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Article

The genus *Tryblionella* W. Smith (Bacillariaceae, Bacillariophyta) in southern Brazil salt marshes

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Abstract: *Tryblionella* is a large epipelic genus, widespread from fresh to marine waters. Most of the studies including the genus are based only in light microscopy. Few recent studies are exclusively dedicated to *Tryblionella* and the ultrastructure of some species is still little known. In this paper we present eleven species of *Tryblionella* found in epiphyton and microphytobenthos in Patos Lagoon salt marshes. All the species are described, illustrated in light and scanning electron microscopy and comments about their taxonomy, distribution and ecology are provided. Two taxa are reported for the first time in the State of Rio Grande do Sul and one in Southern Brazil. The number of species registered in this study comprises nearly a half of the number of species registered in the country. The high richness observed may be related to the dynamics of the salt marshes, which provides both the mixing of fresh and marine waters communities and the diversity of microhabitats. The great variability among the species analyzed allowed to extend the general concept of *Tryblionella*, adding features which were not considered in the previous characterizations of the genus.

Keywords: *diatoms, Patos Lagoon, periphyton, taxonomy, ultrastructure.*

O gênero *Tryblionella* W. Smith (Bacillariaceae, Bacillariophyta) em marismas do Sul do Brasil

Resumo: *Tryblionella* é um gênero de diatomáceas epipélicas, distribuído de águas doces a marinhas. A maioria dos estudos que incluem o gênero baseia-se apenas em microscopia óptica. Poucos estudos recentes são exclusivamente dedicados à *Tryblionella* e a ultraestrutura de algumas espécies ainda é pouco conhecida. No presente artigo, apresentamos onze espécies de *Tryblionella* encontradas no epifíton e no microfitobentos nas marismas da Lagoa dos Patos. Todas as espécies foram descritas, ilustradas em microscopia óptica e eletrônica de varredura e comentários sobre a taxonomia, distribuição e ecologia foram fornecidos. Dois táxons foram registrados pela primeira vez para o estado do Rio Grande do Sul e um para a região Sul do Brasil. O número de espécies registradas neste estudo compreende cerca de metade das espécies registradas para o país. A grande riqueza observada pode estar relacionada à dinâmica das marismas, que proporciona tanto a mistura de comunidades de águas doces e marinhas quanto diversidade de microhabitats. A grande variabilidade entre as espécies analisadas permitiu que o conceito geral de *Tryblionella* fosse ampliado, incluindo características que não haviam sido consideradas nas caracterizações anteriores do gênero.

Palavras-chave: *diatomáceas, Lagoa dos Patos, perifíton, taxonomia, ultraestrutura.*

Introduction

Since the genus *Tryblionella* W. Smith was erected, it has undergone some changes both in its circumscription and in its taxonomic position. Smith (1853) described the genus comparing it to *Campylodiscus* Ehrenberg ex Kützing and *Surirella* Turpin. In the following years, many authors pointed out the resemblance between the genus *Tryblionella* and some species of *Nitzschia* Hassall (Grunow 1862, Rabenhorst 1864, Kitton 1873) and, thus, the genus was transferred to a section of *Nitzschia*, due to the absence of sufficiently distinct features to support the generic entity (Grunow 1879, 1880, Cleve & Grunow 1880). The proposition of the section *Tryblionella* did not conclude the discussion about the taxonomic position of these organisms. During more than one century, a few researchers refused to accept the new status and many suggested changes in the sections of *Nitzschia* (joining or splitting them) in order to better classify the specimens formerly included in the genus *Tryblionella* (Mann 1978).

Round et al. (1990) grouped four sections of *Nitzschia* to raise *Tryblionella* back to the generic status, expecting that the upcoming studies would follow this classification, but it was not applied by several researchers (e.g. Witkowski et al. 2000, 2004, Metzeltin et al. 2005). Recently, molecular studies have shown that *Nitzschia sensu lato* is not monophyletic (Lundholm et al. 2002a, b) and that some groups should be considered separated from it, such as *Psammodyction* and *Tryblionella* (Rimet et al. 2011). Phylogenetic studies with larger data sets, including specimens from various sections of *Nitzschia*, which could finally set a course to the end of this discussion, are still unavailable.

It is estimated that *Tryblionella* comprises 134 specific and infraspecific taxa, of which only 75 are taxonomically accepted (Guiry & Guiry 2019). Twenty-three species have been recorded in Brazil, the majority in the southern region (Cavalcante et al. 2013, Eskinazi-Leça et al. 2015, Bertolli et al. 2019). In the State of Rio Grande do Sul there is a higher concentration of studies in the Central Depression freshwaters and a few species have been registered in the Coastal Plain (Torgan et al. 1999, Bes & Torgan 2008). Although the genus is not considered frequent in brackish and marine waters (Round et al. 1990), it has been found among the genera with greater contribution to the surface sediment diatom assemblages of Patos Lagoon salt marshes (Silva et al. 2010) and, recently, two new species were described at the same salt marsh, undergoing salinity variations (Bertolli et al. 2019).

This study aimed to describe the specific taxonomic composition of the genus *Tryblionella* found in epiphyton and microphytobenthos from Patos Lagoon salt marshes. It also aimed to contribute to a better understanding of their taxonomy, ecology and distribution.

Materials and methods

The study was carried out at the salt marshes adjacent to Patos Lagoon estuary, State of Rio Grande do Sul, Brazil (31º50'-32º09'S 52º00'-52º15'W). Three sites with progressive distances from the Atlantic Ocean were established on the estuary outfall: São José do Norte (32º 06' 49.984" 52º 04' 22.980", 9 km from the outfall), Ilha da Pólvora (32º 01' 14.424" 52º 05' 59.095", 18 km from the outfall) and Saco do Silveira (31º 52' 48.821" 52º 14' 38.762", 36 km from the outfall) as shown in Figure 1.

Four species of herbaceous plants represented the prevailing vegetation of the salt marshes: *Sporobolus montevidensis* (Arechavaleta) Peterson & Saarela (= *Spartina densiflora* Brongniart), *Sporobolus alterniflorus* (Loisel.) Peterson & Saarela (= *Spartina alterniflora* Loiseleur-Deslongchamps), *Bolboschoenus maritimus* (L.) Palla (= *Scirpus maritimus* Linnaeus), and *Juncus kraussii* Hochstetter (1845: 342). Stems of these plants and the surface sediment close to them were gathered in winter (September 2010) and summer (February 2011). Abiotic data of the interstitial water were obtained during the sampling: pH (with PHTEK® pH meter), salinity (with YSI® 30 salinometer) and temperature (with Incoterm® thermometer). The surface sediment was collected with a core with 10 cm of diameter and 2 cm of depth. Live and motile cells were removed from the samples in the laboratory, following the 'Trapping method' (Eaton & Moss 1966 adapted by Laudares-Silva & Cimardi 1989). In addition, in the laboratory, the epiphyton was scrapped of the vegetal stems using a metal blade and deonized water.

Samples were oxidized with nitric acid over heat (15 minutes) and distilled water was rinsed until reaching neutral pH. Epiphytic and microphytobenthic cleaned samples were mounted in glass slides using Naphrax® (RI=1.74) for observation under Light Microscope (LM) Zeiss Axioplan. Images were captured with Axiocam ERc 5s both in bright field and in phase contrast. Aliquots of the cleaned samples were dried in aluminum stubs and covered with gold/palladium (16 nm) for observation under Scanning Electron Microscopes (SEM) Jeol JSM-5200 (20 mm working distance, 25 kV) and Jeol 6060 (10 mm working distance, 25 kV). The slides were housed at Herbarium Alarich Schultz, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil.

Taxa identification followed classic and modern literature such as Bailey (1850), Smith (1853), Grunow (1862, 1880), Cleve & Grunow (1880), Van Heurck (1880-1881, 1986), Kützing (1844), Pritchard (1861), Hustedt (1930), Frenguelli (1942), Cholnoky (1961), Peragallo & Peragallo (1897-1908), Krammer & Lange-Bertalot (1988), Hartley (1996), Witkowski et al. (2000), Metzeltin et al. (2005), Cavalcante et al. (2013) and Bertolli et al. (2019). Morphological terminology for the descriptions followed Hendey (1964), Anonymous (1975), Barber & Haworth (1981) and Round et al. (1990). All images were assembled using Corel Designer X6®.

Results

1. *Taxonomic composition*

A total of eleven species were found. Their descriptions under light and scanning electron microscopy and illustrations are presented as follows.

***Tryblionella acuminata* W. Smith (1853: 36, plate 10, Figure 77)**
Figures 2 A-D; 5 A-C

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, 42.8-49.5 µm long and 7.8-10.8 µm wide. Apices cuneate to subrostrate slightly produced. Transapical ribs parallel in the middle of the valve to radiate in the extremities, 13-16 in 10 µm, interrupted by a very noticeable longitudinal fold, the axial area may extend for almost one-third of the valvar face. Fibulae weakly distinguishable, regularly distributed and coinciding with the transapical ribs.

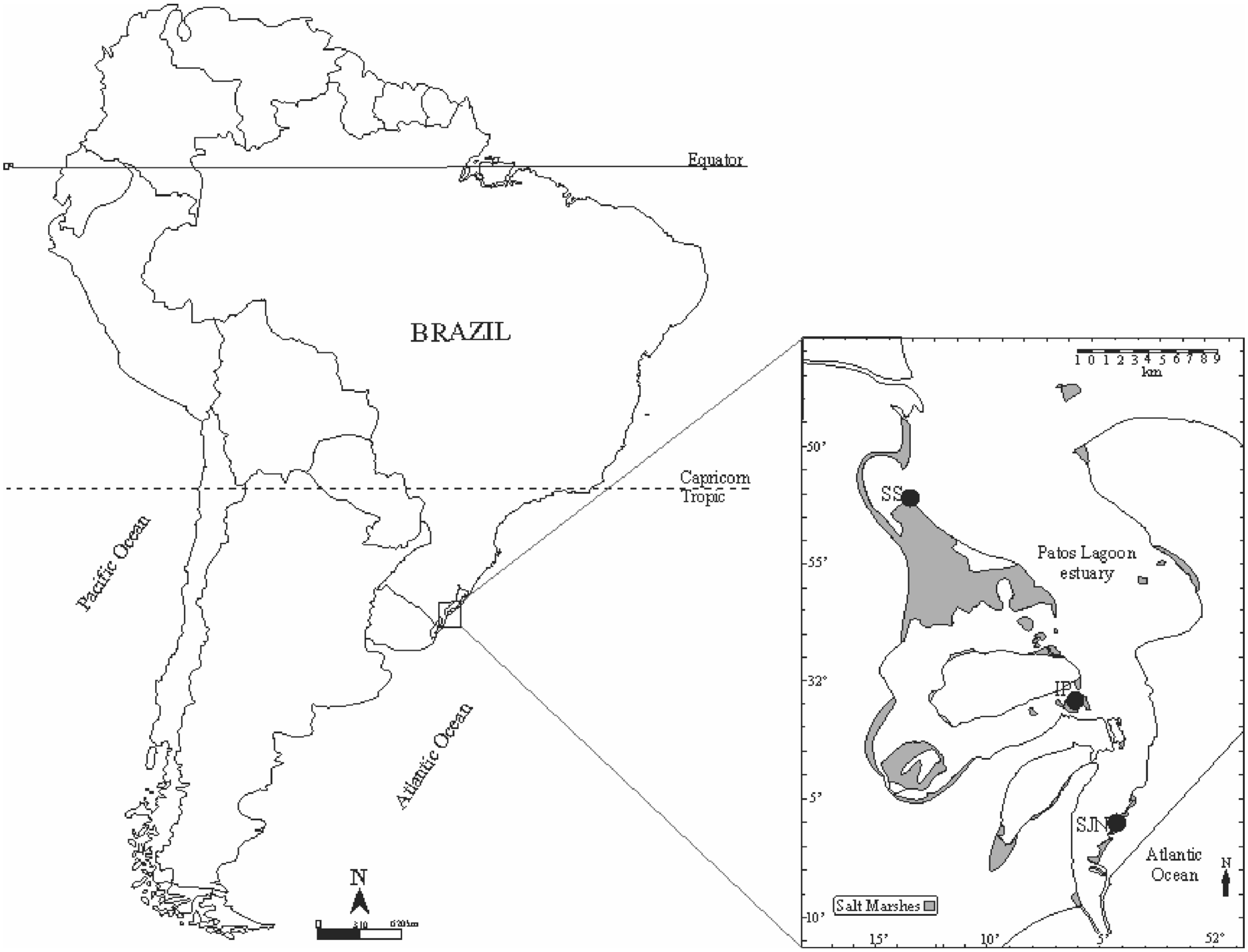

Figure 1. Location of sampling sites: Saco do Silveira (SS), Ilha da Pólvora (IP) and São José do Norte (SJN) in Patos Lagoon estuary, southern Brazil. Modified from Costa (1998).

