



The epizoic marine diatom *Sceptronema orientale* (Licmophoraceae, Licmophorales): epitypification and emendation of specific and generic descriptions

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Abstract

Sceptronema orientale was found epizoic on the harpacticoid copepod *Euterpina acutifrons* (Dana) collected from several locations along Bahía Anegada, Province of Buenos Aires, Argentina. Material was examined with light and scanning electron microscopy and new data about the morphology of the chloroplast and ultrastructural details of the girdle, valves, apical slit fields and rimoportulae pattern were obtained. Based on this new knowledge the descriptions of the species and of the monotypic genus *Sceptronema* are emended. Considering that in the protologue three pictures were designated as iconotype, the material from Ría del Jabalí is chosen as an epitype to serve as the interpretative type of *Sceptronema orientale*. A comparison with the morphologically similar genera *Licmophora* and *Gato* was conducted and the inclusion of *Sceptronema* in the Family Licmophoraceae, Order Licmophorales is proposed.

Keywords: epizoic araphid marine diatom, *Euterpina acutifrons*, morphology, *Sceptronema orientale*, taxonomy

Introduction

Sceptronema is a monotypic genus of araphid marine diatoms described by Takano (1983: 26). It is characterized by the formation of linear colonies and narrow, obovate, heteropolar valves, with a broad head-pole and a slender foot-pole. The sternum is straight and apical slit fields are found on the valve mantle. This genus was included by Takano (1983) in the Sub-Order Araphidineae, Family Diatomaceae. Subsequently, Round *et al.* (1990) recognized the araphid pennates (old Sub-Order Araphidineae of Simonsen 1979) as Class Fragilariophyceae Round, Subclass Fragilariophycidae Round. The Subclass was subdivided into 12 Orders and 14 Families and 54 Genera were listed there. However, *Sceptronema* Takano was not included in their classification scheme although it was listed in the *Index nominum genericorum*.

Sceptronema orientale Takano, type species of the genus by original designation, was found epizoic on the harpacticoid copepod *Euterpina acutifrons* (Dana 1848: 153) from coastal waters off Shimoda City, Shizuoka Prefecture, Japan. The species was analysed only with scanning electron microscopy (SEM) and transmission electron microscopy (TEM) and figures 15, 19 and 20 in the protologue were designated as iconotypes. No slide was designated as holotype.

The species was subsequently reported from inshore waters of the Mediterranean coast of Israel by Kimor *et al.* (1992), who considered the selective relationship between it and an unidentified harpacticoid copepod as strictly seemingly neutral in nature. It was also collected from coastal waters of Port Olímpic, Barcelona, Spain (41.22° 775'N, 02.13° 150' E), NW Mediterranean Sea by Skovgaard & Saiz (2006), who described the association between *Sceptronema orientale* and *Euterpina acutifrons* as an extreme case of host specificity. As part of a large survey examining toxigenic microalgae and toxins in shellfish in coastal waters of Bahía Anegada, Province of Buenos Aires, Argentina, we found *Sceptronema orientale* epizoic on *Euterpina acutifrons*.

The study of this material allowed us to provide new information regarding the cytology and morphology of *Sceptronema orientale* beyond that found in the original description.

Material and methods

The material analysed was collected at several locations along Bahía Anegada: Los Pocitos, Ría del Jabalí and Bahía San Blas, in the southern coast of Buenos Aires Province (Fig. 1), from May 2008 to March 2014. Qualitative samples were taken from the surface layer of the water column (between 0 and 5 m) with 30 µm net hauls and fixed with 4 % formalin.

