

REVISION OF *ODONTELLA ATLANTICA* (FRENGUELLI)
SAR COMB. ET STAT. NOV. WITH COMPARISON TO
TWO RELATED SPECIES, *O. RHOMBUS* (EHRENB.) KÜTZ.
AND *O. RHOMBOIDES* R. JAHN ET KUSBER

Eugenia A. Sar*^{1 2}, Inés Sunesen*, Regine Jahn**,
Wolf-Henning Kusber** & Andrea S. Lavigne*

* Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo,
Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

** Botanic Garden and Botanical Museum, Berlin-Dahlem, Freie Universität Berlin,
Königin-Luise-Str. 6–8, D–14191 Berlin, Germany

Biddulphia rhombus var. *atlantica* was erected by Frenguelli from waters of the South Atlantic Ocean. A revision of its syntype series was carried out with light microscopy, a lectotype was chosen and compared with the lectotype of *Odontella rhomboides* (\equiv *Zygoceros rhombus*), and with the lectotype of *Odontella rhombus* (\equiv *Denticella rhombus*), designated in this paper. As there is no unmounted material available in the Frenguelli Collection, a SEM study was carried out on material collected in Buenos Aires Province coastal waters, Argentina. Differences in pattern of striation and distribution of labiate processes were established as the striking features to distinguish Frenguelli's taxon from the other two species.

Based on the analysis of the fine structure the placement of Frenguelli's var. *atlantica* in the genus *Odontella* according to the modern concept of generic limits within the biddulphioid diatoms was confirmed and the taxon raised to species rank as *Odontella atlantica*, comb. et stat. nov.

Keywords: lectotypes, marine bipolar centric diatoms; *Biddulphia rhombus* var. *atlantica*; *Odontella atlantica*, *Denticella rhombus*, *Zygoceros rhombus*.

INTRODUCTION

In the classical literature and in VanLandingham (1968), most of the species of the genus *Odontella* Agardh (1832) were ascribed to the genus *Biddulphia* Gray (1821). The taxonomic history of the biddulphioid diatoms, the group to which *Odontella* and *Biddulphia* belong, has been reviewed in detail by Ross & Sims (1971), who concluded that both genera are valid taxonomic entities. *Biddulphia* is one of the earliest described diatom genera and is currently characterized by possessing polar elevations with pseudocelli and poroid areolae (Ross & Sims 1971). Round *et al.* (1990) and Hasle & Syvertsen (1997) characterized *Odontella* as possessing elliptical to lanceolate (bipolar) valves, elevations (horns) with distinct ocelli at the poles, rimoportulae with long external tubes located at the valve surface, and areolae with foramina inside and criba outside.

When the genus *Odontella* was erected by Agardh (1832) with *O. aurita* (Lyngbye) Agardh as its type by monotypy, at about the same time two other closely related monotypic genera were described by Ehrenberg: *Denticella* (Ehrenberg 1838) with *D. aurita* (Lyngbye)

¹ Consejo Nacional de Investigaciones Científicas y Técnicas

² Correspondence to E.A. Sar. e-mail: easar@museo.fcnym.unlp.edu.ar

Ehrenberg as the type and *Zygoceros* (Ehrenberg 1839) with *Z. rhombus* Ehrenberg as the type (Fourtanier & Kociolek 1999). Hoban (1983) concluded that *Zygoceros* is not distinguishable from the genus *Odontella* on morphological criteria and synonymized it with *Odontella*, while Simonsen (1974) considered both *Zygoceros* and *Denticella* as synonyms of *Odontella*.

In 1930, Frenguelli described *Biddulphia rhombus* var. *atlantica* from material collected in Buenos Aires Province coastal waters, without designating a holotype but providing a diagnosis and two illustrations. Additionally, Frenguelli commented that material illustrated by him from Mar del Plata coastal waters, Argentina, (Frenguelli 1928) was conspecific with the new variety. In the protologue he compared his new variety with *B. rhombus* (Ehrenberg) W. Smith var. *rhombus*, which currently bears the name *Odontella rhomboides* R. Jahn & Kusber (2004), based on *Zygoceros rhombus* Ehrenberg (1839), non *Odontella rhombus* (Ehrenberg) Kützing (1849), which is based on *Denticella rhombus* Ehrenberg (1844).

In the present study, we examine syntype material of *Biddulphia rhombus* var. *atlantica* as originally described by Frenguelli (1930) by light microscopy, we select the lectotype for this taxon, and because there is no unmounted material available in the Frenguelli Collection, we study recently collected material from Buenos Aires Province coastal waters by scanning electron microscopy. The aims of this study are to give a comprehensive description of *B. rhombus* var. *atlantica*, to compare it with the lectotypes of *Odontella rhomboides* (\equiv *Zygoceros rhombus*) and *Odontella rhombus* (\equiv *Denticella rhombus*), to discuss the differential features among the three taxa and to evaluate the taxonomic position of the studied diatoms.

MATERIALS AND METHODS

Frenguelli (1930) stated that eight series (n° 156, n° 186, n° 189, n° 192, n° 194, n° 197, n° 199 and n° 204) from Miramar contained *Biddulphia rhombus* var. *atlantica*. We examined all the slides of each series (thirty seven in all) and five slides of series n° 167 from Mar del Plata also said to contain var. *atlantica* (Frenguelli 1928, 1930) with light microscopy (LM). Slides of the series mentioned are deposited in the Colección de Diatomeas Argentinas Dr Joaquín Frenguelli, Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo (La Plata, Argentina).

