ORIGINAL ARTICLE

A redescription of the post-larval physonect siphonophore stage known as *Mica micula* Margulis 1982, from Antarctica, with notes on its distribution and identity

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Abstract

The samples obtained during the 2008 Collaborative East-Antarctic MARine Census (CEAMARC) campaign in the Southern Ocean on the TR/V *Umitaka Maru* contained many specimens of the physonect post-larval stage known as *Mica micula*, in varying stages of development, allowing us to complement the existing descriptions. *M. micula* appears to be endemic to the Southern Ocean, and its possible position in the family Pyrostephidae, in particular the species *Pyrostephos vanhoeffeni*, is discussed. For the first time, the definitive necto-phores were observed, but they were still too underdeveloped to be assigned conclusively to any known physonect species.

Introduction

The samples obtained during the 2008 CEAMARC (Collabo-rative East-Antarctic MARine Census) campaign in the Southern Ocean on the TR/V *Umitaka Maru* contained many colonies of the post-larval physonect siphonophore stage known as *Mica micula* Margulis 1982 (Grossmann 2010; Grossmann & Lindsay 2011), in varying stages of development, allowing us to complement existing descrip-tions. As Pugh (1999) and Mapstone (2009) pointed out, this is not a valid species, but a name given to a post-larval stage of a physonect siphonophore, possibly of the family Pyrostephidae. However, it has not yet been possible to con-firm this link, so Margulis' appellation has been retained. The terminology of Haddock *et al.* (2005) is applied for the first time to a post-larval physonect siphonophore (Fig. 1).

Family Incertae Sedis

Genus *Mica* Margulis 1982 (*emend.*)

Non-valid genus, monotypic for the physonect post-larval stage known as *Mica micula* Margulis 1982.

Post-larval stage of a physonect siphonophore, larval nectophore long and hood-like, without descending surface diverticulum, lateral radial canals originating from upper canal, definitive nectophores inserted dorsally on the stem, tentacles with tentilla, stenoteles and a second smaller spherical type of nematocyst.

Type species
Mica micula Margulis 1982

Remarks
Margulis' original generic diagnosis read: 'Small colonies with hood-like long nectophores, a single-chambered elongated pneumatophore and gastrozooids without ten-tilla'. The information on the morphology of the defini-tive nectophore and other information presented in the present manuscript necessitates the amendment of this generic diagnosis. Indeed, only the larval nectophore is hood-like in appearance, and although the pneumato-phore's gas-filled chamber, or pneumatosaccus, is single-chambered, it is hour-glass-shaped in larger preserved material. Furthermore, there are definitely tentilla on the tentacles of the more mature and undamaged specimens.
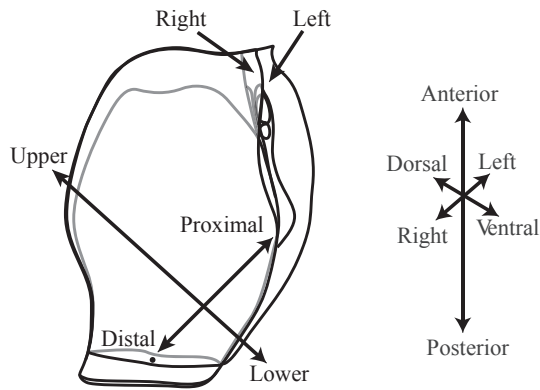
Fig. 1. Schematic diagram of *Mica micula* showing orientation terminology, based on Haddock *et al.* (2005). Axes at right relate to the colony; axes on the larval nectophore relate to the nectophore.

Mica micula Margulis 1982

Diagnosis

With the characters of the genus.

