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Discostella taxa (Bacillariophyta) from the Río Limay basin (northwestern Patagonia, Argentina)

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Discostella stelligera and allied similar taxa are mainly identified by the presence of marginal fultoportulae located at the end of the striae, and not on the interstriae, as occurs in the genus *Cyclotella*, from which they have recently been removed. In this paper, valve morphology and ultrastructure of *D. stelligera*, *D. glomerata*, *D. pseudostelligera* and *D. woltereckii* collected from different environments within the Río Limay basin are described and illustrated. Morphological characters that allow the delimitation of taxa within the group are discussed and the ultrastructure of *D. stelligera* var. *elliptica* comb. nov. is shown for the first time. Two organisms that possess distinct morphological characters, and might be considered new species, are described.

Key words: Argentina, *Discostella stelligera* var. *elliptica*, Patagonia, stelligeroid *Cyclotella*, taxonomy, ultrastructure

Introduction

Cyclotella Kützing is a heterogeneous genus comprising several morphological subgroups (Lowe, 1975; Serieysson, 1981, 1984; Krammer & Lange-Bertalot, 1991), one of which includes *Cyclotella stelligera* Cleve & Grunow and allied taxa. These were referred to as 'stelligeroid' taxa. According to Houk (1992) and Klee & Houk (1996), this group is defined by the following characters: (i) central area of valve face with star-like ornamentation, i.e. radially arranged striae surrounding a central areola or group of areolae, corresponding internally to alveolar chambers; (ii) marginal fultoportulae with more or less distinct external projections, located in the striae and not on the interstriae as in the other members of the genus; (iii) rimoportula situated on valve mantle, unlike other species of *Cyclotella* in which it is located on the valve face or at the valve face/mantle junction.

Recently, Houk & Klee (2004) transferred these taxa into the new genus *Discostella* Houk & Klee, based on the position of both fultoportulae and rimoportula within the striae, in contrast to *Cyclotella* where these processes are located within the interstriae.

Since the species within this new genus are mostly heterovalvar (i.e. one frustule has two distinctly different valves), small and with a similar areolation pattern on the valve face, it is quite difficult to identify them accurately with light microscopy alone.

The purpose of this paper is to present the valve morphology and ultrastructure of several *Discostella* taxa collected at different sites in the Río Limay basin (northwestern Patagonia, Argentina) and to discuss the characters that allow their taxonomic delimitation. We also present the first ultrastructural study of *Discostella stelligera* var. *elliptica* (Frenguelli) Guerrero & Echenique, comb. nov.

Materials and methods

Samples were collected with a 30- μ m mesh plankton net from lakes, rivers and reservoirs within the Río Limay basin (northwestern Patagonia, Argentina) from 1981 to 1997 (Table 1). Material was fixed with 4% formalin or 50% Transeau solution, and has been deposited at the Herbarium of the Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo de La Plata. The sample LP(C) 3313 has also been deposited at the Diatom Herbarium of the Academy of Natural Sciences of Philadelphia (slides A-GC 26791a and A-GC 26791b, and unmounted material A-Mat. #10299).

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The material mentioned in the protologue of *Cyclotella stelligera* var. *elliptica* Frenguelli (Frenguelli, 1942), collected at Río Manso Inferior (Province of Río Negro, Argentina) and included in the Colección de Diatomeas Argentinas ‘Dr. Joaquín Frenguelli’ (series No. 422, slides 2–6) was also examined for comparison. Since Frenguelli (1942) did not designate a holotype, we chose slide No. 4 as the lectotype, since it is the best preserved among the syntype series (see the recommendations of the International Code of Botanical Nomenclature, Greuter *et al.*, 2000).

Material was cleaned to remove organic material according to procedures proposed by Hasle & Fryxell (1970) and mounted as permanent slides with Hyrax. Diatom strews were studied with light microscopy (LM) using a Wild M20 microscope and a Nikon Microphot-FX photomicroscope equipped with phase contrast optics. For scanning electron microscopy (SEM) material was mounted on glass coverslips attached to stubs, coated with gold-palladium and examined with a Jeol JSM T-100 microscope at the Servicio de Microscopia

Table 1. Collecting dates and sites for samples examined in this study. LP(C) refers to the Herbarium of the Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo de La Plata

Sample number	Date	Site
LP(C) 3313	August 1981	Río Collon Cura
LP(C) 3319	January 1981	Río Limay (headwaters)
LP(C) 3321	January 1982	Río Alumine
LP(C) 3333	September 1995	Arroyito Reservoir
LP(C) 3337	October 1994	Piedra del Aguila Reservoir (near dam)
LP(C) 3339	April 1996	Piedra del Aguila Reservoir
LP(C) 3341	August 1981	Lago Nahuel Huapi
LP(C) 3342	August 1981	Río Limay (downstream Arroyo Carbón)
LP(C) 3343	August 1981	Río Traful
LP(C) 3352	August 1981	Río Limay (headwaters)
LP(C) 4502	June 1981	Río Chimehuin
LP(C) 4518	August 1981	Río Limay (at Estancia La Picasa)
LP(C) 4519	October 1997	Alicura Reservoir
LP(C) 4520	April 1996	Piedra del Aguila Reservoir (near dam)

Table 2. Comparative morphological features of the *Discostella* taxa from the Río Limay basin (Argentina)

	Diameter (µm)	Striae/10 µm	Areolae/10 µm	External fultoportula opening	Striae/fultoportulae	Frustule heterovalvar	Valve mantle
<i>D. stelligera</i> var. <i>stelligera</i>	7.5–20	9–12	28–36	With slightly raised rim	2	+	Scarcely developed
<i>D. stelligera</i> var. <i>elliptica</i> ^a	11–20 × 9–15.5 (14.5–23 × 12–20)	10–14 (10–15)	40–50 (45–50)	With slightly raised rim	1–2	–	Scarcely developed
<i>D. glomerata</i>	4–11.5	12–16 (20)	60	Shortly tubular	(1) 2–3	+	Scarcely developed
<i>D. pseudostelligera</i>	5–8	20–24 (28)	55–80	Tubular forked	4–7	+	Developed
<i>D. woltereckii</i>	6.5–7.5	20–22	70–80	Tubular forked	6–7	?	Developed
<i>Discostella</i> sp. 1	20–27.5	9–12	25–30	With slightly raised rim to shortly tubular	1–2	?	Developed
<i>Discostella</i> sp. 2	10.5–18	11–15	50–60	Complex	1–2	+	Developed

^aFigures in brackets correspond to Frenguelli’s material.

Electrónica of the Museo de La Plata. The terminology used is that proposed by Anonymous (1975), Ross *et al.* (1979) and Håkansson (2002).

The study region corresponds to the sector of the Andes known as the Cordillera Neuquina, which is characterized by its mountainous relief and numerous lakes transversely orientated to the ridge, which were formed by Pleistocene glaciers (Holmberg, 1978). These mountain lakes are oligotrophic with bicarbonate and calcium as predominant ions, water temperatures between 7 and 21°C, circumneutral pH (6.9–7.4), low conductivity (20–60 µS cm⁻¹) and reactive silica concentrations of 7–30 mg l⁻¹ (Guerrero *et al.*, 1987; Guerrero & Echenique, 2002). In the mid and low portions of the catchment area, there are several reservoirs whose limnological characteristics indicate that they are oligotrophic to mesotrophic (Labollita & Pedrozo, 1997).