Additionally, we also examined with LM the lectotype of *Zygoceros rhombus* (preparation n° 540211-5 in the Ehrenberg Collection, Museum für Naturkunde, Institut für Paläontologie, Humboldt-Universität zu Berlin, BHUPM), and an isolectotype preparation ("Cuxhaven I" n° 360805-c in BHUPM, see Fig. 3), as well as the lectotype of *Denticella rhombus* (preparation n° 231208-e marked with a white ring, labelled by Ehrenberg as "*Denticella!!*", in BHUPM, see Fig. 4) and the preparation n° 231208-a in BHUPM.

Material from the coastal waters of Buenos Aires Province was collected at several locations (San Clemente del Tuyú, Santa Teresita, La Lucila del Mar, Mar de Ajó, Nueva Atlantis, Pinamar and Villa Gesell: Fig. 1), seasonally from October 1994 to October 1996, bimonthly from October 1996 to January 1999, and monthly from September 1999 to September 2000. Seawater temperatures were 8–24°C and the salinities 31–34.1 psu (unpublished data). 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. In the laboratory, the preserved samples were rinsed with distilled water to remove salt and preservatives, and the organic matter was oxidized according to Hasle & Fryxell (1970). The cleaned material was mounted for light and scanning electron microscopy according to Ferrario *et al.* (1995). Permanent mounts were made with Hyrax® and Naphrax®. The materials were deposited in the Colección de Diatomeas Argentinas, Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo (La Plata, Argentina).

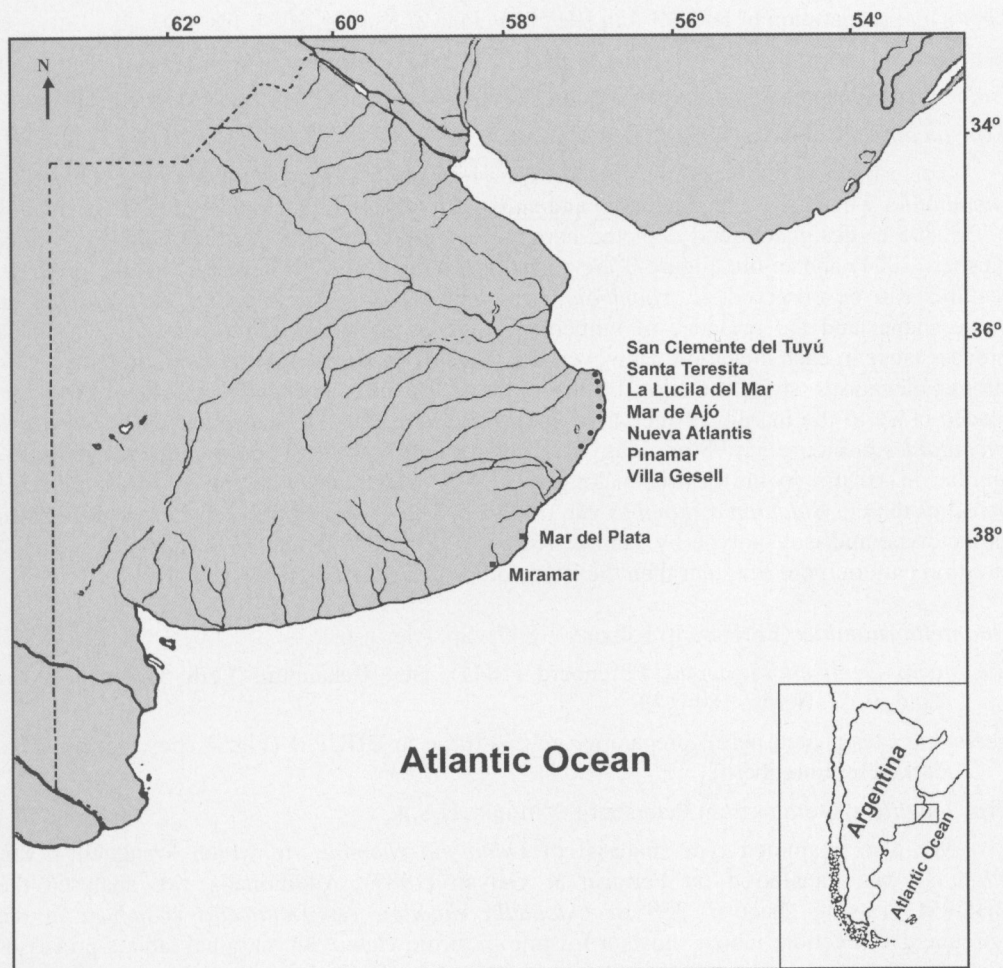


Fig. 1. Map of Buenos Aires Province and location of the study area in Argentina, ● shows our own sampling stations; ■ shows Frenguelli's sampling stations in 1928 and 1930.

Photomicrographs of Frenguelli's and our material were obtained with a light microscope (LM) Nikon Microphot-FX (Yokohama, Japan) under phase contrast and those corresponding to Ehrenberg's material with an Olympus DP 50 and BX 51 (Tokyo, Japan) under bright field. The scanning electron microscope photomicrographs were obtained using a Jeol JSMT 100 (Akishima, Japan).

