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First occurrence of *Beroe forskalii* (Ctenophora) in South American Atlantic coastal waters, with notes on the use of macrociliary patterns for beroid identification

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Abstract

Beroe forskalii Milne Edwards, 1841 is an oceanic ctenophore with a global distribution. The present study provides the first record of *Beroe forskalii* for the South American Atlantic coast, including a redescription of the species and a discussion on the utility of macrociliary patterns for the correct identification of at least some beroid species, exemplified by a comparison of the macrociliary patterns of *Beroe forskalii* and *Beroe ovata* (Chamisso & Eysenhardt, 1821).

Key words: Beroidae, comb jelly, ctenophore, gelatinous zooplankton, Southwest Atlantic

Introduction

Nineteen of the estimated 150 valid ctenophore species (Mills 2013) are known to occur along the South American Atlantic coast (Oliveira *et al.* submitted). Thirteen species have been recorded for Brazil (Oliveira *et al.* 2007), and six were already registered for the São Sebastião Channel, southeastern Brazil (Oliveira & Migotto 2006; 2007). Only two species of Beroidae [*Beroe cucumis* Fabricius, 1780 and *Beroe ovata* (Chamisso & Eysenhardt, 1821)] have been recorded for the area, taking *Beroe gilva* Eschscholtz, 1829 as a junior synonym of *B. ovata* (see Oliveira *et al.* 2007).

The identification of *Beroe* species can be very difficult as many species were only superficially described (Harbison *et al.* 1978) and the number of synonyms is likely to be very high, although determining which species names are synonymous is difficult and ideally requires study of *Beroe* collected from many localities around the world. An anatomical feature useful in discriminating among *Beroe* species is the distributional patterns of oral macrocilia (Tamm & Tamm 1993). Macrocilia are feeding organelles found exclusively inside the mouth of beroid ctenophores (Horridge 1965). Individual macrocilia present a variety of distinct forms and macrociliary fields are also arranged in species-specific patterns (Tamm & Tamm 1993).

The present study provides the first formal record of *Beroe forskalii* from the Brazilian coast, including a redescription of the species and a discussion on how macrociliary patterns can be of paramount importance for correct identification of beroid species.

Material and methods

A single *Beroe forskalii* specimen was collected in the São Sebastião Channel, southeastern Brazil (23.8° S, 45.4° W), in a horizontal plankton tow using a net with 300 µm mesh and mouth diameter of 60 cm. The specimen was then maintained in aquarium seawater at ambient temperature (20–25°C) and photographed alive under a stereomicroscope against a dark background (Oliveira *et al.* 2007). After three days of rearing, the specimen was

preserved in 4% neutralized formalin solution. Additional photos were taken using differential interference contrast microscopy (DIC). The voucher was deposited in the Ctenophora collection of the Museu de Zoologia da Universidade de São Paulo (access number MZUSP00012).

Systematic part

Family **Beroidae** Eschscholtz, 1825

Beroe forskalii Milne Edwards, 1841

(Figures 1–2; Table 1)

Beroe forskalii Milne Edwards, 1841 — Chun 1880; Tamm & Tamm 1991, 1993; Haddock & Case 1999; Mianzan 1999; Wrobel & Mills 2003; Lindsay & Hunt 2005; Lindsay 2006; Shiganova & Malej 2009.

Material examined. MZUSP00012, a single specimen 2.5 cm long from Canal de São Sebastião, 23.8° S, 45.4° W, coll. A. Migotto 8 July 2010, reared to 10 July 2010 then fixed in 4% formalin.

