fig. 117).

COI (L-HCO) data set

Five sequences (four new, one from GenBank; Table 14) were included and analyses were rooted using *Parandalia* sp. (Pilargidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2156, C = 0.1986, G = 0.2037, T = 0.3821); number of substitution types = 6; substitution rate matrix (A↔C = 344699.0000, A↔G = 15672452.0000, A↔T = 0.0000, C↔G = 358084.0625, C↔T = 3512274.0000, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.5350; and gamma distribution shape parameter = 1.3171.

After exclusion of the primer sites, the alignment for the five sequences contained 658 characters, of which 212 were variable and 11 parsimony informative. The MP (tree length = 230, CI = 0.9783 (0.7222), RI = 0.5455, RC = 0.5336) and the ML analysis (–ln L = 1656.12690) found single trees with slightly different topologies (Fig. 117).

COI (3-6W) data set

Five newly acquired sequences (Table 14) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2696, C = 0.1842, G = 0.1770, T = 0.3692); number of substitution types = 6; substitution rate matrix (A↔C = 1708189.3750, A↔G = 3752059.0000, A↔T = 1403652.5000, C↔G = 1733010.1250, C↔T = 5084125.5000, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.0652; and gamma distribution shape parameter = 0.7883.

After exclusion of the primer sites, the alignment for the five sequences contained 421 characters, of which 132 were variable and five parsimony informative. The MP (tree length = 138, CI = 0.9928 (0.8571), RI = 0.8000, RC = 0.7942) and the ML analysis (–ln L = 1012.04140) found single trees with slightly different topologies (Fig. 117).

ITS2 data set

Seven newly acquired sequences (Table 14) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1952, C = 0.2798, G = 0.2677, T = 0.2573); number of substitution types = 6; substitution rate matrix (A↔C = 0.6514, A↔G = 1.8088, A↔T = 1.4737, C↔G = 1.2248, C↔T = 3.7107, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and gamma distribution shape parameter = 7.6482.

After exclusion of the primer sites, the alignment for the seven sequences contained 435 characters, of which 59 were variable and one parsimony informative. The ML analysis (–ln L = 838.06897) yielded three and the MP analysis 101 most parsimonious trees, which are 59 steps long with CI = 1.0000, RI = 1.0000, and RC = 1.0000. The topologies of both strict consensus trees agree completely (Fig. 117).

Discussion of molecular results

The monophyly of Pilargidae was supported by all phylogenetic analyses (see “Molecular phylogeny of abyssal Phyllodocida”). However, the taxon variously resulted as closely related to nephtyids (18S), on the basis to all investigated Phyllodocida (16S), or as sister to the nereidids (COI). The latter hypothesis was also reported by Rousset et al. (2007).

Within the pilargids the analyzed sequences of *Sigambra magnuncus*—a species previously described from the NE Atlantic (Paterson and Glover 2000)—showed complete agreement in the 18S rDNA data and the translated amino acid sequences of the COI gene. The more variable coding (16S, COI) and non-coding regions (ITS2) were also only slightly different from each other. Therefore, no clear population patterns were detected (Fig. 117), which suggests that gene flow for this taxon is not restricted within the Guinea Basin or by the Guinea Rise. Pilargidae have been known to have planktonic larvae (Bhaud 1973; Achari 1975) and this might be the reason for their often wide distribution.

Sphaerodoridae Malmgren, 1867

The Sphaerodoridae are an easily recognizable group of polychaetes that belong to the Phyllodocida, but their precise position is uncertain (Pleijel 2001m; Aguado and Rouse 2006). Their body shape is slender elongate or short and maggot-like, with the surface usually covered by typical macro- and/or microtubercles (Fauchald 1974; Fauchald and Rouse 1997). These sessile or stalked tubercles are often arranged in at least two dorsal rows; additional smaller papillae can be present (Fauchald 1974; Fauchald and Rouse 1997; Wilson 2000h). Furthermore, a more or less distinct, syllid-like muscular proventicle seems to be usually developed (Wilson 2000h; Pleijel 2001m; Aguado and Rouse 2006).

The Sphaerodoridae have a worldwide distribution from the intertidal to abyssal depths, but usually occur in low abundance (Pleijel 2001m). They are sometimes found on hard substrates, but are most common on soft sediments (Wilson 2000h). Fauchald and Jumars (1979) postulated that all sphaerodorids are free-living deposit-feeders probably feeding most frequently on the surface of the mud. However, some species are known to live in commensalism with a sedentary polychaete (Lützen 1961) or with other invertebrates like gorgonians and brittle stars (Martin and Alva 1988; Martin and Britayev 1998). Such symbiotic relationships are not known for the abyssal species examined here.

Of the nine species of Sphaerodoridae collected in the present study, four had been reported earlier only by their original descriptions: *Sphaerodoropsis chardyi* Desbruyères, 1980 from deep waters in the NE Atlantic Gulf of Gascogne; *Sphaerodoridium campanulata* Borowski, 1994, *Sphaerodoropsis furca* Fauchald, 1974 and *Sphaerodoropsis translucida* Borowski, 1994 from the Peru Basin in the E Pacific Ocean. The remaining five species are new to science: *Sphaerephesia regularis* sp. nov., *Sphaerodoropsis longianalpapilla* sp. nov., *Sphaerodoropsis macrotubercula* sp. nov., *Sphaerodoropsis protuberanca* sp. nov., and *Sphaerodoropsis rosehipiformis* sp. nov. In the descriptions below, the interpretations of the prostomium and its appendages, of the peristomium and anterior segments follow Pleijel (2001m) and Aguado and Rouse (2006).

Key to sphaerodorid species from the abyssal SE Atlantic

1. Dorsum with four to eight more or less symmetrically arranged macrotubercles in one or two transverse rows per chaetiger (Figs. 118A, 119A, 123A, 124A, 125A, 126A, 128A, 129A, 130A, 132A, 133A, 135A, 136A) 2
– Dorsum with innumerable, more or less randomly arranged, stalked macrotubercles and papillae (Figs. 121A; 122A, C) .... *Sphaerodoridium campanulata* Borowski
2. Up to four macrotubercles in one transverse row per chaetiger, arranged in distinct longitudinal rows on dorsum (Figs. 118A, 119A, 125A, 126A, 128A, 129A, 132A, 133A) 3
– More than four macrotubercles in two transverse rows per chaetiger, arranged in a more or less distinct pattern on dorsum (Figs. 123A, 124A, 130A, 135A, 136A) 6
3. Macrotubercles distally rounded (Figs. 125E, 126B, 128F, 129B, 132D, 133A); two widely separated double longitudinal rows of macrotubercles situated dorso-laterally on dorsum (Figs. 125A, 126A, 128A, 129A, 132A, 133A) 4
– Macrotubercles with a short terminal papilla (Figs. 118D, 119D); four more closely spaced longitudinal rows of macrotubercles on dorsum (Figs. 118A, 119A) .... *Sphaerephesia regularis* sp. nov.
4. Body surface with some scattered minute papillae, prostomium with a few small globular to conical ones (Figs. 128B, C; 129B; 132B; 133B); macrotubercles all globular (Figs. 128A, 129A, 132A, 133A); specimens often with four red-brown pigmented pharyngeal glands in anterior segments (Figs. 128A, B; 129C; 132A) 5
– Body surface with innumerable globular to conical papillae, prostomium with some more digitiform ones, which resemble antennae (Figs. 125B, C; 126A, B); most macrotubercles globular but posterior ones usually more conical (Figs. 125A, 126A); pharyngeal glands not pigmented .... *Sphaerodoropsis furca* Fauchald
5. Prostomium anteriorly rounded and more or less fused with first segment (Figs. 128B, 129B); medio-ventral anal papilla longer than lateral cirri (Figs. 128E, 129A); pharyngeal glands in a trapezoidal arrangement (Figs. 128A, B; 129C); proventricle well developed, visible through about four segments (Figs. 128A, 129C) .... *Sphaerodoropsis longianalpapilla* sp. nov.
– Prostomium rectangular and more or less distinctly delineated from first segment (Figs. 132A, B; 133B); medio-ventral anal papilla about as long as lateral cirri or slightly shorter (Fig. 132C); pharyngeal glands arranged in one transverse row (Fig. 132A); proventricle indistinctly developed, visible through about two segments (Fig. 133C) .... *Sphaerodoropsis protuberanca* sp. nov.
6. Macrotubercles distally rounded (Figs. 123E, 130C) 7
– Macrotubercles with a cap-like structure or terminal papilla (Figs. 135F, 136A) 8
7. Each transverse row with up to eight globular macrotubercles differing in size and arranged in a loosely set, indistinct zig-zag pattern (Figs. 123A, 124A) .... *Sphaerodoropsis chardyi* Desbruyères
– Each transverse row with up to six very large globular macrotubercles arranged in a tightly set zig-zag pattern (Figs. 130A, 131B) .... *Sphaerodoropsis macrotubercula* sp. nov.
8. Macrotubercles with a cap-like structure (Fig. 135F).................................... *Sphaerodoropsis rosehipiformis* sp. nov.
– Macrotubercles with a terminal papilla (Figs. 136A) .... *Sphaerodoropsis translucida* Borowski

Sphaerephesia Fauchald, 1972

Sphaerephesia regularis sp. nov.

(Figs. 118–120, 137)

Etymology

The species epithet refers to the regularly arranged longitudinal rows of macrotubercles on the dorsum. It is to be treated as a Latin adjective for the purposes of nomenclature.

Material examined

Type material of Sphaerephesia regularis. R/V METEOR 63/2 st. 63 ES-S, 0°8.8′S 2°28.8′W–0°8.2′S 2°28.7′W, 15.iii.2005, 5048–5051 m; holotype: cs/3.0/19/0.8/0.3 (ZMH P25498); paratypes: cs/2.8/19/0.8/0.3, cs/2.6/19/0.8/0.3, cs/2.5/17/0.7/0.3, cs/0.7/5/0.3/0.2 (ZMH P25499, 2 parapodia for DNA).—R/V METEOR 63/2 st. 63 ES-E, 0°8.8′S 2°28.8′W–0°8.2′S 2°28.7′W, 15.iii.2005, 5048–5051 m; paratypes: cs/2.5/19/0.8/0.3, cs/2.4/19/0.9/0.4, cs/2.3/19/0.5/0.2, cs/2.2/18/0.8/0.3 (all ZMH P25497 B), cs/2.1/19/0.7/0.4 (ZMH P25497 A, on SEM stub).

Additional material of Sphaerephesia regularis. See Appendix 1.

Type material of other species. *Sphaerodoropsis laureci*: Campagne POLYGAS du N.O. JEAN CHARCOT st. DS 16, Golfe de Gascogne, 47°36.1′N 8°40.5′W, 19.x.–4.xi.1972, 2325 m; holotype: cs/2.9/22/0.65/0.3 (MNHN Type 1286).—*Sphaerodoropsis longipapillata*:

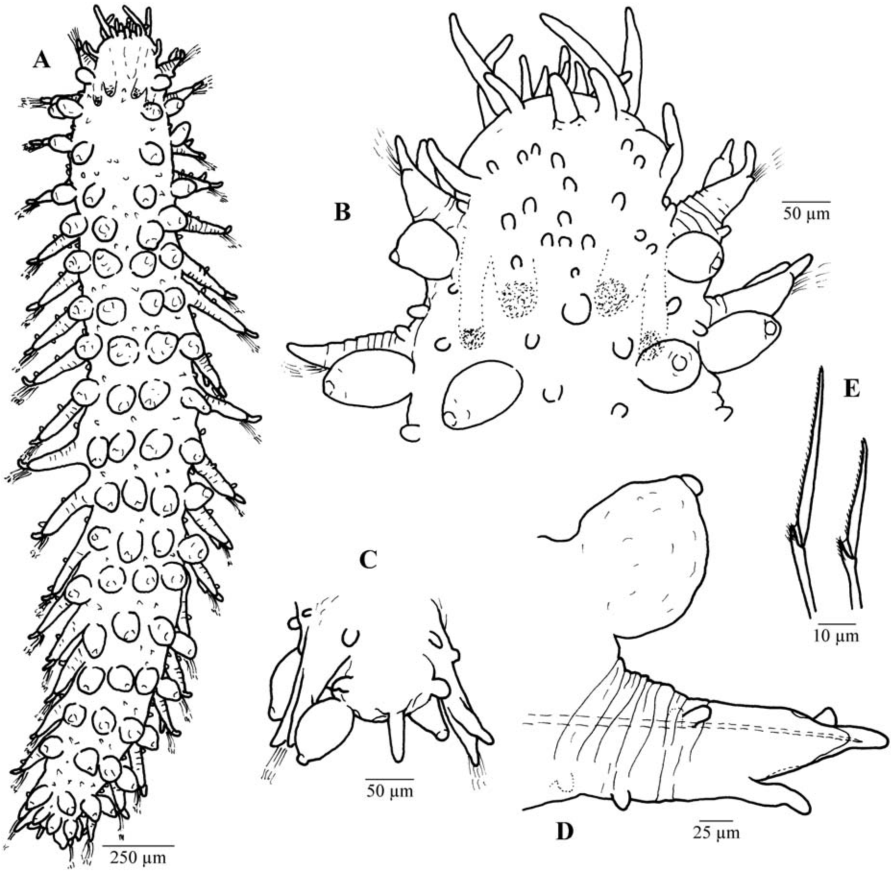

Fig. 118. *Sphaerephesia regularis* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Posterior end; ventral view. (D) Parapodium of mid-body; posterior view, chaetae omitted. (E) Chaetae. (A–C: ZMH P25498; D, E: ZMH P25499).

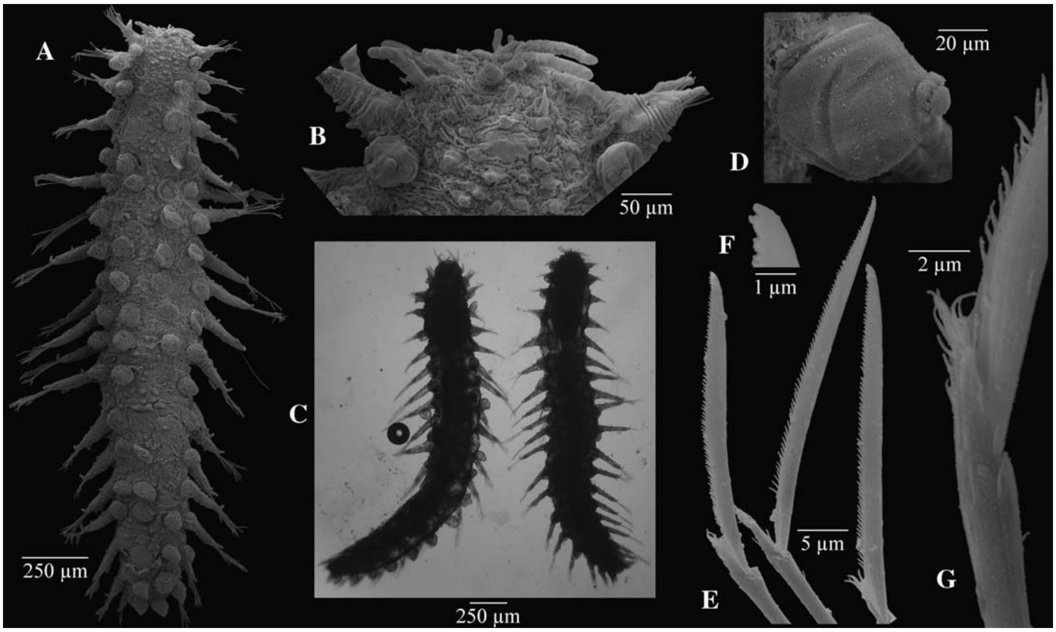

Fig. 119. *Sphaerephesia regularis* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of two complete specimens; dorsal view. (D) Macrotubercle. (E) Chaetae. (F) Tip of chaeta. (G) Detail of chaetal shaft. (A, B, D–G: ZMH P25497 A; C: ZMH P25498 and ZMH P25499).

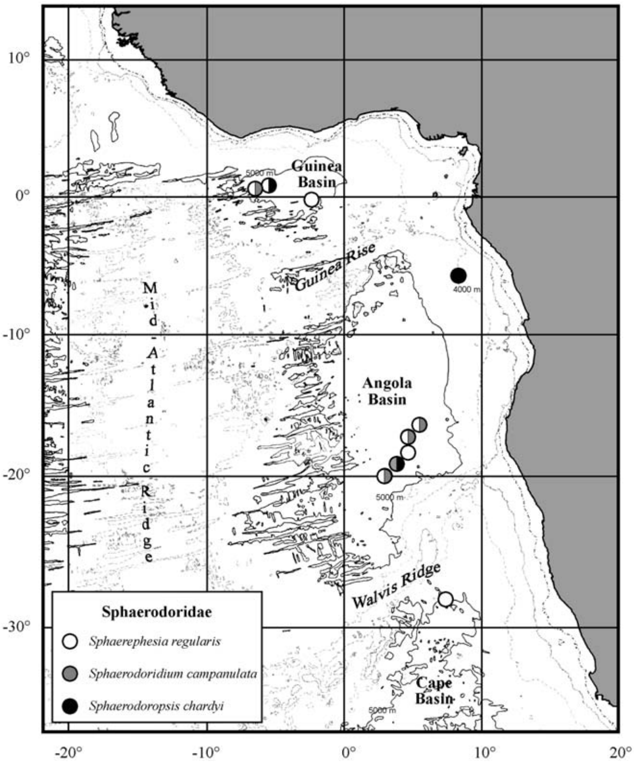

Fig. 120. Distribution of some sphaerodorid species in the studied region.

Campagne BIOGAS V du N.O. CRYOS, Golfe de Gascogne, 47°31′N 9°35′W, 10.–21.vi.1974, 4150 m; holotype: cs/3.9/25/1.0/0.4 (MNHN Type 1283).

Diagnosis

Prostomium with some elongated papillae; four sessile macrotubercles with small, knob-like terminal papilla in one transverse row per chaetiger, regularly arranged in distinct longitudinal rows on dorsum; microtubercles absent; ventral cirri slightly shorter than postchaetal lobes; parapodia with a few papillae; chaetae indistinctly bidentate, not twice as long as parapodia.

Description

Body up to 4.3 mm long with up to 23 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 118A; 119A, C). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and some conical to digitiform papillae (Figs. 118A–C, 119A–C). Frontal antennae and palps all digitiform and of about same length or antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and more conical, inserted more dorsally (Figs. 118A, B; 119A, B). Eyes absent. Nuchal organs not observed.

Proboscis everted in one specimen, without papillae and more or less smooth terminal ring. Proventricle well developed with numerous muscle rings; visible through about three segments (Fig. 119C). Some specimens with two distinct pairs of red-brown pigmented eye-like pharyngeal glands; trapezium-shaped arranged around chaetigers 1–3 (Figs. 118A, 119C).

First segment achaetous, with one pair of digitiform cirri and some small globular to conical papillae; cirri slightly longer than median antenna; inserted laterally (Figs. 118B; 119B).

Second segment with one and following chaetigers with two pairs of dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 118A, B; 119A, B). Parapodia all uniramous with conical to digitiform pre- and distinctly shorter triangular to conical postchaetal lobes; rami more or less distinct wrinkled and with a few globular to conical papillae (Fig. 118D). Macrotubercles large globular to conical, sessile and with small knob-like terminal papilla (Fig. 119D); arranged dorsally in four distinct longitudinal rows (Figs. 118A, 119A). Ventral cirri conical to digitiform; slightly shorter than postchaetal lobes; inserted near terminal end of parapodia (Fig. 118D). Body surface with numerous scattered globular to conical papillae; dorsally more than ventrally (Figs. 118A–C; 119A, B).

All parapodial lobes with one straight acicula (Fig. 118D), and a few falcigerous compound chaetae (Figs. 118E, 119E). Falcigers with slightly different long paring-knife shaped, indistinctly bidentate blades (Fig. 119F); subdistally blades with fine serration over entire length of margin; shafts with some long and slender subdistal spines (Fig. 119G).

Pygidium with anus and a pair of termino-lateral conical and distally knobbed cirri and an additional digitiform medio-ventral papilla, which is about as long as lateral cirri or slightly shorter (Fig. 118C).

Distribution

Angola, Cape and Guinea Basins; 5048–5494 m (Fig. 120).

Discussion

So far, only four species of *Sphaerephesia* were known from intertidal to slope depths: *S. chilensis* Fauchald, 1974; *S. fauchaldi* Kudenov, 1987; *S. longisetis* Fauchald, 1972; and *S. similisetis* Fauchald, 1972. The new species is most closely related to the first two of those, but differs from *S. chilensis* in having much shorter ventral cirri, and from *S. fauchaldi* in lacking dorsal microtubercles (Fauchald 1974; Kudenov 1987).

The remaining two species were originally described without longer prostomial papillae; moreover, the ventral cirri of *S. similisetis* are distinctly larger than in *S. regularis* sp. nov., and prolonged chaetae and microtubercles are present in *S. longisetis* (Fauchald 1972).

The two more or less identical species *Sphaerodoropsis laureci* Desbruyères, 1980 and *S. longipapillata* Desbruyères, 1980 are also very similar, but the respective holotypes (MNHN Types 1286 and 1283) show regularly arranged macrotubercles that are distally rounded and lack terminal papillae, and the entire body surfaces carry much higher numbers of papillae.

Sphaerodoridium Lützen, 1961

Sphaerodoridium campanulata Borowski, 1994

(Figs. 120–122, 137)

Sphaerodoridium campanulata Borowski, 1994—Borowski (1994, p. 194, figs. 1, 2)

Nomenclature

The species epithet "derives from the latin word *campanula* (little bell)" (Borowski 1994, p. 194) but, due to the ending ("-ta") that was attached, looks adjectival, in which case it would have to be changed to match the neuter gender of the genus name. However, as the species name appears to have been used in the original spelling only, the latter is maintained here in accordance with ICZN (1999) Code Article 31.2.2.

Material examined

Type material. Sphaerodoridium campanulata: DISCOL 3 program, R/V SONNE 77 st. KG 1458, Peru Basin, 7°4.184′S 88°27.343′W, 7.ii.1992, 4163 m; holotype: cs/0.6/9/0.24/0.12 (SMF 4486).

Additional material. See Appendix 1.

Diagnosis

Antennae and palps without proximal papillae; median prostomial antenna shorter than frontal antennae; dorsum with innumerable, more or less randomly arranged, stalked macrotubercles and globular, conical or bell/club-shaped papillae; ventral cirri slightly shorter than postchaetal lobes; parapodia usually with one large papilla; venter with longitudinal rows of papillae; chaetae unidentate.

Description

Body up to 1.2 mm long with up to 16 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 121A; 122A, C). Segments uniannulate; indistinctly separated from each other. Preserved

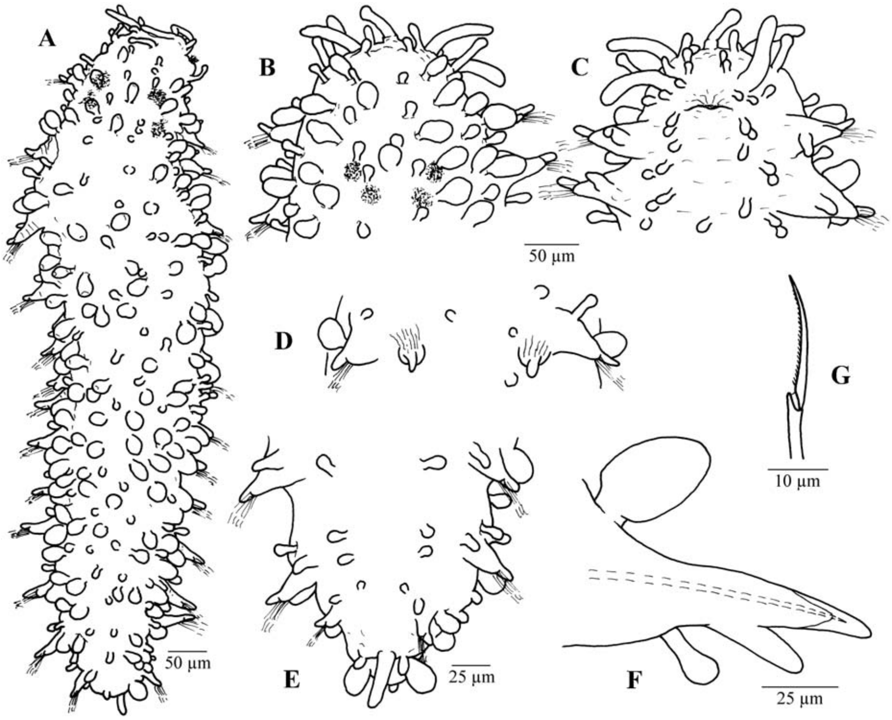

Fig. 121. *Sphaerodoridium campanulata* Borowski. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Chaetiger 6 with specialized ventral cirri; ventral view. (E) Posterior end; ventral view. (F) Parapodium of mid-body; posterior view, chaetae omitted. (G) Chaeta. (A, F, G: ZMH P25510; B–D: ZMH P25509 B; E: ZMH P25509 A).

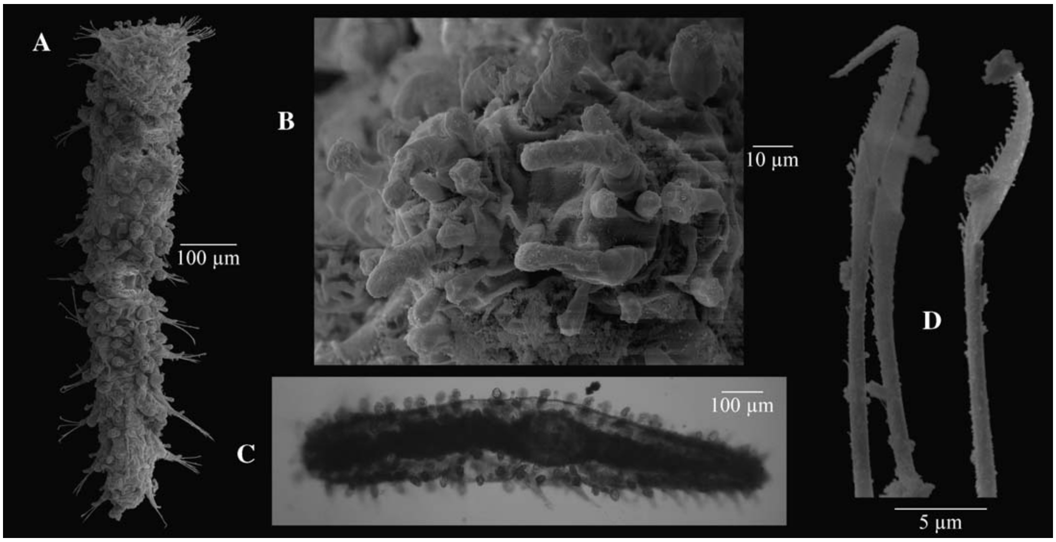

Fig. 122. *Sphaerodoridium campanulata* Borowski. (A) Complete specimen; dorsal view. (B) Anterior end; frontal view. (C) Light micrograph of complete specimen; dorsal view. (D) Chaetae. (A, B, D: ZMH P25511; C: ZMH P25509 B).

specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and numerous conical to digitiform papillae (Figs. 121A–C, 122B). Frontal antennae and palps all digitiform; antennae slightly longer and thinner than palps; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and terminally slightly swollen more club-shaped, inserted more dorsally (Figs. 121B, C; 122B). Eyes absent. One specimen apparently with two ciliated and cushion-like nuchal organs; laterally arranged between prostomium and first segment (Fig. 121A).

Proboscis retracted in all specimens, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about two segments. Some specimens with two distinct pairs of red-brown pigmented eye-like pharyngeal glands; trapezium-shaped arranged around chaetigers 1–2 (Figs. 121A, B; 122C).

First segment achaetous, with one pair of digitiform to club-shaped cirri and some conical to bell-shaped papillae; cirri as long or slightly shorter than median antenna; inserted laterally (Figs. 121A–C; 122B).

Second segment and following chaetigers with dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 121A–C, 122A–C). Parapodia all uniramous with conical to digitiform pre- and distinctly shorter triangular to conical postchaetal lobes; rami sometimes wrinkled and often with one large club-shaped papilla on anterior base (Fig. 121F). Innumerable macrotubercles of slightly different size, large globular to conical, shortly stalked and without terminal papilla; more or less randomly arranged (Figs. 121A; 122A, C). Ventral cirri conical to digitiform; slightly shorter than postchaetal lobes; inserted near middle of parapodia (Fig. 121F); 6th chaetiger of two specimens with basely located cirri, which are inflated and filled with glandular-like tissue (Fig. 121D). Body surface with innumerable scattered globular, conical or bell/club-shaped papillae (Figs. 121A–E, 122A–C).

All parapodial lobes with one straight acicula (Fig. 121F), and a few falcigerous compound chaetae (Figs. 121G, 122D). Falcigers with slightly different long paring-knife to sickle shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with some long and slender subdistal spines (Fig. 122D).

Pygidium with anus and a pair of termino-lateral conical to globular cirri and an additional digitiform medio-ventral papilla, which is distinctly longer than lateral cirri (Fig. 121E).

