

Pseudopodosira boltovskoyi sp. nov. (Pseudopodosiraceae, Bacillariophyta) from coastal waters of Argentina

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ABSTRACT: A new extant marine diatom, *Pseudopodosira boltovskoyi* sp. nov. (Pseudopodosiraceae, Bacillariophyta), is described with light and scanning electron microscopy from Argentinean coastal waters. *Pseudopodosira boltovskoyi* sp. nov. is morphologically distinct with the following combination of characters: (1) cells with numerous lenticular chloroplasts; (2) frustules commonly heterovalvate; (3) valves with concave central area generally occupied by one to several bulges, rarely without bulges; (4) oblique striae located on a horizontal, convex shelf of the valve surface; (5) valve mantle unperforated internally and with variable number of rimmed pores located below the flange externally; (6) one ring of rimoportulae irregularly spaced, not visible externally. *Pseudopodosira calyciflos* (Tempère & Brun) is formally designated as the generitype, and a new name *Pseudopodosira jouseana* nom. nov. is proposed to replace for *Pseudopodosira pileiformis* based on the fact that the protologue quoted the former taxon as a synonym of the latter. We compare the new species with the morphologically allied extinct species *Pseudopodosira modesta*, *P. wittii*, *P. bella*, *P. westii*, *P. hyalina* and *P. himilis*. Although most species of *Pseudopodosira* are extinct, *P. westii*, *P. calyciflos* and *P. echinus* were recorded as extant. Nevertheless, the survival of *P. westii* on European coastal sediments is problematic. *Pseudopodosira calyciflos* was only mentioned in the protologue as living in the Hawaiian Islands but is illustrated by a figure that only shows one valve. As far as we can determine, *P. echinus* and *Pseudopodosira boltovskoyi* sp. nov. are the only extant species.

KEY WORDS: Extant marine species, Morphology, *Pseudopodosira*, Pseudopodosiraceae

INTRODUCTION

Pseudopodosira was described as an extinct marine genus by Jousé based on *Pseudopodosira pileiformis* Jousé in Proschkina-Lavrenko (1949, p. 33, pl. 6, figs 7a, b) from the Kharkov horizon of Kursk, Voronezh and Kharkov regions, in the Late Eocene of Ukraine (Olshtynskaya 1990). Fourtanier & Kociolek (1999) considered *P. pileiformis* to be the type species of this monotypic genus. Nevertheless, Strelnikova *et al.* (2004) established that *P. pileiformis* is an illegitimate name, since the protologue quoted this taxon as a taxonomic synonym of *Porodiscus calyciflos* Tempère & Brun in Brun & Tempère (1889, p. 50, pl. 4, figs 11a, b), and Sheshukova-Poretskaya (1967, p. 177) included the latter as the type of the genus *Pseudopodosira*. Additionally, Strelnikova *et al.* (2004) commented that Tempère & Brun's taxon does not belong in *Porodiscus* Greville. *Porodiscus calyciflos* had been previously transferred to the genus *Pseudopodosira* by Kanaya (1963, p. 24) as *P. calyciflos* (Tempère & Brun) Kanaya.

Jousé in Proschkina-Lavrenko (1949) characterized *Pseudopodosira* as having:

cells solitary; frustules almost spherical, valves hat shaped with a narrow brim; marginal zone (brim)

smooth, sometimes with a circle of small points [spinules]; convex middle area of the valve rises strongly over the edge zone, covered with tubercles [bulges]; along the edges of the convexity [concentric costa], double row of short and thick spines; the spines stand out clearly in lateral position of the valve; the lateral surface of the convexity [vertical part of the valve mantle] is covered by obliquely crossing striae (free translation, terminology interpretations in square brackets are added for readability).

Several extinct species of the genus *Podosira* Ehrenberg with hat-shaped valves, namely, *P. aspera* Jousé (1951, p. 25, pl. 1, fig. 1), *P. hyalina* Jousé in Proschkina-Lavrenko (1949, p. 32, pl. 6, fig. 4), *P. modesta* Jousé in Proschkina-Lavrenko (1949, p. 32, pl. 6, fig. 5), *P. simpla* Jousé in Proschkina-Lavrenko (1949, p. 32, pl. 6, fig. 6), *P. corolla* A.F.H.Schmidt 1888 in Schmidt (1874–1955, pl. 140, figs 11, 12) and *P. wittii* P.Schulz (1935, p. 394, pl. 1, fig. 11) were transferred to the genus *Pseudopodosira* as *P. aspera* (Jousé) Strelnikova (1974, p. 53, pl. 3, fig. 1), *P. hyalina* (Jousé) Sheshukova-Poretskaya (1967, p. 177, pl. 25, fig. 3), *P. modesta* (Jousé) Olshtynskaya (1990, pl. 2, figs 7a, b, 8), *P. simplex* (Jousé) Strelnikova (1974, p. 51, pl. 2, figs 10–11), *P. corolla* (Schmidt) Hajós (1976, p. 824, pl. 1, figs 9, 10) and *P. wittii* (P.Schulz) Vekshina (1961, p. 90), respectively.

Based on knowledge of the extinct species previously described by Jousé in Proschkina-Lavrenko (1949) as belonging to the genus *Podosira*, Vekshina (1961) expanded

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the description of the genus *Pseudopodosira*, pointing out that striae are located in the part of the valve adjacent to the concentric costa with rough spines sometimes present on the concentric costa. Vekshina (1961, p. 90, pl. 1, figs 1, 2) described *Pseudopodosira ternata* and compared it with *Melosira westii* W. Smith (1856, p. 59, pl. 52, figs 333 a, b). Subsequently, Sheshukova-Poretskaya & Glezer (1964, p. 80, pl. 1, figs 4, 5) transferred *M. westii* to the genus *Pseudopodosira* as *P. westii* (W. Smith) Sheshukova-Poretskaya & Glezer, and Olshtynskaya (1990, p. 96) included Vekshina's species as a synonym of *P. westii*. In addition, several extinct species were described in *Pseudopodosira*: *P. bella* Posnova & Glezer in Glezer & Posnova (1964, p. 61, pl. 1, fig. 2, figs text 1, 2), *P. mixta* Posnova in Glezer & Posnova (1964, p. 61, fig. text 2; included as heterotypic synonym of *P. modesta* by Olshtynskaya 1990), *P. dispersa* Sheshukova-Poretskaya in Sheshukova-Poretskaya & Glezer (1964, p. 80, pl. 5, figs 1–3), *P. orientalis* Sheshukova-Poretskaya (1964, p. 75, pl. 2, figs 6, 7), *P. punctata* Strelnikova (1971, p. 42, pl. 1, figs 1, 2), *P. reticulata* Strelnikova (1974, p. 53, pl. 3, fig. 2), *P. marginata* Hajós (1976, p. 824, pl. 1, figs 7, 8), *P. septentrionalis* Loseva (1970, p. 35, pl. 2, figs 2–8, figs text 1–3), *P. areolata* Vishnevskaya & Loginova in Loginova & Vishnevskaya (1993, p. 98, figs 1–11), *P. himilis* Dolmatova (1975, p. 260, pl. 1, figs 2a–c), *P. homanae* Glezer & Olshtynskaya (2000, p. 107, pl. 4, figs 1–3), *P. torosa* Glezer in Glezer & Olshtynskaya (2000, p. 111, pl. 2, figs 1–3) and *P. umbonata* Glezer in Glezer & Olshtynskaya (2000, p. 112, pl. 2, figs 4, 5).

Pseudopodosira kosugii Tanimura & Sato (1997, p. 358, figs 3–24) was described based on material from recent habitat found in salt ponds at the mouth of the Obitsu-gawa River, and it was considered conspecific with *Melosira* sp. previously analyzed from five Holocene sequences on Japanese Islands by Sato *et al.* (1996). Metzeltin *et al.* (2005, p. 204, pl. 4, figs 1–10) transferred *Melosira echinus* Frenguelli (1938, p. 312, pl. 1, figs 43–46) from the Province of Buenos Aires, Argentina, to the genus *Pseudopodosira* as *P. echinus* (Frenguelli) Metzeltin, Lange-Bertalot & García-Rodríguez, including *P. kosugii* as a heterotypic synonym.

The purpose of the present paper is to describe a new extant species of the genus *Pseudopodosira* from Argentinean coastal waters, to report novelties about their morphology and distribution, to compare it with allied taxa, and to propose the necessary taxonomic-nomenclatural changes.