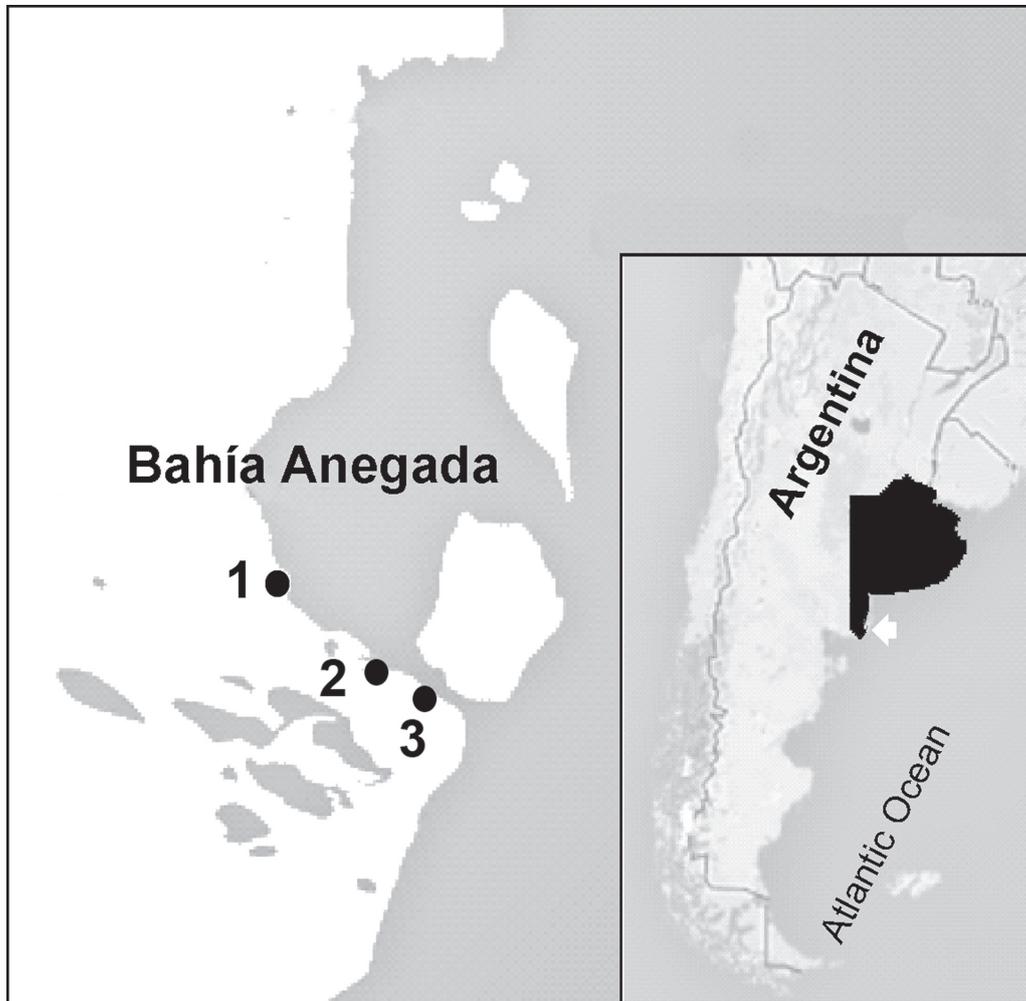


FIGURE 1. Map of Province of Buenos Aires, showing sampling stations and location of the area in Argentina. 1: Los Pocitos, 2: Ría del Jabalí, 3: Bahía San Blas.

In the laboratory, copepods gathered in the plankton samples were analysed with light microscopy (LM) and those with epizoic species were picked with micropipette using a Zeiss Axiovert 40 CFL inverted microscope, rinsed with distilled water to remove salt and preservatives and treated to eliminate organic matter following Prygiel & Coste (2000). Treated and untreated material was mounted for light (LM) and scanning electron microscopy (SEM) after Ferrario *et al.* (1995). Permanent mounts were made with Naphrax (Brunel Microscopes, Chippenham, U.K.).

The material was deposited in the Herbarium of the División Ficología Dr. Sebastián A. Guarrera, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, under the numbers LPC 11601 to LPC 11954.

Observations were made with microscopes Leica DM 2500 (phase contrast and differential interference contrast) and Zeiss Axiovert 40 CFL (phase contrast and Nomarski interference contrast). Photomicrographs were taken with Leica DM 2500 (Leica Microsystems, Wetzlar, Germany), Zeiss Axiovert 40 CFL (Zeiss Microimaging, Göttingen, Germany) microscopes and Jeol JSM 6360 LV (JEOL, Tokyo, Japan) scanning electron microscope.

Terminology follows Ross *et al.* (1979), Takano (1983), Round *et al.* (1990), with some additions proposed by Prasad & Livingston (1993) and Kooistra *et al.* (2009).

Results

Based on the analysis of material from Bahía Anegada, Argentina, we offer an emended description of the species *Sceptronema orientale* that includes data on the morphology of the chloroplast and ultrastructural details of girdle, valves, apical slit fields and rimoportulae. Taking into account that Takano (1983) designated three ultrastructural pictures to serve as iconotype and that these pictures do not allow observation of some differentiating characters, we consider it necessary to designate an epitype to serve as an interpretative type in accordance with Art. 9.8 of the ICN (McNeill *et al.* 2012). Since our understanding of Takano's *Sceptronema orientale* was clarified by the examination of recent material epizoic on *E. acutifrons* collected from coastal waters of Buenos Aires (Argentina), we chose this material to serve as epitype. On the basis of the new knowledge of the generitype of *Sceptronema* we also emend the generic description.

Sceptronema orientale Takano emend. E. A. Sar & I. Sunesen (Figs 2–28)

Iconotype: Figs 15, 19 and 20 designated by Takano (1983).

Type locality: coastal waters off Shimoda City, Shizuoka Prefecture, Japan

Epitype here designated: Slide LPC 11650 (1)!, labeled “epitipo de *Sceptronema orientale*, Ría del Jabalí, 16/02/2009” (deposited in the Herbarium of the División Ficología “Dr. Sebastián A. Guarrera”). Sample LPC 11650!, used to prepare the epitype slide is also available in the Herbarium.

Epitype locality: Ría del Jabalí, Bahía Anegada, Argentina.

Description in LM: Cells are heteropolar in valve view and slightly wedge-shaped in girdle view, with a single, large, butterfly-like, valve-appressed chloroplast (Figs 2–7). The cells are attached to individuals of the copepod *Euterpina acutifrons* by mucilaginous stalks of variable length, cells either solitary or forming linear chains (Figs 2–7, 11–14) by connecting the head-pole of the first cell of the chain to the head-pole of the next cell (Figs 4, 6) and the foot-pole of this one to the foot-pole of the next one. The frustule shows two small septa restricted to the apical region in girdle view (Figs 5, 7, arrowheads). Valve is narrowly obovate, heteropolar, with a wide rostrate head-pole and a narrow capitate foot-pole, with central and straight sternum (Figs 8–10), 31.0–59.0 µm long, 8.7–10.0 µm wide (maximum width). Striae are not visible. The girdle is narrower in the foot-pole than in the head-pole (Figs 4–5, 7). Girdle bands are numerous (Figs 8–9).