Remarks

The specialized inflated ventral cirri of chaetiger six could be interpreted as a penis structure (Moreira et al. 2004), and are also present in the holotype (SMF 4486).

Distribution

Angola and Guinea Basins; 5068–5494 m (Fig. 120).

Discussion

The blades of the chaetae were originally described as smooth (Borowski 1994), but SEM examination shows them to be distinctly serrated.

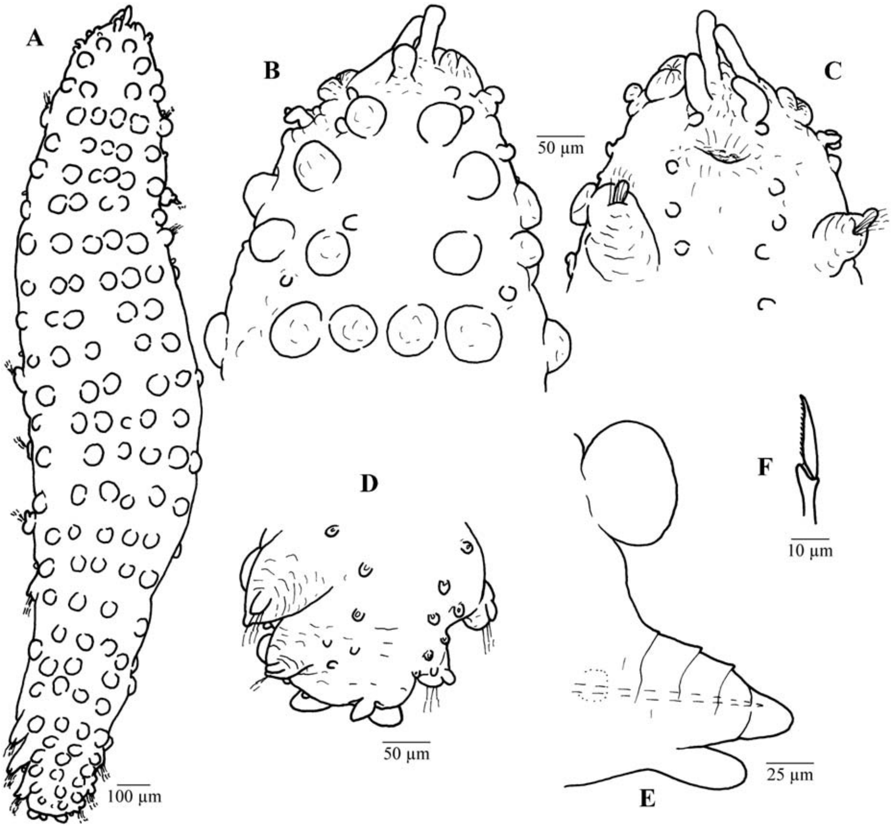

Fig. 123. *Sphaerodoropsis chardyi* Desbruyères. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Posterior end; ventral view. (E) Parapodium of mid-body; posterior view, chaetae omitted. (F) Chaeta. (A–F: ZMH P25513).

Sphaerodoropsis Hartman & Fauchald, 1971

Sphaerodoropsis chardyi Desbruyères, 1980

(Figs. 120, 123, 124, 137)

Sphaerodoropsis chardyi Desbruyères, 1980—Desbruyères (1980, p. 115; pl. 4, figs. A–E)

Material examined

Type material of Sphaerodoropsis chardyi. Campagne BIOGAS IV du N.O. JEAN CHARCOT st. DS 51, Golfe de Gascogne, 44°11.3′N 4°15.4′W, 16.–28.ii.1974, 2430 m; holotype: cs/1.65/14/0.4/0.3 (MNHN Type 1282).

Additional material of Sphaerodoropsis chardyi. See Appendix 1.

Type material of other species. Sphaerodorum distichum: Skagerak Expedition 1933 st. 20, 58°5′N 8°32′E, 4.vii.1933, 460 m; holotype: cs/2.2/15/0.5/0.4 (UUZM 203).

Diagnosis

Prostomium without elongated papillae; up to eight sessile and distally rounded, globular macrotubercles in each of the two transverse rows per chaetiger, arranged in an indistinct zig-zag pattern on dorsum; ventral cirri about as long as postchaetal lobes; parapodia usually with one globular papilla; venter with some scattered small papillae; chaetae unidentate; medio-ventral anal papilla slightly shorter than lateral cirri.

Description

Body up to 2.3 mm long with up to 13 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 123A; 124A). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly slightly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and a few small globular papillae (Figs. 123A–C; 124A, B). Frontal antennae and palps all conical to digitiform; antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and more conical, inserted more dorsally (Fig. 123B, C). Eyes absent. One specimen with two possibly everted large cushion-like nuchal organs; laterally arranged between prostomium and first segment (Fig. 123B, C).

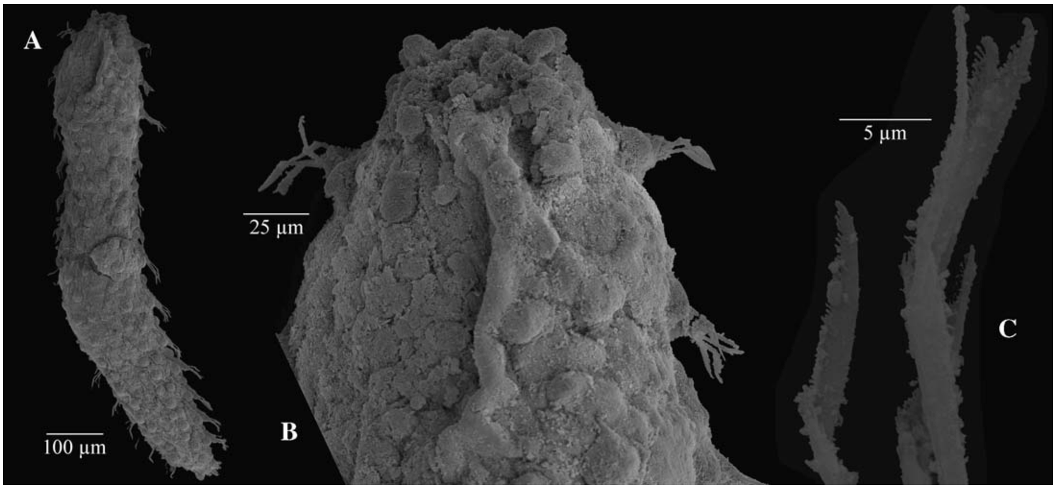

Fig. 124. *Sphaerodoropsis chardyi* Desbruyères. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Chaetae. (A–C: ZMH P25512 B).

Proboscis retracted in all specimens, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about two segments. Some specimens with two pairs of red-brown pigmented eye-like pharyngeal glands; indistinctly trapezium-shaped arranged around chaetigers 1–2.

First segment achaetous, with one pair of conical cirri and a few small globular papillae; cirri about as long as median antenna or slightly shorter; inserted laterally (Fig. 123B, C).

Second segment and following chaetigers with dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 123A, 124A). Parapodia all uniramous with triangular to conical pre- and shorter rounded postchaetal lobes; rami more or less distinct wrinkled and usually with one globular papilla on anterior base (Fig. 123E). Macrotubercles of different size, globular, sessile and without terminal papilla; each chaetiger with two more or less conspicuous transverse rows of up to eight (usually six) tubercles arranged in a more sparsely indistinct zig-zag pattern; number of macrotubercles decreased anteriorly and posteriorly (Figs. 123A, 124A). Ventral cirri conical to digitiform; about as long as postchaetal lobes; inserted on middle of parapodia (Fig. 123E). Body surface with some scattered small globular papillae; ventrally more than dorsally (Figs. 123A–D; 124A, B).

All parapodial lobes with one straight acicula (Fig. 123E), and a few falcigerous compound chaetae (Figs. 123F, 124C). Falcigers with slightly different long paring-knife to sickle shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with some long and slender subdistal spines (Fig. 124C).

Pygidium with anus and a pair of termino-lateral globular cirri and an additional conical medio-ventral papilla, which is slightly shorter than lateral cirri (Fig. 123D).

Distribution

Angola and Guinea Basins; 3961–5468 m (Fig. 120).

Discussion

The specimens are referred to *Sphaerodoropsis chardyi* Desbruyères, 1980, even though the holotype (MNHN Type 1282) from the NE Atlantic carries no more than six macrotubercles per transverse row. *Sphaerodoropsis disticha* (Eliason, 1962) is somewhat similar, but its holotype (UUZM 203) was described as lacking distinct antennae or palps (Eliason 1962).

Sphaerodoropsis furca Fauchald, 1974

(Figs. 125–127, 138)

Sphaerodoropsis furca Fauchald, 1974—Fauchald (1974, p. 272, figs. 3.14–16)

Material examined

See Appendix 1.

Diagnosis

Prostomium with numerous elongated papillae, a few appearing bifurcate; four sessile and distally rounded, globular to conical macrotubercles in one transverse row per chaetiger, dorso-laterally arranged in distinct longitudinal rows on dorsum; ventral cirri longer than postchaetal lobes; parapodia with a few papillae; venter with numerous scattered papillae; chaetae unidentate; medio-ventral anal papilla about as long as lateral cirri.

Description

Body up to 4.0 mm long with up to 22 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 125A; 126A, C). Segments uniannulate but

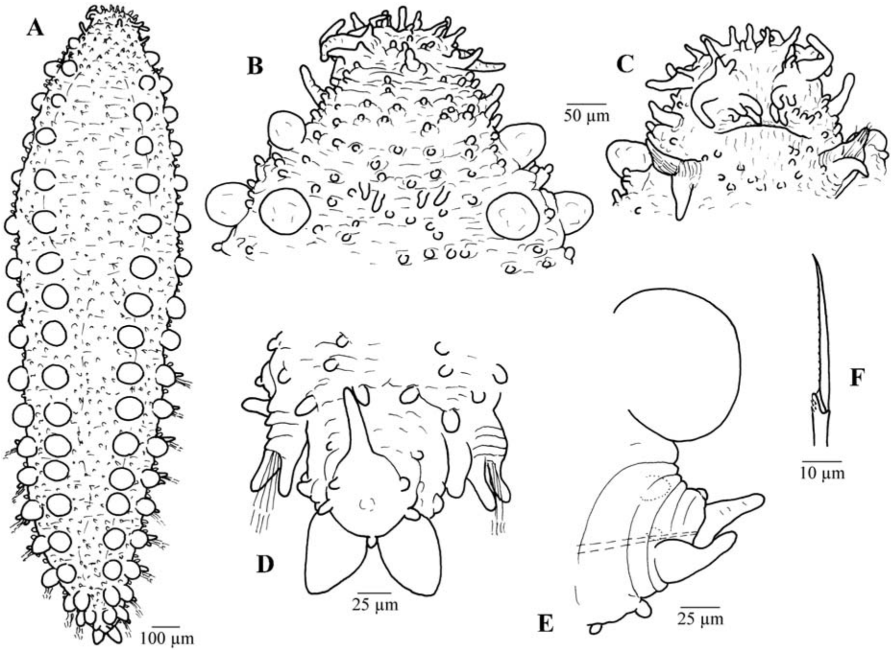

Fig. 125. *Sphaerodoropsis furca* Fauchald. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Posterior end; ventral view. (E) Parapodium of mid-body; posterior view, chaetae omitted. (F) Chaeta. (A–F: ZMH P25514 A).

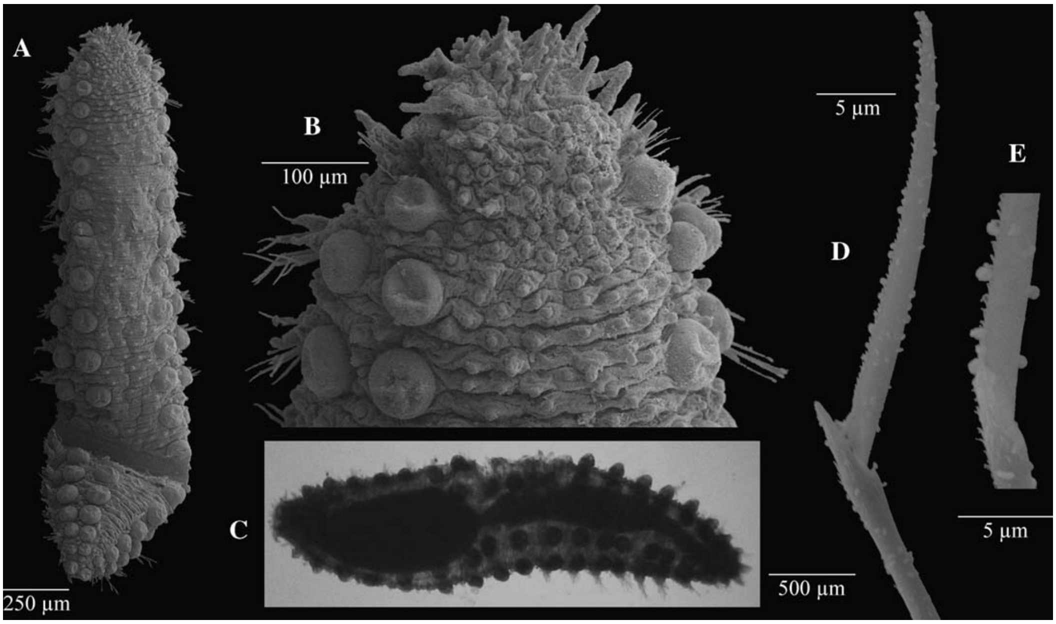

Fig. 126. *Sphaerodoropsis furca* Fauchald. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of complete specimen; dorsal view. (D) Chaeta. (E) Detail of chaeta. (A, B, D, E: ZMH P25514 B; C: ZMH P25514 A).

secundarly ringed; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly slightly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and a few small globular and numerous conical to digitiform papillae which sometimes appear to be bifurcate (Figs. 125A–C, 126B). Frontal antennae and palps all digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and more conical, inserted more dorsally

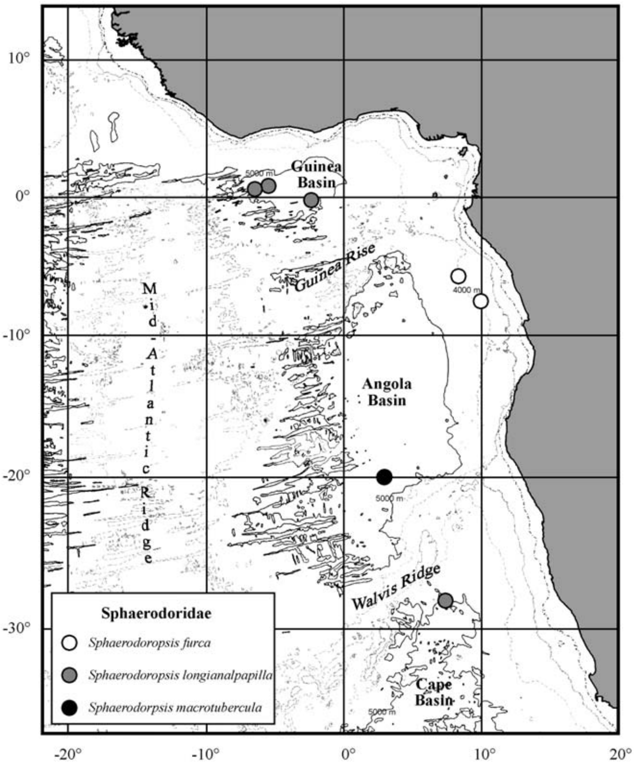

Fig. 127. Distribution of some sphaerodorid species in the studied region.

(Figs. 125A, B; 126B). Eyes absent. Nuchal organs not observed.

Proboscis retracted in all specimens, not observed. Proventricle well developed with numerous muscle rings; visible through about six segments (Figs. 125A, 126C). Pigmented pharyngeal glands not observed.

First segment achaetous, with one pair of conical to digitiform cirri and numerous small globular to conical mirotubercles or papillae; cirri slightly longer than median antenna; inserted laterally (Figs. 125B, C; 126B).

Second segment with one and following chaetigers with two pairs of dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 125A, B; 126A–C). Parapodia all uniramous with conical to digitiform pre- and distinctly shorter more rounded postchaetal lobes; rami more or less distinct wrinkled and with a few globular to conical papillae (Fig. 125E). Macrotubercles large globular, sessile and without terminal papilla; in posterior parapodia usually more conical; arranged dorso-laterally in four distinct longitudinal rows (Figs. 125A, 126A). Ventral cirri conical to digitiform; longer than postchaetal lobes; inserted near terminal end of parapodia (Fig. 125E). Dorsal body surface covered with innumerable globular and some more conical papillae (Figs. 125A, B; 126A, B); venter with numerous scattered globular to conical papillae (Fig. 125C, D).

All parapodial lobes with one straight acicula (Fig. 125E), and a few falcigerous compound chaetae (Figs. 125F, 126D). Falcigers with slightly different long paring-knife shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with a few subdistal spines (Figs. 125F; 126D, E).

Pygidium with anus and a pair of termino-lateral conical cirri and an additional digitiform medio-ventral papilla, which is about as long as lateral cirri (Fig. 125D).

Remarks

In smaller specimens the proventricle is only visible through about two to four segments, and the number and size of the papillae is decreased.

Distribution

Angola Basin; 3945–3994 m (Fig. 127).

Discussion

Sphaerodoropsis furca was originally described with three pairs of antennae: a superior one with a basal spur, and smooth intermediate and inferior ones, which are now interpreted as papillae, antennae and palps (Pleijel 2001m). The species shows great similarities with three other deep-sea taxa: *Sphaerodoropsis anae* Aguado & Rouse, 2006, *S. sibuetae* Desbruyères, 1980, and *S. stellifer* Aguirrezabalaga & Ceberio, 2005. However, bifurcated prostomial papillae are not reported in any of these. Furthermore, the latter two species (from the NE Atlantic) have either terminally star-shaped papillae (*S. stellifer*; Aguirrezabalaga and Ceberio 2005) or a higher number of parapodial papillae (*S. sibuetae*; Desbruyères 1980), whereas *S. anae* (from the Pacific) is equipped with bidentate chaetae (Aguado and Rouse 2006).

Sphaerodoropsis longianalpapilla sp. nov.

(Figs. 127–129, 138)

Etymology

The species epithet refers to the elongate conical medio-ventral papilla of the anus. It is to be treated as a noun in apposition for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 64 ES-S, 0°13.3′S 2°29.9′W–0°13.2′S 2°29.5′W, 16.iii.2005, 5053–5055 m; holotype: cs/2.5/17/0.8/0.5 (ZMH P25537); paratypes: cs/1.9/14/0.7/0.5, cs/1.7/13/0.5/0.3, cs/1.5/13/0.5/0.3, cs/1.4/12/0.6/0.4 (ZMH P25538).—R/V METEOR 63/2 st. 64 ES-E, 0°13.3′S 2°29.9′W–0°13.2′S

2°29.5′W, 16.iii.2005, 5053–5055 m; paratypes: cs/2.0/17/0.6/0.4, cs/1.7/13/0.5/0.3, cs/1.5/12/0.5/0.3, cs/1.1/9/0.5/0.3 (ZMH P25536).

Additional material. See Appendix 1.

Diagnosis

Prostomium without elongated papillae; four sessile and distally rounded, globular macrotubercles in one transverse row per chaetiger, dorso-laterally arranged in distinct longitudinal rows on dorsum; ventral cirri about as long as postchaetal lobes; parapodia without papillae; venter partly with two longitudinal rows of papillae; chaetae unidentate; medio-ventral anal papilla longer than lateral cirri.

Description

Body at least 4.0 mm long with up to 22 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 128A; 129A, C). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and a some small globular to conical papillae (Figs. 128A–C; 129A, B). Frontal antennae and palps all digitiform and of about same length or antennae slightly longer than palps; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and more conical, inserted more dorsally (Figs. 128B, 129B). Eyes absent. Nuchal organs not observed.

Proboscis retracted in all specimens, not observed. Proventricle well developed with numerous muscle rings; visible through about four segments (Figs. 128A, 129C). Some specimens with two distinct pairs of red-brown pigmented eye-like pharyngeal glands; trapezium-shaped arranged around chaetigers 2–4 (Figs. 128A, B; 129C).

First segment achaetous, with one pair of conical cirri and a few small globular to conical papillae; cirri slightly longer than median antenna; inserted laterally (Figs. 128B, C; 129B).

Second segment with one and following chaetigers with two pairs of dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 128A–C; 129A, B). Parapodia all uniramous with conical to digitiform pre- and distinctly shorter triangular to conical postchaetal lobes; rami basally indistinct wrinkled (Fig. 128F). Macrotubercles large globular, sessile and without terminal papilla; arranged dorso-laterally in four distinct longitudinal rows (Figs. 128A, 129A). Ventral cirri conical to digitiform; about as long as postchaetal lobes; inserted on parapodial base (Fig. 128F). Body surface with a few scattered minute papillae (Fig. 129A, B); ventrally partly arranged in two rows near parapodial basis (Fig. 128E).

All parapodial lobes with one straight acicula (Fig. 128F), and a few falcigerous compound chaetae (Figs. 128G, 129D). Falcigers with slightly different long paring-knife shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with some scattered spines (Fig. 129E).

Pygidium with anus and a pair of termino-lateral globular cirri and an additional conical medio-ventral papilla, which is longer than lateral cirri (Fig. 128E).

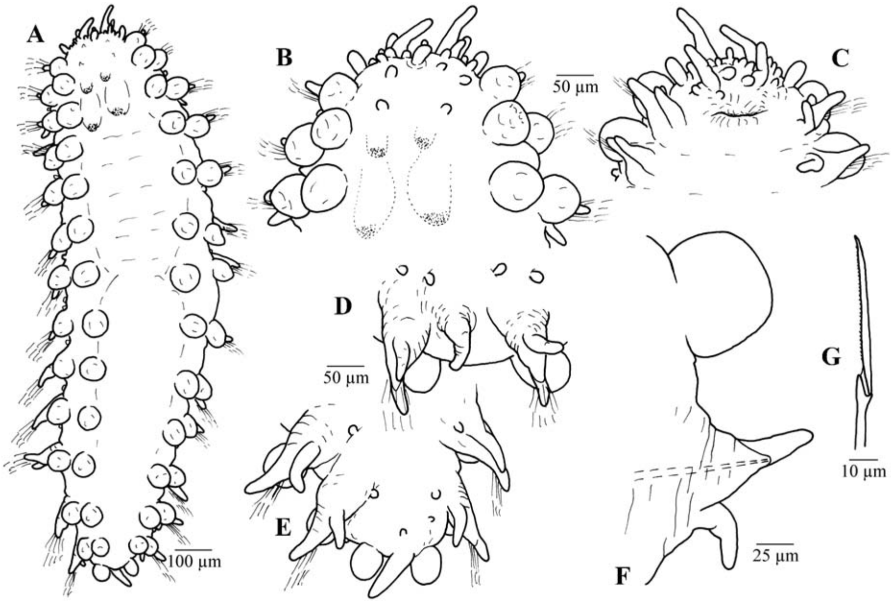

Fig. 128. *Sphaerodoropsis longianalpapilla* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Additional cirrus between chaetigers 7 and 8; ventral view. (E) Posterior end; ventral view. (F) Parapodium of mid-body; posterior view, chaetae omitted. (G) Chaeta. (A–G: ZMH P25538).

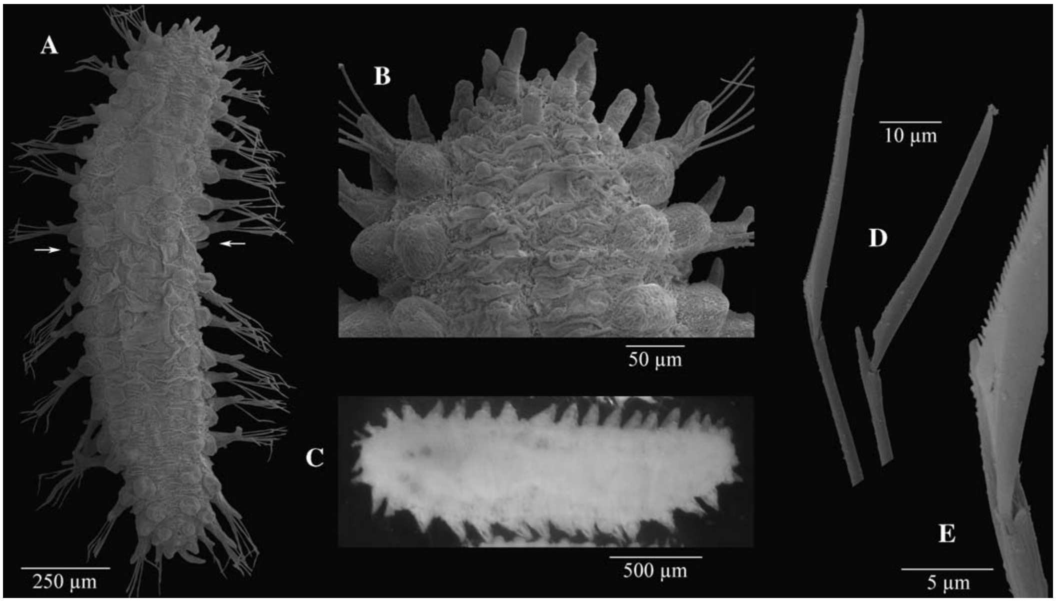

Fig. 129. *Sphaerodoropsis longianalpapilla* sp. nov. (A) Complete specimen with additional cirri (white arrows); dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of complete specimen; dorsal view. (D) Chaetae. (E) Detail of chaeta. (A, B, D, E: ZMH P25535 A; C: ZMH P25537).

Remarks

A few specimens have an additional pair of digitiform cirri located ventro-laterally between chaetigers seven and eight, which might be penis structures (Figs. 128D, 129A).

Distribution

Cape and Guinea Basins; 5048–5443 m (Fig. 127).

Discussion

Sphaerodoropsis longianalpapilla sp. nov. belongs to the *Sphaerodoropsis* Group 1 (sensu Borowski 1994), which is characterized by four longitudinal rows of macrotubercles and one transverse row per segment. Within this group the taxon is most closely related to *Sphaerodoropsis protuberanca* sp. nov., but differs in having the prostomium and first segment more or less fused (rather than delineated), the pharyngeal glands in a trapezoidal arrangement (rather than in one transverse row), the proventricle well developed and visible through about four segments (instead two segments long and indistinct), and especially by a distinctly longer medio-ventral anal papilla.

Sphaerodoropsis macrotubercula sp. nov.

(Figs. 127, 130, 131B, 138)

Etymology

The species epithet refers to the very large macrotubercles. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 48/1 st. 325-7 MC 12, 19°58.4′S 2°59.8′E, 14.vii.2000, 5493 m; holotype: cs/1.2/13/0.3/0.2 (ZMH P25552).—R/V METEOR 48/1 st. 325-7 MC 12, 19°58.4′S 2°59.8′E, 14.vii.2000, 5493 m; paratype: cs/0.7/9/0.3/0.2 (ZMH P25551).

Diagnosis

Prostomium without elongated papillae; up to six sessile and distally rounded, enlarged globular macrotubercles in each of the two transverse rows per chaetiger, arranged in a tightly packed zig-zag pattern on dorsum; ventral cirri about as long as postchaetal lobes; parapodia without papillae; venter with a few scattered minute papillae; chaetae unidentate; medio-ventral anal papilla about as long as lateral cirri or slightly shorter.

Description

Body up to 1.2 mm long with up to 13 chaetigers; short and maggot-like, tapering anteriorly and posteiorly (Figs. 130A, B; 131B). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly slightly rounded, wider than long; more or less fused with first segment; with three antennae, two palps and a few small globular papillae (Fig. 130B). Frontal antennae digitiform and slightly

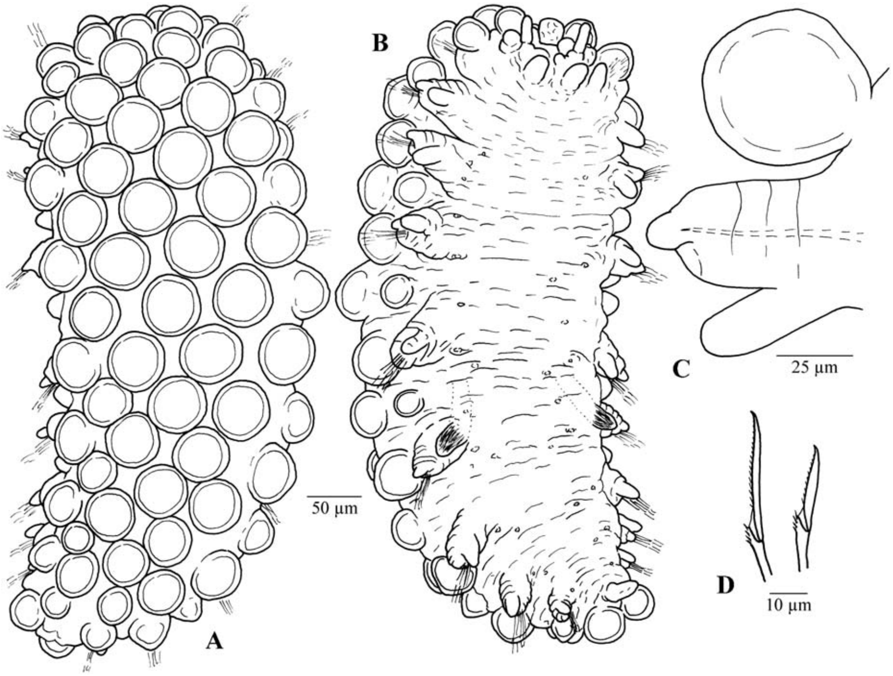

Fig. 130. *Sphaerodoropsis macrotubercula* sp. nov. (A) Complete specimen; dorsal view. (B) Complete specimen; ventral view. (C) Parapodium of mid-body; anterior view, chaetae omitted. (D) Chaetae. (A, B: ZMH P25551, C, D: ZMH P25552).

