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New species of benthopelagic hydromedusae from the Weddell Sea

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Abstract Four medusa species were collected by an epibenthic sledge during the “Polarstern” ANT XV/3 cruise carried out from January to March 1998 in the eastern Weddell Sea. The specimens were collected in the benthic boundary layer at depths ranging between 1,583 and 2,034 m; 2 of the species collected are new to science. The narcomedusa *Sigiweddellia bathypelagica* gen. nov. et sp. nov. is characterised by two types of marginal tentacles and closed marginal statocysts. The trachymedusa *Voragonema laciniata* sp. nov. (known only from the single holotype) is characterised by the number and irregular shape of the centripetal canals. These findings are the first to report benthopelagic hydromedusae in deep Antarctic waters. Examination of several specimens of *Benthocodon pedunculata* (Bigelow 1913) leads us to move it to the genus *Voragonema* Naumov 1971 because of the clear presence of centripetal expansions in the ring canal.

Introduction

In the oceans, the general pattern of biomass and species number decrease as depth increases is an aspect

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of marine biodiversity that has received much attention by the scientific community during the last decade (Gray 1997). Even though many examples of such patterns are known for both planktonic and benthic communities (Angel and Baker 1982; Lampitt et al. 1986), other results support a counter-trend that argues for high diversity in deep-sea benthic communities (Grassle 1989). The existence of a rich fauna and a high biomass of pelagic organisms near the deep-sea floor is generally accepted after the investigations conducted during the last decade, although these faunas are only well known in few selected marine areas (Angel 1990). These studies have pointed out that the deep-sea benthopelagic fauna is distinct and perhaps more diverse than the overlying bathy- and mesopelagic faunas (Childress et al. 1989).

One of the most neglected components of the fauna inhabiting the deep-sea benthic boundary layer appears to be the gelatinous zooplankton. The use of new observation techniques such as submersibles, remotely operated vehicles and underwater cameras has allowed documentation of the near-bottom gelatinous fauna in a way that was previously impossible (Larson et al. 1992). One of the most conspicuous organisms of the deep-sea fauna, the medusa, may develop dense concentrations near the bottom (Smith 1982), with quite different populations in comparison with the better-known mesopelagic ones (Mackie 1985).

Although the main scope of the EASIZ (Ecology of Antarctic Sea Ice Zone) Programme is the study of the coastal and shelf communities, the possibility of also investigating the slope benthopelagic fauna was considered an interesting contribution on cruise ANT XV/3, carried out in the Weddell Sea from January to March 1998. Several deep-water stations were sampled by an epibenthic sledge. A set of rare medusae was collected, which represents the first record of benthopelagic medusae in deep Antarctic waters, where the deep-sea medusa fauna is poorly known (Pagès 1997; Pugh et al. 1997). This report identifies the species collected and describes the new ones.

Materials and methods

Four medusa species were collected during the "Polarstern" ANT XV/3 cruise, carried out from January to March 1998 in the eastern Weddell Sea. Benthopelagic samples were taken by an epibenthic sledge of 1 m mouth width and equipped with a net of 500 μm mesh size bearing a 300- μm mesh size cod-end. Each station was trawled for 10 min over the seafloor at 1 knot mean velocity (Brandt et al. 1999). The gelatinous specimens collected were preserved in 4% formalin immediately after the sledge arrived onboard.

Results

Anthomedusae, Family Bythotiaridae Maas 1905

Calycopsis borchgrevinki Browne 1910

Material. One specimen collected by an epibenthic sledge on 10 February 1998 at st. 48/142, 74°35.8'S 27°17.4'W; bottom depth 1650 m.

Narcomedusae, Family Cuninidae Bigelow 1913

New diagnosis

Narcomedusae with perradial and undivided manubrial pouches, with or without peripheral canal system, with tentacles leaving umbrella in the central edge of each manubrial pouch, equal in number to pouches; pouches not extending beyond points of origin of tentacles; **with** or without secondary tentacles on umbrella margin; with or without otoporpaes; statocysts opened **or enclosed**.

Sigiweddellia gen. nov.