MATERIAL AND METHODS

The material from Argentina was collected at several stations of three areas (Fig. 1):

- the northern coast of the Province of Buenos Aires from November 1994 to September 2000, and from March 2008 to June 2015
- the southern coast of the Province of Buenos Aires in Anegada Bay from May 2008 to December 2015
- the coast of the San Matías Gulf of Río Negro Province from April 1998 to April 2000 and from March 2006 to April 2007.

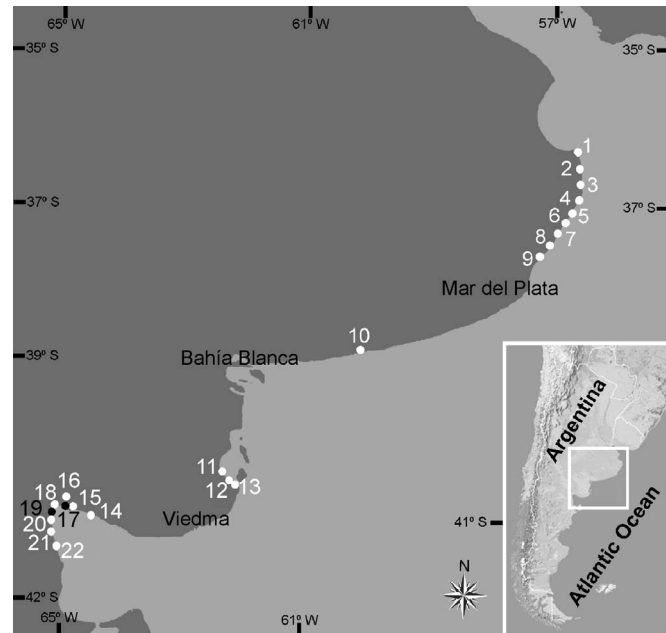


Fig. 1. Map of provinces of Buenos Aires and Río Negro, showing sampling stations and location of the area in Argentina. (1) San Clemente del Tuyú, (2) Santa Teresita, (3) Mar del Tuyú, (4) La Lucila del Mar, (5) Mar de Ajó, (6) Nueva Atlantis, (7) Pinamar, (8) Villa Gesell, (9) Mar Azul, (10) Claromecó, (11) Los Pocitos, (12) Ría del Jabalí, (13) Bahía San Blas, (14) Punta Orenge, (15) Las Garzas, (16) San Antonio Oeste, (17) Banco Reparó, (18) Los Alamos, (19) Las Grutas, (20) Piedras Coloradas, (21) El Sótano, (22) El Fuerte.

This extended region is characterized by strong re-suspension of bottom material caused by winds and tidal currents in the shallow waters, which explains the frequent occurrence of benthic diatom cells in the phytoplankton.

Qualitative samples were taken from the surface layer of the water column in the coastal waters with 30 μ m net hauls and fixed with 4% formalin. In the laboratory, the preserved samples were rinsed with distilled water to remove salt and preservatives, and then the organic matter was oxidized according to Hasle & Fryxell (1970) and Prygiel & Coste (2000). The cleaned material was mounted for light microscopy (LM) and scanning electron microscopy (SEM) after Ferrario *et al.* (1995). Permanent mounts were made with Naphrax (Brunel Microscopes, Chippenham, UK).

The raw and treated samples, slides and stubs material were deposited in the Herbarium (LPC), División Ficología 'Dr. Sebastián A. Guarrera', Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, under the numbers LPC 4250 to 4495, LPC 4550 to 4645, LPC 11001 to 11421, LPC 11601 to 12059 and LPC 13648 to 13685.

Observations and photomicrographs were made with a Leica DM 2500 (phase contrast and differential interference contrast [DIC]; Leica Microsystems, Wetzlar, Germany) and a Zeiss Axiovert 40 CFL (phase contrast and DIC; Zeiss Microimaging, Göttingen, Germany) light microscopes, and a Jeol JSM 6360 LV (JEOL, Tokyo, Japan) scanning electron microscope.

Additionally, unmounted samples and slides, obtained by François Straub from 'Calcaire de Sendai' GE G00110809,

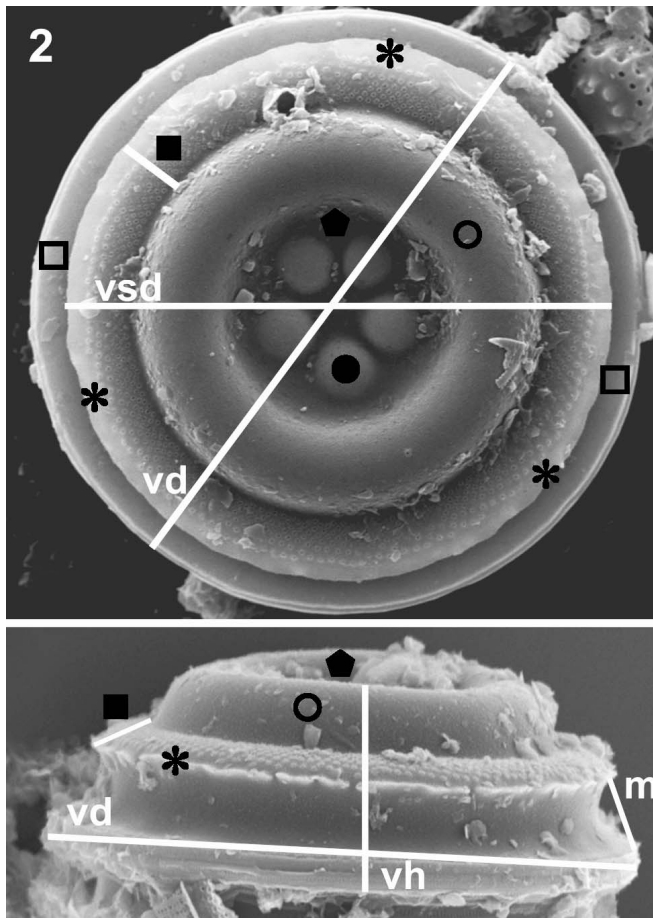


Fig. 2. Morphological features of *Pseudopodosira*. SEM. vd, valve diameter; vsd, valve surface diameter; vh, valve height; m, valve mantle; □, valve mantle edge; ■, valvar shelf; ◆, central concave part of valve surface; *, hyaline fringe; ○, concentric costa; ●, bulge.

were examined with light microscopy searching for original material of *Porodiscus calyciflos* Tempère & Brun in Brun & Tempère (1889). An aliquot of the argillaceous limestone of Sendai & Yedo belonging to the Brun Collection, deposited at Conservatoire et Jardin Botaniques de Genève as ‘Calcaire de Sendai’, was treated by Straub with 1 N HCl (23 July 2015). The diatom material was recovered in two fractions, a coarse and a fine fraction, each mounted in Naphrax (slide leg98–1 and slide leg98–2, respectively) and conserved as unmounted suspension for SEM analysis (Sa1875–1 and Sa1875–2, respectively). This material is deposited in the Straub Collection, housed in Lycee Blaise-Cendrars, La Chaux-de-Fonds, Switzerland. According to Straub (personal communication, 20 August 2016), there is no reference to the ‘Calcaire de Yedo’ in Brun’s manuscript directory in the Brun Collection, Genève. Material from ‘Calcaire de Yedo’ was searched in the Van Heurck Collection deposited at the Botanic Garden Meise, Belgium, and in the Hustedt Collection, deposited at the Institute for Marine Research Bremerhaven, Germany. The search for original material was also made in the Tempère & Peragallo Collection (2nd edition), curated at the Herbarium of the División Ficología of the Facultad de Ciencias Naturales y Museo, Universidad Nacional de La

Plata. The following material was also examined with light microscopy: Tempère & Peragallo (1907–1915) slides 745–750, from marine fossil deposits of Japan; slides 61 and 63 from the Sandwich Islands, in which *P. calyciflos* is quoted; slides 448–449 from marine fossil deposits of Abashiri (Japan) and slides 22–25 from argillaceous limestone of Sendai (Japan) in which *P. calyciflos* is not quoted.

General terminology follows von Stosch (1975), Ross *et al.* (1979) and Round *et al.* (1990) but includes some modifications based on the ultrastructural analysis of valves and frustules of the new species pictured in Fig. 2.

RESULTS

Pseudopodosira boltovskoyi Sar, Lavigne, Wetzel, Ector & Sunesen, sp. nov.

