Fottea, 26(2), 119–132, 2026
doi: 10.5507/fot.2026.004

Czech Phycological Society

Taxonomic revision of *Eunotia indica* and infraspecific taxa (Bacillariophyceae) reported by Frenguelli from the Esteros del Iberá (Argentina)

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Abstract

Eunotia indica, originally described from Banka Island (Indonesia), has been reported worldwide although there is confusion about the identity and actual distribution of this supposedly cosmopolitan species. In 1933 Frenguelli reported 55 different taxa of *Eunotia* from the Esteros del Iberá (Argentina), a vast wetland with a high rate of endemism. One of the species reported was *E. indica* together with two new varieties. We examined the original materials contained in the Frenguelli Collection to study the valve morphology of these taxa and elucidate their taxonomic position. For comparison, we also analyzed the original material of *E. indica* included in the Hustedt Collection. As a result, we conclude that the *E. indica* complex originally reported from Iberá comprises in fact three different species: *Eunotia pseudoindica*, *Eunotia zygodon* and *Eunotia hustedtii nov. nom. et stat. nov.* whereas *Eunotia indica* is not present in this wetland. Since Frenguelli did not designate holotypes for the taxa here studied, we designate herein the corresponding lectotypes.

Keywords

diatoms, Frenguelli Collection, lectotypification, new species, South America, taxonomy, valve morphology

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Article History
Received November 5, 2025
Revised April 16, 2026
Accepted April 28, 2026
Published online September 9, 2026

Supplementary Material
None

How to cite
Vouilloud, A. A., Guerrero, J. M., & Sala, S. E. (2026). Taxonomic revision of *Eunotia indica* and infraspecific taxa (Bacillariophyceae) reported by Frenguelli from the Esteros del Iberá (Argentina). *Fottea*, *26*(2), 119–132. https://doi.org/10.5507/fot.2026.004

Introduction

The diatom genus *Eunotia* was erected by Ehrenberg (1837, p. 44) and later typified by Boyer (1926, p. 215). This large genus, with more than 1300 currently described taxa (Guiry & Guiry, 2025), is characterized by valves asymmetrical to the apical axis, with convex dorsal margin and straight or concave ventral margin, and with short raphe slits positioned at each pole, mostly on the valve mantle (Kociolek *et al.*, 2015). Striae span the valve face from a narrow, ventrally positioned sternum (Siver *et al.*, 2006), and are composed of single rows of round, unoccluded areolae (Round *et al.*, 1990). Rimoportualae are present, usually one per valve, with a simple external opening not discernible from the areolae (Round *et al.*, 1990). Members of this genus prefer acidic, dystrophic or oligotrophic freshwater habitats with low conductivity and generally occur as epiphytic or epilithic (Bukhtiyarova, 2019), with a worldwide distribution and numerous endemics from different continents, and especially, South America (Sala *et al.*, 2023 and references therein). Particularly in the later continent, taxa of *Eunotia* are well-represented in tropical and subtropical regions (Guerrero & Vouilloud, 2022) although diversity is also relatively high in southern Patagonia, mainly associated with peat bogs and moss habitats (Vouilloud, 2003; Casa, 2020).

The subtropical Esteros del Iberá, located in the province of Corrientes (NE Argentina), is a vast wetland (13,000 km^2), one of the largest in South America, comprising a complex environment of interconnected streams, marsh habitats and shallow lakes (Swenson, 2020) that drains in a NE-SW reduced flow to the median basin of the Paraná River. For a detailed description of the study area see Lamaro *et al.* (2021). Frenguelli (1933) surveyed the diatom flora of this area

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and reported 243 taxa (among species and varieties), of which 46 were newly described; representatives of the genus *Eunotia* accounted for 23% of the total number of taxa found and 43% of the new taxa.

In previous contributions about the taxa of *Eunotia* reported by Frenguelli for Iberá, we presented the revision of the infraspecific taxa of *E. luna* Ehrenberg (Guerrero & Vouilloud, 2022) and a study on the *E. camelus* complex of taxa (Sala *et al.*, 2023). The aim of this contribution is to re-examine the materials of the Frenguelli Collection originally reported as *E. indica* Grunow (1865, p. 5) and the two infraspecific taxa described by Frenguelli from Iberá and elucidate their current taxonomic position. The original material of *E. indica* from Indonesia is also studied and its valve morphology is compared with that of Frenguelli's taxon. Since Frenguelli did not designate holotypes, herein we designate the corresponding lectotypes for his new taxa.