Scanning electron microscopy: Longitudinal fold not clearly evident, but a slight depression can be noticed in the axial area region (Figure 5 A). Striae unevenly lengthened near the axial area and formed by a single row of poroids, 50-60 in 10 µm (Figures 5 B, C). Mantle striate, 30 striae in 10 µm (Figure 5 B).

Tryblionella calida **(Grunow) Mann in Round et al. (1990: 678)**

Figures 2 E-H; 5 D-G

Light microscopy: Valves linear-lanceolate, with a very slight constriction in the middle, more noticeable in the fibulate margin, 29.7-46.2 µm long and 8.0-10.3 µm wide. Apices cuneate and produced to slightly rostrate in some specimens. Axial area absent. Transapical ribs parallel in the whole valve extension, 15-17 in 10 µm. Longitudinal fold scarcely visible. Fibulae regularly distributed, 8-9 in 10 µm, the two medians further apart.

Scanning electron microscopy: Longitudinal fold discernible in the middle of the valve, both in external and internal view (Figures 5 D, E). Striae formed by one or two rows of rounded poroids, 50-60 in 10 µm (Figures 5 F, G). A small helictoglossa is visible in each apex of the valve in internal view (Figure 5 E). Mantle striate, 40 striae in 10 µm (Figures 5 D-G). Girdle bands lacking perforations (Figure 5 G).

Tryblionella circumsuta **(Bailey) Ralfs in Pritchard (1861: 792)**

Figures 2 I - J; 6 A - D

Light microscopy: Valves elliptic-lanceolate to obovate with cuneate-rounded apices, 131.1-242.8 µm long and 52.9-68.2 µm wide. Axial area absent. The valvar surface exhibits a rough appearance (Figure 3 A); however, it is not possible to discern striae and areolae in LM. Longitudinal fold conspicuous in the middle of the valve, fibulae equidistant 4-6 in 10 µm.

Scanning electron microscopy: Longitudinal fold very clear in the external face, bearing a narrow ridge of silica (Figure 6 A). Striae (32-40 in 10 µm) formed by a single row of poroids (36-50 in 10 µm), whose openings are rounded to transapically elongate in external view and rounded in internal view (Figure 6 B, C). The pattern of ornamentation of the valve face is different near the raphid margin, presenting narrow stripes of silica, which were defined by Sims & Padock (1982) as a gill-like arrangement of transapical laminae. The valve margin is thickened, and grooves can be observed running parallel with the raphe fissure. Central nodule is diverted in a V-shaped structure. Mantle striate, 32-36 in 10 µm (Figure 6 C). Internally, the poroids openings are rounded (Figure 6 C) and a small helictoglossa is visible at each apex of the valve (Figure 6 C).

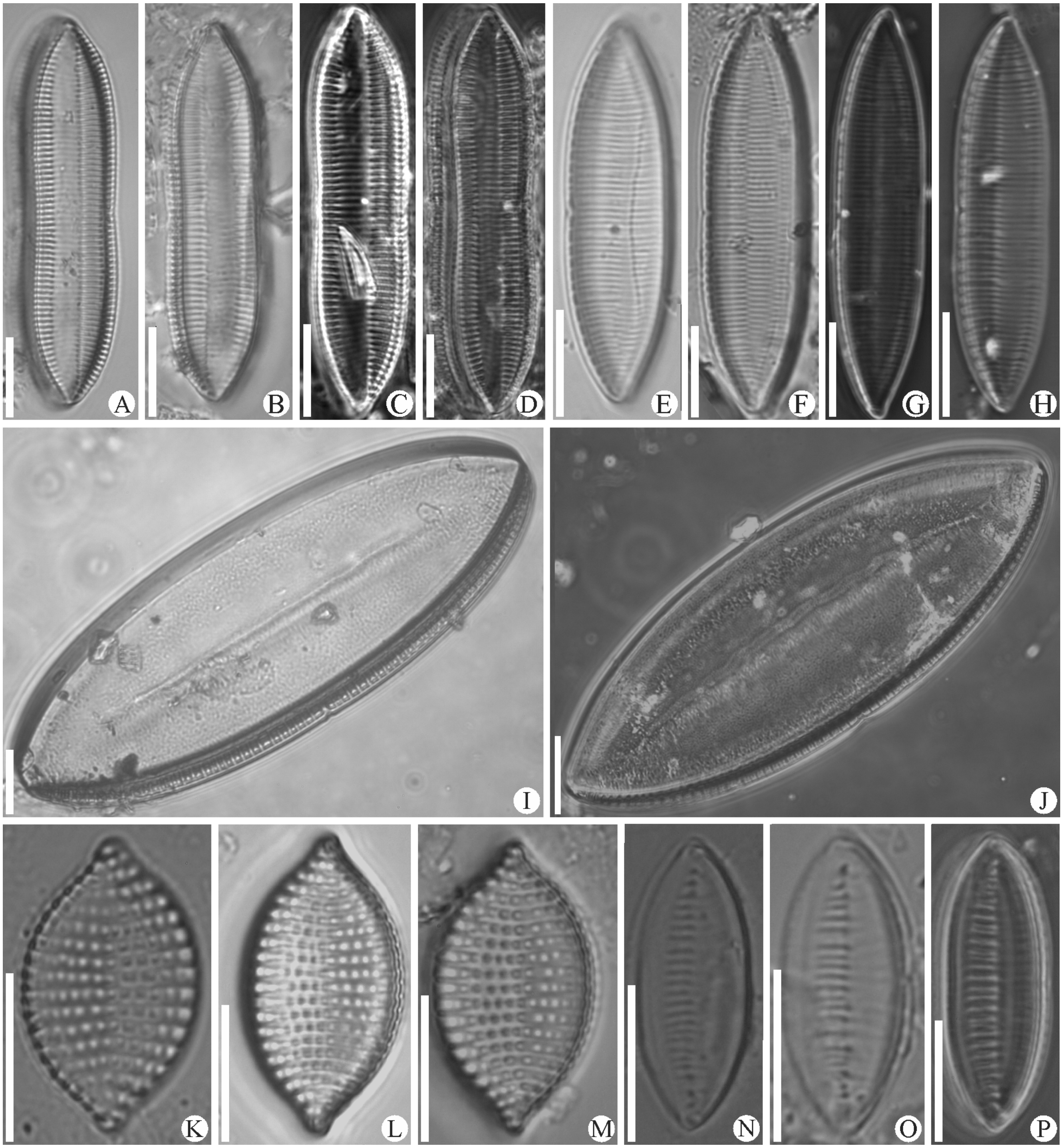

Figure 2. *Tryblionella* species in LM. A-D *T. acuminata*. E-H *T. calida*. I-J *T. circumsuta*. K-M *T. compressa*. N-P* *T. confusa*. Scale bars = 10 µm. *images adapted from Bertolli et al. (2019).

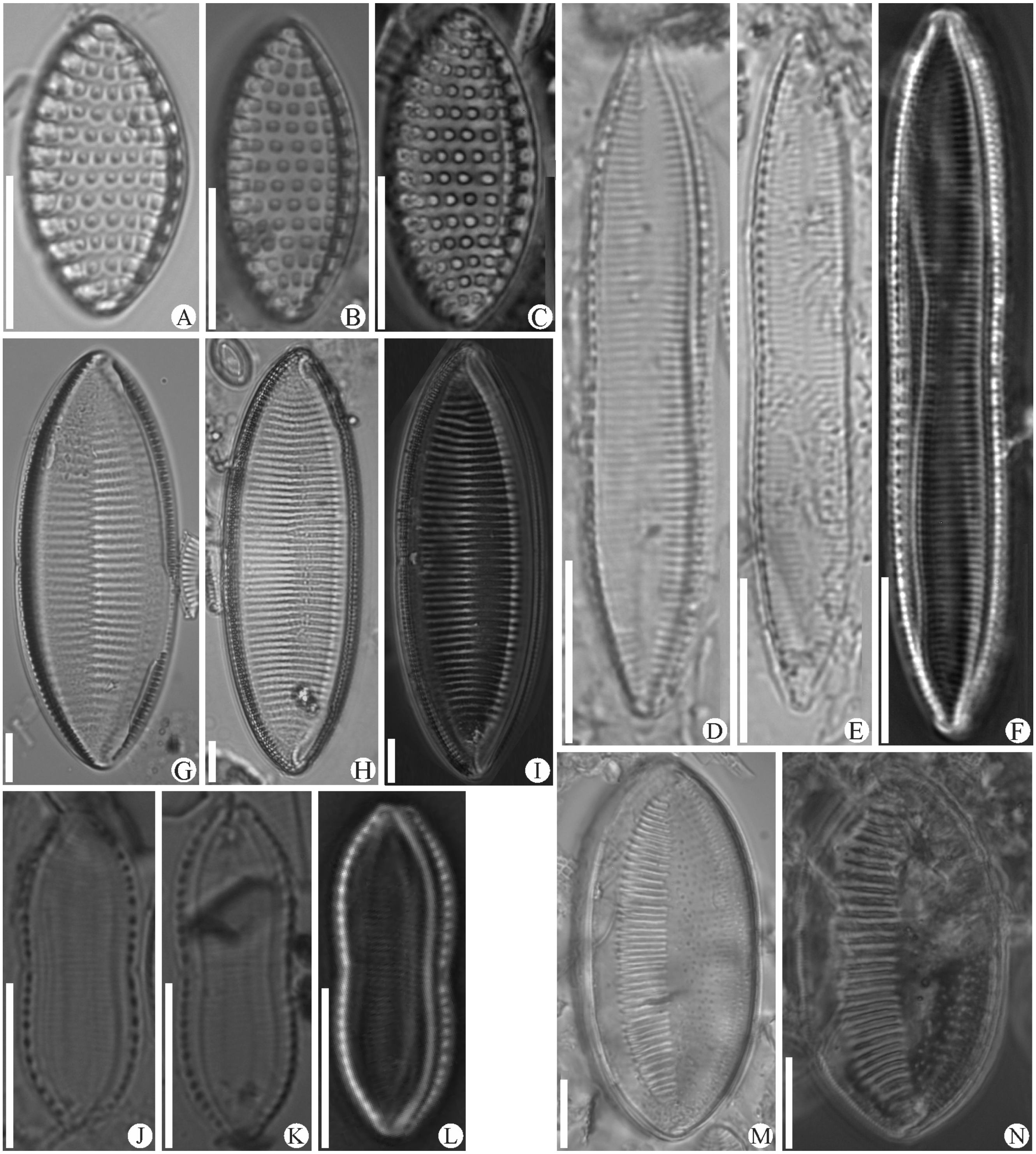

Figure 3. *Tryblionella* species in LM. A-C *T. granulata*. D-F *T. hungarica*. G-I* *T. ornata*. J-L *T. persuadens*. M-N *T. perversa*. Scale bars = 10 µm. *images adapted from Bertolli et al. (2019).