Figs 3–56

DIAGNOSIS: Cells solitary or forming short colonies, with numerous lenticular chloroplasts. Frustules commonly heterovalvate. Valves with concave central area generally occupied by one to several bulges, rarely without bulges. Oblique striae placed on a horizontal, convex shelf of the valve surface. Valve mantle deep and sheave-shaped, unperforated internally and with variable number of rimmed pores located below the flange externally. One ring of rimoportulae irregularly spaced, not visible externally. Marine, extant, epipelagic, occasional in the plankton.

HOLOTYPE: Slide LPC – 11650 (2) here designated, labelled ‘holotipo de *Pseudopodosira boltovskoyi*, Ría del Jabalí, 16/02/2009’ (deposited in the Herbarium of the División Ficología ‘Dr. Sebastián A. Guarrera’).

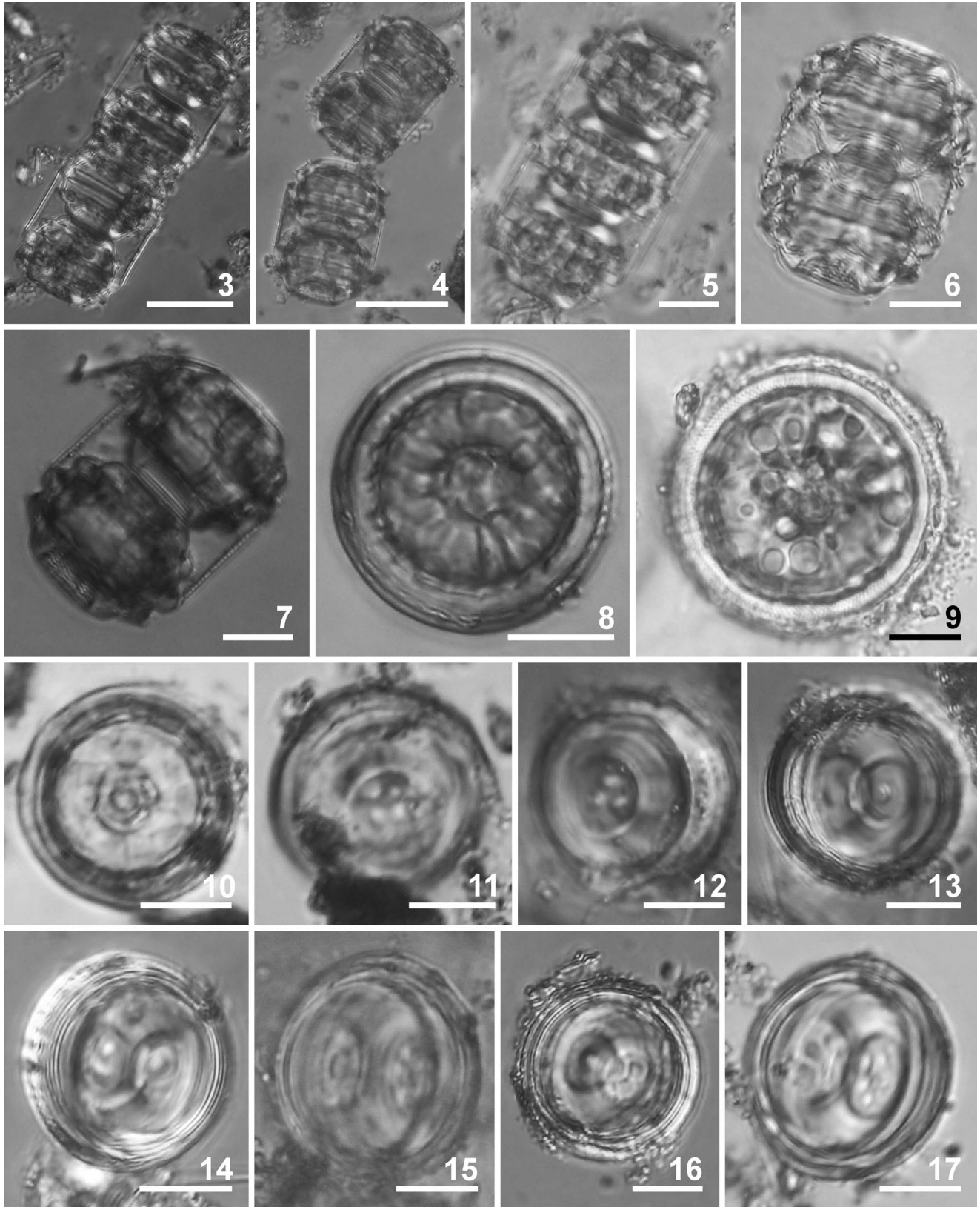
ISOTYPE: Slide LPC – 11650 (3) here designated, labelled ‘isotipo de *Pseudopodosira boltovskoyi*, Ría del Jabalí, 16/02/2009’ (deposited in the Herbarium of the División Ficología ‘Dr. Sebastián A. Guarrera’).

TYPE LOCALITY: Ría del Jabalí, 40°32′25″S–62°17′36″W, Bahía Anegada, Provincia de Buenos Aires, Argentina.

DERIVATION OF THE NAME: This new species is named after Dr. Andrés Boltovskoy, of the División Ficología ‘Dr. Sebastián A. Guarrera’, Argentina, who generously helped us during the preparation of the manuscript.

DISTRIBUTION: *Pseudopodosira boltovskoyi* sp. nov. was found sporadically in phytoplankton samples in all the stations of the studied area. It was rare during most of the year but occasionally abundant during spring and summer.

DESCRIPTION: The cells were single or united in pairs to fours by their girdles (Figs 3–17), circular in valvar view (Figs 8, 9), with diameters of 30–48 µm. Cells irregularly polygonal in girdle view (Figs 6, 7), 16–23 µm height, with numerous lenticular chloroplasts (Figs 3–9). Cells commonly heterovalvate, with only one bulge in the central area of one valve (rarely none) and two or several in the other valve (Figs 10–16); nevertheless, some specimens had equal to similar number of bulges in the central area of both valves (Fig. 17). The frustules were heavy silicified (Figs 24, 25, 28, 30). The valves were high in lateral view (Figs 12–17) with a complex valve surface. LM showed a central depression commonly occupied by one to several more or less uniform bulges enclosed by a concentric costa, which was surrounded by a shelf with an oblique striation pattern (Figs 18–23). SEM of external features showed a concave central area with one to several bulges (Figs 33–39, 41–43) or more rarely without bulges (Fig. 40). The concentric costa was very robust (Figs 24–41) and solid (Fig. 36), and the almost horizontal shelf furnished



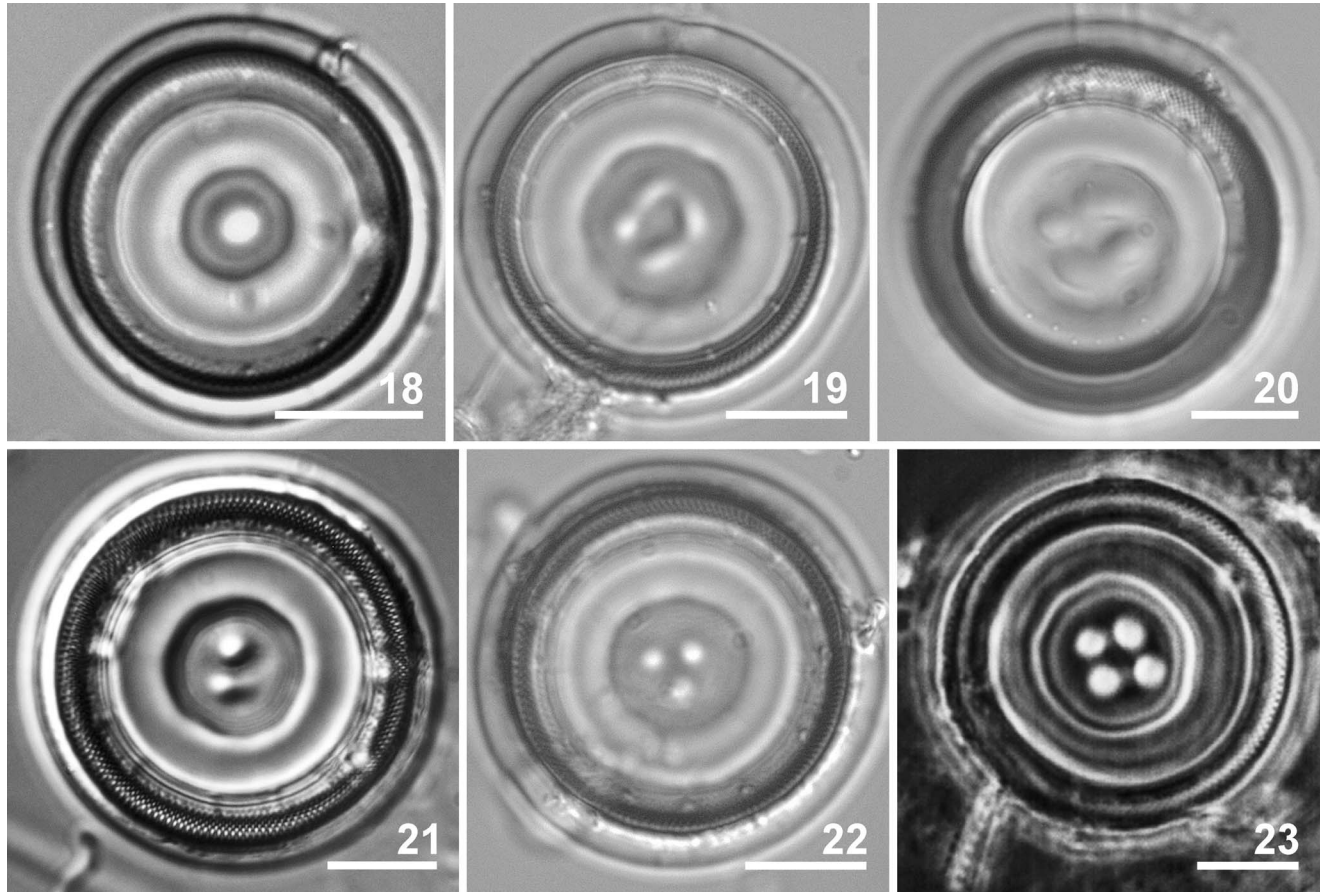
Figs 3–17. *Pseudopodosira boltovskoyi* sp. nov. LM. Scale bars = 20 μ m (Figs 3, 4); 10 μ m (Figs 5–17).