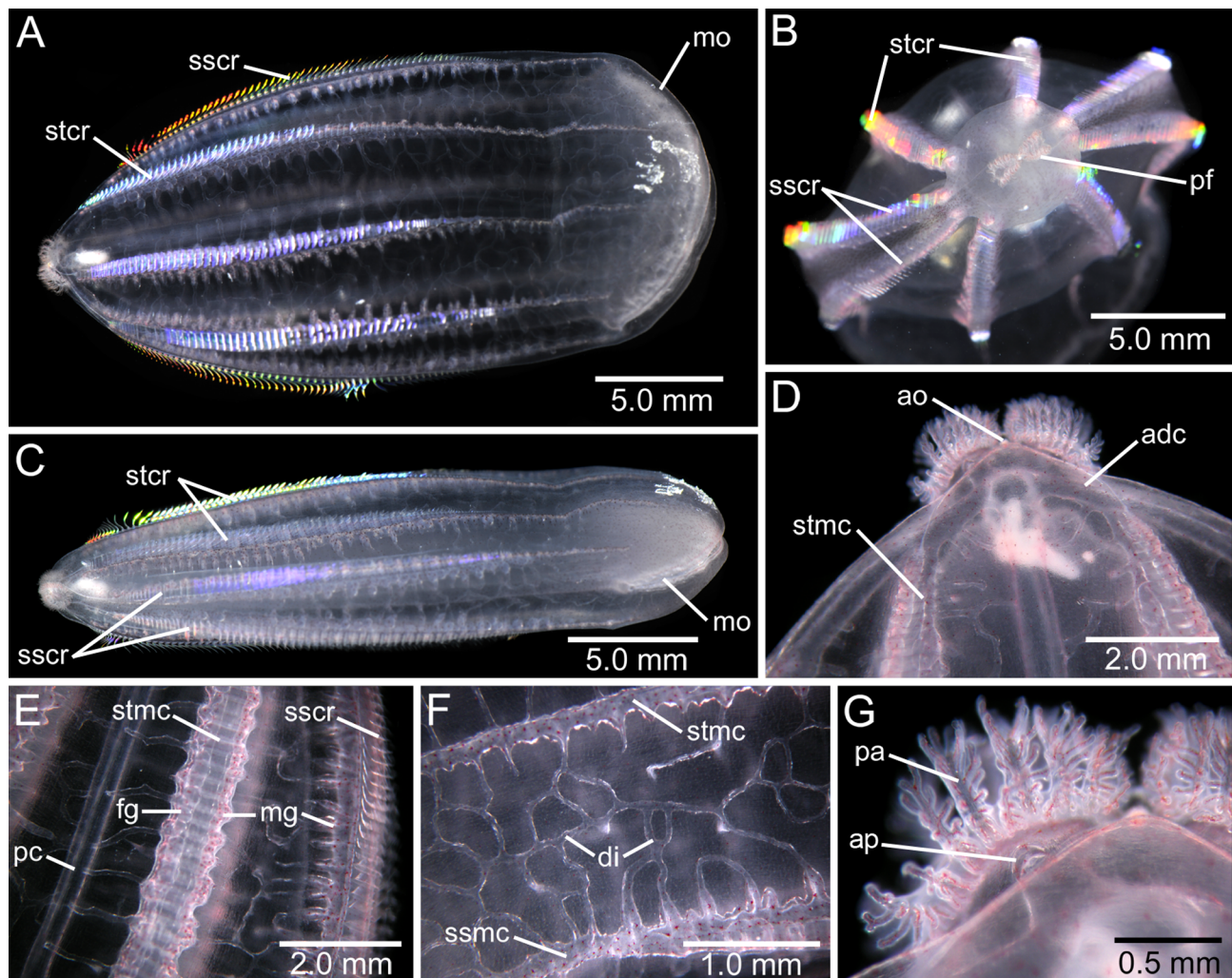


FIGURE 1. *Beroe forskalii* Milne Edwards, 1841. **A**, Entire specimen in stomodeal plane; **B**, same, aboral view; **C**, same, in tentacular plane; **D**, view of the aboral end in stomodeal plane; **E**, close-up of meridional canals and diverticula with male and female gonads; **F**, close-up of anastomosing diverticula near the mouth; **G**, close-up of the aboral end of the body. Abbreviations: adc, adradial canal; ao, apical organ; di, diverticule; fg, female gonads; ap, anal pore; mg, male gonads; mo, mouth; pa, papilla; pc, paragastric canal; pf, polar field; sscr, substomodeal ctene row; stcr, subtentacular ctene row; ssmc, substomodeal meridional canal; stmc, subtentacular meridional canal.