Material Examined

Eighteen specimens from North Pacific Standard net (NORPAC) samples, collected between 0 and 150 m (Grossmann & Lindsay 2011): three larval nectophores and one stem with pneumatophore and small definitive nectophores from station UM08 (65°30′ S, 143° E, 11 February 2008); one colony, four larval nectophores and one stem from station UM12 (66°34′ S, 144°0.3′ E, 10 February 2008); one small colony and two stems from station UM13 (66.45′ S, 144°20′ E, 9 February 2008); two colonies from station UM22 (65°44.5′ S, 140°6.3′ E, 3 February 2008); a single colony in very good condition from station UM23 (65°60′ S, 139°60′ E, 4 February 2008); one colony from station UM24 (64°21′ S, 40°58′ E, 6 February 2008); one larval nectophore from station UM42 (66°20′ S, 139°60′ E, 6 February 2008). Two *Mica micula* colonies and one larval nectophore from a multiple opening-closing net (Multinet) sample collected between 100 and 200 m at station UM11 (66°20′ S, 143°20′ E, 8 February 2008) (Grossmann 2010). One colony (station unknown) and one larval nectophore (station E-217, 0–280 m, 69° S, 24° E) from the 1966–1967 *Magga Dan* expedition to Antarctica. Four specimens from the 1990 Antarktis IX/2 cruise: two larval nectophores from station 108 (100–200 m, 71° S, 13° W) and two very young colonies from station 115 (0–50 and 150–200 m, 71°30′ S, 11° W) (listed as '?*Bargmannia* post-larvae' in Pagès & Kurbjeweit 1994). Additionally, colonies of *Bargmannia amoena* [ref. 2K1204SS2a

(409 m, 35° N, 139°14′ E, 11 July 2000), 2K1227SS3c (441 m, 33°25′ N, 139°40′ E, 17 October 2000), HD305SS2 (438 m, 35°01′ N, 139°22′ E, 14 June 2004), and HD522SS2 (1203 m, 34°42′ N, 139°51′ E, 6 March 2006)], *Bargmannia elongata* [ref. HD296SS2c (470 m, 24°51′ N, 123°50′ E, 21 April 2004)] and *Bargmannia lata* [ref. 3K489SS3b (716 m, 33°30′ N, 139°38′ E, 24 September 2000)] (BISMaL portal; Lindsay & Miyake 2009) as well as 24 definitive nectophores of *Pyrostephos vanhoeffeni* collected by NORPAC net and 31 collected by Multinet during the CEAMARC cruise (Grossmann 2010; Grossmann & Lindsay 2011) were examined. All of the material had lost its pigmentation after several years of storage in the original formalin-seawater preservative.

Description

The colonies had a single larval nectophore, and several buds of definitive nectophores. The definitive nectophores were attached to the stem at the base of the pneumatophore, on the dorsal side. The larval nectophore was attached to the stem by a long external pedicular canal, which gave rise to the and a long internal pedicular canal. The lateral radial canals arose from the upper radial canal. Stenoteles and a second smaller spherical type of nematocyst were present in terminal clumps on the tentilla of the tentacles.

The *Mica micula* larval nectophores varied in height from 1.8 to 3.3 mm and from 0.7 to 2 mm in width, the nectosac being 0.2–0.4 mm shorter than the nectophore (*e.g.* Fig. 2a). The two colonies from the Antarktis IX/2 cruise were at a much younger growth stage, the yolk sac still being prominent and the pneumatophore and siphosome not yet completely differentiated (Fig. 3), yet the larval nectophores were of approximately the same size as those in the more developed CEAMARC specimens (1.2 × 0.67 mm and 2.3 × 0.66 mm). The mesogloea was thicker in the top half of the nectophore. The hydroecium was open at the upper end of the nectophore, forming two small flaps, and extended to the lower end of the nectophore. There was a large velum. The nectosac lay close to the nectophore walls and had a flattened top, similar to that of the nectophore.

