NEW OBSERVATIONS ON FRUSTULE MORPHOLOGY OF *Eupodiscus radiatus* BAILEY AND *Fryxelliella floridana* PRASAD

FERNANDES, L. F.[1]

[1]Universidade Federal do Paraná, Departamento de Botânica, Setor de Ciências Biológicas, Centro Politécnico, C.P. 19031, Jardim das Américas, CEP 81531-970, Curitiba, Paraná, Brazil

Correspondence to: Luciano F. Fernandes, Universidade Federal do Paraná, Departamento de Botânica, Setor de Ciências Biológicas, Centro Politécnico, C.P. 19031, Jardim das Américas, CEP 81531-970, Curitiba, Paraná, Brazil, e-mail: lff@ufpr.br

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ABSTRACT

A study of the diatoms *Eupodiscus radiatus* Bailey and *Fryxelliella floridana* Prasad, mainly focussing on the mantle and cingulum, provided new morphological information. In *E. radiatus* dendritic structures and two types of a palisade-like structure fixed to silica rings were found on the lower valve mantle. Cingulum presented 1-3 bands with areolae arranged in decussate rows. Furthermore, the pars interior of the valvocopula is fimbriate; and the external openings of the rimoportulae are located along the rim of the scalloped extension. The valvocopula of *F. floridana* is open and its copula is ligulate. Both bands possess poroid areolae similar in size to the cribral pores on the valve face. The genus *Eupodiscus* is compared to *Fryxelliella*, based on material sampled in estuaries of Southern Brazil.

Key words: *Eupodiscus*, *Fryxelliella*, taxonomy, diatom, Bacillariophyta, Southern Brazil.

RESUMO

Observações inéditas sobre a morfologia das frústulas de *Eupodiscus radiatus* Bailey e *Fryxelliella floridana* Prasad

Um estudo morfológico sob microscopia eletrônica das diatomáceas *Eupodiscus radiatus* e *Fryxelliella floridana* (Triceratiaceae) foi realizado, enfocando principalmente o manto e o cíngulo. Ornamentações não registradas previamente são descritas. Em *E. radiatus*, estruturas dendríticas semelhantes a estrelas foram encontradas sobre o manto, logo abaixo das ondulações marginais. Dois tipos de paliçada silicosa provida de grânulos e fixada a anéis silicosos também foram observados, todo o conjunto envolvendo o manto. O cíngulo é provido de 1-3 bandas com aréolas ordenadas perpendicularmente ao eixo pervalvar, tendo "fimbrias" nas bordas superiores da valvocópula (pars interior) e encaixadas na parte interna da extremidade do manto. A abertura externa da rimopórtula localiza-se nas margens das ondulações do manto. *F. floridana* possui duas faixas silicosas no manto e um cíngulo ligulado com aréolas semelhantes às da superfície valvar. Adicionalmente, o gênero *Eupodiscus* é comparado à *Fryxelliella* a partir de observações de frústulas de *F. floridana* e *E. radiatus* coletadas em estuários do sul do Brasil.

Palavras-chave: *Eupodiscus*, *Fryxelliella,* taxonomia, diatomácea, estuário, sul do Brasil.

INTRODUCTION

The Genus *Eupodiscus* J. W. Bailey (Triceratiaceae) is readily recognised by the presence of marginal ocelli, rimoportulae intercalated to ocelli, loculate areolae and a scalloped wing-like extension of the valve margin. VanLandinghan (1969) listed 21 taxa of *Eupodiscus*, and Sullivan & Porguen (1990) recently described the new species *E. paracaënsis* Sullivan & Porguen. Sullivan (1988) elucidated some taxonomic problems concerning *Eupodiscus*, and designated a lectotype for the generitype, *E. radiatus* Bailey. All species in the genus are fossil, except for *E. radiatus*, which is found in modern phytoplankton or benthic communities (Prasad & Nienow, 1988; Fernandes *et al.*, 1990; Fernandes *et al.*, 1999).

Studies on *Eupodiscus* taxa using electron microscope techniques have examined the general morphology of the valve (Ross & Sims, 1973; Navarro, 1982; Prasad & Nienow, 1988; Sullivan, 1988; Sullivan & Porguen, 1990; Round *et al.*, 1990), but the mantle and the cingulum received little attention.

Recently, Prasad *et al.* (1997) established the genus *Fryxelliella* Prasad, which is distinguished from other related genera by the presence of a circumferential marginal tube, loculate areolae with a circular pattern of external cribra, a variable number of ocelli, and rimoportulae bearing an external tube, opening to the inner side by means of a labiate fissure. Two species were placed in the genus: *F. floridana* Prasad and *F. inconspicua* (Rattray) Prasad (= *Eupodiscus inconspicuous* Rattray). Although the genus *Fryxelliella* is closely related to *Eupodiscus*, Prasad *et al.* (1997) considered the occurrence of a marginal tube to be a diagnostic character, absent in other diatom taxa.

In this work we have studied the frustular morphology of the generitypes *Eupodiscus radiatus* and *Fryxelliella floridana*, but have mainly focussed on the mantle and cingulum. We describe previously unrecorded structures on the valve of these two species. In addition, we discuss the evolutionary relationships between the two genera in light of our new observations.

MATERIAL AND METHODS

Material for study was obtained from two estuaries of Southern Brazil: Paranaguá Bay (25°25'S-25°35'S and 48°20'W-48°45'W), Paraná State, an estuarine complex with an area of 612 km^2 and average depth of 2.5 meters; and Ratones river estuary (27°15'S-27°29'S and 48°30'W-48°40'W), Santa Catarina State, with an area of 17 km^2 and average depth of 1.8 meter. Both estuaries are influenced by the subtropical climate with two well-defined seasons: rainy in summer and dry in winter. The average annual rainfall is 1,988 mm. Salinity varies from 12 to 34, and the average annual range of the semidiurnal tides is 2.2 m. Mangrove forests, *Spartina* spp. marshes and tidal flats are the main habitats bordering the estuaries.

