

TAXONOMY AND NOMENCLATURE

Species of *Lensia* (Cnidaria: Hydrozoa: Siphonophorae) from southeastern Brazilian waters

Eric Y. Nishiyama^{1*}, Enilma M. Araujo² & Otto M.P. Oliveira¹

¹Centro de Ciências Naturais e Humanas, Universidade Federal do ABC. Rua Arcturus 03, Jardim Antares, 09606-070 São Bernardo do Campo, SP, Brazil.

²Faculdade Pitágoras de Feira de Santana. Avenida Senhor dos Passos 222, Centro, 44001-800 Feira de Santana, BA, Brazil.

*Corresponding author. E-mail: ericukihiro@gmail.com

ABSTRACT. The siphonophores of the Brazilian coast are poorly studied, despite their abundance and ecological importance. *Lensia* is the most diverse genus within Siphonophora, with twenty-six valid species. A total of twenty species of *Lensia* are recorded for South American marine waters. This study presents morphological descriptions and an identification key to the species of *Lensia* that were collected in two oceanographic campaigns throughout the southeastern Brazilian coast. A total of sixty-one specimens were photographed, described, schematized and measured, and fifteen species of *Lensia* were identified.

KEY WORDS. Diphyidae; nectophores; siphonophores; taxonomy.

Siphonophores are a group of cnidarians belonging to the class Hydrozoa (subphylum Medusozoa). They are exclusively marine and mostly holoplanktonic organisms (TOTTON 1965). Their body structure, consisting of polypoid and medusoid zooids with varied functions, is interpreted by many authors as a sophisticated version of a colonial life style (HAECKEL 1869, MACKIE 1963).

Although often overlooked or underestimated in macroplankton samplings, siphonophores are amongst the most abundant and efficient carnivorous animals in the oceans (HADDOCK & DUNN 2005). In view of their abundance, these organisms have great ecological importance (PUGH 1999), and may affect, by predation, the supply of copepods, which also feeds economically important fish species (PAGÈS et al. 2001).

Siphonophores have been traditionally divided into three groups: Cystonectae, characterized by the presence of a pneumatophore and absence of nectophores; Physonectae, characterized by the presence of both a pneumatophore and nectophores; and Calyphorae, characterized by the presence of nectophores and absence of a pneumatophore (TOTTON 1965, PUGH 1999, MAPSTONE 2014).

The majority of known siphonophore species form small rocket-shaped colonies, rarely exceeding 20 cm in total length (GROSSMANN et al. 2014). Most of these species belong to the calyphoran family Diphyidae Quoy & Gaimard, 1827 (MAPSTONE & SCHUCHERT 2015). *Lensia* Totton, 1932, composed of small diphyid calyphoran siphonophores, is one of the most

species-rich genera within the Siphonophora. These diphyid siphonophores have a complex life cycle, composed of multiple different life stages that share few morphological similarities (GROSSMANN et al. 2014).

The largest life stage, which may also be the most durable, is the polygastric stage, usually composed of two large zooids, the anterior and the posterior nectophores, and a siphosomal stem containing many cormidia. The cormidia, composed of gonads, a stomach (gastrozooid) and tentacle, and a protective shield (bract), are released from the posterior end of the polygastric stage in several diphyid species, to form free-living sexual units, called “eudoxids”. In calyphoran siphonophores, identification is commonly, and sometimes exclusively, associated with the morphology of the anterior nectophore of the polygastric stage (GROSSMANN et al. 2014).

The species of the genus *Lensia* belong to the suborder Calyphorae and the family Diphyidae, which contains the greatest number of siphonophore species. This family presents a polygastric stage usually including two serially arranged nectophores (KIRKPATRICK & PUGH 1984). The nectophores are asexual medusoid structures, which contain a muscular structure known as the nectosac, and an opening known as the ostium. Strong contractions of the nectosac force water out of the nectophore, through the ostium, and propels the colony forwards, or in some cases the ostium is directed forwards to allow backward swimming (MACKIE 1964).

The anterior nectophore presents a somatocyst, while the posterior nectophore lacks this structure. The somatocyst usually contains oil droplets that may help controlling the flotation of the colony, and also act as a food store. The nectosac occupies most of the nectophore's length, allowing for fast and active swimming (KIRKPATRICK & PUGH 1984). Additionally, the siphosomal stem can be totally withdrawn into an external hollowed-out chamber known as hydroecium (MAPSTONE 2009, 2014), which is usually reduced in the anterior nectophore (PUGH 1999) (Fig. 1).

Lensia includes the Calycophorae, whose anterior nectophores of the polygastric stage are pentagonal, and may contain up to 15 or more longitudinal ridges. The somatocyst is usually small. The hydroecium is shallow and bordered by a short and divided mouth plate. The radial canals do not possess commissures. The nectosac almost reaches the top of the nectophore (ALVARINO & WOJTAN 1984).

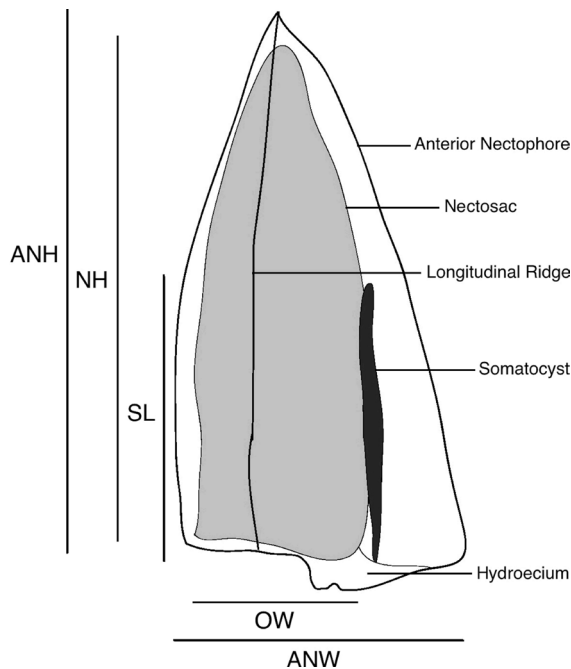


Figure 1. Scheme indicating the main measurements taken and some of the most characteristic structures of the anterior nectophore of specimens of *Lensia*. (ANH) Anterior nectophore height, (ANW) anterior nectophore width, (NH) nectosac height, (OW) ostium width, (SL) somatocyst length.

The posterior nectophores, when present, are fragile and are smaller than the anterior nectophores, being truncated proximally, with a rounded and undivided mouth plate, and no ostial teeth (BOUILLON et al. 2006). The bracts, present in the eudoxids, are structurally simple and helmet-shaped. A special nectophore is absent and the gonophores are truncated at the anterior region, with a small and rounded mouth plate (TOTTON 1965).

Siphonophores are poorly studied due to the extreme difficulty in collecting and preserving specimens, as most of them are found only in deep waters and are very fragile (DUNN et al. 2005). According to OLIVEIRA et al. (2016), twenty species of *Lensia* are found along the South American coast, fifteen of them occurring in Southeastern and Southern Brazilian waters (NISHIYAMA et al. 2016). In this study, we discuss these species of *Lensia* obtained from two oceanographic campaigns made throughout the southwestern Atlantic Ocean.

MATERIAL AND METHODS

The studied specimens were obtained from two oceanographic campaigns made along the southeastern Brazilian coast (FINEP III and Habitats Project). The FINEP III campaign was conducted between Cabo Frio, Rio de Janeiro (23°S) and the south region of Santa Marta Grande Cape, Santa Catarina (29°S), in May 1976. The Habitats Project campaign was conducted in the Campos Basin, Rio de Janeiro (located between 24°S and 20.5°S), from February 2009 to February 2010 (BONECKER et al. 2014). Specimens were conserved in 4% formaldehyde solution and dyed with fuchsine. The anterior nectophores of the analyzed specimens were placed on a hollowed-out microscope slide, and were photographed using a stereomicroscope with digital camera attached (Figs. 2-16). After photographs were taken, the specimens were identified using identification keys and descriptions available (e.g., TOTTON 1965, KIRKPATRICK & PUGH 1984, PAGES & GILI 1992, PUGH 1999). Morphological descriptions of the anterior nectophores of the identified species were made, as well as drawings of the best-preserved specimens using the Adobe Illustrator software (Figs. 17-31). Additionally, all examined specimens were measured using the AxioVision software (Table 1).

Table 1. Measure intervals (mm) of the fifteen species of *Lensia* examined (numbers in parenthesis refer to the quantity of specimens measured). (ANH) Anterior nectophore height, (ANW) anterior nectophore width, (NH) nectosac height, (OW) ostium width, (SL) somatocyst length.