Description in SEM: Valve surface is flat (Figs 15–17, 19–25), valve mantle is very shallow along the sides and deeper at the poles (Figs 19–25). Sternum is conspicuous, central, narrow, straight, extending from pole to pole, slightly raised internally and spatulate at the ends (Figs 21–23). Transapical striae are perpendicular to the sternum, uniseriate, evenly spaced, 40–50 in 10 µm, extending almost to the valve mantle edge (Figs 19–25) except at the poles where they radiate from the end of the sternum (Figs 21–23). Areolae are poroid, 40–45 in 10 µm, elliptical, a little elongated in transapical direction, externally and internally slightly sunken in the siliceous layer and externally occluded (Figs 19–20). At each pole of the valve there is an apical slit field composed of longitudinal lamellae or bars with horizontal sunken cross bars (Fig. 18, arrowheads). The apical slit fields are restricted to the valve mantle. The head-pole field is composed of ca. 16 slits (Figs 21, 23) while the foot-pole field is slightly smaller with ca. 12 slits (Figs 22, 24). At the foot-pole there are 10 to 20 rimoportulae on the valve face and around the apical slit field in the valve mantle (Figs 22, 24, arrowheads). In addition to these, there is a row of 3 to 6 rimoportulae along each valve margin at the basal part of both valves (Figs 20, 25, arrowheads). In only one valve of all analyzed valves an isolated rimoportulae is found at the head-pole (Fig. 23, arrowhead). The rimoportulae are internally sessile, rimmed all around, completely open, sub-circular to elliptical, inserted within the striae taking the place of two areolae (Figs 22, 24–25, arrowheads). Externally they open by sub-circular to elliptical pores without projection (Figs 19, 27, arrowheads). The girdle bands that constitute each cingulum are numerous. Bands are open, tapered towards the ends, with splits nearly 180° apart at poles (Fig. 16). Valvocopula is the widest band, 1.2–1.3 µm wide at the head-pole, open at the foot-pole, with a row of poroids in the pars interior throughout its length (Figs 16, 27–28) and several rows in the pars exterior in the head-pole that shorten towards the ends of the band (Figs 18, 27–28). Pars media is plain in external view (Fig. 27) and thickened forming a longitudinal rib in internal view (Figs 18, 27–28), this rib becomes more prominent and widens in a very short septum at the head-pole (Fig. 28). The width of the other copulae decreases in abvalvar direction and they are structurally similar to the valvocopula (Fig. 18) but without septa at the head-poles. Abvalvar margin of all copulae is plain (Figs 27–28).

