
ON THE OCCURRENCE OF SCYPHOZOAN EPHYRAE (CNIDARIA, SCYPHOZOA, SEMAEOSTOMEAE AND RHIZOSTOMEAE) IN THE SOUTHEASTERN BRAZILIAN COAST

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Biota Neotropica v2 (n2) – <http://www.biotaneotropica.org.br/v2n2/pt/abstract?article+BN02102022002>

Date Received 07/04/2002

Revised 08/03/2002

Accepted 10/02/2002

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Abstract – The occurrence of ephyrae of the scyphozoan orders Semaestomeae and Rhizostomeae is reported for the first time for the Brazilian coast. The specimens, caught in plankton tows in the São Sebastião Channel and the Cananéia lagoon estuarine system, are: *Chrysaora lactea* (Semaestomeae), *Phyllorhiza punctata* (Rhizostomeae), and an unidentified species of *Pelagia* (Semaestomeae). A table with all species of scyphozoan with the known life cycle is provided.

Palavras-chave : Scyphozoa, Semaestomeae, Rhizostomeae, ephyra, life cycle, Brazil.

Resumo – A ocorrência de éfiras de cifozoários das ordens Semaestomeae e Rhizostomeae é registrada pela primeira vez para a costa brasileira. Os espécimes, coletados com arrastos de plâncton no Canal de São Sebastião e no Sistema estuarino-lagunar de Cananéia, são: *Chrysaora lactea* (Semaestomeae), *Phyllorhiza punctata* (Rhizostomeae), e uma espécie não identificada de *Pelagia* (Semaestomeae). Uma tabela, com todas as espécies de cifozoários com ciclo de vida conhecido, é apresentada.

Palavras-chave : Scyphozoa, Semaestomeae, Rhizostomeae, éfira, ciclo de vida, Brasil.

Introduction

The class Scyphozoa is defined, besides other features, by the process of strobilation (Schuchert, 1993), *i.e.* successive vegetative (asexual reproduction) cutting-off of a sequence of new individuals (ephyrae) from one end of a parent benthic polyp (scyphistomae) (Mianzan & Cornelius, 1999: 525, the text in parenthesis was added). These disks (ephyrae) are the young (immature) free-swimming stages of the scyphozoans (Stachowitsch, 1992). Strobilation can be divided into monodisc (one disc produced at a certain time) or polydisc (more than one disc produced at a certain time) (Arai, 1997).

In the life cycle of *Stylocoronella riedli* and *S. variabilis* (members of the order Stauromedusae), the interstitial polyp metamorphoses into a medusa (see Kikinger & Salvini-Plawen, 1995), thus not presenting an ephyra stage. Collins (2002) proposed that the Stauromedusae be separated from the other Scyphozoa, due to the absence of the strobilation process and, consequently, not producing ephyrae. The absence of strobilation and ephyrae, plus the presence of a claustrum led several authors to the conclusion that the Stauromedusae are closely related to the class Cubozoa (cf. Haeckel, 1880; Uchida, 1929; one topology found by Collins, 2002).

Some scyphomedusae present a holopelagic life cycle (absence of the polyp stage, and thus, of strobilation), *e.g.*, the semaeostome *Pelagia noctiluca* (see Rottini Sandrini & Avian, 1983) and the coronate *Periphylla periphylla* (see Jarms *et al.*, 1999).

Besides the general morphological similarity of the ephyra stage of most species, which makes their specific identification difficult, there are few life cycle studies of Scyphozoa, that include detailed accounts of this planktonic stage, to rely on. Out of *ca.* 200 species of scyphozoans (Mianzan & Cornelius, 1999), only about 42 species (almost a quarter of those known) had their life cycles described (see Table 1 in Results and Discussion). Russell (1970) provided a comparative plate of the ephyra stages of the British species. Even among the works devoted to the life cycle of scyphozoan species, only a few [*e.g.*, Silveira & Morandini (1997) and Jarms (2001), for Coronatae; Avian (1986) and Pitt (2000), for Rhizostomeae; Calder (1972) and Gershwin & Collins (2002), for Semaestomeae] included descriptions of ephyrae. For some species, information concerning life cycle stages is scattered throughout the literature, included in systematic or faunistic reports among descriptions of other species, or referring to one or another stage only.

None of the 23 scyphozoans recorded for Brazil (see Migotto *et al.*, 2002) refer to ephyrae collected in nature. Despite their efforts, Silveira & Morandini (1998) could not find the ephyra and medusa of the coronate *Linuche*

unguiculata, a species associated with a calcareous substrate and abundant in the region of São Sebastião. Goy (1979) mentioned the presence of young specimens of *Chrysaora lactea* (as *C. hysoscella*) on the coast of Uruguay, and young *Aurelia aurita* on the coast of Bahia State (Brazil).

This work reports and describes three different ephyrae found on the southeastern coast of Brazil. A table covering the knowledge from literature and our own experiences in life cycles of Scyphozoa (except Stauromedusae) is provided.

Material and Methods

Specimens came from two localities on the coast of São Paulo State, southeastern Brazil: the São Sebastião Channel (23°S – 45°W) (SSC) and the Cananéia lagoon estuarine system (25°S – 48°W) (CES) (see Figure 1).