Species	ANH	ANW	NH	OW	SL
<i>L. campanella</i> (6)	2-2.67	1.12-1.58	1.88-2.63	0.47-0.81	0.32-0.72
<i>L. conoidea</i> (5)	5.26-8.56	2.55-4.07	4.74-7.94	1.79-2.59	2.05-4.15
<i>L. cossack</i> (9)	1.82-4.86	1.23-3	1.77-4.53	0.83-1.83	0.28-1.36
<i>L. fowleri</i> (1)	6.31	1.92	5.79	1.44	0.45
<i>L. grimaldii</i> (1)	7.43	3.71	7.06	2.56	0.71
<i>L. hardy</i> (1)	4.73	2.06	4.27	1.12	0.33
<i>L. havock</i> (3)	5.8-11.29	3.29-5.79	5.43-10.94	2.7-4.41	1.1-2.56
<i>L. hotspur</i> (2)	5.32-7.34	3-3.14	4.88-6.71	1.66-2.43	0.58-0.7
<i>L. hunter</i> (2)	9.15-12.43	4.74-5.11	8.89-11.78	3.18-4.27	1.9
<i>L. leloupi</i> (1)	4.26	2.05	3.86	1.26	1.25
<i>L. lelouvetau</i> (1)	6.72	3.96	6.36	3.11	0.32
<i>L. meteyri</i> (7)	2.18-3.49	1.19-2.36	2.27-3.27	0.73-1.91	0.29-0.61
<i>L. multicristata</i> (2)	4.12-8.37	1.77-3.71	3.89-7.91	1.36-2.68	1.83-3.56
<i>L. subtilis</i> (4)	1.67-2.56	1.03-1.55	1.45-2.34	0.79-0.86	0.53-1.11
<i>L. subtiloides</i> (16)	1.91-4.79	1.14-2.58	1.80-4.43	0.88-1.67	0.32-0.65

Glossary of terminology

Anterior nectophore: Upper nectophore in diphyid calycophorans with two serially arranged nectophores.

Bract: Asexual zooid present in most calycophorans, which functions as a shield for the other zooids.

Cormidium: Group of serially repeated zooids on the siphosomal stem. It is usually composed of gonads, gastrozooids, tentacles and bracts.

Distal lamella: Slim extension from the ostial region of the anterior and posterior nectophores in several diphyid calycophorans. It is usually divided into two lappets in the anterior nectophore. Also designated as “mouth plate” in diphyid calycophorans.

Eudoxid: Free-living sexual stage in the life cycle of most calycophorans. It originates as a cormidium detached from the posterior end of the siphosomal stem. It is composed of bract, gastrozooid, and gonophore.

Gastrozooid: Asexual zooid responsible for feeding, present in the cormidia and the eudoxids.

Hydroecium: Hollowed out external cavity on the proximal or lower surface of a calycophoran nectophore. It houses the siphosomal stem.

Longitudinal ridge: Line that runs along the nectophore, usually from its apex to its base.

Lower-basal facet: Lower surface of the anterior nectophore.

Mouth plate: See “distal lamella”.

Nectophore: Asexual medusoid structure responsible for swimming, containing the muscular nectosac for propulsion.

Nectosac: Internal cavity of the nectophore with an opening (ostium) and muscular walls. It contracts rhythmically to pump out water for colony propulsion.

Ostium: Distal opening of the nectosac.

Pneumatophore: Anterior gas-filled structure in physonect and cystonect siphonophores, responsible for the flotation of the colony.

Polygastric stage: Dominant asexual stage in the life cycle of a siphonophore. Also known as the colony.

Posterior nectophore: Lower nectophore in diphyid calycophorans with two serially arranged nectophores.

Radial canal: Gastrovascular canal present in the nectosac.

Siphosomal stem: Region of the colony bearing the cormidia.

Somatocyst: Structure associated with the gastrovascular system, which may aid in flotation and nutrient storage.

Special nectophore: Asexual nectophore present in eudoxids of some calycophorans, with propulsive function.

Tentacle: Structure arising from the gastrozooid, responsible for prey capture.

Zooid: Unit homologous to a solitary, free-living animal, which forms the siphonophore colony. It may be of polypoid or medusoid origin.

TAXONOMY

A total of sixty one specimens were analyzed, and fifteen species of *Lensia* from Brazilian waters were identified. All identified species had been previously recorded for the southwestern Atlantic Ocean (NISHIYAMA et al. 2016). The morphological descriptions were consistent with the literature, with the exception of some specimens that were damaged or poorly preserved. In those cases, some structures could not be easily distinguished and were not described or measured. For some species, there was only one specimen available, which was damaged, making the observation of some structures difficult. Most species were easily identified by the presence of remarkable structures, such as the varied shape of the somatocyst, the number of longitudinal ridges and the position of the hydroecium and the somatocyst in relation to the ostium. Species descriptions follow the terminology used by HADDOCK et al. (2005) and MAPSTONE (2009), contrasting with the old terminology used to name the longitudinal ridges axes in NISHIYAMA et al. (2016).

Identification key to fifteen species of *Lensia* from southeastern Brazilian waters

1. Absence of longitudinal ridges2
- 1'. Presence of longitudinal ridges.....3
2. Somatocyst globular on long stalk *Lensia subtilis*
- 2'. Somatocyst globular or laterally expanded on short stalk
..... *Lensia meteorii*
3. Up to seven longitudinal ridges.....4
- 3'. More than seven longitudinal ridges.....5
4. Less than seven longitudinal ridges.....6
- 4'. Seven longitudinal ridges7
5. Lateral ridges do not extend below velar ridge, club-shaped somatocyst *Lensia grimaldii*
- 5'. Lateral ridges extend below velar ridge, kidney-shaped somatocyst..... *Lensia lelouvetreau*
6. Five straight, distinct longitudinal ridges.....8
- 6'. Five indistinct longitudinal ridges.....9
7. Lower-lateral ridges bend basally onto mouth plate.....
..... *Lensia havock*
- 7'. Lower-lateral ridges do not bend basally onto mouth plate.
.....10
8. Base of somatocyst above level of the ostium11
- 8'. Base of somatocyst below or at same level of the ostium .12
9. Apex of the nectophore twisted *Lensia campanella*
- 9'. Apex of the nectophore not twisted *Lensia cossack*
10. Somatocyst short and bilobed *Lensia hunter*
- 10'. Somatocyst long and filiform *Lensia multicristata*
11. Somatocyst filiform *Lensia leloupi*
- 11'. Somatocyst club-shaped and slightly bent
..... *Lensia subtiloides*

12. Somatocyst spherical 13
12'. Somatocyst not spherical..... 14
13. Somatocyst located above level of ostium..... *Lensia hardy*
13'. Somatocyst located completely below level of ostium.....
.....*Lensia fowleri*
14. Somatocyst spindle-shaped and about 1/2 the height of the
nectophore.....*Lensia conoidea*
14'. Somatocyst ovate and obliquely inclined*Lensia hotspur*

Phylum Cnidaria Hatschek, 1888

Subphylum Medusozoa Petersen, 1979

Class Hydrozoa Owen, 1843

Order Siphonophorae Eschscholtz, 1829

Diphyidae Quoy & Gaimard, 1827

***Lensia* Totton, 1932**

***Lensia campanella* (Moser, 1917)**

Figs. 2, 17

Galeolaria campanella Moser, 1917: 728.

Lensia campanella petrovskiy Alekseev, 1984: 968.

Lensia eugenioi Alvarino & Wojtan, 1984: 49.

Lensia roomwali Daniel, 1971: 149.

Description. Anterior nectophore: Laterally compressed and measures 2.38 mm in height and 1.33 mm in width. The apex is slightly twisted and obtuse. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 1/2 the width of the nectophore. The mouth plates are small, divided and rounded. The longitudinal ridges are barely visible. The lower-basal facet is bent towards the lower facet of the nectophore at an angle of approximately 45°. The hydroecium is very shallow. The somatocyst is short, ovate, bent slightly toward the lower nectophore surface and measures approximately 1/4 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 5:45 a.m., 2721 m depth, 24°24.8'S-41°07.5'W), one specimen preserved in 4% formaldehyde, 05/09/76, collected by FINEP III campaign, station 1701 leg., LabGel (UFABC); Cabo Frio (collected at 1:00 a.m., 1120 m depth, 23°55.5'S-41°43.0'W), three specimens preserved in 4% formaldehyde, 05/10/76, collected by FINEP III campaign, station 1708 leg., ZUEC CNI 46, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP). *Santa Catarina*: Cabo de Santa Marta Grande (collected at 5:00 a.m., 64 m depth, 25°13.6'S-46°42.2'W), two specimens preserved in 4% formaldehyde, 05/19/76, collected by FINEP III campaign, station 1770 leg., LabGel (UFABC).