Nomenclatural history

Eunotia indica was described by Grunow (1865) from materials collected in Banka Island (Indonesia) (here illustrated in Figure 1) as: "*Eunotia indica Grunow nov. spec. Eunotia valvis sublinearibus parum arcuatis, apice breviter productis oblique truncatis. Striae transversales 24–30 in 0,001". Longit: 0,0020—0,0029", latit. valvae: 0,0003–0,0004". tab. nostr. I. Figure 7. a. b (400/1). Steht der Eunotia regiomontana Schumann (Abhandl. der physik. Oekon. Königsberg. Gesell. 3. Jahrgang tab. VIII. 8) jedenfalls sehr nahe, unterscheidet sich aber durch die nicht herabgebogenen Enden, die auch bei jener Art mehr kopfförmig gestaltet sind. Einige Aehnlichkeit scheint auch Eunotia depressa Ehbg. zu besitzen. var. β ventralis. Bauchseite der Schaalen mit einer kleinen centralen Anschwellung. tab. nostr. I. Figure 7. c (400/1). Beide Formen finden sich vereinzelt in der Aufsammlung, letztere ziemlich selten."*

Here translated: "*Eunotia* with sublinear valves, slightly arched, apex shortly protracted and obliquely truncate. Striae transverse 24–30 in 0,001" (= 12–16 in 10 µm). Length: 0.0020–0.0029" (= 51–74 µm), width: 0.0003–0.0004" (= 9.5–12 µm). table I. Figure 7. a. b (400/1). It is very close to *Eunotia regiomontana* Schumann (Abhandl. der physik. Oekon. Königsberg. Gesell. 3. Jahrgang tab. VIII. 8), but differs in its ends not bent, which are also more capitate in that species. It also has some similarity with *Eunotia depressa* Ehbg. var. β *ventralis*. Ventral side of the valves with a small central swelling. table I. Figure 7. c (400/1). Both forms are found sporadically in the collection, the latter rather rarely."

Lange-Bertalot *et al.* (2011) studied the original material of this taxon, providing an expanded description and images of 4 specimens. Additionally, they considered *E. indica* var. *ventralis* Grunow as a synonym of *E. indica* and commented about the doubtful identification of this taxon from outside the type locality.

Frenguelli (1933) recorded *Eunotia indica* in half of the set of samples from Iberá, detailing its relative frequency in each series in the table in p. 371. He reported this species as "frequent" in series 263, "scarce" in series 261, and "rare" in series 264 and 266.

When describing the specimens of *E. indica* found in Iberá (Figure 2), Frenguelli commented that they differed from Grunow´s original illustrations and from the valves of the material illustrated by Hustedt (in Schmidt, 1913) in the shape of the valve apices, more protracted and slightly attenuated in Frenguelli's material.

Furthermore, Frenguelli (1933) described for Iberá two new varieties of *E. indica*: *E. indica* var. *bigibba* Frenguelli (1933, p. 454) (Figure 3) and *E. indica* var. *gracilis* Frenguelli (1933, p. 454) (Figure 4). The former was reported as "scarce" in series 264 and 265, and as "rare" in series 261 and 263. According to the author, *E. indica* var. *bigibba* differed from the nominate variety by the presence of two prominent humps on the dorsal margin and the valve ends more distinctly capitate. The other variety was created by Frenguelli (1933) to include specimens smaller but with humps relatively more prominent (recorded as "rare" in series 261, 262, 263 and 264), even though he was doubtful about the creation of his new variety (noted both in text and table as "*E. indica* var. *gracilis* n. var.?") and mentioning the high resemblance of this variety with *E. zygodon* var. *gracilis* Hustedt in Schmidt (1913, pl. 287, Figure 10).

In a later publication on diatoms from the Río

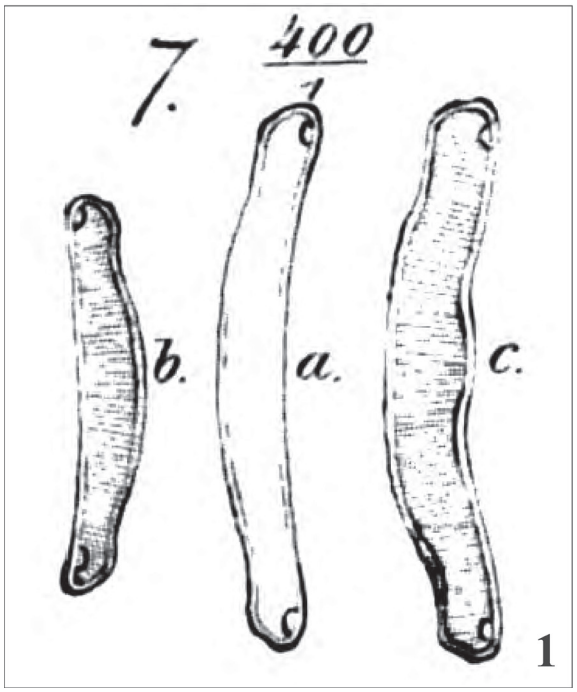


Figure 1. *Eunotia indica* Grunow. Original drawings. **(a, b)** *E. indica*. **(c)** *E. indica* var. *ventralis*