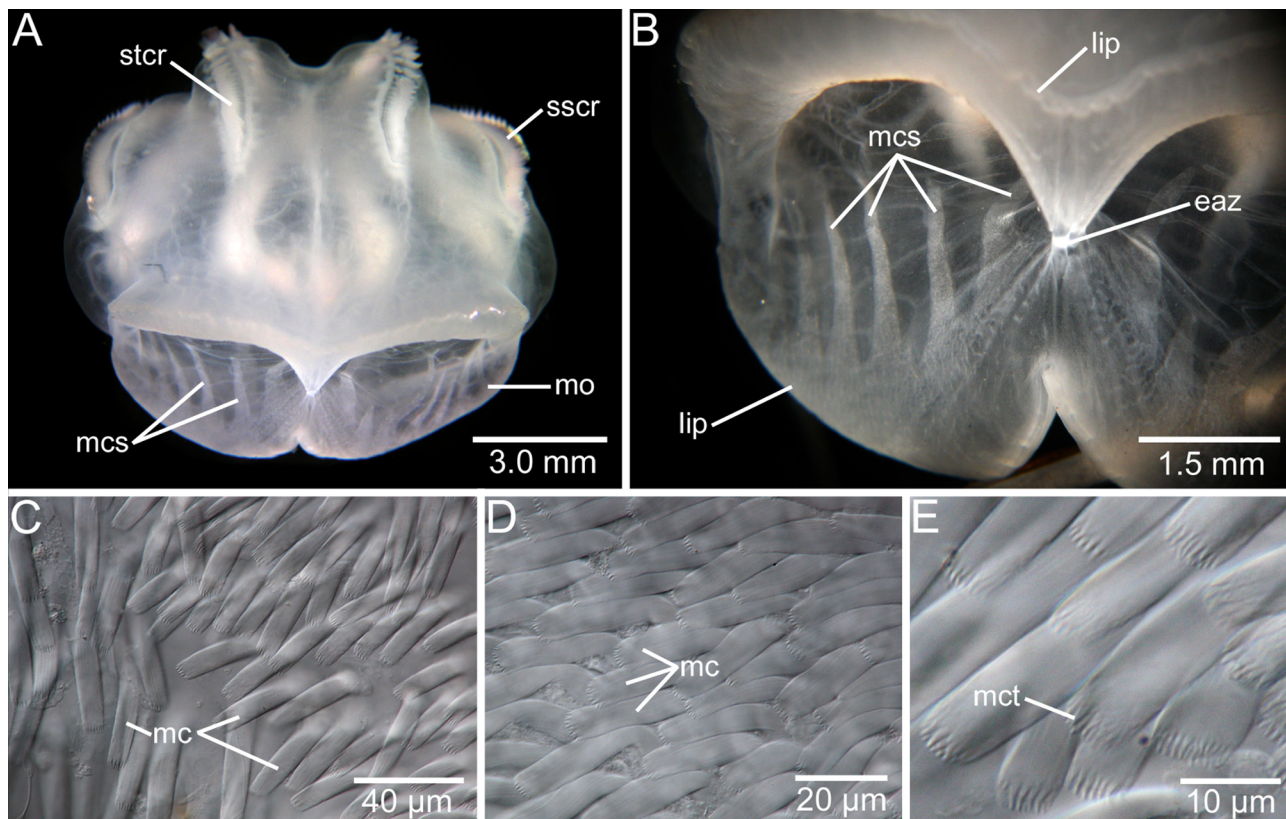


FIGURE 2. *Beroe forskalii* Milne Edwards, 1841. **A**, Partial oral view of the specimen, after two months of preservation in 4% formalin; **B**, interior view of stomodeum through the partially opened mouth, showing the macrociliary stripes; **C**, DIC image of macrocilia oriented toward the base of the stomodeum (two rows of teeth visible); **D**, DIC image of macrocilia oriented toward the mouth (only one row of teeth visible); **E**, DIC image of distal ends of macrocilia oriented toward the base of the stomodeum. Abbreviations: eaz, epithelial adhesive zone; lip, lip edge; mc, macrocilium; mcs, macrociliary stripes; mct, macrocilium teeth; mo, mouth; sscr, substomodeal ctene row; stcr, subtentacular ctene row.