Terminology follows that recommended by Ross *et al.* (1979) and Mayer & Schmid (1995). The bibliography on the fine structure of diatom frustules used is basically that compiled by Gaul *et al.* (1993) and Henderson & Reimer (2003).

RESULTS

Ehrenberg's taxa

Odontella rhomboides R. Jahn & Kusber (2004), Willdenowia, 34: 584.

≡ *Zygoceros rhombus* Ehrenberg (1839), Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin, 1839: 156.

≡ *Biddulphia rhombus* (Ehrenberg) Smith (1856), Brit. Diat., 49.

Lectotype: preparation n° 540043-4 in BHUPM (Jahn & Kusber, 2004, fig. 45).

Isolectotype: preparation n° 540211-5 in BHUPM (Jahn & Kusber, 2004, fig. 44).

Isolectotype (designated here): preparation n° 360805-c in BHUPM (Fig. 3).

Type locality: "Cuxhaven", North Sea, Germany.

To establish the relationship between Frenguelli's var. *atlantica* and *Odontella rhomboides* we analysed the lectotype and an isolectotype BHUPM preparation "Cuxhaven I" n° 360805-c (designated and depicted here as Fig. 3). The valves photographed by Jahn & Kusber (2004) and in our Figure 3 are partially obscured by dirt, nevertheless, the principal features can be observed. *O. rhomboides* resembles *Biddulphia rhombus* var. *atlantica* in valve shape, and the presence of numerous scattered spines on the valve and one labiate process close to each elevation. However, the valve of *O. rhomboides* is more orbicular, with shorter elevations, striae radiating from a more or less circular annulus and large processes placed close to the margin of the valve (arrow-heads in Fig. 3). The specimen of *Odontella rhomboides* in Figure 3 is 98 µm long, 67 µm wide, with 9 striae in 10 µm in the margin and 7 areolae in 10 µm in the centre, making it slightly wider and with lower stria and areola densities than in *Biddulphia rhombus* var. *atlantica*. The valves on the preparations designated as lectotype and isolectotype by Jahn & Kusber (2004, figs 45 and 44 respectively) show a striation pattern more irregular than the isolectotype designated in this paper (Fig. 3).

Odontella rhombus (Ehrenberg) Kützing (1849), Sp. Alg. 136.

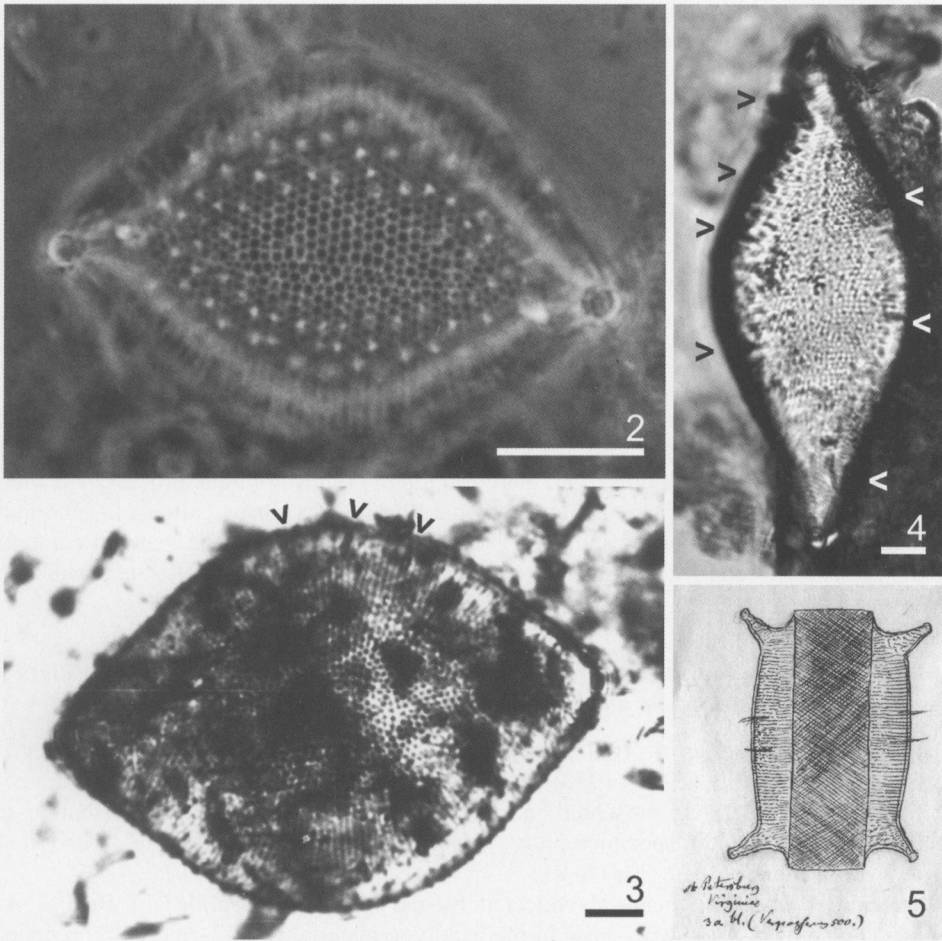
Basionym: *Denticella rhombus* Ehrenberg (1844), Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin, 1844: 79.