Diagnosis. Cuninidae without otoporpaes; with secondary tentacles on the umbrella margin, with marginal sensory clubs enclosed in a polystratified ectodermal vesicle; with a peripheral canal system.

Sigiweddellia benthopelagica sp. nov.

Material. ANT XV/3 cruise: 11 specimens collected by an epibenthic sledge on 4 February 1998 at st. 48/89, 73°27.5'S 22°43.1'W; 1,583 m bottom depth. Five specimens collected by an epibenthic sledge on 8 February 1998 at st. 48/130, 73°23.6'S, 22°09.3'W, 2,034 m depth (Figs. 1, 2, 3).

Additional material examined. ANT XIII/3 cruise, 1 specimen collected by an amphipod trap on 1 March 1996 at st. T6, 70°09'S, 08°16'W; 2,008 m bottom depth. The holotype has been deposited in the Zoologisches Institut und Zoologisches Museum der Universität Hamburg (Germany), where it is entered as C 11654.

The rest of the collection is designated as paratypes, which have been deposited in the Cnidarian Collection

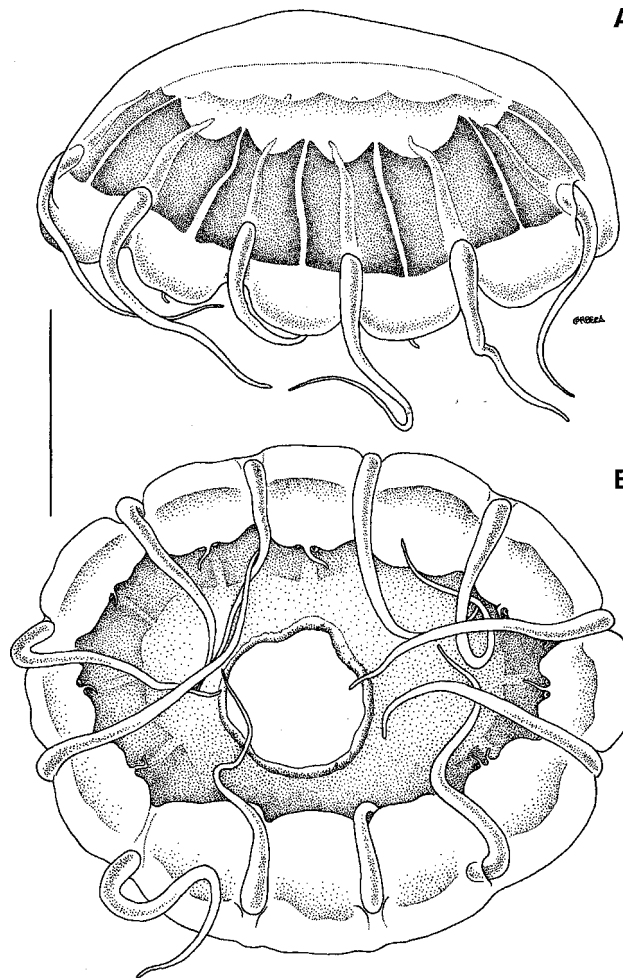


Fig. 1A, B *Sigiweddellia benthopelagica*. Lateral (A) and oral (B) views of a preserved specimen. Scale: 1 cm

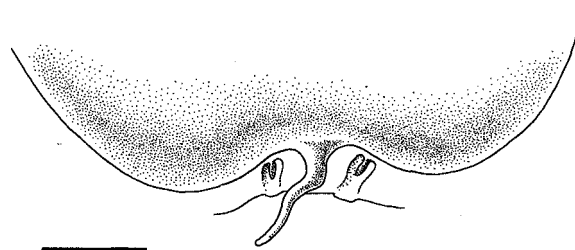


Fig. 2 *Sigiweddellia benthopelagica*: marginal lappet with one secondary tentacle and two multistratified ectodermal vesicles. Scale: 1 mm

of the Institut de Ciències del Mar of Barcelona with the catalogue number.

Etymology. The genus is dedicated to our colleague Sigi Schiel, for her friendship and outstanding contributions to the knowledge of the zooplankton communities of the Weddell Sea. The specific name is related to the apparent benthopelagic habitat, previously unknown in the Narcomedusae.