Description. Body sac-shaped, pinkish, with broad mouth; body width tapering from middle to aboral extremity of body (Fig. 1A); compressed along tentacular plane (Fig. 1C). Eight meridional canals extending from aboral region towards mouth and connected with a circular canal around mouth by a mesh of anastomosing canals; these with lateral diverticulae, mostly with blind ends in aboral half of body, but forming anastomoses along oral half (Fig. 1F). Diverticulae from subtentacular meridional canals connected with paragastric canal (Fig. 1E). Ctene rows located above meridional canals arising at aboral region. Substomodeal ctene rows extending for about 3/4 the length of the meridional canals to oral region. Subtentacular ctene rows limited to aboral 2/3 of body. Mouth wide, semicircular, occupying whole oral region, opening into large pharynx that occupies most of central inner part of animal. Two opposite paragastric canals, extending from aboral pole of pharynx to circular canal around mouth, crossing at tentacular plane. Aboral extremity of body mitriform (Fig. 1D). Apical organ including a statolith at center of polar fields. Aboral papillae prominent, branched (Fig. 1G), projecting from margins of polar fields, forming an “hourglass” figure, oriented in stomodeal plane when in aboral view (Fig. 1B). Each papilla with first- and sometimes second-order branches in a pinnate arrangement; branches curving toward exterior of polar field. The animal is a simultaneous hermaphrodite, with gonads formed at lateral walls of meridional canals and nearby diverticulae (Fig. 1E). Ovaries restricted to portion of meridional canals under ctene rows. Testes lying along all meridional canals and adjacent diverticula. Gonads of adjacent meridional canals facing those of same gender on the adjacent canal, i.e. female gonads face in stomodeal-stomodeal and tentacle-tentacle patterns; male gonads face in a stomodeal-tentacular arrangement. Macrocilia are robust (length 5–7 times width), with about 20 small teeth along edge (Fig. 2), covering extensive area of oral portion of stomodeal cavity, arranged in long tapering stripes that run from lip toward center of stomodeum.

Remarks. The young individual on which the above description is based, was very active for the three days it was kept in the aquarium, swimming quickly, sometimes with the mouth open. It resembled *Beroe mitrata* Moser,

1907, except for the presence of anastomoses and the pointed end of the aboral portion (Wrobel & Mills, 2003). Based on the shape of their macrocilia, these two species form a distinct group within the genus *Beroe* (Tamm & Tamm 1993). In these two species, the macrocilia are very similar, differing only by their pattern of distribution along the stomodeal cavity, comprising a carpet covering all of the oral portion of the stomodeum in *B. mitrata* and long tapering stripes that run from the lip toward the center of the stomodeum in *B. forskalii* (Tamm & Tamm 1993). On this basis, inter alia, the specimen from São Sebastião Channel was certainly *B. forskalii*. The first description of what was probably this species was made by Forskål (1775), as *Beroe rufescens*. This name was not used by later researchers after Milne Edwards (1841) questioned its validity. The combination *Beroe forskalii* has been used in at least 20 publications in the last 50 years and, following the nomenclatural Principle of Stability (ICZN 1999), its use may continue. The author of the combination *Beroe forskalii* is taken as Milne Edwards (1841), not Chun (1880), following the Principle of Priority (ICZN 1999).

Distribution. *Beroe forskalii* is distributed worldwide (e.g. Moser 1910; Mianzan 1999; Lindsay & Hunt 2005; Shiganova & Malej 2009; Oliveira et al. submitted).

TABLE 1. Measurements of a young *Beroe forskalii* (Milne Edwards, 1841) specimen 25.0 mm long in the stomodeal plane (measured on photographs of a living specimen).