Plankton samples were collected using a standard plankton net with a 25 µm mesh. Samples were preserved with buffered formaldehyde (2%) and prepared for light and electron microscopy according to Hasle & Fryxell (1970). An aliquot of each sample was washed with distilled water, and selected specimens were picked out and transferred to electron microscope aluminium stubs. Permanent slides were prepared using Naphrax as a mounting medium. Light microscopy (LM) was performed using an Olympus BX40 microscope equipped with a 100x oil immersion objective. For scanning electron microscopy (SEM), samples were air-dried onto coverslips, which were mounted on aluminium stubs with conductive paint, coated with 16-20 nm gold and examined at an accelerating voltage of 15-30 kV in a Phillips Model XL30 scanning electron microscope. Slides and preserved field material used in this investigation were deposited in the FLOR Herbarium at the Federal University of Santa Catarina (UFSC).

The descriptive terminology follows that of Ross *et al.* (1979) and Round *et al.* (1990).

OBSERVATIONS

Eupodiscus radiatus *J. W. Bailey (Figs. 1-15)*

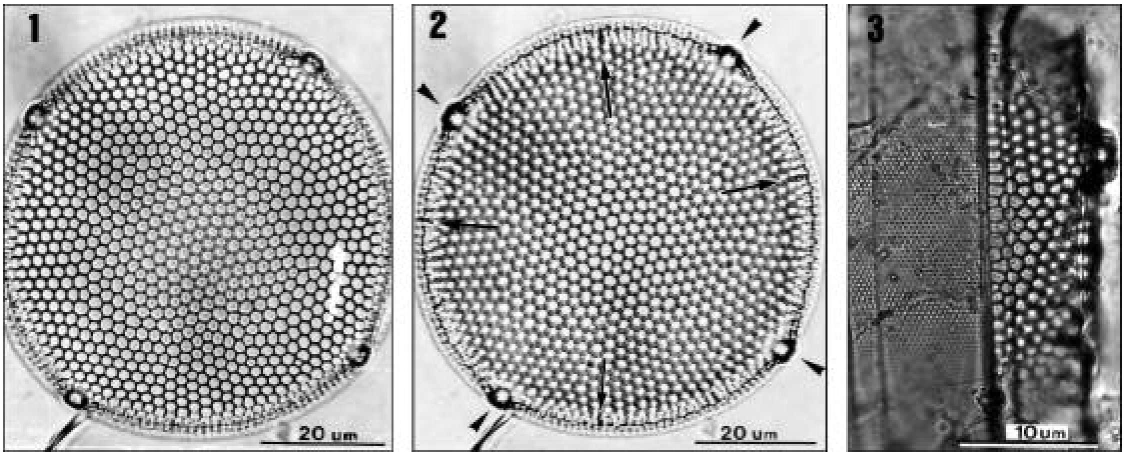
Valve surface. The morphology of the valve surface has already been described in detail by Sullivan (1988); thus only a brief description is furnished here. Living cells contained several ellipsoidal chloroplasts, parietal. Frustules are drum-shaped, strongly silicified, with a range in diameter of 48-133 µm (n = 43). The valve surface is flat or slightly concave, and covered by conspicuous hexagonal areolae (Figs. 1, 2, 6). Each areola bears an external cribra with cribral pores (Fig. 6) arranged in an isostoic pattern (*sensu* Sullivan &Porguen,

1990). The areolae open internally via foramina with slightly raised rims (Figs. 14, 15). Also present are larger cribral pores with a thickened rim (Fig. 6), irregularly scattered on the valve surface and mantle, that is, though some of them are aligned to the row of pores. In the marginal region, there is an undulated projection (Figs. 5, 7-9) in parallel with the valve surface, termed a scalloped wing-like extension by Sullivan (1988). This structure is reinforced by many silica ribs in either the top and the bottom portions (Figs. 8, 9). The margin of the extension presents a delicate reticulation (Fig. 9). The mantle is also areolated (Fig. 3), but these areolae are smaller than those on the valve face.