Lectotype (designated here): preparation n° 231208-e in BHUPM (Fig. 4 showing the valve marked by Ehrenberg).

Type locality: diatomite from Petersburg, Virginia, U.S.A.

We also examined type material of *Odontella rhombus*, to which Frenguelli's var. *atlantica* was transferred by Ferrario & Galván (1989). Additionally, we analysed the BHUPM drawing sheet n° 389 of *Odontella rhombus* (as *Denticella rhombus*) in the Ehrenberg Collection, which shows a frustule in girdle view with marginal labiate processes (Fig. 5). Ehrenberg's diagnosis reads (1844: 79): "*D. testulae subtiliter punctato lineatae, Zygozeroti Rhombo similimae, sed aculeo in quovis latere medio utrinque instructae. Diam. 1/26'''. Petersburg Virg. Cingulum dorsi i.e. pars plana media corpusculorum, neque in Zygozerote neque in hac forma laeve est, sed punctorum minimorum seriebus obliquis caelatum*". (Valves with fine linear punctae, similar to *Zygozeros rhombus*, but three spines in the middle part of both valvar sides [in girdle view]. Planar girdles with structures in the middle parts with oblique series of smallest punctae, not as in *Zygozeros* ... Diameter 86.8 µm. Petersburg, Virginia.)

The lectotype material of *O. rhombus* agrees with Frenguelli's specimens of *Biddulphia rhombus* var. *atlantica* in valve outline and shape, the morphology and direction of the elevations, and presence of numerous scattered spines on the valve and one labiate process close to each elevation. But the two taxa differ in that *B. rhombus* var. *atlantica* lacks the marginal labiate processes, while *O. rhombus*, like *O. rhomboides*, has marginal labiate processes. As regards the striation pattern, *O. rhombus* (Fig. 4) shows areolae arranged in more or less linear striae disposed from a structural centre formed by a lanceolate annulus conformed by disordered areolae. It is 115 µm long, 49 µm wide, with 7 striae in 10 µm in the margin and 8 areolae in 10 µm in the centre. *O. rhombus* is therefore slightly narrower and with lower density of striae and areolae than *Biddulphia rhombus* var. *atlantica*.



Figs 2–4. Light microscopy. **Fig. 2.** *Odontella atlantica*, valve found in lectotype preparation n° 197 (2) from Miramar, Argentina in Frenguelli Collection. Phase contrast. **Fig. 3.** *Odontella rhomboides*, valve on BHUPM preparation n° 360805-c (Ehrenberg Collection) from North Sea, Germany, showing the isolectotype. Bright field. Arrow-heads show lateral labiate processes. **Fig. 4.** *Odontella rhombus*, valve on BHUPM preparation n° 231208-e from Petersburg, USA, showing the lectotype. Bright field. Arrow-heads show position of lateral labiate processes as determined in several planes of focus. **Fig. 5.** Depicted girdle band view of *Denticella rhombus* on drawing sheet n° 389 from the Ehrenberg Collection showing two marginal processes. Scale bars = 10 µm (Figs 2–4).

Frenguelli's taxon

In the original diagnosis, Frenguelli distinguished *Biddulphia rhombus* var. *atlantica* from *B. rhombus* var. *rhombus* (as variety) by the arrangement of the striae on the valve centre and the stria density on the valve and the girdle bands. This diagnosis was clearly made on the basis of comparisons with the illustrations presented by Smith (1856, plate 45, fig. 320 and plate 61, fig. 320). The second illustration shows a specimen with the areolation pattern ordered from a structural centre formed by a circular annulus. Subsequently, Frenguelli's variety was transferred by Ferrario & Galván (1989) to *Odontella rhombus* var. *atlantica* (Frenguelli) Ferrario & Galván.

In order to facilitate the comparison of the three taxa, we here introduce the new status and combination of Frenguelli's taxon; which will be discussed later.

Odontella atlantica (Frenguelli) Sar, **comb. et stat. nov.**

Basionym: *Biddulphia rhombus* var. *atlantica* Frenguelli (1930), An. Mus. Nac. Hist. Nat. "Bernardino Rivadavia", 36: 305, plate 4, figures 1, 2.

≡ *Odontella rhombus* var. *atlantica* (Frenguelli) Ferrario & Galván (1989), 186.

Lectotype (designated here): Slide 197 (2), Colección de Diatomeas Argentinas, Departamento Científico Ficología, Facultad de Ciencias Naturales y Museo, La Plata, Argentina.

Type locality: Miramar, Buenos Aires Province, Argentina, (38° 15' S and 57° 50' W) South Atlantic Ocean.

Frenguelli's slide n° 197 (2) was chosen as the lectotype of *Biddulphia rhombus* var. *atlantica*, following the recommendations of the ICBN (McNeil *et al.* 2006). Figure 2 shows a valve from the lectotype slide. Valve is subrhombic-lanceolate with apical elevations, and a convex valve face. Near each elevation, there is a single, robust, oblique process. The areolae are arranged in uniseriate striae extending out on each side of a narrow, almost linear annulus, and there are numerous scattered spines. All valves found in the syntype material coincide in general appearance and morphometric data with that described and illustrated in the protologue (Table 1).