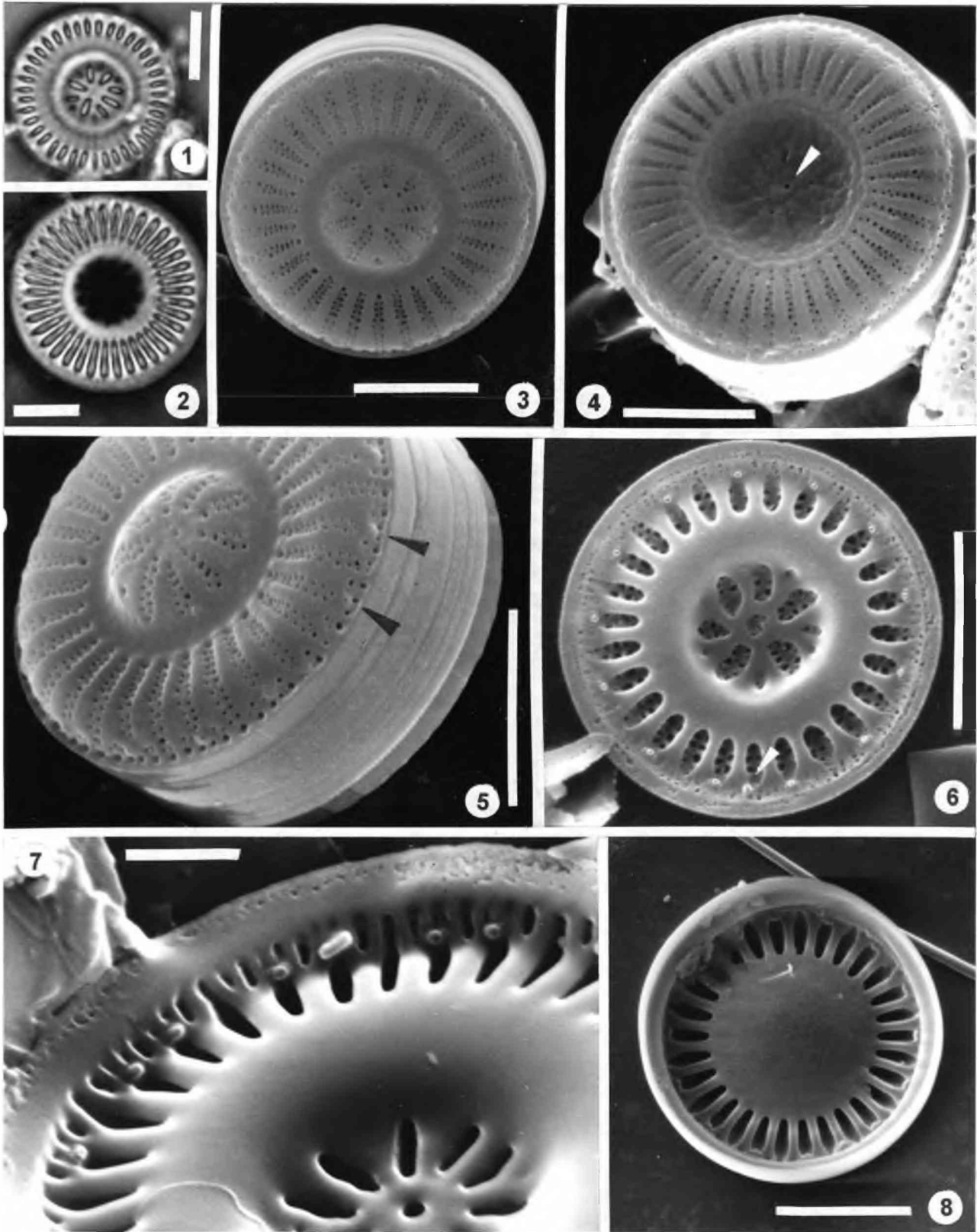
Observations

The main morphological features of the studied taxa are summarized in Table 2.

Discostella stelligera var. *stelligera* (Cleve & Grunow) Houk & Klee (Figs 1–8)

STUDIED MATERIAL: LP(C) 3313; LP(C) 3321; LP(C) 3339 LP(C) 3342 and LP(C) 4518.

Frustules are heterovalvar, shortly cylindrical, 7.5–20 µm in diameter. The valve face is concentrically undulate, with the central area elevated or depressed, separated from the marginal area by a smooth, unornamented ring, hyaline when observed with LM (Figs 1, 2). The convex central area is ornamented by a stellate pattern of radially arranged striae surrounding a single areola or a group of areolae, sometimes alternating with shorter striae and single areolae (Fig. 3). The concave central area is unornamented or has very faint traces of radial striation (‘ghost striae’), occasionally with irregularly scattered areola-like



Figs 1–8. *Discostella stelligera* var. *stelligera*. Figs 1, 2. Light micrographs. Fig. 1. Valve view of a valve with convex central area. Fig. 2. Valve view of a valve with concave central area. Figs 3–8. Scanning electron micrographs. Fig. 3. External view of a valve with a convex central area. Fig. 4. External view of a valve with a concave central area. Note irregularly scattered pores in the central area (arrowhead). Fig. 5. Frustule in girdle view. Arrowheads indicate the external openings of the fultoportulae. Fig. 6. Internal view of a valve with a convex central area. Arrowhead indicates the rimoportula opening. Fig. 7. Detail of preceding figure showing the fultoportula and rimoportula openings. Note costae dividing into two or more branches at the valve mantle. Fig. 8. Internal view of a valve with a concave central area. Scale bars: 5 μm (Figs 1–6, 8); 2 μm (Fig. 7).

openings, only visible in external view since they do not penetrate the siliceous valve (Fig. 4).

The marginal area is occupied by striae (9–12 in 10 μm), each composed of a double row of areolae (Figs 3–5). The areolae (28–36 in 10 μm) tend to fuse towards the centre of the valve, ending in a bigger areola in most cases. The striae are separated by rather poorly defined interstriae and are alveolate internally. In convex valves, the central alveoli are drop-like or elongated (Figs 6, 7), but central alveoli are absent in concave valves and the central area is smooth (Fig. 8). Marginal alveoli are separated by thick costae that divide into two or more branches at the valve mantle (Fig. 7), although in more silicified valves most of the branches are fused.

The valve mantle is hardly developed, although somewhat more extended in convex valves, and there is no clear delimitation between valve face and mantle. The mantle is perforated by larger areolae than the valve face at the ends of striae and interstriae (Fig. 5). The mantle ends in a rim that expands transversely to the pervalvar axis. The fuloportulae are situated at the valve mantle on every other stria. The external fuloportula opening is surrounded by a slightly raised silica rim, located within the stria (Figs 3–5), whilst the internal opening, at the branching point of the costae, has two satellite pores (Figs 6, 7). A single rimoportula is present on the valve mantle, opening to the interior through a sessile labium (Fig. 7). The external aperture could not be identified.

When observed with LM our specimens of *D. stelligera* var. *stelligera* closely resemble those of the type material illustrated by Chang (1991) as Groups B and C. However, in contrast to the type specimens, valves collected from the Río Limay basin exhibit an overall smooth external appearance, without external granules or silica warts. On the concave valves, the central area is smooth and striae are lacking or, at most, very faintly defined. These differences might be related to environmental conditions, such as silica concentration or other water chemistry variables.

The presence of areola-like openings that do not penetrate the valve face has also been reported in *Discostella pliostelligera* (Tanaka & Nagumo) Houk & Klee (Tanaka & Nagumo, 2002).

In Argentina, this taxon has been repeatedly reported as *C. stelligera*, almost exclusively from Patagonian environments (Luchini & Verona, 1972; Tell, 1985; Vouilloud, 2003).

Discostella stelligera var. *elliptica* (Frenguelli)
Guerrero & Echenique, comb. nov. (Figs 9–20)

BASIONYM: *Cyclotella stelligera* var. *elliptica*
Frenguelli in Frenguelli 1942, Revista Mus.

La Plata (nueva serie) Bot., 5: 212, Pl. X, figs 61–62.

LECTOTYPE: Colección de Diatomeas Argentinas 'Dr. Joaquín Frenguelli': series No. 422, slide 4.