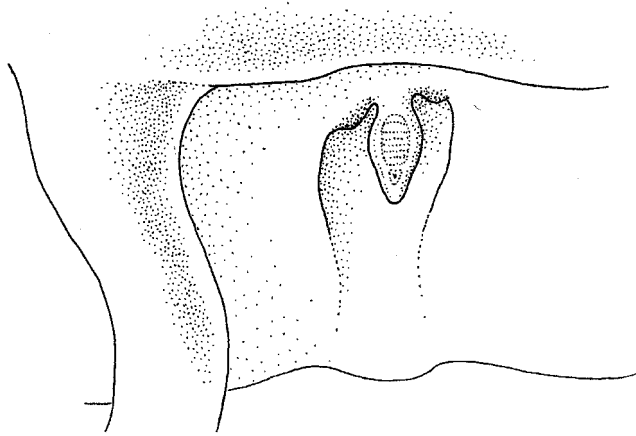


Fig. 3 *Sigiweddellia benthopelagica*: detail of a multistratified ectodermal vesicle that encloses a marginal sensory club. Scale: 0.5 mm

Description. Umbrella up to 30 mm wide and 13 mm high, somewhat flatter than hemispherical, sometimes almost dome-shaped in more contracted specimens (Fig. 1A); mesoglea quite thick and rigid in the centre, thinning slightly at the margin; 10–12 rectangular marginal lappets (Fig. 1B), slightly broader than long, with rounded angles; with a narrow peripheral canal system; manubrium largely conical, with 10–12 rectangular manubrial pouches with elevated, deep, lateral walls (parallelepipedal) and lobed summit in mature specimens, the pouches very close together and only separated by deep, very narrow clefts; endoderm of the gastric pouches with digestive cells full of numerous excretory vacuoles with brown pigments and glandular cells; mouth circular, rather small, 7 mm in diameter, with a thick, dense edge formed by numerous glandular granular cells; velum well developed; 10–12 primary marginal tentacles issuing from umbrella at the upper end of peronia, in the central edge of each manubrial pouch, with root-like endodermal continuations in the apical mesoglea extending up to three-quarters length of marginal pouches; the ectoderm of the manubrial pouches is rich in cnidocysts of two types, apotrichous isorhizas and the other type not determined; 1 or 2 short secondary tentacles at the centre of the margin of each lappet (Figs. 1, 2), some of them sometimes missing, with conical base, sometimes coiled, each one on the central margin of each lappet, with numerous egg-shaped cnidocysts; gonads as irregular longitudinal folds of the manubrial pouches; no otoporphae; 2 marginal sensory clubs, 1 on each side of the secondary tentacles (Fig. 2), enclosed in a multistratified ectodermal vesicle (Fig. 3); manubrium and manubrial pouches coloured brownish by excretory vacuoles.

Diagnosis. The same as the genus.

Remarks. This species undoubtedly belongs to the family Cuninidae by its perradial manubrial pouches. It is nevertheless distinct from the genera *Cunina*, *?Cunissa* and *Solmissus* by the presence of secondary tentacles and closed marginal sensory clubs; the latter morphological

feature is unique among Narcomedusae and the creation of a new genus is thus proposed. This genus has another particular feature: all tissues show a very thick and meaty consistency in comparison with the softness and fragility of the rest of the known Cuninidae.

Trachymedusae, Family Halicreatidae

Botrynema brucei Browne 1908

Material. One specimen collected by an epibenthic sledge on 4 February 1998 at st. 48/089, 73°27.5'S, 22°43.1'W; bottom depth 1,583 m.

Family Rhopalonematidae Russell 1953, Genus *Voragonema* Naumov 1971

Voragonema laciniata sp. nov.

Material. One specimen collected by an epibenthic sledge on 4 February 1997 at st. 48/089, 73°27.5'S, 22°43.1'W; bottom depth 1,583 m. The holotype has been deposited in the Zoologisches Institut und Zoologisches Museum der Universität Hamburg (Germany), where it is entered as C 11653 (Figs. 4, 5).