Geographic distribution: This species occurs in tropical regions of the Atlantic, Pacific and Indian Oceans (DANIEL 1974), and in the Mediterranean Sea (ALVARINO 1971). In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (PAGÉS et al. 2001, PALMA & APABLAZA 2004); and in the Atlantic

Ocean, off French Guiana (LELOUP 1934), and from Brazil to Argentina, from 0° to 38°S (ALVARINO 1968, 1971, CORDEIRO & MONTÚ 1991, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species is recognized by its small size, and by the apical end, which is twisted in preserved specimens (TOTTON 1965).

***Lensia conoidea* (Keferstein & Ehlers, 1860)**

Figs. 3, 18

Diphyes conoidea Keferstein & Ehlers, 1860: 259.

Diphyes truncata Sars, 1846: 41.

Epibulia truncata (Sars, 1846): 41.

Lensia truncata (Sars, 1846): 41.

Description. Anterior Nectophore: Large, with five complete longitudinal ridges converging at the apex. It measures 6.81 mm in height and 3.52 mm in width. The basal end of the upper ridge forms a tooth extending below the level of the ostium. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The somatocyst is spindle-shaped, measuring approximately 1/2 the height of the nectophore, reaching the midpoint of the same. The mouth plate is shallow but broad. The hydroecium is basal and very shallow.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 7:15 a.m., 185 m depth, 25°55.2'S-46°00.0'W), one specimen preserved in 4% formaldehyde, 05/20/76, collected by FINEP III campaign, station 1780 leg., LabGel (UFABC); Campos Basin (250 m depth, 200 µm net, South Atlantic Central Water), four specimens preserved in 4% formaldehyde, 03/25/09, collected by Habitats 14 campaign, station F10 leg., ZUEC CNI 47, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution. In South America, it occurs in the Pacific Ocean, in Chile, from 33°S (Valparaíso) to 55°S (Cape Horn) (LELOUP 1932, PALMA 1973, 1977, 1994, PALMA & ROSALES 1997, PALMA et al. 1999, 2007, 2011, ULLOA et al. 2000, PALMA & ARAVENA 2001, VILLENAS et al. 2009); and in the Atlantic Ocean, off French Guiana (LELOUP & HENTSCHEL 1935), from Brazil to Argentina, from 0° to 60°S (LELOUP 1934, LELOUP & HENTSCHEL 1935, ALVARINO 1968, 1971, 1981, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011), and East of Falklands (Malvinas) Islands (HARDY & GUNTHER 1935).

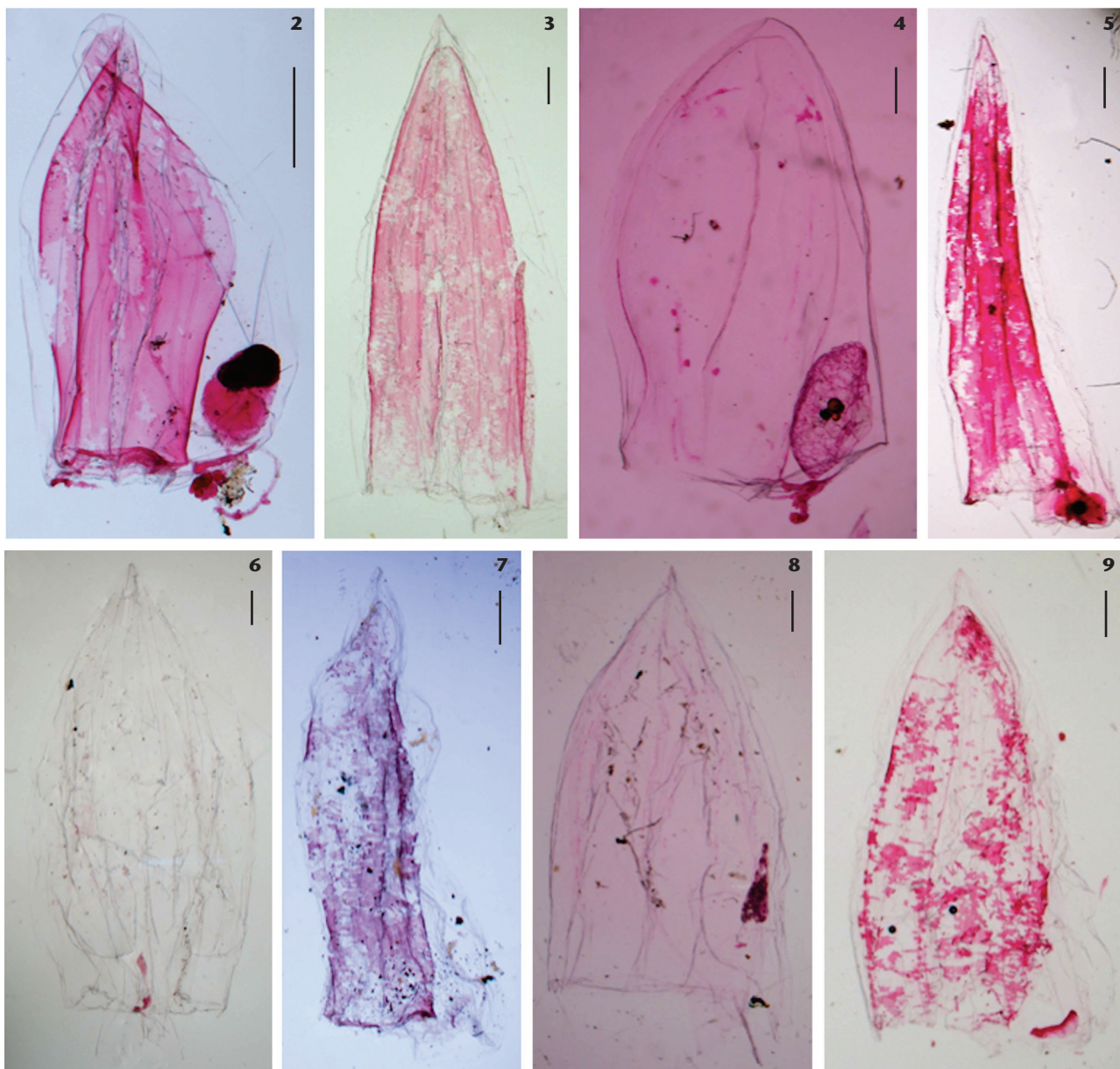
Remarks. This species is distinguished by its large somatocyst, measuring half the height of the nectophore, and its anterior nectophore containing five longitudinal ridges (TOTTON 1965).

***Lensia cossack* Totton, 1941**

Figs. 4, 19

Eudoxia macra Totton, 1954: 118.

Description. Anterior Nectophore: With obtuse apex and turgid appearance. With five incomplete longitudinal ridges: one upper ridge, two lower ridges and two lateral ridges. It measures



Figures 2-9. (2) Lateral view of the anterior nectophore of *Lensia campanella*; (3) lateral view of the anterior nectophore of *Lensia conoidea*; (4) lateral view of the anterior nectophore of *Lensia cossack*; (5) lateral view of the anterior nectophore of *Lensia fowleri*; (6) upper view of the anterior nectophore of *Lensia grimaldii*; (7) lateral view of the anterior nectophore of *Lensia hardy*; (8) lateral view of the anterior nectophore of *Lensia havock*; (9) lateral view of the anterior nectophore of *Lensia hotspur*. Scale bars: 0.5 mm.

4.86 mm in height and 3 mm in width. It has four longitudinal folds, enabling contractions and expansions of the nectophore. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The hydroecium is reduced. The mouth plates are small, with an oblique basal facet. The somatocyst is ovate, oblique and measures approximately 3/10 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 5:45 a.m., 2721 m depth, 24°24.8'S-41°07.5'W), one specimen preserved in 4% formaldehyde, 05/09/76, collected by FINEP III campaign, station 1701 leg., LabGel (UFABC); Cabo Frio (collected at 1:00 a.m., 1120 m depth, 23°55.5'S-41°43.0'W), two specimens preserved in 4% formaldehyde, 05/10/76, collected by FINEP III campaign, station 1708 leg., LabGel (UFABC); Campos Basin (1

m depth, 120 µm net, Tropical Water), one specimen preserved in 4% formaldehyde, 03/23/09, collected by Habitats 14 campaign, station D10 leg., ZUEC CNI 48, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP). *Santa Catarina*: Cabo de Santa Marta Grande (collected at 7:15 a.m., 185 m depth, 25°55.2'S-46°00.0'W), four specimens preserved in 4% formaldehyde, 05/20/76, collected by FINEP III campaign, station 1780 leg., LabGel (UFABC).

Geographic distribution: This species occurs in tropical and subtropical regions of the Atlantic, Pacific and Indian Oceans (DANIEL 1974). In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (PALMA & APABLAZA 2004), and at 33°S off Valparaíso (PALMA & SILVA 2006); and in the Atlantic Ocean, from Brazil to Argentina, from 0° to 42°S (TOTTON 1941, ALVARINO 1968, 1971, 1981, CORDEIRO & MONTÚ 1991, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species is very similar in appearance to *L. campanella*, except for the nectophore apex, which is not twisted in preserved specimens.