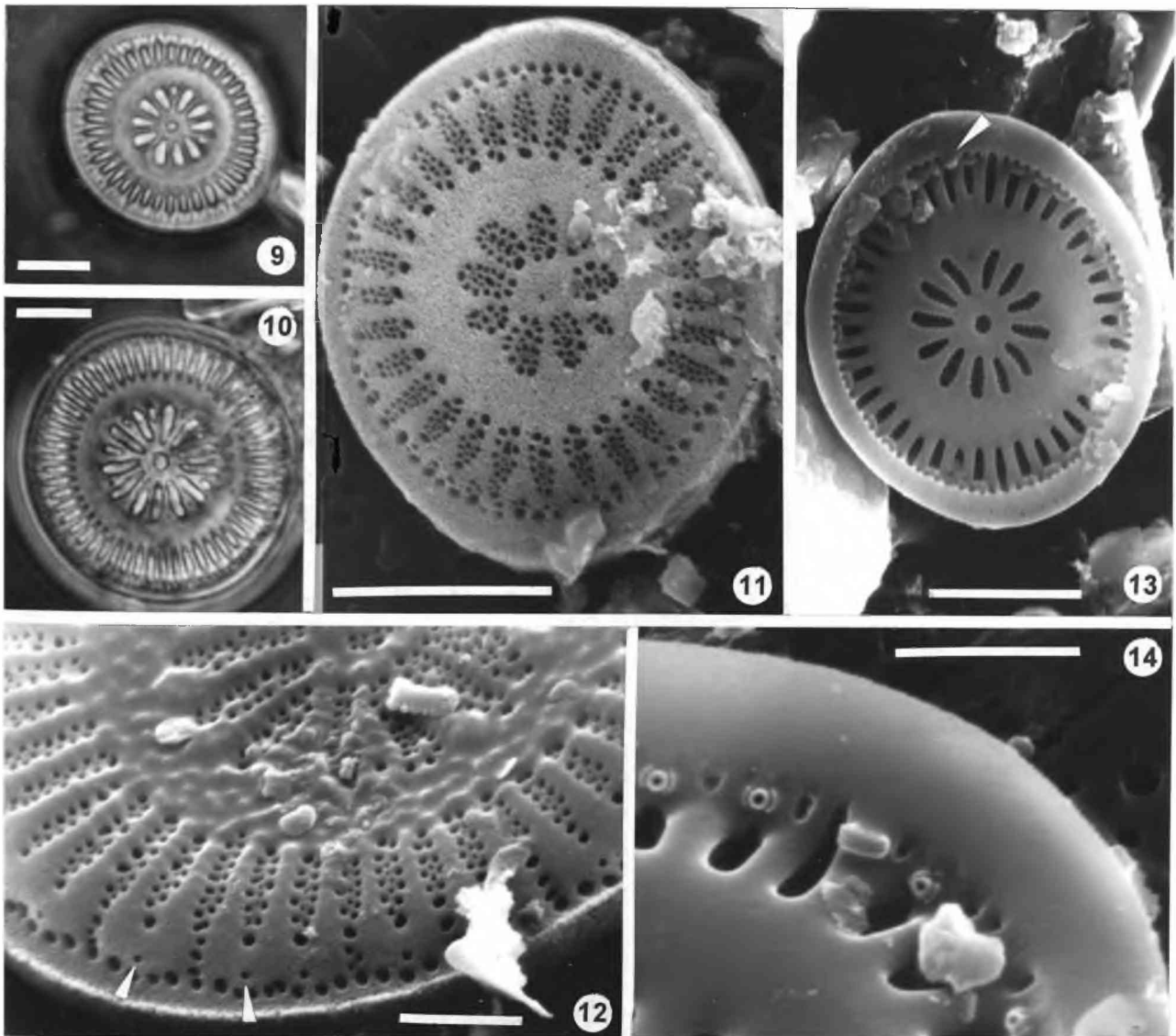
STUDIED MATERIAL: LP(C): 3319; LP(C): 3341; LP(C) 3342 and LP(C): 3352.

In LM the valve face is typically elliptical (Fig. 9) and thus easily distinguishable from the nominate variety with which it often co-occurs. Valve diameter ranges from 11 to 20 μm (greater axis) and from 9 to 15.5 μm (smaller axis). However, some specimens have an almost circular valve face (Fig. 10), mentioned by Frenguelli (1942) in the original description. Nevertheless, even in these cases slight swelling on opposite sides of the valve face allows its identification. Another distinctive feature is that frustules are isovalvar, with flat valve faces, not heterovalvar and concentrically undulate, as in *D. stelligera* var. *stelligera*.

The central area of the valve face is separated from the marginal area by a broad hyaline ring. The central, drop-like or elongated striae are of equal length and surround a central areola in a star-like arrangement. Occasionally shorter striae and small areolae are interspersed among them. SEM reveals that the marginal area is occupied by striae (10–14 in 10 μm) comprising two rows of larger areolae (40–50 in 10 μm), with a third row of smaller areolae between them (Figs 11, 12). A larger areola is generally located at each end of every stria. The interstriae are not very prominent. The striae are internally alveolate, with drop-like or elongated central alveoli (Fig. 13). The marginal alveoli are separated by thick costae that bifurcate into two short branches at the valve mantle (Fig. 14). The fuloportulae are located on every, or every other, stria, opening to the interior between the costal branches and flanked by two satellite pores (Fig. 14). The external opening, surrounded by a slightly raised rim, is located astride the stria (Figs 11, 12). There is one rimoportula on the valve mantle, at one end of the longer axis. Its external aperture is indistinct while the internal aperture has a sessile labium (Figs 12, 14).

The valve mantle is not very developed and is very similar to that of the nominate variety. It is occupied by larger areolae than the valve face, which occur at the ends of striae and interstriae (Figs 11, 12).

We also examined specimens from Frenguelli's material. Both LM and SEM reveal that their valve morphology is very similar (Figs 15–20), but frustule dimensions of specimens on Frenguelli's slides (Table 2) differ from those given in the original description (Frenguelli, 1942).



Figs 9–14. *Discostella stelligera* var. *elliptica* from the Río Limay. Figs 9, 10. Light micrographs. Fig. 9. Valve view of a frustule with an elliptical outline. Fig. 10. Valve view of a frustule with an almost circular valve face. Figs 11–14. Scanning electron micrographs. Fig. 11. External valve view. Fig. 12. Detail of valve mantle showing the external openings of fultoportulae (arrowheads). Fig. 13. Internal valve view. Arrowhead indicates the rimoportula opening. Fig. 14. Detail of internal valve mantle showing the fultoportula and rimoportula openings. Note branching costae. Scale bars: 5 μ m (Figs 9–11, 13); 2 μ m (Figs 12, 14).