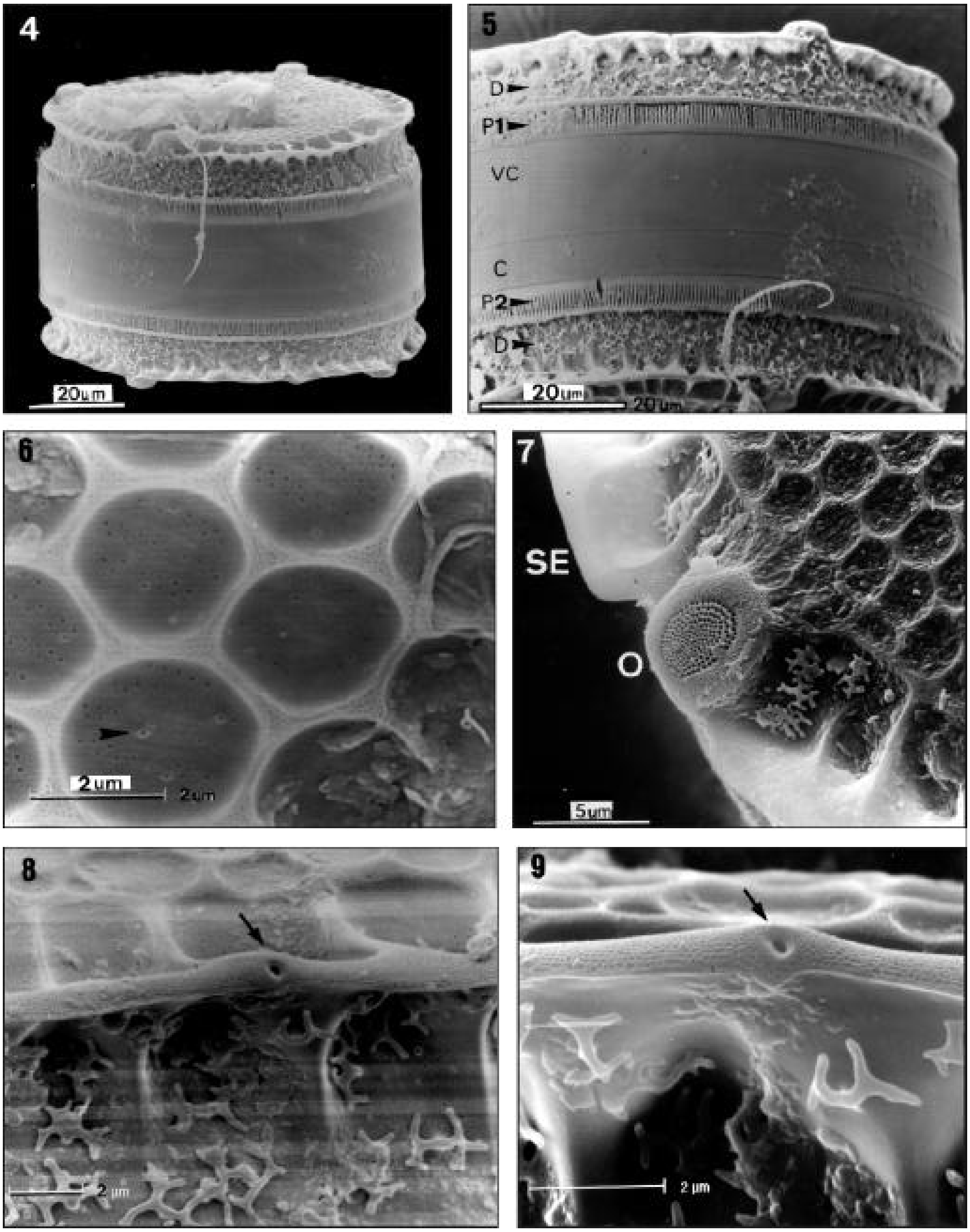
Rimoportulae. Rimoportulae are located in the transition region between the valve surface and mantle (Fig. 2), located approximately midway between two adjacent ocelli. Externally, each rimoportula opens via a circular aperture placed in a small cavity on the scalloped extension (Figs. 8-9). In this area, the rim of the scalloped extension is slightly thickened. Internally, the rimoportula opens via a radially oriented slit flanked by two labia, and located on a hemispherical protuberance (Fig. 14; see also Fig. 10 of Sullivan, 1988).

Ocelli. We found 2-6, equally spaced, ocelli along the margin, (Fig. 2). Smaller valves possessed fewer ocelli (2-3). Each ocellus bears a thickened, hyaline rim surrounding the porelli at the centre (Fig. 7).

Mantle. At the base of the scalloped extension there is a region composed of dendritic structures with irregular ramifications bearing (or not) a central aperture, occupying two thirds of mantle surface (Figs. 5, 10). Following the region of dendritic structures, the base of the mantle in each valve is occupied by a fence-like band (Fig. 5), which we have termed a "palisade" (Latin *vallum*). Two types of palisade are present in the same frustule. The Type 1 palisade is comb-like with the teeth (termed flange from here on) of the comb curving inward and contacting the mantle along its lower one-third (Figs. 5, 10, 11). The base of the comb is flushed with the valvocopula and bears uniseriate rows of small areolae (Fig. 11). The combs also have small granules. The Type 2 palisade appears as two strips of silica encircling the lower one-third of the mantle, with somewhat wavy struts of silica, bearing abundant knob-like structures (or bars) arranged in parallel occurring between the strips (Figs. 5, 12, 13). However, these strips are only connected to the lower strip of silica, which is connected to the valvocopula (Figs. 12, 13). The bars are covered by refringent granules; and some of them show small branching and their distal apices are frequently folded (Fig. 13).



Figs. 1-3 — *Eupodiscus radiatus,* LM. **Figs. 1-2** — Same valve at different focal levels. Note disposition of areolae, rimoportulae (arrows) and ocelli (arrowheads). Scale bars = 20 µm. **Fig. 3** — Partial girdle view of frustule showing loculate areolae of mantle (to the right), an ocellus and decussate poroid areolae of valvocopula and copula (to the left). Scale bar = 10 µm.



Figs. 4-9 — *Eupodiscus radiatus,* SEM, frustule in external views. **Fig. 4** — Complete frustule, with epivalve on bottom. Scale = 20 µm. **Fig. 5** — Girdle view, showing valvocopula (VC) and copula (C) of cingulum, Type 1 palisade (P1) and Type 2 palisade (P2), and dendritic structures (D) on mantle. Scale = 20 µm. **Fig. 6** — Valve surface, cribral pores of loculate areolae in an isostoic pattern. Note some pores are bordered by a thickened rim (arrow). Scale = 2 µm. **Fig. 7** — An ocellus (O) interrupting scalloped wing-like extension (SE) of valve margin. Scale = 5 µm. **Figs. 8-9** — External opening of rimoportula (arrow) on edge of scalloped extension. Note reticulate structure on the surface of this edge. Scales = 2 µm.

Cingulum. The cingulum consists of 2 to 4 open bands, and only the valvocopula was studied in our material. In LM, one can observe the decussate pattern of its areolae, which are much smaller than those of the valve (Fig. 3). Areolae are hexagonal and arranged in transverse rows (Fig. 3), though scanning electron microscopy just shows pores on the external surface (Fig. 11). The areola likely opens to the inner side by means of a small foramen (Fig. 15). The pars interior of the valvocopula possesses delicate fimbriae (to use a term coined by Johnson & Rosowski, 1992), which are flush with the lowermost portion of the internal valve mantle (Figs. 14-15).