de la Plata estuary and based on the above mentioned, Frenguelli (1941) considered that the specimens named *E. indica* from Iberá did not match with *E. indica* Grunow but belonged in a new species he named *E. pseudoindica* Frenguelli (1941, p. 307). With respect to the var. *gracilis*, he made a new combination under the name *E. pseudoindica* var. *gracilis* (Hustedt) Frenguelli (1941, p. 307), erroneously attributing the basionym to *E. zygodon* var. *gracilis*. On the other hand, no mention of var. *bigibba* was made by Frenguelli in this publication. In their Catalogue of diatoms from Argentina and based on the change introduced by Frenguelli in 1941 at the rank of species, Luchini & Verona (1972) proposed for the latter taxon the new combination *E. pseudoindica* var. *bigibba* (Frenguelli) Luchini et Verona (1972, p. 85).

According to Sar *et al.* (2009), the material from Iberá studied by Frenguelli (1933), explicitly linked to *Eunotia pseudoindica* by Frenguelli (1941), must be considered the type material of this species and the description given in the former work as part of its protologue. Although VanLandingham (1969) recognized *E. pseudoindica* as a valid taxonomic entity, Metzeltin & Lange-Bertalot (1998) considered that the illustrations of this species provided by Frenguelli (1941) are insufficient to distinguish it from *E. indica*. This reinforces the need to analyze the type materials of both taxa to establish if they are conspecific or not.