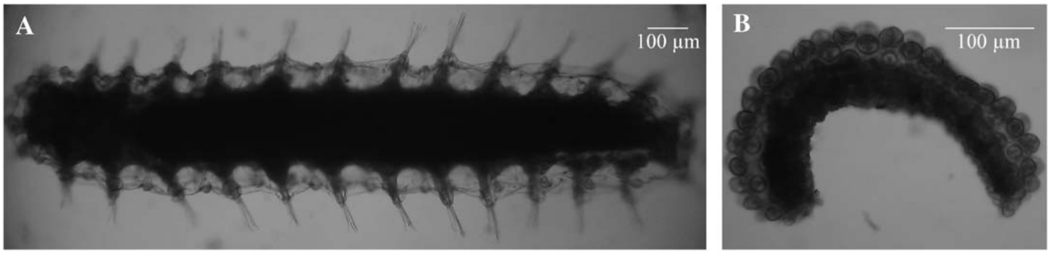

Fig. 131. (A) *Sphaerodoropsis rosehipiformis* sp. nov., complete specimen; dorsal view. (B) *Sphaerodoropsis macrotubercula* sp. nov., complete specimen; lateral view. (A: ZMH P25558; B: ZMH P25552).

longer than more broadly conical palps; inserted latero-dorsally and latero-ventrally; median antenna shorter and more oval to globular, inserted more dorsally (Fig. 130B). Eyes absent. Nuchal organs not observed.

Proboscis retracted in all specimens, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about one or two segments. Pigmented pharyngeal glands not observed.

First segment achaetous, with one pair of oval to globular cirri, which are about as long as median antenna or slightly shorter; inserted laterally (Fig. 130B).

Second segment and following chaetigers with dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 130A, B; 131B). Parapodia all uniramous with conical pre- and shorter rounded postchaetal lobes; rami more or less distinct wrinkled (Fig. 130C). Macrotubercles very large globular, sessile and without terminal papilla; each chaetiger with two transverse rows of up to six tubercles arranged in a tightly packed zig-zag pattern; number of macrotubercles decreased anteriorly and posteriorly (Figs. 130A, 131B). Ventral cirri conical to digitiform; about as long as postchaetal lobes; inserted on middle of parapodia (Fig. 130C), with exception of 6th chaetiger, where cirri are basely located, inflated and filled with glandular-like tissue (Fig. 130B). Ventral body surface with a few scattered minute papillae, usually six per chaetiger (Fig. 130B).

All parapodial lobes with one straight acicula (Fig. 130C), and a few falcigerous compound chaetae (Fig. 130D). Falcigers with slightly different long paring-knife to sickle shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with some long and slender subdistal spines (Fig. 130D).

Pygidium with anus and a pair of termino-lateral globular cirri and an additional conical medio-ventral

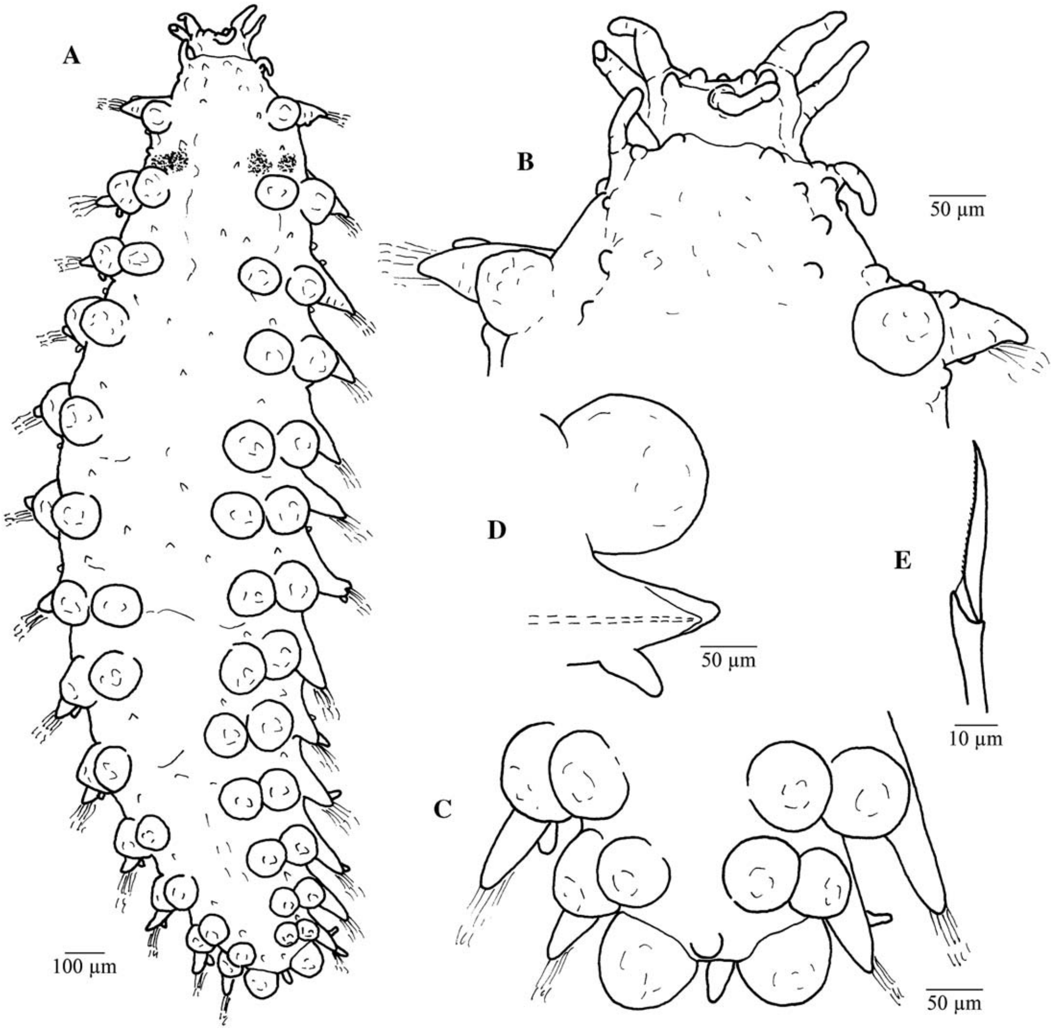

Fig. 132. *Sphaerodoropsis protuberanca* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Posterior end; dorsal view. (D) Parapodium of mid-body; posterior view, chaetae omitted. (E) Chaeta. (A–E: ZMH P25557).

papilla, which is about as long as lateral cirri or slightly shorter (Fig. 130B).

Remarks

The specialized inflated ventral cirri of chaetiger six were previously described by Moreira et al. (2004) for males of *Sphaerodoropsis garciaalvarezi* Moreira, Cacabelos & Troncoso, 2004, and can be interpreted as a penis structure for direct fertilization.

Distribution

Angola Basin; 5493 m (Fig. 127).

Discussion

Sphaerodoropsis macrotubercula sp. nov. belongs to the *Sphaerodoropsis* Group 3 (sensu Borowski 1994), which is characterized by more than four longitudinal rows of macrotubercles and two transverse rows per segment. Within this group the taxon is most closely related to *S. garciaalvarezi*. However, a papilla on the anterior parapodial surface is not observed in *S. macrotubercula* sp. nov., and the macrotubercles are distinctly larger and cover more or less the whole dorsum, which seems to be a unique feature.

Sphaerodoropsis protuberanca sp. nov.

(Figs. 132–134, 139)

Etymology

The anterior end of this species resembles the prostomial frontal protuberance found in some phyllodocid taxa.

Material examined

Type material of Sphaerodoropsis protuberanca. R/V METEOR 63/2 st. 63 ES-S, 0°8.8′S 2°28.8′W–0°8.2′S

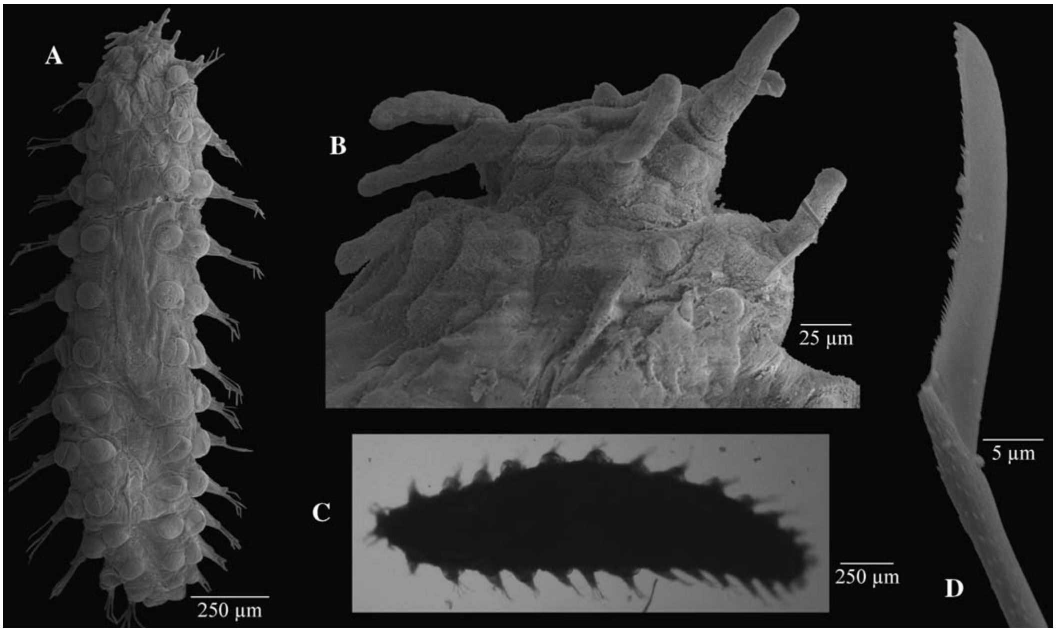

Fig. 133. *Sphaerodoropsis protuberanca* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Light micrograph of complete specimen; ventral view. (D) Chaeta. (A, B, D: ZMH P25555 B; C: ZMH P25557).

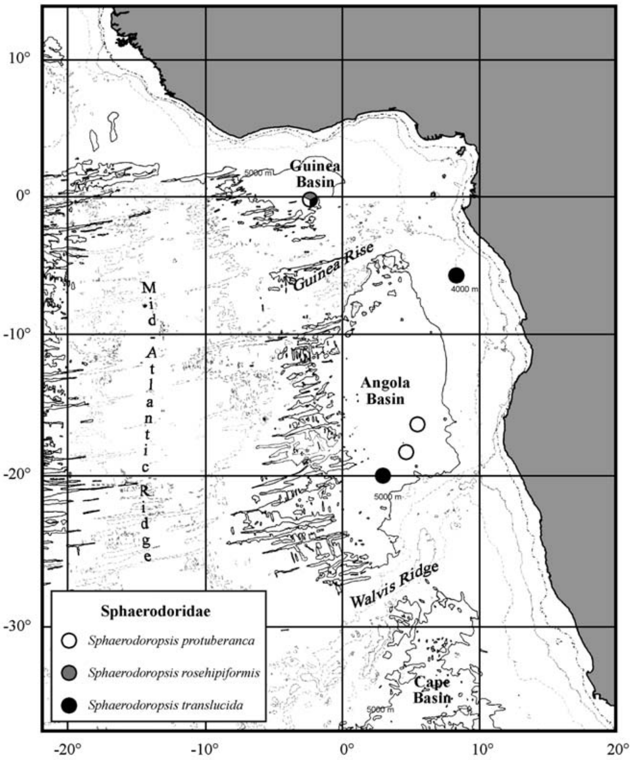

Fig. 134. Distribution of some sphaerodorid species in the studied region.

2°28.7′W, 15.iii.2005, 5048–5051 m; holotype: cs/2.3/13/0.9/0.4 (ZMH P25557); paratypes: cs/2.2/13/0.9/0.5, cs/2.0/12/0.7/0.4 (ZMH P25556).—R/V METEOR 63/2 st. 63 ES-E, 0°8.8′S 2°28.8′W–0°8.2′S 2°28.7′W, 15.iii.2005, 5048–5051 m; paratypes: cs/3.4/22/1.2/0.8 (ZMH P25555 A, 1 parapodium for DNA), cs/2.0/13/0.7/0.4 (ZMH P25555 B, on SEM stub).

Additional material of Sphaerodoropsis protuberanca. See Appendix 1.

Type material of other species. Sphaerodoropsis martinae: Campagne BIOGAS VI du N.O. JEAN CHARCOT st. DS 87, Golfe de Gascogne, 44°5.2′N 4°19.4′W, 16.x.–1.xi.1974, 1913 m; holotype: cs/2.16/15/0.52/0.35 (MNHN Type 1285).

Diagnosis

Prostomium without elongated papillae, distinctly delineated from first segment; four sessile and distally rounded, globular macrotubercles in one transverse row per chaetiger, dorso-laterally arranged in distinct longitudinal rows on dorsum; ventral cirri slightly shorter than postchaetal lobes; parapodia usually with one globular papilla; venter smooth or with a few inconspicuous papillae; chaetae unidentate; medio-ventral anal papilla about as long as lateral cirri or slightly shorter.

Description

Body up to 4.0 mm long with up to 22 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Figs. 132A; 133A, C). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium rectangular, wider than long; more or less distinctly delineated from first segment; with three antennae, two palps and a few small globular papillae (Figs. 132A, B; 133A, B). Frontal antennae and palps all digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna of similar shape but distinctly shorter, inserted more dorsally (Figs. 132B, 133B). Eyes absent. Nuchal organs not observed.

Proboscis retracted in all specimens, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about two segments (Fig. 133C). Some specimens with two distinct pairs of red-brown pigmented eye-like pharyngeal glands; arranged in one transverse row around chaetigers 1–3 (Fig. 132A).

First segment achaetous, with one pair of digitiform cirri and a few small globular papillae; cirri about as long as median antenna; inserted laterally (Figs. 132B, 133B).

Second segment with one and following chaetigers with two pairs of dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Figs. 132A, 133A). Parapodia all uniramous with triangular to conical pre- and slightly shorter postchaetal lobes (Fig. 132D); rami basally indistinct wrinkled and usually with one globular papilla on anterior base. Macrotubercles large globular, sessile and without terminal papilla; arranged dorso-laterally in four distinct longitudinal rows (Figs. 132A, 133A). Ventral cirri conical to digitiform; slightly shorter than postchaetal lobes; inserted near parapodial base (Fig. 132D). Dorsal body surface with some scattered minute papillae (Figs. 132A, 133A); venter smooth or with a few inconspicuous papillae.

All parapodial lobes with one straight acicula (Fig. 132D), and a few falcigerous compound chaetae (Figs. 132E, 133D). Falcigers with slightly different long paring-knife shaped, unidentate blades; subdistally blades with fine serration over entire length of margin; shafts with some scattered spines (Fig. 133D).

Pygidium with anus and a pair of termino-lateral globular cirri and an additional conical medio-ventral papilla, which is about as long as lateral cirri or slightly shorter (Fig. 132C).

Distribution

Angola and Guinea Basins; 5048–5443 m (Fig. 134).

Discussion

Sphaerodoropsis protuberanca sp. nov. belongs to the *Sphaerodoropsis* Group 1 (sensu Borowski 1994), which is characterized by four longitudinal rows of macrotubercles and one transverse row per segment. Within this group the taxon is most closely related to *S. longianalpapilla* sp. nov., but differs in having the prostomium and first segment more or less delineated (rather than fused), the pharyngeal glands in one transverse row (rather than in a trapezoidal arrangement), the proventricle indistinct and visible through about two segments (instead of well developed and four segments long), and by a distinctly shorter medio-ventral anal papilla.

Sphaerodoropsis martinae Desbruyères, 1980 is another very similar species, but its holotype (MNHN Type 1285) lacks a prostomial protuberance, and has blades of the falcigers that seem to be completely smooth.

Sphaerodoropsis rosehipiformis sp. nov.

(Figs. 131A, 134, 135, 139)

Etymology

The species epithet is intended to reflect that the macrotubercles look like rosehips. It is to be treated as a compound adjective with a Latin final component for the purposes of nomenclature.

Material examined

Type material. R/V METEOR 63/2 st. 58 MC 12, 0°0′S 2°25′W, 14.iii.2005, 5065 m; holotype: cs/1.7/14/0.4/0.2 (ZMH P25558).

Diagnosis

Prostomium without elongated papillae; up to six sessile globular macrotubercles with terminal cap-like structure in each of the two transverse rows per chaetiger, arranged in a more or less distinct zig-zag pattern on dorsum; ventral cirri about as long as postchaetal lobes or slightly shorter; parapodia without papillae; venter with a few scattered minute papillae; chaetae unidentate; medio-ventral anal papilla about as long as lateral cirri.

Description

Body 1.7 mm long with 14 chaetigers; short and maggot-like, tapering anteriorly and posteriorly; with integument appears to be more or less detached (Figs. 131A, 135A). Segments uniannulate; indistinctly separated from each other. Preserved specimens without pigment pattern.

Prostomium anteriorly truncate, wider than long; more or less fused with first segment; with three antennae, two palps and a few small globular papillae (Fig. 135A–C). Frontal antennae and palps all conical to digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and conical to oval, inserted more dorsally (Fig. 135B). Eyes absent. Nuchal organs not observed.

Proboscis retracted, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about two segments. Specimen with two pairs of red-brown pigmented eye-like pharyngeal glands; trapezium-shaped arranged in second chaetiger (Fig. 135A, B).

First segment achaetous, with one pair of conical cirri and a few minute papillae; cirri about as long as

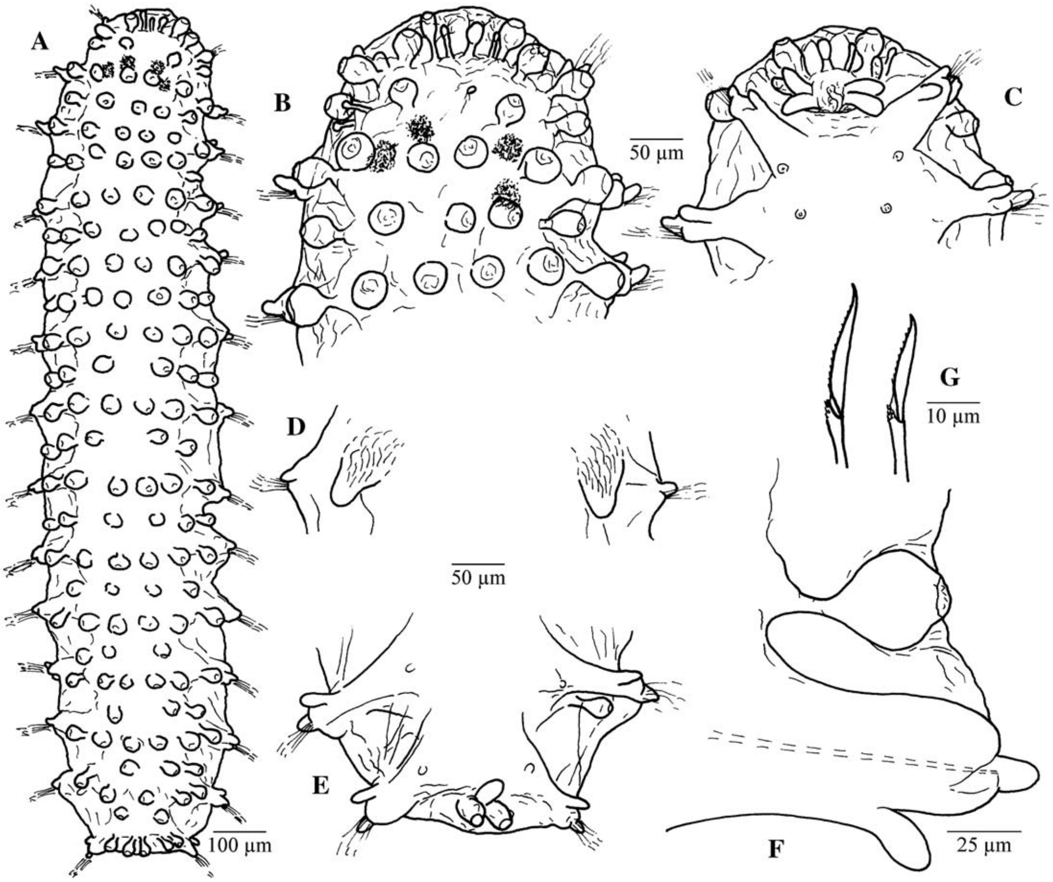

Fig. 135. *Sphaerodoropsis rosehipiformis* sp. nov. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Chaetiger 6 with specialized ventral cirri; ventral view. (E) Posterior end; ventral view. (F) Parapodium of mid-body; posterior view, chaetae omitted. (G) Chaetae. (A–G: ZMH P25558).

median antenna or slightly longer; inserted laterally (Fig. 135B, C).

Second segment and following chaetigers with dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Fig. 135A, B). Parapodia all uniramous with oval to conical pre- and shorter rounded postchaetal lobes (Fig. 135F). Macrotubercles large globular, probably sessile but appear to be stalked by removed integument (Figs. 131A; 135A–C, E, F), and with small cap-like terminal structure; each chaetiger with two more or less conspicuous transverse rows of up to six tubercles arranged in a more or less distinct zig-zag pattern; number of macrotubercles decreased anteriorly and posteriorly (Fig. 135A). Ventral cirri conical to digitiform; about as long as postchaetal lobes or slightly shorter; inserted on middle of parapodia (Fig. 135F), with exception of 6th chaetiger, where cirri are basely located, inflated and filled with glandular-like tissue (Fig. 135D). Body surface especially ventrally with a few scattered minute papillae (Fig. 135C, E).

All parapodial lobes with one straight acicula (Fig. 135F), and a few falcigerous compound chaetae (Fig. 135G). Falcigers with slightly different long paring-knife to sickle shaped, unidentate blades; subdistally blades possibly with fine serration over entire length of margin; shafts with some subdistal spines (Fig. 135G).

Pygidium with anus and a pair of termino-lateral conical to globular and distally papillated cirri and an additional conical medio-ventral papilla, which is about as long as lateral cirri (Fig. 135E).

Remarks

Intestine more or less completely filled with small globular granules (sperm?). The specialized inflated ventral cirri of chaetiger six can be interpreted as a penis structure (Moreira et al. 2004).

Distribution

Guinea Basin; 5065 m (Fig. 134).

Discussion

Sphaerodoropsis rosehipiformis sp. nov. belongs to the *Sphaerodoropsis* Group 3 (sensu Borowski 1994), which

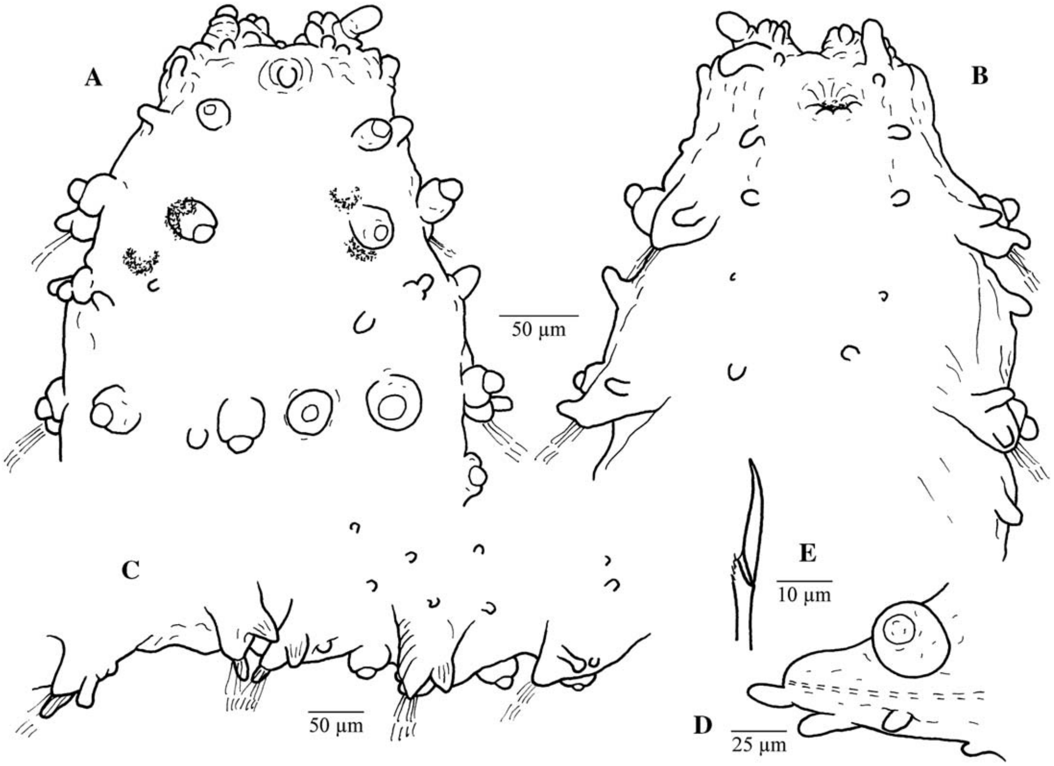

Fig. 136. *Sphaerodoropsis translucida* Borowski. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Left parapodia of chaetigers 7 to 3, ventral view. (D) Parapodium of mid-body; dorsal view, chaetae omitted. (E) Chaeta. (A–E: ZMH P25562).

is characterized by more than four longitudinal rows of macrotubercles and two transverse rows per segment. Within this group the taxon is most closely related to *S. translucida* Borowski, 1994 in having macrotubercles with a terminal structure. However, a distinct terminal papilla is present in the latter species, whereas the macrotubercles of *S. rosehipiformis* sp. nov. resemble rosehips; moreover, the papilla on the anterior parapodial surface reported for *S. translucida* is not observed in *S. rosehipiformis*.

Sphaerodoropsis translucida Borowski, 1994

(Figs. 134, 136, 139)

Sphaerodoropsis translucida Borowski, 1994—Borowski (1994, p. 199, figs. 5, 6)

Material examined

Type material. Sphaerodoropsis translucida: DISCOL 3 program, R/V SONNE 77 st. KG 1477, Peru Basin, 7°7.505′S 88°27.009′W, 14.ii.1992, 4162 m; holotype: cs/1.45/18/0.3/0.2 (SMF 4488).—DISCOL 3 program, R/V SONNE 77 st. KG 1492, Peru Basin, 7°7.477′S 88°26.967′W, 21.ii.1992, 4163 m; paratype: cs/1.45/18/0.3/0.2 (SMF 4544).

Additional material. See Appendix 1.

Diagnosis

Prostomium without elongated papillae; up to six sessile globular macrotubercles with terminal papilla in each of the two transverse rows per chaetiger, arranged in a more or less distinct zig-zag pattern on dorsum; ventral cirri about as long as postchaetal lobes or slightly shorter; parapodia usually with one globular papilla; venter with some scattered small papillae; chaetae unidentate; medio-ventral anal papilla about as long as lateral cirri.

Description

Body up to 1.6 mm long with up to 16 chaetigers; short and maggot-like, tapering anteriorly and posteriorly (Fig. 136A, B). Segments uniannulate; indistinctly separated from each other. Preserved specimens whitish to yellowish, without pigment pattern.

Prostomium anteriorly truncate, wider than long; more or less fused with first segment; with three antennae, two palps and a few small globular to conical papillae (Fig. 136A, B). Frontal antennae and palps all conical to digitiform and of about same length; inserted latero-dorsally and latero-ventrally; median antenna distinctly shorter and more conical, inserted more dorsally (Fig. 136A). Eyes absent. Nuchal organs not observed.

Proboscis retracted in all specimens, not observed. Proventricle indistinctly developed with numerous muscle rings; visible through about 1–2 segments. One specimen with two pairs of red-brown pigmented eye-like pharyngeal glands; trapezium-shaped arranged in first chaetiger (Fig. 136A).

First segment achaetous, with one pair of conical cirri and a few small globular to conical papillae; cirri about as long as median antenna; inserted laterally (Fig. 136A, B).

Second segment and following chaetigers with dorsal macrotubercles, distinct chaetigerous lobes and ventral cirri (Fig. 136A, B). Parapodia all uniramous with oval to conical pre- and shorter rounded postchaetal lobes; often with one globular papilla on anterior base (Fig. 136D). Macrotubercles large globular, sessile and with distinct terminal papilla; each chaetiger with two more or less conspicuous transverse rows of up to six tubercles arranged in a more or less distinct zig-zag pattern; number of macrotubercles decreased anteriorly and posteriorly (Fig. 136A). Ventral cirri conical to digitiform; about as long as postchaetal lobes or slightly shorter; inserted on middle of parapodia (Fig. 136D). Body surface with some scattered small globular to conical papillae; ventrally slightly more than dorsally (Fig. 136A, B).