Lensia fowleri (Bigelow, 1911)

Figs. 5, 20

Diphyes fowleri Bigelow, 1911: 255.

Eudoxia vasconiensis Patriti, 1965: 23.

Description. Anterior Nectophore: With five complete longitudinal ridges. The lateral ridges bend slightly at their basal ends. It measures 6.31 mm in height and 1.92 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/4 the width of the nectophore. The hydroecium is very shallow. The somatocyst is spherical, with a short stalk, and located completely below the level of the ostium. It measures approximately 1/14 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 6:21 a.m., 24°16.3'S-43°49.1'W), one specimen preserved in 4% formaldehyde, 05/12/76, collected by FINEP III campaign, station 1729 leg., ZUEC CNI 49, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution. In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (PALMA & APABLAZA 2004, APABLAZA & PALMA 2006), at 33°S off Valparaíso (PALMA & SILVA 2006); and in the Atlantic Ocean, off French Guiana (LELOUP 1934), and from Brazil to Argentina, from 0° to 45°S (LELOUP & HENTSCHEL 1935, ALVARINO 1971, 1981, PUGH, 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species is very similar to *L. hardy* (TOTTON 1965). It can be distinguished by the somatocyst located completely below the level of the ostium.

Lensia grimaldii Leloup, 1933

Figs. 6, 21

Lensia multicristata forme *grimaldii* Leloup, 1933: 37.

Description. Anterior Nectophore: With a variable number of longitudinal ridges. Only the two lower ridges are complete,

and only five ridges reach the apex. The upper-lateral ridges bend towards the upper surface at their basal ends and bifurcate, forming the velar ridge. It measures 7.43 mm in height and 3.71 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 7/10 the width of the nectophore. The hydroecium is deep, opens as a deep cleft in the narrow lower facet, and this opening extends above the level of the ostium. The somatocyst is club-shaped, has a small stalk, and measures approximately 1/10 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Campos Basin (250 m depth, 200 µm net, South Atlantic Central Water), one specimen preserved in 4% formaldehyde, 08/27/09, collected by Habitats 18 campaign, station D8 leg., ZUEC CNI 50, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution: In South America, it occurs in the Atlantic Ocean, off French Guiana (LELOUP 1934), and in Brazil, from 0° to 34°S (LELOUP & HENTSCHEL 1935, TOTTON 1941, ALVARINO 1971, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species can be recognized by the dorsal bending of the dorso-lateral ridges.

Lensia hardy Totton, 1941

Figs. 7, 22

Anterior Nectophore: With five complete longitudinal ridges. It measures 4.73 mm in height and 2.06 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 1/2 the width of the nectophore. The hydroecium is located below the level of the ostium. The somatocyst is spherical, with a short stalk. It measures approximately 1/14 the height of the nectophore.

Examined material. BRAZIL, *Santa Catarina*: Cabo de Santa Marta Grande (collected at 8:00 a.m., 178 m depth, 28°13.0'S-47°26.5'W), one specimen preserved in 4% formaldehyde, 05/24/76, collected by FINEP III campaign, station 1819 leg., ZUEC CNI 51, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

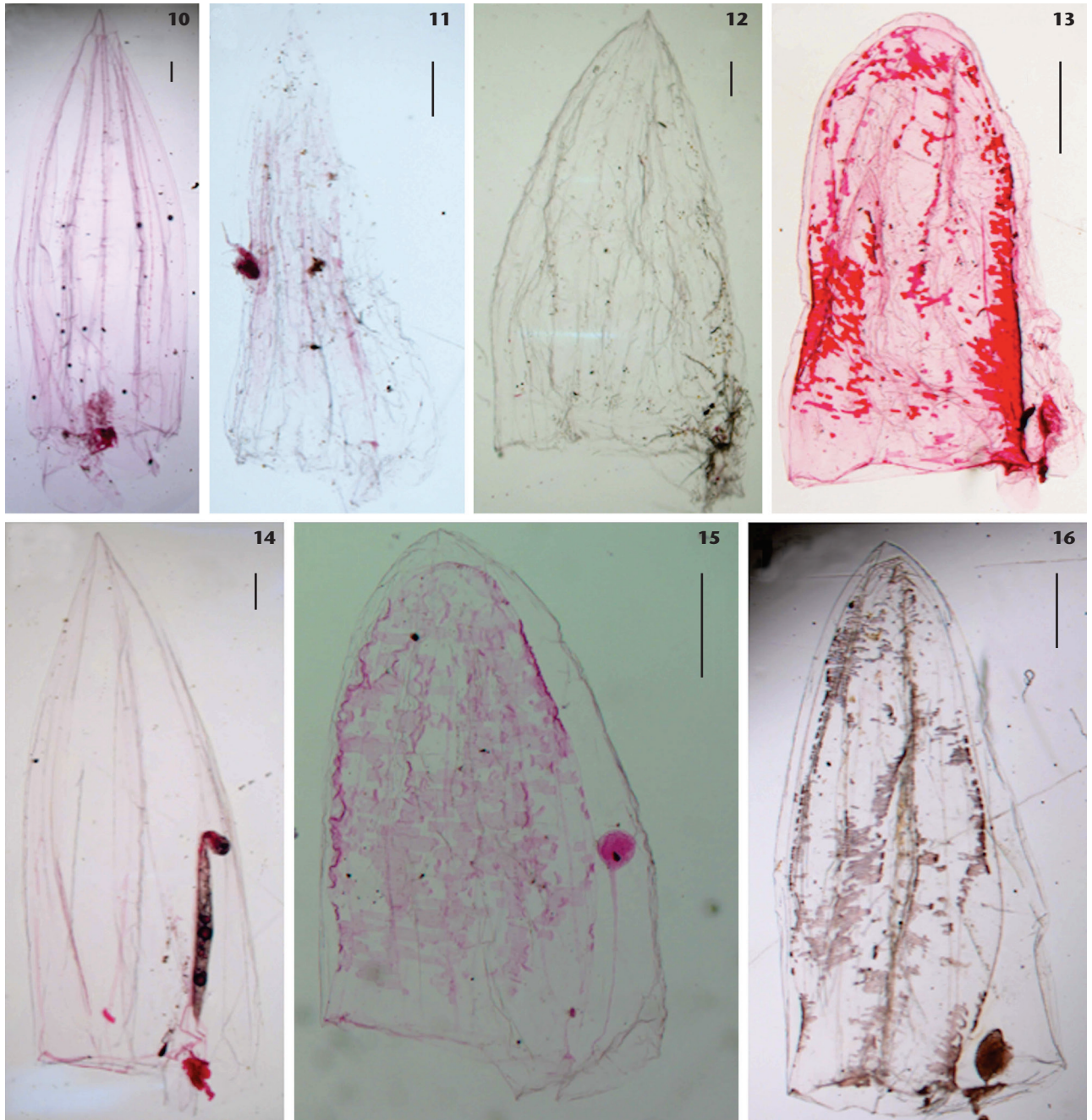
Geographic distribution. In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (APABLAZA & PALMA 2006), at 33°S off Valparaíso (PALMA 1973, 1977); and in the Atlantic Ocean, from Brazil to Argentina, from 0° to 57°S (ALVARINO 1981, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species is very similar to *L. fowleri* (TOTTON 1965), but its somatocyst is located above the level of the ostium.