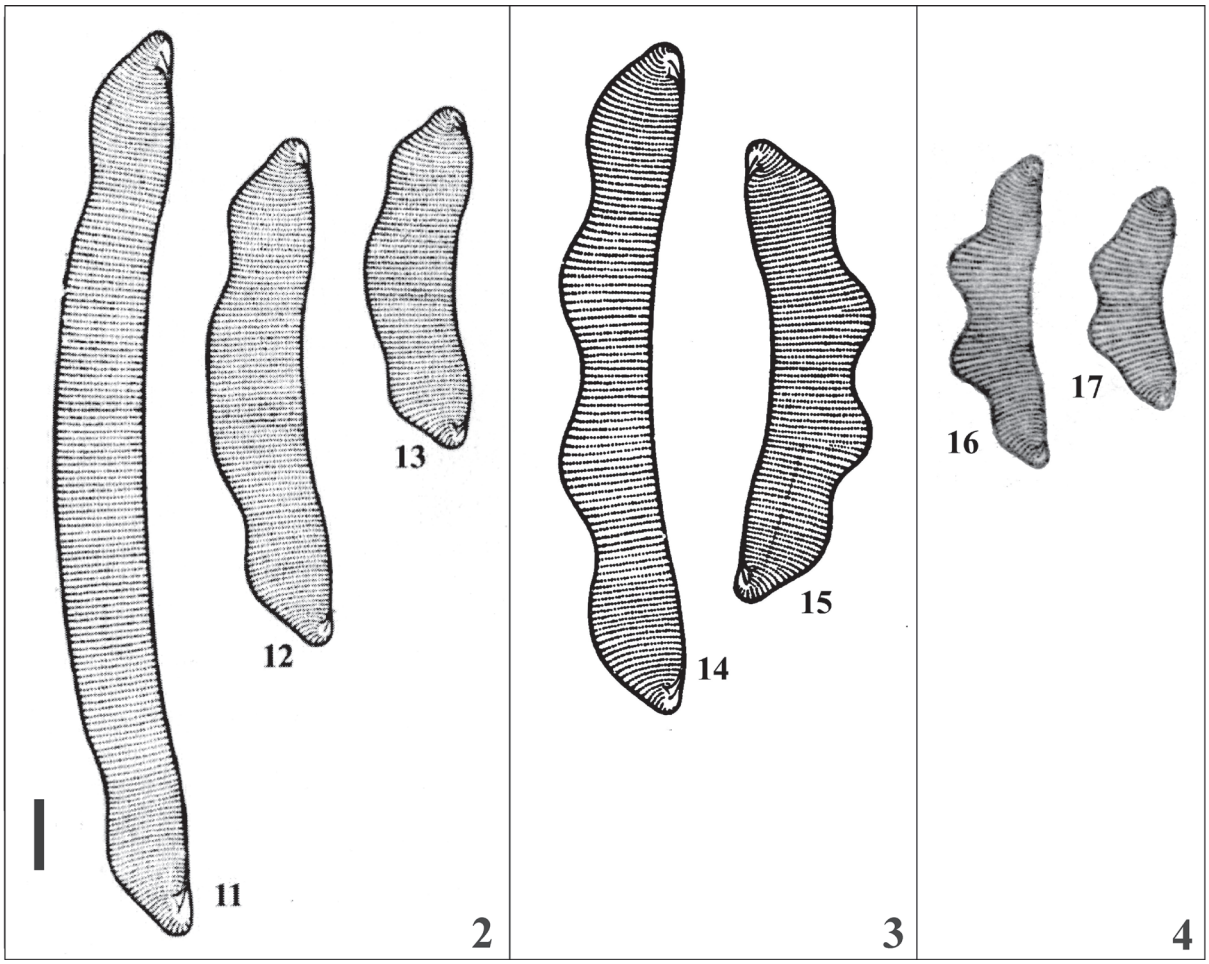
Materials and Methods

Materials from Iberá: The Frenguelli Collection is housed at the Herbarium LPC, Museo de La Plata, Buenos Aires, Argentina. In this study we examined the series (as Frenguelli named his samples) 261 to 266 from Esteros del Iberá, corresponding respectively to:

Series 261: aquatic macrophytes, Estero del Carambola, Corrientes Province, Argentina. December 8th, 1923. 28°28'12"S, 57°49'12"W. Coll. J. Frenguelli. Slides 1–8 and raw material.

Series 262: aquatic macrophytes, Estero del Carambola (lotic zone), near San Miguel town, Corrientes Province, Argentina. December 12th, 1923. 28°4'12"S, 57°24'36"W. Coll. J. Frenguelli. Slides 1–10 and raw material.

Series 263: aquatic macrophytes, Estero Cambá, near Estancia Guayaibí, Corrientes Province, Argentina. December 12th, 1923. 27°58'12"S, 57°25'48"W. Coll. J. Frenguelli. Slides 1–10 and raw material.



Figures 2–4. Original drawings of Frenguelli. **(2)** *Eunotia indica* sensu Frenguelli. **(3)** *E. indica* var. *bigibba* Frenguelli. **(4)** *E. indica* var. *gracilis* Frenguelli.

Series 264: aquatic macrophytes, Estero del Carambola (lentic zone), near San Miguel town, Corrientes Province, Argentina. December 12th, 1923. 28°4'12"S, 57°24'36"W. Coll. J. Frenguelli. Slides 1–10 and raw material.
Series 265: aquatic macrophytes, Estero del Carambola, near Concepción town, Corrientes Province, Argentina. December 8th, 1923. 28°28'29"S, 57°49'46"W. Coll. J. Frenguelli. Slides 1–10 and raw material.
Series 266: aquatic macrophytes, Estero San Juan (between Chavarría and Concepción towns), Corrientes Province, Argentina. December 5th, 1923. 28°46'48"S, 58°12'36"W. Coll. J. Frenguelli. Slides 1–9 and raw material.
Of them, Series 261 (slides 7–8), Series 263 (slides 8–10), Series 264 (slides 8–10), Series 265 (slides 9–10), and Series 266 (slides 7–9) were newly prepared from unmounted raw materials.

Materials from Indonesia: Hustedt Collection: Raw material accession AS 1242, Insel Banka, Süsswasser, Grunow, Rabenhorst. Provided by courtesy of the Hustedt Arbeitsplatz, BRM, Bremerhaven (Hustedt Collection is presently housed at the Botanischer Garten und Botanisches Museum Berlin).

For all samples, raw materials were treated with hydrogen peroxide (H_2O_2), following the procedure outlined in CEN/TC 230 (2002). For light microscopy (LM) analyses, the cleaned materials were mounted in Naphrax to prepare additional permanent slides of materials from Iberá that were incorporated to the Frenguelli Collection, and also new slides of materials from the Hustedt Collection (slides 16654a and 16654b at LPC). The slides were analyzed using a Leica DM 500 microscope with phase contrast optics and equipped with a Leica ICC50 HD digital camera, and a Leica DM2500 microscope with DIC optics, equipped with a Leica DFC 420C digital camera. The specimens representing the selected lectotypes were referenced on the slides using an England Finder™ Graticule. For scanning electron microscopy (SEM) analyses, cleaned material was air-dried onto glass stubs and sputter-coated with gold-palladium. SEM observations were made with a Carl Zeiss NTS SUPRA 40 SEM at the Centro de Microscopías Avanzadas (CMA), Universidad de Buenos Aires, with a JEOL JSM-6360LV at the Servicio de Microscopía Electrónica del Museo de La Plata and with a Size Gemini SEM 360, Laboratorio de Microscopía Electrónica de Barrido del Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires). Terminology used for describing morphological features follows Round *et al.* (1990) and Lange-Bertalot *et al.* (2011).

Results

For the heading in the treatment of Frenguelli's taxa we used the accepted names and the original names given by him (Frenguelli 1933, 1941) were listed as synonyms. The morphometric data obtained from the specimens studied are summarized in Tables 1 and 2.