Figs 3–9. Live material in wet mount.

Figs 3–7. Chains of two, three and four cells with cells irregularly polygonal in girdle view.

Figs 8, 9. Cells in valvar view with numerous lenticular chloroplasts.

Figs 10–17. Fixed material mounted in water.



Figs 18–23. *Pseudopodosira boltovskoyi* sp. nov. LM. Cleaned material mounted in Naphrax. Valves showing central depression with one to four bulges, concentric costa, striated shelf and valve mantle edge. Scale bars = 10 μ m.

Figs 18, 19. Valves with the ring of irregularly spaced rimoportulae.

Fig. 20. Valve showing striation pattern of the shelf.

Fig. 21. Specimen from the holotype slide.

Fig. 22. Valve with rimoportulae more densely arranged than in Figs 18 and 19.

Fig. 23. Valve showing the convexity of the shelf.

by a hyaline flange (Figs 31–43). The concentric costa had an oblique slope toward the central depression and the shelf, and scattered, numerous, very small spinules were present (Figs 42, 43, 45, 47). In some specimens, there were, additionally, rounded granules, larger than spinules (Figs 42, 43, 47). The shelf was slightly convex, with an oblique striation pattern, stria density of 14–17 in 10 μ m (Figs 37–48) and stria angle of approximately 45°. Areolae, 19–22 in 10 μ m, were loculate, surrounded by minute spinules, externally occluded by hymenes with minute spinules (Fig. 46), and internally opening by circular, rimmed foramina (Figs 49–54). The margin of the valve face extended in a scalloped, hyaline flange more or less developed (Figs 33–41, 44, 45). The valve mantle was deep and sheave-shaped, with a variable number of rimmed pores located externally below the flange (Figs 47, 52, 55, 56), which were not distinguishable internally (Figs 49–54). The valve mantle

had a wide, horizontal abvalvar edge that slightly curved upward (Figs 27–32, 40, 41, 43, 47) and minute spinules on the slope and on the edge (Figs 45, 47). Internally, the valve showed a central convex area, enclosed by a concentric structureless costa, surrounded by an oblique fringe of areolae and a valve mantle also unperforated with a curved vertical area and a horizontal wide marginal edge. One ring of irregularly spaced rimoportulae, two to three in 10 μ m, was visible with LM (Figs 18, 19, 22) and internally with SEM, located in the external row of areolae (Figs 49–52). Rimoportulae were not distinguishable externally, while internally opened by short tubes without lipped structures (Figs 53, 54). The bulges were not visible internally. Girdle bands were rarely preserved, smooth valvocopula abutted in a shallow groove of the mantle (Fig. 45), and copulae were numerous, with a line of regularly spaced slits (Figs 26, 28, 29), easily detached.

Fig. 10. Cell with one bulge in the central depression.

Fig. 11. Same cell as in Fig. 10 with four bulges in the central depression.

Fig. 12. Cell with three bulges in the depression.

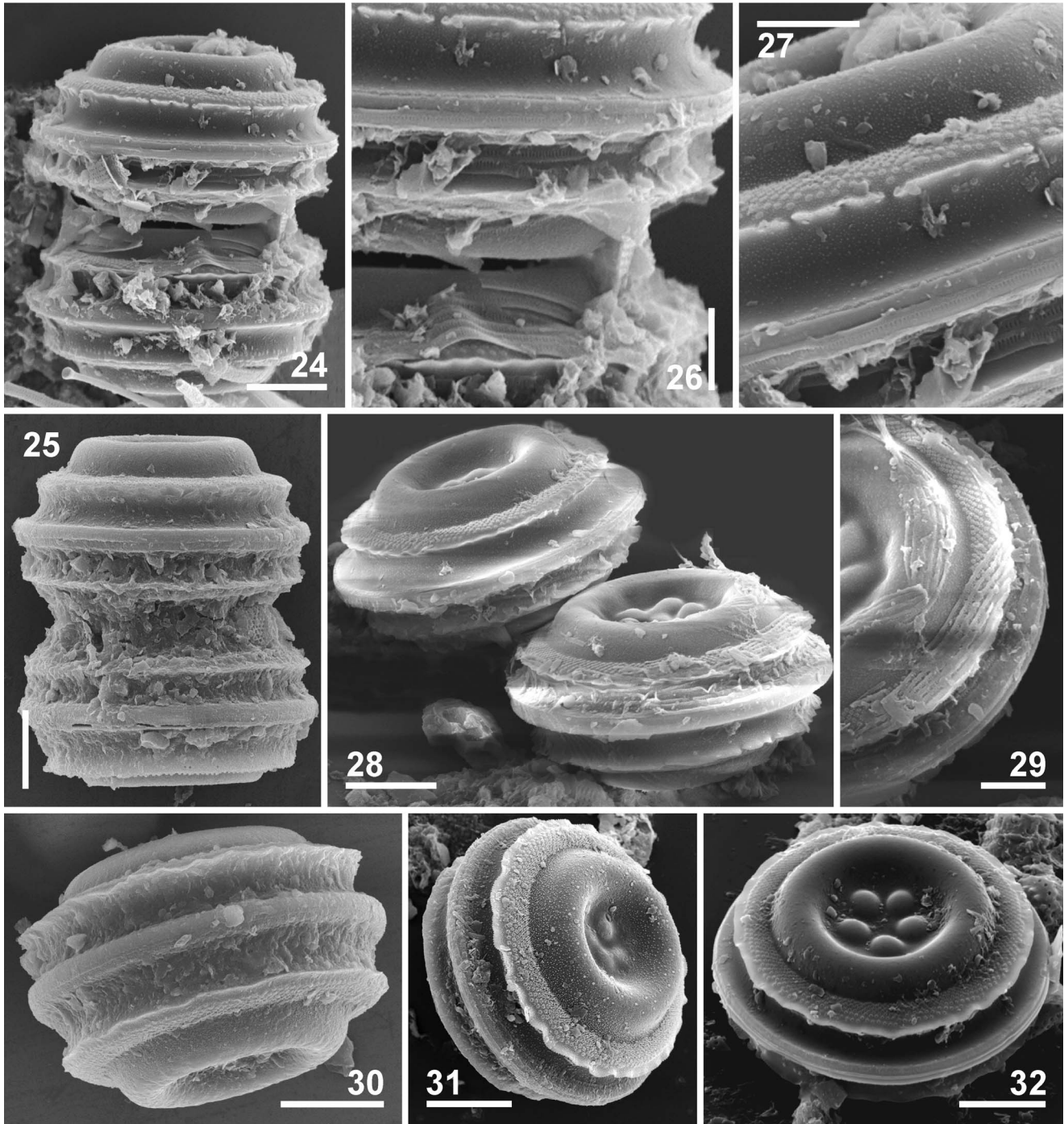
Fig. 13. Same cell as Fig. 12 with only one bulge in the depression.