Lensia havock Totton, 1941

Figs. 8, 23

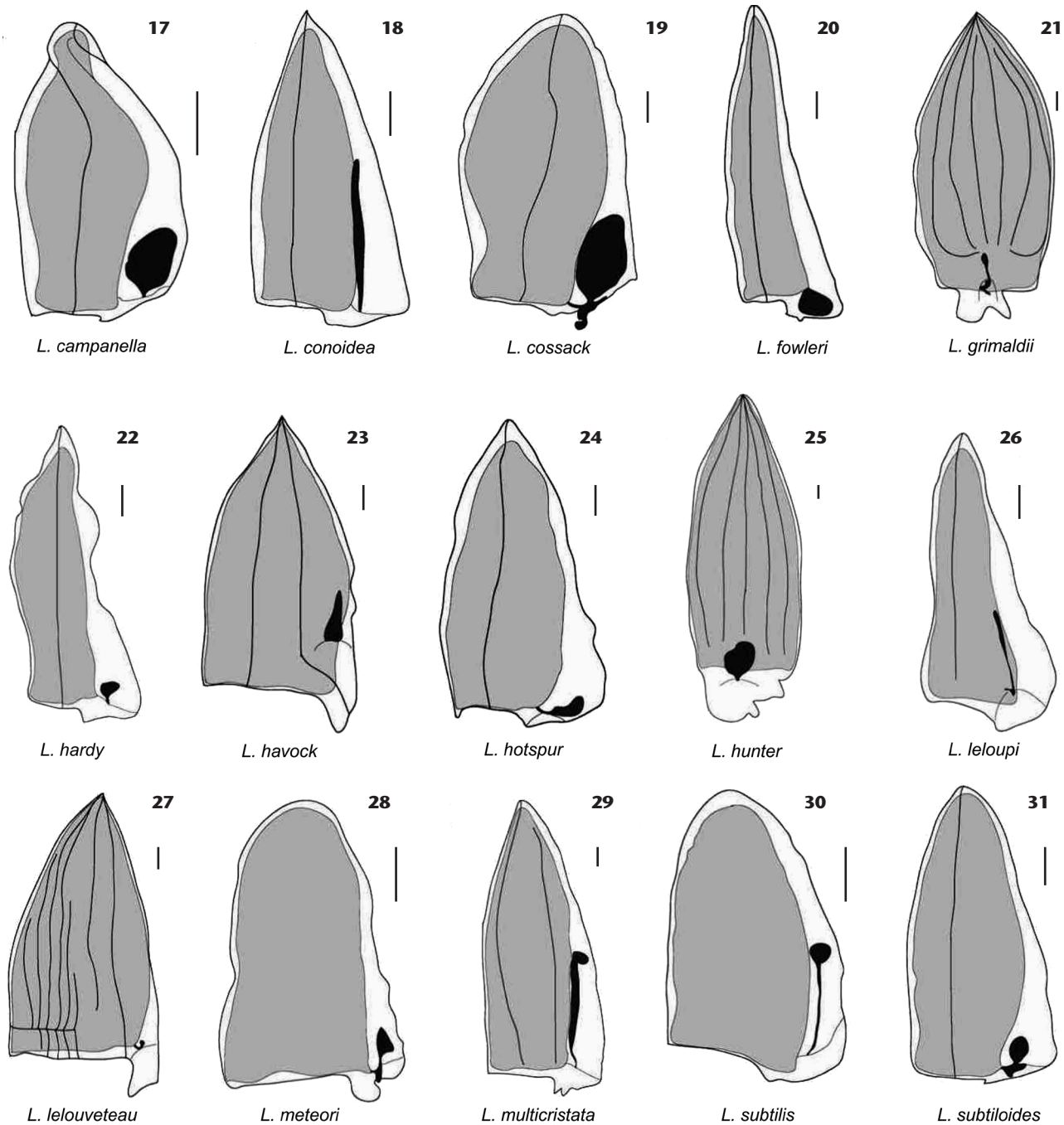
Description. Anterior Nectophore: With seven complete longitudinal ridges, the lower-lateral ridges bending towards the lower surface and passing down onto the mouth plate. It measures 5.8 mm in height and 3.29 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The



Figures 10-16. (10) Lower view of the anterior nectophore of *Lensia hunter*; (11) lateral view of the anterior nectophore of *Lensia leloupi*; (12) lateral view of the anterior nectophore of *Lensia lelouveteau*; (13) lateral view of the anterior nectophore of *Lensia meteori*. (14) lateral view of the anterior nectophore of *Lensia multicristata*; (15) lateral view of the anterior nectophore of *Lensia subtilis*; (16) lateral view of the anterior nectophore of *Lensia subtiloides*. Scale bars: 0.5 mm.

ostium measures approximately 4/5 the width of the nectophore. The hydroecium is deep and extends well above the level of the ostium, and there is a pronounced slit in the lower facet that

extends nearly to the level of the roof of the hydroecium. The somatocyst is short, spindle-shaped and measures approximately 1/5 the height of the nectophore.



Figures 17-31. Comparison of the anterior nectophore morphology of *Lensia* from southeastern Brazilian coast, shown from the same aspects as in Figs. 1-16. Scale bars: 0.5 mm.

Examined material. BRAZIL, *Rio de Janeiro*: Campos Basin (250 m depth, 200 μ m net, South Atlantic Central Water), one specimen preserved in 4% formaldehyde, 03/05/09, collected by Habitats 12 campaign, station A12 leg., ZUEC CNI 52, Museu

de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP); Campos Basin (800 m depth, 120 μ m net, Antarctic Intermediate Water), two specimens preserved in 4% formaldehyde, 08/20/09, collected by Habitats campaign, station A8 leg., LabGel (UFABC).

Geographic distribution. In South America, it occurs in the Atlantic Ocean: Brazil to Argentina, from 0° to 67°S (ALVARIÑO 1981, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. The main characteristics of this species are the hydroecium located above the level of the ostium, and the ventro-lateral ridges bending basally towards the mouth plate.

Lensia hotspur Totton, 1941

Figs. 9, 24

Lensia canopusi Stepanjants, 1977: 72.

Lensia peresi Patriiti, 1970: 103.

Description. Anterior Nectophore: With five complete longitudinal ridges. It measures 5.32 mm in height and 3 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The hydroecium is reduced and located below the level of the ostium, with the hydroecial roof obliquely inclined. The mouth plate is divided into two rounded and slanting lappets. The somatocyst is short, obliquely inclined, ovate, and has a short peduncle. It measures approximately 1/10 the height of the nectophore.

Examined material.

BRAZIL, *Rio de Janeiro*: Campos Basin (250 m depth, 200 µm net, South Atlantic Central Water), two specimens preserved in 4% formaldehyde, 03/18/09, collected by Habitats 12 campaign, station A8 leg., ZUEC CNI 53, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution. This species occurs in tropical regions of the Atlantic (more frequently), Pacific and Indian Oceans (DANIEL 1974). It also occurs in the Mediterranean (PAGÈS & GILI 1992). In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (PALMA & APABLAZA 2004, APABLAZA & PALMA 2006), and at 33°S off Valparaíso (PALMA 1973, 1977, 1994, ULLOA et al. 2000, APABLAZA & PALMA 2006, PALMA & SILVA 2006); and in the Atlantic Ocean, from Brazil to Argentina, from 0° to 43°S (TOTTON 1941, ALVARIÑO 1971, CORDEIRO & MONTÚ 1991, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species is distinguished by the oblique inclination of its somatocyst.

Lensia hunter Totton, 1941

Figs. 10, 25

Description. Anterior Nectophore: With seven straight longitudinal ridges. The upper-lateral ridges do not meet the ostial margin. The lower-laterals do not meet the apex, but curve down and around to meet the lateral edges of the oblique mouth plate. It measures 12.43 mm in height and 5.11 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 4/5 the width of the nectophore. The hydroecium is located below the level of the ostium with the roof curving around gradually to merge

with the lower facet; the lower-lateral ridges both curve around proximally on each side of the hydroecium to meet the lateral edges of the mouth plate. The somatocyst is short, bilobed, and measures approximately 1/7 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Campos Basin (800 m depth, 120 µm net, Antarctic Intermediate Water), one specimen preserved in 4% formaldehyde, 03/05/09, collected by Habitats 12 campaign, station A12 leg., LabGel (UFABC); Campos Basin (800 m depth, 120 µm net, Antarctic Intermediate Water), one specimen preserved in 4% formaldehyde, 08/03/09, collected by Habitats 18 campaign, station C12 leg., ZUEC CNI 54, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution. This species occurs in the Atlantic Ocean. In South America, it occurs from Brazil to Argentina, from 0° to 39°S (ALVARIÑO 1968, 1981, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species can be distinguished by its bilobed somatocyst (TOTTON 1965).

Lensia leloupi Totton, 1954

Figs. 11, 26

Lensia nagabhushanami Daniel, 1971: 150.

Description. Anterior Nectophore: With five straight longitudinal ridges, the laterals not reaching the ostium. It measures 4.26 mm in height and 2.05 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The mouth plate is oblique. The hydroecium is bell-shaped, extending above the level of the ostium. The somatocyst is filiform and measures approximately 1/3 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Campos Basin (250 m depth, 120 µm net, South Atlantic Central Water), one specimen preserved in 4% formaldehyde, 08/20/09, collected by Habitats 18 campaign, station A8 leg., ZUEC CNI 55, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP).

Geographic distribution. In South America, it occurs in the Pacific Ocean, in Colombia, at 7.5°N 78.6°W (ALVARIÑO 1976); and in the Atlantic Ocean, in Brazil, from 0° to 28°S (ALVARIÑO 1968, 1971, CORDEIRO & MONTÚ 1991, PUGH 1999, MIGOTTO et al. 2002).

Remarks. This species resembles *Lensia subtiloides*, but is larger and has a deeper hydroecium (TOTTON 1965).

Lensia lelouvetteau Totton, 1941

Figs. 12, 27

Lensia multicristata forme *grimaldii* Leloup, 1934: 36.

Description. Anterior Nectophore: With groups of longitudinal ridges, most of them complete. It measures 6.72 mm in height and 3.96 mm in width. It has a velar ridge, crossing the longitudinal ridges, and located above the ostium. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 4/5 the width of the nectophore. The lower ridges curve towards the mouth plate at their ostial

ends. The hydroecium is deep and open on the lower surface as a long slit in the lower facet; it also extends above the level of the ostium. The somatocyst is squat and kidney-shaped, measures approximately 1/20 the height of the nectophore, and is very difficult to distinguish.