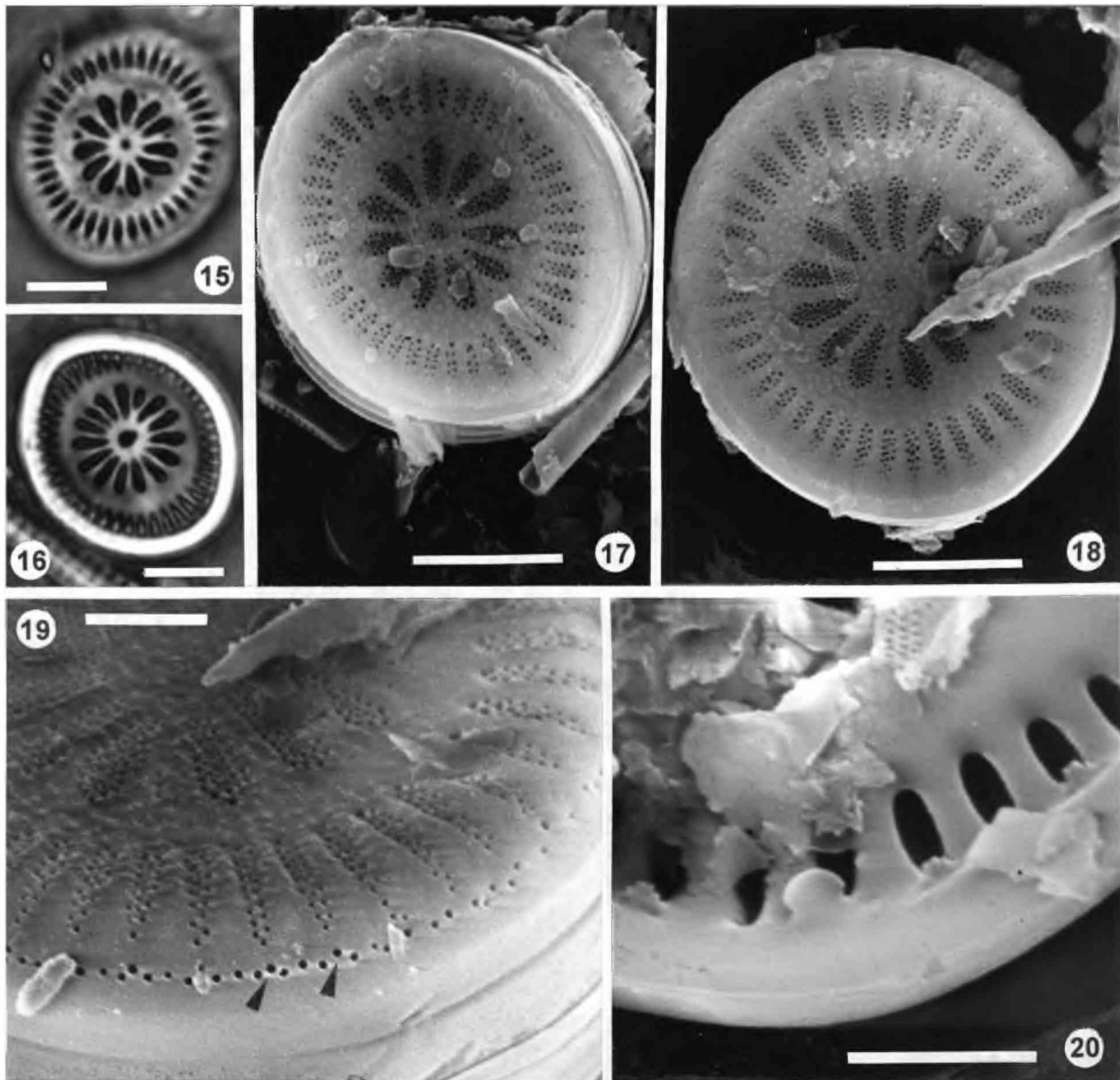
Both Frenguelli's material and our specimens were collected from oligotrophic water-bodies. Although *D. stelligera* var. *elliptica* has repeatedly been recorded for the Patagonian Andes (Luchini & Verona, 1972; Tell, 1985; Vouilloud, 2003), to which it appears restricted, it has not been previously studied with SEM.

Comparison with *Discostella tasmanica* (Haworth & Tyler) Houk & Klee (Haworth & Tyler, 1993), another stelligeroid taxon with an elliptical valve face, reveals that the latter is heterovalvar, has a concentrically undulate valve face and a very distinct outer extension of the mantle fultoportulae, the dorsal side extended to form a broad spine.

Discostella glomerata (Bachmann) Houk & Klee
(Figs 21–26)

STUDIED MATERIAL: LP(C) 3333; LP(C) 3337; LP(C) 3342 and LP(C) 4502.

The frustules of this tiny species are heterovalvar, shortly cylindrical. The valve face is concentrically undulate, 4–11.5 μ m in diameter, with a convex or concave central area, separated from the marginal area by a hyaline ring (Figs 21, 22). The elevated central area is ornamented by a stellate pattern consisting of radially arranged striae surrounding a single areola, which may sometimes be lacking (Figs 21, 23). The depressed central area is ornamented with very faint traces



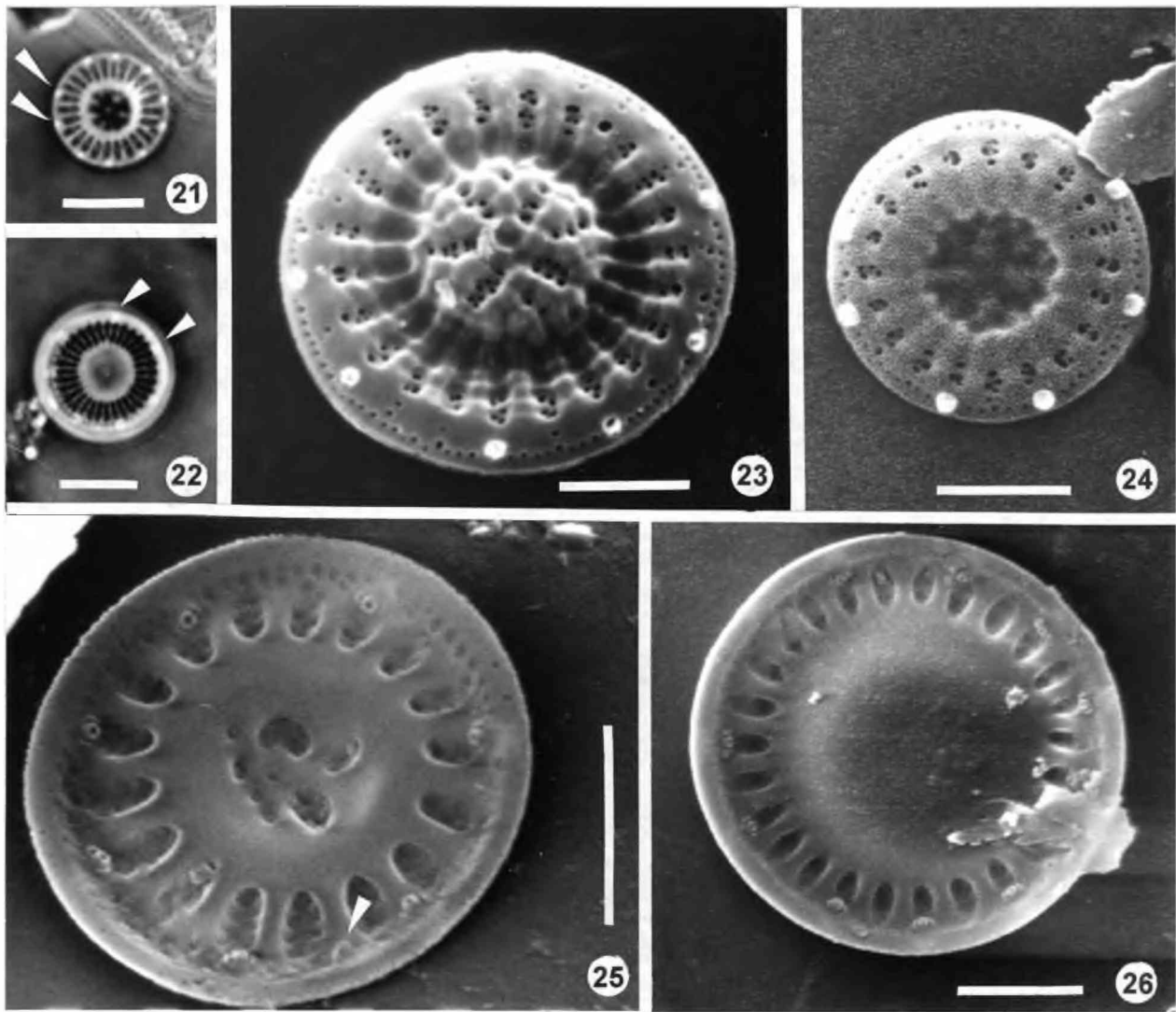
Figs 15–20. *Discostella stelligera* var. *elliptica* from Frenguelli’s material. Figs 15, 16. Light micrographs. Fig. 15. External view of valve face. Fig. 16. Internal view of valve face. Figs. 17–20. Scanning electron micrographs. Fig. 17. External view of a valve with an elliptical outline. Fig. 18. External view of a valve with an almost circular valve face. Fig. 19. Detail of external valve mantle showing the fultoportula openings (arrowheads). Fig. 20. Detail of internal of valve face/mantle junction showing the fultoportula and rimoportula openings. Scale bars: 5 μm (Figs 15–18); 2 μm (Figs 19, 20).

of radial striation ('ghost striae'), separated by interstriae that are continuous to the margin (Fig. 24). There are 12–16 (20) striae in 10 μm in the striated marginal area, each stria composed of 2 (rarely 3) rows of areolae (60 in 10 μm), separated by elevated interstriae. Internally, striae form partially closed alveolar chambers. In convex valves, the central alveoli are drop-like (Fig. 25), while in concave valves the central area is smooth and unornamented (Fig. 26). Marginal alveoli are separated by thick costae that split into two or more branches at the valve mantle (Fig. 25).