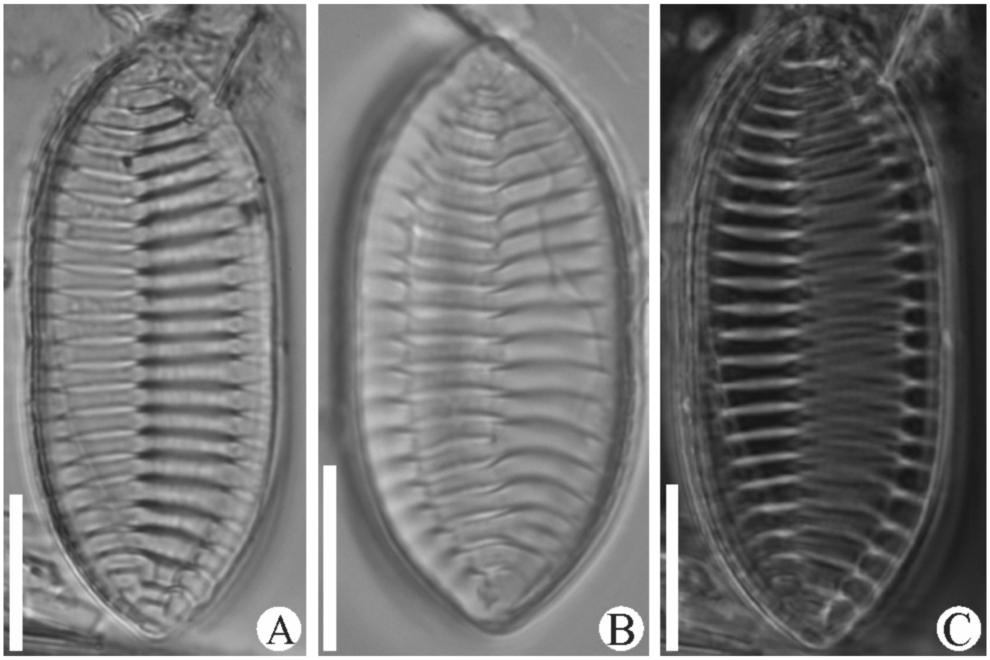

Figure 4. *Tryblionella* species in LM. A-C *T. victoriae*. Scale bars = 10 µm.

Tryblionella compressa **(J. W. Bailey) M. Poulin in Poulin et al. (1990: 96, Figure 98)**

Figures 2 K-M; 6 E-G

Light microscopy: Valves broadly lanceolate with produced rostrate or somewhat apiculate apices, 17.3-25.9 µm long and 8.9-12.7 µm wide. Longitudinal fold not distinguishable. Axial area absent. Fibulae weakly distinguishable (9-11 in 10 µm). Striae uniseriate, equidistant and parallel across the entire valve (9-11 in 10 µm), formed by large rounded poroids, 12-14 in 10 µm.

Scanning electron microscopy: Valve face remarkably undulated (Figures 6 E,F). A line of warts can be observed disposed on the external transapical costae at one margin (Figure 6 E). Poroids occluded by a delicate vola (Figure 6 G). Girdle bands lacking perforations (Figure 6 E).

Tryblionella confusa **Bertolli & Torgan in Bertolli et al. (2019: 175, Figures 2-21)**

Figures 2 N-P; 7 A-C

Light microscopy: Valves elliptic-lanceolate, slightly constricted in the middle, with slightly cuneate to rounded apices, 16.3-27.6 µm long and 7.2-10.0 µm wide. Axial area absent. Fibulae weakly distinguishable (7-10 in 10 µm). Unequally spaced transapical ribs (13-16 in 10 µm) occupying only one side of the valvar face.

Scanning electron microscopy: Asymmetric transapical ribs, with spatulate ends towards the valve center (Figures 7 A, B). Striae parallel, 40-42 in 10 µm, formed by a single line of rounded poroids, 80 in 10 µm (Figures 7 B, C). Valve margin thickened in the raphe side (Figure 7 A). A flattened silica projection is deflected towards the valve face, as well as distal raphe endings (Figure 7 B). Cingulum composed by several non-perforated bands (Figures 7 A, B). The mantle is striated, 40-42 in 10 µm, (Figures 7 A-C).

Tryblionella granulata **(Grunow) Mann in Round et al. (1990: 678)**

Figures 3 A-C; 7 D-F

Light microscopy: Valves elliptic-lanceolate with apices rounded to slightly cuneate, 17.1-26.8 µm long, 8.7-13.9 µm wide. Axial area absent. Fibulae equidistant (6-8 in 10 µm). Striae equidistant (6-8 in 10 µm), uniseriate to biseriate towards the fibulate margin, parallel in the middle of the valve and slightly radiate at the apices. Large rounded or elliptical poroids (8-12 in 10 µm).

Scanning electron microscopy: Longitudinal fold slightly apparent in external view, as a light depression (Figure 7 D). Striae formed by a single row of large poroids occluded by vola in the valve face (Figures 7 E, F) and by a double row of smaller poroids towards the valve mantle (Figure 7 D). Valvocopula presenting a row of large perforations (Figure 7 D).

Tryblionella hungarica **(Grunow) Frenguelli (1942: 178, plate 8, Figure 12)**

Figures 3 D-F; 8 A-F

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, 41.6-63.0 µm long and 6.0-10.0 µm wide. Apices subrostrate, somewhat produced. Transapical ribs very remarkable, 17-20 in 10 µm, interrupted by an axial area not always clearly distinguishable. Fibulae irregularly distributed, 8-10 in 10 µm.

Scanning electron microscopy: Longitudinal fold slightly perceptible, by the depression in the axial area region (Figures 8 A,B). Axial area ornamented with small granules (Figures 8 C, E). Both striae and transapical ribs are unevenly lengthened (Figures 8 D, F). Striae formed by a double row of poroids (80 in 10 µm), that may become single closer to the axial area (Figures 8 D, F). Distal raphe endings deflected (Figure 8 D). Mantle striate, 30 striae in 10 µm (Figures 8 C, E). Girdle bands lacking perforations and presenting rows of small granules (Figure 8 C).

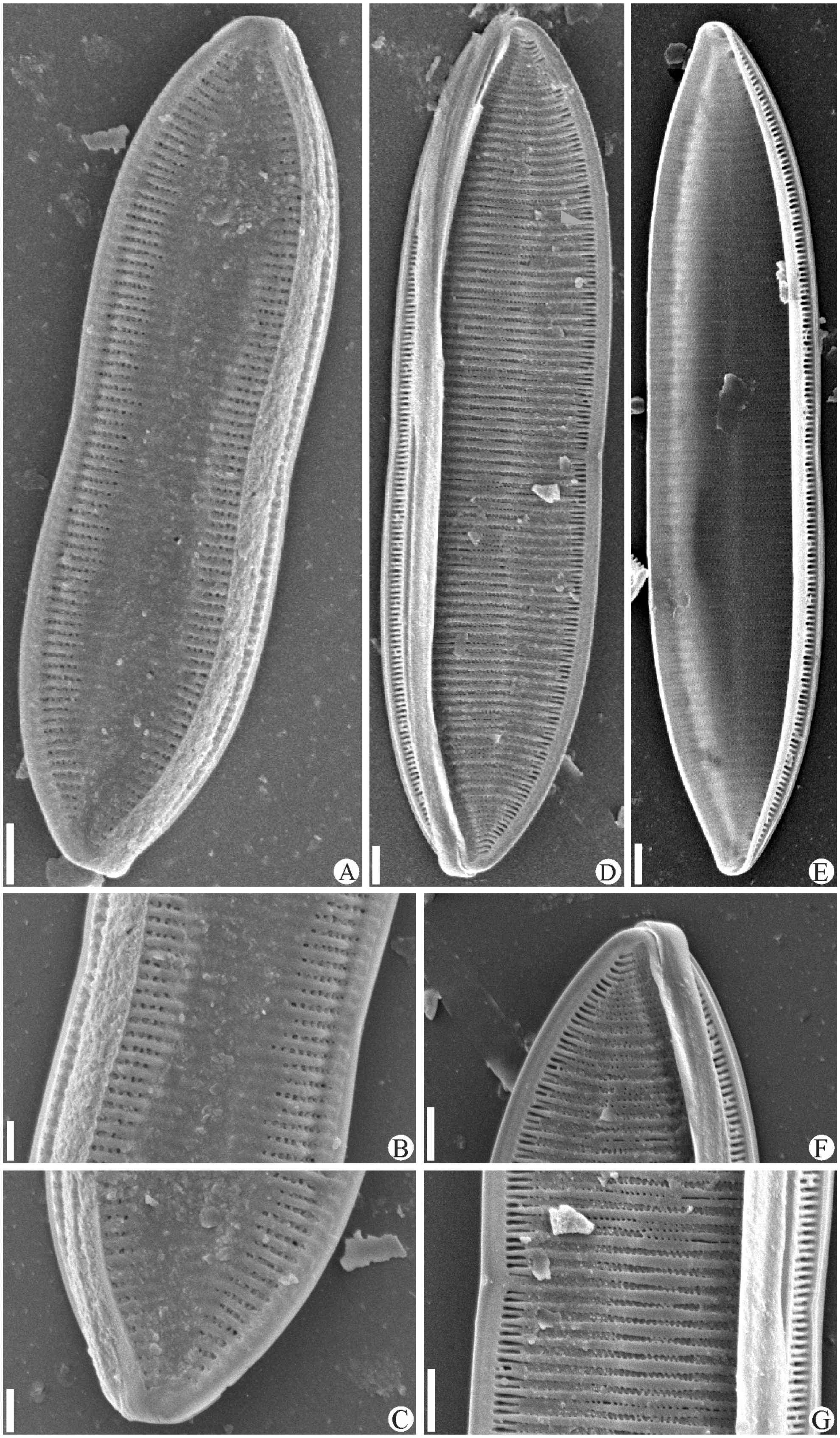

Figure 5. *Tryblionella* species in SEM. A-C *T. acuminata*. D-G *T. calida*. Scale bars = 1 µm (A), 2 µm (B-G).

