Stephanopyxis species (Bacillariophyceae) from shelf and slope waters of the Argentinean Sea: Ultrastructure and distribution

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Abstract: *Stephanopyxis* is a cosmopolitan planktonic marine diatom genus. It comprises a large number of fossil species but only four living species: *S. nipponica*, *S. orbicularis*, *S. palmeriana* and *S. turris*. In this study, the morphology and occurrence of *Stephanopyxis* species were studied by means of light and scanning electron microscopy from the inner shelf to slope waters of the Argentinean Sea. Two species, *S. nipponica* and *S. turris*, were found. In both species the ultrastructure of the valve showed two different morphological forms. One form had true poroid aereolae, with an external foramen and an internal cribral velum while the second one had a network of hexagonal compartments with an external opening but lacking an internal cribral velum. The structure of the linking rimoportulae and the presence of acceptant process in the vegetative cells of *S. nipponica* distinguished this species from the other living *Stephanopyxis* species. We consider that the orientation of the rimoportulae located on the mantle margin as well as the presence of scattered rimoportulae on the valve surface in the resting spores are not useful taxonomic characters to differentiate between the vegetative and resistance cells of *S. nipponica*. *Stephanopyxis turris'* main morphometric and ultrastructural features coincided with the diagnosis of this species. However, some lightly silicified specimens presented a different type of areolae in the valvar mantle, not previously described. We give also new information on cingulum structure for *S. turris*, which is high with a narrow valvocopula and numerous segmented girdle bands, similar to other species of the genus. Finally, we provide data on the *S. nipponica* and *S. turris* occurrence, cell abundance and environmental data in the Argentinean Sea, including remarks on their distribution in southern South America.

Key words: *Stephanopyxis*, diatom, morphology, distribution, Argentinean Sea.

Introduction

The taxonomic status of the genus *Stephanopyxis* Ehrenberg has been discussed on several occasions, not being easy to place in the upper taxonomic levels. Early studies based on light microscopy placed *Stephanopyxis* in the family Melosiraceae (Simonsen 1979). Later investigations with electron microscopy provided additional morphological information, leading to a different classification. Glezer et al. (1988) placed *Stephanopyxis* in the family Pyxidiculaceae Nikolaev, which is characterized mainly by the location of a velum in the areolae on the internal surface of the valve. On the other hand, Round et al. (1990) included this genus into Stephanopyxidaceae Nikolaev.

Stephanopyxis is a diatom genus restricted to marine plankton, occurring from polar to tropical regions (Garrison 1991, Hoppenrath et al. 2009). The genus comprises a large number of species, most of them belonging to the fossil record (Jousé 1978, Haga 1997). By contrast, only four living species are known: *S. palmeriana* (Greville) Grunow, *S. turris* (Greville & Arnottt) Ralfs, *S. nipponica* Gran & Yendo and *S. orbicularis* Wood, Crosby & Cassie (Haga 1997). The most relevant characteristics for species identification include the areola density, the morphology of external processes, the presence of acceptant processes, the density of cribral pores and the orientation of the marginal rimoportulae (Cupp 1943, Round 1973, Haga 1997). However, some of these characteristics sometimes overlap, complicating species identification (Haga 1997, Gómez 2008).

Stephanopyxis has been frequently mentioned in lists of phytoplankton species from the South Atlantic (Ferrario & Galvan 1989), making the region ideal to study diversity in this genus. However, morphological descriptions by light microscopy are only available for *S. turris* (Frenguelli 1928, Sar 1996). The ultrastructure by electron microscopy, distribution and abundance of *Stephanopyxis* species have never been studied in the Argentinean Sea.

The aim of this work is to analyse the morphology and occurrence of *Stephanopyxis* species by means of light and scanning electron microscopy in the Argentinean Sea, from inner shelf to slope waters. In addition, we provide comments on their distribution in the southern South American waters (Brazil, Uruguay, Argentina, and Chile), including remarks on cell abundance and environmental data.

Materials and methods

The continental shelf and slope waters of the Argentinean Sea were sampled from 8 to 28 October 2005 (austral spring) onboard R/V "Puerto Deseado". Phytoplankton samples for qualitative and quantitative analyses were taken at 74 stations distributed along 9 on-offshore transects located approximately between 38–55°S and 55–68°W (Fig. 1).