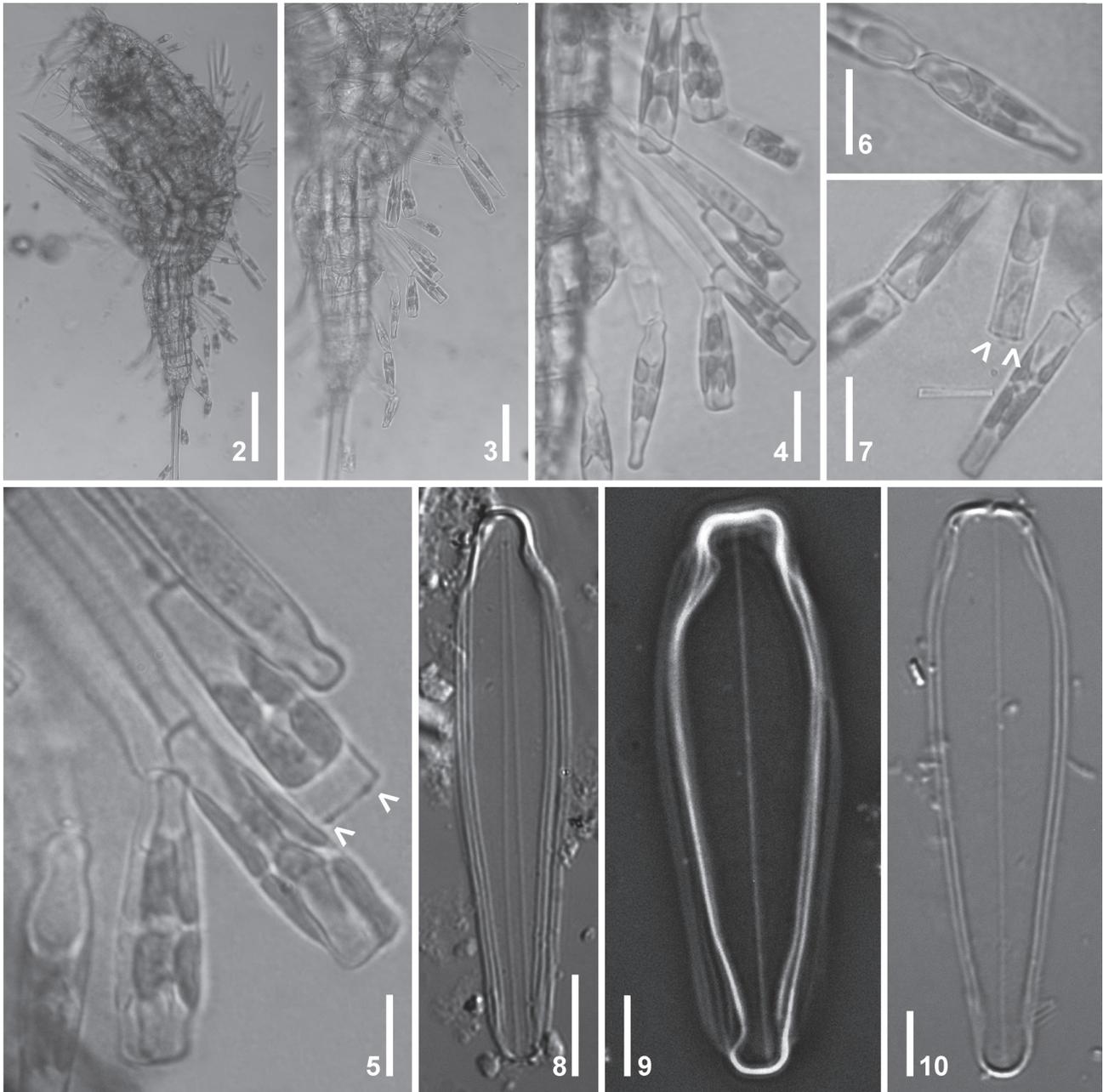


FIGURE 2–10. *Scytronema orientale*. LM. Figs 2–7. Sample LPC 11650. Figs 2–4. Several live colonies on *Euterpina acutifrons*. Figs 5–7. Details of these colonies. Fig. 5. Cells with one chloroplast, attached by mucilaginous stalks. Arrowheads show short septa. Fig. 6. Cells in valvar view with the head-pole attaching by a mucilaginous pad to the head-pole of the adjacent cell of the colony. Fig. 7. Cells in girdle view. Arrowheads show septa. Figs 8–10. Slide LPC 11650 (1), cleaned material, epitype here designated. Fig. 8. Complete frustule. Figs 9–10. Valves with girdle bands. Note the central, straight sternum. Scale bars: Fig. 2 = 100 µm; Fig. 3 = 50 µm; Figs 4, 6–7 = 20 µm; Figs 5, 8 = 10 µm; Figs 9–10 = 5 µm.

Ecology: the species was only found attached on the exoskeleton of marine copepods by Takano (1983), Kimor *et al.* (1992) and Skovgaard & Saiz (2006). Fernandes & Calixto-Feres (2012) analysed epizoic diatoms on several species of copepods and they only found *Pseudohimantidium pacificum* Hustedt & Krasske in Krasske (1941: 272) on *Euterpina acutifrons* from Paranaguá Bay, Paraná State, Brazil.

In this study *Scytronema orientale* occurred on *Euterpina acutifrons* in only two samples collected during the summer from Ría del Jabalí (LPC11650, 16 February of 2009) and Los Pocitos (LPC 11952, 4 March of 2014) enlarging its range of geographic distribution from Japan and the Mediterranean Sea to the coastal waters of the Southwestern Atlantic Ocean. A previous record of *S. orientale* from the phytoplankton of the Ribeirão da Fazenda, Santa Catarina State, Brazil, given by Souza-Mosimann & Moro Roos-Oliveira (1998) is a misidentification of another slightly heteropolar araphid diatom with a coarser stria density (15 in 10 µm) as seen in figure 45 of these authors.

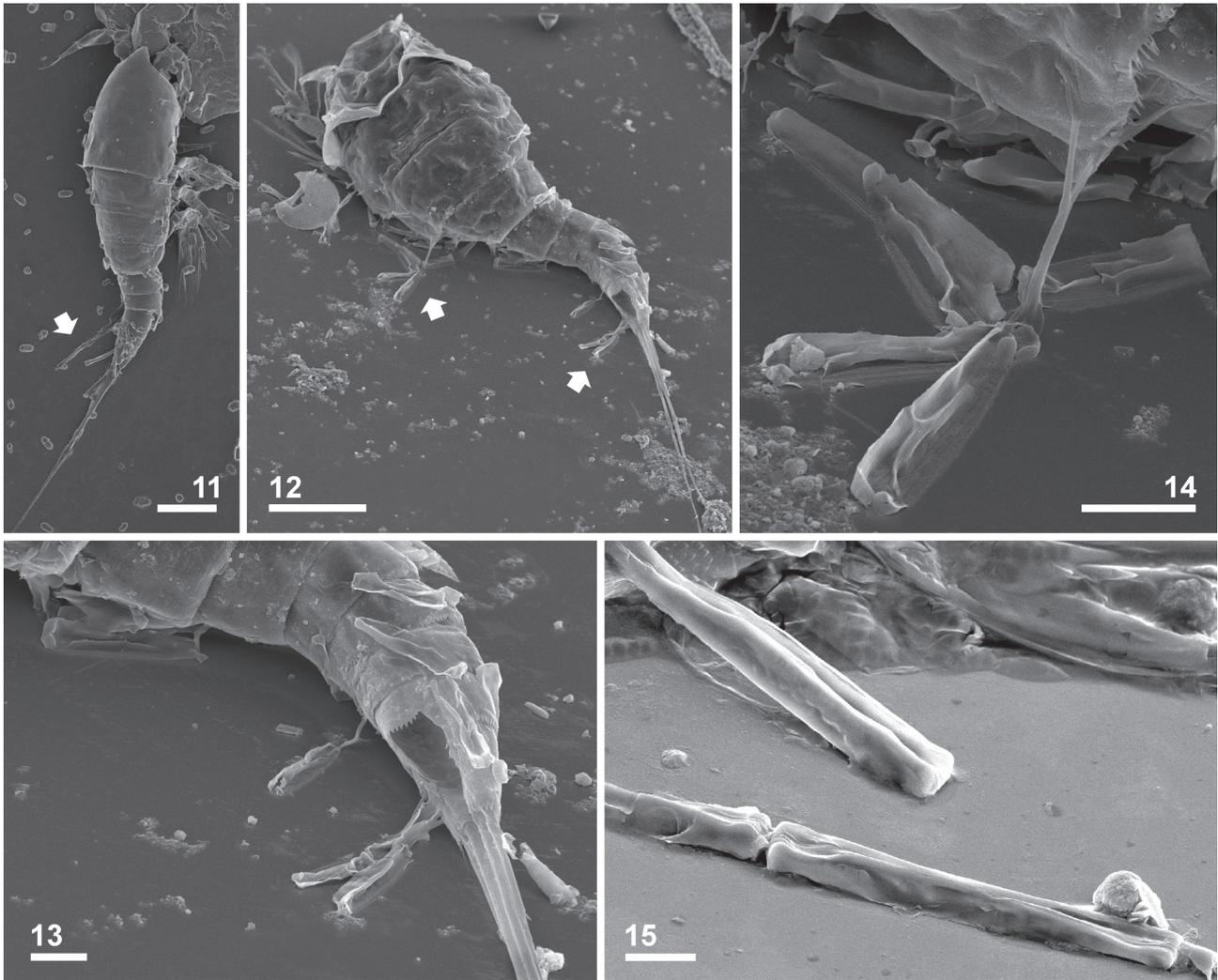


FIGURE 12–15. *Sceptronema orientale* on *Euterpina acutifrons*. SEM. Sample LPC 11650. Figs 11–13. Note cells attached to the copepod by mucilaginous stalks. Fig. 14. Detail of several coiled mucilaginous stalks. Fig. 15. Frustules tilted showing valvar and partial girdle views. Scale bars: Figs 11–12 = 100 μm ; Figs 13–14 = 20 μm ; Fig. 15 = 10 μm .