All parapodial lobes with one straight acicula (Fig. 136D), and a few falcigerous compound chaetae (Fig. 136E). Falcigers with slightly different long paring-knife to sickle shaped, unidentate blades; subdistally blades appear smooth under light microscope but possibly with fine serration over entire length of margin; shafts with some long and slender subdistal spines (Fig. 136E).

Pygidium with anus and a pair of termino-lateral globular and distally papillated cirri and an additional conical medio-ventral papilla, which is about as long as lateral cirri.

Remarks

The intestine of some smaller specimens is more or less completely filled with small globular granules. One specimen (ZMH P25562) shows slightly inflated and more conical to triangular ventral cirri on chaetigers 4–6, which might be penis structures (Fig. 136C).

Distribution

Angola and Guinea Basins; 3945–5494 m (Fig. 134).

Discussion

The distal ends of the macrotubercles in this species were originally described as "more or less set off, but without terminal papilla" (Borowski 1994). However, in the examined type material (SMF 4488, 4544) more or less distinct papillae are present. This character state is in contrast to the currently accepted diagnosis of *Sphaerodoropsis* (Hartman and Fauchald 1971), and has been known only from the genera *Ephesiella* Chamberlin, 1919; *Ephesiopsis* Hartman & Fauchald, 1971; *Sphaerephesia* Fauchald, 1972; and *Sphaerodorum* Örsted, 1843. However, members of these four genera exhibit four longitudinal rows of macrotubercles or two macro- and two microtubercles in only one transverse row per chaetiger.

Abundance of Sphaerodoridae

A total of 204 specimens or fragments were found in all investigated areas. Most of them belong to *Sphaerodoropsis longianalpapilla* sp. nov. (61), *Sphaerephesia regularis* sp. nov. (53), *Sphaerodoropsis furca* (47) or *Sphaerodoropsis protuberanca* sp. nov. (21). *Sphaerephesia regularis* sp. nov. is widely distributed, with the highest abundance in the Angola and Guinea Basins (DIVA-1 areas 5–6, DIVA-2 areas 3–4). *Sphaerodoropsis longianalpapilla* sp. nov. and *S. protuberanca* sp. nov. were present in two of the investigated basins, with the highest abundance in the Guinea Basin or the Angola Basin, whereas *Sphaerodoropsis furca* was found only in the BIOZAIRE material (Figs. 137–139). Findings of *Sphaerodoridium campanulata* (8), *Sphaerodoropsis chardyi* (4) and *Sphaerodoropsis translucida* (7) were scattered in the Angola and Guinea Basins (Figs. 137, 139), whereas *Sphaerodoropsis macrotubercula* sp. nov. (2) and *S. rosehipiformis* sp. nov. (1) were only found at one station in the Angola and Guinea Basins, respectively (Figs. 138, 139). The epibenthic sledge was the most effective gear for quantitative sampling of sphaerodorids, but only six of the nine taxa were taken by it. Seven species were found in the multicorer samples, though in much lower numbers, whereas the box corer was sometimes also useful for quantitative sampling (Figs. 137–139).

Molecular data

The phylogenetic position of the Sphaerodoridae varied with the sequences analyzed. The 18S rDNA data highly support a close relationship of *Sphaerephesia regularis* sp. nov. to goniadids and nereidids, whereas the COI amino acid analyses indicate *Sphaerodoropsis protuberanca* sp. nov. as sister to a Glyceriformia clade (see "Molecular phylogeny of abyssal Phyllodocida"). The latter hypothesis is in agreement with an obsolete morphology-based superfamily concept named Glyceroidea (Hartmann-Schröder 1996).

The two examined non-coding ITS2 sequences (Table 15) of *Sphaerodoropsis longianalpapilla* sp. nov.

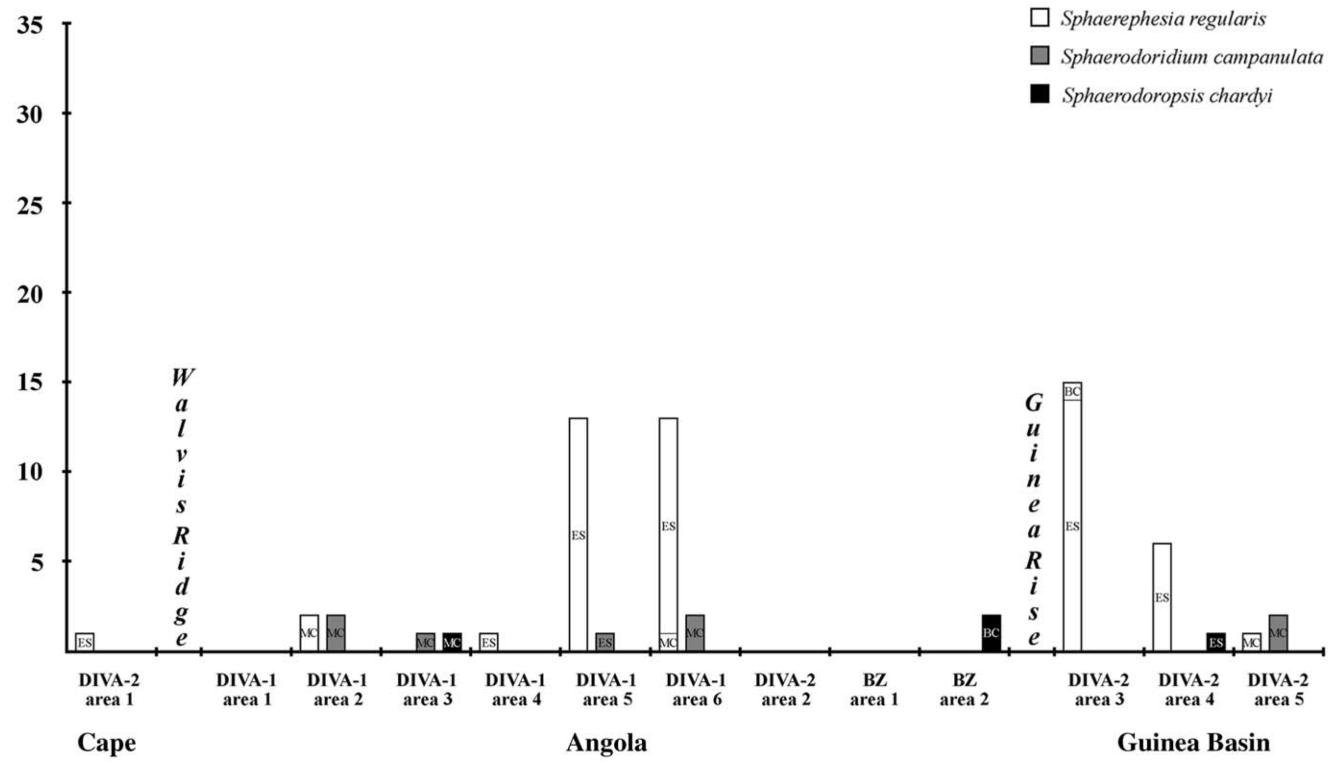

Fig. 137. Abundance of the sphaerodorids *Sphaerephesia regularis*, *Sphaerodoridium campanulata* and *Sphaerodoropsis chardyi* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

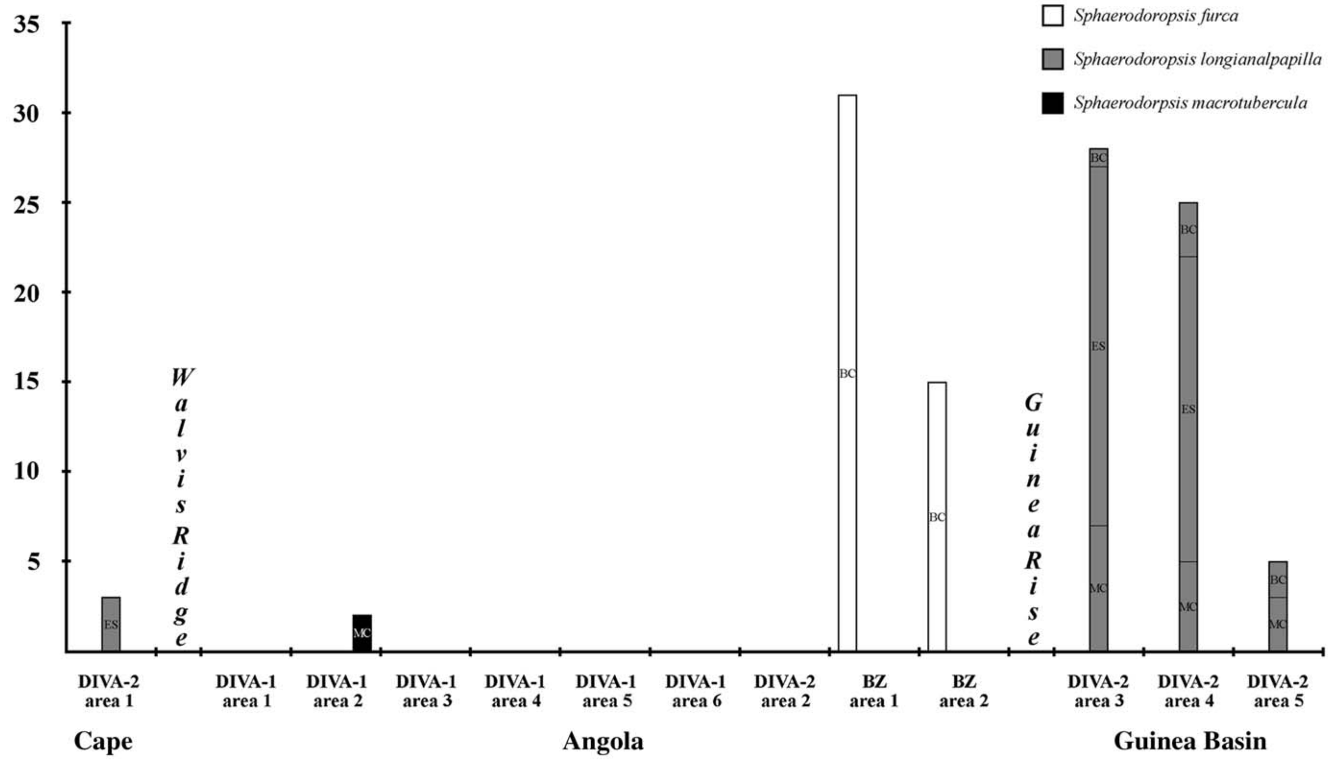

Fig. 138. Abundance of the sphaerodorids *Sphaerodoropsis furca*, *S. longianalpapilla* and *S. macrotubercula* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

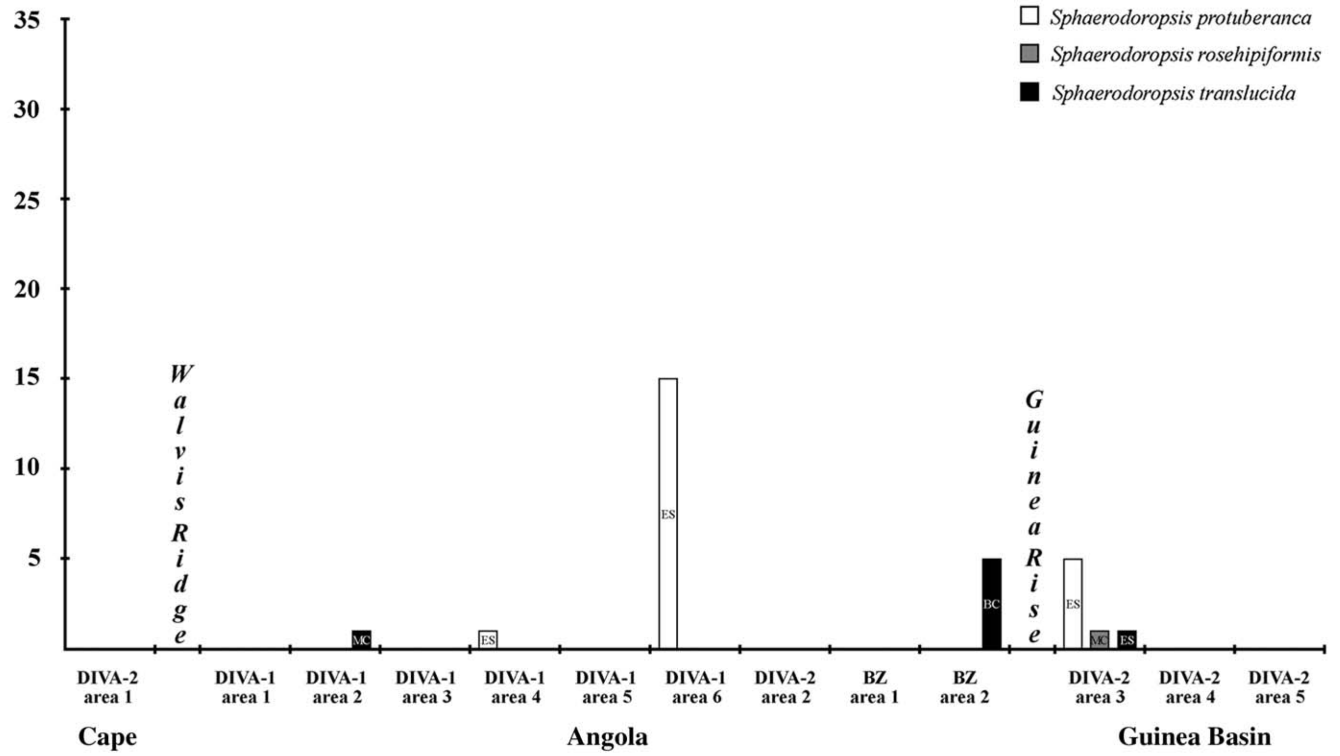

Fig. 139. Abundance of the sphaerodorids *Sphaerodoropsis protuberanca*, *S. rosehipiformis* and *S. translucida* in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

Table 15. List of taxa and corresponding sequences in Sphaerodoridae used for phylogenetic analyses.

Taxon	Geographic origin	Voucher	GenBank accession numbers			
			18S rDNA	COI (3-6W)	ITS1	ITS2
SPHAERODORIDAE						
Sphaerephesia regularis sp. nov.	Guinea Basin					
	D-2 st. 63 ES-S	ZMH P25499	GQ426596	–	–	–
Sphaerodoropsis longianalpapilla sp. nov.	D-2 st. 63 ES-S	ZMH P25535 C	–	–	GQ426702	GQ426702
	D-2 st. 90 ES-S	ZMH P25547 B	–	–	–	GQ426747
Sphaerodoropsis protuberanca sp. nov.	D-2 st. 63 ES-E	ZMH P25555 A	–	GQ426691	–	–

differed in only one position, which suggests that gene flow between the populations in the Guinea Basin is ongoing.

Syllidae Grube, 1850

The Syllidae are a large and variable group; they clearly belong to the Phyllodocida, but their lower-level classification is less certain (Pleijel 2001n; Aguado et al. 2007). One of their most obvious characters is the anterior part of the digestive tract, which is generally visible through the body wall. Especially the uniquely-muscularised proventicle is probably an autapomorphy of the whole group (Glasby 2000b). However, the presence of a muscular proventricle has been noted also in Sphaerodoridae (e.g. Wilson 2000h; Aguado and Rouse 2006).

The Syllidae show their greatest diversity in shallow warm waters, especially on coral reefs (Pleijel 2001n). However, they are also common in other regions, even in soft sediments of the deep sea. Most species are free living and considered to be carnivorous, piercing the surface of the prey with their often armed, eversible proboscis and using the proventricle as a pumping organ (Fauchald and Jumars 1979). Other species, especially those associated with muddy bottoms, are reported to be highly selective surface deposit-feeders or to feed on diatoms (Fauchald and Jumars 1979).

In the present study, specimens of four species of Syllidae were identified; an additional median fragment appears to represent a species of *Exogone* Oersted, 1845 but cannot be determined precisely. In *Anguillosyllis capensis* Day, 1963 and *Guillermogonita abyssicola* gen. et sp. nov. the pharyngeal tube is unarmed, whereas in *Parexogone wolfi* (San Martín, 1991) and *Typosyllis* sp. the tube carries a large dorsal tooth; therefore, the latter two species might be carnivorous. *Parexogone wolfi* is a well known taxon previously reported from subtidal to abyssal depths off Florida, the Gulf of Mexico, the Capbreton Canyon (Bay of Biscay), the Eastern Mediterranean, Western Australia and the Angola Basin (e.g. San Martín 1991, 2003, 2005; San Martín et al. 1996; Böggemann and Purschke 2005). *Anguillosyllis capensis* is known only from the Agulhas Bank (Day 1963b, 1967) and the Angola Basin (Böggemann and Purschke 2005). All mentioned taxa are morphologically described in this paper and molecular methods are used for *Anguillosyllis capensis*.

Key to syllid species from the abyssal SE Atlantic

1. Prostomium with two palps and three antennae (Figs. 140A; 141A, C; 145A); first segment with one or two pairs of cirri 2
– Prostomium with two palps only, antennae absent (Figs. 143A, B; 144A); first segment with two pairs of smooth, short cirri .... *Guillermogonita abyssicola* sp. nov.
2. Palps fused for at least half their length, antennae and cirri all smooth (Figs. 140A; 141A, C; 145A, B); first segment with one pair of cirri 3
– Palps separated, antennae and dorsal cirri (Fig. 147C) all articulated; first segment with two pairs of cirri .... *Typosyllis* sp.
3. Antennae subequal in length (Figs. 140A; 141A, C); dorsal cirri much longer than parapodial lobes (Fig. 140D); chaetae with unidentate tips (Figs. 140E, 141F) .... *Anguillosyllis capensis* Day
– Median antenna much longer than lateral ones (Fig. 145A); dorsal cirri not longer than parapodial lobes (Fig. 145C, D); chaetae with bidentate tips (Fig. 146D–F) .... *Parexogone wolfi* (San Martín)

Anguillosyllis Day, 1963

Anguillosyllis capensis Day, 1963

(Figs. 140–142, 148)

Anguillosyllis capensis Day, 1963—Day (1963b, p. 400, fig. 5a–d); Day (1967, p. 271, fig. 12.10.z–zzz); Böggemann and Purschke (2005, p. 222, fig. 1); Aguado and San Martín (2008, p. 36, fig. 1)

?*Braniella palpata* Hartman, 1967—Hartman (1967, p. 55; pl. 14, figs. A–D)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three smooth antennae of subequal length; palps fused for at least half their length; eyes absent; first segment with one pair of smooth, short cirri; parapodia with possibly contractile dorsal projection; dorsal cirri smooth and much longer than parapodial lobes, present on all parapodia; ventral cirri digitiform, inserted distally; compound chaetae with unidentate tips; pharyngeal tooth absent, proventricle barrel-shaped.

Description

Body up to 5 mm long, with up to 11 chaetigers; widest in middle, tapering both anteriorly and posteriorly (Fig. 141A). Fixed specimens without pigmentation (Fig. 141B). Integument smooth.

Prostomium considerably wider than long (Figs. 140A, 141A–C); bearing three short antennae and two palps. Palps considerably longer than prostomium, somewhat bean-shaped, fused for half to throughout their length, except for a terminal notch, from which a median furrow runs backwards (Figs. 140A, 141C). Antennae smooth digitiform of subequal length (Figs. 140A; 141A, C); median antenna arising near posterior margin, lateral antennae close to anterior margin. Eyes absent (but see “Remarks”).

Pharyngeal tube extending through about 3–5 segments (Figs. 140A, 141B), unarmed, with about 10 terminal papillae (Figs. 140B, 141D). Proventricle barrel-shaped (Figs. 140A, 141B), extending through

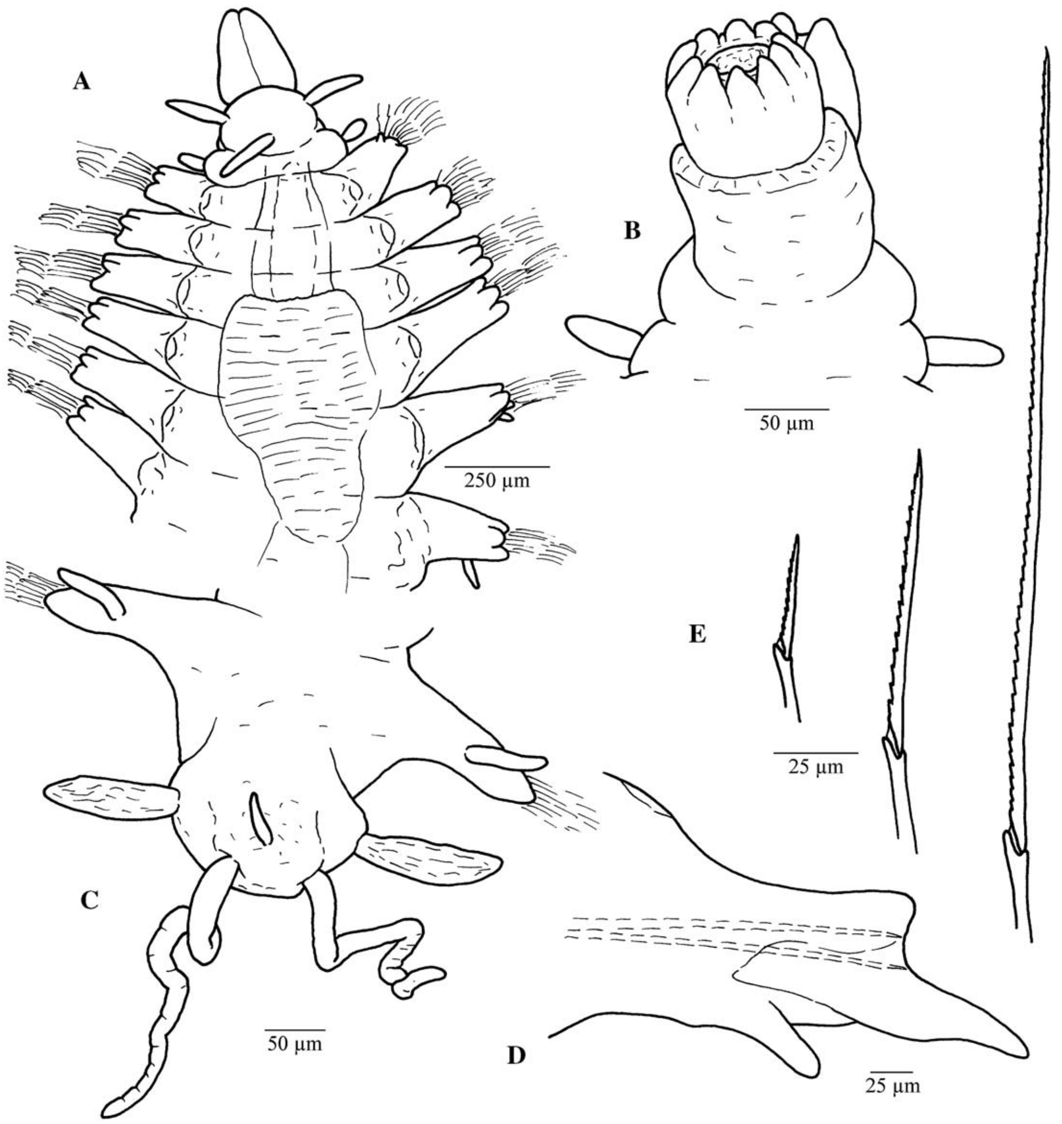

Fig. 140. *Anguillosyllis capensis* Day. (A) Anterior end; dorsal view. (B) Anterior end with everted pharyngeal tube; ventral view. (C) Posterior end; ventral view. (D) Right parapodium of chaetiger 4; posterior view, chaetae omitted. (E) Chaetae. (A: ZMH P25611 B; B: ZMH P25612 B; C: ZMH P25571 C; D: ZMH P25586 A; E: SMF 13694).

about two segments and with indistinct number (13–18?) of muscle rings.

First segment achaetous (Figs. 140A, 141A–C), laterally with a pair of smooth cirri, shorter than antennae and more conical.

Parapodia uniramous (Fig. 140D), with smooth long and often coiled dorsal cirri, which are mostly broken off, and smooth digitiform ventral cirri, inserted near distal end of parapodia. Each chaetigerous lobe with a tapered dorsal projection (Fig. 140D), which seems to be retractile (see Day 1963b). Anterior chaetigers with about 2–7 and posterior chaetigers with 1–4 aciculae having pointed tips. Chaetigers with numerous compound chaetae having unidentate, differently long blades (Figs. 140E, 141F), their lengths decreasing inferiorly, and their shape changing from pseudospiniger to paring-knife-shaped falcigers within each bundle; subdistally blades with saw-like serration over entire length of margin; shafts appearing always smooth (Figs. 140E; 141F, G).

Pygidium (Figs. 140C, 141E) with one pair of lateral club-shaped appendages, one pair of terminal smooth and slender cirri, and a short, smooth, digitiform to conical medio-ventral cirrus; all of these structures are mostly broken off, especially the club-shaped appendages are only present in a very small number of specimens.

Remarks

A few of the specimens have four spots on the posterior part of the prostomium which might be eyes.

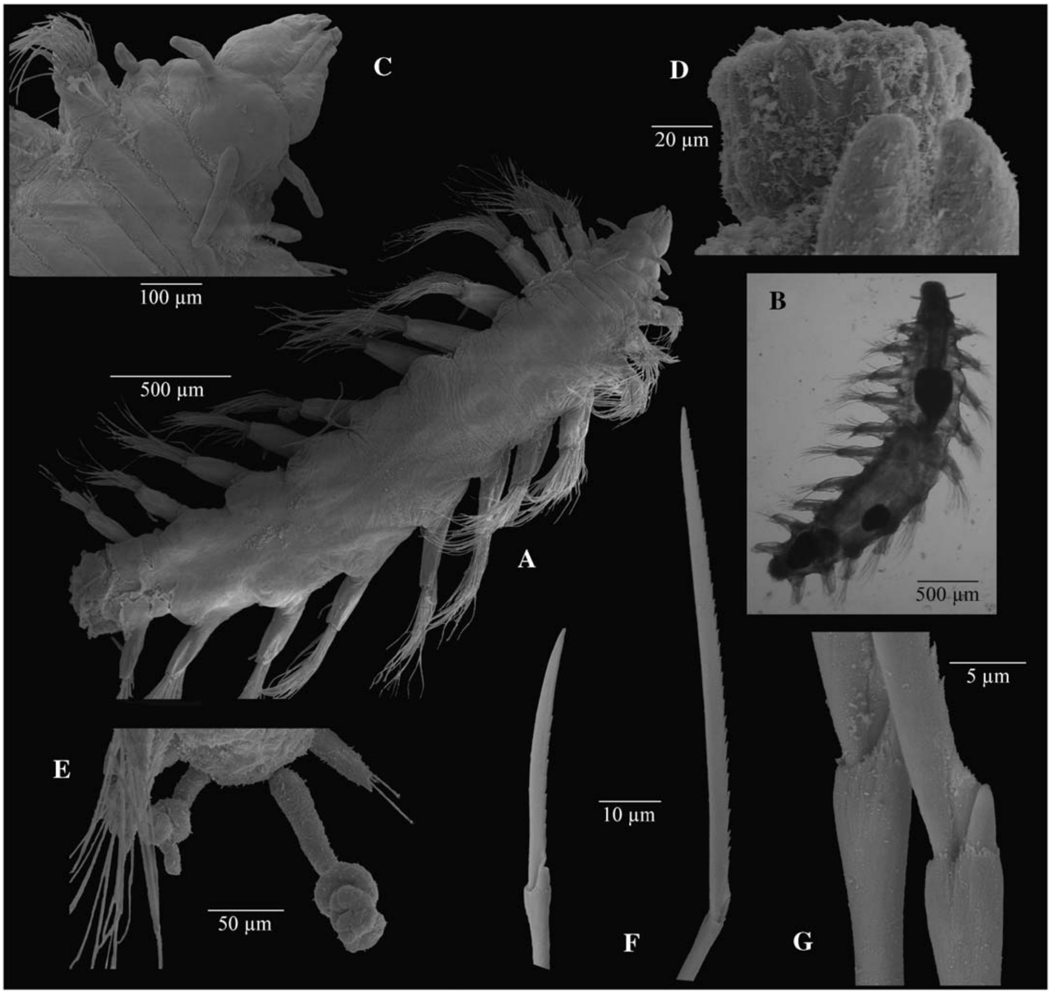

Fig. 141. *Anguillosyllis capensis* Day. (A) Complete specimen; dorsal view. (B) Light micrograph of complete specimen; dorsal view. (C) Anterior end; dorsal view. (D) Anterior end with everted pharyngeal tube. (E) Pygidium; dorsal view. (F) Chaetae. (G) Chaetae with details. (A, C, F, G: ZMH P25586 B; B: ZMH P25588 B; D, E: ZMH P25578 Y).

Distribution

Angola, Cape and Guinea Basins; 3950–5655 m (Fig. 142).

Discussion

Anguillosyllis capensis shows great similarities with *Braniella palpata*, which was described by Hartman (1967) from Antarctic seas. They might be conspecific, but better-preserved material is necessary to address this question. However, it is obvious that *Braniella* Hartman, 1965 is a junior synonym of *Anguillosyllis* Day, 1963 (Aguado and San Martín 2008).