Surface samples were collected at 3 m depth using a continuous seawater pumping system (Balestrini et al. 2000). Qualitative samples were taken using a 20 μm mesh net, whereas quantitative samples were collected in 250 ml bottles. All samples were fixed with Lugol's iodine solution. Water temperature and salinity were measured continuously with Sea-Bird SBE 1621 and 37SI sensors.
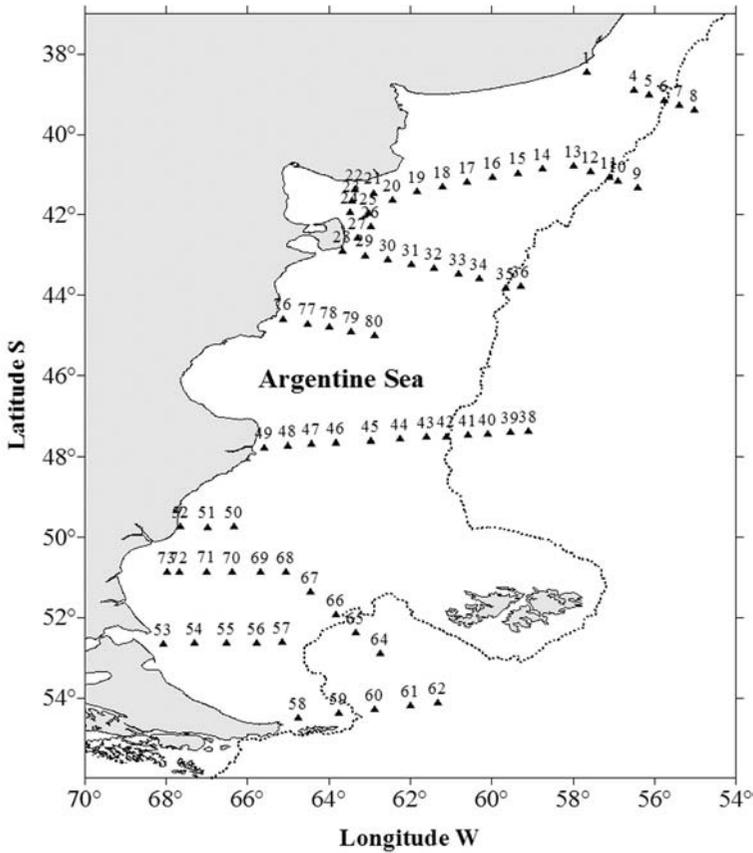
Fig. 1. Map of the study area showing the location of transects and sampling stations.

For morphological species identification, net samples were cleaned of organic matter according to Hasle & Fryxell (1970) and Prygiel & Coste (2000), and dried onto cover glasses for mounting in Naphrax medium for light microscopy (LM) and onto stubs subsequently shadowed with gold-palladium for scanning electron microscopy (SEM, Ferrario et al. 1995). LM observations were made using a phase contrast and a differential interference contrast Leica DM 2500 microscopes equipped with a Leica DFC420 C digital camera. SEM observations were done with a Jeol JSM-6360 LV located at the Museo de La Plata. Voucher material and permanent glass slides were stored at the Diatom Collection (LPC), of the División Ficología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina.

For quantitative estimations, cells fixed in Lugol were enumerated using a phase contrast Leica DMIL LED inverted microscope according to the procedures described by Utermöhl (1958). The whole chamber (100 ml) was scanned at 20× to count *Stephanopyxis* specimens.

The terminology in this study follows mainly von Stosch (1975), Round et al. (1990), Haga (1997) and Hasle & Syvertsen (1997).

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Results

Stephanopyxis nipponica Gran & Yendo   Figs 2a–b, 3a–f, 4a–f

Cupp (1943), p.43, fig. 5 a–b; Haga (1997), p. 217–228, figs 1–20.

MORPHOLOGY: Cells with numerous discoid chloroplasts and connected by long and slender processes that link up to 4 cells in straight chains (Figs 2a, b). The frustules are cylindrical in girdle view (Fig. 3a), the valves are domed with a high valve mantle (Fig. 3b), 21–42 µm in diameter.

The areolae (4–6 in 10 µm) are hexagonal and arranged in tangentially curved striae (Fig. 3c). They have a large external circular foramen and the inner face covered by a continuous sheet of very small cribral pores (5–6 in 1 µm) radially distributed (Fig. 3d). Different from a true areola sensu Hasle & Syvertsen (1997), the cribral pores are not restricted to the floor of the areola; rather they are continuously distributed from the valve centre, uninterrupted by the vertical locular walls.

There are two different types of connecting processes in this species. One of these, called linking rimoportulae, has an external long tubular extension and a buttress at its base, lacking a fusion line mid way between cells. They are placed close to the valve centre in number of 2–5 (Fig. 3e). The other one, termed acceptant process, without internal rimoportula, is short and associated with the long tubular extension linking to the adjoining valve (Fig. 3f). Other smaller rimoportulae, without external tubular prolongation, are arranged in a ring at the marginal valve mantle with parallel or oblique orientation to the margin (Figs 3b, d).

Resting spores are heterovalvar, highly silicified and nearly hemispheric in shape. The domed valve presents 2 to 5 tubular linking processes that, unlike those observed in vegetative cells, are generally shorter and grouped at the valve center (Figs 4 a–c). Similar to the vegetative cells, other smaller rimoportulae are arranged in a ring placed at the marginal valve mantle (Fig. 4c). The other valve is relatively flat and has no tubular linking processes (Fig. 4d). The distribution of the cribral pores in these resting spores is different in each type of valve. In the flat valves, they are continually distributed from the valve centre to the margin, similar to the vegetative cells, whereas in the domed valves the cribral pores sensu stricto are confined to the centre of each areola (Fig. 4e).

The structure of the cingulum could not be observed, and only some resting spores presented an apparent remnant valvocopula, which has small pores (4–4.5 in 1 µm) arranged in parallel rows (Fig. 4f).