Examined material. BRAZIL, *Rio de Janeiro*: Campos Basin (800 m depth, 120 µm net, Antarctic Intermediate Water), one specimen preserved in 4% formaldehyde, 08/09/09, collected by Habitats campaign, station C12 leg., ZUEC CNI 56, Museu de Zoologia “Prof. Dr. Adão José Cardoso” (UNICAMP).

Geographic distribution. In South America, it occurs in the Pacific Ocean, in Chile, at 33°S off Valparaíso (ULLOA et al. 2000); and in the Atlantic Ocean, in Brazil, from 0° to 33°S (TOTTON 1941, ALVARINO 1971, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. The presence of a velar ridge and the shape of its somatocyst distinguish this species.

Lensia meteori (Leloup, 1934)

Figs. 13, 28

Galettia meteori Leloup, 1934: 15.

Description. Anterior Nectophore: Delicate, with rounded apex, apparently without longitudinal ridges. It measures 2.61 mm in height and 1.75 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 4/5 the width of the nectophore. The hydroecium is narrow, high, and slants upwards towards the lower surface. The roof of the hydroecium is located above the level of the ostium. The mouth plate is divided into two lappets. The somatocyst is spherical, expanding laterally, with a short stalk, and measures approximately 1/10 the height of the nectophore.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 1:00 a.m., 1120 m depth, 23°55.5'S-41°43.0'W), three specimens preserved in 4% formaldehyde, 05/10/76, collected by FINEP III campaign, station 1708 leg., ZUEC CNI 57, Museu de Zoologia “Prof. Dr. Adão José Cardoso” (UNICAMP); Campos Basin (250 m depth, 120 µm net, South Atlantic Central Water), four specimens preserved in 4% formaldehyde, 03/22/09, collected by Habitats 14 campaign, station D8 leg., LabGel (UFABC).

Geographic distribution. This species occurs in tropical and temperate regions of the Atlantic, Pacific, and Indian Oceans (ALVARINO 1971, DANIEL 1974). In South America, it occurs in the Pacific Ocean, in Chile, at 33°S off Valparaíso (PALMA & ROSALES 1995, ULLOA et al. 2000), and from 47°S to 53°S in the fjords and channels of southern Chile (PALMA et al. 1999); and in the Atlantic Ocean, from Brazil to Argentina, from 0° to 39°S (LELOUP 1934, SEGUIN 1965, ALVARINO 1971, 1981, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. The anterior nectophore of this species is very similar to that of *Lensia subtilis*, except for the almost vertical basal facet, the larger mouth plates, and the short peduncle and laterally expanded shape of the somatocyst (TOTTON 1965).

Lensia multicristata (Moser, 1925)

Figs. 14, 29

Galeolaria multicristata Moser, 1925: 165.

Lensia multicristata forme typica Leloup, 1934: 33.

Description. Anterior Nectophore: Elongate, with seven longitudinal ridges. Neither of the pairs of the laterals reach the ostium, and the lower-lateral pair also do not reach the apex. It measures 8.37 mm in height and 3.71 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 7/10 the width of the nectophore. The hydroecium is relatively shallow, and located below the level of the ostium. The mouth plates are divided, rounded and overlap each other. The somatocyst is long, filiform and measures approximately 2/5 the height of the nectophore, reaching nearly the midpoint of the same.

Examined material. BRAZIL, *Rio de Janeiro*: Cabo Frio (collected at 5:45 a.m., 2721 m depth, 24°24.8'S-41°07.5'W), one specimen preserved in 4% formaldehyde, 05/09/76, collected by FINEP III campaign, station 1701 leg., LabGel (UFABC); Campos Basin (250 m depth, 120 µm net, South Atlantic Central Water), one specimen preserved in 4% formaldehyde, 03/25/09, collected by Habitats 14 campaign, station F10 leg., ZUEC CNI 58, Museu de Zoologia “Prof. Dr. Adão José Cardoso” (UNICAMP).

Geographic distribution: This species is cosmopolitan and distributed in all world's oceans (KIRKPATRICK & PUGH 1984). It occurs in tropical and subtropical regions of the Atlantic, Pacific, and Indian Oceans (DANIEL 1974), and in the Mediterranean (ALVARINO 1971). In South America, it occurs in the Pacific Ocean, in Colombia, from 5°N to 3.1°N, 78.3°W to 79.2°W (ALVARINO 1976), and Chile, at 33°S off Valparaíso (ULLOA et al. 2000, PALMA & SILVA 2006); and in the Atlantic Ocean, off French Guiana (LELOUP 1934, LELOUP & HENTSCHEL 1935), and from Brazil to Argentina, from 0° to 57°S (LELOUP & HENTSCHEL 1935, TOTTON 1954, ALVARINO 1968, 1971, 1981, CORDEIRO & MONTÚ 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species can be recognized by its long, filiform somatocyst, reaching almost half the height of the anterior nectophore in most specimens, and its anterior nectophore, which has seven longitudinal ridges.

Lensia subtilis (Chun, 1886)

Figs. 15, 30

Diphyes subtilis Chun, 1886: 681.

Description. Anterior Nectophore: Conical, laterally compressed, with rounded apex, and apparently without longitudinal ridges. It contains four longitudinal folds and measures 2.56 mm in height and 1.32 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The lower ridges bordering the lower facet are rounded at their proximal ends, and the mouth plate is small and divided, each distal lamella being rounded distally. The roof of the hydroecium

curves obliquely upwards towards the lower facet. The hydroecium is shallow and wide below ostial level. The somatocyst is spherical with a long stalk, and measures approximately 1/4 the height of the nectophore.

Examined material. **BRAZIL**, *Rio de Janeiro*: Cabo Frio (collected at 5:45 a.m., 2721 m depth, 24°24.8'S-41°07.5'W), one specimen preserved in 4% formaldehyde, 05/09/76, collected by FINEP III campaign, station 1701 leg., LabGel (UFABC); Cabo Frio (collected at 1:00 a.m., 1120 m depth, 23°55.5'S-41°43.0'W), one specimen preserved in 4% formaldehyde, 05/10/76, collected by FINEP III campaign, station 1708 leg., LabGel (UFABC); Campos Basin (1200 m depth, 120 µm net, Upper Circumpolar Water), one specimen preserved in 4% formaldehyde, 03/17/09, collected by Habitats 12 campaign, station A10 leg., ZUEC CNI 59, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP). *Santa Catarina*: Cabo de Santa Marta Grande (collected at 12:20 a.m., 1170 m depth, 28°29.0'S-46°46.0'W), one specimen preserved in 4% formaldehyde, 05/24/76, collected by FINEP III campaign, station 1821 leg., LabGel (UFABC).

Geographic distribution. This species occurs in tropical and temperate regions of the Atlantic, Pacific and Indian Oceans (DANIEL 1974), as well as the Mediterranean Sea (ALVARIÑO 1971). In South America, it occurs in the Pacific Ocean, in Chile, at 23°S off Antofagasta (PAGÈS et al. 2001, PALMA & APABLAZA 2004, APABLAZA & PALMA 2006), and at 33°S off Valparaíso (PALMA & ROSALES 1995); and in the Atlantic Ocean, off French Guiana (LELOUP 1934), and from Brazil to Argentina, from 0° to 48°S (LELOUP 1934, ALVARIÑO 1968, 1971, 1981, CORDEIRO & MONTÚ 1991, NOGUEIRA & OLIVEIRA 1991, PUGH 1999, MIGOTTO et al. 2002, SILVEIRA & MORANDINI 2011).

Remarks. This species resembles *L. meteori*, but has a longer somatocyst peduncle.

Lensia subtiloides (Lens & van Riemsdijk, 1908)

Figs. 16, 31

Diphyes subtiloides Lens & van Riemsdijk, 1908: 46.

Description. Anterior Nectophore: With firm consistency and five complete longitudinal ridges that converge at the apex. It measures 3.96 mm in height and 1.94 mm in width. The nectosac measures approximately 9/10 the height of the nectophore. The ostium measures approximately 3/5 the width of the nectophore. The mouth plate is small, with two small distal lamellae, and the hydroecium is shallow and located at the same level as the ostium. The somatocyst is small, club-shaped, slightly bent, and measures approximately 1/10 the height of the nectophore.