There were four radial canals and an ostial ring canal. The upper and lower radial canals originated from the internal pedicular canal slightly above the middle of the nectosac, and ran straight to join the ostial ring canal. The lateral canals originated from the upper radial canal close to the top of the nectosac (about 1/6th of the nectosac length from the top of the nectosac) and were curved. They joined the ostial ring canal at equal distances from the upper and lower radial canals. The junction of the lateral canals with the upper radial canal was
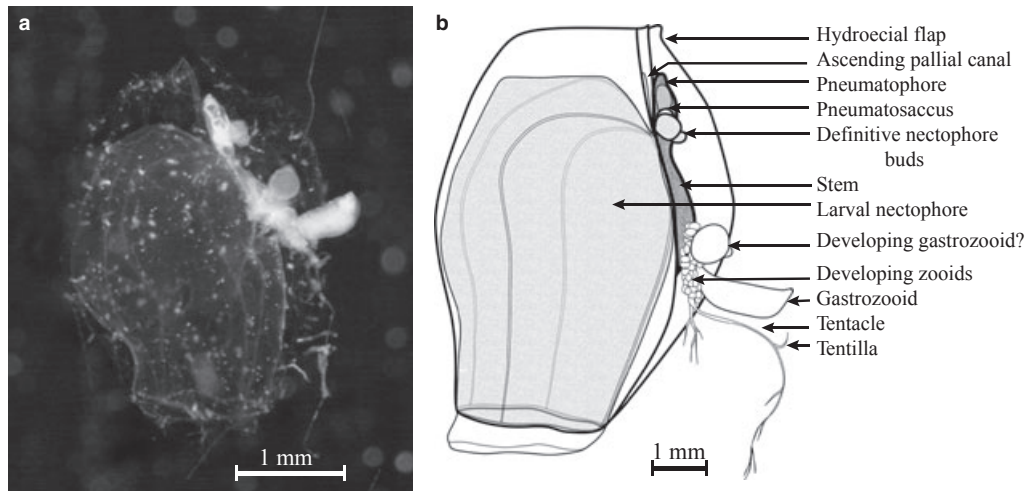
Fig. 2. Photograph (a) and line drawing (b) of the *Mica micula* specimen found in the NORPAC net at station UM23 (65°60′ S, 139°60′ E, 4 February 2008). Scale bars: 1 mm.
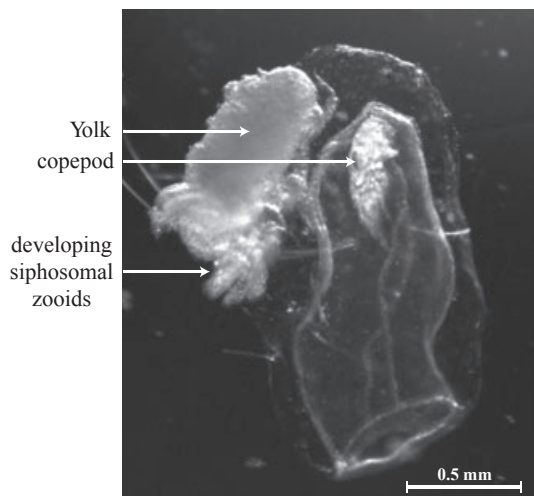

Fig. 3. Photograph of the *Mica micula* specimen from the Antarktis IX/2 station 115 (71°30′ S, 11° W), Multinet 5, showing the yolk and some developing siphosomal buds. Scale bar: 0.5 mm. There is a copepod in the nectosac of the larval nectophore.

variable in form, with three different kinds of arrangements observed in the eight nectophores where the canals could be clearly observed. In three specimens (nectophores 2 × 1.3 mm; 3.2 × 1.7 mm; 3 × 1.2 mm), the left and right laterals met the upper radial at the same place, forming a flattened 'V' shape. In four specimens (nectophores 3.3 × 2 mm; 2.9 × 1.7 mm; 3 × 1.3 mm; 2.4 × 1 mm), the lateral canals bent upwards to meet the upper radial canal, the right lateral joining up to 0.2 mm below the left lateral (about 1/12th of the necto-sac height). Finally, in the last specimen (nectophore

2.4 × 1.1 mm), the lateral canals met the upper radial canal at right angles, the left lateral canal joining slightly lower than the right. The different structures of the junction were not correlated with the size of the larval necto-phore or of the pneumatosaccus.