Sceptronema Takano emend. E. A. Sar & I. Sunesen

Generitype: *Sceptronema orientale* Takano emend. E. A. Sar & I. Sunesen

Description in LM: Cells solitary or colonial, attached by mucilaginous stalks, heteropolar in valve view and slightly wedge-shaped in girdle view, with a butterfly-like, valve-appressed chloroplast. Frustule with two small septa restricted to the head-pole in girdle view. Valve narrowly obovate, heteropolar, with central and straight sternum. Girdle narrower in the foot-pole than in the head-pole.

Description in SEM: Valve surface flat, valve mantle shallow. Sternum central, narrow, straight, extending from pole to pole. Transapical striae, perpendicular to the sternum, uniseriate, extending through the valve mantle. Areolae poroid. One apical slit field composed of longitudinal lamellae or bars restricted to the valve mantle at each pole of the valve. Several rimoportulae placed on the valve face and around the apical slit field in the valve mantle at foot-pole and additional ones forming a row near each valve margin at the basal part of the valve. Rimoportulae internally sessile, rimmed all around, completely open, sub-circular to elliptical, inserted in the striae opened by sub-circular to elliptical pores. Cingulum with numerous open bands, tapered towards the ends, with splits nearly 180° apart at poles. Valvocopula wider than copulae, opened at foot-pole, with a very short septum at head-pole. Copulae structurally similar to the valvocopula without septa in the head-poles.