Total length of the body	25.0 mm
Maximum width of the body	12.3 mm
Length of the subtentacular ctene rows	11.9 mm
Length of the substomodeal ctene rows	17.5 mm
Maximum width between substomodeal and subtentacular ctene rows	up to 3.8 mm
Maximum width between subtentacular ctene rows	up to 4.8 mm
Width of the mouth	11.8 mm
Number of ctene plates in subtentacular ctene rows	65–76
Number of ctene plates in substomodeal ctene rows	74–78
Length of the polar field	2390 µm
Number of papillae	36
Length of the papillae	up to 480 µm
Diameter of the meridional canals	up to 715 µm
Diameter of the diverticulae	up to 81 µm
Diameter of the paragastric canals	up to 235 µm
Diameter of the adradial canal	up to 490 µm
Diameter of the radial canal	up to 140 µm
Width of the ctene plates	214–700 µm
Distance between ctene plates	59–295 µm
Diameter of the statocyst	118 µm

Discussion on the use of macrociliary patterns for *Beroe* identification

Macrociliary patterns are very useful for the identification of *Beroe* species. Strikingly different patterns can be found among species or even among different populations (Tamm & Tamm 1993). Two major groups of Beroidae can be distinguished by these patterns (see Tamm & Tamm 1991, fig. 10; 1993). The *Beroe ovata* group is composed of species with a single band of macrocilia around the inside of the lips. The other, *Beroe forskalii* group, includes species with macrocilia covering an extensive portion of the stomodeal cavity. Furthermore, the macrocilia of both groups are different in transverse section: hexagonal in the former and wedge-shaped in the later (Horridge 1965; Tamm & Tamm 1993). The number and size of the teeth on the edge of the macrocilia are also good characters for distinguishing species (Tamm & Tamm 1993). The remarkable differences between the patterns in the two groups certainly relates to differences in feeding methods. Apparently, the simple band of macrocilia in

the *B. ovata* group is used to bite and cut off pieces of large prey (Swanberg 1974; Matsumoto & Harbison 1993). There is some evidence that macrociliary beating is activated during prey ingestion (Swanberg 1974; Tamm 1988). In the *B. forskalii* group the stomodeal macrocilia are considered to rasp and scrape ingested prey, assisting the digestion process (Tamm & Tamm 1993).