Comparison of syntype material corresponding to series n° 167 from Mar del Plata and our own material of *Odontella atlantica*, LM

In Frenguelli's series n° 167 from Mar del Plata we found specimens smaller than described by Frenguelli (1928, 1930) and wider ranges of the morphometric parameters (Table 1). The illustrations presented in both publications are perfectly coherent to each other and coincide with the specimen photographed in the lectotype slide (Fig. 2) and in slide n° 167 (3) from Mar del Plata (Figs 6–8).

Specimens from the material collected by us in several localities of Buenos Aires Province (Figs 9–11) agree with those in the lectotype material (Fig. 2) and with Frenguelli's illustrations in frustule shape, valve outline, valve shape, areolation pattern, and distribution of labiate processes. There are slight differences in valve dimensions and striae density in valve and girdle (Table 1) but we nevertheless are confident that our material is conspecific with Frenguelli's.

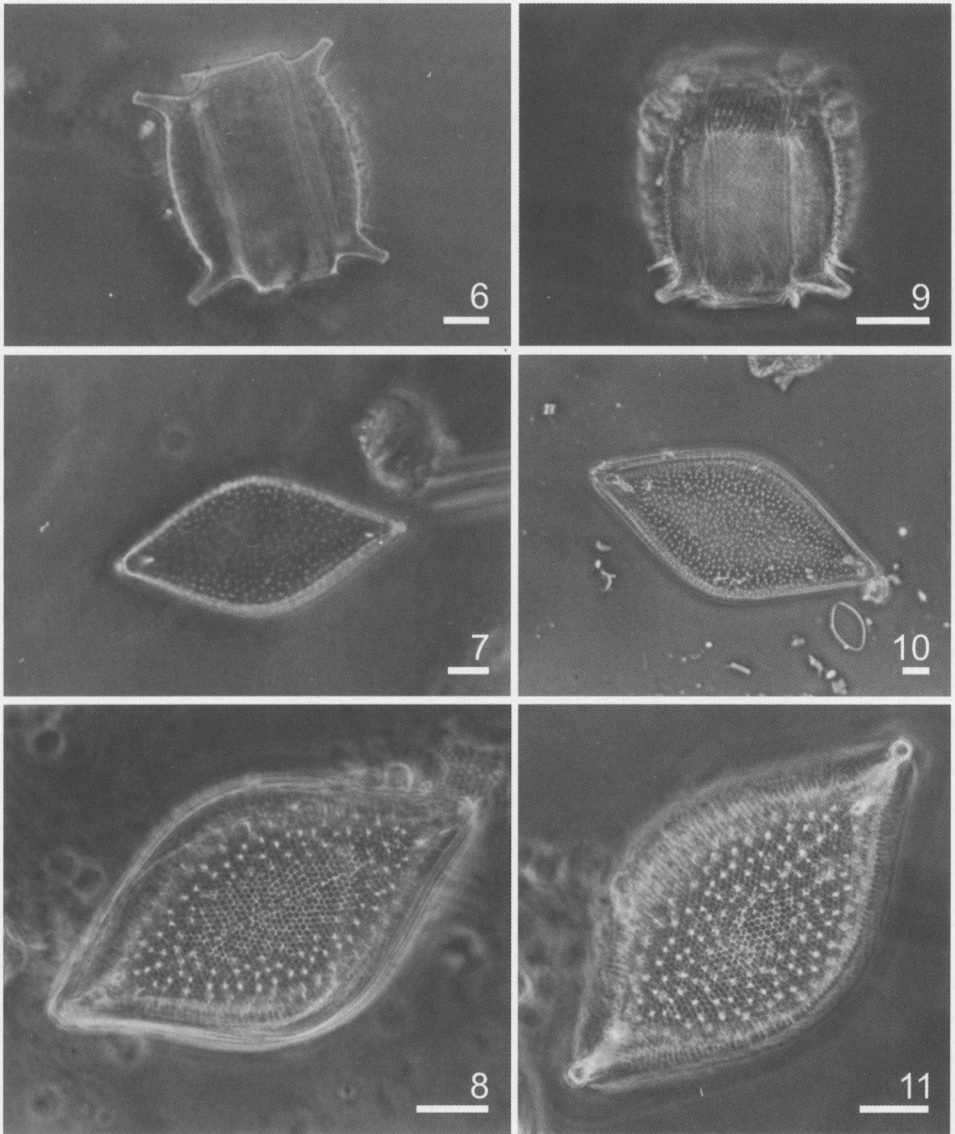
SEM:

In material from coastal waters of Buenos Aires Province the frustules are rectangular to quadrangular in broad girdle view, with protracted apical elevations, convex valve face, and external tubes of the two labiate processes placed near the elevations and curving polewards (Fig. 12). The girdle is composed of three split bands, a wide valvocopula, with areolae arranged in striae running in the peralvar direction and secondarily in decussate rows, and two narrower copulae, which are more densely areolate (Figs 12–13).