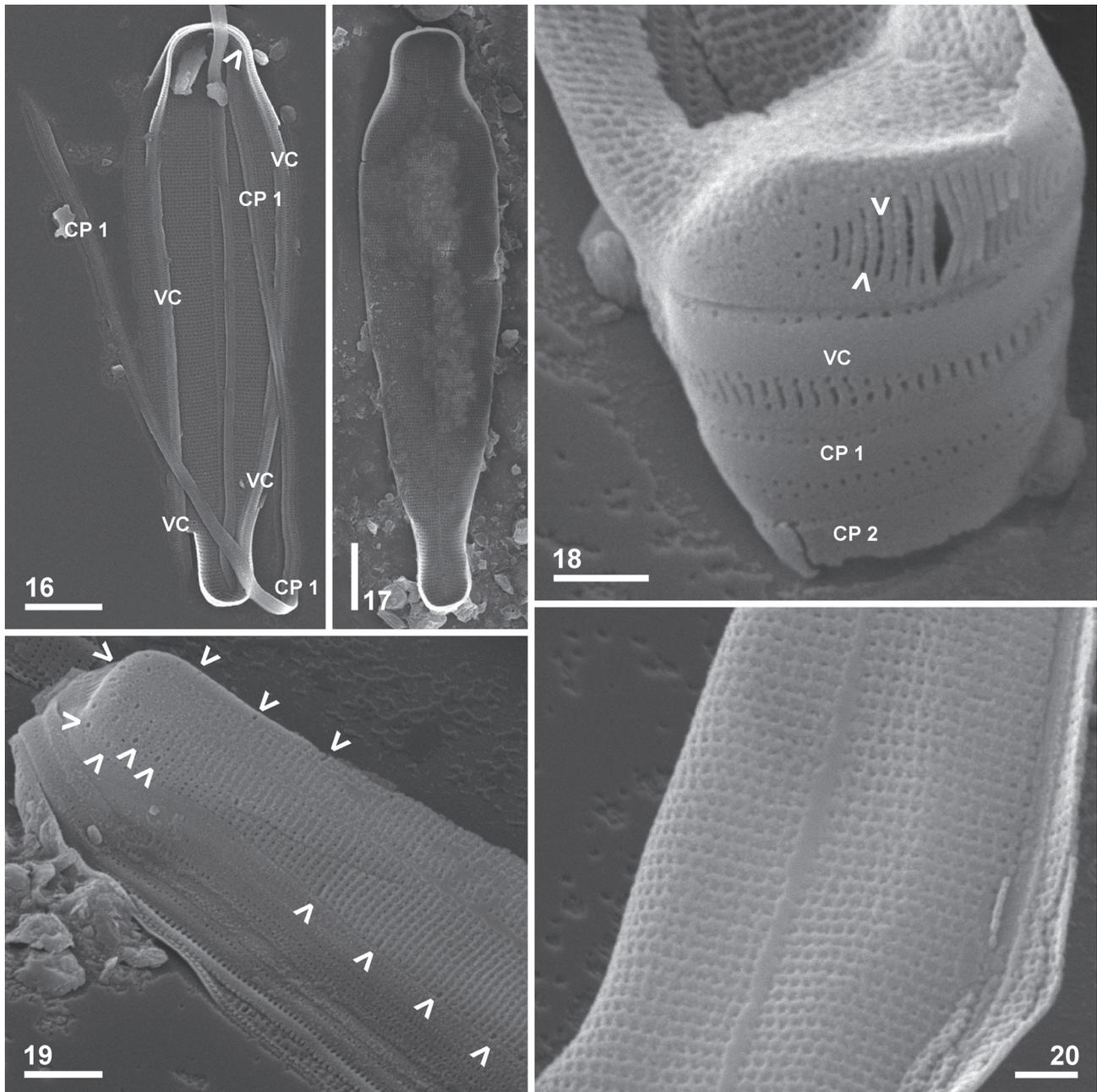


FIGURE 16–20. *Sceptronema orientale*. SEM. Sample LPC 11650. Figs 16–17. Internal valve view. Note open bands in Fig. 16 (VC valvocopula, CP 1 1st copula). Figs 18–20. External views. Fig. 18. Valve mantle of the head-pole with an apical slit field and girdle. Arrowheads show sunken cross bars of the slits (VC valvocopula, CP 1 1st copula, CP 2 2nd copula). Fig. 19. Foot-pole of a valve showing rimoportulae opening by subcircular to elliptical pores (arrowheads). Fig. 20. Central part of valve showing straight sternum and transverse, uniseriate striae. Scale bars: Figs 16–17 = 5 μ m; Fig. 19 = 2 μ m; Figs 18, 20 = 1 μ m.

Discussion

Araphid pennate diatoms were considered as a non-monophyletic group by Kooistra *et al.* (2003), Medlin & Kaczmarek (2004) and Williams & Kociolek (2007) among other authors. This point of view was subsequently reconfirmed by Sato *et al.* in Sato (2008) based on phylogenetic relationships estimated using multi-gene markers. Groups recognized by Sato *et al.* in Sato (2008) ('Core araphid' and 'Basal araphid') were not formally described as explained by Medlin & Sato (2009) and were comprehensively questioned by Williams & Kociolek (2010), thus, we follow the classification scheme presented by Round *et al.* (1990), understanding that requires urgent review. Based on morphological analysis of *Sceptronema orientale* carried out in this study, the genus *Sceptronema* should be included in the Class Fragilariophyceae, Subclass Fragilariophycidae since it possesses a sternum and a pennate arrangement