Additional material examined. Holotype of *Benthocodon hyalinus* (Larson and Harbison 1990); USNM 87603, deposited at the Smithsonian Institution, National Museum of Natural History, Washington, D.C. Six specimens of *Benthocodon pedunculata* (Bigelow 1913) collected in Monterey Canyon, California, United States of America, and kindly supplied by George Matsumoto. Kodachrome photograph of *Benthocodon pedunculata* taken by Claudia E. Mills and collected in the Bahamas. **Etymology** *laciniata* (Latin) inspired by the jagged edge of the ring canal.

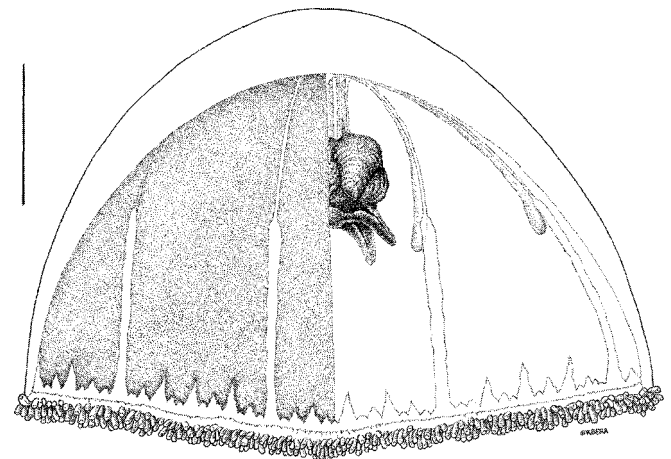


Fig. 4 Lateral view of the holotype of *Voragonema laciniata*. The left half shows the dark subumbrella, which has been deleted in the right half to illustrate the peduncle, the manubrium and the gonads. Scale: 1 cm

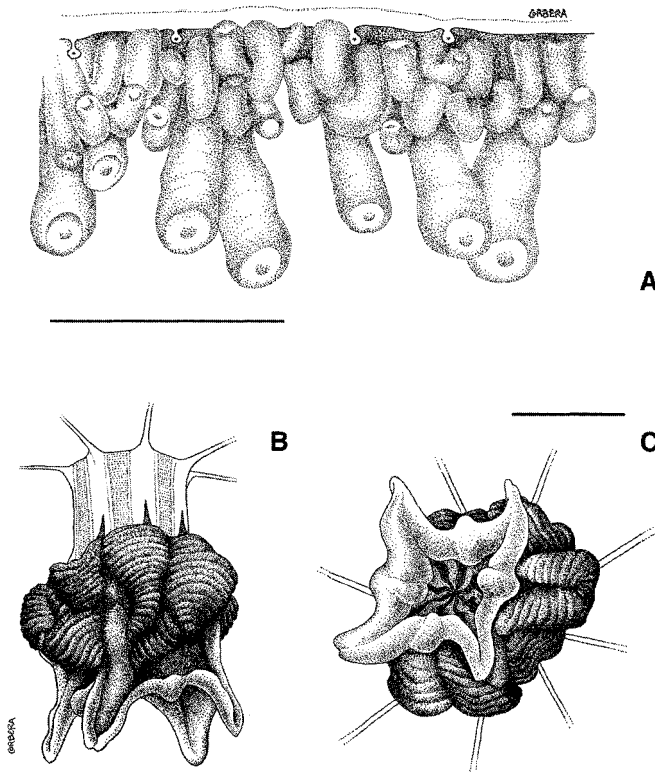


Fig. 5A–C *Voragonema laciniata*. **A** detail of the bell margin showing the proximal part of marginal tentacles superimposed in several rows together with the free statocysts placed among them; drawn from the inside, looking out. Scale: 5 mm. **B** Infralateral view of the peduncle and manubrium on which the gastric pouches stand out. Scale: 5 mm. **C** Oral view of the manubrium showing the perradial lips. Scale: 5 mm

Diagnosis. *Voragonema* with subumbrella brownish-coloured, circular canal with irregular conical centripetal expansions; about 1,200 marginal tentacles.