The valves are subrhombic-lanceolate, with apical elevations, convex, with the valve mantle indented, curving out again to the margin (Figs 13–16). The areolae are arranged in linear striae disposed from a structural centre formed by a line or a linear annulus (Figs 15, 19, 20). The areolae are loculate, with an internal foramen and an external velum (Fig. 18). The vela are centrally imperforate, with several holes around the periphery (Fig. 17). The areolation pattern is not easily visible in external view because of the presence of numerous buttressed spines with simple (Fig. 16) or blunt lobed tips (Figs 13–15). In internal view,

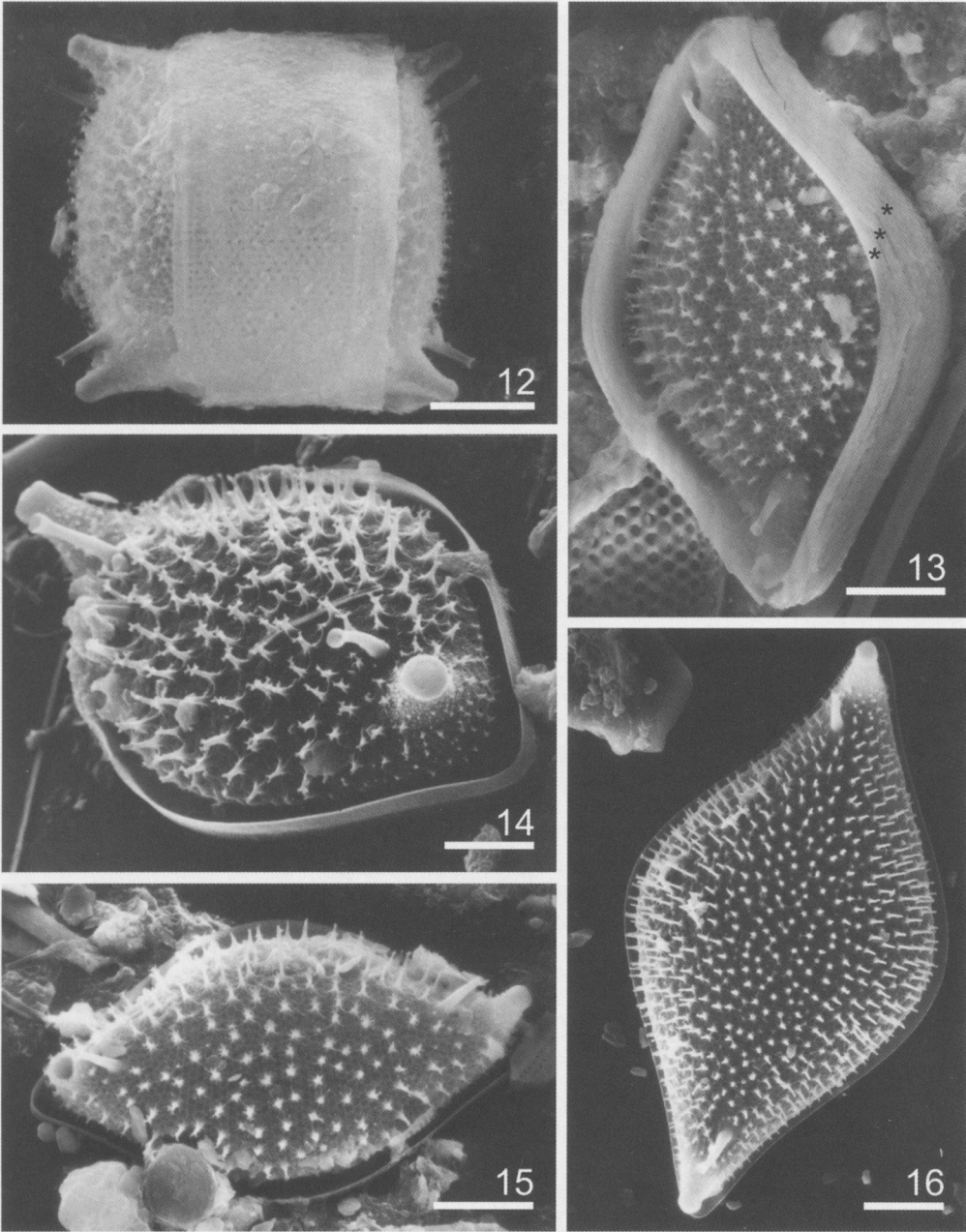
Table 1. Morphometric comparison among *Odontella atlantica* populations found in syntype material, Mar del Plata material, and our own material. Asterisk = data reported by Frenguelli; nd = no data.

Analysed material	Seen in	Apical axis in μm	Transapical axis in μm	Pervalvar axis in μm	Striae in 10 μm (valve)	Striae in 10 μm (girdle)	Areolae in 10 μm (valve)	Areolae in 10 μm (girdle)
Material found in the syntype series corresponding to Frenguelli (1930)	LM	24.5-69	16.5-36	25.5-30.5	10-15	13-14	9-14	12-13
		33-80*	21-43*	nd*	12-13*	12*	9-14*	12-14*
Material found in the serie n° 167 corresponding to Frenguelli (1928)	LM	48-92	19.2-42.4	36.8-40	10-14	12-13*	9-13	nd*
		42-80*	43*	45-51*	nd*	nd*	nd*	nd*
Our own material from Buenos Aires coastal water	LM	31-118	24-56	24-30	11-15	14	10-13	12-14
		SEM	36-74	22-40	32-40	13-16	13-15	12-14