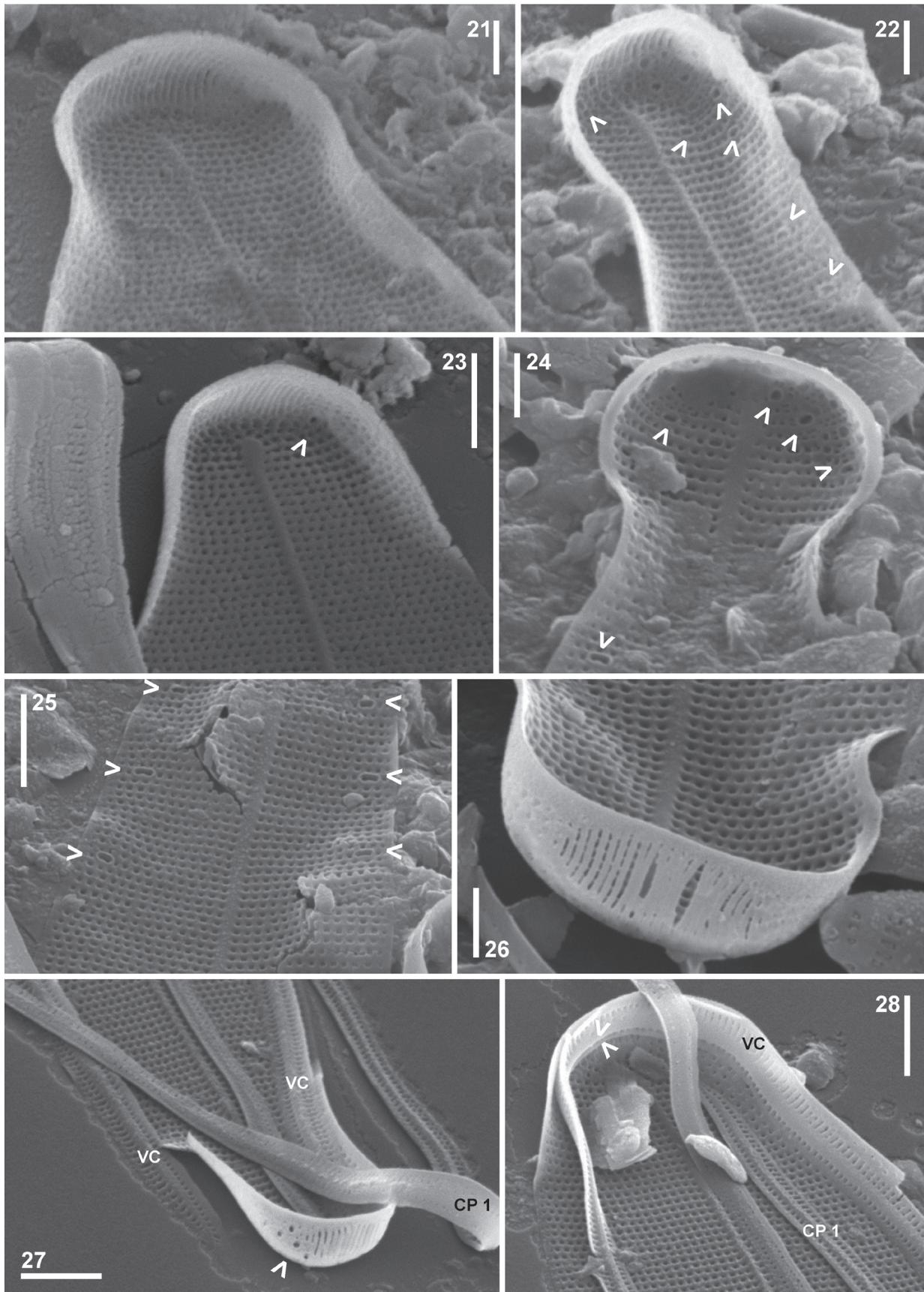


FIGURE 21–28. *Sceptronema orientale*. SEM. Sample LPC 11650. Internal views. Figs 21, 23. Head-poles showing apical slit field on the valve mantle. Figs 22, 24. Foot-poles showing apical slit field on the valve mantle and several rimmed, sessile rimoportulae (arrowheads). Fig. 25. Rows of rimoportulae near each valve margin. Note rimoportulae are inserted within the striae (arrowheads). Fig. 26. Apical slit field on the head-pole. Fig. 27. Foot-pole of the valve of fig. 16. Note valvocopula in internal view and the next copula in external and internal view (VC valvocopula, CP 1 1st copula). Fig. 28. Head-pole of the valve of fig. 16 showing valvocopula with a very short septum formed on the pars media (arrowheads, VC valvocopula, CP 1 1st copula). Scale bars: Figs 23, 25, 27–28 = 2 μ m; Figs 21–22, 24, 26 = 1 μ m.

of striae. Furthermore, it should be placed in the Order Licmophorales Round, Family Licmophoraceae Kützing by having cuneate cells in valve and girdle view, foot-pole attached to the substrate by mucilage pad or stalk, valvocopula bearing a short, apical, septum and attached lifestyle. The genus *Sceptronema* shares all these features with *Licmophora* Agardh (1827: 628), generitype of the Licmophoraceae, which is the genus morphologically most similar. Additionally, both genera have valves with a narrow, central sternum and transapical, uniseriate striae, cingula formed by open copulae with one row of pores towards the pars interior, a plain pars media, and one or more rows of pores towards the pars exterior. Despite these similarities both genera show several differences in apical slit fields, mode of colony formation and morphology and pattern of distribution of the rimoportulae (Table 1).

Sceptronema bears an apical slit field on the valve mantle at both poles while *Licmophora* has only one at the foot-pole. The apical slit field is composed of longitudinal bars and slits with horizontal sunken cross bars reminiscent of *Hyaloneis hyalinum* (Hustedt) Amspoker (Amspoker 2008: 12, figs 15–24) in *Sceptronema*, while slits are relatively shorter, without cross bars in *Licmophora* [Sar & Ferrario 1990: 404, figs 7–9, 13 for *L. flabellata* (Carmichael ex Greville) Agardh emend Sar & Ferrario; Honeywill 1998: figs 1 g–i for *L. flabellata* (Carmichael ex Greville) Agardh 1831: 42, figs 3 f, h for *L. ehrenbergii* (Kützing) Grunow 1867: 36, figs 8 d–f for *L. grandis* (Kützing) Grunow in Van Heurck 1881: pl. 48, figs 2–3]. Apical slit fields of *Sceptronema* resemble those of *Neosynedra* Williams & Round (1986: 332) for being placed at both poles of the cell, however the slits of *Neosynedra* differs from those of *Sceptronema* because they are intermittently interrupted by conspicuous cross-pieces which link the bars (similarly to those of *Cyclophora* Castracane 1878: 10). On the other hand *Neosynedra* (Fragilariales, Fragilariaceae) clearly differs from *Sceptronema* by having solitary, isopolar cells in valve and girdle view, without apical septum.

The mode of colony formation in *Sceptronema* is different than in the other araphid diatoms with an attached lifestyle as the cells are united in short linear chains. The first cell is attached to the copepod by a unbranched mucilaginous stalk formed from the foot-pole and with the head-pole attaching by a mucilaginous pad to the head-pole of the second cell and foot-pole of second cell attaching to the foot-pole of the third cell. In contrast the morphology of colonies of araphid genera according to Kooistra *et al.* (2009) exhibits the following variation: fan-shaped (*Licmophora*), bunches (*Protoraphis* Simonsen 1970: 384, *Ulnaria* (Kützing) Compère 2001: 100 and *Synedropsis* Hasle, Medlin & Syvertsen 1994: 248), ribbon-shaped [*Staurosira* Ehrenberg 1843: 45, *Nanofrustulum* Round, Hallsteinsen & Paasche 1999: 245, *Fragilaria* Lyngbye 1819: 182 and *Fragilariforma* Williams & Round 1988: 265] and zigzag chains [*Grammatophora* Ehrenberg 1840: 46, *Hyalosira* Kützing 1844: 125, *Rhabdonema* Kützing 1844: 126 and *Tabellaria* Ehrenberg ex Kützing 1844: 127].

The rimoportulae of *Sceptronema* were not described by Takano (1983); nevertheless, they were pictured in Takano's figs 2 c, 15 (iconotype), 17 (detail of the iconotype) and 19 (iconotype). The pattern of rimoportulae distribution in *Sceptronema* appears to be unique: several are placed at the foot-pole on the valve face and around the apical slit field on the valve mantle and additional ones form a row along each valve margin in the basal part of the valve. The pattern of rimoportulae distribution in *Licmophora* is completely different and shows some variability. According to Honeywill (1998) there are 2 or 3 rimoportulae per cell placed at the poles, if 2 one is placed at the basal pole of one valve and the other at the head-pole of the other valve, if 3 one is placed at the basal pole of one valve and one at the head-pole of each valve. Two species of *Licmophora* show several additional sessile rimoportulae forming an irregular row along the sternum, *L. flabellata* (Sar & Ferrario 1990: figs 2, 4, 6; Honeywill 1998: figs d, f; Lobban *et al.* 2011: figs 29, 33) and *L. connavmaria* Lobban & Scheffer (2013: 2, fig. 3 a–c, fig. 4 c, e, fig. 5 b, d).