Fryxelliella floridana *Prasad (Figs. 16-28)*

Valvar surface. Valves are circular. The valve diameter ranges from 20 to 40 µm (n = 70), but is usually less than 32 µm. The valve surface is convex and covered by hexagonal loculate areolae arranged in radial and concentric rows (Figs. 16-18). In the central region, the areolae are larger and more widely spaced than elsewhere on the valve. The areolae are slightly sunken on the valve surface. The external cribrum of each the areola is perforated by 7-13 cribral pores (Fig. 19), which are mainly arranged in a circular pattern, although some pores may be present at the centre of an areola. Internally, the areolae open via foramina with slightly raised rims (Figs. 26, 27). The valvar margin has a ring of refringent granules encircling the external tube of the rimoportulae but not the ocelli (Figs. 20, 21). Between the marginal granules and the valve face areolae a hyaline area is present (indicated by MT in Fig. 20), which is interrupted only by the ocelli and rimoportulae. At the edge of the valvar margin are numerous triangular to elliptical holes (or apertures) encircled by silica rims (Figs. 20-22). Each hole continues down the uppermost part of the mantle as a fissure (Fig. 21).

Rimoportulae. Three, sometimes two, rimoportulae are intercalated to the ocelli, and located on the valvar margin (Fig. 16). Each rimoportula has a short external tube (Fig. 22), and opens internally via a radially directed slit flanked by two labia (Fig. 27).

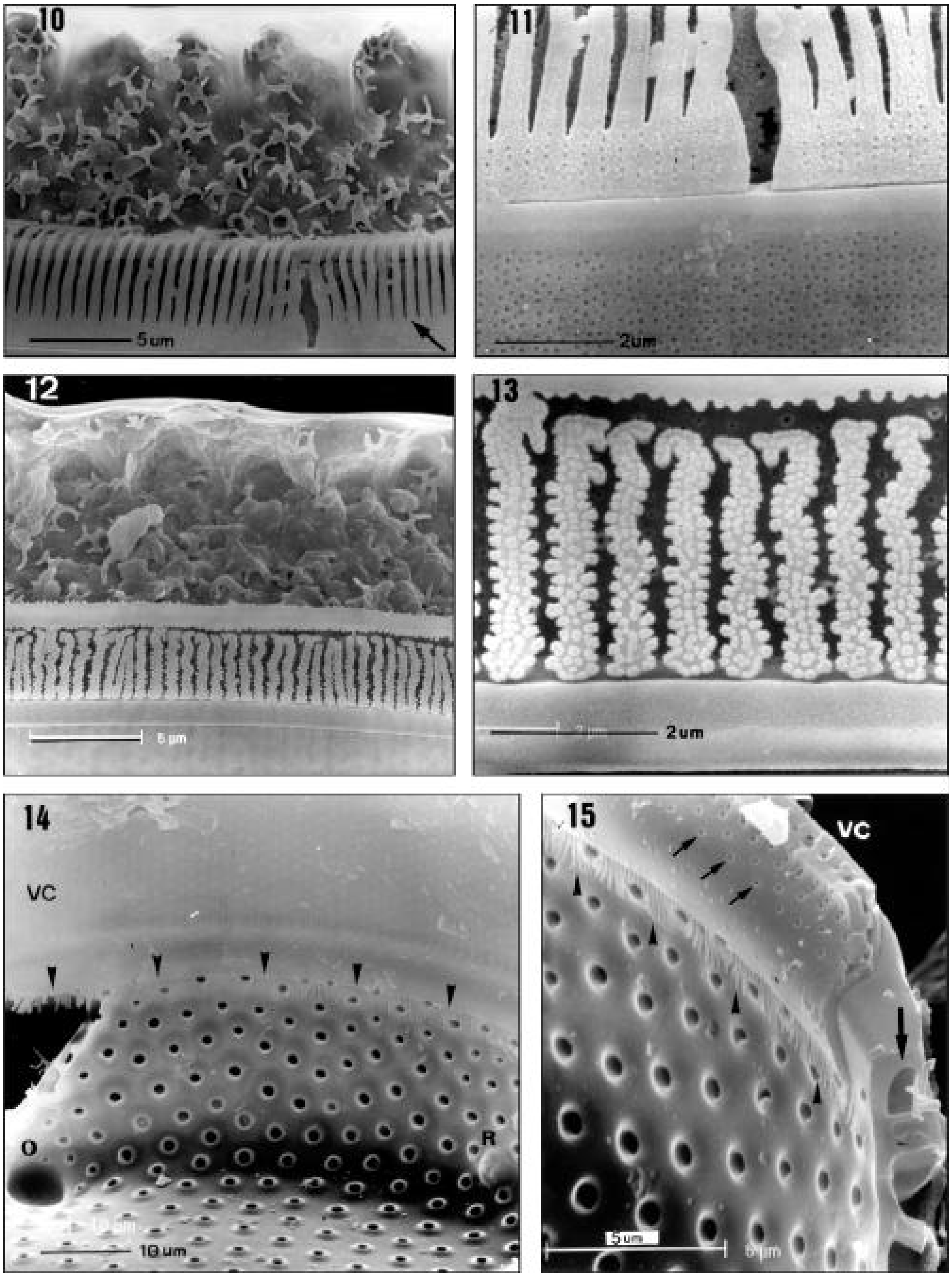
Ocelli. Three, sometimes two, marginal ocelli are equally spaced around the valve perimeter (Figs. 16-18). Each ocellus bears concentric rows of porelli, surrounded by a thickened hyaline rim (Figs. 20-21). The Fig. 25 illustrates a fracture through an ocellus in an internal view showing the unoccluded, small channels of the porelli.

Mantle. The valvar mantle is divided in two well-defined regions (Figs. 21-22), separated by a sulcus: (i) an upper hyaline strip interrupted by pervalvarly directed fissures of marginal triangular holes slightly elevated above the margin of the valve surface and (ii) a lower series of juxtaposed quadrangular plates bearing fine granules. A marginal circumferential tube is present along the outer edge of the valve (Figs. 20, 26) that is, occupying the internal structure of the mantle. Externally, the marginal tube opens through the triangular holes (Figs. 20-22). The marginal tube is interrupted in the ocelli (Figs. 23, 24). Internally, the marginal tube is perforated by small pores, which are radially arranged (Figs. 26-27).