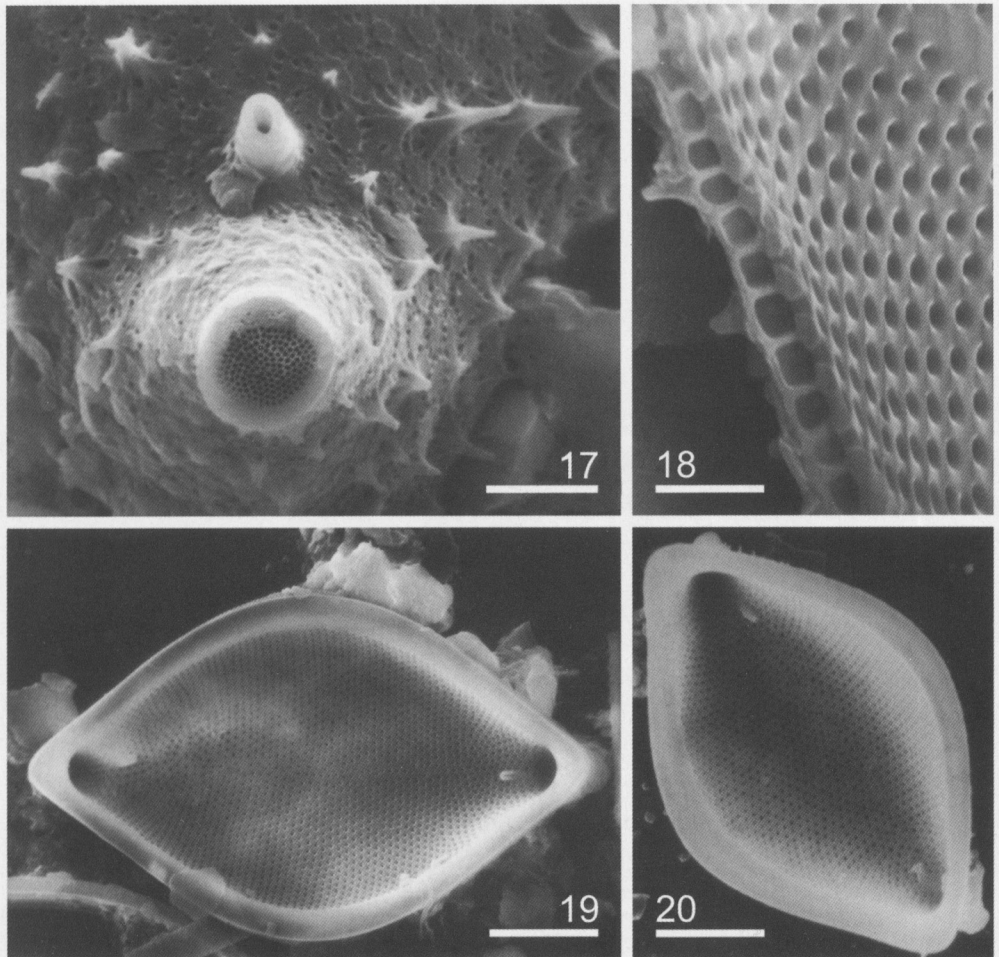


Figs 6–11. *Odontella atlantica*, light microscope, phase contrast. **Figs 6–8.** Specimen and valves found in slide 167 (3) from Mar del Plata, Argentina, in Frenguelli Collection. **Fig. 6.** Frustule. **Figs 7, 8.** Valvar views. **Figs 9–11.** Specimen and valves found in Santa Teresita. **Fig. 9.** Frustule. **Figs 10, 11.** Valvar views. Scale bars = 10 μm (Figs 6–11).

however, the arrangement of the areolae is more obvious (Figs 19, 20). The elevations are low and blunt and directed diagonally outwards. Each bears a terminal ocellus consisting of a plate perforated by densely packed porelli and surrounded by a solid rim (Fig. 17). There are two labiate processes per valve, placed close to the bases of the elevations and diagonally opposite each other, furnished by robust oblique external tubes (Figs 12–16). The tip of the processes has a cup-like expansion (Fig. 14). Internally the processes have sessile lips in an almost apical position (Figs 19, 20).



Figs 12–16. *Odontella atlantica*, scanning electron microscopy. **Fig. 12.** Specimen found in San Clemente del Tuyú. Frustule rectangular to quadrangular in broad girdle view. Note the three girdle bands, the wide valvocopula with rows of areolae, and two narrower copulae densely areolate. **Fig. 13.** Specimen found in San Clemente del Tuyú. Hypovalve enclosed by the epicingulum. Note valve pattern of striation and girdle bands opened at one end. Asterisks show each band. **Figs 14–16.** Valves found in Villa Gesell, San Clemente del Tuyú and Nueva Atlantis respectively. Valves in external view showing elevations, labiate processes and spines. **Fig. 15.** Note the pattern of striation. Scale bars = 10 μ m (Figs 12, 13, 15, 16); 5 μ m (Fig. 14).



Figs 17–20. *Odontella atlantica*, scanning electron microscopy. **Fig. 17.** Valve found in Santa Teresita. Elevation with ocellus showing porelli. Note imperforated velum with several holes around the periphery and buttressed spines. **Fig. 18.** Valve found in Mar de Ajó. Broken valve showing loculate areolae with internal foramen and external velum. **Figs 19, 20.** Valves found in San Clemente del Tuyú and Villa Gesell respectively. Valves in internal view. Note pattern of striation and sessile lips of the labiate processes in almost apical position. Scale bars = 2 μm (Figs 17, 18); 10 μm (Figs 19, 20).