The morphology of the rimoportulae in *Sceptronema* is somewhat similar to the “sessile rimoportulae” of *L. flabellata* [which were overlooked for a long time until they were first described by Sar & Ferrario (1990)] but the lips are less developed and the pattern of distribution is completely different. Besides being internally sessile these processes are rimmed all around more than lipped, completely open, sub-circular to elliptical, inserted in the striae taking the place of two areolae and externally opened by sub-circular to elliptical pores without projections. Rimoportulae of *Sceptronema* are morphologically very similar to the “rimmed pores” described by Lobban & Navarro (2013) in the protologue of the araphid, heteropolar, marine, epiphytic and monotypic genus *Gato* Lobban & Navarro (2013: 23). The authors chose this designation “to avoid the assumption that they are homologous to rimoportulae” (sic Lobban & Navarro, 2013) and reserved the term rimoportulae for those placed at both poles at or beyond the end of the subtle sternum of *Gato*. As mentioned by Lobban & Navarro (2013) the term “rimmed pore” was previously used by Round *et al.* (1990) in referring to a small opening in the middle of some valves of *Podocystis* Bailey (1854: 11); however this structure is completely different and only visible in external valve view. In contrast the rimoportulae were defined by Round *et al.* (1990) as tubes that open to the inside of the cell by a lip-shaped slit and to the outside by a simple aperture or tubular structure, similar to the “rimmed pores” of *Gato hyalinus* Lobban & Navarro (2013: 23) despite subtle differences in the shape of the slit and the lipped part of the process. Thus, we consider that these structures in *Gato* should be considered rimoportulae. These type of sessile rimoportulae are typically placed in series of 4–5 on each side of the foot-pole on the valve with a pedicellate rimoportula (figs 7–11 in Lobban & Navarro 2013) or in series of only 3 on those without a foot-pole pedicellate rimoportula (figs 12, 14–15 in Lobban & Navarro 2013).

Additionally, some sessile rimoportulae form a row near each valve margin at the basal part of the valve (fig. 15 in Lobban & Navarro 2013). The pattern of rimoportulae distribution of *Gato* is more similar to that of *Sceptronema* than to that of *Licmophora* (described above); nevertheless, it clearly differs by the presence of pedicellate rimoportulae at both poles or at the head-pole (Table 1). The mode of colony formation in *Gato* is different from that of the other araphid diatoms with attached lifestyle including *Sceptronema* and *Licmophora*, cells form mucilage branched tubes.

TABLE 1. Comparison among *Sceptronema*, *Gato* and *Licmophora* based on data obtained from: 1 Takano (1983), 2 this study, 3 Lobban & Navarro (2013), 4 Sar & Ferrario (1990), 5 Honeywill (1998), 6 Lobban *et al.* (2011), 7 Lobban & Schefter (2013).

	<i>Sceptronema orientale</i> 1, 2	<i>Gato hyalinus</i> 3	<i>Licmophora</i> spp. 4, 5, 6, 7
Colony	linear chain, attached by mucilaginous stalks of variable length	tube dwelling	fan-shaped, bushy, attached by mucilaginous pad or stalk/single cells at tips of long branched stalks
Cell shape	heteropolar in valve view and slightly wedge-shaped in girdle view	heteropolar in valve view and slightly wedge-shaped in girdle view	heteropolar in valve view and wedge-shaped in girdle view
Chloroplast	one, large, butterfly-like, valve-appressed along their length	numerous, elongate-lenticular, radiating around a center (central nucleus?)	two H-shaped with large pyrenoid/ numerous round, oval, discoid, lenticular plate-like or irregularly shaped distributed throughout the cell/ numerous long lenticular radiating around the central nucleus
Valve outline	narrowly obovate, heteropolar, with a wide rostrate head-pole and a narrow capitate foot-pole	broadly oval, slightly narrower at the foot-pole	cuneate, spatulate, clavate, with pointed or inflated head-pole and attenuate or inflated foot-pole
Sternum	central, narrow, straight, slightly raised internally	central, narrow, irregular	central, narrow, straight, slightly raised internally
Striation pattern	transverse, perpendicular to the sternum, striae uniseriate, extending through the valve mantle until the plain valvar margin except at the poles where they radiate from the end of the sternum	transverse, perpendicular to the sternum, striae uniseriate, extending through the valve mantle until the plain valvar margin except at the poles where they radiate from the end of the sternum	transverse, perpendicular to the sternum, striae uniseriate, extending through the valve mantle until the plain valvar margin except at the poles where they radiate from the end of the sternum
Areolae	poroid, elliptical, elongate in transapical direction and externally occluded	poroid, elliptical, elongate in transapical direction	poroid, elongate in transapical or in apical direction and externally occluded
Sessile rimoportula pattern	several at foot-poles on valve surface and mantle, isovalvar distribution	several at foot-poles, heterovalvar distribution	absent/several along the sternum in some species
Pedicellate rimoportula pattern	absent	2 or 3, heterovalvar distribution	2 or 3, heterovalvar distribution
Apical slit field	present at both poles, slits with horizontal cross bars	absent	present at foot-pole, slits without horizontal cross bars
Valvocopulae	open in the foot-pole, with a row of poroids in the pars interior through their length and several rows in the pars exterior in the head-pole that shorten towards the poles of the band	unknown	open in the foot-pole, with a narrower pars interior than pars exterior, several rows of poroids in pars exterior in the head-pole that shorten towards the poles of the band.
Septum	short septum at the head-pole on each valvocopulae	unknown	most species with short or deep septum on each valvocopulae
Copulae	open, tapered towards the ends, with splits nearly 180° apart at poles, decreases in width in abvalvar direction	finely punctate, similar to the valve surface	open, tapered towards the ends, with splits nearly 180° apart at poles, decreases in width in abvalvar direction

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