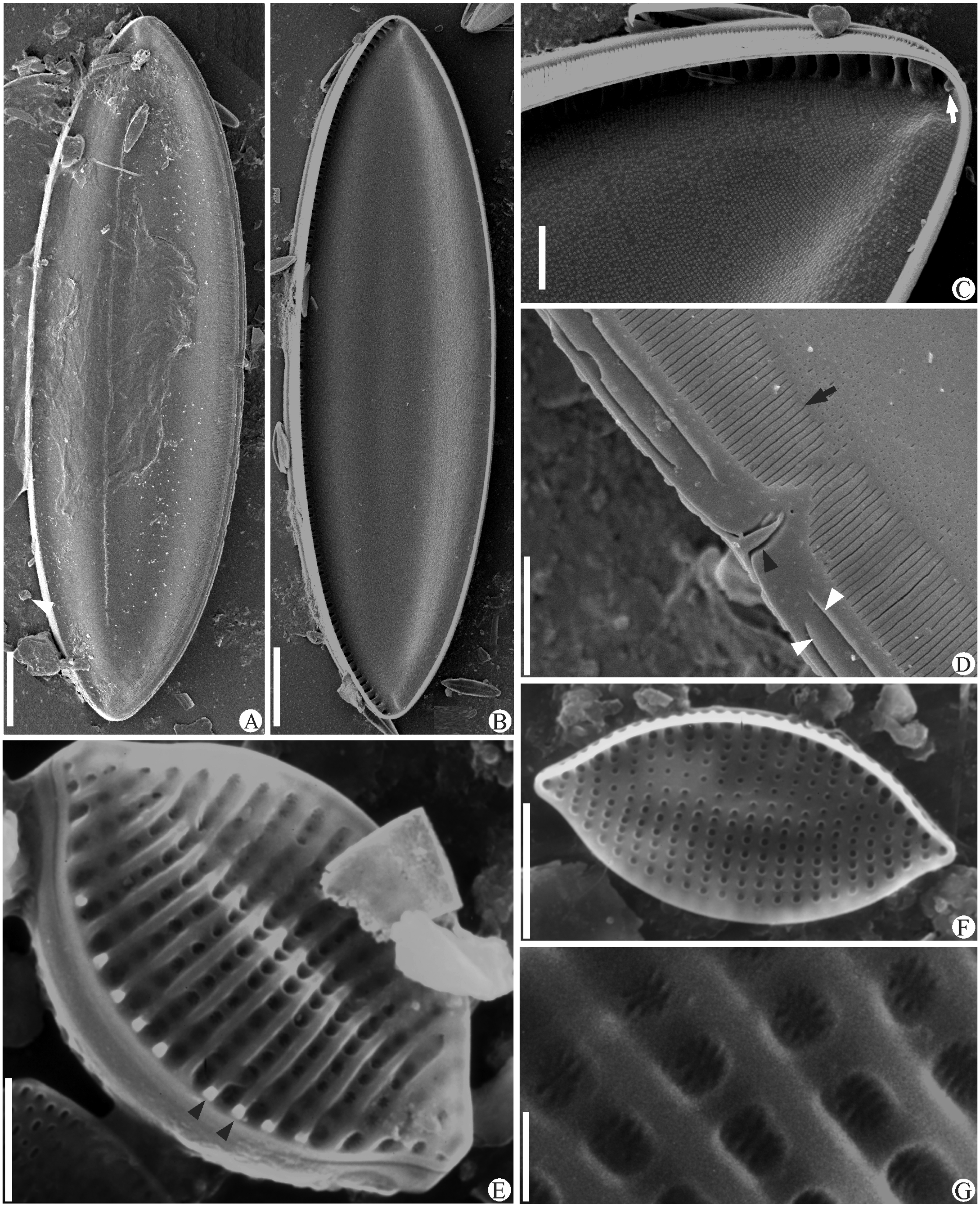

Figure 6. *Tryblionella* species in SEM. A-D *T. circumsuta*. Note the small helictoglossa (white arrow in Fig. 6 C) and the "gill-like" arrangement of transapical laminae (black arrow), the grooves parallel to the raphe fissure (white arrow heads) and central nodule (black arrow head) in figure 6 D. E-G *T. compressa*. Note the warts on the transapical costae (black arrow heads in Fig. 6 E). Scale bars = 20 µm (A, B), 10 µm (F), 5 µm (C-E), 1 µm (G).

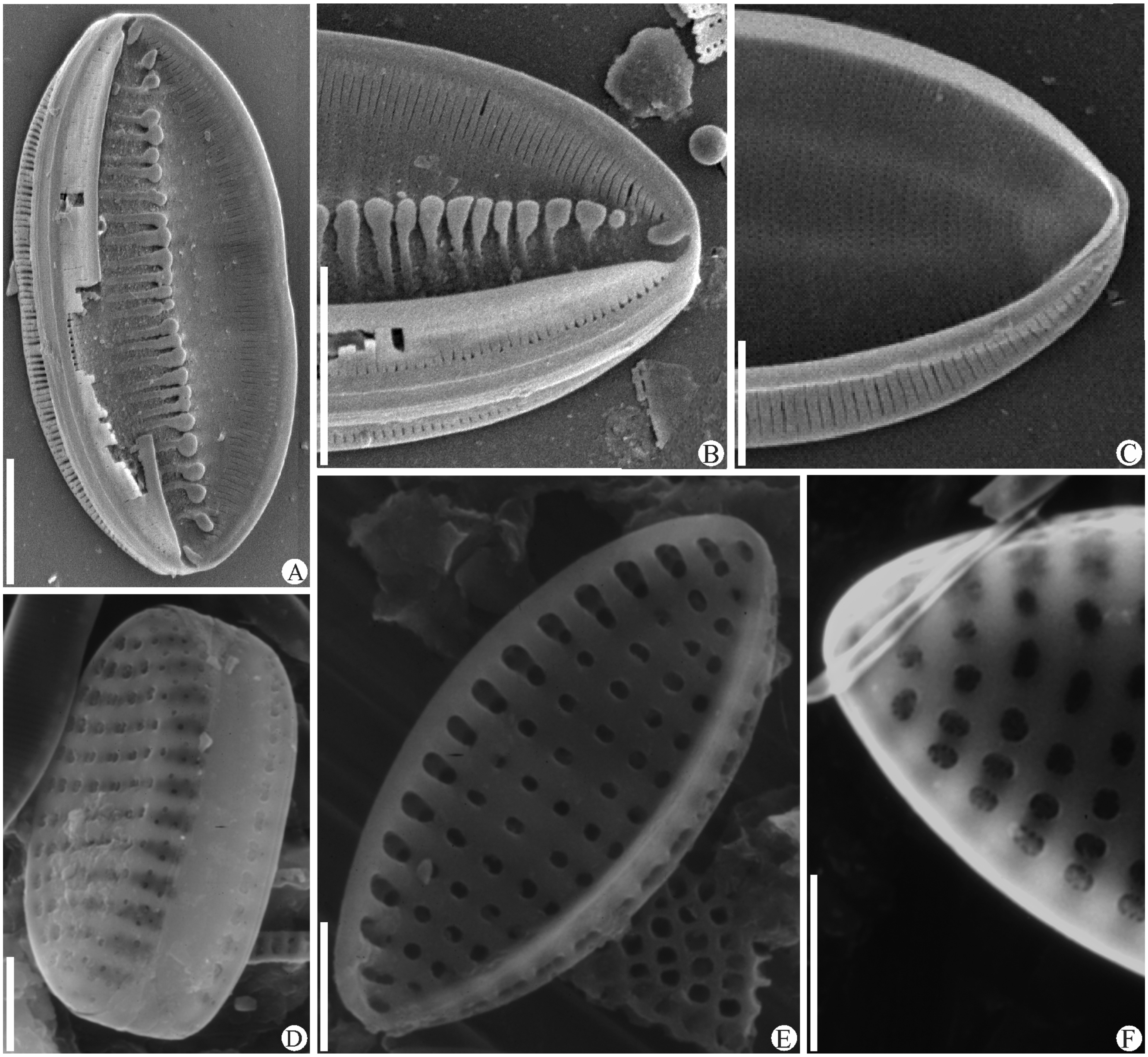

Figure 7. *Tryblionella* species in SEM. A-C *T. confusa*. D-F *T. granulata*. Scale bars = 5 µm (A, B, D-F), 1 µm (C*). *image adapted from Bertolli et al. (2019).

***Tryblionella ornata* Bertolli, Talgatti & Torgan in Bertolli et al. (2019: 178, figs. 22-40)**

Figures 3 G-I; 9 A-C

Light microscopy: Valves broadly lanceolate with cuneate apices, 85.7-108.3 µm long and 31.4-35.0 µm wide. Remarkable transapical ribs, 5-7 in 10 µm, sometimes presenting branches. Axial area absent. Fibulae equidistant, 6-8 in 10 µm.

Scanning electron microscopy: the space between two consequent transapical ribs is ornamented by a pattern that reminds a lace texture (Figure 9 B). Striae (36 in 10 µm) formed by single rows of poroids (40 in 10 µm). Proximal raphe endings deflected towards the valve face, forming a small obtuse central nodule (Figure 9 A). Valve margins thicker than the valve face with irregular grooves throughout its extension (Figures 9 A, B). Mantle striate, 10 striae in 10 µm (Figures 9 A, B). A very small helictoglossa is visible at each valve end (Figure 9 C).

***Tryblionella persuadens* (Cholnoky) Cavalcante, Tremarin & Ludwig in Cavalcante et al. (2013: 1420)**

Figures 3 J-L; 10 A, B

Light microscopy: Valves slightly panduriform with cuneate to subrostrate apices, 17.6-25.3 µm long and 5.8-6.5 µm wide. Striae parallel in almost all the valve extension, becoming slightly radiate on the apices, 24-28 in 10 µm. Axial area absent. Fibulae irregularly distributed, the two medians further apart, 14-16 in 10 µm.

Scanning electron microscopy: Longitudinal fold noticeable by the presence of a depression in the middle of the valve (Figures 10 A, B). Striae formed by a single row of poroids rounded to more rectangular nearer the non fibulate margin, 35 in 10 µm (Figure 10 A). Mantle striate 40 striae in 10 µm (Figure 10 A). A small helictoglossa is observed at each valve end internally (Figure 10 B).

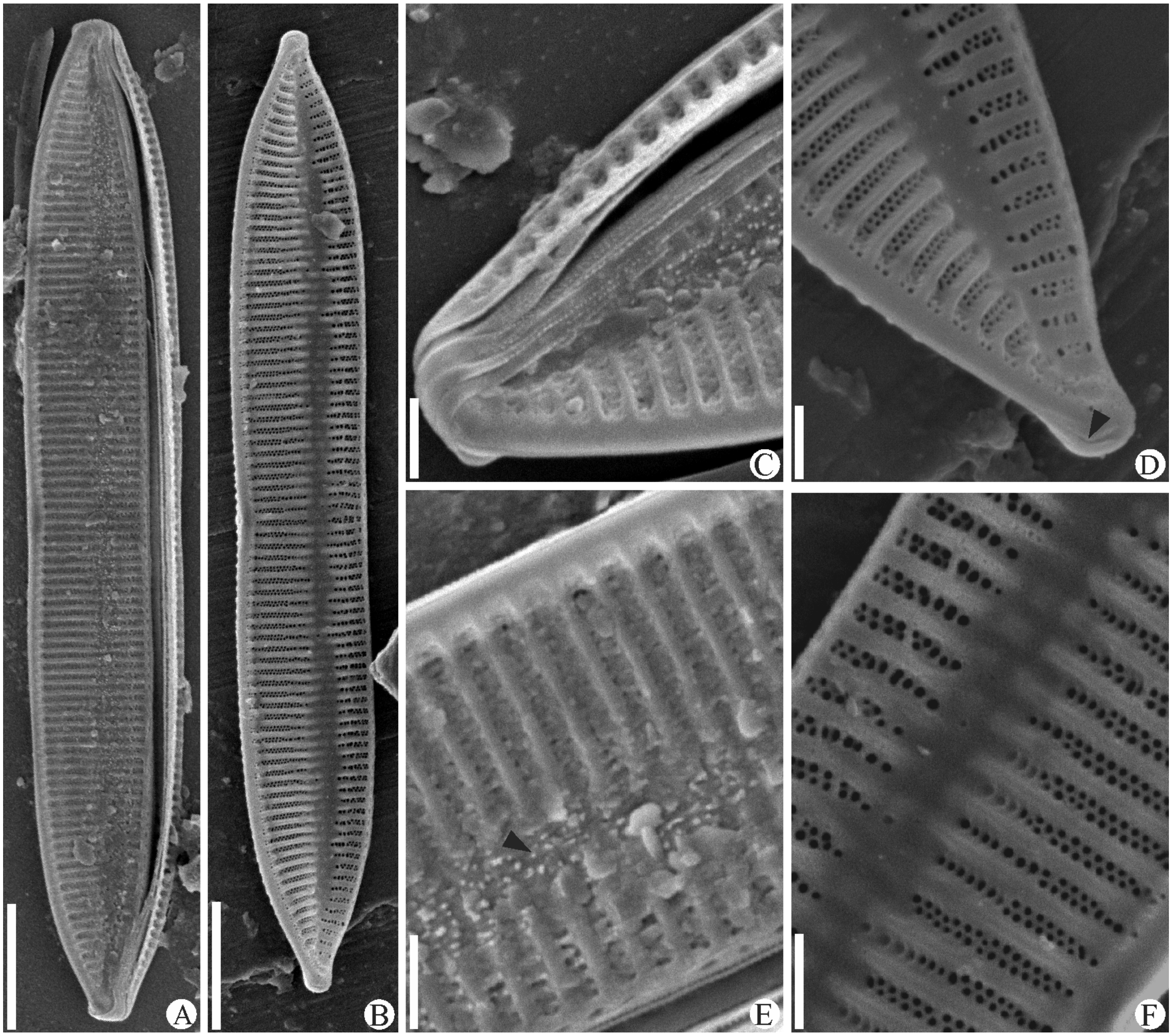

Figure 8. *Tryblionella* species in SEM. A-F *T. hungarica*. Note the distal raphe ends deflected (black arrow head in Fig. 8 D) and the small granules in the axial area (black arrow head in Fig. 8 E). Scale bars = 5 µm (A, B), 1 µm (C-F).