Exogone Oersted, 1845

Exogone sp.

(Fig. 147A–C)

Material examined

See Appendix 1.

Description

Median fragment 2.0 mm long, with 13 chaetigers. Integument smooth.

Parapodia uniramous (Fig. 147A), with long conical lobes and shorter, smooth dorsal and ventral cirri of subequal length. Dorsal cirri conical and ventral cirri digitiform, both inserted near base of parapodia. One food-shaped acicula in all parapodial lobes (Fig. 147B). Chaetigers supra-acicularly with one simple chaeta; finely spinulose subterminally and with conical tip (Fig. 147C). Compound chaetae including one long pseudospiniger and 2–4 short paring-knife to sickle-shaped falcigers in each bundle; both types with bidentate blades; subdistal tooth distinctly larger than distal one; rest of blade faintly serrated with long spines; shafts with fine subdistal spines (Fig. 147C). Posterior chaetigers with one inferiormost simple chaeta; slightly sigmoid; bidentate, subdistal tooth distinctly larger than distal one; subdistally minutely serrated with long spines (Fig. 147C).

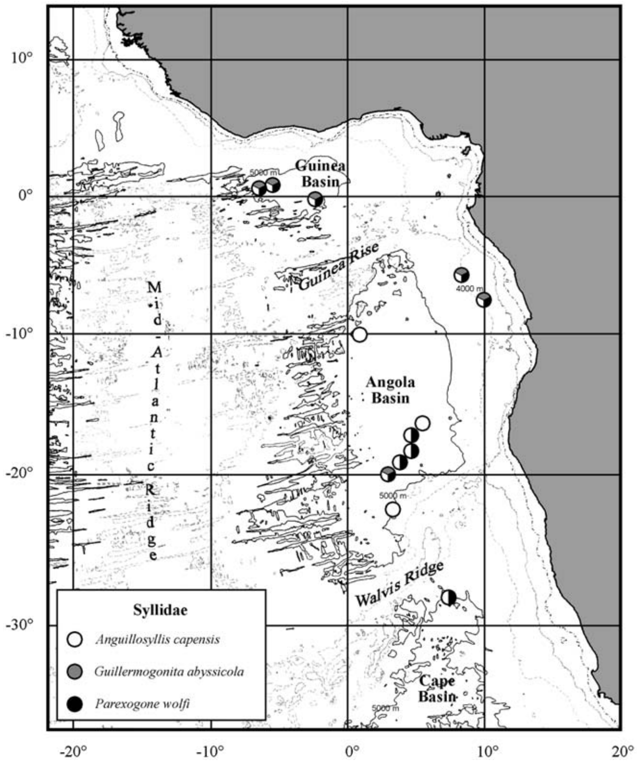

Fig. 142. Distribution of syllid species in the studied region.

Distribution

Guinea Basin; 5029 m.

Discussion

The fragment shows chaetae as are typical for the genus *Exogone*, especially for *E. dispar* (Webster, 1879), which might be cosmopolitan, and for *E. longispinulata* San Martín, 1991, which was described from Puerto Rico (512 m depth). However, definite identification of the specimen is not possible without the anterior part of the body.

Guillermogonita gen. nov.

Etymology

The first part of the genus name is chosen in honour of the syllid expert Guillermo San Martín. The second part is taken from *Exogonita*, a name proposed by Hartman and Fauchald (1971) for an abyssal taxon originally also characterised by absence of prostomial antennae and presence of two pairs of cirri on the first segment, but later synonymised with *Exogone* Oersted by San Martín and Parapar (1990).

Type species

Guillermogonita abyssicola sp. nov.

Diagnosis

Body slightly flattened dorso-ventrally, with tapered anterior and posterior ends. Prostomium with two palps but without antennae; palps not fused. Pharyngeal tube unarmed; proventricle without distinct muscle rings. First segment achaetous, with two pairs of smooth, short cirri. Parapodia uniramous, with smooth, short, oval to digitiform dorsal and ventral cirri of subequal length. Chaetigers with falcigerous compound chaetae with bidentate tips; sometimes additional simple chaetae on posterior parapodia. Pygidium with one pair of anal cirri.

Remarks

Guillermogonita gen. nov, is difficult to assign to any of the traditionally recognised subfamilies of Syllidae. Overall it resembles the Exogoninae Langerhans, 1879, but the palps are separated as in some members of Syllinae Grube, 1850, whereas the compound chaetae are very similar to those in some members of the hesionid genus *Podarke* Ehlers, 1864. Better-preserved material of *Guillermogonita* is needed to clarify its systematic relations.

Guillermogonita abyssicola sp. nov.

(Figs. 142–144, 148)

Etymology

The species epithet (Latin -cola = dweller, inhabitant) refers to the environment in which the species was found. It is to be treated as a noun in apposition for the purposes of nomenclature.

Material examined

Type material. R/V L'ATALANTE st. 23 BC, 7°40.5′S 9°59.7′E, 8.i.2001, 3993 m; holotype: af/1.2/17/0.3/0.1 (MNHN Type 1505).—R/V METEOR 63/2 st. 62 MC 6, 0°0′S 2°25′W, 15.iii.2005, 5062 m; paratype: af/0.7/12/0.5/0.2, 1 mf + 2 pf with 2–11 chaetigers (all ZMH P25621 A), 1 mf with 8 chaetigers (ZMH P25621 B, on SEM stub)

Additional material. See Appendix 1.

Diagnosis

Prostomium with two separated palps, without antennae; eyes absent; first segment with two pairs of smooth, short cirri; dorsal and ventral cirri present; compound chaetae falcigerous with bidentate tips; pharyngeal tooth absent, proventricle without distinct muscle rings.

Description

Body at least 1.2 mm long, with at least 18 chaetigers. Fixed specimens without pigmentation. Integument smooth.

Prostomium wider than long (Figs. 143A, 144A); bearing two palps but no antennae. Palps slightly longer than prostomium, somewhat bean-shaped to globular; ventrally located and apparently completely free from each other (Fig. 143A, B). Eyes absent.

Pharyngeal tube extending through about 3 segments, not appearing to have teeth or a trepan. Proventricle without distinct muscle rings; sometimes slightly coiled; about two times longer than pharyngeal tube.

First segment achaetous (Fig. 143A, B), ventrolaterally with two pairs of smooth, short oval to conical cirri of subequal length.

Parapodia uniramous (Fig. 143D), with smooth dorsal and ventral cirri of subequal length, which are oval to conical in a few anterior chaetigers and than more slender conical to digitiform. Dorsal cirri starting from 1st chaetiger, inserted near base of parapodia (Fig. 143A, D). Ventral cirri starting from 3rd chaetiger, inserted on middle of parapodia (Fig. 143B, D). Prechaetal lobes conical and distinctly longer than rounded postchaetal lobes with up to two aciculae (Fig. 143D). Chaetigers with compound chaetae having bidentate, differently long blades (Figs. 143E, 144B–F), their lengths decreasing superiorly and inferiorly, and their shape changing from pseudospiniger to paring-knife-shaped falcigers within each bundle; distal tooth curved and slightly larger than subdistal one (Fig. 144F); subdistally blades with saw-like serration over entire length of margin; shafts appearing always smooth (Fig. 144E). Sometimes a few posterior chaetigers with one additional slender, slightly sigmoid chaeta, with bidentate tip and some small subdistal spines on margin (Figs. 143F, 144G).

Pygidium (Fig. 143C) with one pair of smooth digitiform cirri.

Remarks

All specimens are very small, fragmented and not well preserved.

Distribution

Angola and Guinea Basins; 3962–5496 m (Fig. 142).

Discussion

Guillermogonita abyssicola sp. nov. and *Exogone oculata* (Hartman & Fauchald, 1971) are the only syllids characterised by the absence of prostomial antennae and presence of two pairs of cirri on the first segment. However, *E. oculata* differs from the new species, among other features, in the fused palps, presence of a pharyngeal tooth, absence of dorsal cirri on the second chaetiger, the shape of the chaetae, and in having two pairs of eyes. Moreover, San Martín and Parapar (1990) mentioned that the type material of *E. oculata* shows only one pair of cirri on the first segment, rather than two as originally described.

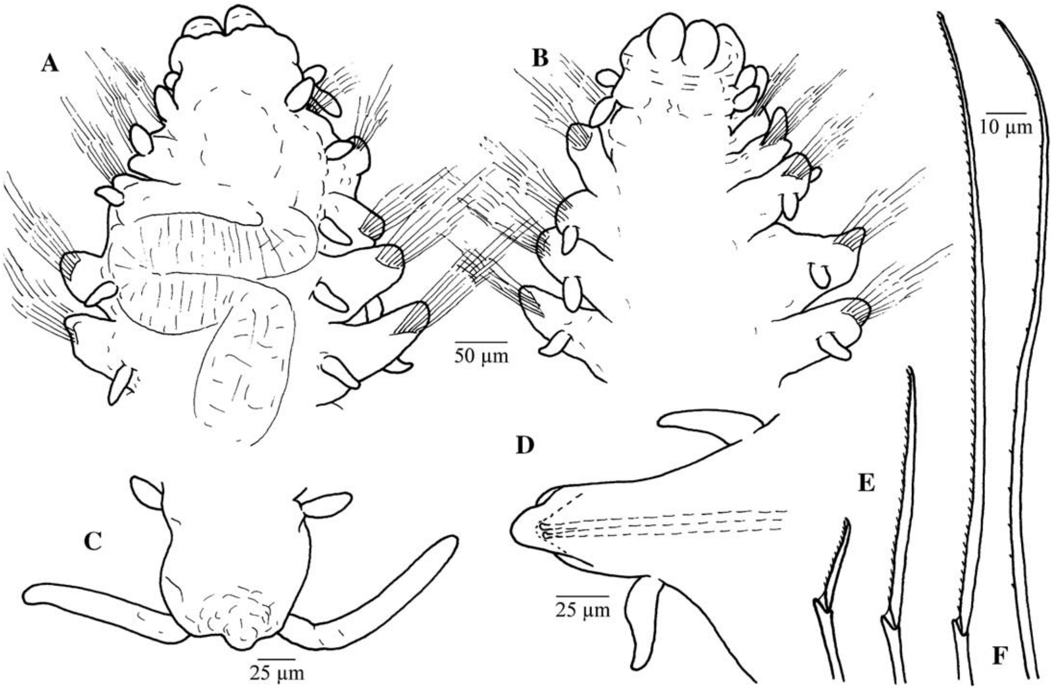

Fig. 143. *Guillermogonita abyssicola* gen. et sp. nov. (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Posterior end; dorsal view. (D) Parapodium of chaetiger 11; anterior view, chaetae omitted. (E) Compound chaetae. (F) Simple chaeta. (A–F: ZMH P25621 A).

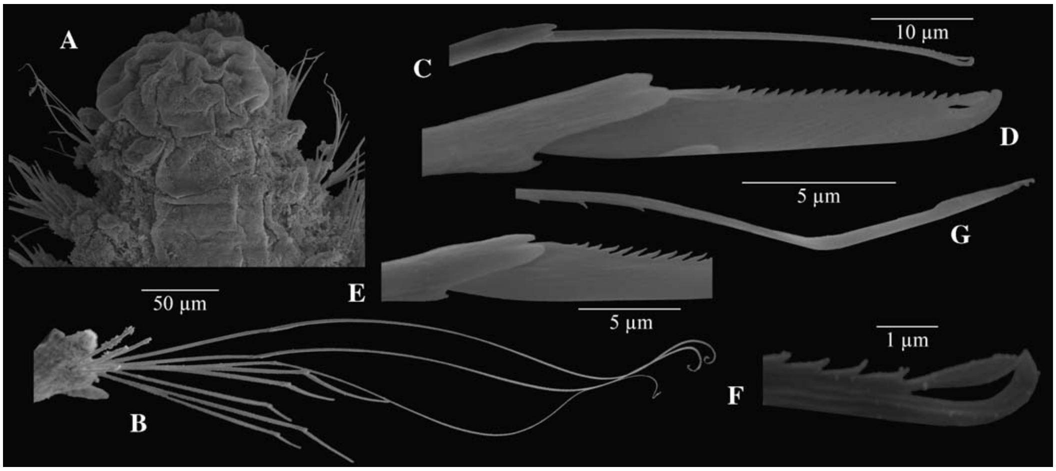

Fig. 144. *Guillermogonita abyssicola* gen. et sp. nov. (A) Anterior end; dorsal view. (B) Parapodium of mid-body. (C) Chaeta with bread knife-shaped blade. (D) Chaeta with paring knife-shaped blade. (E) Shaft of pseudospingerous chaeta. (F) Tip of pseudospingerous chaeta. (G) Simple chaeta. (A, C–G: ZMH P25625; B: ZMH P25621 B).

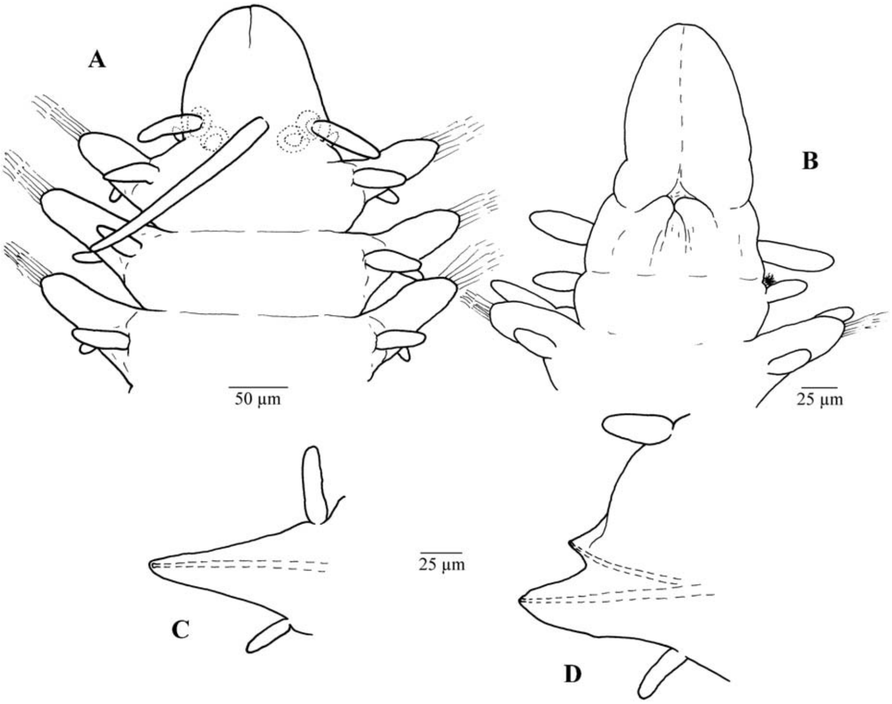

Fig. 145. *Parexogone wolfi* (San Martín). (A) Anterior end; dorsal view. (B) Anterior end; ventral view. (C) Uniramous parapodium; anterior view, chaetae omitted. (D) Biramous parapodium; anterior view, chaetae omitted. (A, C, D: ZMH P25639; B: ZMH P25634).

Parexogone Mesnil & Caullery, 1918

Parexogone wolfi (San Martín, 1991)

(Figs. 142, 145, 146, 148)

Exogone (*Parexogone*) *wolfi* San Martín, 1991—San Martín (1991, p. 726, fig. 6a–f); San Martín et al. (1996, p. 252, fig. 3A–I); San Martín (2003, p. 243, figs. 129, 130; 2005, p. 111, fig. 64)

Parexogone wolfi (San Martín)—Böggemann and Purschke (2005, p. 223, fig. 2)

Material examined

See Appendix 1.

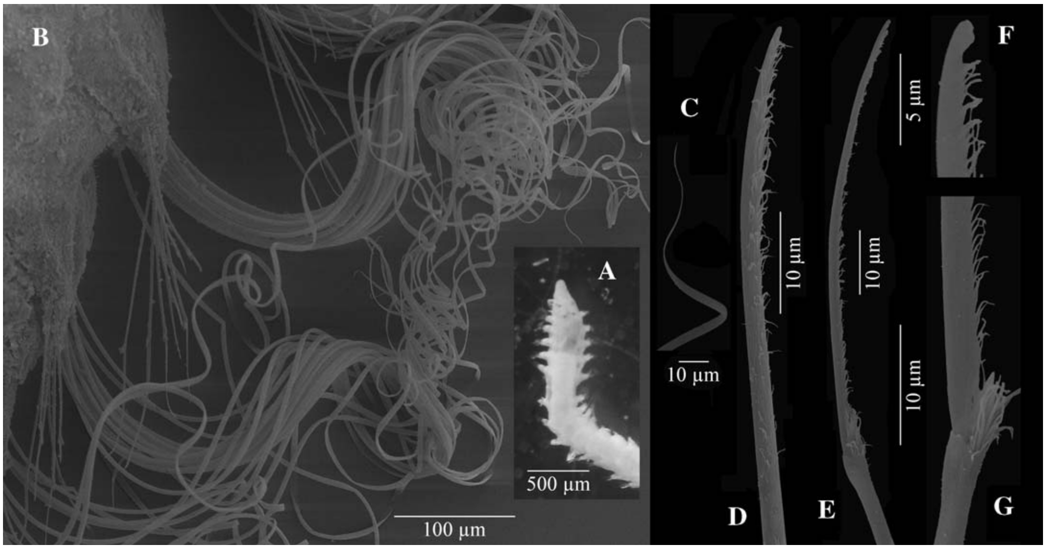

Fig. 146. *Parexogone wolfi* (San Martín). (A) Light micrograph of anterior end; dorsal view. (B) Parapodia of mid-body; ventral view. (C) Natatory chaeta. (D) Inferior simple chaeta. (E) Chaeta with pseudospiniger blade. (F) Tip of compound chaeta. (G) Chaetal shaft with very long spines. (A: ZMH P25640; B–G: ZMH P25631 G).

Diagnosis

Prostomium with three smooth antennae, median one much longer than lateral ones; palps fused throughout their length; first segment with one pair of smooth, short cirri; dorsal and ventral cirri smooth and not longer than parapodial lobes, present on all parapodia; compound chaetae falcigerous with bidentate tips; pharyngeal tooth present near anterior opening, proventricle barrel-shaped.

Description

Body up to 10.2 mm long, with up to 67 chaetigers. Fixed specimens usually without pigmentation, but sometimes a few mid-body segments with pink colouration and one specimen dorsally with two brown spots on posterior margin of brain (Fig. 146A). Integument smooth.

Prostomium about twice as wide as long (Fig. 145A), partly retracted into peristomium; bearing three antennae and two palps. Palps distinctly longer than prostomium; fused throughout their length, with a median furrow running backwards (Fig. 145A, B). Antennae smooth and digitiform (Fig. 145A), arising nearly at same level near posterior margin of prostomium; lateral antennae distinctly shorter than median one. Eyes mostly absent, but in some specimens two pairs of spherical-lensed eyes in almost trapezoidal arrangement in posterior half of prostomium (Figs. 145A, 146A).

Pharyngeal tube extending through 3–4 segments (Fig. 146A), with one large tooth near anterior opening. Proventricle with 18–21 muscle rings; about as long as pharyngeal tube (Fig. 146A).

First segment achaetous (Fig. 145A, B), laterally with a pair of smooth cirri, similar in shape to antennae, but distinctly shorter. Lateral pair of ciliated knobs (nuchal organs?) present.

Parapodia usually uniramous (Fig. 145C), with smooth digitiform dorsal cirri of subequal length; ventral cirri conical to papilliform, inserted near parapodial base. Anteriorly about nine chaetigers probably with two, following chaetigers with one strong acicula with bent tips. Supra-acicularly one slightly sigmoid bidentate simple chaeta, beginning usually from 3rd to 19th chaetiger; distal tooth about as large as subdistal one; subdistally with curved and distally directed very long spines. Anterior chaetigers with subacicular bundles of 5–15 compound chaetae, posterior chaetigers with 2–6 chaetae with differently long bidentate blades (Fig. 146E–G), their lengths decreasing inferiorly, and their shape changing from pseudospiniger (Fig. 146E) to paring-knife-shaped falcigers within each bundle; distal tooth slightly larger than subdistal one; subdistally blades with long spines over entire length of margin; shafts with very long spines subdistally (Fig. 146F, G). Sometimes a few posteriormost chaetigers with one inferiormost simple chaeta; slender, slightly sigmoid and bidentate, distal tooth about as large as subdistal one; subdistally with curved and distally directed very long spines (Fig. 146D).

Pygidium with one pair of smooth conical to digitiform cirri.

Remarks

Juveniles have upper and lower simple chaetae on all parapodia. In reproductive specimens the mid-body (chaetigers 10–44) shows enlarged, biramous parapodia (Figs. 145D, 146B) filled with gametes. Notopodia possess one strong, slightly curved acicula (Fig. 145D) and a bundle of numerous smooth and very long natatory chaetae (Fig. 146B, C). The species exhibits external gestation (Böggemann and Purschke 2005).

Distribution

Angola, Cape and Guinea Basins; 3964–5497 m (Fig. 142).

Typosyllis Langerhans, 1879

Typosyllis sp.

(Fig. 147D–F)

Typosyllis sp.—Böggemann and Purschke (2005: 225)

Material examined

See Appendix 1.

Diagnosis

Prostomium with three articulated antennae, median one distinctly longer than lateral ones; palps separated; eyes absent; first segment with two pairs of articulated cirri; dorsal cirri articulated and distinctly longer than parapodial lobes, present on all parapodia; ventral cirri digitiform, as long as parapodial lobes; falcigerous compound chaetae with bidentate tips; pharyngeal tooth present near anterior opening, proventricle barrel-shaped.

Description

Complete specimen 2.4 mm long, with 23 chaetigers. Fixed specimen of bad condition, without pigmentation, with red-brown pharyngeal tube. Dorsal integument smooth.

Prostomium considerably wider than long. Palps slightly longer than prostomium, large and bean-shaped; separated from each other along their entire length. Antennae articulated, articles somewhat wider than long to subquadrangular, distal article sometimes longer than wide; median antenna with 12–13 articles, arising near posterior margin of prostomium; anterolateral antennae shorter, with nine articles. Eyes absent.

Pharyngeal tube extending through 4–5 segments with large tooth near anterior opening. Proventricle with about 50 muscle rings; slightly longer than pharyngeal tube.

First segment achaetous, laterally with two pairs of cirri, articulation similar in shape to that of antennae; dorsal ones with 11 articles, ventral ones distinctly shorter with four articles.

Parapodia uniramous (Fig. 147D); articles of dorsal cirri subquadrangular, distal article sometimes longer than wide; ventral cirri digitiform, as long as parapodial lobes, inserted near parapodial bases. Dorsal cirri of different lengths, decreasing in length posteriorly and articulated as follows: 1st with 12–15, 2nd with 6, 3rd with 6–7, 4th with 9, 5th with 8, 6th with 4, 7th with 4–5, 8th with 4, 9th with 8, 10th with 4, 11th with 8, 12th with 4, 13th with 6, 14th with 4, 15th not present, 16th with 3,

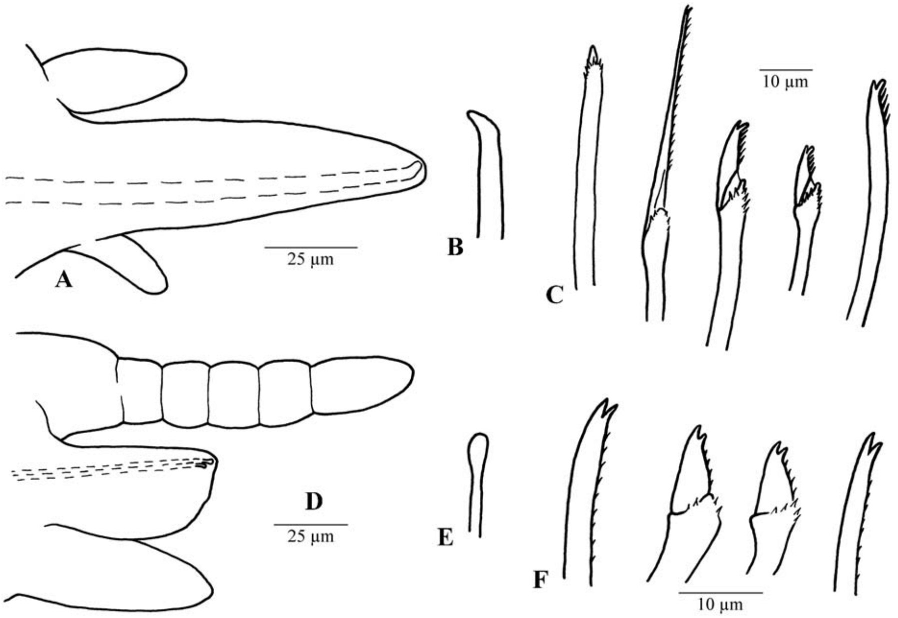

Fig. 147. (A–C) *Exogone* sp. (A) Parapodia of mid-body; posterior view, chaetae omitted. (B) Acicula. (C) Chaetae. (D–F) *Typosyllis* sp. (D) Parapodia of chaetiger 2; posterior view, chaetae omitted. (E) Acicula. (F) Chaetae. (A–C: ZMH P25618; D–F: SMF 13687).

17th with 5, 18th with 3, 19th with 5, 20th with 3, 21st with 2, 22nd with 1, 23rd with 1 article. Anterior chaetigers possibly with two aciculae, other clearly with a single match-shaped acicula (Fig. 147E). Seven posteriormost chaetigers supra-acicularly with one bidentate simple chaeta; teeth about the same size; subdistally with minute serration (Fig. 147F). Chaetigers with subacicular bundles of 2–6 subequal falcigers with paring-knife to sickle-shaped, bidentate blades; secondary tooth about as large as primary one; rest of blade minutely serrated; shafts with fine subdistal spines (Fig. 147F). Three posteriormost chaetigers with one slender inferiormost simple chaeta (Fig. 147F).

Pygidium incomplete, lacking anal cirri.

Distribution

Angola Basin; 5468 m.

Discussion

Additional material would be needed to describe a new taxon, because the present specimen might be a juvenile or an aberrant form of a known species (Böggemann and Purschke 2005).

Abundance of Syllidae

A total of 489 specimens or fragments were found in the investigated areas. Most of them (393) belong to *Anguillosyllis capensis*. This species was present in all three basins (Fig. 148), sometimes in very high abundance (DIVA-1 area 6, DIVA-2 area 4, BIOZAIRE area 1). *Parexogone wolfi* was found in the same basins, but in lower numbers (altogether 75 specimens or fragments) and with the highest abundance in DIVA-1 areas 2 and 3. The 19 specimens or fragments of *Guillermogonita abyssicola* gen. et sp. nov. from box and multicorer samples were taken only in the Angola and Guinea Basins. The median fragment of *Exogone* sp. comes from the Guinea Basin (DIVA-2 area 3); the anterior fragment of *Typosyllis* sp. from the Angola Basin (DIVA-1 area 3). The most effective gear for collecting syllids was the box corer. However, multicorer and epibenthic sledge where also very useful. The sledge samples have the advantage of being generally rapidly fixed in ethanol; therefore, the material was more or less useful for molecular analyses.

Molecular data

All analyses were conducted using the branch-and-bound algorithm. Gaps were treated as missing and characters were unordered and unweighted. Clade support values were calculated with nonparametric bootstrapping with 100 (ML: 18S rDNA, ITS2), 1,000 (ML: 16S rDNA, COI, ITS1) or 100,000 replicates (MP).

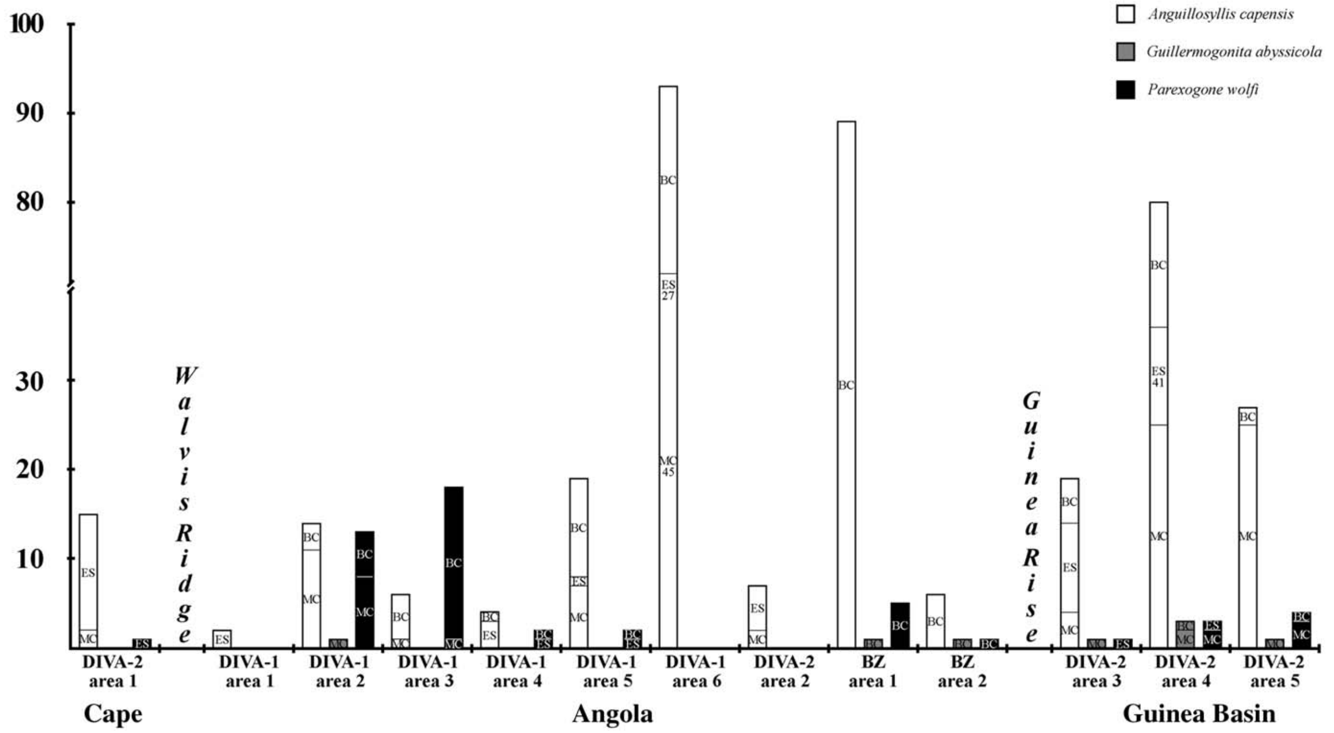

Fig. 148. Abundance of the three syllid species in the sampling areas; only complete specimens, anterior fragments and fragments distinctly representing separate specimens counted. BC = box corer, ES = epibenthic sledge, MC = multicorer.