The valve mantle is scarcely developed and is occupied by one row of areolae (Figs 23, 24).

The fultoportulae are situated at the valve face/mantle junction, at the end of every (1) 2–3 striae. The external opening of the fultoportulae, a short tubulus (Figs 23, 24) rather than a domed pore, allows accurate identification of this species. The internal opening has two satellite pores (Figs 25, 26). One rimoportula with a sessile internal labium is located on the valve mantle (Fig. 25). The external aperture is indistinct.

The overall appearance of the valve and the tubular external opening of the fultoportulae in our specimens are very similar to those illustrated in Lowe (1975), Haworth & Hurley (1986) and Kling & Håkansson (1988). Although *D. glomerata* is often described as colonial (Lowe, 1975;



Figs 21–26. *Discostella glomerata*. Figs 21–22. Light micrographs. Fig. 21. Valve view of a valve with a convex central area showing the external fultoportula openings (arrowheads). Fig. 22. Valve view of a valve with a concave central area showing the external fultoportula openings (arrowheads). Figs 23–26. Scanning electron micrographs. Fig. 23. External view of a valve with a convex central area. Fig. 24. External view of a valve with concave central area. Fig. 25. Internal view of a valve with convex central area. Arrowhead indicates the rimoportula opening. Fig. 26. Internal view of a valve with a concave central area. Scale bars: 5 μm (Figs 21, 22); 2 μm (Figs 23–26).

Kling & Håkansson, 1988; Krammer & Lange-Bertalot, 1991), in our untreated, formalin-fixed samples the frustules were always solitary.

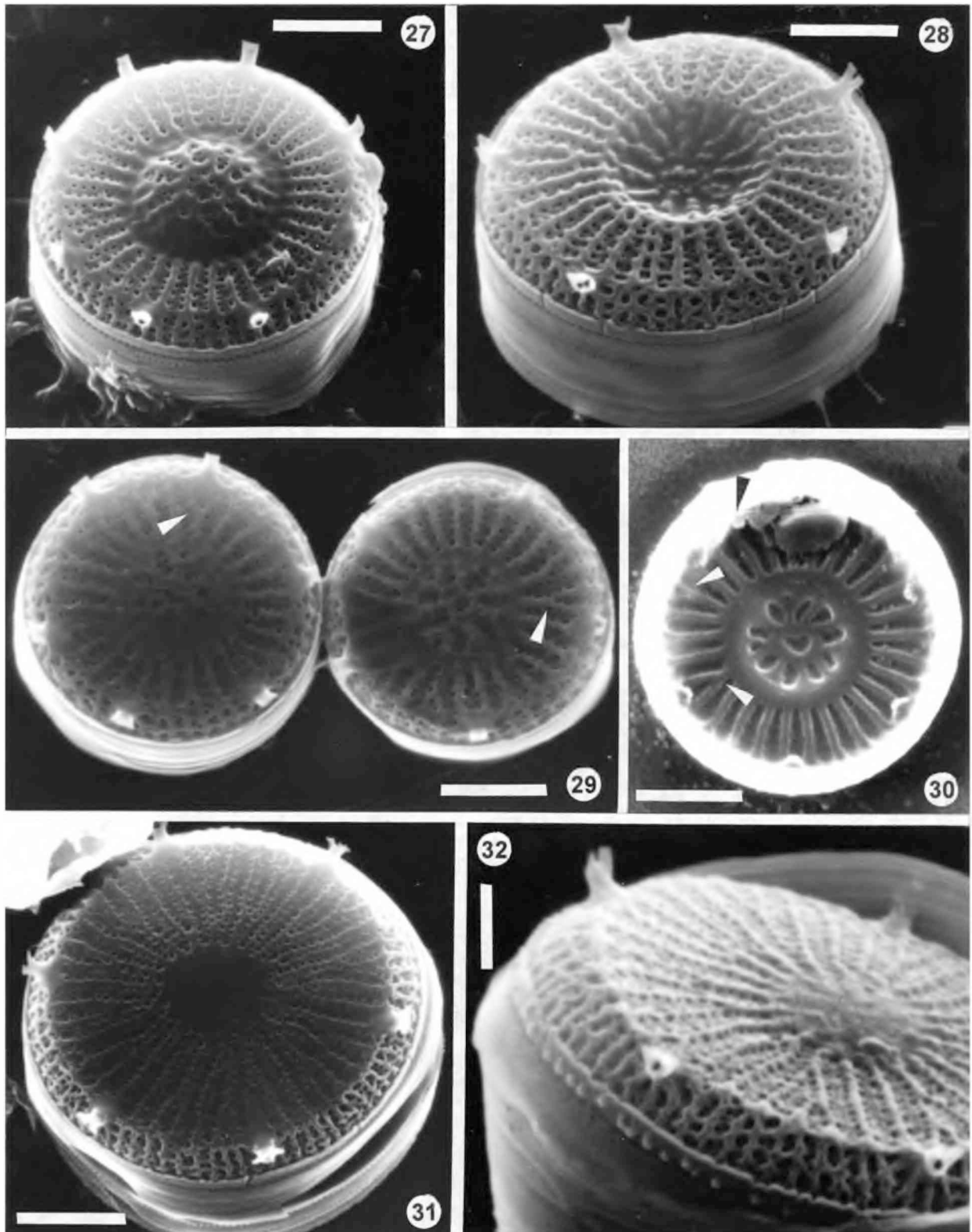
This species has occasionally been reported for Argentina (Anselmi de Manavella & García de Emiliani, 1995; García de Emiliani, 1997; Echenique & Guerrero, 2003).

Discostella pseudostelligera (Hustedt) Houk & Klee (Figs 27–30) and *Discostella woltereckii* (Hustedt) Houk & Klee (Figs 31, 32)

STUDIED MATERIAL: LP(C): 3339.

Specimens identified here as *D. pseudostelligera* have heterovalvar, shortly cylindrical frustules, 5–8 μm in diameter. The valve face is concentrically undulate, with a convex or concave central area.

The elevated central area is occupied by short striae in a star-like arrangement surrounding a group of areolae, separated from the marginal area by an unornamented ring (Figs 27, 29). The depressed central area is ornamented with ridges extending from the marginal area, with occluded striae between them (Fig. 28). The striated marginal area has 20–24 (28) striae in 10 μm , each consisting of two rows of areolae (55–80 in 10 μm) and separated by elevated interstriae (Figs 27, 29). Some of the interstriae bifurcate towards the margin of the valve face and thus shorter striae are formed (Figs 28, 29). In internal view, the striae are sunk in grooves, the central striae are drop-like, while the marginal ones are separated by thick costae (Fig. 30). The costae branch at different distances from the valve margin.