Description. Umbrella almost as high (30 mm) as wide (35 mm) (Fig. 4); mesoglea 4 mm thick in the apex and tapering towards the umbrella margin; exumbrella transparent with fine ridges, subumbrella dark-red-brownish, with circular and crossed oblique-radial muscles in the subumbrella; dark-red-brownish colour due to pigmented cells.

Gastric peduncle large (Figs. 4, 5B), circular from above and slightly octagonal from the subumbrellar cavity (Fig. 5B), 4.2 mm in diameter and 5.0 mm in height; ectodermal walls of the gastric peduncle dark-red.

Radial canals 8, white-cream coloured, straight; peduncular part 5.0 mm long and 1.5 mm wide; proximal half of the subumbrellar part narrow, 0.5 mm wide, distal half broader, 1.3 mm wide.

Manubrium short, broad, square, dark-red, slightly longer than the peduncle, with thick muscular walls; mouth with four prominent and elongated perradial lips and swollen interradianal edges; manubrial cavity divided into eight longitudinally folded gastric pouches that open into the radial canals; peduncle and manubrium height is half that of the subumbrella (Fig. 5B, C).

Gonads extending along the proximal half of the radial canals, flattened, with distal part slightly pendent.

Circular canal whitish and wide, with numerous centripetal, conical and irregular expansions; bell margin thickened by a conspicuous whitish ring of cnidocysts; velum dark-red, 6.0 mm wide, with marked circular muscles.

Tentacles with reddish ectodermal pigment, superimposed in 5–6 rows, each with an adnate base, about 150 in number per octant; size increases from the adaxial to the abaxial side; younger tentacles are 2.0 mm in length and 0.15 mm in diameter; maximum length unknown; numerous free statocysts with a single large statolith, placed among the marginal tentacles (Fig. 5A).

Remarks. This new species belongs to the genus *Voragonema* Naumov 1971 because of the presence of centripetal expansions arising from the ring canal. *V. laciniata* differs markedly from *V. profundicola* by the coloured subumbrellar surface, a higher number of marginal tentacles and by the number and irregular shape of the centripetal canals (Table 1). The description of *V. profundicola* was rather poor (Naumov 1971) and some of the characters (e.g. the shape of the centripetal canals) are only known from the holotype illustration, which contains little detail.

In this new species, the presence of septal pouches in the manubrial cavity presumably increases the absorption surface of the endoderm. This morphological feature is physiologically similar to the gastric digitations observed by Bouillon (1988) in the anthomedusan genus *Koellikerina*. Likewise, the length of larger tentacles is unknown since none of them were recovered. However, all tentacles are cut off at the same level and their bases show identical structure; the ectoderm seems to cover the endodermal layer of the hollow tentacle. This feature suggests that *V. laciniata* is able to autotomise the marginal tentacles during adverse conditions, as has been observed in other Trachymedusae like *Colobonema sericeum* and *Benthocodon pedunculata* (Larson and Harbison 1990; Matsumoto et al. 1997), as well as in most other trawl-collected Trachymedusae.

The strong musculature of the wide velum suggests that *V. laciniata* is at least periodically a powerful swimmer. Matsumoto et al. (1997) observed in situ that *Benthocodon pedunculata*, a closely related species, performs upwards-swimming and sinking bouts. The genus *Benthocodon* was created for the new Antarctic species *Benthocodon hyalinus* (Larson and Harbison 1990). This genus differs mostly from the closely related genus *Crossota* by the presence of a gastric mesoglean peduncle non-existent in the genus *Crossota*, with the exception of the species *Crossota pedunculata*. This latter species was therefore moved to the genus *Benthocodon*. The strong morphological similarities between *Benthocodon* and *Voragonema*, already noted by Larson and Harbison (1990), caused us to investigate the main differences between the genera.