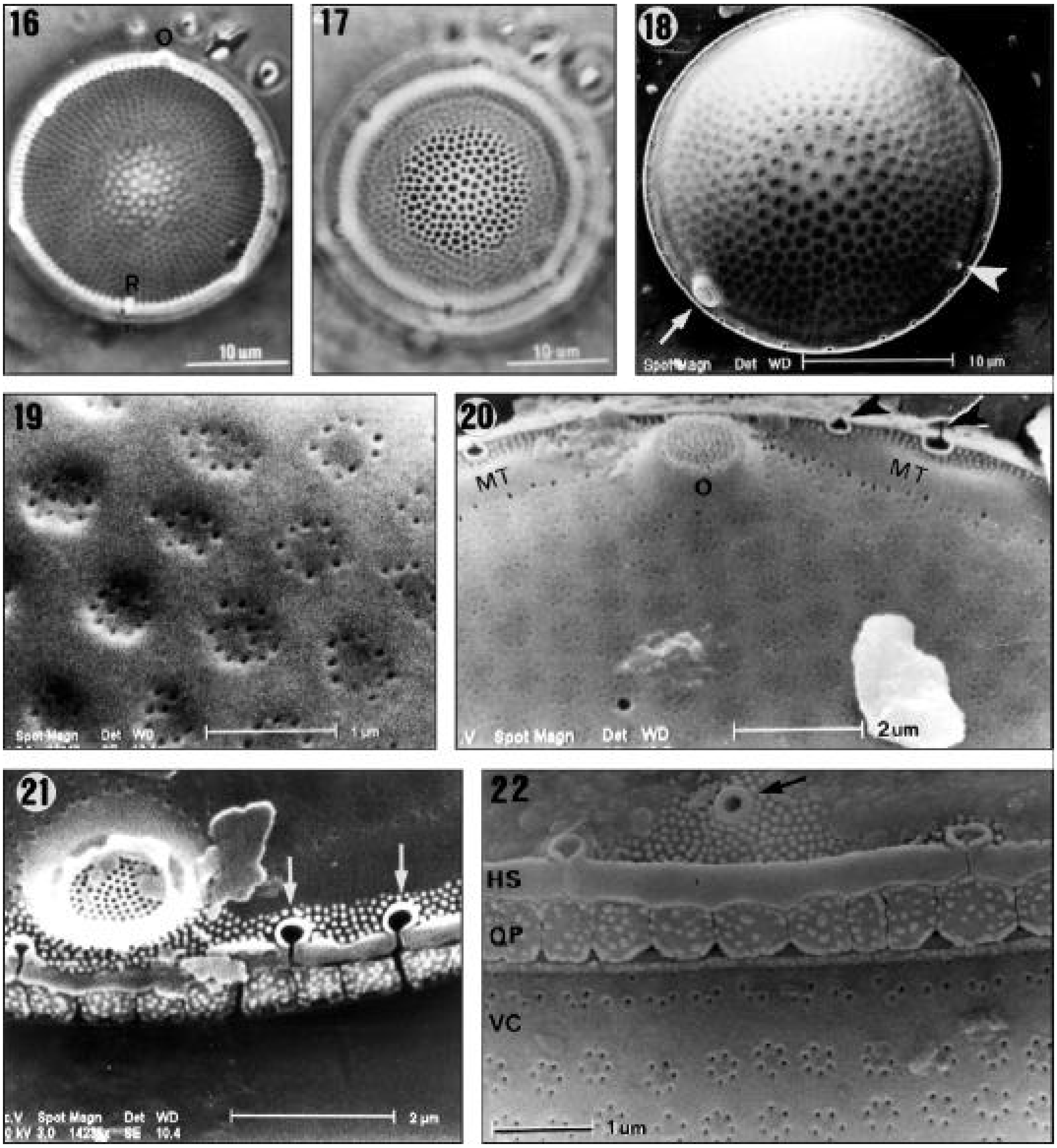
Cingulum. Some interpretations of the cingulum structure were made based on Figs. 24 and 28. We only observed frustules with two bands. A wide valvocopula is connected to the mantle by its pars interior, which underlaps the marginal tube (Fig. 24). Fimbriae are absent. The areolae of the valvocopulae are poroid and arranged in transverse rows (Fig. 22); pores are disposed in small circles of 5 to 6 pores (Figs. 22, 28). The copula is narrow and ligulate. Ligula is rounded (Fig. 28).