As described by Pagès & Gili (1989), the external pedicular canal arose from the stem just anterior to the siphosome. In the largest specimen (Station UM23), the stem, external and internal pedicular canals were all in close contact with the hydroecial wall of the larval necto-phore, making their exact junction points difficult to discern (Fig. 4a). In the two smallest specimens found during the CEAMARC cruise (nectophores 2.2 × 1.1 mm and 1.8 × 1 mm for stations UM12 and UM13, respectively), the pneumatosaccus was less developed, similar to that figured in Pagès & Gili's 1989 paper. On the colony from the *Magga Dan* expedition (Fig. 4b), as in the specimen from CEAMARC station UM12 (Fig. 4c), it was possible to see the external pedicular canal running anteriorly to about the height of the base of the pneumatos-accus. It then split, the anterior branch, the ascending pallial canal, extending to the same height as the top of the nectosac, and the lower branch, the internal pedicular canal, running along the wall of the hydroecium to its point of junction with the upper and lower canals of the nectosac. In the two colonies from the Antarktis cruise, the external pedicular canal was very short, due to the small extent of the stem. However, it clearly branched in its distal part, the ascending pallial canal running up to the same height as the anterior-most extent of the necto-sac; the internal pedicular canal running posteriorly to meet the upper and lower radial canals at about mid-nectosac (Fig. 4d). Most of the specimens illustrated by
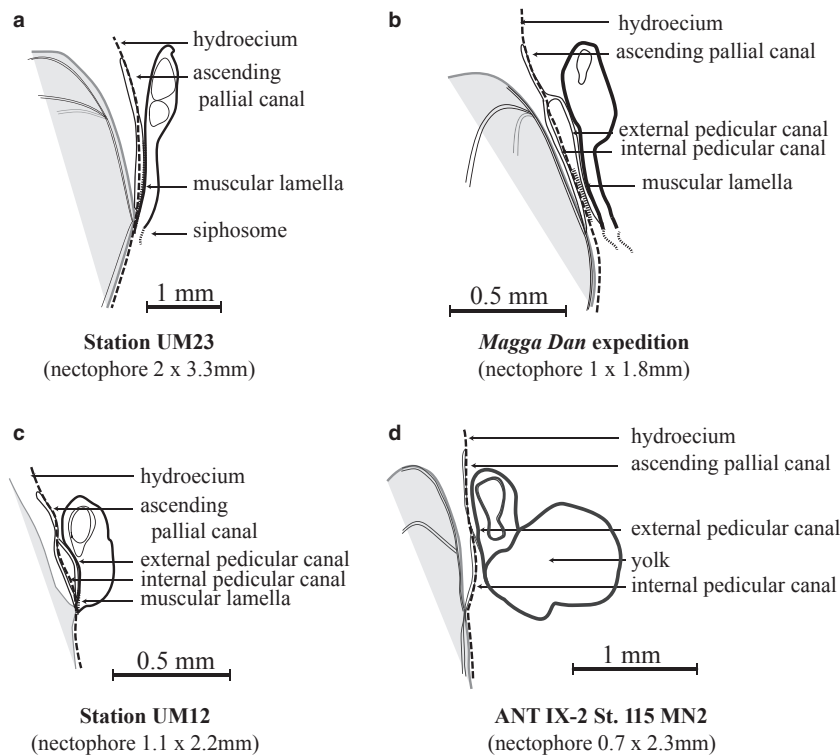
Fig. 4. Schematic diagrams of the canal structure near the point of attachment of the larval nectophore to the stem. Colonies are ordered in reverse order of their developmental stages; (a) *Mica micula* specimen from CEAMARC station UM23 (65°60′ S, 139°60′ E, 4 February 2008); (b) *Mica micula* specimen from the *Magga Dan* expedition (station unknown); (c) *Mica micula* specimen from CEAMARC station UM12 (66°34′ S, 144°0.3′ E, 10 February 2008); (d) *Mica micula* specimen from Antarktis IX/2 station 115 (71°30′ S, 11° W). Scale bar: 1 mm (a, d), 0.5 mm (b, c).

Margulis (1982) had lost their stems or were not figured in enough detail to conclude about how the nectophore was attached to the stem.

It would seem the stem becomes more compressed against the larval nectophore as it develops, a fact which may also have been observed by Pagès and Gili, as they state in their 1989 redescription that the canal structure was more visible in the smaller colony. Additionally, the muscular lamella joining the larval nectophore to the stem was particularly developed near the point of junction of the internal pedicular canals with the radial canals, even in the smaller colonies.

The posterior end of the pneumatophore was positioned slightly posterior to the level of the junction of the lateral canals with the upper radial canal. In the largest specimen (CEAMARC station UM23), the pneumatosaccus was hour-glass-shaped, the anterior and posterior portions of the single chamber communicating through a circular opening in the central constriction. In the smaller CEAMARC samples, as in the larger of the Antarktis colonies and the *Magga Dan* one, the lower portion of the pneumatosaccus was less developed than the upper one, giving it a teardrop shape. No apical pore was visible. On the youngest specimen (Antarktis IX/2 cruise, station 115), the pneumatosaccus was not yet clearly differentiated from the yolk (Fig. 3). At the posterior end of the pneumatophore, on the dorsal side, a varying number of definitive nectophore buds could be seen.