DISCUSSION

All the studied taxa possess ocelli and therefore belong to *Odontella*, according to the modern concept of the genus established by Hoban (1979) and Round *et al.* (1990).

In contrast to current taxonomic understanding and nomenclatural practice, Kützing (1849) pointed out that *Odontella rhombus* (Ehrenberg) Kützing (\equiv *Denticella rhombus*), is not conspecific with *Odontella rhomboides* R. Jahn & Kusber (as *Zygoceros rhombus*). Nevertheless, when Van Heurck (1880–1885) and Hustedt (1930) described and illustrated *Biddulphia rhombus* (Ehrenberg) Smith, they listed *Zygoceros rhombus* Ehrenberg, *Denticella rhombus* Ehrenberg and *Odontella rhombus* (Ehrenberg) Kützing as synonyms. In their illustrations these authors show specimens subcircular, broadly lanceolate and subrhombic,

with some differences in the striation pattern but agree in presenting marginal processes. Hoban (1979) too mentioned in the conclusions of his Ph.D. Thesis that *Zygoceros rhombus* is a heterotypic synonym of *Odontella rhombus*. However, Jahn & Kusber (2004) renamed this taxon as *Odontella rhomboides* R. Jahn & Kusber due to the fact that the epithet *rhombus* was preoccupied in the genus *Odontella* and to avoid the creation of a later homonym.

Although the lectotypes of *Odontella rhomboides* and *O. rhombus* share a similar pattern of distribution of labiate processes, not found elsewhere in the genus *Odontella*, and the density of the valve areolae, they differ in valve outline and striation pattern, *O. rhomboides* (recent European material from the 1830s) having a sub-circular annulus but *O. rhombus* (diatomite from the USA) having a linear lanceolate annulus. Taking into account that the observations were made on a few specimens and that we only found valvar views, we doubt their conspecificity as proposed by Van Heurck (1880–1885), Hustedt (1930) and Hoban (1979).

Odontella atlantica differs from *O. rhomboides* and *O. rhombus* in the striation pattern, with parallel striae extending bilaterally from a structural centre formed by a line or a linear annulus, and in the distribution of the labiate processes, there being one process per pole, without processes at the valve margins. Additionally, Frenguelli's taxon can be smaller and have a higher areola density on the valve than the others.

Since, there is no unmounted original material of either *Denticella rhombus* or *Zygoceros rhombus* in the Ehrenberg Collection, we have to use published images for SEM comparisons. Ross & Sims (1971) studied material from Tampa, Florida, that they identified as *Biddulphia rhombus* (Ehrenberg) Smith, i.e. *Odontella rhomboides*. The specimens they examined resemble ours in general aspect, morphology of the loculate areolae, with a centrally imperforate velum, and the morphology of the spines. However, they differ in areola density in the centre (7.5 in Tampa's *Odontella rhomboides* and 9–14 in 10 µm in our specimens), and in striation pattern (with structural centre formed by a point in the former and by a line in the latter) and labiate process distribution (one per pole plus three or four close to each lateral margin of the valve in the former and one per pole in the latter). Overall, we consider that the distribution of labiate processes and the striation pattern, when taken together, are the striking features to distinguish *Odontella atlantica* from the other two taxa and are sufficient to raise this variety to the rank of species. *O. atlantica* has a pattern of labiate process distribution that is very common in the genus, whereas *O. rhombus* and *O. rhomboides* present a different and unique pattern, which was not described by Simonsen (1974, 1979) for this genus.

The taxon analysed with SEM by Ricard (1987) as *Odontella rhombus* is in fact the pseudoloculate *Triceratium dictyotum* Sims & Ross (1990)³, and was therefore not treated in our study.

Emended description

Odontella atlantica (Frenguelli) Sar (Figs 2, 5–20)

Frustules rectangular to quadrangular in broad girdle view, with protracted apical elevations and convex valve face. Girdle composed of three split bands, valvocopula wide with areolae arranged in perivalvar striae secondarily in decussate rows, and copulae narrower, more densely areolate.

Valves subrhombic-lanceolate. Valve mantle indented, curving out again to the margin. Areolae arranged in linear striae disposed from a structural centre formed by a line or a linear annulus. Areolae loculate, with internal foramen and external velum. Vela centrally

³ *Triceratium dictyotum* is the new name given by Sims & Ross (1990) to *Biddulphia reticulata* Roper which ultrastructural analysis was presented in Ross & Sims (1971).

imperforated, with several holes around the periphery. Areolation pattern not easily visible in external view by the numerous buttressed spines with simple or blunt lobed tips. Elevations low and blunt, directed diagonally outwards, and provided with ocelli. Labiate processes placed close to the bases of the elevations, diagonally opposite each other, furnished by external tubes strong, oblique and curve polewards, with cup-like expansion on tips and internal sessile lips in almost apical position.

Morphometric data: apical axis, 24.5–118 μm ; transapical axis, 16.5–56 μm ; perivalvar axis, 24–51 μm ; striae in 10 μm , valve: 10–15, girdle: 12–15; areolae in 10 μm , valve: 9–14, girdle, 12–14.

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