In the SSC, two ephyrae were collected with vertical plankton tows (300 and 500 µm mesh sizes; maximum depth 40 m) in August and October 1999, and reared in the laboratory until the first signs of gonadal tissue were detected. The ephyrae were isolated in glass containers filled with filtered seawater (changed daily) and kept in a constant temperature chamber at 20-21°C. The medusae were fed daily with *Artemia* sp. nauplii, besides other planktonic organisms (especially copepods) and small pieces of muscle and gonads of mussels (*Perna perna*).

In the CES, ephyrae were collected with horizontal (0.5 m below surface) and vertical (maximum depth 12 m) plankton tows (500 and 200 µm mesh sizes) in April 2001, and January and February 2002. The ephyrae were transferred to culture dishes, kept in a constant temperature chamber at 22°C and reared as described by Jarms *et al.* (*in press*). Mature medusae of *Chrysaora lactea* collected at CES and reared in “planktonkreisel” (according to Greve, 1968) produced planulae that settled on the “planktonkreisel” walls and originated scyphistomae; these were transferred to culture dishes, there producing ephyrae.

Fixed and live specimens were photographed under a stereomicroscope; the live ones were relaxed in a mixture of 1:1 of seawater and 7.5% MgCl₂ solution before being photographed. When the specimens from the SSC attained a size larger than 15 mm in diameter they were also periodically photographed, without being anaesthetized, in an aquarium using a 35mm camera and a flashgun.

Class	Order	Species	Reference
SCYPHOZOA	CORONATAE	<i>Atorella japonica</i>	Kawaguti & Matsuno 1981
		<i>Atorella vanhoeffeni</i>	Werner 1966
		<i>Linuche unguiculata</i>	Ortiz-Corp's <i>et al.</i> 1987
		<i>Nausithoe aurea</i>	Silveira & Morandini 1997
		<i>Nausithoe eumedusoides</i>	Werner 1974
		<i>Nausithoe globifera</i>	Jarms 1997
		<i>Nausithoe hagenbecki</i>	Jarms 2001
		<i>Nausithoe maculata</i>	Jarms 1990
		<i>Nausithoe marginata</i>	Jarms 1990
		<i>Nausithoe planulophora</i>	Werner & Hentschel 1983
		<i>Nausithoe punctata</i>	Werner 1979
		<i>Nausithoe racemosa</i>	Komai & Tokuoka 1939
		<i>Nausithoe thieli</i>	Jarms 1990
		<i>Nausithoe weneri</i>	Jarms 1990
		<i>Periphylla periphylla</i>	Jarms <i>et al.</i> 1999
<i>Thecoscyphus zibrowii</i>	Sötje & Jarms 1999		
SEMAEOSTOMEAE		<i>Aurelia aurita</i>	Lucas 2001
		<i>Aurelia labiata</i>	Gershwin 2001
		<i>Chrysaora achlyos</i>	*Gershwin & Collins 2002
		<i>Chrysaora colorata</i>	Gershwin & Collins 2002
		<i>Chrysaora fuscescens</i>	*Gershwin & Collins 2002
		<i>Chrysaora hysoscella</i>	*Delap 1901
		<i>Chrysaora melanaster</i>	Kakinuma 1967
		<i>Chrysaora quinquecirrha</i>	Littleford 1939; Calder 1972
		<i>Cyanea capillata</i>	*Gröndahl 1988
		<i>Cyanea lamarckii</i>	*Gröndahl 1988
		<i>Pelagia noctiluca</i>	Goette 1893; Russell 1970
		<i>Phacellophora camtschatica</i>	*Wrobel & Mills 1998 (picture of the polyp stage, p.22)
		<i>Sanderia malayensis</i>	Uchida & Sugiura 1978
<i>Stygiomedusa fabulosa</i>	Russel & Rees 1960		
RHIZOSTOMEAE		<i>Cassiopea andromeda</i>	Gohar & Eisawy 1960
		<i>Cassiopea xamachana</i>	Bigelow 1900
		<i>Catostylus mosaicus</i>	Pitt 2000
		<i>Cephea cephea</i>	*Sugiura 1966
		<i>Cotylorhiza tuberculata</i>	Kikinger 1992
		<i>Mastigias papua</i>	Uchida 1926
		<i>Phyllorhiza punctata</i>	Lange & Kaiser 1995
		<i>Rhizostoma pulmo</i>	*Paspaleff 1938
		<i>Rhopilema esculenta</i>	Ding & Chen 1981
		<i>Rhopilema nomadica</i>	Lotan <i>et al.</i> 1992
		<i>Rhopilema verrilli</i>	Calder 1973
		<i>Stomolophus meleagris</i>	Calder 1982

Table 1. Scyphozoan species with known life cycles (except Stauromedusae), adapted from several sources. The most recent references or those with the most complete description regarding their life cycle were included. A reference which mentions one or another stage was included and marked with an “*”.