18S rDNA data set

Seven newly acquired sequences (Table 16) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the General Time Reversible model with invariant gamma distribution (GTR + I + G), selected as the optimal model based on the Akaike Information Criterion (AIC). Accordingly, the priors were set to: base frequencies (A = 0.2439, C = 0.2272, G = 0.2734, T = 0.2555); number of substitution types = 6; substitution rate matrix (A↔C = 0.9057, A↔G = 5.4180, A↔T = 2.7036, C↔G = 0.5494, C↔T = 9.2971, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.4915; and gamma distribution shape parameter = 0.8356.

After exclusion of the primer sites, the alignment for the seven sequences contained 1,679 characters, of which 104 were variable and three parsimony informative. The MP (tree length = 105, CI = 0.9905 (0.7500), RI = 0.8000, RC = 0.7924) and the ML analysis (–ln L = 2863.77927) yielded three trees each, with slightly different topologies between the respective strict consensus trees (Fig. 149).

16S rDNA data set

Five newly acquired sequences (Table 16) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.3527, C = 0.1306, G = 0.1847, T = 0.3320); number of substitution types = 6; substitution rate matrix (A↔C = 0.2063, A↔G = 5.9097, A↔T = 2.9697, C↔G = 0.0000, C↔T = 6.1278, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.3486; and gamma distribution shape parameter = 1.6406.

After exclusion of the primer sites, the alignment for the five sequences contained 496 characters, of which 199 were variable and 71 parsimony informative. The MP (tree length = 266, CI = 0.8947 (0.7705), RI = 0.6056, RC = 0.5419) and the ML analysis (–ln L = 1663.34379) found single trees with slightly different topologies (Fig. 149).

COI (L-HCO) data set

Four sequences (3 new, 1 from GenBank; Table 16) were included and analyses were rooted using *Parandalia* sp. (Pilargidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2226, C = 0.1549, G = 0.2080, T = 0.4145); number of substitution types = 6; substitution rate matrix (A↔C = 0.8336, A↔G = 8.5635, A↔T = 1.4666, C↔G = 1.5769, C↔T = 4.7907, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.0438; and gamma distribution shape parameter = 0.3525.

After exclusion of the primer sites, the alignment for the four sequences contained 658 characters, of which 289 were variable and 45 parsimony informative. The MP (tree length = 397, CI = 0.9597 (0.7377), RI = 0.6444, RC = 0.6185) and the ML analysis (–ln L = 2314.94916) found single trees with identical topologies (Fig. 149).

COI (3-6W) data set

Five newly acquired sequences (Table 16) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.2351, C = 0.1403, G = 0.2145, T = 0.4101); number of substitution types = 6; substitution rate matrix (A↔C = 1.5794, A↔G = 14.8451, A↔T = 2.1854, C↔G = 5.3773, C↔T = 14.7065, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.4610; and gamma distribution shape parameter = 1.3236.

After exclusion of the primer sites, the alignment for the five sequences contained 421 characters, of which 157 were variable and 72 parsimony informative. The MP (tree length = 221, CI = 0.9050 (0.8205), RI = 0.7083, RC = 0.6410) and the ML analysis (–ln L = 1402.29600) found single trees with slightly different topologies (Fig. 149).

ITS1 data set

Five newly acquired sequences (Table 16) were included and analyses were rooted using *Paralacydonia paradoxa* Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1704, C = 0.2932, G = 0.3009, T = 0.2355); number of substitution types = 6; substitution rate matrix (A↔C = 0.8868, A↔G = 1.5525, A↔T = 2.2505, C↔G = 0.3426, C↔T = 2.4449, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0; and gamma distribution shape parameter = 1.4387.

After exclusion of the primer sites, the alignment for the five sequences contained 596 characters, of which 279 were variable and 65 parsimony informative. The MP (tree length = 313, CI = 0.9712 (0. 9053), RI = 0.8615, RC = 0.8368) and the ML analysis (−ln L = 1815.34355) found single trees with identical topologies (Fig. 149).

ITS2 data set

Eight newly acquired sequences (Table 16) were included and analyses were rooted using *Paralacydonia*

Table 16. List of taxa and corresponding sequences in Syllidae, Paralacydoniidae and Pilargidae used for phylogenetic analyses.

TAXON	Geographic origin	Voucher	GenBank acession numbers					
			18S rDNA	16S rDNA	COI		ITS1	ITS2
					(LCO-HCO)	(3-6W)		
SYLLIDAE								
Anguillosyllis capensis Day	Cape Basin							
	D-2 st. 40 ES-S	ZMH P25586 A	–	–	–	–	–	GQ426748
	D-2 st. 41 ES-S	ZMH P25587	GQ426597	GQ426626	GQ426644	GQ426692	GQ426703	GQ426703
	Walvis Ridge							
	Angola Basin							
	D-2 st. 45 ES-E	ZMH P25588 A	GQ426598	GQ426627	–	GQ426693	GQ426715	GQ426749
	D-2 st. 45 ES-S	ZMH P25588 B	–	–	–	–	–	GQ426750
	Guinea Rise							
	Guinea Basin							
	D-2 st. 63 ES-E	ZMH P25593 A	GQ426599	GQ426628	GQ426645	GQ426694	GQ426716	GQ426751
	D-2 st. 64 ES-S	ZMH P25594	GQ426600	GQ426629	–	–	GQ426717	GQ426752
	D-2 st. 89 ES-E	ZMH P25611 A	GQ426601	–	–	GQ426695	–	–
	D-2 st. 89 ES-S	ZMH P25611 B	GQ426602	–	GQ426646	–	–	–
	D-2 st. 90 ES-E	ZMH P25612 A	–	–	–	–	–	GQ4267453
PARALACYDONIIDAE								
Paralacydonia paradoxa Fauvel	France, Banyuls-s.-M.		GQ426587	GQ426619	–	GQ426684	GQ426700	GQ426700
PILARGIDAE								
Parandalia sp.	Australia, Darwin		–	–	EU835664*	–	–	–

*Sequence obtained from GenBank.

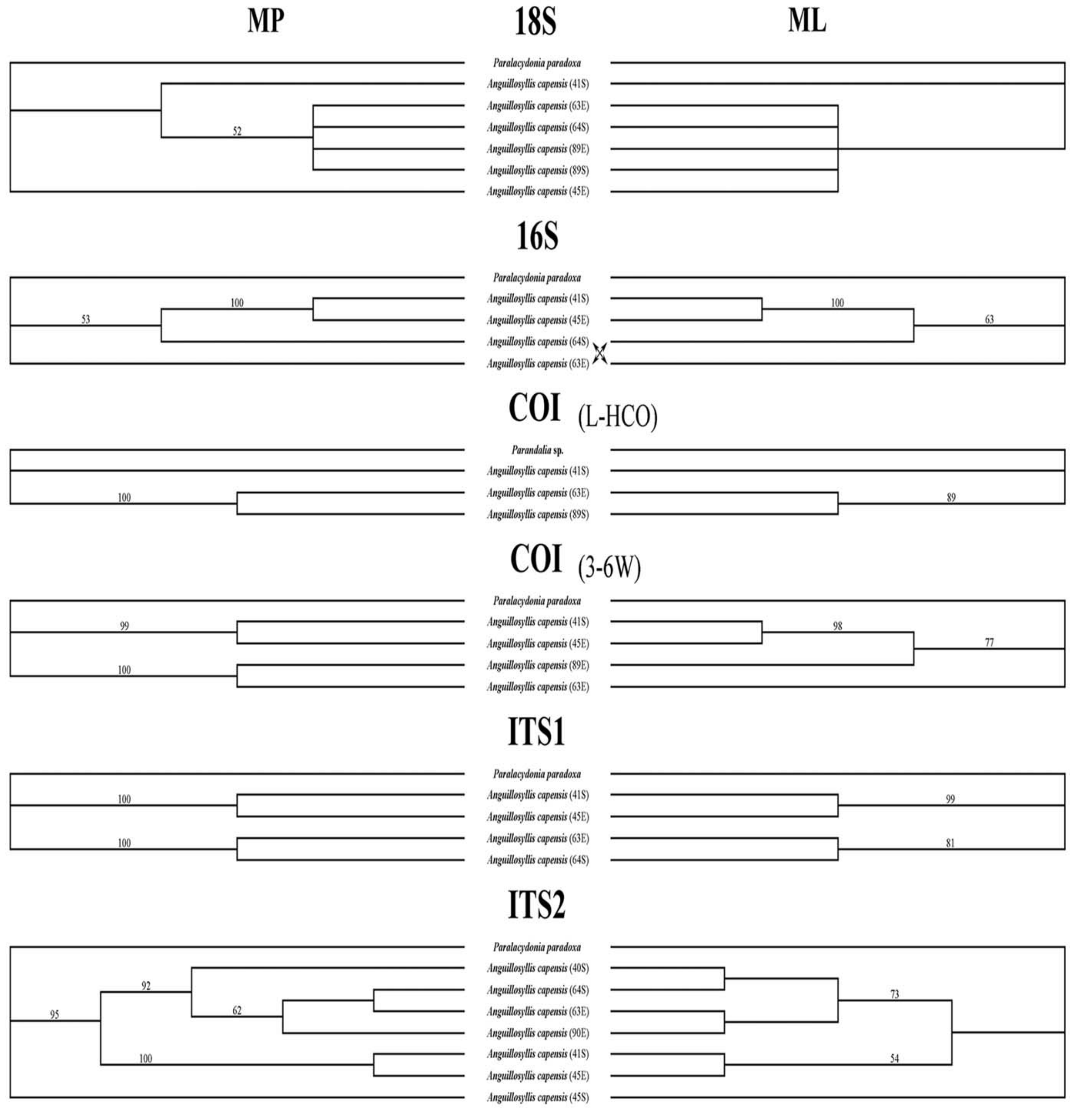

Fig. 149. Cladograms obtained from MP and ML analysis of the 18S, 16S, COI, ITS1 and ITS2 sequences. Bootstrap values > 50 shown above branches.

paradoxa Fauvel (Paralacydoniidae) as outgroup. ML was performed using the GTR + I + G model, selected as optimal based on the AIC. Accordingly, the priors were set to: base frequencies (A = 0.1716, C = 0.3104, G = 0.2708, T = 0.2472); number of substitution types = 6; substitution rate matrix (A↔C = 1.5625, A↔G = 3.5578, A↔T = 2.3263, C↔G = 0.9515, C↔T = 4.0642, G↔T = 1.0000); among-site rate variation with proportion of invariable sites = 0.1488; and gamma distribution shape parameter = 3.6651.

After exclusion of the primer sites, the alignment for the eight sequences contained 358 characters, of which 187 were variable and 72 parsimony informative. The MP (tree length: 283, CI = 0.8445 (0. 6986), RI = 0.5849, RC = 0.4940) and the ML analysis (−ln L = 1577.61054) found single trees with slightly different topologies (Fig. 149).

Discussion of molecular results

The phylogenetic results documented the monophyly of Syllidae, but the group's position varied with the sequences analyzed. The 18S rDNA data support a closer relationship to nephtyids and pilargids, whereas the 16S rDNA sequences grouped them near nephtyids and nereidids, and the COI amino acid analyses proposed Syllidae to be sister to all other examined Phyllodocida (see "Molecular phylogeny of abyssal Phyllodocida"). However, none of the reported hypotheses received strong support.

Anguillosyllis capensis was originally described from 183 m depth in the Agulhas Bank (Day 1963b) and later reported from the abyssal Angola Basin (Böggemann and Purschke 2005). Therefore, the species has a wide geographical and vertical distribution. However, the examined sequences of both, the more conservative coding regions (18S rDNA, 16S rDNA, COI) and the more variable non-coding internal transcribed spacers (ITS1 + 2), suggest that this taxon could be divided in at least two groups (Fig. 149). The molecular data usually indicated that the specimens from the Cape and Angola Basins were more closely related to each other, thus could be separated from the Guinea Basin specimens. This conclusion is often supported by high bootstrap values. On the other hand, the ITS2 analysis gave a closer relationship between specimens from the Cape Basin (st. 40S) and the Guinea Basin. Therefore, more well preserved material is necessary to elucidate these patterns and to clarify whether the name *Anguillosyllis capensis* as presently applied represents widespread populations with gene flow between them, i.e. a single species, or a complex of cryptic species.

Tomopteridae Grube, 1848

The pelagic Tomopteridae are an easily recognizable group of polychaetes which clearly belongs to the Phyllodocida, even though its position is highly uncertain (Pleijel 2001o). Nevertheless, a typical apomorphy is the presence of a pair of long cirri on the second segment, which are supported by a single internal acicula, whereas external chaetae are totally absent (Fauchald and Rouse 1997; Wilson 2000i).

The Tomopteridae are active swimmers; they have a worldwide distribution in ocean waters from the surface to considerable depths (at least 3000 m), but most records are from less than 500 m (Pleijel 2001o; Wilson 2000i). They are considered holopelagic carnivores, feeding on chaetognaths, fish larvae and pelagic tunicates (Fauchald and Jumars 1979). In all taxa the animals are transparent, but one or more of the four different types of parapodial glands may occur as pigmented spots, some of which, e.g. the rosette glands, have been described as bioluminescent organs (Greeff 1882, 1885). However, no such glands are present in the species examined here.

The single tomopterid collected in the present study, *Tomopteris* cf. *elegans* Chun, 1888, was previously reported as a holopelagic cosmopolitan in surface waters down to 1800 m (e.g. Chun 1888; Apstein 1900; Støp-Bowitz 1948, 1951, 1992; Dales 1957a, 1957b; Tebble 1960, 1962; Imajima and Hartman 1964; Day 1967; Dales and Peter 1972; Uschakov 1972; Pleijel and Dales 1991; Jiménez-Cueto and Suárez-Morales 1999; Fernández-Álamo 2000, 2006). The new material was taken with an epibenthic sledge at a depth below 5000 m.

Tomopteris Eschscholtz, 1825

Tomopteris cf. *elegans* Chun, 1888

(Figs. 150, 151)

Tomopteris elegans Chun, 1888—Chun (1888, p. 18; pl. 3, figs. 4, 5)

Material examined

See Appendix 1.

Diagnosis

Short anterior cirri of first segment present; pinnules completely bordering parapodial rami; rosette glands absent; often indistinct hyaline glands in dorsal pinnules of parapodia 3–4; tail-like posterior region absent.

Description

Body of single specimen 1.6 mm long with 10 segments; dorso-ventrally flattened with tapering anterior and posterior ends (Fig. 150A). Segments indistinctly separated. Preserved specimen transparent, without pigment patterns.

Prostomium rectangular to oval, wider than long; with two palps (variously labeled 'tentacles' and 'antennae' in previous literature; see Pleijel 2001o), antennae absent (Fig. 150A–C). Palps long, broad and digitiform, of about same length; distinctly longer than prostomium; inserted termino-laterally, terminal border with pronounced central indentation. One pair of small lensed eyes present in posterior half of prostomium, situated directly on the brain (Fig. 150A, B). Inconspicuous nuchal epaulettes on dorso-lateral margins.

Proboscis more or less completely retracted, not observed (Fig. 150C).

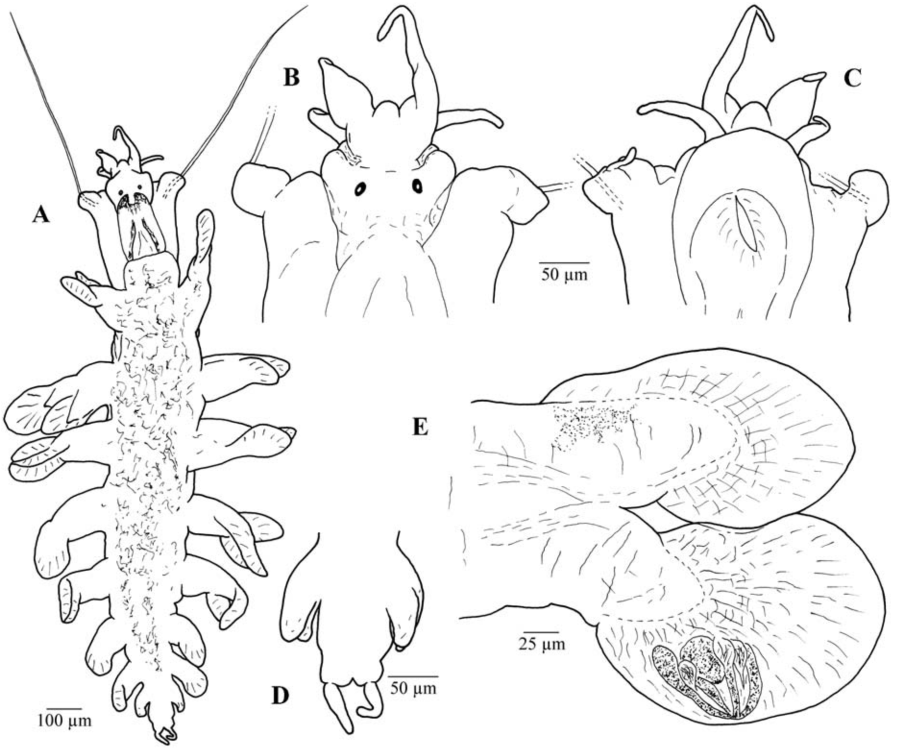

Fig. 150. *Tomopteris* cf. *elegans* Chun. (A) Complete specimen; dorsal view. (B) Anterior end; dorsal view. (C) Anterior end; ventral view. (D) Posterior end; dorsal view. (E) Fourth right biramous parapodium; posterior view. (A–E: ZMH P25650).

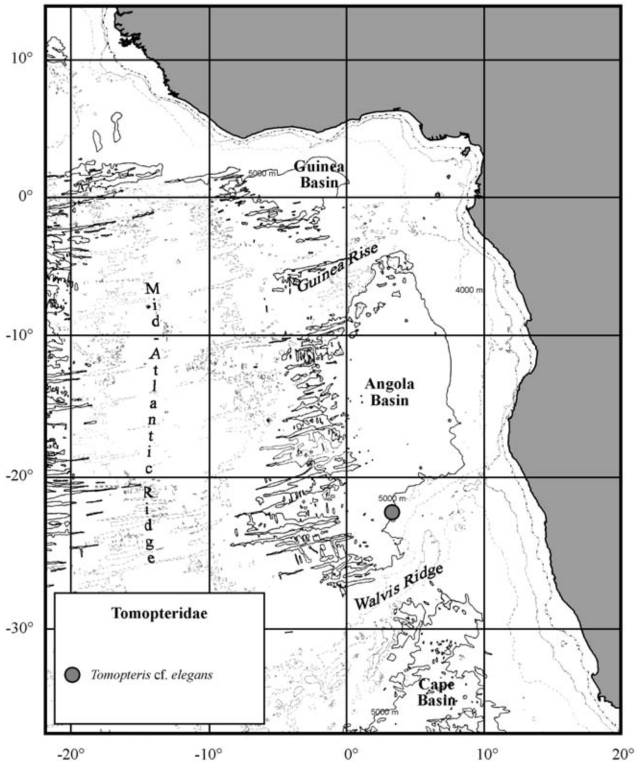

Fig. 151. Distribution of *Tomopteris* cf. *elegans* in the studied region.

First segment reduced, more or less fused with prostomium; ventrally with one pair of short and thin digitiform cirri, which are about half as long as palps (Fig. 150A–C). Second segment with one pair of parapodial lobes, with enlarged base and slender, elongated extension, which are supported throughout their length by a single internal acicula; normally posteriorly directed, reaching about two-thirds length of body (Fig. 150A). Following eight pairs of parapodia all biramous with conical parapodial lobes, which are completely surrounded by paddle-like pinnules (Fig. 150E); decreasing in size posteriorly, but without tail-like region with rudimentary parapodia (Fig. 150A, D). Chromophil glands well developed from fourth foot onwards, situated below tip of neuropodial ramus (Fig. 150E); hyaline glands not observed, but normally restricted to notopodial pinnules of third and fourth foot, situated at apex of pinnule; rosette and spur glands not present.

With exception of second segment all other parapodia without aciculae and chaetae.

Pygidium with a pair of lateral conical to digitiform cirri (Fig. 150D).

Remarks

The sample was taken with an epibenthic sledge provided with a closing mechanism; thus, the examined specimen of this holopelagic species was caught directly above the abyssal sea floor.

Distribution

Angola Basin; 5179–5180 m (Fig. 151).

Discussion

The probably juvenile specimen, without obvious dorsal gonads, is tentatively referred to *Tomopteris elegans* Chun, even though the hyaline glands typical of this species are not evident, because the notopodial pinnules are more or less damaged in this region. However, these structures are often difficult to see, except in sexually mature adults (Støp-Bowitz 1948; Tebble 1960; Day 1967; Uschakov 1972). Therefore, juveniles can be confused with other, similar species, e.g. with *Tomopteris cavallii* Rosa, 1907 or *T. planktonis* Apstein, 1900. However, in both latter species the cirri of the first segment are always absent, whereas another closely related species with these cirri, *T. kefersteinii* Greeff, 1879, has distinct rosette glands in noto- and neuropodial pinnules.

Typhloscolecidae Uljanin, 1878

The pelagic Typhloscolecidae are an aberrant group of polychaetes, which might belong within Phyllodocida, although the group's closer affinities are uncertain (Uschakov 1972; Pleijel 2001h). Possible apomorphies for this taxon are the anteriormost forwardly directed, foliose cirri, which often enfold the prostomium, and a glandular or retort organ of unknown function in the dorsal part of the eversible pharynx (Fauchald and Rouse 1997; Wilson 2000j).

The Typhloscolecidae are holopelagic worms with a worldwide distribution from the surface to abyssal depths (Pleijel 2001h; Wilson 2000j). Little is known about their biology, but species of the genera *Sagitella* Wagner, 1872 and *Typhloscolex* Busch, 1851 are reported to be predators or ectoparasites on much larger chaetognaths which decapitate their hosts and eat only the head (Feigenbaum 1979; Øresland and Pleijel 1991; Øresland and Bray 2005).

The only typhloscolecid collected in the present study is a single specimen of *Typhloscolex muelleri* Busch, 1851. This species was previously reported as a holopelagic cosmopolitan in surface waters down to 3000 m (e.g. Busch 1851; Wagner 1872; Uljanin 1878; Reibisch 1895, 1905; Støp-Bowitz 1949, 1951, 1977, 1992; Friedrich 1950a, 1950b; Dales 1957a; Tebble 1960, 1962; Hartman 1964; Imajima and Hartman 1964; Day 1967; Dales and Peter 1972; Uschakov 1972; Øresland and Bray 2005; Fernández-Álamo 2006). The specimen reported here was collected with a box corer, but see the "Remarks" below.

Typhloscolex Busch, 1851

Typhloscolex muelleri Busch, 1851

(Figs. 152, 153)

Typhloscolex Müllери Busch, 1851 [incorrect original spelling]—Busch (1851, p. 115; pl. 11, figs. 1–6)

Sagitella "*Kowalewskii* forme B" [= *Sagitella barbata* Uljanin; see below]—Wagner (1872, p. 345)

Sagitella Bobretzkii Wagner, 1872—Wagner (1872, p. 347, figs. E, F)

Sagitella barbata Uljanin, 1878—Uljanin (1878, p. 6; pl. 1, figs. 2, 4, 5; pl. 2, figs. 12, 14, 15; pl. 3, fig. 18; pl. 4, fig. 30)

Sagitella præcox Uljanin, 1878—Uljanin (1878, p. 8; pl. 1, fig. 3; pl. 4, fig. 27)

Material examined

See Appendix 1.

Diagnosis

Prostomium with a median antenna/papilla; nuchal organs as large, ciliated flaps dorsally and ventrally on prostomium, with additional pair of dorso-lateral lobes.

Description

Body of single specimen 0.8 mm long with 19 chaetigers; cylindrical, stout anteriorly and markedly tapering posteriorly (Fig. 152A, B). Segments indistinctly separated. Preserved specimen whitish, semi-transparent; without pigment patterns.

Prostomium blunt conical, wider than long; extending forwards into a median antenna/papilla; palps and paired antennae absent (Fig. 152A). Eyes absent. Nuchal organs present, forming large ciliated flaps dorsally and ventrally on prostomium with additional pair of freely projecting oval dorso-lateral lobes (Fig. 152A).

Proboscis retracted, not observed.

Anterior three segments reduced; each with one pair of enlarged and flattened cirri which enfolded the prostomium; remaining only on left side of first segment (Fig. 152A). Next two segments achaetous, with dorsal and ventral cirri which are all broken off. Following parapodia all uniramous with short conical chaetigerous lobes and distinctly longer oval to conical dorsal and ventral cirri, which are of about equal length and inserted near parapodial bases (Fig. 152C); cirri often lost in examined specimen (Fig. 152A, B).

All chaetigers with one straight acicula, which barely extending beyond tip of lobe (Fig. 152C), and two

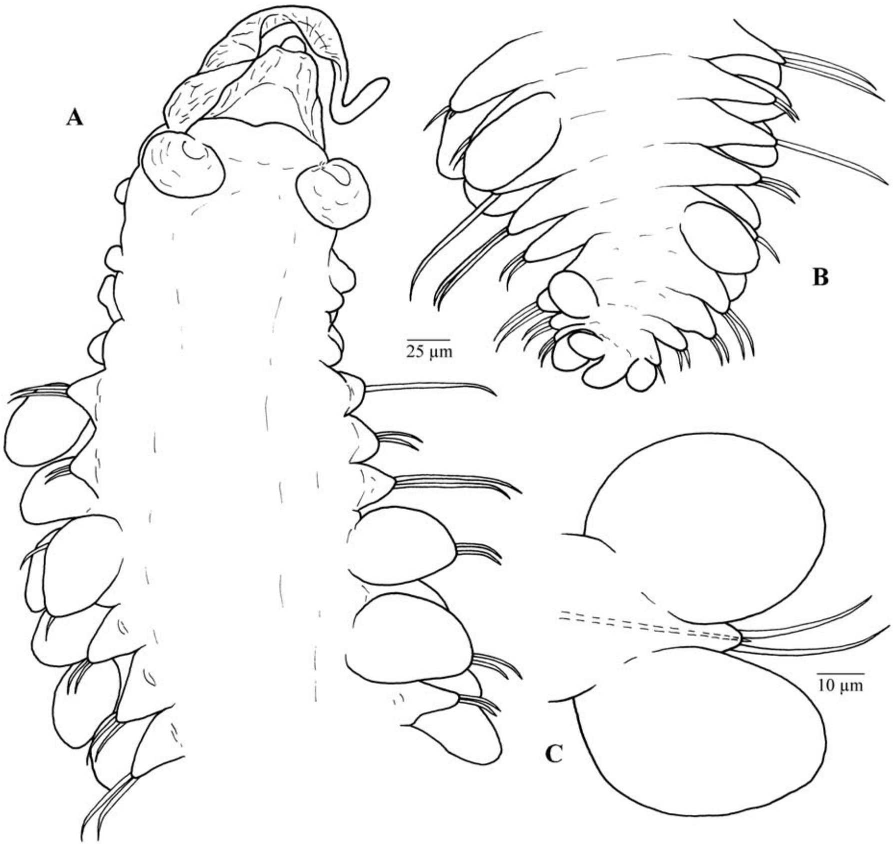

Fig. 152. *Typhloscolex muelleri* Busch. (A) Anterior end; dorsal view. (B) Posterior end; dorsal view. (C) Parapodium of mid-body; posterior view. (A–C: ZMH P25651).