Tryblionella perversa **(Grunow) Mann in Round et al. (1990: 679)**
Figures 3 M, N; 10 C

Light microscopy: Valves broadly elliptic-lanceolate, with a slight constriction in the middle and cuneate to slightly obtuse apices, 39.6-51.2 µm long and 19.4-20.8 µm wide. The valvar face presents two different patterns of ornamentation. One side presents radiate transapical ribs (9-12 in 10 µm) and the other side lacks these structures and presents irregularly distributed granules. Axial area absent. Fibulae are weakly distinguishable at the granulate side margin.

Scanning electron microscopy: Valve margins presenting longitudinal stripes, similar to the gill-like structures observed in *T. circumsuta* (Figure 10 C). The granulate area may advance towards the apices of the transapical ribs side (Figure 10 C). The internal aspects of the valve were not observed.

Tryblionella victoriae **Grunow (1862: 553, plate 28, Figure 34)**
Figures 4 A-C; 11 A-D

Light microscopy: Valves linear-lanceolate, slightly constricted in the middle, with cuneate to sub-rostrate apices, 33.6-39.1 µm long and 15.2-16.9 µm wide. Large equidistant transapical ribs (6-7 in 10 µm) distributed alternately on both sides of the remarkable longitudinal fold, producing a zigzag pattern appearance. Axial area absent. Fibulae eccentric, equidistant, the two medians further apart (6-10 in 10 µm).

Scanning electron microscopy: Striae are delicate (50-60 in 10 µm) formed by a row of small poroids, 6-7 in 10 µm (Figures 11 A-D). Thin apical silica projections rise from the transapical ribs and extend to the areolate areas, sometimes connecting two consequent ribs (Figures 11 A, B, D). The transapical ribs may cross all the valve face or be interrupted in the longitudinal fold region (Figure 11 D). Internally, a

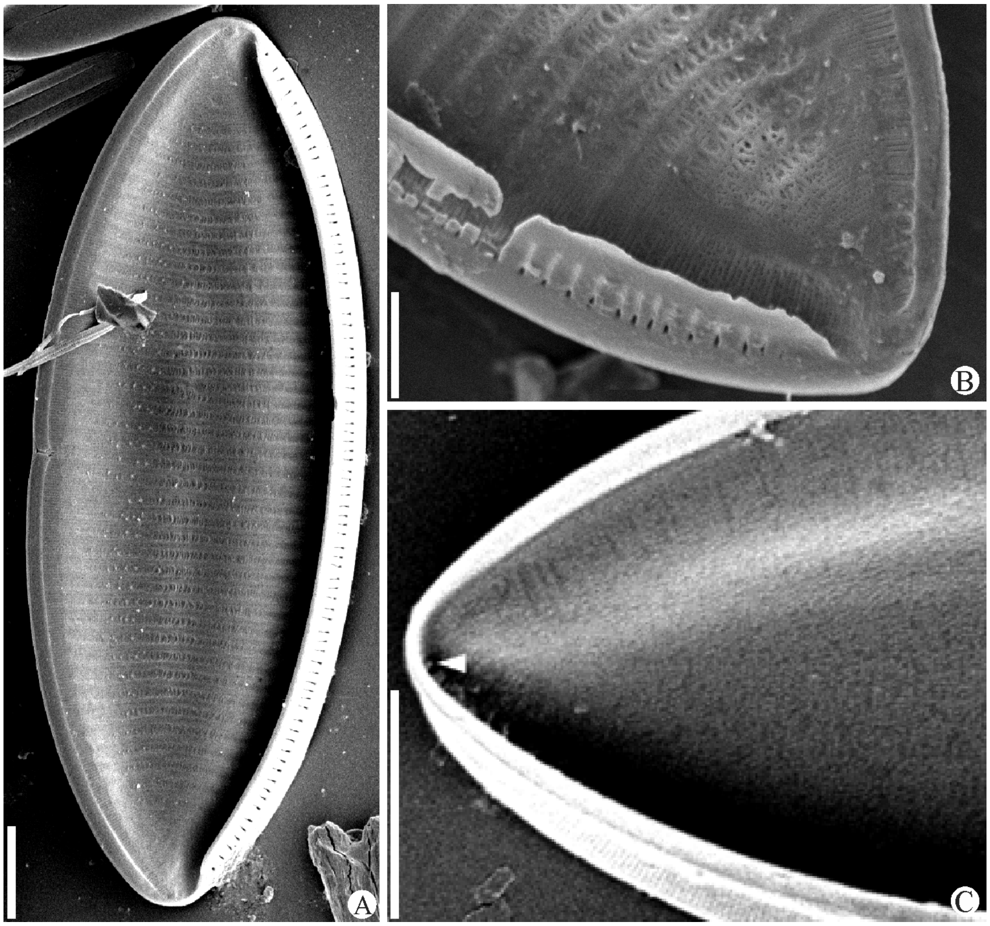

Figure 9. *Tryblionella* species in SEM. A-C *T. ornata*. Note the small helictoglossa (white arrow head) in Fig. 9 C. Scale bars = 10 µm (A*, C*), 5 µm (B). *images adapted from Bertolli et al. (2019).

small helictoglossa is visible at each valve end (Figure 11 C), and the striation pattern continues throughout the fibulae (Figure 11 C). The girdle bands lack perforations and present small granules (Figures 11 B, D).

2. *Species distribution and environmental data*

The distribution of the species in the sites, seasons and substrates is summarized in Table 1. All the taxa showed wide distribution in the study area, and no species was restricted to a certain substrate, site or season. However, the distribution of the taxa showed some differences among the sites. On Ilha da Pólvora site, *T. circumsuta* was not registered in summer, all the other species were registered, at least in one substrate. In Saco do Silveira site, *T. acuminata* was observed only in summer microphytobenthic samples. *Tryblionella ornata* and *T. persuadens* occurred only in winter microphytobenthic samples and *T. perversa* occurred only in epiphytic samples. In São José do Norte site, *T. persuadens* occurred only in winter microphytobenthic samples.

The environmental data of the sampling sites are shown in Table 2. Salinity ranged from 1.5 to 3.4 and 4.2 to 14.0 on Ilha da Pólvora, from 0.1 to 0.3 and 15.0 to 16.0 in Saco do Silveira and from 0.7 to 1.9 and 10.0 to 30.0 (winter and summer, respectively). The values of pH varied from slight acid to slight alkaline, with few registers of more intense acidity (Ilha da Pólvora and São José do Norte during summer).

3. *Extending the interpretation of Tryblionella*

Round et al. (1990) defined some diagnostic features to identify *Tryblionella*, such as elliptical, linear or panduriform valves, with bluntly rounded or apiculate poles, striae formed by small round poroids, occluded by hymenes and girdle narrow, containing plain or sparsely porous, open bands. The treatment used by Lowe (2013) does not add new features to the genus characterization, but points out the undulation along the apical axis as a diacritical feature among *Tryblionella* and *Nitzschia*. The examination of the specimens found in Patos Lagoon salt marsh revealed several features which are not included in the former descriptions. It shows that the concept used previously does not reach the entire diversity of the genus. Our findings were assembled to Round et al. (1990) characterization, providing a broader interpretation of the genus.

Tryblionella specimens are characterized by solitary cells, usually lying in valve view. Frustules diagonally symmetrical about the median valvar plane. Two plastids, one at each end of the cell. Valves robust, broad and symmetric both by apical and transapical axis, presenting an undulation along the apical axis and frequently constricted in the middle portion. Valve outlines vary from linear to elliptic, may be panduriform, lanceolate, elliptic or obovate. Apices rounded, rostrate, cuneate or apiculate, produced or not. Valve face undulate, ornamented by warts, granules, ridges or transapical ribs, which may be parallel radiate or convergent, symmetric or asymmetric by the transapical plane, disposed

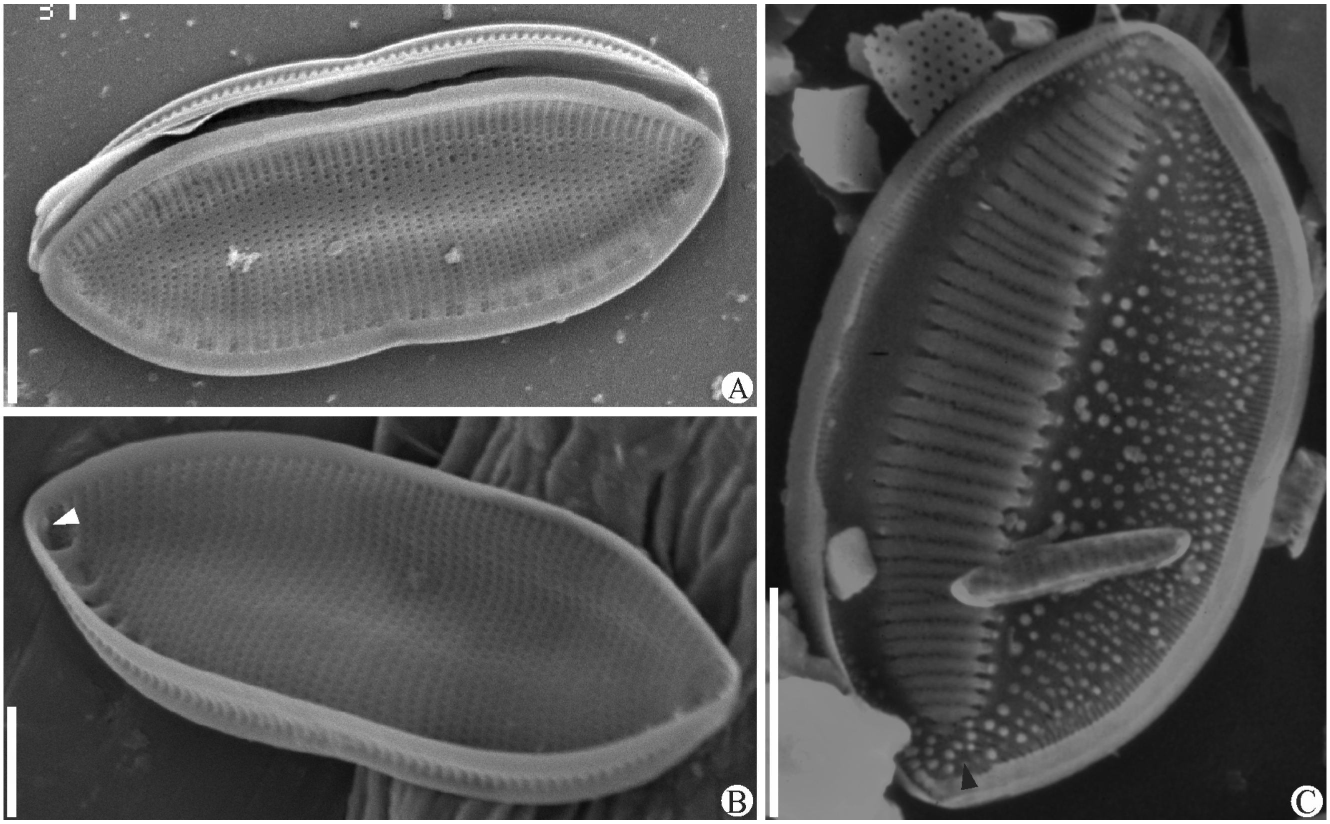

Figure 10. *Tryblionella* species in SEM. A-B *T. persuadens*. Note the small helictoglossa (white arrow head) in Fig. 10 B. C *T. perversa*. Scale bars = 2 µm (A-B), 10 µm (C). Note the granules advancing towards the transapical ribs side (black arrow head) in Fig. 10 C.

in one or both sides of the valve face, sometimes disposed alternately forming a 'zig-zag' pattern. The pattern of ornamentation may vary along the valve face, silica projections rising from the transapical ribs may be present. Striae uniseriate to multiseriate, containing small rounded, rectangular or elongate poroids, occluded by hymenes or volae; rarely alveolate. Striae may be interrupted by broad or narrow axial area (one or more), sometimes ornamented with small granules. Valve face bounded on one side by the keeled raphe system, sometimes presenting narrow stripes of silica (gill-like arrangement) at this margin; on the other side often bearing a marginal ridge. Valve margins may be thickened and present groves. Mantle shallow, plain or presenting elongate striae. Raphe system strongly eccentric, keeled, fibulate. Proximal external raphe endings close together slightly expanded or deflected; occasionally absent. Terminal fissures short, deflected, internally ending in a double helictoglossa. Fibulae squat, often as broad or broader apically than transapically, equidistant or irregularly distributed, the two medians further apart; striate like the valve or hollow. Narrow girdle, formed by opens bands, plain or containing sparse porous, open bands, sometimes presenting small granules. A benthonic genus, occurring more frequently in epipelon, but also in periphyton, widespread in marine and brackish waters but also present in high conductivity fresh waters.