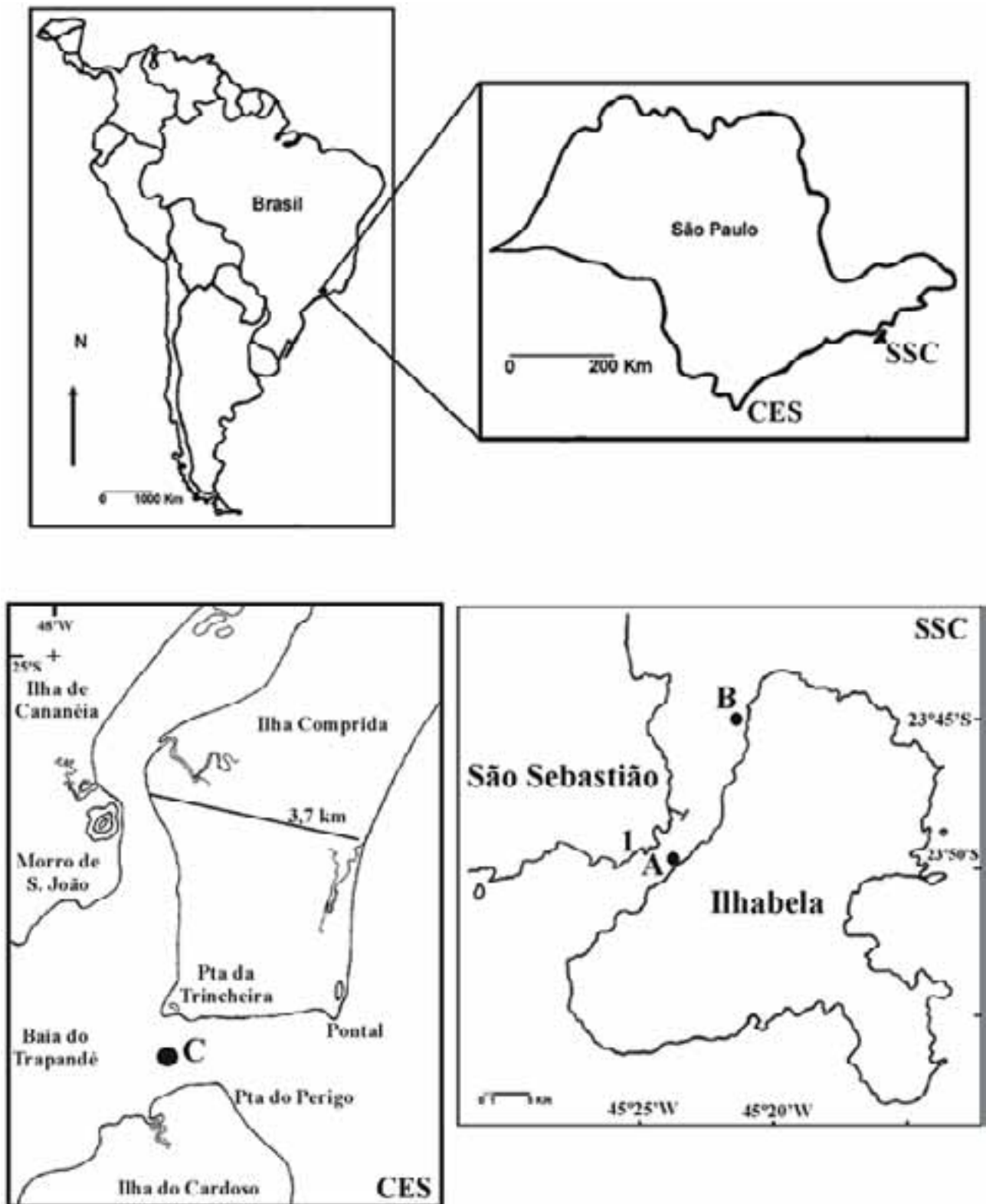


Figure 1. Map showing the collecting areas: CES = Cananéia lagoon estuarine system; SSC = São Sebastião Channel; I= Centro de Biologia Marinha laboratory (CEBIMar-USP); A= collection of *Chrysaora lactea* (23°49.89S-045°25.36W); B= collection of *Pelagia* (23°44.85S-045°20.92W); C = collection of *Phyllorhiza punctata*.

Results and Discussion

Known life cycle

A review of scyphozoan literature was performed to build up a list with all scyphozoan species (except for the order Stauromedusae) in which the life cycle is known. This list is presented here as Table 1. We tried to provide the most complete or the most recent reference for each species. But, for some of them there is little information on life cycle stages, and we decided to include references which mentioned one or another stage (these are marked with a "*" in the table). As mentioned in the Introduction, life cycles have been described of only about 42 species, this means almost a quarter of the known scyphozoan species. The order with more species with known life cycles is Coronatae (16 spp.), followed by Semaestomeae (14 spp.), the last being Rhizostomeae (12 spp.).

Order Rhizostomeae

Phyllorhiza punctata von Lendenfeld, 1884

Seven specimens (Figure 2), found in the waters of CES (salinity 20-24‰; temperature 28°C) measuring 1.5-2.5 mm in diameter when collected, were reared for 54 days. Their tissues were filled with zooxanthellae, and they presented 8 lobes with rounded lappets and 4 gastric filaments; some specimens had small warts on the exumbrella. By the 7th day (Figure 3), the marginal lappets started to grow between the lobes, and the manubrium became more elongated. By the 10th day the oral arms showed the first signs of oral tentacles and began to bifurcate. On the 40th day the mouth closed and the exumbrellar warts were more conspicuous.

These ephyrae were identified as *Phyllorhiza punctata* by the presence of zooxanthellae and the white warts on the exumbrella. In the same period that the studied specimens were found, large medusae were also present in the area. Ephyrae obtained from laboratory cultures measured 1.5 mm when detached from the scyphistomae, suggesting that the specimens collected in the plankton tows had been newly released. Although recent articles (Garcia, 1990; Rippingale & Kelly, 1995) mention the occurrence of the ephyrae stage of *P. punctata*, until now there is no morphological description of it in the literature. D'Ambra *et al.* (2001) commented on the flow and prey capture of young *P. punctata* (1.4-7.4 cm in diameter).