Examined material. **BRAZIL**, *Rio de Janeiro*: Cabo Frio (collected at 6:21 a.m., 240 m depth, 24°16.3'S-43°49.1'W), two specimens preserved in 4% formaldehyde, 05/12/76, collected by FINEP III campaign, station 1729 leg., LabGel (UFABC); Cabo Frio (collected at 2:10 a.m., 186 m depth, 24°19.3'S-44°17.0'W), one specimen preserved in 4% formaldehyde, 05/13/76, collected by FINEP III campaign, station 1737 leg., LabGel (UFABC); Campos Basin (250 m depth, 120 µm net, South Atlantic

Central Water), one specimen preserved in 4% formaldehyde, 08/09/09, collected by Habitats 18 campaign, station C12 leg., LabGel (UFABC). *Santa Catarina*: Cabo de Santa Marta Grande (collected at 4:27 a.m., 128 m depth, 25°30.5'S-45°26.8'W), one specimen preserved in 4% formaldehyde, 05/15/76, collected by FINEP III campaign, station 1758 leg., ZUEC CNI 60, Museu de Zoologia "Prof. Dr. Adão José Cardoso" (UNICAMP); Cabo de Santa Marta Grande (collected at 7:15 a.m., 185 m depth, 25°55.2'S-46°00.0'W), two specimens preserved in 4% formaldehyde, 05/20/76, collected by FINEP III campaign, station 1780 leg., LabGel (UFABC); Cabo de Santa Marta Grande (collected at 12:50 a.m., 218 m depth, 26°24.5'S-46°33.3'W), two specimens preserved in 4% formaldehyde, 05/21/76, collected by FINEP III campaign, station 1791 leg., LabGel (UFABC); Cabo de Santa Marta Grande (collected at 13:30 a.m., 230 m depth, 27°33.9'S-47°17.1'W), two specimens preserved in 4% formaldehyde, 05/23/76, collected by FINEP III campaign, station 1811 leg., LabGel (UFABC); Cabo de Santa Marta Grande (collected at 12:20 a.m., 1170 m depth, 28°29.0'S-46°46.0'W), one specimen preserved in 4% formaldehyde, 05/24/76, collected by FINEP III campaign, station 1821 leg., LabGel (UFABC); Cabo de Santa Marta Grande (collected at 4:00 a.m., 640 m depth, 28°41.7'S-47°16.0'W), two specimens preserved in 4% formaldehyde, 05/25/76, collected by FINEP III campaign, station 1827 leg., LabGel (UFABC); Cabo de Santa Marta Grande (collected at 9:00 a.m., 128 m depth, 28°23.0'S-47°55.0'W), two specimens preserved in 4% formaldehyde, 05/25/76, collected by FINEP III campaign, station 1829 leg., LabGel (UFABC).

Geographic distribution. In South America, it occurs in the Atlantic Ocean, in Brazil, from 0° to 28°S (NISHIYAMA et al. 2016).

Remarks. It is the type species of *Lensia* (TOTTON 1965).

ACKNOWLEDGMENTS

The authors are grateful to Alvaro E. Migotto and Charles M.D. Santos for their valuable suggestions on an early version of this manuscript; to the anonymous referee that gave valuable suggestions to the improvement of the manuscript; to Renato Nagata and Karine Nascimento for their help in the early identification of the samples from Habitats and FINEP III; and to Guilherme C. Ribeiro for the use of his lab. This research was sponsored by a Master's fellowship to EYN provided by CAPES and UFABC, and research grants to OMPO (FAPESP 2007/06560-7, CNPq 481227/2007-5, PETROBRAS/CENPES).

LITERATURE CITED

- ALEKSEEV DO (1984) New species and subspecies of the genus *Lensia* (Calycophorae). *Zoologicheskii Zhurnal* 63: 965-970.
ALVARIÑO A (1968) Los quetognatos, sifonoforos y medusas en la región del Atlántico ecuatorial bajo la influencia del Amazonas. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 1: 41-76.

- ALVARIÑO A (1971) Siphonophores of the Pacific with a review of the world distribution. **Bulletin of the Scripps Institution of Oceanography** 16: 1-432.
- ALVARIÑO A (1976) El zooplancton del océano Pacífico colombiano y las pesquerías, p. 206-271. In: VEGAS M, ROJAS R (Eds.) **Memorias del primer Seminario sobre el Océano Pacífico Sudamericano**, Cali, Septiembre 1 a 5 de 1976. Santiago de Cali, Univalle-Colciencias.
- ALVARIÑO A (1981) Siphonophorae, p. 383-441. In: BOLTOVSKOY D (Ed.) **Atlas del zooplancton del Atlántico sudoccidental y métodos de trabajo con el zooplancton marino**. Mar del Plata, Publicación especial del INIDEP.
- ALVARIÑO A, WOJTAN JM (1984) Three new species of *Lensia*, and description of the eudoxia stages of *Lensia reticulata* and *Lensia lelouveteau* (Calycophorae: Siphonophorae). **Proceedings of the Biological Society of Washington** 97: 49-59.
- APABLAZA P, PALMA S (2006) Efecto de la zona de mínimo oxígeno sobre la migración vertical de zooplancton gelatinoso en la bahía de Mejillones. **Investigaciones Marinas** 34: 81-95. doi: 10.4067/S0717-71782006000200009
- BIGELOW HB (1911) The Siphonophorae. Reports of the scientific research expedition to the tropical Pacific. Albatross XXIII. **Memoirs of the Museum of Comparative Zoology at Harvard College** 38: 173-401.
- BONECKER SLC, ARAUJO AV, CARVALHO PF, DIAS CO, FERNANDES LFL, MIGOTTO AE, OLIVEIRA OMP (2014) Horizontal and vertical distribution of mesozooplankton species richness and composition down to 2,300 m in the southwest Atlantic Ocean. **Zoologia** 31: 45-462. doi: 10.1590/S1984-46702014000500005
- BOUILLON J, GRAVILI C, PAGÈS F, GILI JM, BOERO F (2006) **An introduction to Hydrozoa**. Paris, Publications Scientifiques du Muséum, 591p.
- CHUN C (1886) Über Bau und Entwicklung der Siphonophoren. **Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin** 35: 681-688.
- CORDEIRO TA, MONTÚ M (1991) Distribuição dos Siphonophorae Calycophorae (Cnidaria) em relação às massas de água ao largo dos estados do Paraná e de Santa Catarina, Brasil (28°S-31°S). **Nerítica** 6: 107-126.
- DANIEL R (1971) Some new species of Siphonophora (Coelenterata) from the Indian Ocean. **Journal of the Zoological Society of India** 22: 147-156.
- DANIEL R (1974) Siphonophora from the Indian Ocean. **Memoirs of the Zoological Survey of India** 15: 1-242.
- DUNN CW, PUGH PR, HADDOCK SHD (2005) Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialization. **Systematic Biology** 54: 916-935. doi: 10.1080/10635150500354837
- GROSSMANN MM, COLLINS AG, LINDSAY DJ (2014) Description of the eudoxid stages of *Lensia havock* and *Lensia leloupi* (Cnidaria: Siphonophora: Calycophorae), with a review of all known *Lensia* eudoxid bracts. **Systematics and Biodiversity** 12: 163-180. doi: 10.1080/14772000.2014.902867
- HADDOCK SHD, DUNN CW (2005) The complex world of siphonophores. **JMBA Global Marine Environment** 2: 24-25.
- HADDOCK SHD, DUNN CW, PUGH PR (2005) A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. **Journal of the Marine Biological Association of the United Kingdom** 85: 695-707. doi: 10.1017/S0025315405011616
- HAECKEL E (1869) **Ueber Arbeitsteilung in Natur-und Menschenleben**. Berlin, Berliner Handwerker-Vereins, 40p.
- HARDY AC, GUNTHER ER (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. **Discovery Reports** 11: 1-456.
- KEFERSTEIN W, EHLERS E (1860) Auszug aus den Beobachtungen über die Siphonophoren von Neapel und Messina angestellt in Winter 1859-60. **Nachrichten von der königlichen Gesellschaft der Wissenschaften zu Göttingen** 23: 254-262.
- KIRKPATRICK PA, PUGH PR (1984) Siphonophores and Velellids. **Synopses of the British Fauna New Series** 29: 1-154.
- LELOUP E (1932) Contribution à la répartition des siphonophores calycophorides. **Bulletin du Musée Royal d'Histoire Naturelle de Belgique** 8: 1-30.
- LELOUP E (1933) Siphonophores calycophorides provenant des Campagnes du Prince Albert 1er de Monaco. **Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1er, Prince Souverain de Monaco** 87: 1-35.
- LELOUP E (1934) Siphonophores calycophorides de l'océan Atlantique tropical et austral. **Bulletin du Musée Royal d'Histoire Naturelle de Belgique** 10: 1-87.
- LELOUP E, HENTSCH E (1935) Die Verbreitung der calycophoren Siphonophoren im Südatlantischen Ozean. **Wissenschaftliche Ergebnisse der Deutschen Atlantischen Expedition "Meteor" (1925-1927)** 12: 1-31.
- LENS AD, VAN RIEMSDIJK T (1908) The Siphonophora of the "Siboga" Expedition. **Siboga Expedition** 9: 1-130.
- MACKIE GO (1963) Siphonophores, Bud Colonies and Superorganisms, p. 329-337. In: DOUGHERTY EC (Ed.) **The Lower Metazoa**. Berkeley, University of California Press.
- MACKIE GO (1964) Analysis of locomotion in a siphonophore colony. **Proceedings of the Royal Society B: Biological Sciences** 159: 366-391.
- MAPSTONE GM (2009) **Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters**. Ottawa, NRC Research Press, 302p. doi: 10.1139/9780660198439
- MAPSTONE GM (2014) Global diversity and review of the Siphonophorae. **PLOS One** 9: e87737. doi: 10.1371/journal.pone.0087737
- MAPSTONE GM, SCHUCHERT P (2015) Siphonophorae. In: SCHUCHERT P (Ed.) **World Hydrozoa Database**. Available online at: <http://www.marinespecies.org/hydrozoa/aphia.php?p=tax-details&id=1371> [Accessed: 14/06/2015].
- MIGOTTO AE, MARQUES AC, MORANDINI AC, SILVEIRA FL (2002) Checklist of the Cnidaria Medusozoa of Brazil. **Biota Neotropica**