Microscopical examination of six specimens of *Benthocodon pedunculata*, collected in Monterey Bay (Calif-

Table 1 Main morphological features of the three species of the genus *Voragonema* and *Benthocodon hyalinus*. Key interspecific differences are in **bold**

	Exumbrella	Subumbrella	Radial canals	Peduncle	Manubrium	Mouth	Gonads	Centripetal canals	Tentacles	Statocysts	Velum	Distribution and depth	Main references
<i>Voragonema profundicola</i> Naumov 1971	10 mm high; 15 mm wide; transparent	Transparent , hemispherical	Eight, slightly undulated along the peduncle, uniformly narrow along the subumbrella	Short, solid, cylindrical in section	Narrow	With four simple oral lips	Unknown	Eight per octant, triangle- shape, regular in length and width	About 500	Unknown	Rather wide	Kurile- Kamchatka Trench, 8,700- 6,800 m	Naumov (1971)
<i>V. pedunculata</i> (Bigelow 1913)	Up to 31 mm high and 41 mm in diameter; transparent with a little rusty pigment, with many fine meridional furrows	Dark-reddish- brown , more conical than hemispherical	Eight, white-cream, proximal half narrow, distal half broader	Short, small	Short, broad, square, dark-red, folded gastric pouches	With four flared lips	White-cream, thin, proximal half attached along the radial canal, distal half free, pendent	Eight per octant, triangle- shape, regular in length and width	Superimposed in 4-5 rows; 1,000-2,000 in number; 2 types: outermost, solid and heavily pigmented; inner, hollow, shorter and thinner	Up to 30 per octant	6.0 mm wide	Northwest USA, 90 m; Bahamas, 830-910 m; Virgin Is. 870-900 m; Monterey Canyon, California, 175-975 m	Bigelow (1913); Larson et al. (1992); Matsumoto et al. (1997); Wrobel and Mills (1998)
<i>V. laciniata</i> Bouillon, Pages and Gili	Almost as high (30 mm) as wide (35 mm in diameter); transparent with numerous fine meridional ridges	Dark-red- brownish , circular and crossed oblique-radial muscles	Eight, white-cream, proximal half narrow, distal half broader	Large, circular from above and slightly octagonal from below	Short, broad, square, dark-red, thick muscular walls; divided by eight longitudi- nal and folded gastric pouches	With four prominent elongated, perradial lips and with prominent interradial swellings	Whitish, thin, proximal half attached along the radial canal, distal half free, pendent	11-13, usually 12 per octant, triangle- shape, irregular in length and width	Superimposed in 5-6 rows, about 1,200 in number, 2 types: outermost row, solid, with adnate base; shorter and thinner in the innermost rows	Free, numerous, with a single and large statolith	6.0 mm wide	Weddell Sea, 1,583 m	This study
<i>Benthocodon pedunculata</i> Larson and Harbison 1990	Dome-shaped, 40 mm in diameter, 25 mm high; thick, smooth	Transparent, hemispherical	Eight, proximal half narrow, distal half broader	Cylindrical, 1/4 the length of the manu- brium or longer	Tubular, extends to the margin in living specimens; reddish- brown	With four flared oral lips with smooth margin	White, as wavy bands along most of the radial canals	Absent	Superimposed in at least 5 rows, more than 800 in number, 1 type	Not seen	Thin, fairly broad	McMurdo Sound, Ross Sea, 20-0 m depth	Larson and Harbison (1990)

fornia) and kindly supplied by Dr. George Matsumoto, showed the existence of many short centripetal expansions in the ring canal, a conspicuous feature apparently not detected in previous studies (Larson and Harbison 1990; Larson et al. 1992; Matsumoto et al. 1997; Wrobel and Mills 1998), although visible in one photograph of a specimen collected in Bahamas waters and produced by Claudia E. Mills (Fig. 6). This finding demonstrates that this species actually belongs to the genus *Voragonema* and we propose to move the species *pedunculata* to this genus. Unfortunately, the holotype of *V. profundicola* could not be examined for comparison.