REMARKS: *S. nipponica* can be distinguished from other living *Stephanopyxis* species by an unusual character, the acceptant process, located in the vegetative cells (Haga 1997), whereas other morphological distinctions are generally more subtle.

Different from Haga's (1997) observations, the orientation of the rimoportulae found at the marginal valve mantle can have not only a perpendicular or parallel orientation to the valve margin but also an oblique one. These three types of orientations were observed in the same valve, both in vegetative cells as well as in resting stages (Figs 3d and 4e). On the other hand, unlike Haga's (1997) observations on the spores of
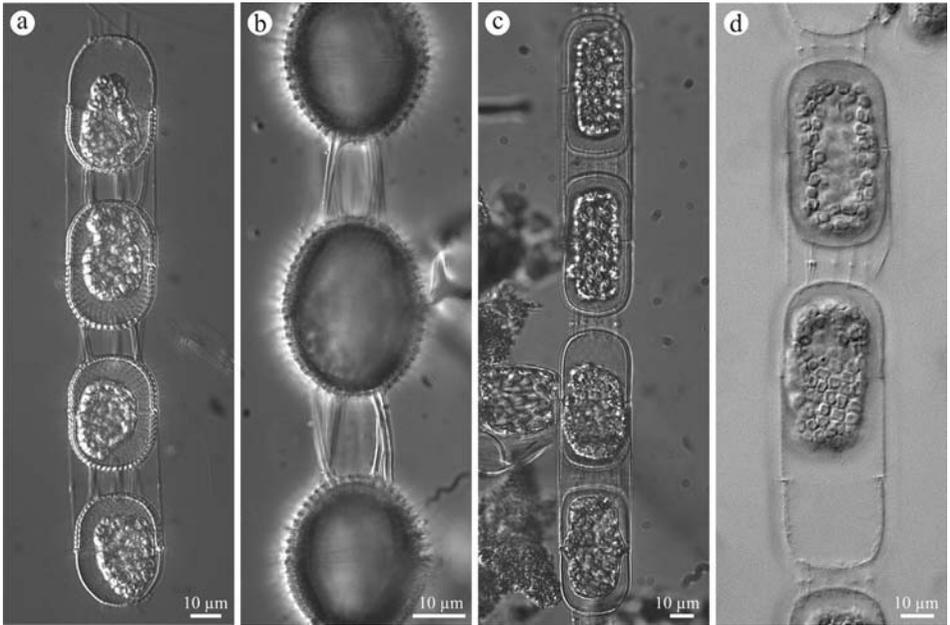
Fig. 2. *Stephanopyxis nipponica* (a–b) and *S. turris* (c–d). LM. (a) Chain of four cells; 40×. (b) Detail of linking rimoportulae; 100×. (c) Chain of four cells; 40×. (d) Detail of linking rimoportulae with distinctive fusion line; 100×.

resistance, the specimens we analyzed showed no additional rimoportulae scattered on the valve face.

DISTRIBUTION: *S. nipponica* has been reported as a neritic species found in north temperate to arctic waters (Horner 2002). In southern South America, this species has been cited only in Chile and Argentina. In Chilean waters, it was observed as a frequent species during winter at ≈41–43°S, significantly contributing to total phytoplankton biomass (Valenzuela & Avaria, 2009). In the Argentinean Sea, it has been previously recorded between 52-56°S at temperatures ranging from 5.35 to 6.84°C (Balech 1971, 1978). During the present study *S. nipponica* was observed in 23% of the samples examined. Its distribution was restricted to colder waters (4.8–7.1°C) of the southern shelf and shelf-break (Fig. 5). The highest abundances were recorded at stations 60 and 61 (≈54°S), where it reached a maximum of about 1,500 cells l^{-1}, at temperatures of 5.5–5.7°C and salinities of 33.84–33.95 psu.

Stephanopyxis turris (Greville & Arnott) Ralfs   Figs 2c–d, 6a–f, 7a–f

Hasle (1973), pag. 127, figs 9197, 104–112. Simonsen (1974), pag. 7–8. Hoppenrath et al. (2009), pags 42–44, figs 17 a–j.