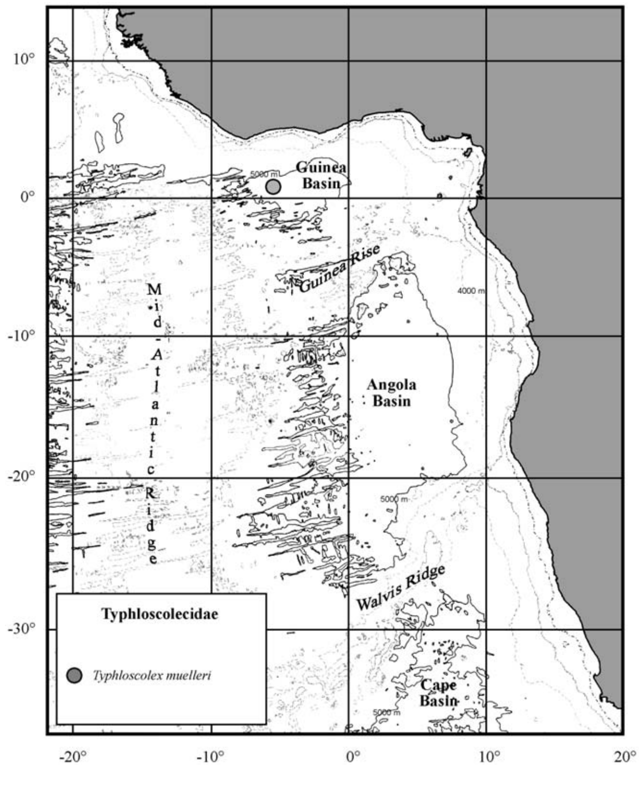

Fig. 153. Distribution of *Typhloscolex muelleri* in the studied region.

simple spines on each side of the acicula, which are distally slightly curved (Fig. 152C).

Pygidium with a pair of blunt conical cirri (Fig. 152B).

Remarks

The specimen of this reportedly holopelagic species was collected with a box corer, presumably only by chance. It is unclear whether it was captured right above the abyssal sea floor or during the vertical haul of the gear, or entered the sample during on-board sieving with seawater.

Distribution

Guinea Basin; 5136 m (Fig. 153).

Discussion

Friedrich (1950a) characterised most of the other species of *Typhloscolex* (*T. leuckarti* Reibisch, 1895; *T. phyllodes* Reibisch, 1895; *T. reibischi* Friedrich, 1950(a); *T. robusta* Friedrich, 1950(a)), especially using the form of the prostomium and the position and structure of the nuchal organs. Some other authors, e.g. Tebble (1960) and Dales and Peter (1972), suggested that those species might represent only variations or sexually maturing specimens of *Typhloscolex muelleri*. Furthermore, *Typhloscolex grandis* Støp-Bowitz, 1948, which was originally questionably referred to this genus, is now believed to belong to a different group (Støp-Bowitz 1984).

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Appendix 1. Supplementary material

This appendix, presenting a list of all specimens and fragments examined, their geographic origins, collections of deposition and type or voucher numbers, can be found in the online edition at: doi:10.1016/j.ode.2009.10.001.

References

Achari, G.P.K., 1975. Studies on new or little known polychaetes from the Indian Seas. 4. On a new record of *Sigambra tentaculata* (Treadwell) (Pilargidae), from the southwest coast of India along with observations on its early larval stages. J. Mar. Biol. Ass. India 17, 238–241.

Aguado, M.T., Nygren, A., Siddall, M.E., 2007. Phylogeny of Syllidae (Polychaeta) based on combined molecular analysis of nuclear and mitochondrial genes. Cladistics 23, 552–564.

Aguado, M.T., Rouse, G.W., 2006. First record of Sphaerodoridae (Phyllodocida: Annelida) from hydrothermal vents. Zootaxa 1383, 1–21.

Aguado, M.T., San Martín, G., 2008. Re-description of some enigmatic genera of Syllidae (Phyllodocida: Polychaeta). J. Mar. Biol. Ass. UK 88, 35–56.

Aguirrezabalaga, F., Ceberio, A., 2005. *Sphaerodoropsis amoureuxi* and *S. stellifer*, two new species of Sphaerodoridae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic). Cah. Biol. Mar. 46, 9–20.

Aguirrezabalaga, F., San Martín, G., Petersen, M.E., Ceberio, A., 1999. Presencia de *Dysponetus gracilis* Hartman, 1965 (Polychaeta, Chrysopetalidae) en las costas europeas, Golfo de Vizcaya. Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.) 95 (3–4), 21–25.

Amoureux, L., 1982. Annélides Polychètes recueillies sur la pente continentale de la Bretagne a l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. Cah. Biol. Mar. 23, 29–51.

Amoureux, L., 1986. Annélides Polychètes abyssaux de la campagne Abyplaine au lage de Madère. Bull. Mus. Natl. Hist. Nat., 4me Sér., Sect. A. 8, 591–615.

Apstein, C., 1900. Die Alciopiden und Tomopteriden der Plankton-Expedition, in: Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 Ausgeführten Plankton-Expedition der Humboldt-Stiftung, Bd. 2. Lipsius & Tischer, Kiel and Leipzig, pp. 1–62, pl. 1–14.

Arwidsson, I., 1899. Studien über die Familien Glyceridæ und Goniadidæ. Bergens Mus. Aarbog 11, 1–69.

Audouin, J.V., Milne Edwards, H., 1830. Première classe des animaux articulés. Les Annélides. In: Cuvier, G. (Ed.), Le Règne Animal Distribué d'apres son Organisation, pour Servir de Base a l'Histoire Naturelle des Animaux et d'Introduction a l'Anatomie Comparée, nouv. éd., t. III. Déterville, Paris.

Audouin, J.V., Milne Edwards, H., 1833. Classification des Annélides, et description de celles qui habitent les côtes de la France. Ann. Sci. Nat. 29, 195–269 pl. 13–18.

Averincev, V.G., 1972. Benthic polychaetes Errantia from the Antarctic and Subantarctic collected by the Soviet Antarctic Expeditions [in Russian]. Issled. Fauny Morei (=Explor. Fauna Seas) 11 (19), 88–293.

Baco, A.R., Smith, C.R., 2003. High biodiversity levels on deep-sea whale skeletons. Mar. Ecol. Prog. Ser. 260, 109–114.

Bakken, T., Wilson, R.S., 2005. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. Zool. Scr. 34, 507–547.

Balzer, W., Alheit, J., Emeis, K.-C., Lass, H.U., Türkay, M., 2006. South-East Atlantic 2000 Cruise No. 48, 6 July – 3 November 2000, Walvis Bay – Walvis Bay. Meteor-Ber. 06 (5), I–XV.

Banse, K., 1977. Gymnonereidinae new subfamily: the Nereididae (Polychaeta) with bifid parapodial neurocirri. J. Nat. Hist. 11, 609–628.

Barnett, P.R.O., Watson, J., Connelly, D., 1984. A multiple corer for taking visually undisturbed samples from shelf, bathyal and abyssal sediments. Oceanol. Acta 7, 399–408.

Beesley, P.L., Ross, G.J.B., Glasby, C.J., 2000. Fauna of Australia, Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula., Vol. 4A. CSIRO Publishing, Melbourne, pp. 1–465.

Benham, W.B., 1921. Polychæta. Australasian Antarctic Expedition 1911–14. Sci. Rep., Ser. C Zool. Bot. 6 (3), 1–128 pl. 5–10, 1 map.

Bett, B.J., Vanreusel, A., Vincx, M., Soltwedel, T., Pfannkuche, O., Lambshead, P.J.D., Gooday, A.J., Ferrero, T., Dinet, A., 1994. Sampler bias in the quantitative study of deep-sea meiobenthos. Mar. Ecol. Prog. Ser. 104, 197–203.

Bhaud, M., 1973. *Ancistrosyllis groenlandica*, Pilargidae, nouvelle espèce d'Annélide Polychète benthique a larve planctonique. Vie Milieu, Sér. A: Biol. Mar. 23, 263–272.

Blake, J.A., 1985. Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific. I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae and Maldanidae. Biol. Soc. Wash. Bull. 6, 67–101.

Blake, J.A., 1988. New species and records of Phyllodocidae (Polychaeta) from Georges Bank and other areas of the western North Atlantic. Sarsia 73, 245–257.

Blake, J.A., 1991. A new species of *Hesiocaeca* (Polychaeta: Hesionidae) from hydrothermal vents at the Mariana back-arc basin with notes on other polychaetes. Proc. Biol. Soc. Wash. 104, 175–180.

Blake, J.A., 1994. 5. Family Lacydoniidae Bergström, 1914, In: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4 – The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 187–195.

Blake, J.A., 1997a. 4. Family Phyllodocidae Oersted, 1843, in: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4, rev. ed.—The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 109–177.

Blake, J.A., 1997b. 10. Family Pilargidae Saint Joseph, 1899, in: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4, rev. ed.—The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 261–284.

Bleidorn, C., Vogt, L., Bartolomaeus, T., 2005. Molecular phylogeny of lugworms (Annelida, Arenicolidae) inferred from three genes. Mol. Phyl. Evol. 37, 673–679.

Böggemann, M., 2002. Revision of the Glyceridae Grube 1850 (Annelida: Polychaeta). Abh. Senckenb. Naturforsch. Ges. 555, 1–249.

Böggemann, M., 2005. Revision of the Goniadidae (Annelida, Polychaeta). Abh. Naturwiss. Ver. Hamburg (NF) 39, 1–354.

Böggemann, M., 2006. Worms that might be 300 million years old. Mar. Biol. Res. 2, 130–135.

Böggemann, M., Fiege, D., Purschke, G., 2000. Ultrastructure of the proboscidial papillae in some *Glycera* species (Annelida: Polychaeta: Glyceridae). Cah. Biol. Mar. 41, 143–153.

Böggemann, M., Purschke, G., 2005. Abyssal benthic Syllidae (Annelida: Polychaeta) from the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 221–226.

Bohn, J.M., 2005. On two rare abyssal Myriotrochidae (Echinodermata: Holothuroidea: Apodida) new to the South Atlantic: *Siniotrochus myriodontus* Gage and Billett, 1986 and *Neolepidotrochus parvidiscus angolensis* subsp. nov. Org. Divers. Evol. 5 (Suppl. 1), 231–238.

Borowski, C., 1994. Three new deep-sea species of Sphaerodoridae (Annelida, Polychaeta) from the eastern tropical South Pacific. Zool. Scr. 23, 193–203.

Brandt, A., 2001. *Acanthaspidia namibia* sp. nov. from the deep Angola Basin. Beaufortia 51, 91–101.

Brandt, A., 2002. New species of Nannoniscidae (Crustacea, Isopoda) and *Saetoniscus* n. gen. from the deep sea of the Angola Basin. Zootaxa 88, 1–36.

Brandt, A., 2004. New deep-sea species of the Macrostylidae (Asellota: Isopoda: Malacostraca) from the Angola Basin off Namibia (South West Africa). Zootaxa 448, 1–35.

Brandt, A., Barthel, D., 1995. An improved supra- and epibenthic sledge for catching *Peracarida* (Crustacea, Malacostraca). Ophelia 43, 15–23.

Brandt, A., Brenke, N., Andres, H.-G., Brix, S., Guerrero-Kommritz, J., Mühlenhardt-Siegel, U., Wägele, J.-W., 2005. Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 105–112.

Brenke, N., Brix, S., Knuschke, T., 2005. A new deep-sea isopod species from the Angola Basin: *Prochelator angolensis* sp. nov. (Asellota: Desmosomatidae). Org. Divers. Evol. 5 (Suppl. 1), 179–188.

Brito, M.C., Núñez, J., Bacallado, J.J., Ocaña, O., 1996. Anélidos poliquetos de Canarias: Orden Phyllodocida (Chrysopetalidae, Pisionidae, Glyceridae, Sphaerodoridae, Hesionidae y Pilargidae). In: Llinás, O., González, J.A., Rueda, M.J. (Eds.), Oceanografía y Recursos Marinos en el Atlántico Centro-Oriental. Monogr. Inst. Canario Cienc. Mar. 1, pp. 157–179.

Bröhldick, K.S.T., 2005. A new taxon of Idyanthidae (Copepoda, Harpacticoida) from the deep sea of the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 43–57.

Brökeland, W., Wägele, J.W., 2004. Redescription of three species of *Haploniscus* Richardson, 1908 (Isopoda, Asellota, Haploniscidae) from the Angola Basin. Org. Divers. Evol. 4, 237–239.

Busch, W., 1851. Beobachtungen über Anatomie und Entwicklung einiger wirbellosen Seethiere. August Hirschwald, Berlin.

Buzhinskaja, G.N., 2001. Class Polychaeta. In: Sirenko, B.I. (Ed.), List of Species of Free-living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters. Issled. Fauny Morei (= Explor. Fauna Seas). 51(59), 52–66.

Buzhinskaja, G.N., 2004. Class Polychaeta, In: Sirenko, B.I. (Ed.), Fauna and ecosystems of the Laptev Sea and adjacent deep waters of the Arctic Basin, pt. II. Issled. Fauny Morei (= Explor. Fauna Seas). 54(62), 120–127.

Chun, C., 1888. Die pelagische Thierwelt in grösseren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna. Bibl. Zool. 1, 1–66 pl. 1–5.

Corliss, J.B., Dymond, J., Gordon, L.I., Edmond, J.M., Herzen, R.P.V., Ballard, R.D., Green, K., Williams, D., Bainbridge, A., Crane, K., Vanandel, T.H., 1979. Submarine thermal springs on the Galapagos rift. Science 203, 1073–1083.

Cristobo, F.J., Urgorri, V., Ríos, P., 2005. Three new species of carnivorous deep-sea sponges from the DIVA-1 expedition in the Angola Basin (South Atlantic). Org. Divers. Evol. 5 (Suppl. 1), 203–213.

Dahlgren, T.G., 1996. Two new species of *Dysponetus* (Polychaeta: Chrysopetalidae) from Italy and Papua New Guinea. Proc. Biol. Soc. Wash. 109, 575–585.

Dahlgren, T.G., Glover, A.G., Baco, A., Smith, C.R., 2004. Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysopetalidae) from the deep Pacific Ocean. Deep-Sea Res. I 51, 1873–1887.

Dahlgren, T.G., Pleijel, F., 1995. On the generic allocation of *Chrysopetalum caecum* Langerhans, 1880 (Polychaeta, Chrysopetalidae). Mitt. Hamb. Zool. Mus. Inst., Ergänz.bd. 92, 159–173.

Dales, R.P., 1955. The evolution of the pelagic alciopid and phyllodocid polychaetes. Proc. Zool. Soc. London. 125, 411–420.

Dales, R.P., 1957a. Pelagic polychaetes of the Pacific Ocean. Bull. Scripps Inst. Oceanogr. 7, 99–168.

Dales, R.P., 1957b. Pelagic polychaetes from the Bay of Biscay. Ann. Mag. Nat. Hist., 12th Ser. 10,, 661–664.

Dales, R.P., Peter, G., 1972. A synopsis of the Pelagic Polychaeta. J. Nat. Hist. 6, 55–92.

Day, J.H., 1963a. Polychaete Fauna of South Africa: part 7. Species from depths between 1,000 and 3,330 metres west of Cape Town. Ann. South African Mus. 46, 353–371.

Day, J.H., 1963b. The polychaete fauna of South Africa. part 8: new species and records from grab samples and dredgings. Bull. Brit. Mus. (Nat. Hist.), Zool. 10, 381–445.

Day, J.H., 1967. A Monograph on the Polychaeta of Southern Africa. Part I. Errantia and Part II. Sedentaria. Brit. Mus. (Nat. Hist.), London, Publ. 656, 1–878.

Desbruyères, D., 1980. Sphaerodoridae (Annélides Polychètes) profonds du Nord-Est Atlantique. Bull. Mus. Natl. Hist. Nat., Paris, 4me Sér., Sect. A 2, 109–128.

Desbruyères, D., Segonzac, M., Bright, M. (Eds.), 2006. Handbook of Deep-Sea Hydrothermal Vent Fauna, 2nd ed. Denisia 18, pp. 1–544.

Desbruyères, D., Toulmond, A., 1998. A new species of hesionid worm, *Hesiocaeca methanicola* sp. nov. (Polychaeta: Hesionidae), living in ice-like methane hydrates in the deep Gulf of Mexico. Cah. Biol. Mar. 39, 93–98.

Detinova, N.N., 1985. Polychaetous annelids of Reykjanes Ridge (North Atlantic) [in Russian]. Trudy Inst. Okean. (= Trans. P.P. Shirshov Inst. Oceanol.) 120, 96–136.

Ebbesmeyer, C.C., Ingraham Jr., W.J., 1994. Pacific toy spill fuels ocean current pathways research. Earth in Space 7 (2), 7–9.

Ehlers, E., 1913. Die Polychaeten-Sammlung der Deutschen Südpolar-Expedition 1901–1903, In: Drygalski, E. von (Ed.), Deutsche Südpolar-Expedition, 1901–1903, Bd. XIII, Zool. 5(4), 397–598, pl. 26–46.

Eibye-Jacobsen, D., 1991. A Revision of *Eumida* Malmgren, 1865 (Polychaeta: Phyllodocidae). Steenstrupia 17, 81–140.

Eibye-Jacobsen, D., 1993. On the phylogeny of the Phyllodocidae (Polychaeta Annelida): an alternative. Z. Zool. Syst. Evol.forsch. 31, 174–197.

Eklöf, J., Pleijel, F., Sundberg, P., 2007. Phylogeny of benthic Phyllodocidae (Polychaeta) based on morphological and molecular data. Mol. Phyl. Evol. 45, 261–271.

Eliason, A., 1951. Polychaeta. Rep. Swedish Deep-Sea Exped. 1947–1948. Zool. 2 (11), 129–148 pl. 1–2.

Eliason, A., 1962. Die Polychaeten der Skagerak-Expedition 1933. Zool. Bidr. Uppsala 33, 207–293.

Emson, R.H., Young, C.M., Paterson, G.L.J., 1993. A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea-urchin *Archeopneustes hystrix* (A. Agassiz, 1880). J. Nat. Hist. 27, 1013–1028.

Fauchald, K., 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. Allan Hancock Monogr. Mar. Biol. 7, 1–575.

Fauchald, K., 1974. Sphaerodoridae (Polychaeta: Errantia) from world-wide areas. J. Nat. Hist. 8, 257–289.

Fauchald, K., 1977a. The polychaete worms. Definitions and keys to the orders, families and genera. Nat. Hist. Mus. Los Angeles Co., Sci. Ser. 28, 1–188.

Fauchald, K., 1977b. Some nereid polychaetes from deep water. In: Reish, D.J., Fauchald, K. (Eds.), Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman. Allan Hancock Foundation, University of Southern California Los Angeles, pp. 157–171.

Fauchald, K., Hancock, D.R., 1981. Deep-water polychaetes from a transect off central Oregon. Allan Hancock Monogr. Mar. Biol. 11, 1–73.

Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Annu. Rev. Oceanogr. Mar. Biol. 17, 193–284.

Fauchald, K., Rouse, G., 1997. Polychaete systematics: past and present. Zool. Scr. 26, 71–138.

Fauvel, P., 1913. Quatrième note préliminaire sur les Polychètes provenant des campagnes de l'Hirondelle et de la Princesse-Alice, ou déposées dans le Musée Océanographique de Monaco. Bull. Mus. Océanogr. Monaco 270, 1–80.

Feigenbaum, D., 1979. Predation on chaetognaths by typhloscolecid polychaetes, one explanation for headless specimens. J. Mar. Biol. Ass. UK 59, 631–633.

Fernández-Álamo, M.A., 2000. Tomopterids (Annelida: Polychaeta) from the eastern tropical Pacific Ocean. Bull. Mar. Sci. 67, 45–53.

Fernández-Álamo, M.A., 2002. Composition and distribution of Lopadorhynchidae (Annelida-Polychaeta) in the eastern tropical Pacific Ocean. In: Färber Lorda, J. (Ed.), Oceanography of the Eastern Pacific II. CICESE, pp. 41–59.

Fernández-Álamo, M.A., 2006. Composition, abundance and distribution of holoplanktonic polychaetes from the expedition "El Golfo 6311-12" of Scripps Institution of Oceanography. Sci. Mar. 70S3, 209–215.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotech. 3, 294–299.

Friedrich, H., 1950a. Beiträge zur Kenntnis der Polychätenfamilie Typhloscolecidae. (Die pelagischen Polychaeten der „Meteor"-Expedition, II.) Zoolog. Jahrb., Abt. Syst. Ökol. Geogr. Tiere 79, 309–320.

Friedrich, H., 1950b. Vorkommen und Verbreitung der pelagischen Polychaeten im Atlantischen Ozean. Auf Grund der Fänge der „Meteor"-Expedition. Kieler Meeresforsch. 7, 5–23.

Gad, G., 2005a. Giant Higgins-larvae with paedogenetic reproduction from the deep sea of the Angola Basin—evidence for a new life cycle and for abyssal gigantism in Loricifera? Org. Divers. Evol. 5 (Suppl. 1), 59–75.

Gad, G., 2005b. A parthenogenetic, simplified adult in the life cycle of *Pliciloricus pedicularis* sp. n. (Loricifera) from the deep sea of the Angola Basin (Atlantic). Org. Divers. Evol. 5 (Suppl. 1), 77–103.

Gardiner, S.L., 1976 ("1975"). Errant polychaete annelids from North Carolina. J. Elisha Mitchell Sci. Soc. 91, 77–220.

Gathof, J.M., 1984. Chapter 34: Family Lacydoniidae Bergström 1814. In: Uebelacker, J.M., Johnson, P.G. (Eds.), Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, Vol. 5. Vittor & Assoc., Metairie, LA, pp. 1–5.

Glasby, C.J., 2000a. Family Pilargidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula., Vol. 4. CSIRO Publishing, Melbourne, pp. 148–150.

Glasby, C.J., 2000b. Family Syllidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula., Vol. 4. CSIRO Publishing, Melbourne, pp. 161–167.

Grassle, J.F., 1987. The ecology of deep-sea hydrothermal vent communities. Adv. Mar. Biol. 23, 301–362.

Gravier, C., 1911. Expédition artarctique française du "Pourquoi-Pas", dirigée par le Dr. J.-B. Charcot (1908–1910). Espèces nouvelles d'Annélides Polychètes. Bull. Mus. Natl. Hist. Nat. 17, 310–316.

Greeff, R., 1876. Untersuchungen über die Alciopiden. Nova Acta Ksl. Leop.-Carol. Dt. Akad. Naturf. 39, 34–132.

Greeff, R., 1879. Ueber pelagische Anneliden von der Küste der canarischen Inseln. Z. Wiss. Zool. 32, 237–283 pl. 13–15.

Greeff, R., 1882. Über die rosettenförmigen Leuchtorgane der Tomopteriden und zwei neue Arten von *Tomopteris*. Zool. Anz. 116, 1–4.

Greeff, R., 1885. Über die pelagische Fauna an den Küsten der Guinea-Inseln. Z. Wiss. Zool. 42, 432–458 pl. 12–14.

Guerrero-Kommritz, J., 2003a. *Portaratruma*, a new genus of deep-sea Tanaidacea (Crustacea) with description of two new species. Zootaxa 282, 1–14.

Guerrero-Kommritz, J., 2003b. Agathotanaididae (Crustacea: Tanaidacea) from the Angola Basin. Zootaxa 330, 1–15.

Guerrero-Kommritz, J., 2005. Notes on the Tanaidacea (Crustacea: Peracarida) of the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 171–177.

Guerrero-Kommritz, J., Błażewicz-Paskowycz, M., 2004. New species of *Tanaella* Norman et Stebbing, 1886 (Tanaidacea: Crustacea) from the deep-sea of the Antarctic and the Angola Basin. Zootaxa 459, 1–20.

Guerrero-Kommritz, J., Heard, R.W., 2003. A new genus and species of deep-sea apseudomorph tanaidacean (Crustacea: Malacostraca: Peracarida) from the Angola Basin. Mitt. Hamb. Zool. Mus. Inst. 100, 127–137.

Guerrero-Kommritz, J., Schmidt, A., Brandt, A., 2002. *Paranarthura* Hansen 1913 (Crustacea: Tanaidacea) from the Angola Basin, description of *Paranarthura angolensis* n. sp. Zootaxa 116, 1–12.

Halanych, K.M., Cox, L.N., Struck, T.H., 2007. A brief review of holopelagic annelids. Integr. Comp. Biol. 47, 872–879.

Halanych, K.M., Janosik, A.M., 2006. A review of molecular markers used for annelid phylogenetics. Int. Comp. Biol. 46, 533–543.

Hartman, O., 1964. Polychaeta Errantia of Antarctica. Antarct. Res. Ser. 3, 1–131.

Hartman, O., 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. Vol. 28, Allan Hancock Found. Publ., Occas. Pap. pp. 1–378.

Hartman, O., 1967. Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. Allan Hancock Monogr. Mar. Biol. 2, 1–387.

Hartman, O., 1971. Abyssal polychaetous annelids from the Mozambique Basin off Southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. J. Fish. Res. Bd. Can. 28, 1407–1428.

Hartman, O., 1978. Polychaeta from the Weddell Sea Quadrant, Antarctica. Biology of the Antarctic Seas VI. Antarct. Res. Ser. 26 (4), 125–223.

Hartman, O., Fauchald, K., 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas Part II. Allan Hancock Monogr. Mar. Biol. 6, 1–327.

Hartmann-Schröder, G., 1974. Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. Veröff. Inst. Meeresforsch. Bremerh. 14, 169–274.

Hartmann-Schröder, G., 1975. Polychaeten der Iberischen Tiefsee, gesammelt auf der 3. Reise der METEOR im Jahre 1966. Mitt. Hamb. Zool. Mus. Inst. 72, 47–73.

Hartmann-Schröder, G., 1977a. The genera *Ceratocephale* Malmgren, *Olganereis* n. gen., and *Profundilycastis* n. gen. (Nereidae, Polychaeta) with a key to the nereid genera without chitinous paragnaths. In: Reish, D.J., Fauchald, K. (Eds.), Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman. Allan Hancock Foundation, University of Southern California, Los Angeles, pp. 141–155.

Hartmann-Schröder, G., 1977b. *Profundilycastis profundus* (Hartman, 1965) (Nereidae, Polychaeta. Wiederbeschreibung des Holotypus. Mitt. Hamb. Zool. Mus. Inst. 74, 45–48.

Hartmann-Schröder, G., 1979. Die Polychaeten der „Atlantischen Kuppenfahrt" von F.S. „Meteor" (Fahrt 9c, 1967). 1. Proben aus Schleppgeräten. Meteor Forsch.-Ergeb., Reihe D Biol. 31, 63–90.

Hartmann-Schröder, G., 1983. Zur Kenntnis einiger Foraminiferengehäuse bewohnender Polychaeten aus dem Nordostatlantik. Mitt. Hamb. Zool. Mus. Inst. 80, 169–176.

Hartmann-Schröder, G., 1996. Annelida, Borstenwürmer, Polychaeta. In: Die Tierwelt Deutschlands und der Angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise, 2. Aufl. 58, 1–648.

Hartmann-Schröder, G., Rosenfeldt, P., 1992. Die Polychaeten der „Polarstern"-Reise ANT V/1 in die Antarktis 1986. Teil 1: Euphrosinidae bis Iphitimidae. Mitt. Hamb. Zool. Mus. Inst. 89, 85–124.

Hessle, C., 1925. Einiges über die Hesioniden und die Stellung der Gattung *Ancistrosyllis*. Arkiv Zool. 17A (10), 1–36 pl. 1–2.

Hilbig, B., 1997a. 9. Family Hesionidae Sars, 1862. In: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4, rev. ed.—The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 235–260.

Hilbig, B., 1997b. 12. Family Nereididae Johnston, 1845. In: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4, rev. ed.—The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 291–316.

Hilbig, B., 1997c. 13. Family Nephtyidae Grube, 1850. In: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 4, rev. ed.—The Annelida Part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae). Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 317–349.

Hilbig, B., 2005. *Melinnopsis angolensis* (Annelida: Polychaeta: Ampharetidae), a new species from the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 215–220.

Hillis, D.M., Dixon, M.T., 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. Q. Rev. Biol. 66, 411–453.

Horst, R., 1910. On the genus *Chloeia* with some new species from the Malay-Archipelago, partly collected by the Siboga-Expedition. Notes Leyden Mus. 32, 169–175.

Horst, R., 1912. Polychaeta Errantia of the Siboga Expedition. Part I Amphinomidae. Siboga-Exped. Uitk. Zool. Bot. Oceanogr. Geol. Geb. Verz. Nederl. Oost-Indië 1899–1900 24a, 1–43, pl. 1–9.

Hutchings, P.A., 2000a. Family Amphinomidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 107–110.

Hutchings, P.A., 2000b. Family Aphroditidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 117–120.

Hylleberg, J., Nateewathana, A., 1988. Polychaetes of Thailand. Nereididae (Part 2): *Ceratocephale* and *Gymnonereis*, with description of two new species and notes on the subfamily Gymnonereidinae. Phuket Mar. Biol. Cent. Res. Bull. 49, 1–20.

ICZN = International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature, London.

Imajima, M., Hartman, O., 1964. The polychaetous annelids of Japan. Part I. Allan Hancock Found. Publ., Occas. Pap. 26, 1–237.

Jannasch, H.W., 1985. Leben in der Tiefsee auf chemosynthetischer Basis. Naturwissenschaften 72, 285–290.