DISCUSSION

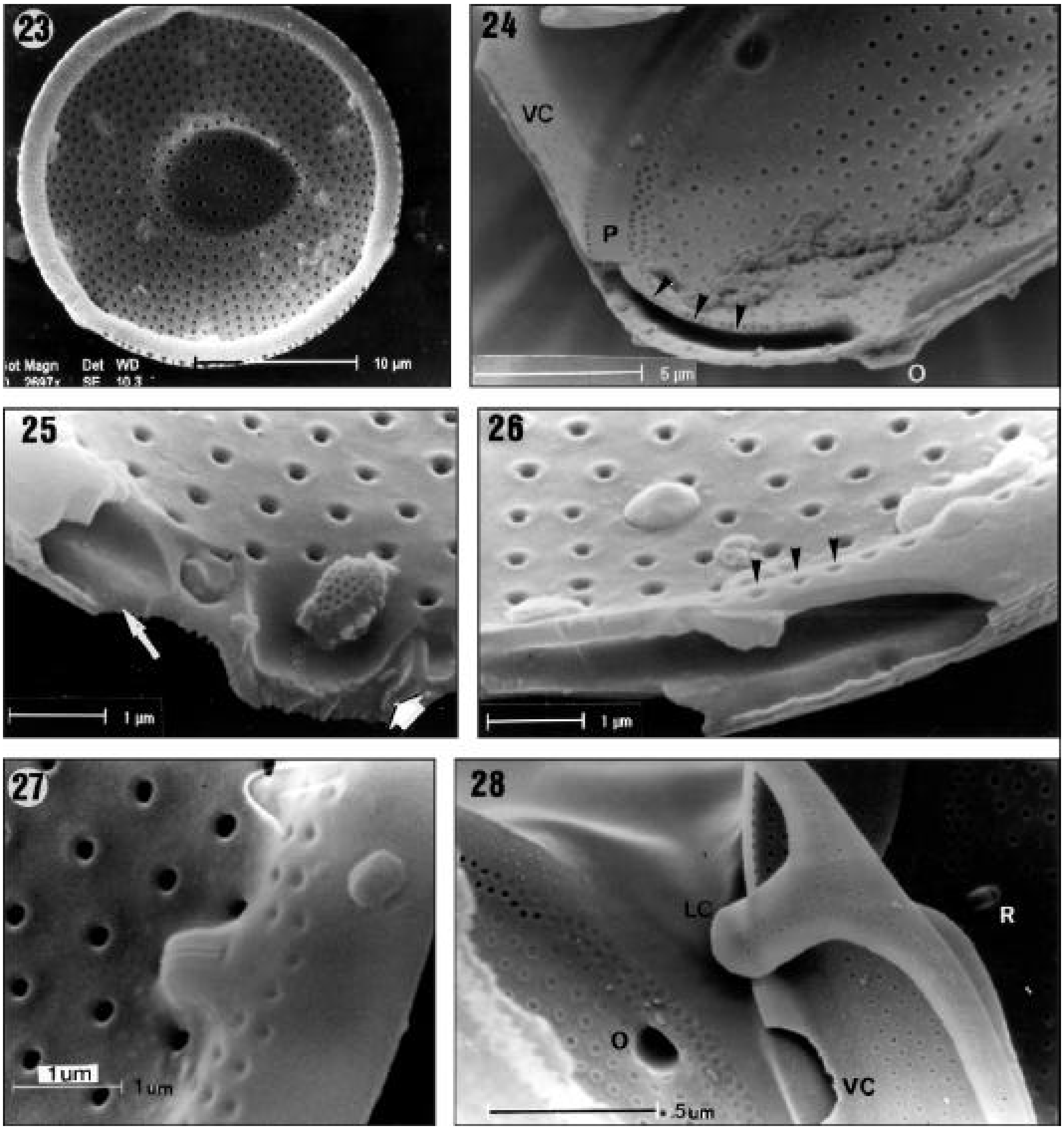
Taxonomic studies on diatoms are traditionally based on frustule morphology as viewed in the light and electron microscopes. The usual methodology for preparing material involves cleaning of cells through harsh chemical reactions, generally using potassium permanganate and strong acids. Although this technique makes valvar structures evident, it may preclude important observations concerning the cingulum and mantle. For instance, the bands of the cingulum may be dissociated during the cleaning process. Our work illustrates well the disadvantages of using harsh cleaning methods. The new structures (palisade and dendritic structures) found in this work were well preserved because an aliquot of the material was not submitted to acid attack. On the other hand, judging from material described and photographed by other authors and our personal observations, those structures disappear when valves are prepared by conventional procedures using strong acids.



Figs. 10-15 — *Eupodiscus radiatus,* SEM, external views (Figs. 10-13, entire frustule), and internal views (Figs. 14-15). **Fig. 10** — Valve mantle showing dendritic structures and Type 1 palisade. Note flanges (arrows). Scale = 5 µm. **Fig. 11** — Detail of Type 1 palisade showing small granules and tiny pores at this base. Note valvocopula with poroid areolae. Scale = 2 µm. **Fig. 12** — Valve mantle illustrating Type 2 palisade with its bars attached to lower silica strip. Scale = 5 µm. **Fig. 13** — Detail of palisade. Note broad granules on vertical silica bars. Scale = 2 µm. **Fig. 14** — Overlap of valve mantle and valvocopula (VC). Arrowheads indicate fimbriae at the edge of pars interior. Note internal opening of ocellus (O) and internal opening of rimoportula (R). Scale = 10 µm. **Fig. 15** — Detail of broken mantle and valvocopula (VC). Note fimbriae (arrowheads) and small poroids (small arrows) of valvocopula. Also indicated is a chamber (large arrow) at the base of a palisade that could correspond to an areola or a marginal tube. Scale = 5 µm.



Figs. 16-22 — *Fryxelliella floridana*, LM (Figs. 16-17), and SEM (Figs. 18-22), all external views. **Figs. 16-17** — Same valve at different focal levels showing ocelli (O) and rimoportulae (R). Note radial and concentric arrangement of areolae. Scale bars = 10 µm. **Fig. 18** — Whole valve with two ocelli (arrows) and two rimoportulae (arrowheads). Scale = 10 µm. **Fig. 19** — Detail of valve face, showing cribral pores of loculate areolae. Note circular pattern of cribral pores. Scale = 1 µm. **Fig. 20** — Marginal region of valve showing ocellus (O), hyaline portion of the marginal tube (MT), and subcircular apertures at the valve face edge (arrowheads). Scale = 2 µm. **Fig. 21** — Detail of ocellus and narrow mantle. Note subcircular apertures (arrows) surrounded by row of granules. Scale = 2 µm. **Fig. 22** — Detail of valve margin and valvocopula. Upper portion of mantle is a longitudinal hyaline strip (HS) interrupted by fissures of apertures, and its lower portion is a series of quadrangular plates (QP) bearing fine granules. Note circles of poroid areolae on valvocopula (VC) and external opening of rimoportula (arrow). Scale = 1 µm.



Figs. 23-28 — *Fryxelliella floridana,* SEM, internal views. **Fig. 23** — Whole valve with two ocelli and two rimoportulae. Scale = 10 µm. **Fig. 24** — Valve fractured through part of marginal tube (arrowheads) Note ocelli in internal and side views and non-frimbiate pars interior (P) of valvocopula (VC). Scale = 5 µm. **Fig. 25** — Detail of fractured valve showing marginal tube (arrow) and porellar plate of ocellus (white arrow). Scale = 1 µm. **Fig. 26** — Fracture through marginal tube. Note pores on its internal surface (arrowheads). Scale = 1 µm. **Fig. 27** — Internal opening of rimoportula, located at the transition between valve mantle and surface (i.e. where marginal tube begins). Scale = 1 µm. **Fig. 28** — Detail of frustule with valves partially opened, illustrating ligulate copula (LC), and valvocopula (VC) with small poroid areolae. Ocellus (O) and rimoportula (R) are also indicated. Scale = 5 µm.