Fig. 14. Cell with one bulge in one depression and two in the other.

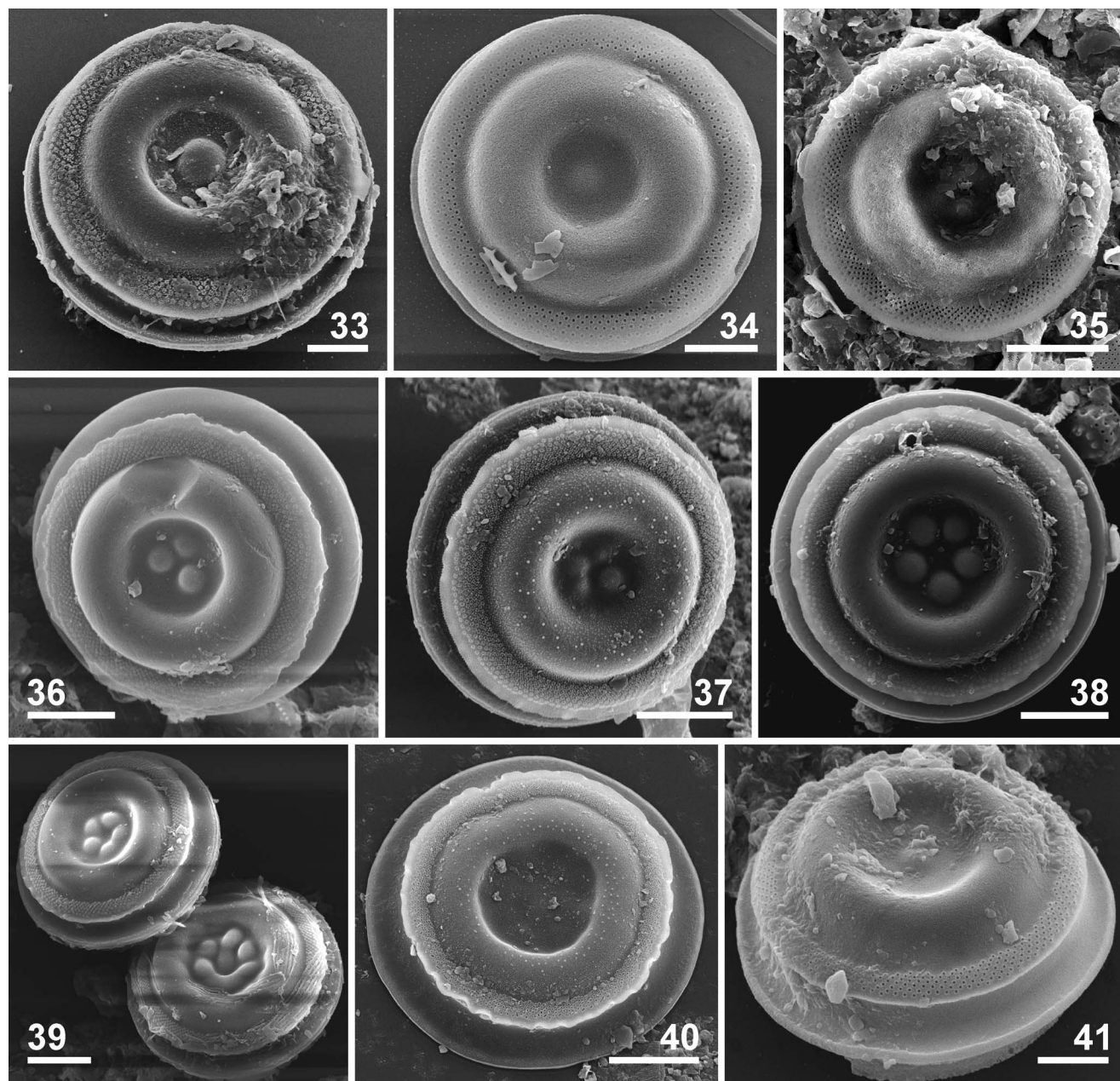
Fig. 15. Cell with one bulge in one depression and five in the other.

Fig. 16. Cell with one bulge in one depression and three in the other.

Fig. 17. Cell with several bulges in both central depressions.



Figs 24–32. *Pseudopodosira boltovskoyi* sp. nov. SEM. Scale bars = 10 μ m (Figs 24, 25, 28, 30–32); 5 μ m (Figs 26, 27, 29).
Figs 24–25. Girdle view of two celled chains with irregularly polygonal cells.
Fig. 26. Detail of Fig. 24 with collapsed girdle bands and line of regularly spaced slits.
Fig. 27. Detail of Fig. 24 showing an epivalve with depression, concentric costa, shelf with a hyaline flange and a deep, sheave-shaped valve mantle.
Fig. 28. General aspect of two frustules.
Fig. 29. Detail of one of the frustules in Fig. 28 showing collapsed girdle.
Fig. 30. Frustule in lateral oblique view.
Figs 31–32. Frustules in oblique view with hyaline scalloped flanges.



Figs 33–41. *Pseudopodosira boltovskoyi* sp. nov. SEM. Scale bars = 10 μm (Figs 35–40); 5 μm (Figs 33, 34, 41).

Figs 33–38. Frustules in valvar view showing variability in size, number and form of bulges in the central depression; in the extension of the hyaline flange and in the extension of the horizontal edge of the valve mantle.

Fig. 39. Frustules with some confluent bulges.

Fig. 40. Valve with no bulge in the central depression.

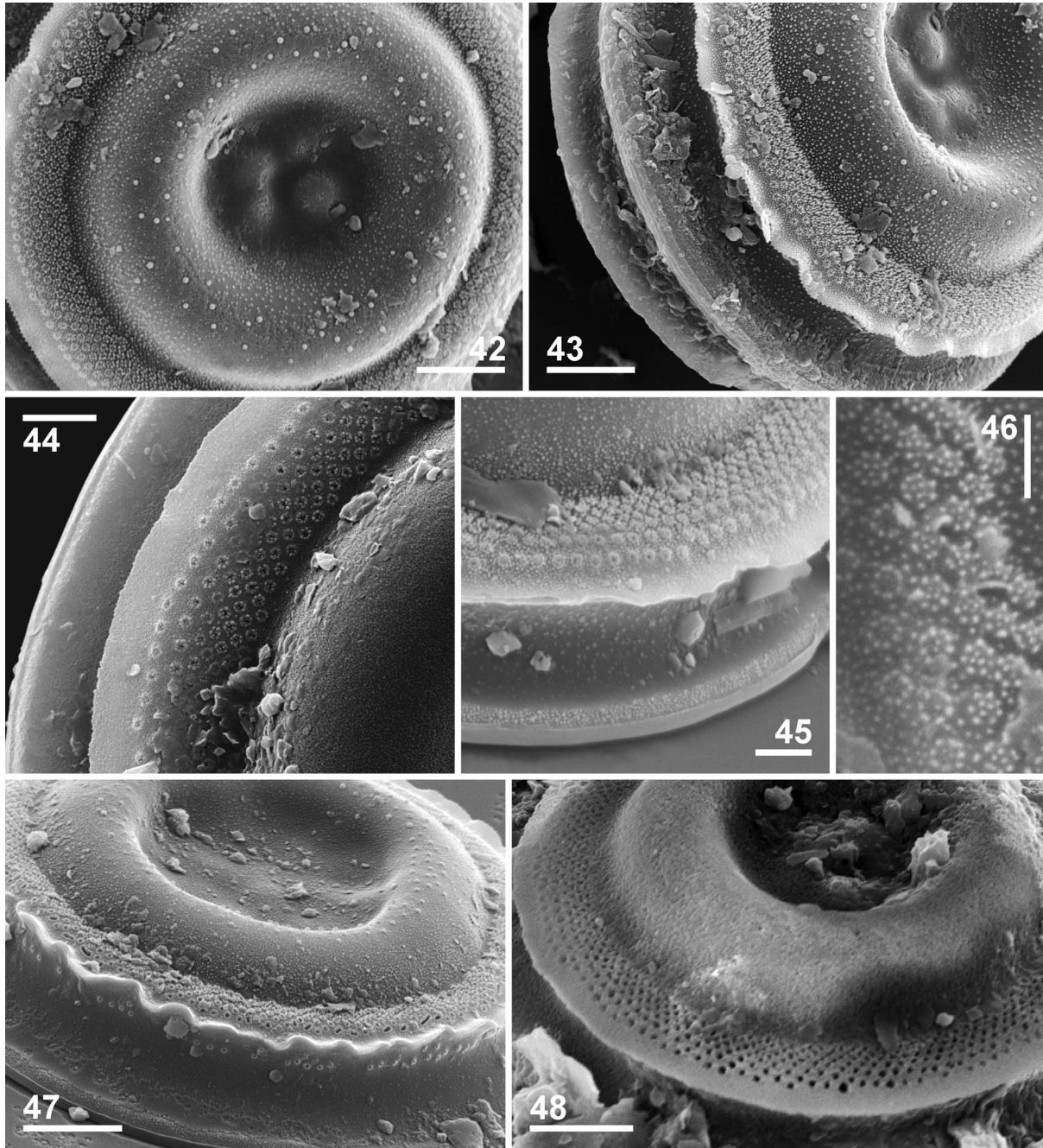
Fig. 41. Cell in lateral oblique view showing deep sheave-shaped valve mantle.