The diagnosis of the genus *Benthocodon* mentions that centripetal canals are absent (Larson and Harbison 1990). The holotype of *Benthocodon hyalinus*, which is quite damaged, showed no tracks of centripetal expansions of the ring canal when examined under the microscope. The lack of centripetal expansions suggests keeping *Benthocodon* as a valid genus because *Voragonema* is characterised by this uncommon feature, not shown in the rest of the Rhopalonematidae. An excellent photograph of a living specimen of *Benthocodon hyalinus* published under the name *Arctapodema* (Curtsinger 1986) makes evident its strong morphological similarity in comparison to *V. pedunculata* (Fig. 6, Larson et al. 1992). However, the presence of centripetal expansions in the ring canal is an outstanding feature, unknown in other Trachymedusae except the family Geryoniidae, which warrants the maintenance of both genera. *Voragonema* and *Benthocodon* are quite different in comparison to other genera in the family Rhopalonematidae for the very large number of tentacles and the separation of small downward-pointing tentacles and larger outward-pointing ones, seemingly an adaptation to a benthopelagic lifestyle. *Crossota* and *Vampyrocrossota* are two genera of Rhopalonematidae morphologically similar to *Voragonema* and *Benthocodon*. However, *Crossota* has

pendent gonads (Wrobel and Mills 1998) and *Vampyrocrossota* shows the tentacles arranged in a single row (Thuesen 1993).

In summary, the genus *Voragonema* comprises three species at present: *V. profundicola* Naumov 1971, *V. pedunculata* (Bigelow 1913) and the new species *V. laciniata*. The main morphological features that distinguish them are the colour of the subumbrella and the number of centripetal canals (Table 1).

Outlook

The bathypelagic fauna has a close relationship with the benthic communities on which many planktonic crustaceans (Cartes 1998) and gelatinous organisms (Matsumoto et al. 1997) feed. Interest in the role of this bathy-benthopelagic fauna in plankton-benthos coupling processes is increasing. The study of these processes is one of the main objectives of the EASIZ-SCAR Programme. However, while pelagic-benthic interactions are increasingly well studied on the high-Antarctic shelf (Gili et al. 2001), their importance in the deep sea is as yet unknown. This contribution is a first step towards understanding these processes in deep water.

Acknowledgements We are greatly indebted to Claudia E. Mills for valuable comments on the content, style and language of the manuscript, permission to reproduce her photograph of *Voragonema (Benthocodon) pedunculata*, as well as her field notes on this species. Valuable comments by Nando Boero and Peter Schuchert are acknowledged. We thank the officers and crew of the FS "Polarstern" and many colleagues, especially Covadonga Orejas, Pablo López-González, Wolf Arntz and Angelika Brandt, for their help during the EASIZ XV/3 (EASIZ II) cruise. We are grateful to George Matsumoto and Jenny Paduan (Monterey Bay Aquarium Research Institute) for the gift of several specimens of *Voragonema pedunculata*. We thank Steve Cairns and the Smithsonian Institution for the loan of the holotype of *Benthocodon hyalinus*. Financial support for this study was provided by a CICYT Spanish grant (ANT97-1533-E). J.B. acknowledges the "Fondation David et Alice Van Buuren". The figures were drawn by Jordi Corbera.

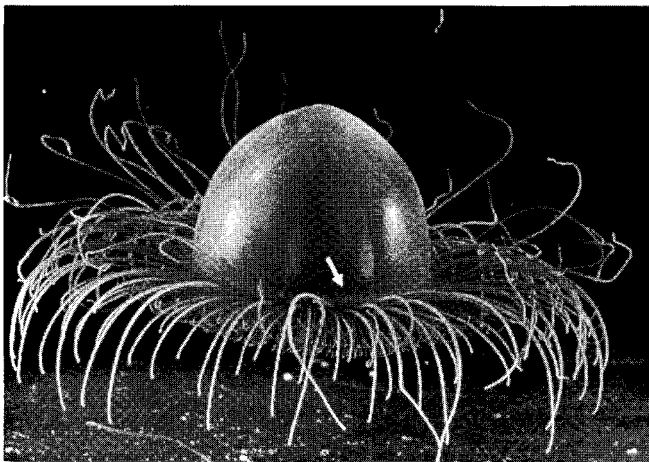


Fig. 6 Specimen of *Voragonema (Benthocodon) pedunculata* collected in Bahamas waters on 5 November 1989 and photographed in an aquarium on board ship. Note the regularly spaced triangular centripetal expansions on the ring canal. Photograph by Claudia E. Mills

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