For instance, in illustrations of *Eupodiscus radiatus* furnished by Sullivan (1988), Round *et al.* (1990) and Navarro (1982) one may only observe vestiges of the thickened marginal strips that sustain the palisade, as well as the refringent points that could be the basis of the dendritic structures. On the other hand, the scutella of *E. paracaënsis* endured the harsh cleaning methods used by Sullivan & Porguen (1990).

In *E. radiatus* we found, for the first time, the external openings of rimoportulae located on the outer edge of the scalloped extension. Prasad & Nienow (1988) and Prasad *et al.* (1997) commented that these external openings were flushed with the valve surface and could not be viewed, or they did not exist. The location of the external opening of the rimoportulae is interesting from a phylogenetic viewpoint. They could have surfaced as an independent external tube before the scalloped extension evolved, to which it later fused to the tube. If we assume that rimoportulae in *Eupodiscus* are older than a scalloped extension, and the hypothesis is true, then *E. radiatus* would be closely related to other *Eupodiscus* taxa with rimoportula bearing external tubes. To date, the rimoportula of *E. paracaënsis* has a conspicuous external tube located on the mantle, just below the scalloped extension (Sullivan & Porguen, 1990). In *E. oculatus* Greville, the external tubes are short, with the same location as in *E. paracaënsis* (Ross & Sims, 1973). Sullivan & Porguen (1990) also suggested that *E. radiatus* was a more recent species than *E. paracaënsis* and *E. oculatus*, based on the eventual **loss** of the external tube in *E. radiatus*. Our findings indicate that this view should be changed, as the external tube in *E. radiatus* was not lost but fused to the scalloped extension.

The two types of palisade were observed in all frustules analysed, to which we used gentle methods of valve cleaning. When samples were prepared with harsh methods, only traces of the palisade and dendritic structures remained on the mantle. Round *et al.* (1990) recorded “dendritic structures” in *E. radiatus*, and they should correspond to the ornamentations found in our material. In *E. paracaënsis*, which is closely related to *E. radiatus*, there is a series of plates (scutella) on the mantle base which encircle the valve (Sullivan & Porguen, 1990). Moreover, *E. paracaënsis* shows a marginal silica strip on the lower one-third of the mantle similar to that observed in *E. radiatus*. This structure could be the support for other ornamentations, as we observed for *E. radiatus*.

In *Cerataulus* Ehrenberg, which also belongs to Triceratiaceae, there are structures on the mantle edge very similar to that in the palisade of *E. radiatus*, and they are also sustained by silica strips. Furthermore, in figure “g” of Round *et al.* (1990, p. 234) for *Cerataulus* one can discern that the bars of the palisade appear eroded, their former presence suggested by a row of granules on the mantle base.

As for *Eupodiscus*, *Pleurosira laevis* (Ehrenberg) Compère bears projecting flanges with spines on the mantle, which partially cover the valvocopula (Johnson & Rosowski, 1992, Fig. 3). These authors suggested the flanges (and the mucilage recovering the cells) might function as adhesion mechanisms between valve and cingulum. The palisade of *E. radiatus* could carry out the same function. Examples of associations between mantle and valvocopula occur in other diatom genera. Flanges at the base of the mantle and a fimbriate pars interior of the valvocopula also appear in *Melosira* Agardh and *Odontella* Agardh (Crawford, 1975; Round *et al.*, 1990). In the pennate genera *Gomphonema* Ehrenberg and *Luticola* D. G. Mann, the valvocopula bears undulated projections which underlap the valve mantle (Round *et al.*, 1990).

If mantle characteristics are taken into account, two groups may be distinguished in the Family Triceratiaceae *sensu* Round *et al.* (1990): (i) pseudoloculi present on the mantle and siliceous strips plus accompanying structures absent (*Amphitetras* Ehrenberg, *Sheshuskovia* Glezer, *Triceratium* Ehrenberg *partim*), and (ii) siliceous strip present bearing specific structures such as scutella, flanges, a palisade and granules; with pesudoloculi absent (*Auliscus* Ehrenberg (?), *Cerataulus* Ehrenberg, *Eupodiscus*, *Fryxelliella*, *Pleurosira* (Meneghini) Trevisan, *Pseudoauliscus* A. Schmidt, *Triceratium partim*). The genus *Lampriscus* A. Schmidt is problematic since it possesses pseudocellus and linking spines, and shares some features with *Isthmia* Agardh of the Biddulphiaceae. Therefore, its placement in Triceratiaceae *sensu* Round *et al.* (1990) is questionable.

The mantle and cingulum of *Fryxelliella floridana* showed structures not previously recorded (Prasad *et al.*, 1997). Two silica strips separated by a sulcus were observed on the mantle edge, resembling the ornamentations found in *Cerataulus* (Round *et al*., 1990). In the latter, there is only one single silica strip, but it also possesses granular plates, as in *F. floridana*. Prasad *et al.* (1997) also observed the silica strip bearing granules, but not the smooth strip, perhaps because their Figs. 34 and 35 masked it due to the valve positioning in the stub. The bands of the cingulum in *F. floridana* have poroid areolae, similar in size to the cribral pores of the loculate areolae on the valve surface. In the Family Triceratiaceae, such complex feature is shared with *Amphitetras* (Round *et al.*, 1990) and *Eupodiscus* (this work); in other genera we generally found simple poroid areolae or rotae.

It is useful to compare *Eupodiscus* and *Fryxelliella* in view of similarities between the two genera pointed out by Prasad *et al.* (1997) and of the evolutionary relationships among the "eupodiscoid" group. Both genera have marginal ocelli, loculate areolae, rimoportulae between the ocelli, and girdle bands bearing complex poroid areolae. All these characteristics lead to the inclusion of these genera in the Triceratiaceae. *Fryxelliella* is distinguished from *Eupodiscus* by the existence of a marginal circumferential tube along the valve edge. Furthermore, cribral pores arranged in circles in contrast to parallel rows in *Eupodiscus*, and the presence of triangular apertures on the valve margin of *Fryxelliella* are further features claimed by Prasad *et al.* (1997) to distinguish the two genera.