DISCUSSION

Taxonomic-nomenclatural analysis of the genus *Pseudopodosira* and its generic type

José in Proschkina-Lavrenko (1949) described *Pseudopodosira* without designating a type species, but the name was legitimized by a generic description in Russian. The author simultaneously described a new species, *Pseudopodosira pileiformis* José, and included a previously described

species, *Porodiscus calyciflos* Tempère & Brun in Brun & Tempère (1889), as a taxonomic (heterotypic) synonym. According to the Article 52.1 of the International Code of Nomenclature (McNeill *et al.* 2012) the name *Pseudopodosira pileiformis* is illegitimate (as was previously mentioned by Strelnikova *et al.* 2004). It must be rejected since it was nomenclaturally superfluous when published because the taxon to which it was applied included the type (as qualified in Art. 52.2 e) of the taxon *Porodiscus calyciflos* Tempère &

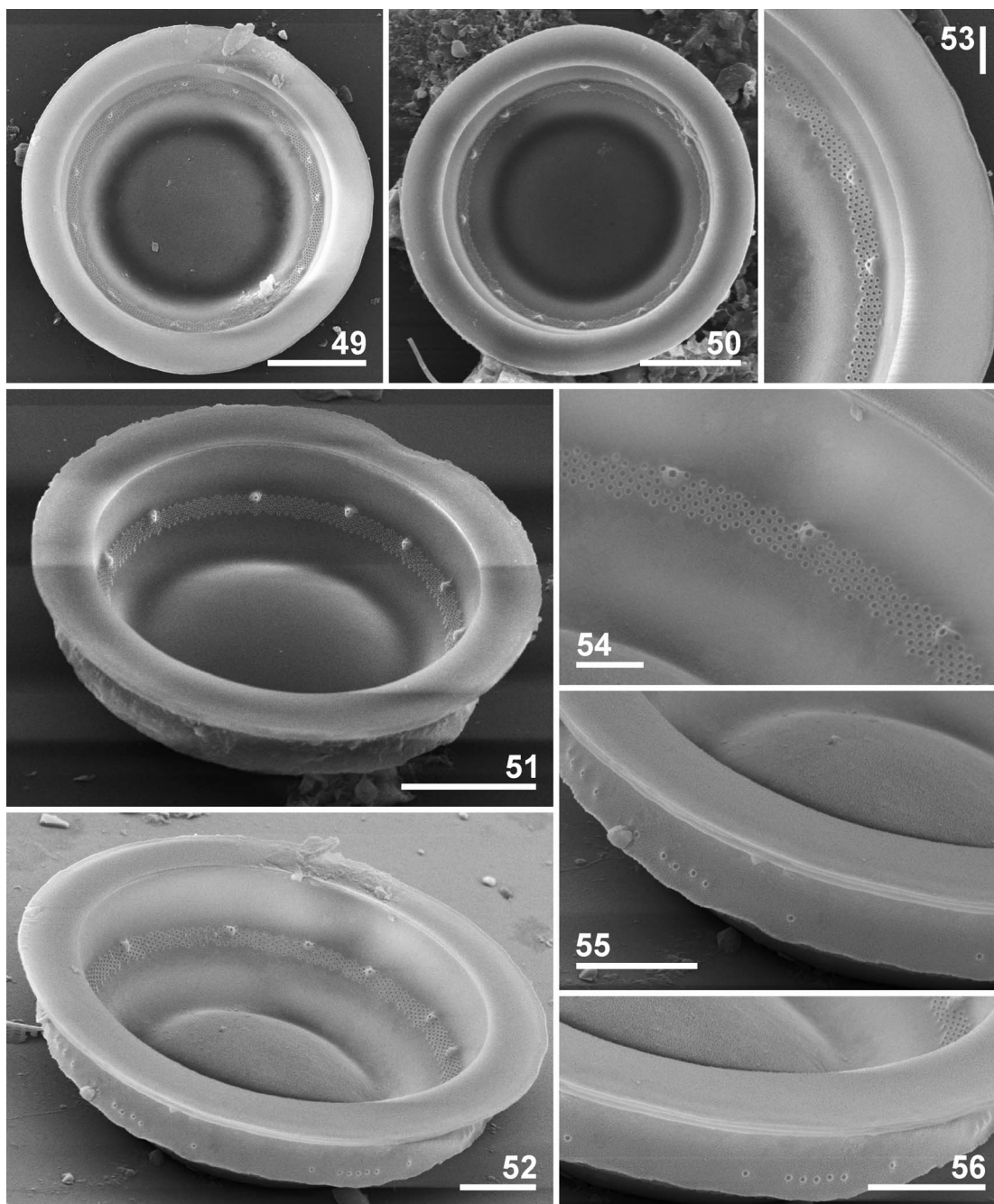


Figs 42–48. *Pseudopodosira boltovskoyi* sp. nov. SEM, external views. Scale bars = 5 μm (Figs 42, 43, 47, 48); 2 μm (Figs 44, 45); 1 μm (Fig. 46).
Figs 42–43. Details of Fig. 37 showing minute spinulae and rounded granules on the concentric costa.
Figs 44–45. Detail of the striate shelf showing the sawed edge of the hyaline flange, the areolae surrounded by minute spinules and scattered minute spinulae in the edge of the valve mantle.
Fig. 46. Detail of externally occluded areolae.
Fig. 47. Detail of Fig. 40 in lateral oblique view showing the valve mantle with rimmed pores located below the flange.
Fig. 48. Eroded valve.

Brun, whose epithet ought to have been adopted under the rules. Nevertheless, in accordance with Article 9.3, the original material comprises ‘those specimens and illustrations (both unpublished and published either prior to or together with the protologue) upon which it can be shown that the description or diagnosis validating the name was based’, and it is clearly based on those published for

Pseudopodosira pileiformis that conflicts with that published for *Porodiscus calyciflos*.

A necessary nomenclatural change is to replace the illegitimate name *P. pileiformis* Jousé by the replacement name *Pseudopodosira jouseana* nov. nom. Additionally, considering that the author did not designate a holotype of the species, figure 7a in Proschkina-Lavrenko (1949, pl. 6), one of



Figs 49–56. *Pseudopodosira boltovskoyi* sp. nov. SEM, internal views. Scale bars = 10 μ m (Figs 49–51); 5 μ m (Figs 52, 55, 56); 2 μ m (Figs 53, 54).

Figs 49–50. Valve showing a concentric areolate band with a ring of irregularly spaced rimoportulae.

Figs 51–52. Oblique lateral view of the valve showing a central dome corresponding to the external depression, a concentric area with oblique slope corresponding to the concentric costa, an oblique fringe of areola corresponding to the areolate shelf, a curve area corresponding to the vertical area of the valve mantle and a horizontal wide area of the valve mantle.

Figs 53–54. Detail of Fig. 49 showing the oblique fringe of areolae with rimmed foramina and two rimoportulae with a short tube and without a lipped structure.

Figs 55–56. Detail of the valve mantle showing an irregular ring of rimmed pores and the groove of the mantle edge.

the two figures given in the protologue, is chosen as lectotype based on Article 9.2.

Porodiscus calyciflos was transferred to *Pseudopodosira* by Kanaya (1963) as *Pseudopodosira calyciflos* (Tempère & Brun) Kanaya.

Thus, the illustration showed by Tempère & Brun in Brun & Tempère (1889, pl. 4, fig. 11b) should be considered the holotype of *Pseudopodosira calyciflos* according to Article 9.1 based on the fact it is the only figure from Yedo ('Edo': 'bay-entrance' or 'estuary' in Japanese, also romanized as Yedo,

Jeddo or Yeddo is the former name of Tokyo, Japan) while figure 11a in the same plate (the only figure mentioned by Kanaya 1963, 50) corresponds to extant material from Sandwich Islands, additionally mentioned by the authors in the protologue.