The most developed definitive nectophores were elongate, with small axial wings (Fig. 5a) and a bi-lobed mouthplate. Denser cell concentrations could be observed on the nectosac, but the form of the radial canals could not be discerned. Although some morphological similarities were noted, a comparison with the smallest definitive nectophores of *Bargmannia* spp. colonies [*e.g.* Fig. 5b (Dunn 2005; fig. 6, modified): nectophore at bottom left] was inconclusive. However, these latter were all more than twice as large as the most developed definitive nectophores of the *Mica micula* colonies.

Slightly posterior to the junction point with the external pedicular canal, the stem carried several cormidia and developing cormidial buds. No bracts were present. In the figured animal (Fig. 2), the following elements were present: a mass of developing zooids, enveloping the whole posterior part of the stem; a globular zooid with a conical distal end, possibly a developing gastrozooid; and,
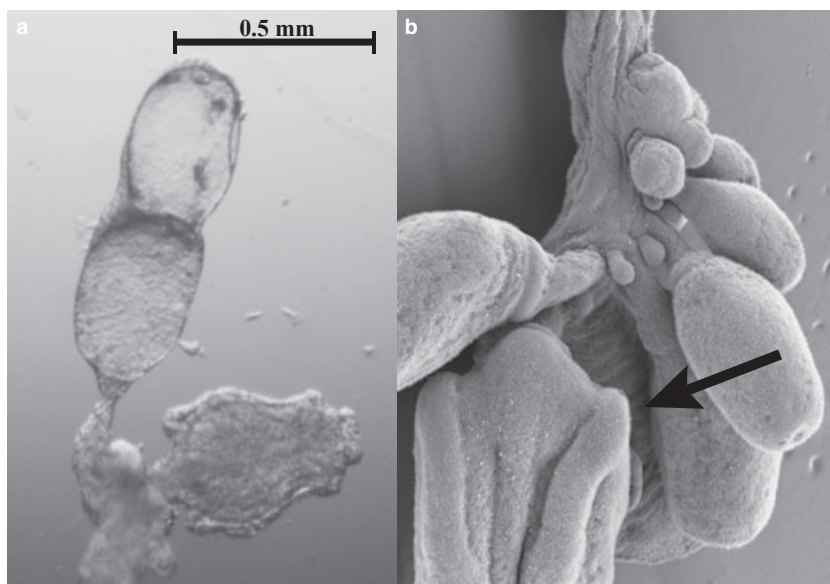
Fig. 5. (a) Pneumatosaccus and developing definitive nectophore of the *Mica micula* stem collected at station UM12 (66°34′ S, 144°0.3′ E, 10 February 2008). (b) Scanning electron micrograph of the *Bargmannia elongata* nectosomal growth zone (view from left, anterior up, dorsal to the right of the page). Modified from Dunn (2005) (Fig. 6). The arrow indicates a developing definitive nectophore. Scale bar: 0.5 mm.

finally, a large elongated gastrozooid with a small mouth at the distal end. The long thin tentacle had several tentilla carrying nematocyst clumps at their extremity. A study of one of the tentilla showed there were two kinds of nematocysts, an oval kind measuring 25 × 30 μm, and a small spherical kind measuring 5 × 10 μm in diameter (Fig. 6). No discharged nematocysts could be seen, but the larger nematocysts appeared to be stenoteles.

The study of the two young colonies from the Antarktis IX cruise confirmed their development to be similar to that described by Carré (1971) for *Halistemma rubrum*, the larval nectophore being produced first, followed by the pneumatophore, stubs of the definitive nectophores and siphosomal cormidia.

Fig. 6. Nematocyst clump from the tentilla of the *Mica micula* colony from station UM23 (65°60′ S, 139°60′ E, 4 February 2008). Scale: 50 μm.

Distribution

Mica micula was caught in seven 330-μm mesh NORPAC nets, between 0 and 150 m (65–66° S, 140–144° E) and in a 100-μm mesh Multinet at station UM11 in the Winter Water (−1.7 to −1.3 °C), between 100 and 200 m (66°20′ S, 143°20′ E). No animals were caught north of the Antarctic Shelf Front (ASF) in the present study (Fig. 7a).