Eunotia indica Grunow 1865

Synonym: *Eunotia indica* var *ventralis* Grunow non *E. indica* Grunow sensu Frenguelli 1933 (Figures 5–16)

Description

LM (Figures 5–14): Valves asymmetrical to the apical axis. Ventral margin barely concave, slightly tumid in the middle in some specimens, and dorsal margin convex. Ends subcapitate clearly differentiated from the main body of the valve by a constriction of the dorsal margin. Apices rounded, curved to the ventral margin. Raphe barely extended from the ventral margin. Striae uniseriate, irregularly spaced and parallel over almost the entire length of the valve, occasionally alternating with shorter striae on the dorsal margin; near the apices striae become radiate and curved around the distal end of the raphe; striae composed of round areola.

SEM (Figures 15–16): The only specimen found under SEM was observed in internal view. Apices with a distinct pseudoseptum. Mantle with striae parallel composed of round areolae. Internal valve face areolae openings are round and are located in narrow troughs. Additionally, the specimen observed exhibited short dorsal striae variably extending onto the valve face. Due to the presence of detrital material that partially covers the valve, no details are visible regarding the internal raphe fissure and the presence of rimoportula. Valvocopula open at one pole, ornamented with rows of round poroids.

Morphometric data (n=6): length: 48.5–63.0 µm; width: 8.0–11.0 µm; striae in 10 µm: 9–11; areolae in 10 µm: 27–30.

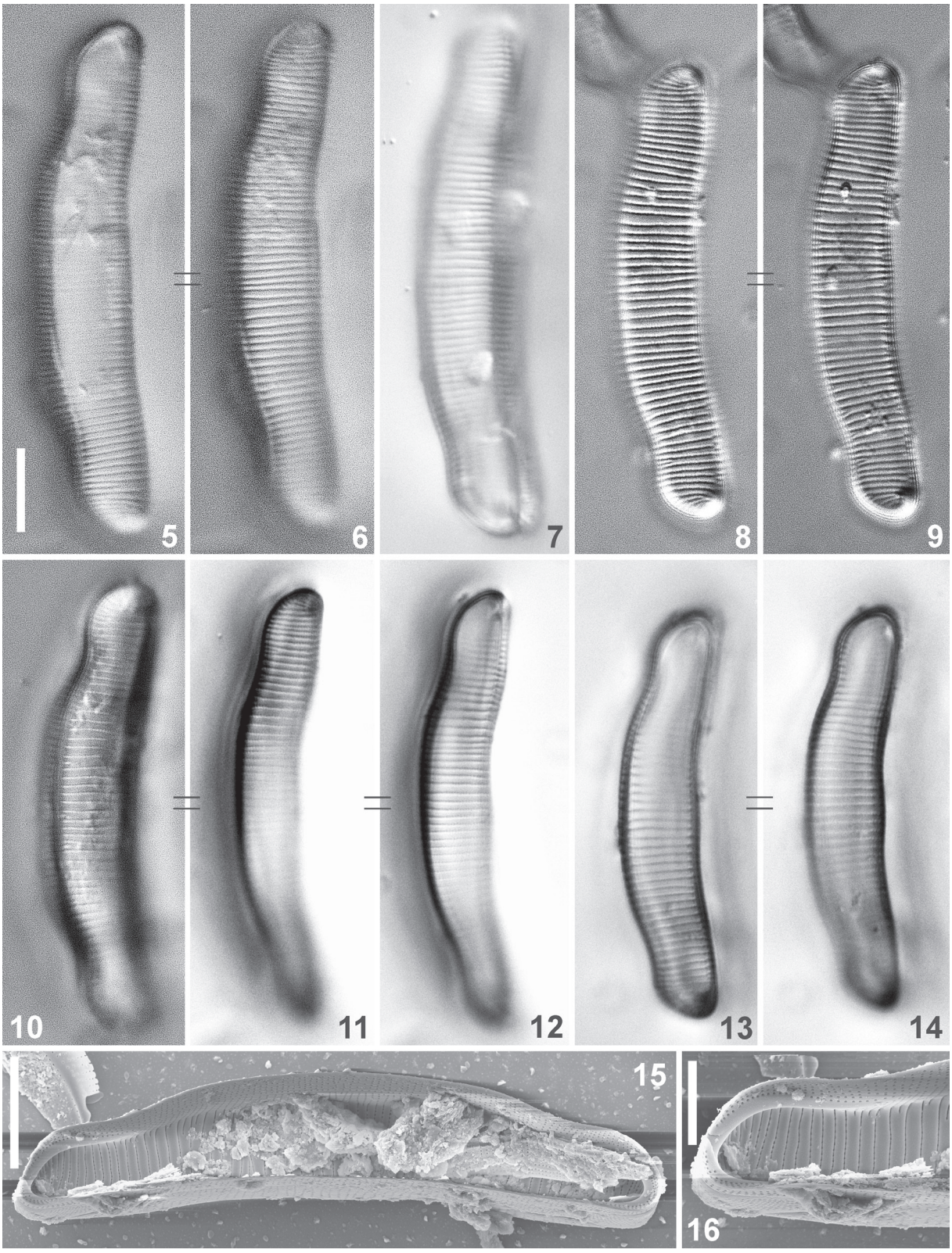
Remarks: The specimens in the original material of *Eunotia indica* we examined, with valves arcuate and ends subcapitate with round apices, fit quite well the original description and illustrations by Grunow (1865, Figures 7 a, b). Some valves have a slightly tumid ventral margin at the middle, conforming to what Grunow described as *E. indica* var. *ventralis* (Grunow 1865, Figure 7 c). This swelling is subtle and there is not a clear distinction between valves with ventral margin straight or swollen; it rather seems an expression of the range of variation within the analyzed population. The valves of the original material from Banka illustrated in Lange-Bertalot *et al.* (2011) are coincident in shape and morphometrics with the specimens we examined (Table 1); these authors included *E. indica var. ventralis* in the list of synonymies of *E. indica,* with which we agree.