The original material of *Pseudopodosira calyciflos* was searched with the purpose of choosing an epitype to serve as an interpretative type of the holotype. We examined the slides leg98–1 and leg98–2 and both unmounted suspensions Sa1875–1 and Sa1875–2 from Calcaire of Sendai & Yedo, and slides 22–25, 61 and 63, 448–449, 745–750, from Tempère & Peragallo Collection (2nd edition) but the species was not found. A single slide from the Calcaire de Yedo labelled ‘*Campylodiscus taeniatus* A.S. (fossile) Calcaire de Yedo, Prof. J. Brun, Genève’, deposited in the Van Heurck Collection was also analyzed, and it only contains four valves of *Campylodiscus*. Four slides deposited in the Hustedt Collection are from Yedo; however, they do not correspond to the ‘Calcaire de Yedo’; two are labelled as ‘Schlamm’ (= mud), and two as coming from the Challenger expedition (one of these from Cleve). Taking into account that original material of *P. calyciflos* is not available, the epitypification of the taxon was not possible.

The comparison between the lectotype of *Pseudopodosira jouseana* and the holotype of *Pseudopodosira calyciflos* allowed us to determine that both taxa are similar in having external tubes of rimoportulae and a striated valve mantle. Nevertheless, they clearly differ based on the following: (1) the diameter of the cells that were smaller in *P. jouseana* than in *P. calyciflos*, (2) the size and morphology of the central concave part of the valve surface, with larger and more numerous bulges in *P. jouseana*, and (3) the distribution of the rimoportulae, in two circles, one placed on the concentric costa and the other on the mantle in *P. jouseana* but in only one circle located on the mantle in *P. calyciflos*.

Taking into account that the species are not conspecific, that they belong to the genus *Pseudopodosira*, and that *Pseudopodosira pileiformis* is a name nomenclaturally superfluous by the unwarranted change of epithet, *P. calyciflos* should be established as the generic type typified by the holotype of the basionym (see Nomenclatural changes proposed in this study) despite the fact that it does not exactly fit with the description of the genus. This problem is completely solved by the emendation of the description of *Pseudopodosira* given by Vekshina (1961).

Comparison of *Pseudopodosira boltovskoyi* sp. nov. with related species

Glezer & Olshtynskaya (2000) made a comprehensive comparative-morphological analysis of the frustules and valves of numerous *Pseudopodosira* species. They described two types of frustule structure: in the first type the valves have a structure more or less homogeneous (*P. hyalina* and *P. himilis*), and in the second, the valves have a more complex valve relief (*P. modesta*, *P. wittii*, *P. bella* and *P. westii*). *Pseudopodosira boltovskoyi* sp. nov. shows a valvar relief that better agrees with the second morphological type, i.e. with species characterized by having a central depression commonly sculpted with one or several bulges, enclosed by a concentric costa surrounded by a shelf with striae (Table 1). *Pseudopodo-*

sira boltovskoyi shares these features with specimens of *P. modesta* and *P. wittii*, which show several bulges in the concave central depression, and with specimens of *P. bella* and *P. westii*, which show only one bulge in the concave central depression. In the case of specimens lacking bulges in the concave central depression, the new species also shares valve morphology with two members of the first morphological type, *P. hyalina* and *P. himilis*.

More similar to *Pseudopodosira boltovskoyi* in morphological and morphometric features is *P. modesta* (Table 1); however, they differ in the proportion of the valve surface occupied by the central concave depression, which is smaller in the former species. They also differ in the extension of the horizontal shelf, which is wider and convex in *P. boltovskoyi*. With respect to density of striae, it is lower in *P. boltovskoyi*, and in the constriction of the sheave-shaped valve mantle, *P. boltovskoyi* is more constricted in the central part (Figs 33–41; figs 7, 8 in Olshtynskaya 1990). *Pseudopodosira boltovskoyi* differs from *P. wittii* by size of the valve (30–48 µm in diameter in and 80–108 µm, respectively), and in the number and distribution of bulges, generally one or several, more or less concentrically located in *P. boltovskoyi* (Figs 18–41), and very numerous and randomly distributed in *P. wittii* (pl. 1, fig. 11 in Schulz 1935; pl. 40, figs 8–10 in Schmidt 1874–1955, mentioned in the protologue).

Pseudopodosira boltovskoyi differs from *P. bella* by its larger valves, the lower stria density (14–17 in 10 µm vs 36 in 10 µm) and the presence of short radial ribs between the central bulge and the concentric costa in the latter (pl. 1, fig. 2 in Glezer & Posnova 1964; figs 2–4 in Olshtynskaya 1990; pl. 3, figs 6–8 in Glezer & Olshtynskaya 2000), which are absent in the former (Figs 18, 33, 34, 41). *Pseudopodosira westii* differs from *P. boltovskoyi* by having the central depression with only one large central bulge higher than the contiguous costa, costa continuous or in sections, and a wide shelf with striae on the advalvar part of the valve mantle below the marginal hyaline flange (pl. 1, figs 4, 5 in Sheshukova-Poretskaya & Glezer 1964; figs 13–15 in Olshtynskaya 1990).

Cells of *Pseudopodosira boltovskoyi* sp. nov. that lack bulges (Figs 40, 46) differ from *P. hyalina* (pl. 6, fig. 4 in Proschkina-Lavrenko 1949) by the smaller diameter of the central depression, higher valve and wider shelf. The new species differs from *P. himilis* (pl. 1, figs 2a, b in Dolmatova 1975; pl. 1, figs 5, 6 in Glezer & Olshtynskaya 2000) by the smaller diameter of the central depression and by the morphology of the shelf, convex in the former and concave in the latter.

Although most species of *Pseudopodosira* are extinct, *P. westii*, *P. calyciflos* and *P. echinus* (= *P. kosugii*) have been mentioned as extant. Nevertheless, Witkowski *et al.* (2000, p. 41) pointed out that according to Hustedt (1930, p. 269) it is necessary to check whether *P. westii* still survives on European coastal sediments. *Pseudopodosira calyciflos* has never been confirmed as extant, it was mentioned in the protologue as living in the Hawaiian Island (as Sandwich Islands) and illustrated by Brun & Tempère (1889, pl. 4, fig. 11a) that only shows one valve. As far as we can determine, *P. echinus* is the only extant species able to grow in culture (Tanimura & Sato 1997). These authors determined that the species also had been documented in sedimentary Holocene sequences from Japan by Sato *et al.* (1996). *Pseudopodosira echinus* was described

Table 1. Comparison of morphometric, morphological and stratigraphic data among *Pseudopodosira boltovskoyi* sp. nov. and morphologically related taxa. Abbreviations: nd, no data; *, observed in published images.

Taxon	Reference	Valve diameter	Valve height	Striae in 10 µm	Rimoportulae	Bulges in central depression	Morphology of the shell	Extant/fossil stratigraphic occurrence
<i>P. boltovskoyi</i> sp. nov.	This study	30–48	8–12	14–17, oblique	one ring 10–14, 2–3 in 10 µm	1–6, rarely 0	convex	Extant
<i>P. bella</i> Posnova & Glezer	Posnova & Glezer in Glezer & Posnova (1964)	12–14	6–8	nd	nd	1, surrounded by short radial ribs	nd	Late Eocene–Early Oligocene
<i>P. echinus</i> (Frenguelli)	Olshynskaya (1990)	14–25	6–8	36, oblique	one ring 6–10	1 surrounded by short radial ribs	slightly concave*	Early Paleocene–Late Miocene
Metzeltin <i>et al.</i> = <i>P. kosugii</i> Tanimura & Sato	Tanimura & Sato (1997)	5–15	1.7*	15–30, on valve surface and mantle	one marginal ring	no bulges, very small depression*	not differentiated*	Extant Holocene
<i>P. himilis</i> Dolmatova	Dolmatova (1975)	nd	low	15–20, oblique	nd	no bulges, weakly and ample depression*	nd	Late Eocene
<i>P. hyalina</i> (Jousé)	Glezer & Olshynskaya (2000)	25–45	low	15–20	nd	no bulges, ample depression*	concave*	Middle to Late Eocene
Sheshukova-Poretzkaya	Jousé in Proshkina-Lavrenko (1949)	25–30	5	nd	nd	no bulges, ample depression*	nd	Middle to Late Eocene
	Sheshukova-Poretzkaya (1967)	28–33	2–4	radial	nd	no bulges, ample depression*	nd	Late Eocene–Early Oligocene
<i>P. modesta</i> (Jousé)	Jousé in Proshkina-Lavrenko (1949)	57	5–6	nd	nd	nd	nd	nd
Olshynskaya	Olshynskaya (1990)	25–57	nd	20–25, radial and oblique	one ring	1 central surrounded by 6, 7, sometimes confluent*	concave*	Early Paleocene to Late Eocene; Middle Eocene to Late Pliocene (Glezer & Olshynskaya 2000)
<i>P. westii</i> (Smith)	Sheshukova-Poretzkaya & Glezer (1964)	23–44	nd	16–18, oblique	nd	1, occupying all the central depression*	nd	Early Eocene to Late Miocene
Sheshukova-Poretzkaya & Glezer	Olshynskaya (1990)	12–74	nd	16–18, oblique extended in the advalvar part of the mantle*	one ring	1, occupying all the central depression*	convex*	Early Eocene to Late Miocene; Pleistocene (Glezer & Olshynskaya 2000)
<i>P. vittii</i> (P. Schulz) Vekshina	Schulz (1935) and Glezer & Olshynskaya (2000)	80–108	nd	nd	nd	numerous, randomly located	nd	Late Cretaceous to Early Eocene