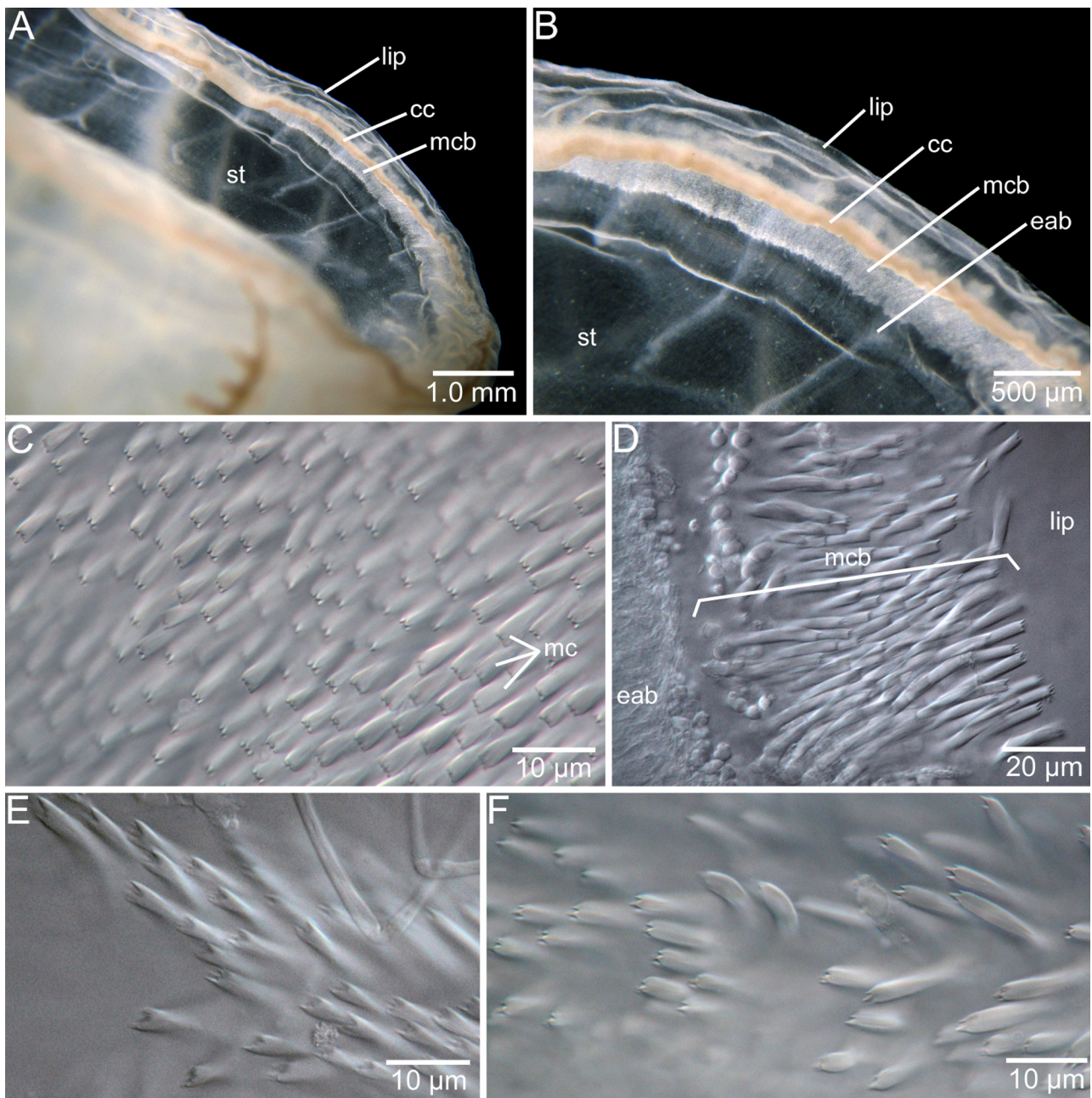


FIGURE 3. *Beroe ovata* (Chamisso & Eysenhardt, 1821). **A**, view of part of the mouth of a specimen after two months of preservation in 4% formalin; **B**, close-up of the edge of the mouth of the same specimen, showing the narrow macrociliary band; **C**, DIC image of macrocilia oriented toward the base of the stomodeum; **D**, DIC image of a narrow portion of the macrociliary band, showing macrocilia oriented toward the mouth; **E**, **F**, DIC images of detached patches of macrocilia, showing teeth configurations in diverse orientations. Abbreviations: eab, epithelial adhesive band; lip, lip edge; mc, macrocilium; mcb, macrociliary band; cc, circular canal; st, stomodeum.

A careful comparison between *B. ovata* and *B. forskalii* makes evident the distinctive differences in the external morphology of these species. The former is not as flattened as the latter, which also has a pointed aboral end with much more prominent papillae than in *B. ovata* (cf. Oliveira & Migotto 2006 and the present study). The swimming behavior of both species in aquaria is also very distinct, *B. forskalii* being more active and raptorial. In this regard, the macrociliary patterns represent an additional character for species distinction. *Beroe ovata* contains

thin macrocilia (length nine times the width), with about five sharp teeth at the edge (Fig. 3), arranged in a narrow band around the inside of the lips. Comparison of macrociliary patterns in the two species, which co-occur in the São Sebastião Channel, allows them to be unequivocally distinguished (Table 2). However, definitive identification of the young specimen of *B. forskalii* from São Sebastião Channel (25 mm length vs 200 mm larger specimens from other areas) was possible only using the macrociliary pattern. Whereas obvious morphological differences are observed between larger specimens of *B. forskalii* and *B. mitrata* (see Wrobel & Mills, 2003), young specimens have a very similar morphology, differing chiefly in the pattern of the macrocilia. While it is true that molecular biology can be very helpful in ctenophore identification, for rapid field identification relying only on morphology, macrociliary patterns prove to be a very reliable character for the distinction of different *Beroe* species.

TABLE 2. Comparison between macrociliary patterns of *Beroe forskalii* Milne Edwards, 1841 and *Beroe ovata* (Chamisso & Eysenhardt, 1821) from southeastern Brazilian waters (after two months preserved specimens).

Structure	<i>B. forskalii</i>	<i>B. ovata</i>
Macrociliary field	Broad stripes running from the lips, tapering towards the inner stomodeum.	Narrow band (150–250 µm wide) inside lips.
Macrocilium length	40–55 µm	15–20 µm
Macrocilium diameter	7–9 µm	2–3 µm
Tooth number	18–26	4–6
Tooth size	Equal, 2–3 µm in length.	One larger, ca. 1 µm in length.

Acknowledgments

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