Order Semaestomeae

Chrysaora lactea Eschscholtz, 1829

One ephyra (Figure 4a) was found in SSC (salinity: 34‰; temperature 20.8°C), and reared for 38 days. When collected it had a transparent body, was 1.2 mm in diameter, had a manubrium with red pigment spots, pointed lappets (3

lappets were probably damaged during collecting, regenerated during the first week), and nematocyst clusters at the base of each marginal lappet (*i.e.*, in the typical *Chrysaora*-pattern, cf. Russell, 1970; Gershwin & Collins, 2002). From days 10-19 the beginning of the 8 marginal tentacles were noted, and from days 20-29 the pigmentation of the manubrium became pale and smaller (Figure 5). From days 30-37, 5-9 gastric filaments were observed in each quadrant. At the 38th day the young medusa reached a diameter of 2 cm and the manubrium a length of 4 cm (Figure 6). At this stage, secondary tentacle buds were observed growing from below the lappets (Figure 7), totaling 24 tentacles.

The number of tentacles and the nematocyst clusters arranged in a pattern are diagnostic characters of *Chrysaora*; as the only species of the genus that occurs on the Brazilian coast is *Chrysaora lactea*, the specimen is identified as that. With this, secondary tentacles arising below the marginal lappets are diagnostic characters of *C. lactea*. The ephyrae obtained in the laboratory from mature medusae of *C. lactea* collected at CES were identical to the nature-collected specimen, except for the lack of pigmentation (Figure 4b). Calder (1972) noted that ephyra of *C. quinquecirrha* obtained from scyphistomae raised in the laboratory had no pigmentation. Little information on the biology of the species exists. Mianzan (1989a, 1989b) mentioned that some ephyrae of *C. lactea* were collected in plankton tows along the Argentinean coast.

Pelagia Péron & Lesueur, 1810

One ephyra (Figure 8), found in the waters of SSC (salinity: 34-36‰; temperature: 20.5°C), had a diameter of 2.4 mm when collected. It was reared for 76 days. In the laboratory, from days 1-19, it acquired 2 gastric filaments, 4 milky spots on the stomach, red pigment on the manubrium and nematocyst clusters around the central disk. From days 20-39, 2 marginal tentacles and 4-5 gastric filaments on each quadrant developed, the manubrium attained a length of 4.3 mm, and warts on the umbrella and manubrium (Figure 9) were visible; at the same time the milky spots on the stomach disappeared. From days 40-70 many gastric filaments (up to 10 in each quadrant) were observed in each quadrant, the number of warts increasing. On the 76th day, the young medusa was 3 cm in diameter, the manubrium was 5.3 cm long, there were 8 tentacles and the beginning of the gonads was noted.

The long rearing period (compared to the *Chrysaora* ephyra) and the appearance of gonadal tissue indicate that the specimen had achieved the maximum number of tentacles (totaling 8). The presence of 8 marginal tentacles is diagnostic for the genus *Pelagia*. Nevertheless, specific identification was hindered due to the small size of the medusa. For the Brazilian coast, the species *Pelagia noctiluca* (Forskål, 1775) is reported off the Pernambuco and Santa Catarina states (Migotto *et al.*, 2002).