- 2: 1-31. doi: 10.1590/S1676-06032002000100010
- MOSER F (1917) Die Siphonophoren der Adria und ihre Beziehungen zu denen des Weltmeeres. **Sitzungsberichte der Akademie der Wissenschaften in Wien** 126: 703-763.
- MOSER F (1925) Die Siphonophoren der Deutschen Südpolar-Expedition 1901-1903. **Zoologie. Deutsche Südpolar-Expedition** 18: 1-541.
- NISHIYAMA EY, RIBEIRO GC, OLIVEIRA OMP (2016) Phylogenetic analysis of the genus *Lensia* (Cnidaria, Hydrozoa, Siphonophora), based on the species morphology. **Zootaxa** 4132: 493-508. doi: 10.11646/zootaxa.4132.4.2
- NOGUEIRA CR, OLIVEIRA JR SR (1991) Siphonophores from the coast of Brazil (17°S to 24°S). **Boletim do Instituto Oceanográfico** 39: 61-69. doi: 10.1590/S0373-55241991000100004
- OLIVEIRA OMP, MIRANDA TP, ARAUJO EM, AYÓN P, CEDENO-POSSO CM, AMANCAY A, CEPEDA-MERCADO AA, CÓRDOVA P, CUNHA AF, GENZANO GN, HADDAD MA, MIANZAN HW, MIGOTTO AE, MIRANDA LS, MORANDINI AC, NAGATA RM, NASCIMENTO KB, NOGUEIRA JR M, PALMA S, QUIÑONES J, RODRIGUEZ CS, SCARABINO F, SCHIARITI A, STAMPAR SN, TRONOLONE VB, MARQUES AC (2016) Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. **Zootaxa** 4194: 001-256. doi: 10.11646/zootaxa.4194.1.1
- PAGÈS F, GILI JM (1992) Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). **Scientia Marina** 56: 65-112.
- PAGÈS F, GONZÁLEZ H, RAMÓN M, SOBARZO M, GILI JM (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). **Marine Ecology Progress Series** 210: 13-24. doi: 10.3354/meps210013
- PALMA S (1973) Contribución al estudio de los sifonóforos encontrados frente a la costa de Valparaíso. I. Taxonomía. **Investigaciones Marinas, Valparaíso** 4: 17-88.
- PALMA S (1977) Contribución al estudio de los sifonóforos encontrados frente a la costa de Valparaíso. Aspectos ecológicos, p. 119-133. In: Memorias II Simposio Latinoamericano de Oceanografía Biológica, Cumaná, Venezuela, vol. 2.
- PALMA S (1994) Distribución del macroplankton gelatinoso en un área de desove de peces frente a la costa central de Chile (32°-33°S). **Revista de Biología Marina** 29: 23-45.
- PALMA S, APABLAZA P (2004) Abundancia estacional y distribución vertical del zooplankton gelatinoso carnívoro en un área de surgencia en el norte del Sistema de la Corriente de Humboldt. **Investigaciones Marinas** 32: 49-70. doi: 10.4067/S0717-71782004000100005
- PALMA S, ARAVENA G (2001) Distribución de quetognatos, eufáusidos y sifonóforos en la región magallánica. **Ciencia y Tecnología del Mar** 24: 47-59.
- PALMA S, ROSALES S (1995) Composición, distribución y abundancia estacional del macroplankton de la bahía de Valparaíso. **Investigaciones Marinas** 23: 49-66. doi: 10.4067/S0717-71781995002300003
- PALMA S, ROSALES S (1997) Sifonóforos epipelágicos de los canales australes chilenos (41°30'-46°40'S). **Ciencia y Tecnología del Mar** 20: 125-146.
- PALMA S, SILVA N (2006) Epipelagic siphonophores assemblages associated with water masses along a transect between Chile and Easter Island (eastern Pacific Ocean). **Journal of Plankton Research** 28: 1-9. doi: 10.1093/plankt/fbl044
- PALMA S, ABAPLAZA P, SOTO D (2007) Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). **Investigaciones Marinas** 35: 71-82. doi: 10.4067/S0717-71782007000200008
- PALMA S, SILVA N, RETAMAL MC, CASTRO L (2011) Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile. **Continental Shelf Research** 31: 260-271. doi: 10.1016/j.csr.2010.04.007
- PALMA S, ULLOA R, LINACRE L (1999) Sifonóforos, quetognatos y eufáusidos de los canales australes entre el golfo de Penas y el estrecho de Magallanes. **Ciencia y Tecnología del Mar** 22: 111-142.
- PATRITTI G (1965) Contribution à l'étude de siphonophores calycophores recueillis dans le Golfe de Gascogne. Note préliminaire 2. Campagne du "Job ha Zélian" (Octobre-Novembre 1964). **Recueil des Travaux de la Station marine d'Endoume, Faculté des Sciences de Marseille** 38: 15-31.
- PATRITTI G (1970) Note sur deux nouvelles espèces du genre *Lensia*, recueillies dans les eaux du large de Tulear (S. W. de L'Océan Indien, Madagascar). **Recueil des Travaux Station marine d'Endoume, Fascicule hors série supplement** 10: 103-106.
- PUGH PR (1999) Siphonophorae, p. 467-513. In: BOLTOSKOY D (Ed.) **Zooplankton**. Leiden, Backhuys Publishers, vol. 1.
- SARS M (1846) **Fauna littoralis Norvegiae oder Beschreibung und Abbildungen neuer oderwenig bekannter Seethiere, nebst Beobachtungen über die Organisation, Lebensweise und Entwicklung derselben**. Christiania, Johann Dahl, 194p.
- SEGUIN G (1965) Contribution a la connaissance du plancton des eaux cotieres du Brésil (copepodes et amphipodes excepts) et comparaison avec celui du Senegal (Campagne de la Calypso, Janv.-Feb. 1962). **Bulletin de L'Institut Océanographique d'Algerie** 2: 7-44.
- SILVEIRA FL, MORANDINI AC (2011) Checklist dos Cnidaria do Estado de São Paulo, Brasil. **Biota Neotropica** 11: 1-10. doi: 10.1590/S1676-06032011000500016
- STEPANJANTS SD (1977) Siphonophora of the central part of the Pacific Ocean. **Issledovaniya Fauny Morei** 20: 54-81.
- TOTTON AK (1932) Siphonophora. **Scientific Reports of the Great Barrier Reef Expedition** 4: 317-374.
- TOTTON AK (1941) New species of Siphonophora genus *Lensia* Totton 1932. **Annual Magazine of Natural History, Series** 11, 8: 145-168.
- TOTTON AK (1954) Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. **Discovery Reports** 27: 1-162.

- TOTTON AK (1965) **A Synopsis of the Siphonophora**. London, Trustees of the British Museum (Natural History), 230p.
- ULLOA R, PALMA S, LINACRE L, SILVA N (2000) Seasonal changes in the bathymetric distribution of siphonophores, chaetognaths and euphausiids associated to water masses off of Valparaiso, Chile (Southeast Pacific), p. 72-83. In: FARBER J (Ed.) **Oceanography in the Eastern Pacific**. Ensenada, CICESE.
- VILLENAS F, SOTO D, PALMA S (2009) Cambios interanuales en la biomasa y biodiversidad de zooplancton gelatinoso en el sur de Chile (Primaveras 2004 y 2005). **Revista de Biología Marina y Oceanografía** 44: 309-324. doi: 10.4067/S0718-19572009000200005

Submitted: 2 June 2016

Received in revised form: 7 October 2016

Accepted: 10 October 2016

Editorial responsibility: Rosana M. da Rocha

Author Contributions: EMA and OMPO were responsible for the samples curatorship; EYN analyzed, photographed and depicted the material; EYN, EMA and OMPO wrote the paper.

Competing Interests: The authors have declared that no competing interests exist.