MORPHOLOGY: Cells with numerous discoid chloroplasts and connected by short linking processes to form straight chains, usually four cells long. The frustules are cylindrical
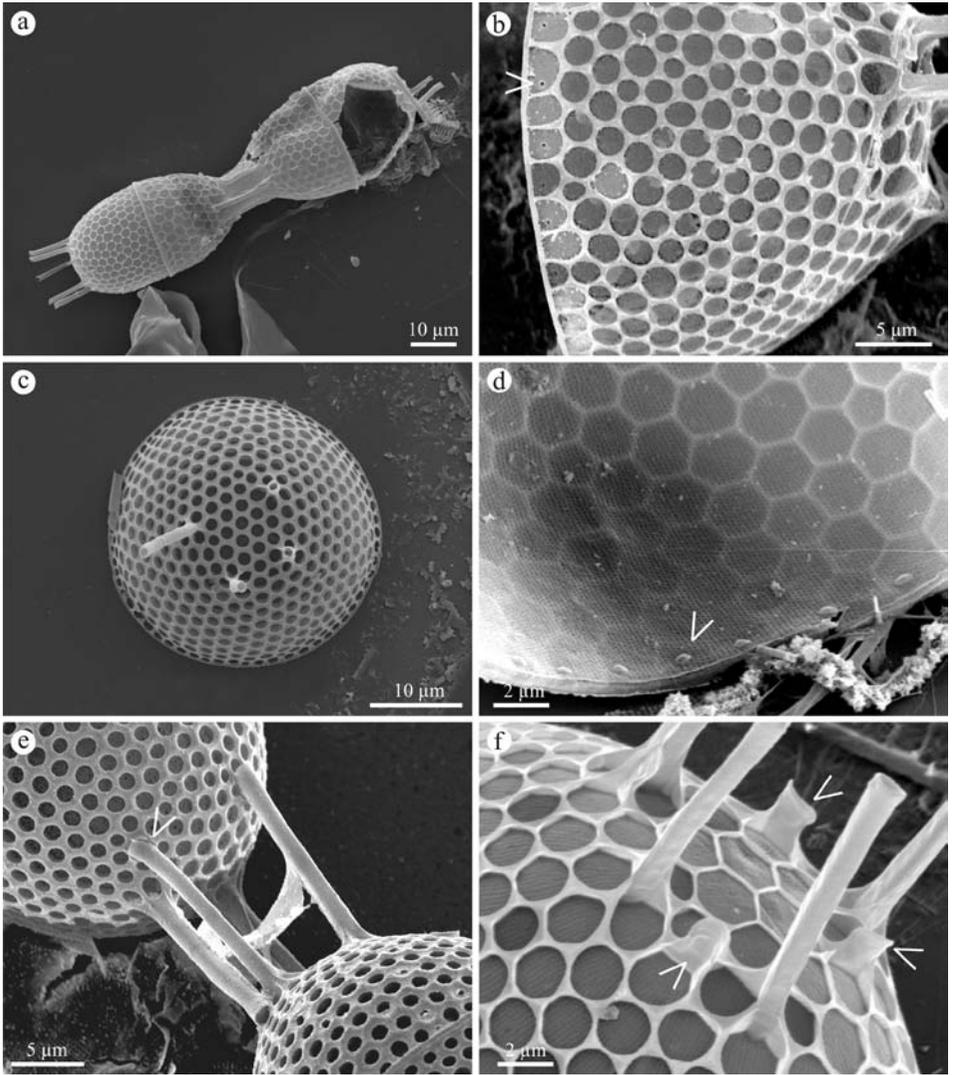
Fig. 3. *Stephanopyxis nipponica*. SEM. (a) Part of colony showing the cylindrical shape in girdle view. (b) Domed valve with a high mantle. Note the rimoportulae arranged in a ring at the marginal valve mantle (arrowhead). (c) Arrangement of the areolae in tangential curved striae. (d) Internal valve view showing a continuous sheet of very small cribral pores radially distributed. Note the marginal rimoportulae with parallel or oblique orientation (arrowhead). (e) Linking rimoportulae and acceptant processes (arrowhead) placed close to the valve centre. (f) Detail of acceptant processes (arrowhead).

in girdle view (Figs 2c, d), the valves are domed with a high valve mantle (Fig. 6a), 27–48 μm in diameter.
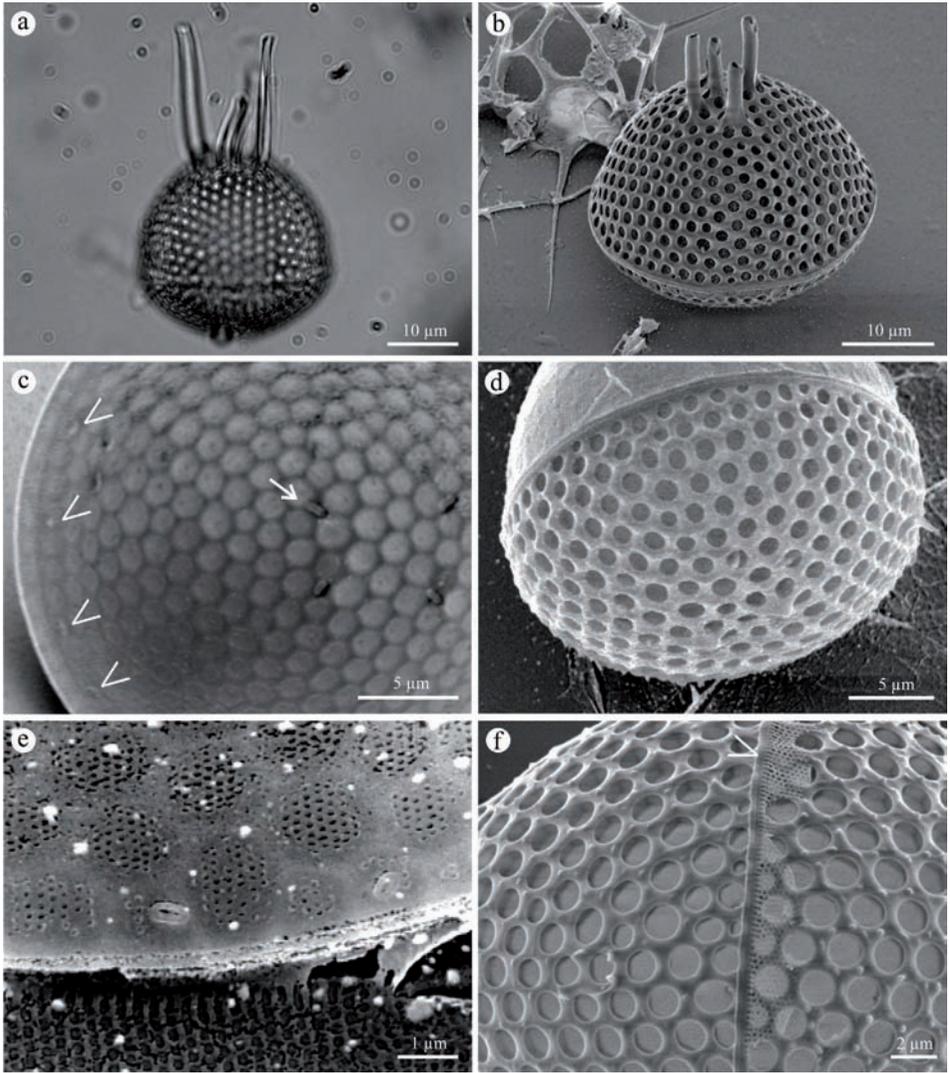
Fig. 4. *Stephanopyxis nipponica.* Resting spores. (a) LM. (b–f) SEM. (a–b) Different specimens showing domed valve with linking rimoportulae, absent on flat valve. (c) Internal valve view showing four linking rimoportulae (arrow) and part of the marginal ring of rimoportulae (arrowhead). (d) Flat valve without tubular linking processes. (e) Cribral pores confined to the centre of each areola. (f) Remains of the valvocopula with pores arranged in parallel rows.