Discussion

Tryblionella's characterization, especially under LM, is complex, since many metric and meristic characters are overlapping and some species may present, for example, a broad variation of valve or apices outlines. The analysis under SEM provided a more detailed characterization of the taxa, leading to better understand their morphology. Due to the morphological overlapping and, sometimes, to nomenclatural issues, many species can be misinterpreted and misidentified. Our attempt to better understand *Tryblionella's* morphological variability, by adding new features to its characterization, seems far from ending the genus' taxonomic issues. The great variability in the features observed may indicate a great phenotypic plasticity, which may occur not only among the species, but also among specimens of the same species in response to environmental variation. However, we can't ignore the possibility of being grouping different lineages of diatoms under the same genus over the centuries, since phylogenetic studies are scarce. Not only *Tryblionella*, but the whole Bacillariaceae family should be the focus of an extensive revision, including phylogenetics and large data sets, and then, we will be closer to more trustworthy interpretations and circumscriptions of the taxa.

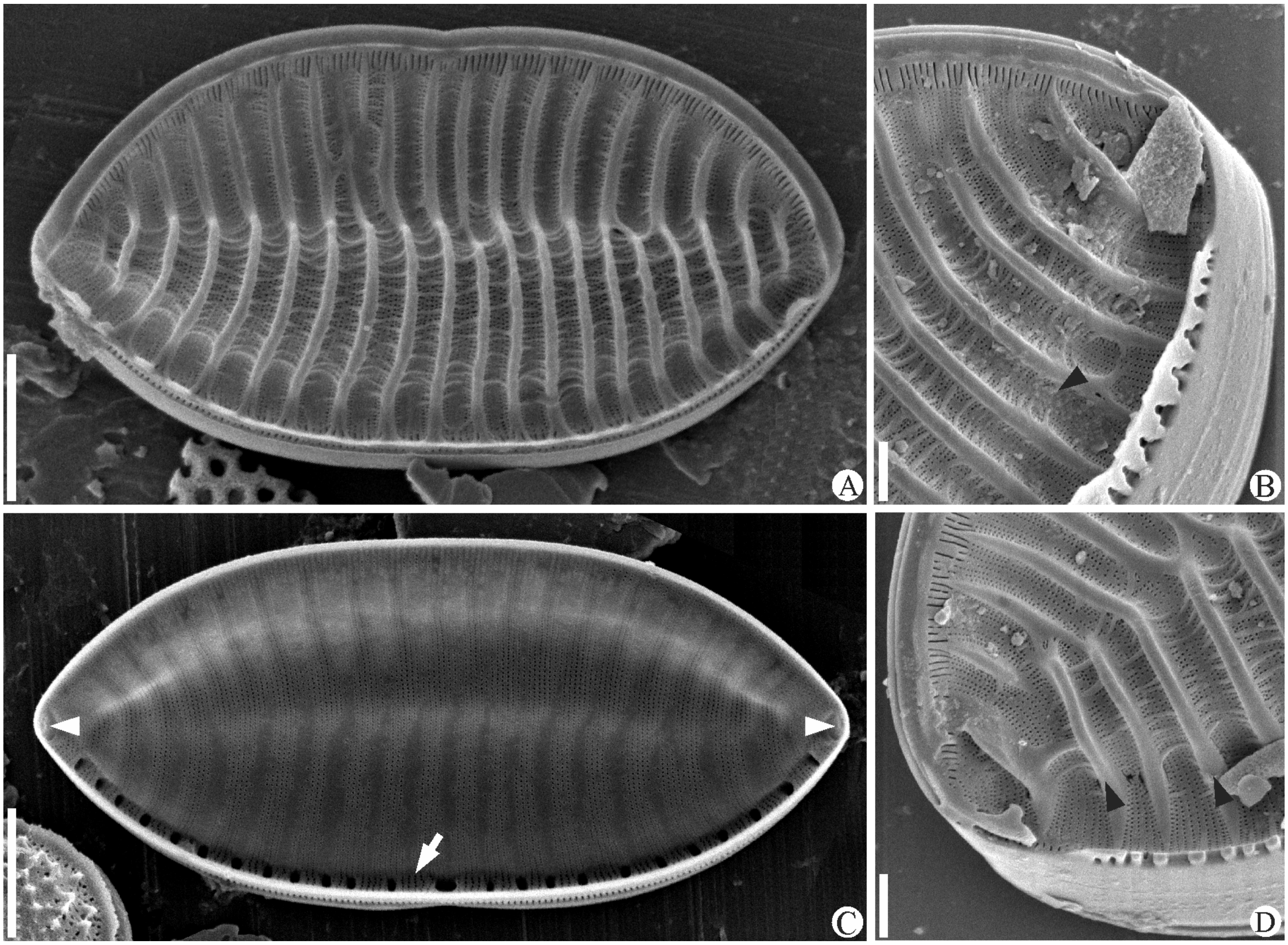

Figure 11. *Tryblionella* species in SEM. A-D *T. victoriae*. Scale bars = 5 µm (A, C), 2 µm (B, D). Note the silica projections between two transapical ribs (black arrow head in Fig. 11 B), the small helictoglossa (White arrow heads) and the striation continuing throughout the fibulae (white arrow) in Fig. 11 C, and the transapical rib interrupted in the longitudinal fold region (black arrow head in Fig. 11 D).

Table 1. Distribution of the *Tryblionella* species in the sites along the Patos Lagoon Estuary in the winter of 2010 and the summer of 2011. Abbreviations: (EPP) epiphyton, (MPB) microphytobenthos.

	Ilha da Pólvora				**Saco do Silveira**				**São José do Norte**			
	Winter		**Summer**		**Winter**		**Summer**		**Winter**		**Summer**	
	EPP	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**	**EPP**	**MPB**
T. acuminata	-	X	X	X	-	-	-	X	X	X	X	-
T. calida	X	X	X	X	X	X	X	X	X	X	X	X
T. circumsuta	X	X	-	-	X	X	X	X	X	X	X	X
T. compressa	X	X	X	X	X	X	X	X	X	X	X	X
T. confusa	X	X	X	X	X	X	X	X	X	X	X	X
T. granulata	X	X	X	X	X	X	X	X	X	X	X	X
T. hungarica	X	X	X	X	X	X	X	X	X	X	X	X
T. ornata	X	X	X	X	-	X	-	-	X	X	-	X
T. persuadens	X	X	X	-	-	X	-	-	-	X	-	-
T. perversa	X	X	X	X	X	-	X	-	X	-	X	X
T. victoriae	X	X	X	-	-	X	X	X	X	X	X	X

Table 2. Samples code, type of vegetal substrate, sediment main component, epiphyton (EPP) and microphytobenthos (MPB) slide numbers at Herbarium Alarich Schultz, Temperature (T, ºC), salinity. (Sal., ‰) and pH ranges of the interstitial water registered in the three sampling sites in Winter (September 2010) and Summer (February 2011). IP: Ilha da Pólvora, SS: Saco do Silveira, SJN: São José do Norte.

Sample	Vegetal substrate	Sediment main component	Sal.	T	pH	EPP slide number	MPB slide number
Winter							
IPA	*Bolboschenus maritimus*	Sand	1.6	16.7	7.3	6520	6242
IPB	*Sporobolus montevidensis*	Sand	1.6	15.4	7.2	6523	6244
IPC	*B. maritimus*	Sand	1.5	15.9	6.8	6526	6246
IPE	*B. maritimus*	-	2.8	16.0	7.5	6532	-
IPG	*S. montevidensis*	-	3.4	16.2	6.0	6538	-
IPH	*S. montevidensis*	-	3.4	19.5	7.2	6540	-
SSA	*Juncus kraussii*	Sand	0.1	20.6	8.8	6548	6263
SSB	*J. kraussii*	Sand	0.3	21.2	7.8	6553	6249
SSC	*S. montevidensis*	Sand	0.3	20.4	7.1	6554	6251
SSE	*Sporobolus alterniflorus*	-	0.1	21.0	7.5	6561	-
SSF	*J. kraussii*	-	0.2	19.6	6.9	6565	-
SSJ	*S. alterniflorus*	-	0.3	19.9	6.5	6577	-
SJNA	*S. alterniflorus*	Silt	1.2	17.0	7.2	6579	6254
SJNC	*J. kraussii*	-	0.7	17.0	7.3	6584	-
SJNE	*J. kraussii*	-	1.2	20.4	7.3	6590	-
SJNF	*S. alterniflorus*	-	1.3	20.6	7.7	6593	-
SJNG	*S. montevidensis*	Silt	1.9	21.5	7.7	6596	6260
SJNI	*S. alterniflorus*	Sand	1.9	19.1	7.7	6602	6256
Summer							
IPA	*S. alterniflorus*	Sand	14.0	28.0	8.6	6610	6497
IPB	*B. maritimus*	-	7.2	27.0	6.8	6611	-
IPC	*B. maritimus*	Sand	8.0	29.0	6.6	6614	6499
IPF	*S. alterniflorus*	-	10.0	29.0	8.8	6624	-
IPG	*S. alterniflorus*	Sand	4.2	29.0	7.2	6626	6503
IPI	*B. maritimus*	-	8.2	30.0	5.2	6632	-
SSA	*J. kraussii*	Sand	15.0	27.0	7.9	6639	6505
SSC	*S. montevidensis*	-	15.0	26.0	7.9	6644	-
SSD	*J. kraussii*	Sand	16.0	25.0	7.5	6647	6507
SSE	*J. kraussii*	-	15.0	26.0	8.0	6652	-
SSF	*S. montevidensis*	Sand	15.0	26.0	6.8	6653	6509
SSH	*S. montevidensis*	-	15.0	29.0	7.8	6660	-
SJNC	*J. kraussii*	-	13.0	31.0	7.0	6676	-
SJND	*J. kraussii*	Silt	16.0	27.0	7.3	6678	6511
SJNE	*J. kraussii*	-	15.0	27.0	7.4	6680	-
SJNG	*S. alterniflorus*	Silt	30.0	27.0	4.0	6686	6514
SJNI	*S. alterniflorus*	Silt	15.0	28.0	7.4	6692	6516
SJNJ	*S. alterniflorus*	-	10.0	26.0	8.2	6696	-

The *Tryblionella acuminata* specimens observed are smaller than the originally described to the taxon (63.5-106.7 of length, Smith 1853); however, the valve outline and striae density are conserved. The species occurs from fresh to marine waters (Smith 1853, Hartley 1996, Witkowski et al. 2004). In southern Brazil the species have been recorded in a wide range of salinity, occurring in lakes, rivers, lagoons and estuaries (Torgan et al. 1999, Procopiak et al. 2006). Silva et al. (2010) recorded *Tryblionella apiculata* Gregory in the Patos Lagoon salt marsh, however the individual illustrated presents characteristics, such as valve outline, apices and axial area width, that fits more with *T. acuminata* than with the referred taxon.