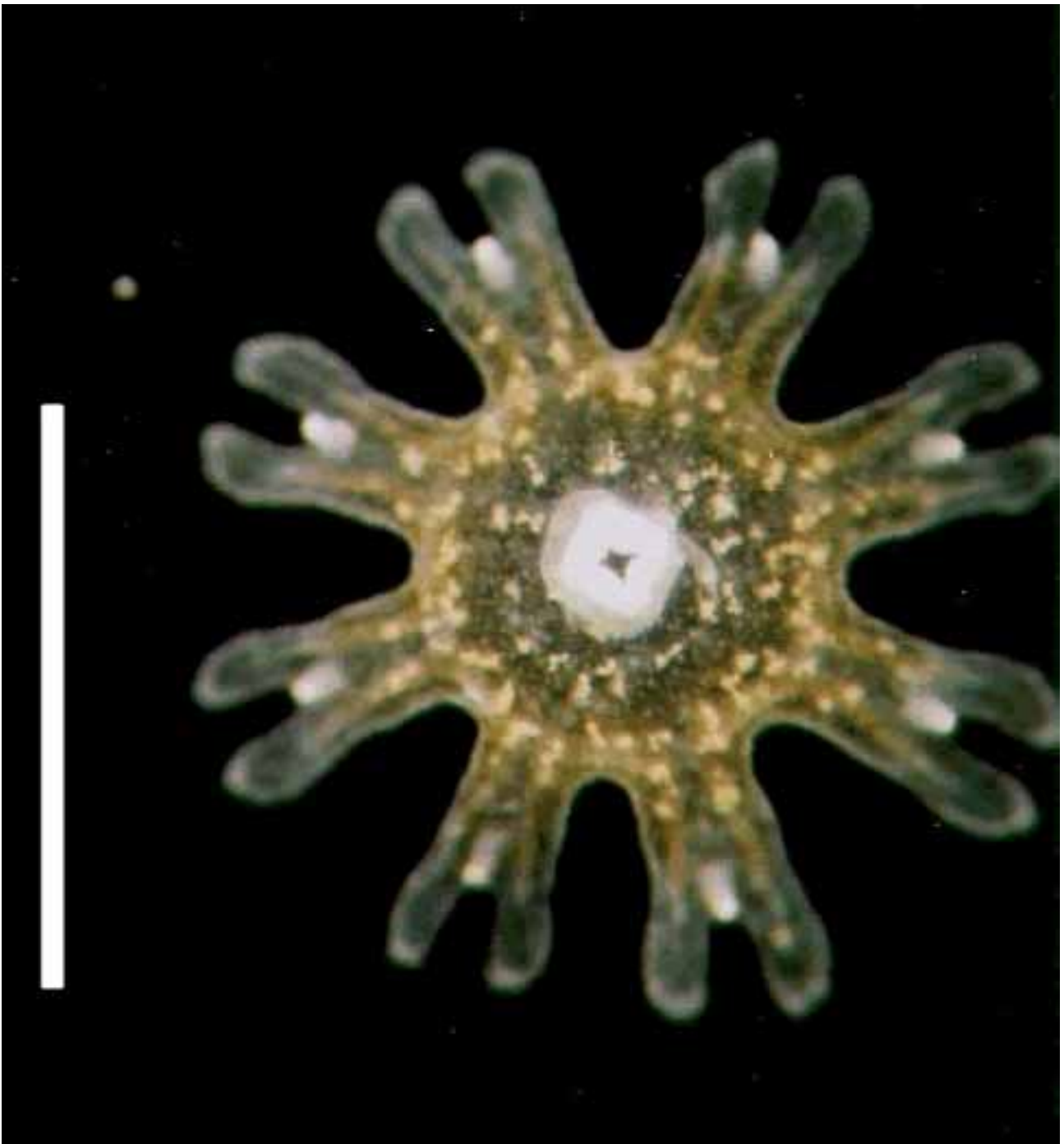


Figure 2. Oral view of ephyra of *Phyllorhiza punctata* von Lendenfeld, 1884, collected in the Cananéia lagoon estuarine system in January 2002, two days after collecting. Note the zooxanthellae and rounded lappets. Scale bar = 1 mm.



Figure 3. Oral view of ephyra of *Phyllorhiza punctata* von Lendenfeld, 1884, collected in the Cananéia lagoon estuarine system in April 2001, seven days after collecting. Note the zooxanthellae, the beginning of lappet formation and the exumbrellar warts. Scale bar = 1 mm