The areolae (4–5 in 10 μm) are mainly hexagonal, with a large external circular foramen (Fig. 6b) and the inner face is covered by a continuous sheet of very small cribral pores (4–6 in 1 μm) (Fig. 6c). Similar to *S. nipponica*, the cribral pores are not restricted to the aerola base rather they are placed in a continuous sheet covering the valve interior.
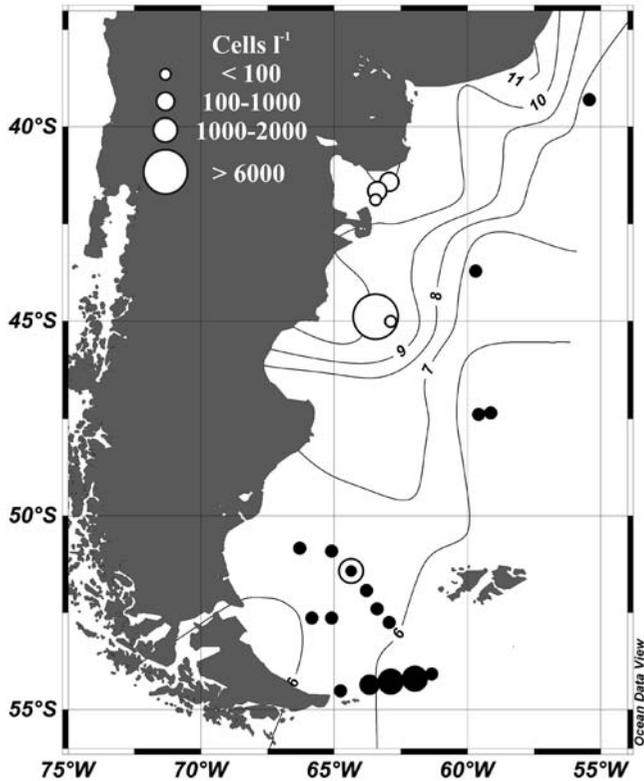
Fig. 5. Distribution and abundance of *S. nipponica* (black circles) and *S. turris* (white circles) in continental shelf and slope waters of the Argentine Sea. Isolines refer to horizontal distribution of surface temperature (°C) in the study area.

The linking rimoportulae are situated at irregular intervals in a ring between the valve face and the valve mantle, in number of 5 to 12 (Fig. 6d). Each one is slightly thickened at the tip highlighting a distinctive fusion line mid way between the cells of a chain (Figs 2c, d). Smaller rimoportulae, without external tubular prolongation, are located in a ring at the marginal valve mantle (Figs 6e and 7d). Occasionally a few additional rimoportulae processes were also observed both at the edge valve mantle (Fig. 6f) as well as close to the ring of linking rimoportulae (Fig. 7a).

The cingulum is high and extremely fragile, with numerous girdle bands, each of them formed of several segments (Figs 7b, c).The valvocopula is narrow, apparently not segmented, and has the same ornamentation as the other bands, with pores (4–4.5 in 1 µm) arranged in parallel rows (Fig. 7d).