Tryblionella calida was originally recorded in thermal fountains in Hungary (Cleve & Grunow 1880), however, nowadays it is considered widespread in slightly brackish and in electrolyte rich inland waters (Witkowski et al. 2000). *Tryblionella calida* was registered in freshwater environments (unpublished data) in the State of Paraná, southern Brazil (Tremarin et al. 2009). This is the first record of the taxon in the State of Rio Grande do Sul.

Tryblionella circumsuta resembles some specimens of *T. littoralis* (Grunow) Mann. However, the latter species is characterized by smaller specimens (30-100 µm versus 130-300 µm) and a higher number of fibulae in 10 µm (3-5 versus 6-9) as noticed by Krammer & Lange-Bertalot (1988). The species is considered cosmopolitan, occurring in brackish and marine waters (Hartley 1996, Witkowski et al. 2000). In southern Brazil it has been recorded in coastal waters in the State of Paraná (Procopiak et al. 2006), in the State of Santa Catarina (Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998, Souza-Mosimann & Laudares-Silva 2005) and in the State of Rio Grande do Sul at Patos Lagoon, both in salt marsh surface sediment (Silva et al. 2010) and in core sediment samples (Abreu et al. 1987).

Tryblionella compressa is sometimes identified as *Tryblionella* (or *Nitzschia*) *punctata* W. Smith (Van Heurck 1896, Gandhi 1967). We chose to use the epithet '*compressa*' assuming that the species is a synonym of *Pyxidicula compressa* Bailey as also considered by Krammer & Lange-Bertalot (1988) and Lopez-Fuerte et al. (2010). *Pyxidicula compressa* has nomenclatural priority since it was formerly published (Bailey 1850 vs. Smith 1853). It is considered a marine to brackish-water species, widespread on marine coasts (Hartley 1996; Witkowski et al. 2000). There are many records of *T. compressa* in the coastal waters of the State of Santa Catarina (Souza-Mosimann 1982;1988; Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998). In the State of Paraná, the species has been mentioned as *T. punctata* (Procopiak et al. 2006). Rosa & Garcia (2013) registered *Nitzschia pararostrata* (Lange-Bertalot) Lange-Bertalot, in a stream nearby Patos Lagoon, the species is similar to *T. compressa*, but differs by the smaller dimensions and areolae density (Lange-Bertalot et al. 1996). This is the first record of the species in the State of Rio Grande do Sul.

Tryblionella confusa may resemble specimens of *T. perversa* (Grunow) Mann and *Tryblionella debilis* Arnot ex O'Meara in light microscopy, however, the analysis under scanning electron microscopy reveals several differences among the taxa, especially the pattern of ornamentation. *Tryblionella confusa* was recently proposed and its distribution is still limited to Patos Lagoon salt marshes (Bertolli et al. 2019).

Tryblionella granulata presents dimensions and coarse areolation similar to *T. compressa*, however, the species are distinguishable by the valve shape. *T. granulata* does not present elongated valves towards the ends, forming produced apices, as occurs in *T. compressa*. It is considered a cosmopolitan species, especially common in tidal flats (Witkowski et al. 2000). The species was registered in Patos Lagoon core sediment samples (Santos-Fischer et al. 2016) and in the coastline along the States of Paraná and Santa Catarina (Araújo et al. 1989; Fernandes et al. 1990, Felício-Fernandes 1996, Souza-Mosimann 1988, Souza-Mosimann & Roos-Oliveira 1998, Souza-Mosimann & Laudares-Silva 2005, Procopiak et al. 2006, Souza-Mosimann et al. 2011).

Tryblionella hungarica is very frequently recorded and considered a cosmopolitan species, inhabiting brackish and freshwater environments (Krammer & Lange-Bertalot 1988). The current concept of *T. hungarica* (see Witkowski et al. 2000, Metzeltin et al. 2005 and Hofmann et al. 2011, for example) is somewhat different from the original illustrated by Grunow (1862) and also by Frenguelli (1942). It is more likely that a complex of similar species has been misidentified as *T. hungarica* throughout the years, what may explain the wide range of dimensions, valve outlines and ends shapes observed in the literature. A detailed examination of the type material and the phylogenetic analysis of similar morphotypes would help to better circumscribe the species. The species is largely recorded in southern Brazil, occurring in continental and coastal environments (Torgan et al. 1999, Procopiak et al. 2006, Tremarin et al. 2009, Bes & Torgan 2008) and in core sediment samples in the State of Rio Grande do Sul (Hermany et al. 2013).

Tryblionella ornata may resemble specimens of *T. circumsuta* and *T. victoriae*, however the morphometric patterns and the features of the transapical ribs allow the differentiation. *Tryblionella ornata* was recently described, its distribution is still restricted to Patos Lagoon salt marshes (Bertolli et al. 2019).

Tryblionella persuadens is similar to *T. aerophila*; however, it presents a higher density of fibulae in 10 µm (12-16 versus 9-11) and lacks the longitudinal axial area formed by the interruption in the striae observed in the referred species (Cavalcante et al. 2013). The species was originally described for brackish waters (Cholnoky 1961) however, it has already been found in freshwaters in northeastern Brazil (Cavalcante et al. 2013). This is the first record of the species in southern Brazil.

Krammer & Lange-Bertalot (1988, p. 271, Figures 10 and 11) and Witkowski et al. (2000, p. 813, Figures 8-10) illustrated specimens that raise doubts about their determination as *T. perversa* or *T. debilis*. However, the valvar shape and the arrangement of the granules over the valvar face made us believe that the specimens are more similar to *T. perversa*. The species is considered estuarine (Cleve & Grunow 1880). It has been recorded to coastal environments in southern Brazil (Fernandes et al. 1990, Felício-Fernandes 1996, Procopiak et al. 2006), in Patos Lagoon salt marsh by Silva et al. (2010) and in core sediment samples from different geologic formations in the State of Rio Grande do Sul (Abreu et al. 1987, Santos-Fischer et al. 2016).

Tryblionella victoriae is similar to *T. levidensis* W. Smith and has already been considered one of its many varieties. The differentiation is based on the higher width/length ratio and the number of transapical ribs (seven or less in 10 µm) presented by *T. victoriae* (Witkoswki et al. 2000). The species has been originally found in freshwaters (Grunow 1862) but is also spread in marine and brackish waters (Hartley 1996, Witkoswki et al. 2000). In southern Brazil it is widely recorded in continental and coastal waters (Souza-Mosimann 1982, Felício-Fernandes 1996, Souza-Mosimann & Roos-Oliveira 1998, Torgan et al. 1999, Souza-Mosimann & Laudares-Silva 2005, Procopiak et al. 2006, Tremarin et al. 2009, Bes & Torgan 2008, Bes et al. 2012), in Patos Lagoon salt marsh by Silva et al. (2010) and in in core sediment samples from different geologic formations in the State of Rio Grande do Sul (Hermany et al. 2013, Santos-Fischer et al. 2016).

A high number of *Tryblionella* species was observed in Patos Lagoon salt marsh, comprising nearly a half of the richness known to the country. The spatial heterogeneity of the salt marshes, which favors the formation of microhabitats, allied to the mixing of communities from fresh and marine waters, may be responsible for the high richness observed. The occurrence of species concomitantly in epiphyton and in microphytobenthos was already observed in other species in the same sites and is probably related to the environmental dynamics (Talgatti et al. 2014, Bertolli et al. 2016, 2019). The temperature variation among the seasons was expected. However, the fluctuations among sites and samples may be related to the depth of water column in each circumstance. The abiotic conditions were affected by the seasonal period and by the distance of the sites from the Atlantic Ocean, resulting in different marine water input. Nevertheless, such environmental variation did not seem to interfere in the presence of *Tryblionella* species, since they occured in a broad spectrum of pH, salinity and temperature. The occurrence of the species in the three sites, in both periods, in both substrates and in a wide range of environmental variables, evidences a community adjusted to the fluctuations observed in Patos Lagoon estuary.

Two species were firstly registered in the State of Rio Grande do Sul and one in southern Brazil. This study represents an important contribution to *Tryblionella*, since there are few studies dedicated to the genus, and little is known about some species' ultrastructure, such as *T. compressa* and *T. perversa*. Besides that, these results reinforce the importance of studying this kind of heterogenous environment to diatom biodiversity knowledge.

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Authors contributions

Lucielle Merlym Bertolli: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Dávia Marciana Talgatti: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Thamires Mariah da Silveira Nascimento: Contribution to data collection; Contribution to data analysis and interpretation.

Lezilda Carvalho Torgan: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Conflict of interests

The authors declare that they have no conflict of interest related to the publication of this manuscript.

References

ABREU, V.S., TORGAN, L.C., ESTEVES, I.R.F. & KOTZIAN, S.C. 1987. Estudo paleogeográfico do Quaternário de Morretes, RS, Brasil. In Anais do 1º Congresso ABEQUA (I.C.S. Correia, ed). ABEQUA, Porto Alegre, p. 177-189.

ANONYMOUS 1975. Proposals for standardization of diatom terminology and diagnoses. Beiheft zur Nova Hedwigia 53: 323-354.

ARAÚJO, N.B., SOUZA-MOSIMANN, R.M. & FERNANDES, L.F. 1989. Contribuição ao estudo das diatomáceas (Bacillariophyceae) da foz do rio Ararangúá, Santa Catarina, Brasil. Ínsula 19: 305-334.

BAILEY J.W. 1850. Microscopical observations made in South Carolina, Georgia, and Florida. Smithsonian Contr. Know. 2(8): 1-48.

BARBER, H.G. & HAWORTH, E.V. 1981. A guide to the morphology of the diatom frustule with a key to the British freshwater genera. Freshwat. Biol. Assoc. Sci. Publ. 44: 1-112.

BERTOLLI, L.M., TALGATTI, D.M. & TORGAN, L.C. 2016. *Nitzschia papillosa* (Bacillariaceae, Bacillariophyta): a new species from a Brazilian salt marsh. Phytotaxa 247(1): 75-84.

BERTOLLI, L.M., TALGATTI, D.M., NASCIMENTO, T.M.S. & TORGAN L.C. 2019 Two new species of *Tryblionella* W. SMITH (Bacillariaceae, Bacillariophyta) from a southern Brazil salt marsh. Phytotaxa 399(3): 173-186.

BES, D. & TORGAN, L.C. 2008. O gênero *Tryblionella* (Bacillariophyta, Bacillariaceae) em ambientes lacustres da planície costeira do Rio Grande do Sul, Brasil. In Aplicações da Ficologia, Anais do XI Congresso Brasileiro de Ficologia e Simpósio Latino-Americano sobre Algas Nocivas (Sociedade Brasileira de Ficologia, org.). Museu Nacional, Rio de Janeiro, p. 27-34.

BES, D., ECTOR, L., TORGAN, L.C. & LOBO, E.A. 2012. Composition of the epilithic diatom flora from a subtropical river, Southern Brazil. Iheringia (Bot.). 67(1): 93-125.

CAVALCANTE, K.P., TREMARIN, P.I., FREIRE, E.G. & LUDWIG T.A.V. 2013. *Tryblionella persuadens comb. nov.* (Bacillariaceae, Diatomeae): new observations on frustule morphology of seldom recorded diatom. Ann. Braz. Acad. Sci. 85(4): 1419-1426.

CHOLNOKY, B.J. 1961. Ein Beitrag zur Kenntnis der Diatomeenflora der venetianischen Lagunen. Hydrobiologia. 17(4): 287-325.

CLEVE, P.T. & GRUNOW, A. 1880. Beiträge zur Kenntniss der Arctischen Diatomeen. K. Sven. Vetensk. Akad. Hand. 17(2): 1-121.

COSTA, C.S.B. 1998. Irregularly flooded marginal marshes. In Subtropical convergence environments: the coast and sea in the Southwestern Atlantic (U Seeliger, C. Odebrecht & J.P. Castello., eds). Springer-Verlag, Berlin. p. 72-77.

EATON, J.W. & MOSS, B. 1966. The estimation of numbers and pigment content in epipelic algal populations. Limnol. Oceanogr. 11: 584-595.