Figs 27–32. Scanning electron micrographs of *Discostella pseudostelligera* (Figs 27–30) and *D. woltereckii* (Figs 31–32). Fig. 27. External view of a valve with a convex central area. Fig. 28. External view of a valve with a concave central area. Fig. 29. Frustules in external view. Arrowheads indicate branching interstriae. Fig. 30. Internal valve view showing branching costae (white arrowheads) and the rimoportula opening (black arrowhead). Fig. 31. *Discostella woltereckii*. External valve view. Fig. 32. Detail of external valve mantle. Scale bars: 2 μ m (Figs 27–31); 1 μ m (Fig. 32).

The valve mantle is ornamented by costae joined by transverse bars, resulting in a reticulate appearance (Figs 27, 28), and the margin ends in a conspicuous silica rim. Each valve has

5–8 fultoportulae, every 4–7 striae, at the valve face/mantle junction. The external opening is an elongated, frequently forked tubulus, supported by thick silica struts (Figs 27–29) and the internal

opening has two satellite pores (Fig. 30). The rimoportula is located on the mantle, without a distinct external aperture, opening internally in a sessile labium (Fig. 30).

In the same sample we found two specimens, here referred to as *D. woltereckii*, which are similar to *D. pseudostelligera*, but differ in the following details. The valves are flat rather than concentrically undulate, 6.5–7.5 µm in diameter. The central area is small and smooth, without any striae or pores (Figs 31, 32). The striated marginal area occupies two thirds of the valve diameter with 20–22 striae in 10 µm, composed of two rows of fine areolae, 70–80 in 10 µm, separated by slightly raised interstriae (Fig. 31). The ornamentation of the valve mantle (Fig. 32) is similar to that of *D. pseudostelligera*. Each valve has 5–6 fuloportulae, every 6–7 striae, at the valve face/mantle junction (Figs 31, 32). The external opening of the rimoportula could not be identified. The few specimens in our samples were only seen in external valve view with SEM and details of the internal valve morphology could not be examined.

Our specimens resemble LM micrographs of type specimens of *D. woltereckii* (Simonsen, 1987; figs 9, 12), specimens illustrated by Hübener (1999; figs 3, 4) and those described by Haworth & Hurley (1986; figs 19, 20) as *C. stelligera* var. *pseudostelligera* f. *wolterecki* (Hustedt) Haworth & Hurley. Compared to the illustrations given by Klee & Houk (1996) in their study of the type material of *D. woltereckii*, our specimens are similar to their figs 12, 13 (LM), but do not resemble any of their specimens studied with SEM.

Discostella pseudostelligera was previously recorded for Argentina as *Cyclotella pseudostelligera* Hustedt by Ferrario *et al.* (1989), Anselmi de Manavella & García de Emiliani (1995) and Echenique & Guerrero (2003). *Discostella woltereckii* has only been recorded for Argentina by Echenique & Guerrero (2003).

Discostella pseudostelligera and *D. woltereckii* are very closely related species that share several morphological features: fuloportula openings, mantle ornamentation and branching interstriae at the valve face. Haworth & Hurley (1986) consider *D. woltereckii* to be a form of *D. pseudostelligera*, illustrating a frustule comprising a valve of *D. woltereckii* and one of *D. pseudostelligera* (Haworth & Hurley, 1986; fig. 21).

Comparison of the original descriptions and drawings of *D. pseudostelligera* (Hustedt, 1939; figs 1–2) and *D. woltereckii* (Hustedt, 1942; figs 11–13) reveals differences in the central area morphology. In *D. pseudostelligera* the central area occupies half the valve diameter and is ornamented

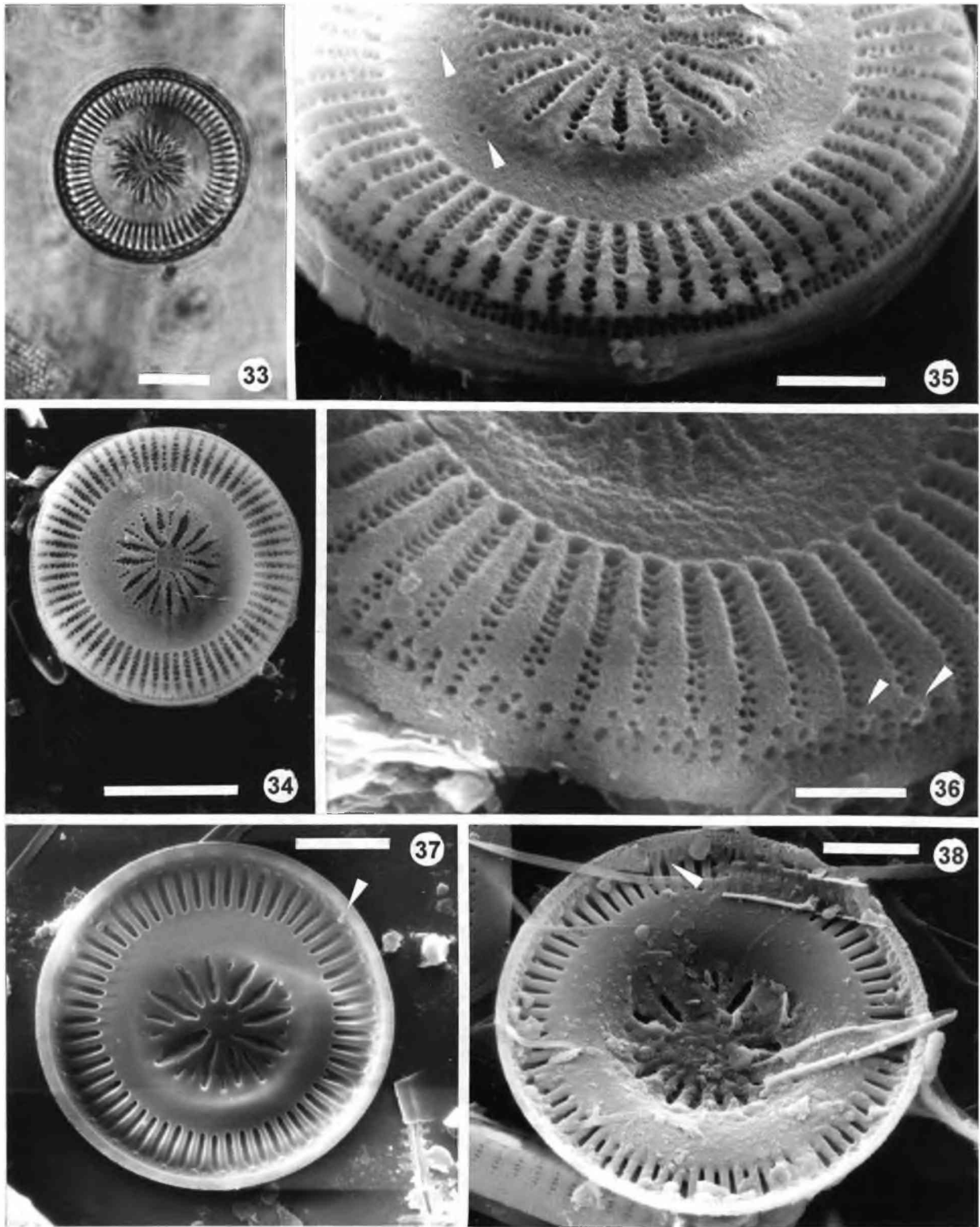
with a ring of areolae or short striae surrounding an isolated central areola. On the other hand, in *D. woltereckii* the central area is very small, either reduced to an isolated central areola, or with a ring of more or less regular smaller areolae, with or without a central areola (the original illustrations show only valves of the first type). Nevertheless, these differences are not always clear according to further studies of the type material. The LM pictures provided by Simonsen (1987) of the specimens present in Hustedt's slides containing the type material of both species show that *D. pseudostelligera* (Simonsen, 1987; pl. 371; figs 26–30) exhibits a distinct broad hyaline ring between the stellate central area and the radially striated marginal zone, the latter occupying approximately half the valve diameter. On the other hand, *D. woltereckii* (Simonsen, 1987; pl. 400; figs 7–14) lacks a hyaline ring and the marginal area extends over two thirds or more of the valve face, the central area sometimes being reduced to an isolated areola. However, LM and SEM studies of the type material of *D. woltereckii* (Klee & Houk, 1996) showed that this taxon comprises a wide range of morphological patterns, ranging from flat valves with dichotomously branching costae (so-called 'dichotomous valve pattern' of Klee & Houk, 1996), to concave or convex valves with costae branching near the margin ('stellate valve pattern'), thus including specimens similar to *D. pseudostelligera*. A similarly wide spectrum of valve morphologies has been reported by Hübener (1999) in natural populations of *D. woltereckii* from Northern Germany. This may be further evidence that environmental factors could play an important role in morphology variation and that the taxonomic separation of these taxa is unjustified, as Haworth & Hurley (1986) have already speculated.