REMARKS: In the present study we were not able to distinguish any resistance spores, as previously described for *S. turris* (Hasle 1973).
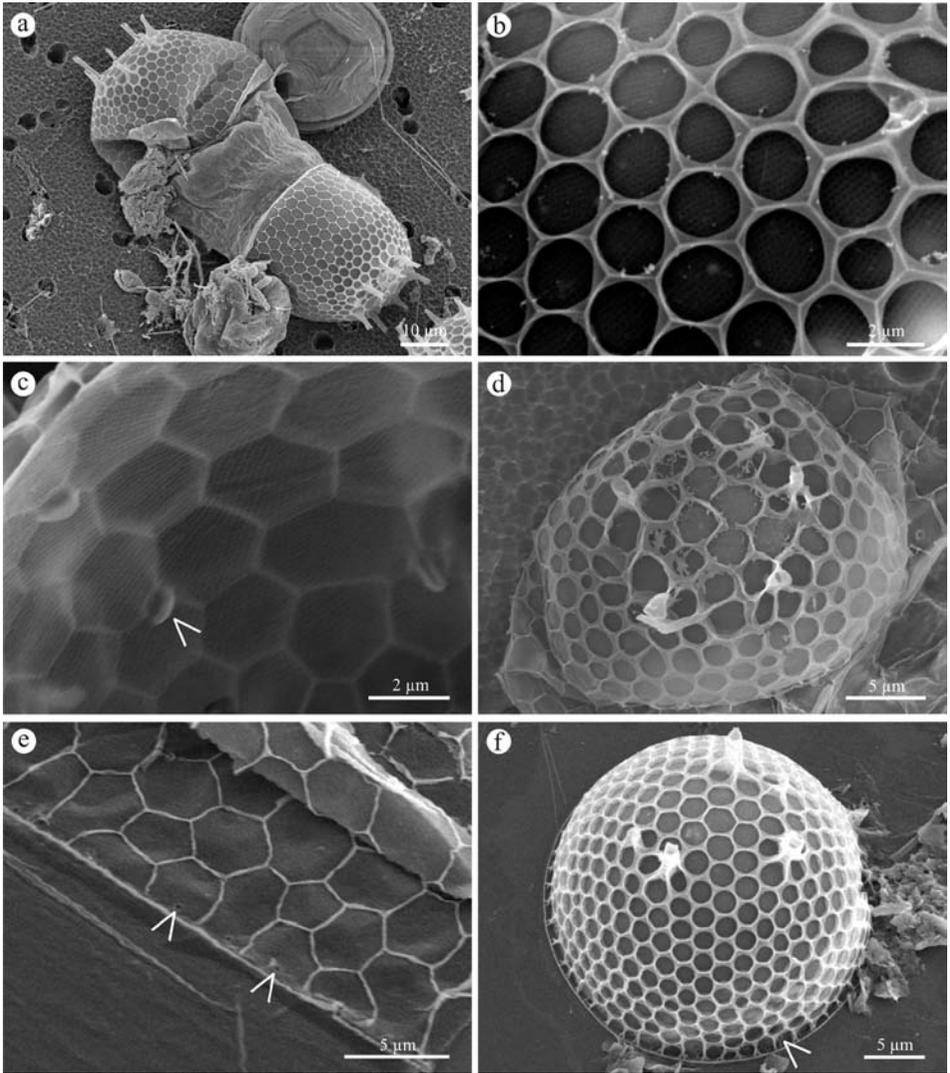
Fig. 6. *Stephanopyxis turris*. SEM. (a) Domed valve with a high mantle and linking rimoportulae. (b). Hexagonal areolae in external view, showing a large circular foramen. (c) Internal valve view covered by a continuous sheet of very small cribral pores. Note the linking rimoportulae (arrowhead). (d) Linking rimoportulae arranged irregularly in a ring. (e) Small rimoportulae arranged in a ring at the marginal valve mantle (arrowhead). (f) Same type of ring but showing additional rimoportulae processes (arrowhead).