Eunotia pseudoindica Frenguelli 1941

Synonym: *Eunotia indica* Grunow sensu Frenguelli 1933 (Figures 17–33)

Description

LM (Figures 17–26): Valves asymmetrical to the apical axis, ventral margin slightly concave and dorsal margin convex. Ends subcapitate, clearly differentiated from the main body of the valve by a constriction of the dorsal margin, Apices cuneate, curved to the ventral margin. Raphe extended half-way towards the dorsal margin; distal fissure absent, raphe endings surrounded by a hyaline area. Striae uniseriate, parallel over almost the entire length of the valve, slightly radi-



Figures 5–16. *Eunotia indica* Grunow. Specimens from sample AS 1242 (Hustedt Collection). **(5–14)** LM. Size decreasing series. **(15–16)** SEM. **(15)** Internal view of an entire valve. **(16)** Internal view of the valve apex. Scale bars 10 µm (5–16) and 3 µm (16).

Table 1. Morphometric data of *Eunotia pseudoindica* Frenguelli and allied taxa.

Taxon	Length (µm)	Width (µm)	Striae in 10 µm (centre)	Striae in 10 µm (apices)	Areolae in 10 µm	Reference
Eunotia pseudoindica Frenguelli	42.5–81.5	9.5–11.5	14–18	18–22	28–34	This study
	42.0–135.0	12.0–15.0	10–12	nd	nd	Frenguelli (1933)
Eunotia indica Grunow	51.0–74.0	9.5–12.0	12–16	nd	nd	Grunow (1865)
	38.0–100.0	8.8–11.0	10–13	15–16	30	Lange-Bertalot *et al.* (2011)
	48.5–63.0	8.0–11.0	9–11	nd	27–30	This study
Eunotia xystriformis Manguin	57.5–112.0	11.5–15.0	13–16	nd	nd	Bourrelly & Manguin (1952)
Eunotia platyvalva Burliga *et* Kociolek	70.7–127.0	9.4–12.1	18–20	21–23	35–40	Burliga & Kociolek (2012)
Eunotia helodesiana Kociolek *et* Burliga	42.4–97.0	9.5–13.3	18–20	20–22	32–36	Burliga & Kociolek (2012)
Eunotia monodontiforma Lange-Bertalot *et* Nörpel-Schempp	50.0–120.0	10.0–15.0	10–13	16	35	Rumrich *et al.* (2000)

nd: no data.