In addition to the above taxa, we found specimens that are similar to *C. stelligera* var. *stelligera* with LM, but have quite different ultrastructure (SEM). We will refer to these taxa as *Discostella* sp. 1 and *Discostella* sp. 2.

Discostella sp. 1 (Figs 33–38)

STUDIED MATERIAL: LP(C) 3313; LP(C) 3339; LP(C) 3343 and LP(C) 4518.

The frustules of this diatom are larger than any other *Discostella* present in our samples. The valve face is slightly concave, 20–27.5 µm in diameter, with a raised central area ornamented with radially arranged striae (Figs 33, 34). The striae are arranged around an areola or a group of areolae, with one or, more rarely, two rows



Figs 33–38. *Discostella* sp. 1. Fig. 33 Light micrograph. Valve view. Figs 34–38 Scanning electron micrographs. Fig. 34. External valve view. Fig. 35. Detail of a valve in external view. Note the two rows of pores located beneath the opening of the fuloportulae. Arrowheads point the scattered pores in the hyaline ring between the central and marginal areas. Fig. 36. Detail of the external valve mantle showing the openings of the fuloportulae (arrowheads). Fig. 37. Internal valve view. Arrowhead points the opening of the fuloportulae. Fig. 38. Internal valve view. Arrowhead points costae dividing in two or more branches at the valve mantle. Scale bars: 10 μm (Figs 33, 34); 5 μm (Figs 35, 37, 38); 2 μm (Fig. 36).

of areolae, alternating with shorter striae and isolated areolae. Central and marginal areas are separated by a very broad hyaline ring (Figs 33–36), ornamented with scattered pores.

The marginal area is clearly delimited from the hyaline ring and consists of biseriate striae, 9–12 in 10 μm , separated by raised interstriae (Figs 35, 36). The striae have 25–30 areolae in 10 μm . In internal

view, striae are alveolate (Figs 37, 38); the central alveoli are elongated and alternate with smaller ones, while the thick costae separating the marginal alveoli divide into two or more branches at the valve mantle (Fig. 38).

The high valve mantle is occupied by two rows of areolae below the openings of the fuloportulae, while a third row of areolae lies at the end of the striae on a level with the fuloportulae (Figs 35, 36). The valve margin ends in a broad, unornamented rim. The fuloportulae are situated at the end of every, or every other, stria; the external opening is slightly domed to shortly tubular (Figs 35, 36), whereas the internal opening, above the point of costal branching, has two satellite pores. The rimoportula has a sessile internal aperture (Fig. 37); the outer opening is inconspicuous and could not be identified.

Valves of this unidentified species were rather scarce in our samples. All observed valves presented the same ultrastructure and we therefore assume that the frustules are isovalvar. They differ from the other taxa of the group by their greater size, the development of a broader hyaline ring between central and marginal areas and the presence of a double row of areolae in the valve mantle. In LM this taxon closely resembles *D. stelligera* var. *hyalina* (Hustedt) Houk & Klee (Hustedt, 1935), but, comparison with Hustedt's illustrations (Hustedt, 1935) and with LM photographs of the type material (Simonsen, 1987) reveals that the central area in our specimens is more distinctively striated. *Discostella* sp. 1 is also similar in LM to one of Grunow's drawings of the type material (Houk & Klee, 2004, fig 22a) and to the specimens studied by Chang (1991) in the type material of *D. stelligera*, named Group A by him (Chang, 1991, figs 2a, 2a' and 2b). However, the ultrastructure of *Discostella* sp. 1 is quite different with regard to its valve mantle, which is more developed and ornamented by a double row of areolae.

Discostella sp. 2 (Figs 39–43)

STUDIED MATERIAL: LP(C) 3339; LP(C) 4519 and LP(C) 4520.

The frustules are shortly cylindrical, 10.5–18 µm in diameter. The valve face bears the typical stelligeroid pattern, with the concave central area occupied by radially arranged striae surrounding a central pore, which may sometimes be lacking (Fig. 39–41). The central and marginal areas are separated by a broad hyaline ring. The marginal striae, 11–15 in 10 µm, have two rows of areolae, 50–60 in 10 µm, occasionally with a third row of smaller areolae between them (Fig. 42). The raised

interstriae merge into the valve face/mantle junction, ending at the same level as the striae (Fig. 42).

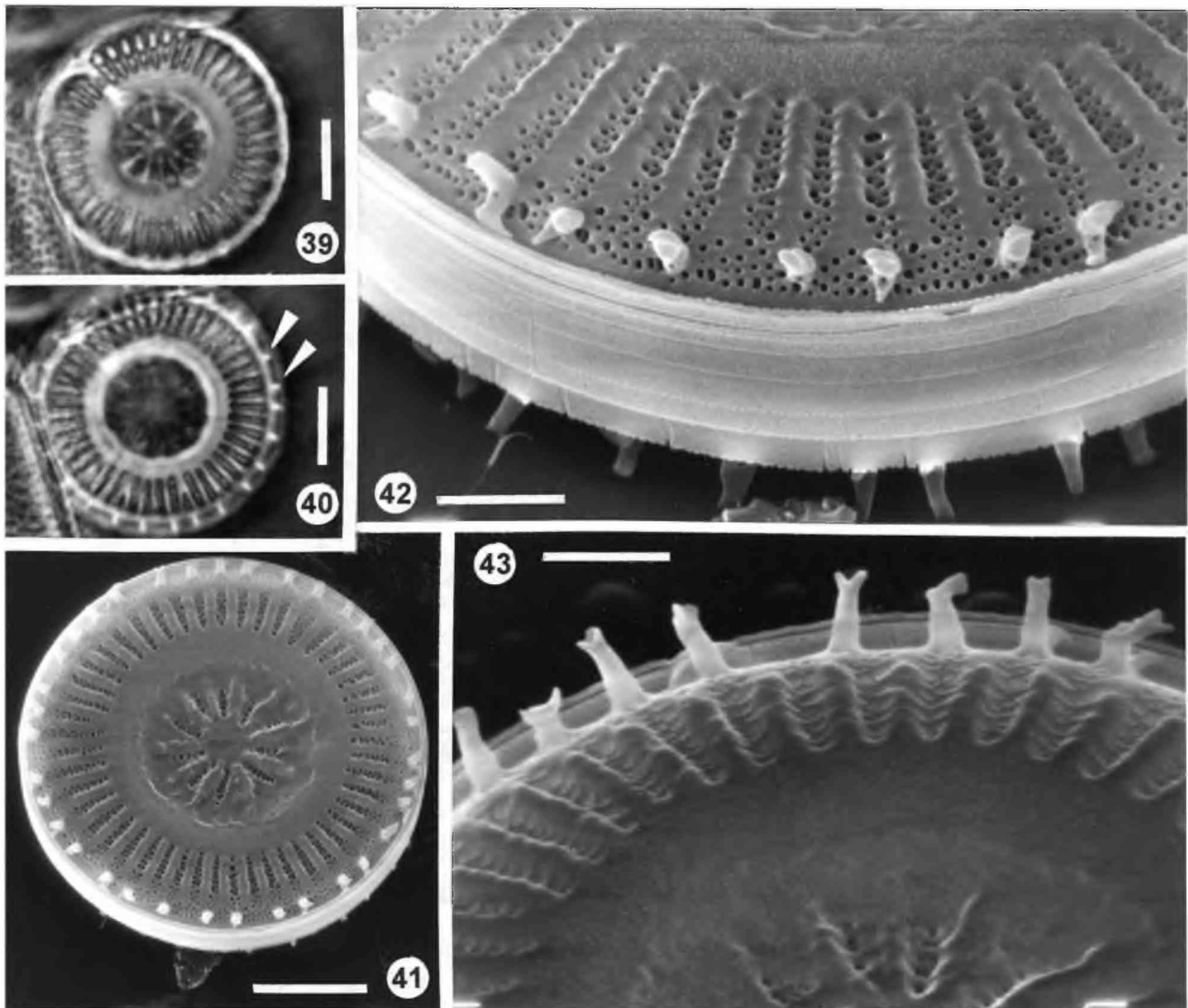
Two differentiating features of this taxon are the ornamentation of the valve mantle and the external extension of the fuloportulae. The valve mantle is quite high and is occupied by a large number of irregularly arranged, different sized areolae (Fig. 42), resembling the mantle of *D. pliostelligera* (Tanaka & Nagumo, 2002). However, the mantle areolae are somewhat more regularly arranged in parallel rows in the latter. The fuloportulae are located at the valve face/mantle junction, at the end of every, or every other, stria; the distinctive external opening is ornamented by two branches, one dorsal, longer and generally forked, the other ventral, slightly shorter and sometimes bent (Figs 42, 43). As with other stelligeroid taxa, the external opening of the rimoportula could not be recognized. The few available specimens studied with SEM were seen in external view and it was not possible to examine the valve interior.