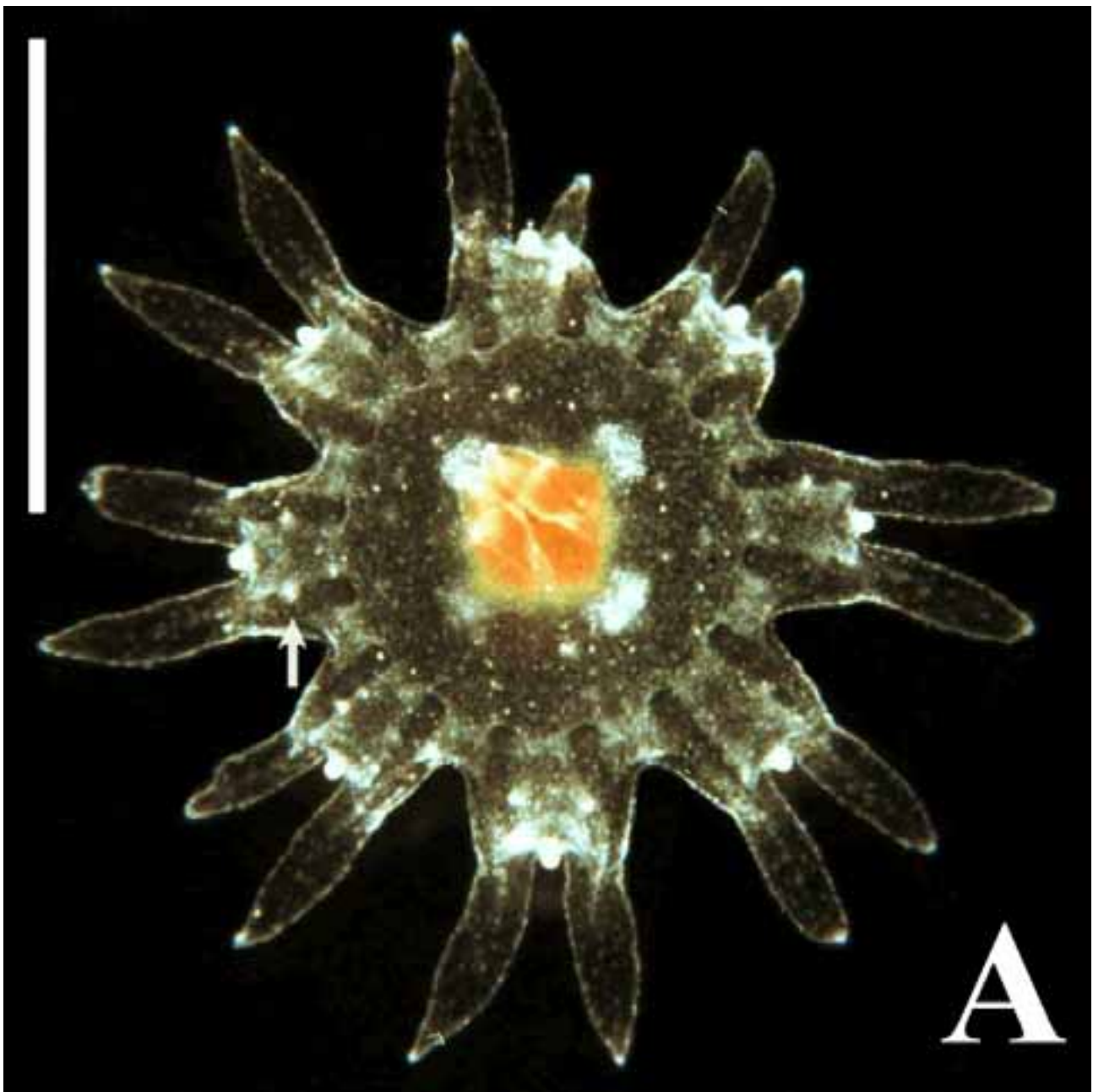


Figure 4. A. Oral view of ephyra of *Chrysaora lactea* Eschscholtz, 1829, collected in the São Sebastião Channel in August 1999, two days after collecting. Note the red pigment on the manubrium, the nematocyst clusters (arrows) and the pointed lappets. Scale bar = 1 mm. **B.** Oral view of just released ephyra of *Chrysaora lactea* Eschscholtz, 1829, from laboratory cultures. Note the absence of pigmentation, and the nematocyst clusters (arrows). Scale bar = 1 mm

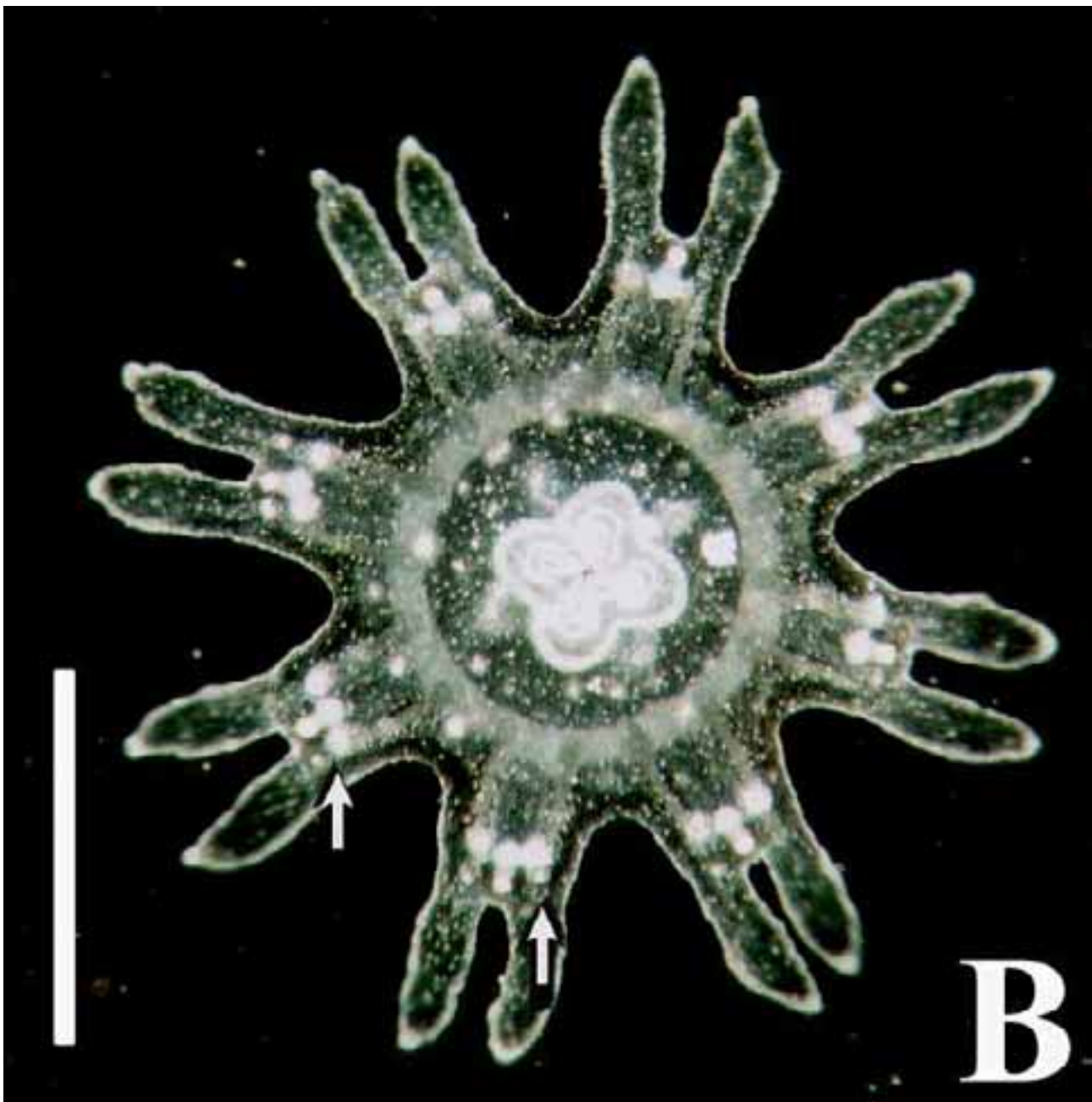


Figure 4. **A.** Oral view of ephyra of *Chrysaora lactea* Eschscholtz, 1829, collected in the São Sebastião Channel in August 1999, two days after collecting. Note the red pigment on the manubrium, the nematocyst clusters (arrows) and the pointed lappets. Scale bar = 1 mm. **B.** Oral view of just released ephyra of *Chrysaora lactea* Eschscholtz, 1829, from laboratory cultures. Note the absence of pigmentation, and the nematocyst clusters (arrows). Scale bar = 1 mm