The only previous records of this species are also from Antarctic and sub-Antarctic waters. The material used for Margulis' original description (1982) was caught between 0 and 110 m with a 280–300 μm mesh Juday net, south of the Falkland Islands (52–54° S, 53–56° W). In 1992, Margulis recorded them in the Cosmonaut Sea and Commonwealth Bay (66–69° S, 31–51° E and 60° S, 55–90° E, respectively), from 2000 m to the surface, using the same kind of net (Margulis 1992). The specimens used by Pagès & Gili 1989 in their 1989 redescription of *Mica micula* were sampled from 0–4500 and 0–250 m at 68°50′ S, 26°31′ E with a 300-μm mesh Indian Ocean standard net. A further nectophore from that *Magga Dan* expedition was collected between 0 and 280 m at about 23° E, 68° S. *M. micula* was also found between 0 and 500 m in a 100-μm mesh Multinet net in the Weddell Sea (62°30′–71° S, 53–12° W) during the 1990 Antarktis IX/2 cruise (Pagès & Kurbjeweit 1994, listed as '?*Bargmannia* post-larvae'). This seems to indicate that it is endemic to the Southern Ocean, and mainly epipelagic. The lack of further records may be due to the diminutive size of the colonies, as they would probably not have been sampled using nets with a mesh aperture larger than 500 μm. Additionally, although *M. micula* appears to be
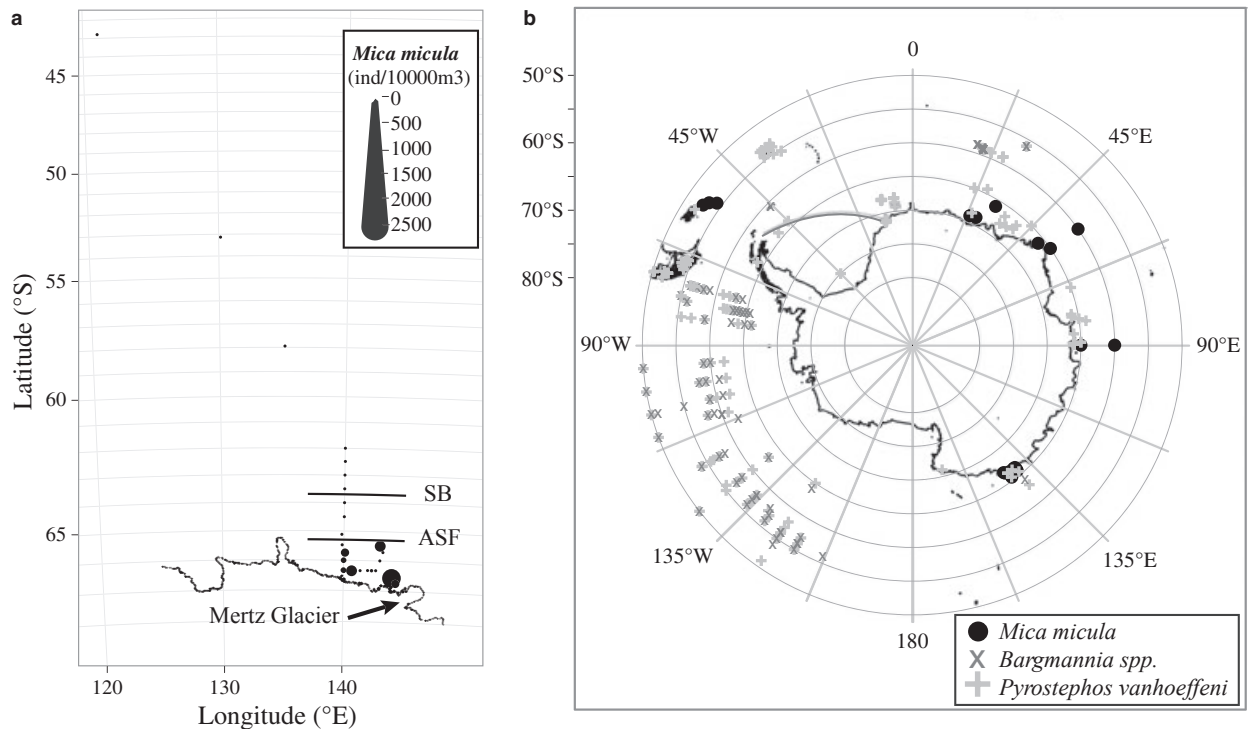
Fig. 7. (a) Abundance and distribution of *Mica micula* sampled during the CEAMARC campaign (continuous size scale, in ind.10 000·m^{-3}). ASF, Antarctic Slope Front (65.3° S), SB, Southern Boundary of the Antarctic Circumpolar Current (63.7° S). (b) Map of all published records of *M. micula* (circles), *Bargmannia* spp. (×) and *Pyrostephos vanhoeffeni* (+), south of 50° S. Data from GBIF (Global Biodiversity Information Facility); data portal; Alvariño *et al.* 1990; Grossmann 2010; Hardy & Gunther 1936; Hopkins 1985; Margulis 1982, 1992; Moser 1925; Pagès & Gili 1989; Pagès & Kurbjeweit 1994 (represented by the line of sampled stations, more detailed information being unavailable); Pagès & Schnack-Schiel 1996; Palma & Aravena 2001; Palma *et al.* 1999; Panasiuk-Chodnicka & Žmijewska 2010; Pugh *et al.* 1997; Toda *et al.* 2010;. Coastline map from NOAA; Coastline extractor, World Vector Shoreline (designed for 1:250 000) database (50–90°S).