Some specimens with extremely thin walls were observed in our material, showing areolae of different size and shape, which as far as we know have not been described previously. The areolae were hexagonal and sometimes smaller over the valve face and part of the mantle, polygonal and larger in the rest of the valve mantle (Figs 7e, f).
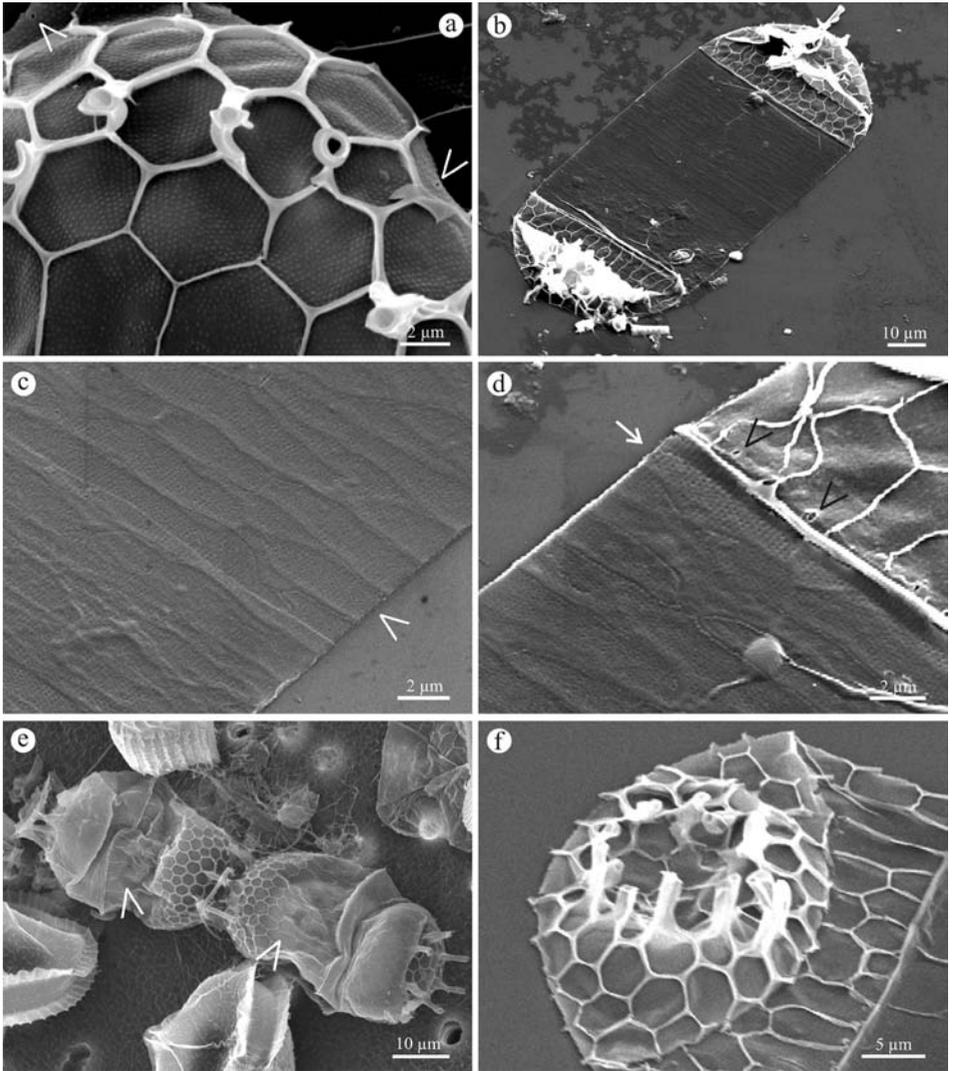
Fig. 7. *Stephanopyxis turris*. SEM. (a) External valve view showing the continuous sheet of very small cribral pores, the linking rimoportulae and the additional rimoportulae processes (arrowhead). (b) General girdle view. (c) Cingulum with numerous segmented bands (arrowhead). (d) Valvocopula, apparently not segmented, with pores arranged in parallel rows (arrow). Note also the marginal rimoportulae (arrowhead). (e) Specimens with different size and shape of areolae (arrowhead), (f) detail of the areolae.

DISTRIBUTION: *S. turris* is a neritic species found in tropical/subtropical to temperate waters of all oceans (Simonsen, 1974). In southern South American, it has been frequently cited in the Atlantic coast of Brazil, south of 23°S (Villac et al. 2008), Uruguay (Muller-Melchers 1959) and Argentina (Ferrario & Galvan 1989). In the

Pacific, it was recorded in Chile from 18º28'S to the Magellan Strait (≈53°S) (Rivera 1983). In the Argentinean Sea, it has been previously recorded both in coastal and neritic areas between 36–54°S and temperatures between 5.64 and 17°C (e.g. Hendey 1937, Balech 1971, Lange 1985). Although cell densities are not available, it is usually mentioned as a rare species (Frenguelli & Orlando 1959, Olguin et al. 2007). More recently this species was observed as a conspicuous component of diatom assemblages within the range of 20–200 μm in the southern Patagonian shelf (Sabatini et al. in press). During the present study *S. turris* was observed in only 8.1% of the examined samples. Its distribution was confined to shelf waters between 41 and 45°S (9.3–11.4°C), except for a record at 51°S at a temperature of 6.32°C (Fig. 5). The highest abundance was recorded at station 79, where it reached a maximum of 6,720 cells l^{-1}, at a temperature of 9.8°C and a salinity of 33.24 psu.

Discussion and conclusions

Two *Stephanopyxis* species, *S. nipponica* and *S. turris*, were found and described from inner shelf and oceanic waters of the Argentinean Sea by light and scanning electron microscopy.

In both species the ultrastructure of the valve showed two different morphological forms. One form had true poroid aereolae, with an external foramen and an internal cribral velum, while the second one did not present true aerolae (Figs 4c, e). Instead, we observed a network of hexagonal compartments with varying wall height, with a circular external opening but lacking an internal cribral velum (Figs 3d and 7a). By SEM analyses, it was possible to observe that there is a continuous inner sheet of silica perforated by cribral pores, which is not interrupted by the vertical compartment walls (Figs 3d and 6c). This structure was seen in the vegetative cells of both species, whereas true poroid areolae were only observed in the resting spores of *S. nipponica*.

Based on the analysis of our material, we consider that the orientation of the rimoportulae located on the mantle margin as well as the presence of scattered rimoportulae on the valve surface in the resting spores, proposed previously as differential characters between the vegetative and resistance cells in *S. nipponica* (Haga 1997), were not diagnostic characters possible to implement.