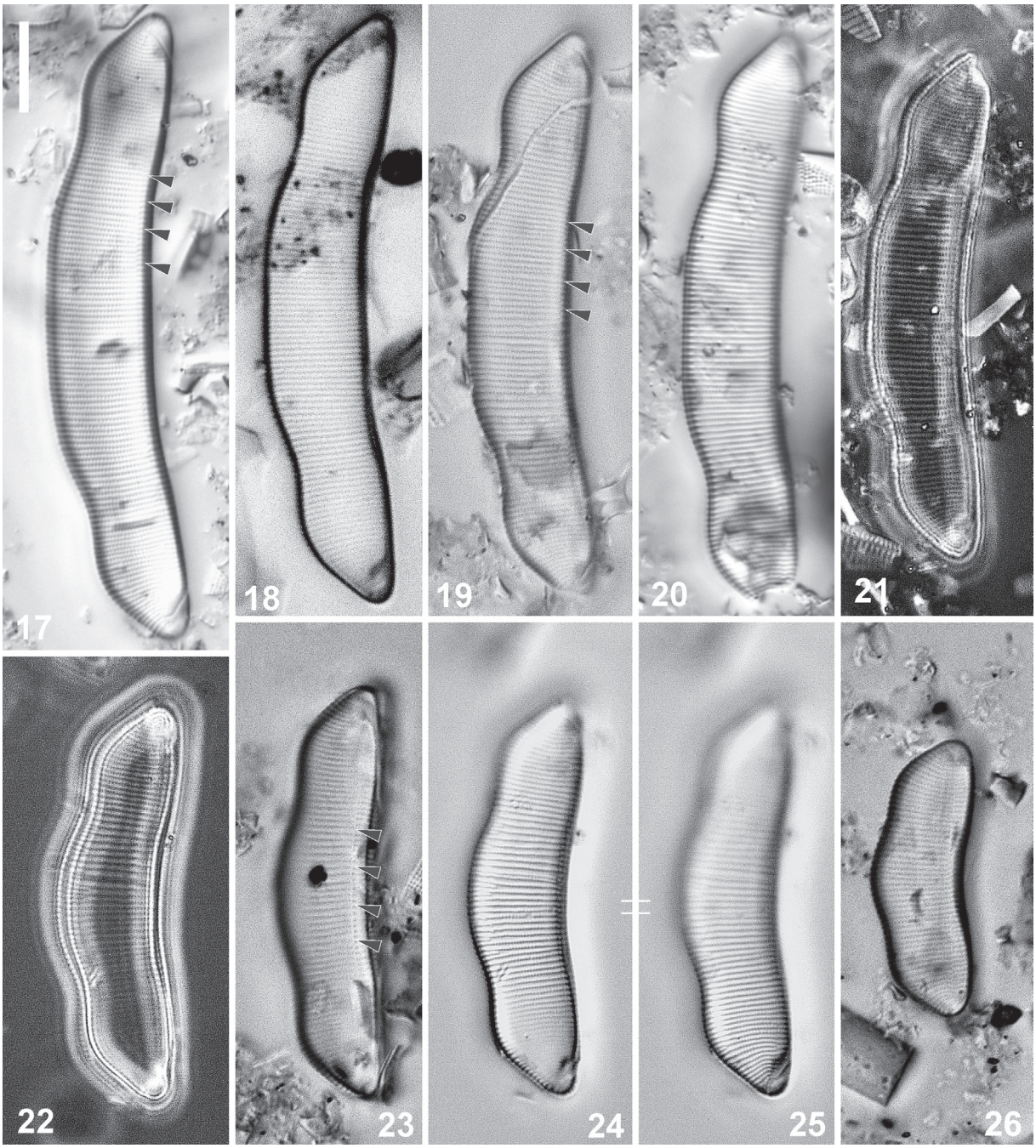
Table 2. Morphometric data of *Eunotia. indica* var. *bigibba* Frenguelli, *E. pseudoindica* var. *gracilis* (Frenguelli) Frenguelli and allied taxa.

Taxon	Length (µm)	Width (µm, centre)	Width (µm, maximum)	Striae in 10 µm (centre)	Striae in 10 µm (apices)	Areolae in 10 µm	Reference
Eunotia indica var. *bigibba* Frenguelli	35.5–89.5	8.0–11.5	9.5–13.0	12–16	14–18	24–28	This study
	57.0–129.0	12.0–14.0	nd	9–10	nd	nd	Frenguelli (1933)
Eunotia zygodon Ehrenberg	53.3	8.0*	10.0*	10–11	15–16*	24–26*	Reichardt (1995)
	43.0–54.5*	7.5–8.0*	9.5*	12–14*	17–18*	22–24*	Metzeltin & Lange-Bertalot (1998)
Eunotia pseudoindica var. *gracilis* (Frenguelli) Frenguelli	29.5–52.5	7.5–8.5	8.5–10.5	13–16	16–20	24–28	This study
Eunotia zygodon var. *gracilis* Hustedt	33.0–46.0	9.0	nd	12–13	nd	nd	Frenguelli (1933)
	52.5*	7.5*	10.5*	14*	22*	25–26*	Simonsen (1987)

nd: no data; *measured on the figures in the text.

ate in smaller specimens, and occasionally alternating with shorter striae on the dorsal margin; near the apices striae become radiate and curved around the distal end of the raphe. Areolae distinct. Near the ventral margin the striation pattern is discontinuous and forms a subtle, hyaline line parallel to the margin (Figures 17, 19, 23, arrowheads).