ESKINAZI-LEÇA, E., MOURA, C.W.N., CUNHA, M.G.G.S., SANTIAGO, M.F., BORGES, G.C.P., LIMA, J.C., SILVA, M.H., FERREIRA, L.C., AQUINO, E., DA SILVA, W.J. & MENEZES, M. 2015. Bacillariophyceae: Lista de Espécies da Flora do Brasil, Jardim Botânico do Rio de Janeiro, Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB98220. Last access 15/04/2019.

FELÍCIO-FERNANDES, G. 1996. Diatomáceas no rio Tavares, manguezal do rio Tavares, Florianópolis, Santa Catarina, Brasil. II. Penatae. Ínsula 25: 69-192.

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. Ínsula 20: 11-112.

FRENGUELLI, J. 1942. Diatomeas del Neuquén (Patagonia). Rev. Mus. La Plata, Sec. Bot. 5(20): 73-219.

GANDHI, H.P. 1967. Notes on the Diatomaceae from Ahmedabad and its Environs. VI. On some diatoms from Fountain Reservoir of Seth Sarabhai's Garden. Hydrobiologia 30(2): 248-272.

GRUNOW, A. 1862. Die österreichischen Diatomaceen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Uebersicht der bisher bekannten Gattungen und Arten. Erste Folge. Epithemieae, Meridioneae, Diatomeae, Entopyleae, Surirelleae, Amphipleureae. Zweite Folge. Familie Nitzschieae. Verh. K.K. Zool.-Bot. Ges. Wien. 12: 315-472, 545-588.

GRUNOW, A. 1879. New species and varieties of Diatomaceae from the Caspian Sea, translated with additional notes by F. Kitton. J. R. Microsc. Soc. 2: 677-691.

GRUNOW, A. 1880. On some new species of *Nitzschia* (with notes by Kitton). J.R. Microsc. Soc. 3(1): 394-397.

GUIRY, M.D. & GUIRY, G.M. 2019. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org/. Last access 15/04/2019.

HARTLEY, B. 1996. An Atlas of British Diatoms. Biopress Ltd, Bristol.

HENDEY, N.I. 1964. An introductory account of the smaller algae of British coastal Waters - V. Bacillariophyceae (Diatoms), Fishery Investigations Series, London. H. Maj. Stat. Off. 4(5): 1-317.

HERMANY, G., SOUZA, P.A. & TORGAN L.C. 2013. Paleoecologia do sistema Pinguela-Palmital-Malvas, Holoceno da Bacia de Pelotas, RS: uma abordagem focada na utilização de análises multivariadas para obtenção de diatomáceas descritoras. Pesq. Geociênc.40(1): 31-49.

HOFMANN, G., WERUM, M. & LANGE-BERTALOT, H. 2011. Diatomeen im Süβwasser-Benthos von Mitteleuropa. Bestimmungsflora Kieselalgen für die ökologische Praxis. Über 700 der häufigsten Arten und ihre Ökologie. A.R.G. Gantner, Ruggell.

HUSTEDT, F. 1930. Bacillariophyta (Diatomeae). In Die Süsswasser-Flora Mitteleuropas. Heft 10. (A. Pascher, ed.) Gustav Fischer Verlag, Jena. p. 1-466.

KITTON, F. 1873. A description of some new species of Diatomaceae. Mon. Microsc. J. 10: 205-207.

KRAMMER, K. & LANGE-BERTALOT, H. 1988. Bacillariophyceae, 2. Teil: Bacillariaceae. Epithemiaceae, Surirellaceae. In Süsswasserflora von Mitteleuropa (begründet von A. Pascher). Band 2/2. (H. Ettl, J. Gerloff, H. Heynig & Mollenhauer D., eds.) Gustav Fischer Verlag, Stuttgart. p. 1-596.

KÜTZING, F.T. 1844. Die Kieselschaligen. Bacillarien oder Diatomeen. Fr. Fritsch, Nordhausen.

LANGE-BERTALOT, H., KÜLBS, K., LAUSER, T., NÖRPEL-SCHEMPP, M. & WILLMANN, M. 1996. Diatom taxa introduced by Georg Krasske, documentation and revision. In Iconographia Diatomologica, Annotated Diatom monographs. Vol. 3. Taxonomy (H. Lange-Bertalot, ed.). Koeltz Scientific Books, Königstein. p. 1-358.

LAUDARES-SILVA, R., CIMARDI, J.M. 1989. Nota sobre a utilização do 'Trapping Method' no estudo das diatomáceas epipélicas do manguezal de Ratones, Florianópolis, SC. Ínsula 19: 299-304.

LÓPEZ-FUERTE, F.O., SIQUEIROS-BELTRONES, D.A. & NAVARRO, N. 2010. Benthic diatoms associated with mangrove environments in the northwest region of México. Conabio-UABCS-IPN, México City.

LOWE, R.L. 2003. Keeled and canalled raphid diatoms. In Freshwater Algae of North America: ecology and Classification. (J. D. Wehr & R. G. Sheath, eds.). Elsevier, San Diego, p. 669-684.

LUNDHOLM, N., DAUGBJERG, N. & MOESTRUP, Ø. 2002a. Phylogeny of the Bacillariaceae with emphasis on the genus *Pseudo-nitzschia* (Bacillariophyceae) based on partial LSU rDNA. Eur. J. Phycol. 37: 115-134.

LUNDHOLM, N., HASLE. G.R., FRYXELL, G.A. & HARGRAVES, P.A. 2002b. Morphology, phylogeny and taxonomy of species within the *Pseudo-nitzschia americana* complex (Bacillariophyceae) with descriptions of two new species, *Pseudo-nitzschia brasiliana* and *Pseudo-nitzschia linea*. Phycologia 41(5): 480-497.

MANN, D.G. 1978. Studies in the Nitzschiaceae (Bacillariophyta). PhD Thesis. University of Bristol, England.

METZELTIN, D., LANGE-BERTALOT, H. & GARCÍA-RODRÍGUEZ, F. 2005. Diatoms of Uruguay. In Iconographia Diatomologica, Annotated Diatom monographs. Vol. 15. Taxonomy-Biogeography-Diversity. (H. Lange-Bertalot, ed.). ARG Gartner, Ruggell. p.1-736.

PERAGALLO, H. & PERAGALLO, M. 1897-1908. Diatomées marines de France et des districts maritimes voisins. Micrographe-Editeur, Grez-sur-Loing.

POULIN, M., BÉRARD-THERRIAULT, L., CARDINAL, A. & HAMILTON, P.B. (1990). Les Diatomées (Bacillariophyta) benthiques de substrats durs des eaux marines et saumâtres du Québec. 9. Bacillariaceae. Le Naturaliste Canadien 117(2): 73-101.

PRITCHARD, A. 1861. A history of infusoria, living and fossil: arranged according to Die infusionsthierchen of CG Ehrenberg; containing colored engravings, illustrative of all the genera, and descriptions of all the species in that work, with several new ones; to which is appended an account of those recently discovered in the chalk formations. Edition IV. Whittaker and Co., London.

PROCOPIAK, L.K., FERNANDES, L.F. & MOREIRA-FILHO, H. 2006. Diatomáceas (Bacillariophyta) marinhas e estuarinas do Paraná, Sul do Brasil: lista de espécies com ênfase em espécies nocivas. Biota Neotrop. 6(3): 1-28.

RABENHORST, L. 1864. Flora Europaea Algarum aquae dulcis et submarinae. Sectio I. Algas diatomaceas complectens, cum figuris generum omnium xylographice impressis. Apud Eduardum Kummerum, Lipsiae.

RIMET, F., KERMARREC, L., BOUCHEZ, A., HOFFMANN, L., ECTOR, L. & MEDLIN, L. 2011. Molecular phylogeny of the family Bacillariaceae based on 18S rDNA sequences: focus on freshwater *Nitzschia* of the section *Lanceolatae*. Diatom Res. 26: 273-291.

ROSA, V.C. & GARCIA M. 2013. Diatomáceas (Bacillariophyceae) epífitas em *Acrostichum danaeifolium* (Pteridaceae) no Arroio Pseudônimo, Pelotas, Rio Grande do Sul, Brasil. Sitientibus Ciê. Biol. 13: 1-14.

ROUND, F.E., CRAWFORD, R.M. & MANN, D.G. 1990. The Diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge.

SANTOS-FISCHER, C.B., CORRÊA, I.C.S., WESCHENFELDER, J., TORGAN, L.C. & STONE, J.F. 2016. Paleoenvironmental insights into the Quaternary evolution of the Southern Brazilian coast based on fossil and modern diatom assemblages. Palaeogeogr., Palaeoclimatol., Palaeoecol. 446: 108-124.

SILVA, J.G., TORGAN, L.C. & CARDOSO, L.S. 2010. Diatomáceas (Bacillariophyceae) em marismas no sul do Brasil. Acta Bot. Bras. 24: 935-947.

SIMS, P.A. & PADDOCK, T.B.B. 1982. The fenestral fibula: A new structure in the diatoms. Bacillaria. 5: 7-21.

SMITH, W. 1853. Synopsis of British Diatomaceae. John Van Voorst, London.

SOUZA-MOSIMANN, R.M. 1982. Diatomáceas da represa do córrego Grande (Poção) Florianópolis, Santa Catarina, Brasil (Chrysophyta, Bacillariophyceae). Ínsula. 12: 1-38.

SOUZA-MOSIMANN, R.M. 1988. Estudo preliminar das diatomáceas (Chrysophyta-Bacillariophyceae) da baía sul, Florianópolis, Santa Catarina, Brasil. Ínsula. 18: 23-74.

SOUZA-MOSIMANN, R.M. & LAUDARES-SILVA, R. 2005. Diatomáceas (Bacillariophyta) do complexo lagunar do sul do estado de Santa Catarina, Brasil. Ínsula. 34: 39-82.

SOUZA-MOSIMANN, R.M., LAUDARES-SILVA, R., TALGATTI, D.M. & D'AQUINO-ROSA, V. 2011. The Diatom flora in Conceição Lagoon, Florianópolis, SC, Brazil. Ínsula. 40: 25-54.

SOUZA-MOSIMANN R.M. & ROOS-OLIVEIRA, A.M. 1998. Diatomáceas (Bacillariophyceae) planctônicas do Ribeirão da Fazenda, Manguezal do rio Tavares, Florianópolis, SC, Brasil. Ínsula. 27: 59-98.

TALGATTI, D.M., BERTOLLI, L.M. & TORGAN, L.C. 2014. *Seminavis recta comb. nov. et. stat. nov.*: morphology and distribution in salt marshes from southern Brazil. Fottea. 14 (2): 141-148.

TORGAN, L.C., BECKER, V. & PRATES, H.M. 1999. Checklist das diatomáceas (Bacillariophyta) de ambientes de águas continentais e costeiros do estado do Rio Grande do Sul, Brasil. Iheringia (Bot). 52: 89-144.

TREMARIN, P.I., FREIRE, E.G., BERTOLLI, L.M. & LUDWIG, T.A.V. 2009. Catálogo das diatomáceas (Ochrophyta-Diatomeae) continentais do estado do Paraná. Iheringia (Bot.). 64(2): 79-107.

VAN HEURCK, H. 1880-1881. Synopsis des Diatomées de Belgique. Atlas. Ducaju & Cie, Anvers.

VAN HEURCK, H. 1896. A Treatise on the Diatomaceae. William Wesley & Son, London.

WITKOWSKI, A., LANGE-BERTALOT, H. & METZELTIN, D. 2000. Diatom flora of marine coasts I. In Iconographia Diatomologica Annotated Diatom Monographs (H. Lange-Bertalot. Ed.). Vol. 7 Taxonomy-Biogeography-Diversity. ARG Gartner. Ruggell, p. 1-925.

WITKOWSKI, A., LANGE-BERTALOT, H., KOCIOLEK, J.P., RUPPEL, M., WAWRZYNIAK-WYDROWSKA, B., BAK, M. & BRZEZYNSKA, A. 2004. Four new species of *Nitzschia* sect. *Tryblionella* (Bacillariophyceae) resembling *N. parvula*. Phycologia. 43: 579-595.

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