endemic, it is only one of the developmental stages of a physonect siphonophore, and so we cannot come to a conclusion as to the endemicity of the adult.

Discussion

Mica micula colonies showed some characteristics associated with the family Pyrostephidae, such as the presence of stenoteles and a smaller spherical kind of nematocyst on the tentilla of the tentacles, (Pugh 1999; Mapstone 2009), as well as the dorsal insertion of the nectophores on the stem. The larval nectophores of *M. micula* also lacked a descending pallial canal, and the lateral radial canals originated from the upper radial canal, characters associated with definitive nectophores of the family Pyrostephidae. However, it is not known whether the characteristics observable on the larval nectophore are also found in the definitive nectophores.

Margulis (1982), Pugh (1999) and Mapstone (2009) hypothesized that *Mica micula* might be a post-larval stage of a *Bargmannia* siphonophore. However, no *Bargmannia* nectophores or bracts were found in the Multinet or NORPAC samples, and in fact were found only once during the CEAMARC cruise, in an RMT net at station UM18 (64° S, 140° E; unpublished data). A map of the published records of *Bargmannia* in the Southern Ocean shows very little correlation between the areas of distribution of *M. micula* and *Bargmannia* (Fig. 7b). However, *Pyrostephos vanhoeffeni*, another species in the family Pyrostephidae, was present in the sampling area (Grossmann 2010; Grossmann & Lindsay 2011) and its areas of distribution, based on published records, overlap those of *M. micula*.

If the adult form of *Mica micula* were a Southern Ocean endemic, as the post-larval stage seems to be, and if the characters of the larval nectophores were to be carried on into the definitive nectophores, then *Pyrostephos vanhoeffeni* would be the most likely candidate for the adult form of *M. micula*.

Conclusion

Although this study does not allow *Mica micula* to be definitively assigned to any known physonect species,

some additional morphological characteristics of the stem and larval nectophore are described, such as the origin of the lateral radial canals on the upper canal, the different arrangements this junction can have, and the absence of a descending pallial canal. The study of two very young colonies confirmed their development to be similar to that of *Halistemma rubrum*, the larval nectophore being produced first, followed by the pneumatophore and then the definitive nectophores and siphosomal cormidia. The cormidia of the oldest specimens were composed of both gastrozooids and gonozooids, but no bracts were observed. Contrary to the generic characteristics established by Margulis (1982), the tentacles do have tentilla. Stenoteles and a second smaller spherical type of nematocyst were present in clumps at the extremities of the tentilla of the larger tentacle. For the first time, the definitive nectophores were observed. However, they were still too underdeveloped to be assigned to any known physonect species.

As in the family Pyrostephidae, the nectophores are attached to the dorsal side of the stem, a characteristic shared only by the Agalmatidae. It has been hypothesized (Margulis 1982; Pugh 1999; Mapstone 2009) that *Mica micula* might be a post-larval stage of a *Bargmannia*. However, *Bargmannia* colonies have rarely been collected in the same geographic locations as *M. micula*, whereas *Pyrostephos vanhoeffeni*, another species of the family Pyrostephidae, seems to have overlapping areas of distribution. Further samplings of *M. micula*, using small-meshed nets, genetic analysis or rearing experiments may be necessary to definitively link *M. micula* to its adult stage.

Acknowledgements

Conflicts of Interest

None of the authors have any potential conflict of interest.

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