Figure 5. Oral view of ephyra of *Chrysaora lactea* Eschscholtz, 1829, collected in the São Sebastião Channel in August 1999, 26 days after collecting. Note the absence of red pigment on the manubrium and the already developed primary tentacles. Scale bar = 2 mm.



Figure 6. Lateral view of young medusa of *Chrysaora lactea* Eschscholtz, 1829, collected in the São Sebastião Channel in August 1999, 32 days after collecting. Note the elongated manubrium, , there was food in the manubrium and stomach. Scale bar = 1 cm.

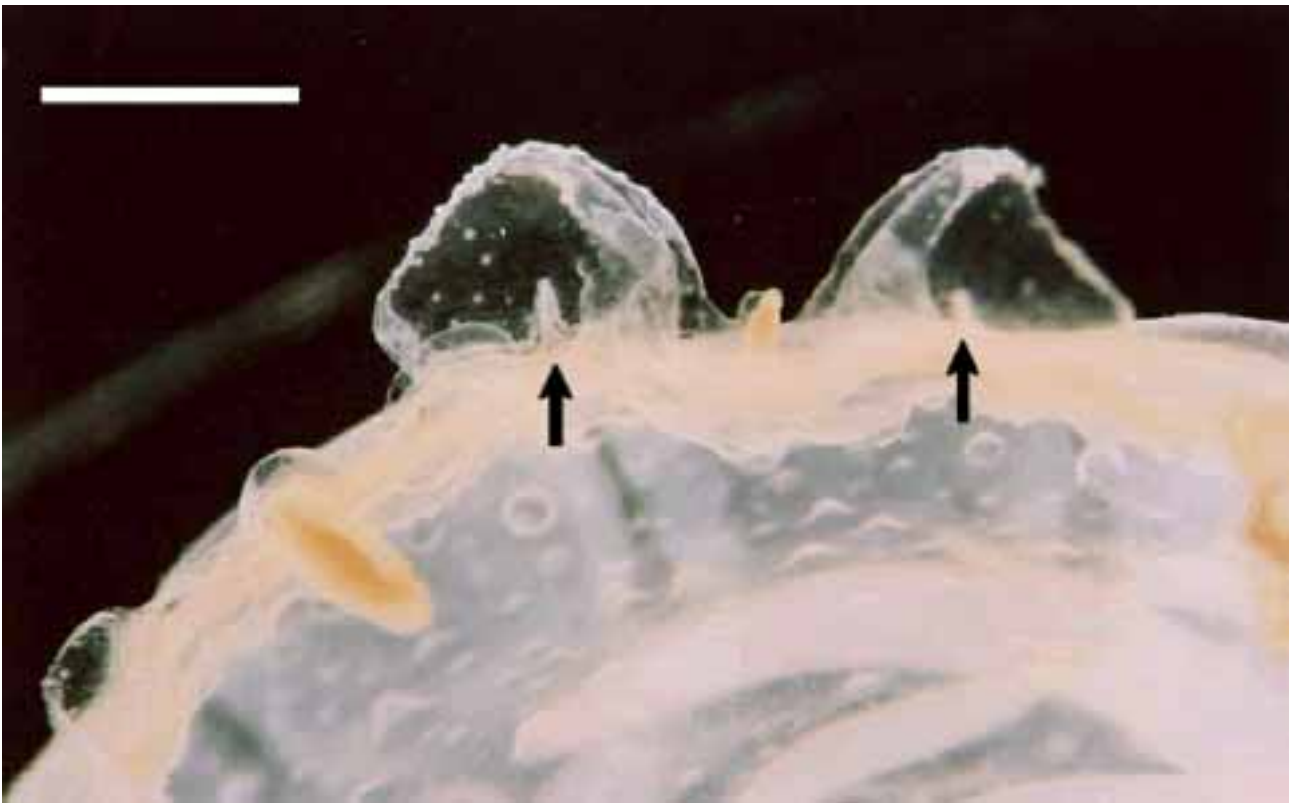


Figure 7. Detail of umbrella margin of preserved young medusa of *Chrysaora lactea* Eschscholtz, 1829, collected in the São Sebastião Channel in August 1999, 38 days after collecting. Note the small secondary tentacles arising from below the marginal lappets (arrows). Scale bar = 2.5 mm.



Figure 8. Lateral view of ephyra, upstroke, of *Pelagia Péron & Lesueur, 1810*, collected in the São Sebastião Channel in October 1999, nine days after collecting. Note pointed lappets. Scale bar = 2 mm.