Jannasch, H.W., Mottl, M.J., 1985. Geomicrobiology of deep-sea hydrothermal vents. Science 229, 717–725.

Jiménez-Cueto, S., Suárez-Morales, E., 1999. Tomopterids (Polychaeta: Tomopteridae) of the Western Caribbean Sea. Bull. Inst. R. Sci. Nat. Belg., Biol. 69, 5–14.

Jördens, J., Struck, T., Purschke, G., 2004. Phylogenetic inference regarding Parergodrilidae and *Hrabeiella periglandulata* ('Polychaeta' Annelida) based on 18S rDNA, 28S rDNA and COI sequences. J. Zool. Syst. Evol. Res. 42, 270–280.

Johnson, H.P., 1901. The Polychaeta of the Puget Sound region. Proc. Boston Soc. Nat. Hist. 29, 381–437.

Jones, M.L. (Ed.), 1985. Hydrothermal Vents of the Eastern Pacific: an overview, Biol. Soc. Wash., Bull. 6, 1–547.

Kato, T., Pleijel, F., 2003. A revision of *Paranaitis* Southern, 1914 (Polychaeta: Phyllodocidae). Zool. J. Linn. Soc. 138, 379–429.

Katzmann, W., Laubier, L., Ramos, J., 1974. Pilargidae (Annélides Polychètes errantes) de Méditerranée. Bull. Inst. Océanogr., Monaco 71 (1428), 1–40.

Kirkegaard, J.B., 1980. Abyssal benthic polychaetes from the northeast Atlantic Ocean southwest of the British Isles. Steenstrupia 6, 81–98.

Kirkegaard, J.B., 1983. The Polychaeta of West Africa. Part II. Errant species. 1. Aphroditidae to Nereididae. Atlantide Rep. 13, 181–240.

Kirkegaard, J.B., 1994. The biogeography of some abyssal Polychaetes. In: Dauvin, J.-C., Laubier, L., Reish, D.J. (Eds.), Actes de la 4ème Conférence Internationale des Polychètes. Mém. Mus. Natn. Hist. Nat. 162, pp. 471–477.

Kirkegaard, J.B., 1995. Bathyal and abyssal polychaetes (errant species). Galathea Rep. 17, 7–56.

Kiseleva, M.I., 1996. On a new name of the genus *Victoriella* (Polychaeta, Chrysopetallidae [sic!]) [in Russian with English summary]. Zool. Zh. 75, 1092.

Knox, G.A., Cameron, D.B., 1998. The marine fauna of the Ross Sea: Polychaeta. NIWA Biodivers. Mem. 108, 1–125.

Kojima, S., Segawa, R., Hashimoto, J., Ohta, S., 1997. Molecular phylogeny of vestimentiferans collected around Japan, revealed by the nucleotide sequences of mitochondrial DNA. Mar. Biol. 127, 507–513.

Kröncke, I., Türkay, M., 2003. Structural and functional aspects of the benthic communities in the deep Angola Basin. Mar. Ecol. Prog. Ser. 260, 43–53.

Kudenov, J.D., 1987. Five new species of Sphaerodoridae (Annelida: Polychaeta) from the Gulf of Mexico. Proc. Biol. Soc. Wash. 100, 927–935.

Kudenov, J.D., 1993. Amphinomidae and Euphrosinidae (Annelida: Polychaeta) principally from Antarctica, the Southern Ocean, and Subantarctic regions. Antarct. Res. Ser. 58, 93–150.

Kudenov, J.D., 1995. 7. Family Amphinomidae Lamarck, 1818. In: Blake, J.A., Hilbig, B., Scott, P.H. (Eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 5—The

Annelida Part 2. Polychaeta: Phyllodocida (Syllidae and Scale-Bearing Families), Amphinomida, and Eunicida. Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 207–215.

Langerhans, P., 1880. Die Wurmfauna Madeiras. II. Z. Wiss. Zool. 33, 271–316 pl. 14–17.

Laubier, L., 1975. *Lacydonia laureci* sp. n., annelide polychete nouvelle de l'étage abyssal de Méditerranée Orientale. Vie Milieu, Sér. A: Biol. Mar. 25, 75–82.

Leese, F., Brenke, N., 2005. *Chauliodoniscus coronatus* sp. nov., a new deep-sea species from the Angola Basin (Crustacea, Isopoda, Asellota, Janiroidea, Haploniscidae). Org. Divers. Evol. 5 (Suppl. 1), 189–201.

Levenstein, R.J., 1975. The polychaetous annelids of the deep-sea trenches of the Atlantic sector of the Antarctic Ocean [in Russian]. Trudy Inst. Okean. (= Trans. P.P. Shirshov Inst. Oceanol.) 103, 119–142.

Levinsen, G.M.R., 1879. Om to nye slægter af arctiske chætopode Annelider. Vidensk. Meddel. Naturh. Foren. Kjöbenhaven 31/32, 9–18, pl. 1.

Levinsen, G.M.R., 1885. Spolia atlantica. Om nogle pelagiske Annulata. Vidensk. Selsk. Skr., 6. Række, Naturvidensk. Math. Afd. 3, 321–344, 1 pl.

Licher, F., Westheide, W., 1994. The phylogenetic position of the Pilargidae with a cladistic analysis of the taxon—facts and ideas. In: Dauvin, J.-C., Laubier, L., Reish, D.J. (Eds.), Actes de la 4ème Conférence Internationale des Polychètes. Mém. Mus. Natn. Hist. Nat. 162, pp. 223–235.

Lützen, J., 1961. Sur une nouvelle espèce de polychète *Sphaerodoridium commensalis*, n. gen., n. spec. (Polychaeta Errantia, famille des Sphaerodoridae) vivant en commensal de *Terebellides stroemi* Sars. Cah. Biol. Mar. 2, 409–416.

Malyutina, M.V., Wägele, J.W., Brenke, N., 2001. New records of little known deep-sea Echinothambematidae (Crustacea: Isopoda: Asellota) with redescription of *Vemathambema elongata* Menzies, 1962 and description of a new species from the Argentina Basin. Org. Divers. Evol. 1, 321–322.

Manaranche, R., Thieffry, M., Israel, M., 1980. Effect of the venom of *Glycera convoluta* on the spontaneous quantal release of transmitter. J. Cell Biol. 85, 446–458.

Martin, D., Alva, V., 1988. Un polychète nouveau *Sphaerodorum ophiurophoretos* nov. sp. (Polychaeta: Sphaerodoridae), symbiotique de l'ophiure *Amphipholis squamata* (Delle Chiaje, 1828). Bull. Inst. R. Sci. Nat. Belg., Biol. 58, 45–49.

Martin, D., Britayev, T.A., 1998. Symbiotic polychaetes: review of known species. Annu. Rev. Oceanogr. Mar. Biol. 36, 217–340.

Martínez Arbizu, P., Schminke, H.K., 2005. DIVA-1 expedition to the deep sea of the Angola Basin in 2000 and DIVA-1 workshop in 2003. Org. Divers. Evol. 5 (Suppl. 1), 1–2.

Mattson, S., 1981. Burrowing and feeding of *Goniada maculata* Ørsted (Polychaeta). Sarsia 66 (1), 49–51.

McIntosh, W.C., 1879. On the Annelida obtained during the Cruise of H.M.S. 'Valorous' to Davis Strait in 1875. Trans. Linn. Soc. London, 2nd Ser., Zool. 1, 499–511 pl. 65.

McIntosh, W.C., 1885. Report on the Annelida Polychæta collected by H.M.S. Challenger during the years 1873–76. Rep. Sci. Res. Voyage H.M.S. Challenger 1873–76. Zool. 12, 1–554.

McIntyre, A.D., Warwick, R.M., 1984. Meiofauna techniques. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell, Oxford, pp. 217–244.

Mettam, C., 1980. On the feeding habits of *Aphrodita aculeata* and commensal polynoids. J. Mar. Biol. Ass. UK 60, 833–834.

Monro, C.C.A., 1930. Polychaete worms. Discovery Rep. 2, 1–222.

Monro, C.C.A., 1936. Polychaete worms. II. Discovery Rep. 12, 59–198.

Moreira, J., Cacabelos, E., Troncoso, J.S., 2004. A new species of *Sphaerodoropsis* (Polychaeta: Sphaerodoridae) from north-east Atlantic, with comments on other species of the genus. J. Mar. Biol. Ass. UK 84, 995–1000.

Mühlenhardt-Siegel, U., 2003. A new Cumacea genus (Crustacea: Peracarida: Diastylidae) from the deep-sea expedition DIVA-1 with RV "Meteor" to the Angola Basin. Beaufortia 53, 159–165.

Mühlenhardt-Siegel, U., 2005a. New Cumacea species (Crustacea: Peracarida) from the deep-sea expedition DIVA-1 with RV "Meteor" to the Angola Basin in July 2000. Families Lampropidae, Bodotriidae. Org. Divers. Evol. 5, (Suppl. 1), 113–130.

Mühlenhardt-Siegel, U., 2005b. Cumacea species (Crustacea: Peracarida) from the deep-sea expedition DIVA-1 with RV "Meteor" to the Angola Basin in July 2000. Family Nannastacidae. Org. Divers. Evol. 5 (Suppl. 1), 131–149.

Mühlenhardt-Siegel, U., 2005c. Cumacea species (Crustacea: Peracarida) from the deep-sea expedition DIVA-1 with RV "Meteor" to the Angola Basin in July 2000. Family Nannastacidae. Org. Divers. Evol. 5 (Suppl. 1), 151–170.

Nicholas, K.B., Nicholas, H.B. Jr., 1997. GeneDoc: a Tool for Editing and Annotating Multiple Sequence Alignments. Software distributed by the authors.

Ockelmann, K.W., Vahl, O., 1970. On the biology of the polychaete *Glycera alba*, especially its burrowing and feeding. Ophelia 8, 275–294.

O'Connor, B.D.S., Shin, P.K.S., 1983. *Hesiospina similis* (Hessle) (Polychaeta, Hesionidae) from Galway Bay, west coast of Ireland, with notes on its taxonomic status and distribution. Cah. Biol. Mar. 24, 355–361.

Øresland, V., Pleijel, F., 1991. An ectoparasitic typhloscolecid polychaete on the chaetognath *Eukrohnia hamata* from the Antarctic Peninsula. Mar. Biol. 108, 429–432.

Øresland, V., Bray, R.A., 2005. Parasites and headless chaetognaths in the Indian Ocean. Mar. Biol. 147, 725–734.

Ørsted, A.S., 1842. Udtog af en beskrivelse af Grønlands Annulata dorsibranchiata. Naturhist. Tidsskr. 4, 109–127.

Orensanz, J.M., 1972. Los anelidos poliquetos de la Provincia Biogeografica Argentina. I. Palmyridae (= Chrysopetalidae), Amphinomidae y Euphrosinidae. Physis 31 (83), 485–501.

Orrhage, L., Eibye-Jacobsen, D., 1998. On the anatomy of the central nervous system of Phyllodocidae (Polychaeta) and the phylogeny of phyllodocid genera: a new alternative. Acta Zool. 79, 215–234.

Oug, E., 1980. On feeding and behavior of *Ophiodromus flexuosus* (Delle Chiaje) and *Nereimyra punctata* (O.F. Müller) (Polychaeta, Hesionidae). Ophelia 19, 175–191.

Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L., Grabowski, G., 1991. The Simple Fool's Guide to PCR. University of Hawaii, Honolulu Ver. 2.0.

Paterson, G.L.J., Glover, A.G., 2000. A new species of *Sigambra* (Polychaeta, Pilargidae) from the abyssal plains of the NE Atlantic. Bull. Nat. Hist. Mus., London (Zool.) 66, 167–170.

Paull, C.K., Hecker, B., Commeau, R., Freemanlynde, R.P., Neumann, C., Corso, W.P., Golubic, S., Hook, J.E., Sikes, E., Curray, J., 1984. Biological communities at the Florida escarpment resemble hydrothermal vent taxa. Science 226, 965–967.

Pettibone, M.H., 1963. Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae. US Natl. Mus., Smithson. Inst., Bull. 227, 1–356.

Pettibone, M.H., 1966. Revision of the Pilargidae (Annelida: Polychaeta), including descriptions of new species, and redescription of the pelagic *Podarmus ploa* Chamberlin (Polynoidae). Proc. US Natl. Mus. 118 (3525), 155–207.

Pettibone, M.H., 1970. Polychaeta Errantia of the Siboga-Expedition. Part IV: some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. Siboga-Exped. Monogr. 24 (1d), 199–270.

Pettibone, M.H., 1971. Revision of some species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaeta: Nereididae). Smithson. Contr. Zool. 104, 1–53.

Piatkowski, U., Diekmann, R., 2005. A short note on the cephalopods sampled in the Angola Basin during the DIVA-1 expedition. Org. Divers. Evol. 5 (Suppl. 1), 227–230.

Pleijel, F., 1988. *Phyllodoce* (Polychaeta, Phyllodocidae) from northern Europe. Zool. Scr. 17, 141–153.

Pleijel, F., 1991. Phylogeny and classification of the Phyllodocidae (Polychaeta). Zool. Scr. 20, 225–261.

Pleijel, F., 1993a. Polychaeta Phyllodocidae. Mar. Invert. Scandinavia 8, 1–159.

Pleijel, F., 1993b. Taxonomy of European species of *Amphiduros* and *Gyptis* (Polychaeta: Hesionidae). Proc. Biol. Soc. Wash. 106, 158–181.

Pleijel, F., 1993c. *Gyptis crypta*, a new hesionid species from the USA east coast, with a redescription of *G. vittata* Webster & Benedict, 1887 (Annelida: Polychaeta). Proc. Biol. Soc. Wash. 106, 237–242.

Pleijel, F., 1998. Phylogeny and classification of Hesionidae (Polychaeta). Zool. Scr. 27, 89–163.

Pleijel, F., 2001a. Amphinomida Lamarck, 1818. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 145–147.

Pleijel, F., 2001b. Aphroditoidea Malmgren, 1867. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 73–76.

Pleijel, F., 2001c. Chrysopetalidae Ehlers, 1864. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 89–90.

Pleijel, F., 2001d. Glyceriformia Fauchald, 1977. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 111–114.

Pleijel, F., 2001e. Hesionidae Grube, 1850. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 91–93.

Pleijel, F., 2001f. *Lacydonia* Marion, 1874. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 117–118.

Pleijel, F., 2001g. Lopadorhynchidae Claparède, 1868. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 119–120.

Pleijel, F., 2001h. 'Minor' holopelagic Phyllodocida. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 121–123.

Pleijel, F., 2001i. Nephtyidae Grube, 1850. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 127–129.

Pleijel, F., 2001j. Nereididae Johnston, 1865. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 96–98.

Pleijel, F., 2001k. Phyllodocidae Örsted, 1843a. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 132–135.

Pleijel, F., 2001l. Pilargidae Saint-Joseph, 1899. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 99–101.

Pleijel, F., 2001m. Sphaerodoridae Malmgren, 1867. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 136–138.

Pleijel, F., 2001n. Syllidae Grube, 1850. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 102–105.

Pleijel, F., 2001o. Tomopteridae Johnston, 1865. In: Rouse, G.W., Pleijel, F. (Eds.), Polychaetes. Oxford University Press, Oxford, pp. 132–135.

Pleijel, F., 2004. A revision of *Hesiospina* (Psamathini, Hesionidae, Polychaeta). J. Nat. Hist. 38, 2547–2566.

Pleijel, F., Dahlgren, T.G., 1998. Position and delineation of Chrysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). Cladistics 14, 129–150.

Pleijel, F., Dales, R.P., 1991. Polychaetes: British phyllodocoideans, typhloscolecoideans and tomopteroideans. In: Kermack, D.M., Barnes, R.S.K. (Eds.), Synopses of the British Fauna (New Series) 45, 1–202.

Pleijel, F., Fauchald, K., 1993. *Scalispinigera oculata* Hartman, 1967 (Scalibregmatidae: Polychaeta. senior synonym of *Lacydonia antarctica* (Lacydoniidae) Hartmann-Schröder & Rosenfeldt, 1988. Proc. Biol. Soc. Wash. 106, 673–677.

Pleijel, F., Rouse, G.W., Ruta, C., Wiklund, H., Nygren, A., 2008. *Vrijenhoekia balaenophila*, a new hesionid polychaete from a whale fall off California. Zool. J. Linn. Soc. 152, 625–634.

Pleijel, F., Rouse, G., Nygren, A., 2009. Five colour morphs and three new species of *Gyptis* (Hesionidae, Annelida) under a jetty in Edithburgh, South Australia. Zool. Scr. 38, 89–99.

Posada, D., Crandall, K.A., 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14, 817–818.

Quatrefages, A. de, 1866 ("1865"). Histoire Naturelle des Annelés Marins et d'Eau Douce. Annélides et Géphyriens, 3 vols. plus Atlas. Roret, Paris.

Reibisch, J., 1895. Die pelagischen Phyllodociden und Typhloscoleciden der Plankton-Expedition. Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 Ausgeführten Plankton-Expedition der Humboldt-Stiftung, Bd. 2. Lipsius & Tischer, Kiel and Leipzig, 1–63, pl. 1–8.

Reibisch, J., 1905. Anneliden. Nordisches Plankton, Zool. Teil 3 (10), 1–10.

Rice, S.A., 1987. Reproductive biology, systematics, and evolution in the polychaete family Alciopidae. Biol. Soc. Wash. Bull. 7, 114–127.

Rouse, G.W., Goffredi, S.K., Vrijenhoek, R.C., 2004. *Osedax*: Bone-eating marine worms with dwarf males. Science 305, 668–671.

Rouse, G.W., Pleijel, F., 2001. Polychaetes. Oxford University Press, Oxford.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C., Siddall, M.E., 2007. A molecular phylogeny of annelids. Cladistics 23, 41–63.

Ruta, C., Nygren, A., Rousset, V., Sundberg, P., Tillier, A., Wiklund, H., Pleijel, F., 2007. Phylogeny of Hesionidae (Aciculata, Polychaeta), assessed from morphology, 18S rDNA, 28S rDNA, 16S rDNA and COI. Zool. Scr. 36, 99–107.

Salazar-Vallejo, S.I., 1986. Pilargidae (Annelida: Polychaeta) de Mexico: Lista de especies, nueva especie y biografia. Cah. Biol. Mar. 27, 193–209.

San Martín, G., 1991. *Grubeosyllis* and *Exogone* (Exogoninae, Syllidae, Polychaeta) from Cuba, the Gulf of Mexico, Florida and Puerto Rico, with a revision of *Exogone*. Bull. Mar. Sci. 49, 715–740.

San Martín, G., 2003. Annelida, Polychaeta II: Syllidae. In: Ramos, M.A. (Ed.), Fauna Ibérica, vol. 21. Museo Nacional de Ciencias Naturales CSIC, Madrid, pp. 1–554.

San Martín, G., 2005. Exogoninae (Polychaeta: Syllidae) from Australia with the description of a new genus and twenty-two new species. Rec. Aust. Mus. 57, 39–152.

San Martín, G., Ceberio, A., Aguirrezabalaga, F., 1996. *Exogone* species (Polychaeta: Syllidae: Exogoninae) from the Capbreton Canyon (Bay of Biscay, NE Atlantic). Cah. Biol. Mar. 37, 249–258.

San Martín, G., Parapar, J., 1990. *Exogone acerata* (Exogoninae: Syllidae: Polychaeta), a new species without antennae from the Mediterranean Sea. Proc. Biol. Soc. Wash. 103, 687–690.

Sars, M., 1862. Uddrag af en af detaillerede afbildninger ledsaget udførlig beskrivelse over følgende norske Annelider. Forh. Vidensk. Kristiania 1861, 87–95.

Schmid, C., Brenke, N., Wägele, J.W., 2002. On abyssal isopods (Crustacea: Isopoda: Asellota) from the Angola Basin: *Eurycope tumidicarpus* n. sp. and redescription of *Acanthocope galathea* Wolff, 1962. Org. Divers. Evol. 2, 87–88.

Schram, T.A., Haaland, B., 1984. Larval development and metamorphosis of *Nereimyra punctata* (O.F. Müller) (Hesionidae, Polychaeta). Sarsia 69, 169–181.

Shaffer, P.L., 1979. The feeding biology of *Podarke pugettensis* (Polychaeta: Hesionidae). Biol. Bull. 156, 343–355.

Smith, C.R., Baco, A.R., 2003. The ecology of whale falls at the deep-sea floor. Annu. Rev. Oceanogr. Mar. Biol. 41, 311–354.

Smith, C.R., Baco, A.R., Glover, A.G., 2002. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep relationships. Cah. Biol. Mar. 43, 293–297.

Southern, R., 1909. Polychaeta of the coasts of Ireland. II. Pelagic Phyllodocidae. Sci. Invest., Dept. Agr. Tech. Instr. Ireland, Fish. Branch 3 5, 1–11 pl. 1–3.

Southward, E.C., 1982. Bacterial symbionts in Pogonophora. J. Mar. Biol. Ass. UK 62, 889–906.

Støp-Bowitz, C., 1948. Polychaeta from the "Michael Sars" North Atlantic deep-sea expedition 1910. Rep. Sci. Res. "Michael Sars" North Atlantic Deep-Sea Exped. 5 (8), 1–91.

Støp-Bowitz, C., 1949. Polychétes pélagiques des expéditions norvégiennes antarctiques de la «Norvegia» 1927–1928, 1928–1929 et 1930–1931. Sci. Res. Norw. Antarctic Exped. 1927–1928 et sqq 31, 1–25.

Støp-Bowitz, C., 1951. Polychétes pélagiques de l'expédition suédoise antarctique 1901–1903. Further Zool. Res. Swed. Antarctic Exped. 1901–1903 4 (7), 1–14.

Støp-Bowitz, C., 1977. Polychétes pélagiques des expéditions du „Willem Barendsz" 1946–1947 et 1947–1948 et du „Snellius" 1929–1930. Zool. Meded. 51, 1–23.

Støp-Bowitz, C., 1984. A short note on the problems with systematics of some pelagic polychaetes. In: Hutchings, P.A. (Ed.), Proceedings of the First International Polychaete Conference, Sydney, Australia, July 1983. Linnean Society New South Wales, Kingsford, pp. 86–90.

Støp-Bowitz, C., 1992. Polychétes Pélagiques des Campagnes de «l'Ombango» dans les Eaux Equatoriales et Tropicales Ouest-africaines. Editions ORSTROM, Paris.

Struck, T., Hessling, R., Purschke, G., 2002. The phylogenetic position of the Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the 'Polychaeta', based on molecular data from 18S rDNA sequences. J. Zool. Syst. Evol. Res. 40, 155–163.

Swofford, D.L., 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). ver. 4.0b. Sinauer Associates, Sunderland, MA.

Tebble, N., 1960. The distribution of pelagic polychaetes in the South Atlantic Ocean. Discovery Rep. 30, 161–299.

Tebble, N., 1962. The distribution of pelagic polychaetes across the North Pacific Ocean. Bull. Brit. Mus. (Nat. Hist.), Zool. 7, 371–492.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 24, 4876–4882.

Treadwell, A.L., 1937. *Hemipodia canadensis* a new polychaetous annelid from Nova Scotia. J. Biol. Bd. Can. 3, 348–349.

Türkay, M., 2006. South-East Atlantic 2000 Part 1 Cruise No. 48, Leg 1, 6 July – 2 August 2000, Walvis Bay – Walvis Bay. Meteor-Ber. 06-5, 1–37.

Uebelacker, J.M., 1984. Chapter 28: Family Hesionidae Sars, 1862. In: Uebelacker, J.M., Johnson, P.G. (Eds.), Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, vol. 4. Vittor & Assoc., Metairie, LA, pp. 1–39.

Uljanin, M., 1878. Sur le genre *Sagitella* (N. Wagn.). Arch. Zool. Exp. Gén. 7, 1–32 pl. 1–4.

Uschakov, P.V., 1958. Two new species of marine Polychaeta of the family Phyllodocidae from abyssal depths of the

Kuril-Kamchatka trench [in Russian]. Trudy Inst. Okean. (= Trans. P.P. Shirshov Inst. Oceanol.) 27, 204–207.

Uschakov, P.V., 1962. Polychaetous annelids of the fam. Phyllodocidae and Aphroditidae from the Antarctic and Subantarctic [in Russian]. Issled. Fauny Morei (= Explor. Fauna Seas) 1 (9), 129–189.

Uschakov, P.V., 1972. Fauna of the USSR. Polychaetes. Volume I. Polychaetes of the suborder Phyllodociformia of the Polar Basin and the northwestern part of the Pacific (Families Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, and Lacydoniidae) [in Russian]. Akad. Nauk SSSR, New Ser. 102, 1–271 [English transl. 1974 by Israel Program for Scientific Translations, Jerusalem].

Uschakov, P.V., 1975. Deep-water Pyhllodocidae (Polychaeta) from the South-Sandwich Trench collected by the R/V «Akademic Kurchatov» in 1971 [in Russian]. Trudy Inst. Okean. (= Trans. P.P. Shirshov Inst. Oceanol.) 103, 143–150.

Vanhöffen, E., 1897. Die Fauna und Flora Grönlands. In: Drygalski, E. von (Ed.), Grönland-Expedition der Gesellschaft für Erdkunde zu Berlin 1891–93, Bd. 2, Teil 1. Gesellschaft für Erdkunde, Berlin, pp. 1–383.

Veit-Köhler, G., 2005. First deep-sea record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda: Harpacticoida) with the description of *Kliopsyllus diva* sp. n.—the most abundant member of Paramesochridae at two different sites of the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 29–41.

Viguier, C., 1886. Études sur les animaux inférieurs de la Baie d'Alger. Recherches sur les Annélides pélagiques. Arch. Zool. Exp. Gén., Sér. 2 (4), 347–442.

Wagner, N., 1872. Nouveau groupe d'Annélides [in Russian]. Trudy St.-Peterb. Obscestva Estest. (= Trav. Soc. Nat. Saint-Pétersbourg). 3, 344–347.

Watson Russell, C., 1986. *Paleaequor*, a New Genus of polychaete worm (Chrysopetalidae). Rec. Aust. Mus. 38, 153–174.

Watson Russell, C., 1991. *Strepternos didymopyton* Watson Russell in Bhaud & Cazaux, 1987 (Polychaeta: Chrysopetalidae) from experimental wooden panels in deep waters of the western North Atlantic. Ophelia Suppl. 5, 283–294.

Watson Russell, C., 2000. Family Chrysopetalidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 121–125.

Wesenberg-Lund, E., 1951. Polychaeta. Zool. Iceland 2 (19), 1–182.

Westheide, W., Hass-Cordes, E., 2001. Molecular taxonomy: description of a cryptic *Petitia* species (Polychaeta: Syllidae) from the island of Mahé (Seychelles, Indian Ocean) using RAPD markers and ITS2 sequences. J. Zool. Syst. Evol. Res. 39, 103–111.

Westheide, W., Haß-Cordes, E., Krabusch, M., Müller, M.C.M., 2003. *Ctenodrilus serratus* (Polychaeta: Ctenodrilidae) is a truly amphi-Atlantic meiofauna species – evidence from molecular data. Mar. Biol. 142, 637–642.

Wiklund, H., Glover, A.G., Johannessen, P.J., Dahlgren, T.G., 2009. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. Zool. J. Linn. Soc. 155, 774–785.

Wiklund, H., Nygren, A., Pleijel, F., Sundberg, P., 2008. The phylogenetic relationships between Amphinomidae, Archinomidae and Euphrosinidae (Amphinomida: Aciculata: Polychaeta), inferred from molecular data. J. Mar. Biol. Ass. UK 88, 509–513.

Willen, E., 2005. A new species of *Paranannopus* Lang, 1936 (Copepoda, Harpacticoida, Pseudotachidiidae) with atrophic mouthparts from the abyssal of the Angola Basin. Org. Divers. Evol. 5 (Suppl. 1), 19–27.

Wilson, R.S., 2000a. Family Alciopidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 115–117.

Wilson, R.S., 2000b. Family Hesionidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 131–133.

Wilson, R.S., 2000c. Family Lacydoniidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 134.

Wilson, R.S., 2000d. Family Lopadorhynchidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 134–136.

Wilson, R.S., 2000e. Family Nephtyidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 136–137.

Wilson, R.S., 2000f. Family Nereididae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 138–141.

Wilson, R.S., 2000g. Family Phyllodocidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 145–148.

Wilson, R.S., 2000h. Family Sphaerodoridae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 160–161.

Wilson, R.S., 2000i. Family Tomopteridae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 167–168.

Wilson, R.S., 2000j. Family Typhloscolecidae. In: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), Polychaetes & Allies: The Southern Synthesis. Fauna of Australia, vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, pp. 168–169.

Worsaae, K., Nygren, A., Rouse, G.W., Giribet, G., Persson, J., Sundberg, P., Pleijel, F., 2005. Phylogenetic position of Nerillidae and *Aberranta* (Polychaeta, Annelida), analysed by direct optimization of combined molecular and morphological data. Zool. Scr. 34, 313–328.

Wu, B., Hua, L., 1994. Phylogeny of Alciopidae (pelagic polychaetes): a cladistic analysis. In: Dauvin, J.-C., Laubier, L., Reish, D.J. (Eds.), Actes de la 4ème Conférence Internationale des Polychètes. Mém. Mus. Natn. Hist. Nat. 162, 317–321.