Discostella sp. 2 differs from the other taxa of the group in the distinctive external fuloportula opening, the distal portion of the interstriae merging with the valve face/mantle junction and the presence of different sized areolae scattered over the valve mantle. Although with rapid LM examination *Discostella* sp. 2 could be misidentified as *D. stelligera* var. *stelligera*, more careful study at higher magnifications allows the external extension of the fuloportulae to be distinguished.

Discostella sp. 1 and *Discostella* sp. 2 undoubtedly belong within the newly described genus, based on the position of the mantle fuloportulae and the striation pattern at the valve centre. Their characteristic mantle ornamentation and external fuloportula openings have not been seen in other species of the group, suggesting that we are probably dealing with new taxa. Nevertheless, we think that many more specimens should be examined before they are described as such.

Discussion

The position of the fuloportulae within the striae instead of at the end of the interstriae, in most cases accompanied by a stellate pattern in at least one of the valves, was a unique character within the genus *Cyclotella*, indicating that the stelligeroid taxa comprised a natural group (Houk, 1992; Klee & Houk, 1996) and, according to Håkansson (2002), the 'stelligeroid' morphology justified their classification in a special group. Recently, Houk & Klee (2004) erected the new genus *Discostella*, mainly based on the position of both fuloportulae and rimoportula within the striae. The description of *Discostella mascarenica*



Figs 39–43. *Discostella* sp. 2. Figs 39, 40 Light micrographs. Fig. 39. Valve view focusing central area. Fig. 40. Valve view focusing marginal area. Note the external openings of the fultoportulae (arrowheads). Figs 41–43 Scanning electron micrographs. Fig. 41. External valve view. Fig. 42. Detail of external valve face/mantle junction. Note the distinctive morphology of the external opening of the fultoportulae. Fig. 43. Detail of the marginal area in valve view. Note the forked dorsal branch of the fultoportulae. Scale bars: 5 μ m (Figs 39–41); 2 μ m (Figs 42, 43).

(Klee, Houk & Bielsa) Houk & Klee (Klee *et al.*, 2000), a species with a typical stellate pattern at the valve centre, very similar to *D. stelligera* var. *stelligera* and *D. glomerata*, but with mantle fultoportulae on both striae and interstriae is a partial exception to this rule. With regard to the position of the rimoportula, we observed some specimens of *D. stelligera* var. *elliptica* (Figs 13–14) and *D. glomerata* (Fig. 25) with the internal opening of the rimoportula located on a costa. Although a rimoportula at the valve mantle was also mentioned as characteristic of *Discostella* (Klee & Houk, 1996), the rimoportula is in a similar position in species of the genus *Cyclotella*, as circumscribed by Håkansson (2002).

The morphological variability within the new genus *Discostella* has often caused confusion and erroneous interpretation of the taxonomy

and nomenclature of the group (Klee & Houk, 1996). Haworth (1983) and Haworth & Hurley (1986) postulated that the occurrence of specimens with intermediate morphological features, in apparent response to environmental conditions, precludes clear delimitation of *D. stelligera* and allied taxa. Nevertheless, they retained the separation of the taxa at the varietal level, considering that this distinction might provide ecologically useful information.

Although the specimens we studied exhibited some intrapopulation variability, we have not found transitional forms between the species, despite their co-occurrence, and very similar forms under LM can be quite easily identified when examined with SEM. The study of the ultrastructure reveals that each taxon has specific morphological characters that remain almost

invariable (type of costa, type of fultoportula external opening, fultoportulae/costae ratio, development and ornamentation of the valve mantle, ornamentation of central area, etc.).

We acknowledge that specimens of *Discostella* taxa are generally quite scarce in our samples, which consequently makes the study of the morphological variability of each species in natural populations difficult. Low abundances of *D. stelligera* in nature and consequent lack of information on developmental stages have also been reported by Chang (1991). We therefore think that culture studies would help to clarify the taxonomy of the group as a whole, e.g. allowing the study of morphological variability of known taxa, and revealing whether unidentified specimens, such as *Discostella* sp. 1 and *Discostella* sp. 2, are new taxa, part of the life-cycle of other species, or responses to changing environmental conditions. Culture studies of some 'stelligeroid' taxa by Chang & Steinberg (1989) revealed a wide range of morphological variability, and produced forms attributable to different species.

Emended diagnosis

Discostella stelligera var. *elliptica* (Frenguelli) Guerrero & Echenique, comb. nov.

BASIONYM: *Cyclotella stelligera* var. *elliptica* Frenguelli, J. Diatomeas del Neuquen (Patagonia). Revista Mus. La Plata (nueva serie) Bot., 5: 73–219, 1942.

LECTOTYPE: Colección de Diatomeas Argentinas 'Dr. Joaquín Frenguelli': series No. 422, slide 4.

Light microscopy. Frustules isovalvar. Valve face flat, elliptical to almost circular, diameter 11–23 µm (greater axis), 9–20 µm (smaller axis). Central area of the valve face separated from the marginal area by a broad hyaline ring. Central striae drop-like or elongated, equally long and surrounding a central areola in a star-like arrangement, occasionally with shorter striae and small areolae among them. Marginal area occupied by striae of nearly equal length, separated by narrow interstriae, 10–15 in 10 µm. Dark spots at the end of almost every stria correspond to the positions of the fultoportulae.

Scanning electron microscopy. Valve face with central area separated from the marginal area by a broad unornamented ring. Externally central striae with two rows of areolae and one-to-three rows of smaller areolae between them, surrounding a central areola or a group of areolae in a star-like arrangement. Marginal striae consisting of two rows of areolae with a third row of smaller areolae

between them. 40–50 areolae in 10 µm. There is usually a larger areola at each end of every stria. Striae separated by interstriae, internally alveolate. Marginal alveoli separated by thick costae bifurcating in two short branches at the valve mantle. Fultoportulae located on every, or every other, stria; internal opening between the branches of the costae with two satellite pores; external opening at the centre of a slight dome within the striae. One rimoportula located on the valve mantle at one end of the longest valvar axis; external aperture indistinct, internal opening with a sessile labium. Valve mantle not very developed, with larger areolae located at the ends of both striae and interstriae.

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