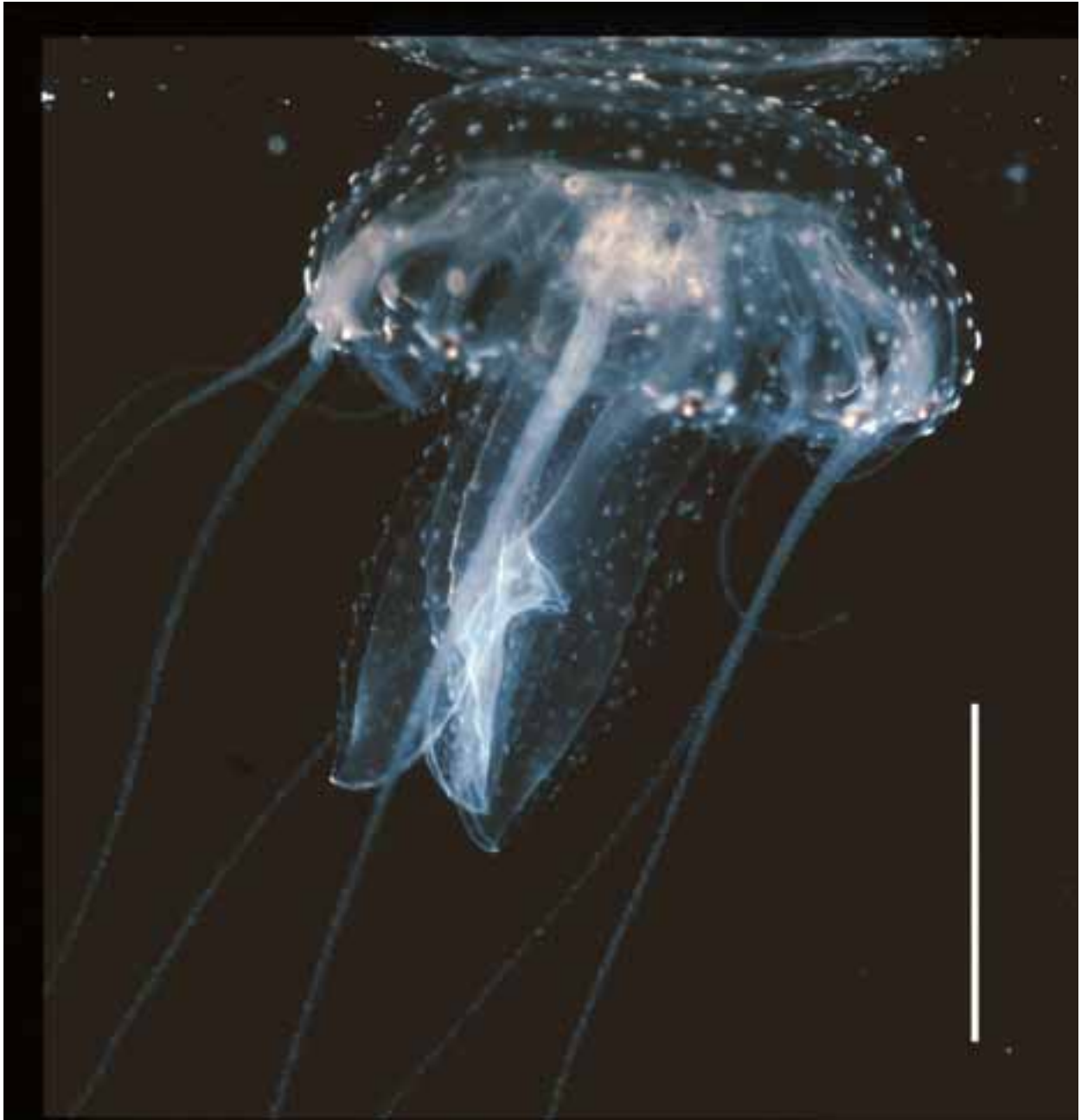


Figure 9. Lateral view of a young medusa of *Pelagia Péron & Lesueur, 1810*, collected in the São Sebastião Channel in October 1999, 35 days after collecting. Note the warts on the umbrella and manubrium. Scale bar = 3 mm.



Figure 10. Lateral view of a young medusa of *Pelagia Péron & Lesueur*, 1810, sampled in the São Sebastião Channel in October 1999, 71 days after collecting. Note the elongated manubrium. Scale bar = 2 cm.

Acknowledgements

We are grateful to Dr Fábio L. da Silveira (IB-USP, Brazil) for assistance and the critical reading of the manuscript. We also thank the Departamento de Zoologia (IB-USP), Instituto Oceanográfico da Universidade de São Paulo (IO-USP), and Centro de Biologia Marinha (CEBIMar-USP) for providing collecting and logistic support. Dr. H.W. Mianzan (INIDEP, Argentina) and MSc. A. Lindner (Duke University, USA) provided important literature. VBT and AEM had financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and from CAPES/DS/PROAP. ACM received financial support from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 99/05374-7).

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Title: On the occurrence of scyphozoan ephyrae (Cnidaria, Scyphozoa, Semaestomeae and Rhizostomeae) in the southeastern Brazilian coast

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Biota Neotropica, Vol. 2 (number 2): 2002

<http://www.biotaneotropica.org.br/v2n2/pt/abstract?article+BN02102022002>

Date Received 07/04/2002

Revised 08/03/2002

Accepted 10/02/2002

ISSN 1676-0611