based on material from the Province of Buenos Aires, Argentina, and was found in Rocha Lagoon, Uruguay, by García-Rodríguez & Witkowski (2003, figs 1–13) and Metzeltin *et al.* (2005, p. 204, pl. 4, figs 1–10) as a reliable indicator of Holocene sea level variation.

Like *Pseudopodosira echinus*, *P. boltovskoyi* was found with chloroplasts and able to grow in culture. These taxa are very different with respect to (1) size (30–47 µm diameter in *P. boltovskoyi* vs 5–15 µm in *P. echinus*); (2) chloroplasts number (numerous in *P. boltovskoyi* and three to seven in *P. echinus*); (3) distribution of areolae [limited to the shelf in the valve surface forming oblique striae in *P. boltovskoyi* (Figs 33–41) vs ordered in rows radiating from the central part of the valve in *P. echinus* (figs 11, 20, 22, 23 in Tanimura & Sato 1997; pl. 4, fig. 10 in Metzeltin *et al.* 2005)]; (4) spinules, if present, only visible with SEM in *P. boltovskoyi* (Figs 42, 43, 48) vs robust spines visible with LM scattered on the valve face in *P. echinus* (figs 7a, b in Tanimura & Sato 1997; pl. 4, figs 1–8 in Metzeltin *et al.* 2005).

Nomenclatural changes proposed in this study

Pseudopodosira Jousé in Proschkina-Lavrenko (1949, p. 33, pl. 6, figs 7a, b) emended by Vekshina (1961, p. 89)

GENERITYPE: *Pseudopodosira calyciflos* (Tempère & Brun) Kanaya (*A survey of fossils from Japan illustrated in classical monographs Part VI. Brun & Tempère (1889): Diatomées fossiles du Japon – Espèces marines et nouvelles des calcaires argileux de Sendai & de Yedo.* Palaeontological Society of Japan, 25th Anniversary, 1963, p. 24).

BASIONYM: *Porodiscus calyciflos* Tempère & Brun in Brun & Tempère (*Diatomées fossiles du Japon. Espèces marines et nouvelles des calcaires argileux de Sendai et de Yedo. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* 1889, 30 (9): 50, pl. 4, fig. 11b).

HOLOTYPE: Here designated according Article 9.1 McNeill *et al.* (2012), figure 11b in Brun & Tempère (1889, pl. 4, fig. 11b). This figure was considered the only element from Yedo in which the protologue is based, while figure 11a was included as pertaining to a material found alive in the Sandwich Islands (Hawaiian Islands).

TYPE LOCALITY: Limestone clay from Yedo (Tokyo), Japan.

OCCURRENCE: Extinct and extant from marine habitats in Yedo and Hawaiian Islands, respectively.

Pseudopodosira jouseana nom. nov. [replacement name for the illegitimate name *Pseudopodosira pileiformis* Jousé in Proschkina-Lavrenko (*Diatomovyi Analis. Kniga 2.* Botanicheskii Institut im V.L. Komarova Akademii Nauk S.S.S.R. Gosudarstvennoe Izdatelystvo Geologicheskoi Literaturny, Moskva-Leningrad, 1949, 2 (1), p. 33)]

LECTOTYPE: Here designated according to Article 9.2 in McNeill *et al.* (2012), fig. 7a in Proschkina-Lavrenko (1949, p. 33, pl. 6, fig. 7a).

TYPE LOCALITY: Deposits level of Kharkov, Ukraine.

OCCURRENCE: Marine extinct species.

Prospects for future studies of *Pseudopodosira*

The morphological analysis of the new species informs relationship with *Pseudopodosira bella*, *P. modesta* and *P.*

westii and clear differences with *P. jouseana*, *P. calyciflos*, *P. homanae* Glezer & Olshtynskaya (2000, p. 107, pl. 4, figs 1–3), which have external tubes of the rimoportulae and striae on the valve mantle (not on the shelf, absent in these species) and with *P. echinus*, which has striae on valve and mantle. A revision of the type material of several species described only with LM analysis would be necessary to establish all the morphological range found in the genus and to evaluate if it should be split.

The occurrence of two extant species (*P. boltovskoyi* and *P. echinus*) in marine and estuarine recent sediments, respectively, from diverse geographic locations suggests that the genus may be more diverse than presently known. *Pseudopodosira boltovskoyi* was found in phytoplankton samples from marine coastal waters and in sediments from Ría del Jabalí, with temperatures between 8.0°C and 24.5°C and with a salinity range between 26.2 and 34.8. The sediments from Ría de Jabalí were characterized as mud clay-loam, dark black in colour, with scattered fine quartz gravels well rounded.

Recently, Álvarez-Blanco & Blanco (2014) determined a material, supposedly alive, collected by scrapping coastal rocks from Palma de Mallorca, España, as *Pseudopodosira westii*. A specimen depicted by Álvarez-Blanco & Blanco (2014, pl. 2, fig. 9, 30 µm in diameter measured in picture) with only one small bulge in the depressed area, better coincides with *P. boltovskoyi* than with *P. westii*, in which the bulge occupies all the central depression. The analysis of the Mediterranean material should be useful to determine if *P. westii* is an extant species as suggested by Álvarez-Blanco & Blanco (2014) or if *P. boltovskoyi* has a more extended distribution. Further research of estuarine and marine coastal waters would be necessary, including analysis of phytoplankton, sediments, stones, benthic algae and other substrata of each area, to check whether more extant species appear, to determine the distribution of extant species previously known, and to confirm whether species are tytoplanktonic and benthic and the substrata they grow on.

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Table 2. Latitude and longitude of the sampling stations.

1: San Clemente del Tuyú	36° 21' 16" S–56° 42' 54" W
2: Santa Teresita	36° 32' 30" S–56° 41' 09" W
3: Mar del Tuyú	36° 34' 37" S–56° 41' 07" W
4: La Lucila del Mar	36° 39' 30" S–56° 40' 40" W
5: Mar de Ajó	36° 42' 36" S–56° 40' 17" W
6: Nueva Atlantis	36° 45' 47" S–56° 40' 23" W
7: Pinamar	37° 07' 22" S–56° 51' 26" W
8: Villa Gesell	37° 16' 50" S–56° 58' 52" W
9: Mar Azul	37° 20' 22" S–57° 01' 24" W
10: Claromecó	38° 51' 29" S–60° 01' 28" W
11: Los Pocitos	40° 25' 40" S–62° 25' 10" W
12: Ría del Jabalí	40° 32' 25" S–62° 17' 36" W
13: Bahía San Blas	40° 32' 05" S–62° 16' 36" W
14: Punta Orengo	40° 50' 57" S–64° 39' 49" W
15: Las Garzas	40° 46' 46" S–64° 51' 08" W
16: San Antonio Oeste	40° 43' 44" S–64° 53' 24" W
17: Banco Reparo	40° 48' 05" S–64° 54' 59" W
18: Los Alamos	40° 47' 21" S–65° 01' 13" W
19: Las Grutas	40° 49' 03" S–65° 05' 04" W
20: Piedras Coloradas	40° 50' 32" S–65° 06' 23" W
21: El Sótano	40° 54' 17" S–65° 04' 34" W
22: El Fuerte	41° 06' 29" S–65° 07' 02" W