If we analyze the characters that differentiate the four living species in the genus, *S. palmeriana*, *S. orbicularis, S. turris* and *S. nipponica,* we find they are applicable to all species with the exception of *S. orbicularis* (Table 1). Based on the original description, this latter species could correspond to any of the other three. Therefore, it would be advantageous to analyze *S. orbicularis* type material with SEM in order to confirm its taxonomic status.

The architecture of the linking rimoportulae and the acceptant processes allow the separation of *S. niponnica* from *S. palmeriana* and *S. turris*. The two latter species can be differentiated by the aereolae density, where *S. turris* has a similar number of aereolae in the valvar surface and mantle and *S. palmeriana* has larger areolae on the valve face than on the valve mantle (Table 1).

Table 1: Comparison between morphological and ecological characteristics of living *Stephanopyxis* species.

Stephanopyxis species	*S. nipponica*	*S. orbicularis*[2]	*S. palmeriana*[7]	*S. turris*
Cell shape	Cylindrical-domed	Orbicular	Cylindrical	Cylindrical
Chloroplasts	Numerous and discoids	n/d	Numerous [3]	Numerous
Diameter (µm)	21–42	25–30	27–71 [4]	27–48
External structure of linking rimoportulae	Without fusion line mid way between cells	n/d	With distinctive fusion line mid way between cells [4]	With distinctive fusion line mid way between cells
Acceptant processes	Present	n/d	Not present	Not present
Rimoportulae without external extension.	One ring placed at the marginal valve mantle	n/d	One ring placed at the marginal valve mantle [5]	One ring placed at the marginal valve mantle
Density areolae	Same size (4–6 in 10 µm)	n/d	Two different sizes, valve surface 1,5–2,5 in 10 µm and valve mantle (3,5–5,5 in 10 µm) [6]	Same size (4–5 in 10 µm)
Density cribral pores	5–6 in 1 µm	n/d	n/d	4–6 in 1 µm
Cingulum	Valvocopula complete? Bands segmented [1]	Delicate without visible sculpture	Valvocopulae and bands segmented [7]	Valvocopula complete? Bands segmented
Habitat	Neritic to oceanic	Neritic	Neritic [3, 6]	Neritic
Distribution	Temperate to cold waters [5]	n/d	Temperate to warm waters [4]	Tempate to warm waters

n/d, no data. [1] Haga (1997). [2] Wood et al. (1959). [3] Hoppenrath et al. (2009). [4] Hasle & Syvertsen (1997). [5] Hasle (1973). [6] Cupp (1943). [7] von Stosch (1975).

In this paper we provide new information on cingulum structure for *S. turris*. The cingulum in this species was similar to that of *S. palmeriana,* described in detail by Von Stosch (1975), *S. nipponica* (Haga 1997) and also to the information provided for the genus (Round 1973, Round et al. 1990).

Although the main morphometric and ultrastructural features of *S. turris* coincided with the diagnosis of this species, some lightly silicified specimens presented a different type of aerolae in the valvar mantle (Figs 7c, f), not previously described. Further analysis of these samples by molecular techniques (mainly from Stations 21, 23 and 24 in Fig. 1) could shed light if this difference could be used as an intraspecific diagnostic tool.

With the exception of the presence of *S. turris* at station 67 (6.32°C), the distribution of *Stephanopyxis* species was as expected, with *S. turris* found at higher and *S. nipponica* at lower water temperatures. Argentinean continental shelf waters north of ~46°S, where *S. turris* occurred, were characterized by temperatures between 9.3 and 11.4°C. Towards the south of ~50°S and on the continental slope between 38–55°S, *S. nipponica* occurrence was associated to temperatures between 4.8 and 7.1°C. Shelf waters have a sub-Antarctic origin, with important input from waters of the Magellan Strait and the southern fjords, and they are diluted from south to north by the continental discharge (Guerreo & Piola, 1997; Piola & Rivas, 1997). The continental slope defines an area with high biological diversity and productivity, and it is directly influenced by the Malvinas Current, which runs along the slope from Drake Passage to ~38°S (Bianchi et al. 2005). Stations 21, 23 and 24, opposite Gulf of San Matías, where *S. turris* appeared restricted to a small area, are locations with particular characteristics: high water temperatures and salinities due to a thermal anomaly resulting from waters of long residence time originating from within the gulf (Piola & Scasso, 1988; Rivas & Beier, 1990, Bianchi et al. 2005).

The results presented here allow us to confirm *S. nipponica* as a cold-water species, typical of neritic environments. However, it was also observed in oceanic waters, as previously mentioned by Balech (1971, 1978) increasing its known northern distribution in the western South Atlantic ocean to 39.26°S. By contrast, the distribution of *S. turris* was mainly confined to temperate waters (9.3 to 11.4°C) but it was exceptionally found in cold waters (6.32°C). In the southern South American waters (Brazil, Uruguay, Argentina, and Chile), *S. nipponica* had only been reported previously in Argentina and Chile while *S. turris* had been found in all four countries.

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