Comparing *Fryxelliella* to *Triceratium*, on the mantle edge of *Triceratium favus* Ehrenberg there is a 'circumferential canal' with small pores opening to the inside (Miller & Collier, 1978) very similar in structure to the marginal circumferential tube found in *Fryxelliella*. If the two structures are homologous, then *Triceratium* and *Fryxelliella* exhibit more affinity to each another than previously believed. At least, the species *T. favus* and *Fryxelliella* spp. could represent an evolutionary line apart from the other genera of Triceratiaceae.

Although Prasad *et al.* (1997) maintained that a marginal tube did not occur in *Eupodiscus*, the authors did not provide any illustration (or evidence from the literature) proving that the structure definitely does **not** exist in *Eupodiscus*. Despite our efforts, we also were not able to determine its presence in valves of *E. radiatus* studied in the present work. The best illustration we have obtained (Fig. 15) hampers a reliable conclusion, but the figure shows a chamber that could correspond to an areola or a marginal tube. In this way, the absence of evidences pointing out the presence of marginal tube in *Eupodiscus* cast doubts on the validity of *Fryxelliella*, though other characters such as triangular apertures, rimoportula positioning and morphology of marginal tube would support the validation of the genus.

In spite of differences in opinion concerning the choice of criteria to circumscribe taxonomic categories, both genera seem to constitute an evolutionary group closely related. However, choosing phylogenetic criteria will better help the resolution of taxonomic problems into the large Family Triceratiaceae towards a more natural system of classification. Proposed earlier by Simonsen (1979), this phylogenetic viewpoint was recently advocated by Kociolek (1998), who invited diatomists to adopt criteria based on a more evolutionary perspective, especially when proposing new *taxa* or diatom systems.

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REFERENCES

CRAWFORD, R. M., 1975, The taxonomy and classification of the diatom genus *Melosira* C. Ag. I. The type species *M. nummuloides* C. Ag.. *Br. Phycol. J., 10*: 323-338.

FERNANDES, L. F., SOUZA-MOSIMANN, R. M. & FELÍCIO-FERNANDES, G., 1990, Diatomáceas (Bacillariophyceae) do Rio Ratones, Florianópolis, Santa Catarina, Brasil. I. Baixo curso e estuário. *Insula, 20*: 11-112.

FERNANDES, L. F., BRANDINI, F. P., GUTSEIT, K. S., FONSECA, A. L. & PELLIZZARI, F. M., 1999, Benthic diatoms growing on glass slides in the Paranaguá Bay, Southern Brazil: taxonomic structure and seasonal variation. *Insula, 28*: 53-100.

HASLE, G. R. & FRYXELL, G. A., 1970, Diatoms: cleaning and mounting for light and electron microscopy. *Trans. Am. Microscop. Soc*., *89*: 469-474.

JOHNSON, L. M. & ROSOWSKI, J. R., 1992, Valve and band morphology of some freshwater diatoms. V. Variations in the cingulum of *Pleurosira laevis* (Bacillariophyceae). *J. Phycol.*, 28: 247-259.

KOCIOLEK, J. P., 1998, Does each genus of diatoms have at least one unique feature? – a reply to Round. *Diatom Res.*, *13*: 177-179.

MILLER, W. I. & COLLIER, A., 1978, Ultrastructure of the frustule of *Triceratium favus* (Bacillariophyceae). *J. Phycol.*, *14*: 56-62.

NAVARRO, J. N., 1982, Marine diatoms associated with mangrove prop roots in the Indian river, Florida, U.S.A. *Bibl. Phycol.*, *61*: 1-151.

PRASAD, A. K. S. K. & NIENOW, J. A., 1988, Rimoportulae in *Eupodiscus radiatus* (Bacillariophyceae) from the Northeast Gulf of Mexico. *J. Phycol.*, *24*: 120-123.

PRASAD, A. K. S. K., RIDDLE, K. A. & LIVINGSTON, R. J., 1997, Fine structure, taxonomy, and systematics of the centric diatom *Fryxelliella* gen. nov. (Eupodiscaceae, Bacillariophyta) having a new valve structure, the circumferential marginal tube, with descriptions of *F. floridana* sp. nov. and *F. inconspicua* (Rattray) comb. nov.. *Phycologia, 36*: 305-323.

ROSS, R., COX, E. J., KARAYEVA, N. I., MANN, D. G., PADDOCK, T. B. B., SIMONSEN, R. & SIMS, P. A., 1979, An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia*, Beih., *64*: 513-533.

ROSS, R. & SIMS, P. A., 1973, Observations on family and generic limits in the Centrales. *Nova Hedwigia*, Beih., *45*: 97-128.

ROUND, F. E., CRAWFORD, R. M. & MANN, D. G., 1990, *The diatoms. Biology and morphology of the Genera*. Cambridge University Press, Cambridge, 747p.

SIMONSEN, R., 1979, The diatom system: ideas on phylogeny. *Bacillaria, 2*: 9-71.

SULLIVAN, M. J., 1988, A light and scanning electron microscope study of *Eupodiscus radiatus* Bailey (Eupodiscaceae). *In*: M. Ricard (ed.), *Proceedings of the Eighth International Diatom Symposium, 1986*. O. Koeltz, Koenigstein, pp. 113-123.

SULLIVAN, M. J. & PORGUEN, V., 1990, A new species of *Eupodiscus* closely related to the generitype *E. radiatus* (Eupodiscaceae). *In*: H. Simola (ed.), *Proceedings of the Tenth International Diatom Symposium, 1988*. O. Koeltz, Koenigstein, p. 117-126.

VANLANDINGHAN, S. L., 1969, *Catalogue of the fossil and recent genera and species of diatoms and their synonyms*. Part III. *Coscinosphaena* through *Fibula*. J. Cramer Verlag, Vaduz, pp. 1087-1756.