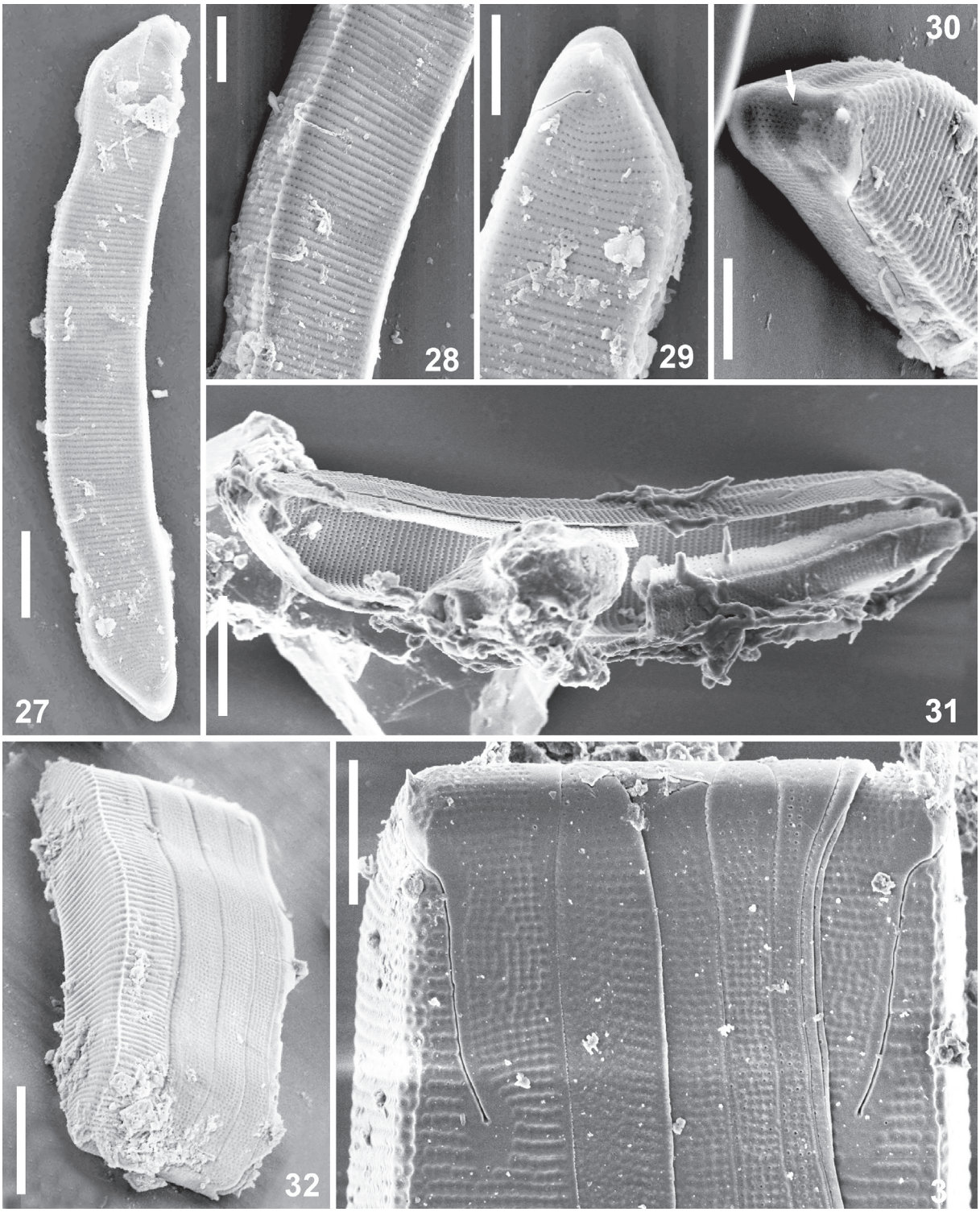
SEM (Figures 27–33): Frustules rectangular in girdle view. Valve face flat with a thin, irregular marginal ridge. A distinct conical spine located apically at the valve face/mantle junction. Striae composed of round, unoccluded areolae. Interstriae raised and thickened. Raphe branches short, mostly positioned on the ventral mantle; distal raphe endings simple, slightly expanded, without terminal fissure, located onto the valve face near the apices. One rimoportula per valve located at the apex; the external opening is a longitudinal slit located on the mantle; internal opening not observed. Mantle striae parallel; those beneath the raphe and around the apices more densely arranged and composed of smaller areolae. At least 4 open girdle bands, ornamented with parallel rows of small poroids.



Figures 17–26. *Eunotia pseudoindica* Frenguelli. LM. Size decreasing series. **(17–18, 22–26)** Specimens of Series 261 (type population). **(19–20)** Specimens of Series 264. **(21)** Specimen of Series 260. Specimen in Figure 17 represents the lectotype, note hyaline line parallel to the ventral margin (arrowheads in Figures 19, 23). Scale bar 10 µm.

Morphometric data (n=24): length: 42.5–81.5 µm; width: 9.5–11.5 µm; striae in 10 µm: 14–18 (at mid-valve), 18–22 (near the apices); areolae in 10 µm: 28–34; poroids on girdle bands: 28–32 in 10 µm. The specimens were found in series 261, 263, 264 and 266. **Lectotype (here designated)**: LPC Frenguelli Collection (Museo de La Plata, Buenos Aires, Argentina) Slide 261(2), represented by the specimen in Figure 17 (Finder N31/4).

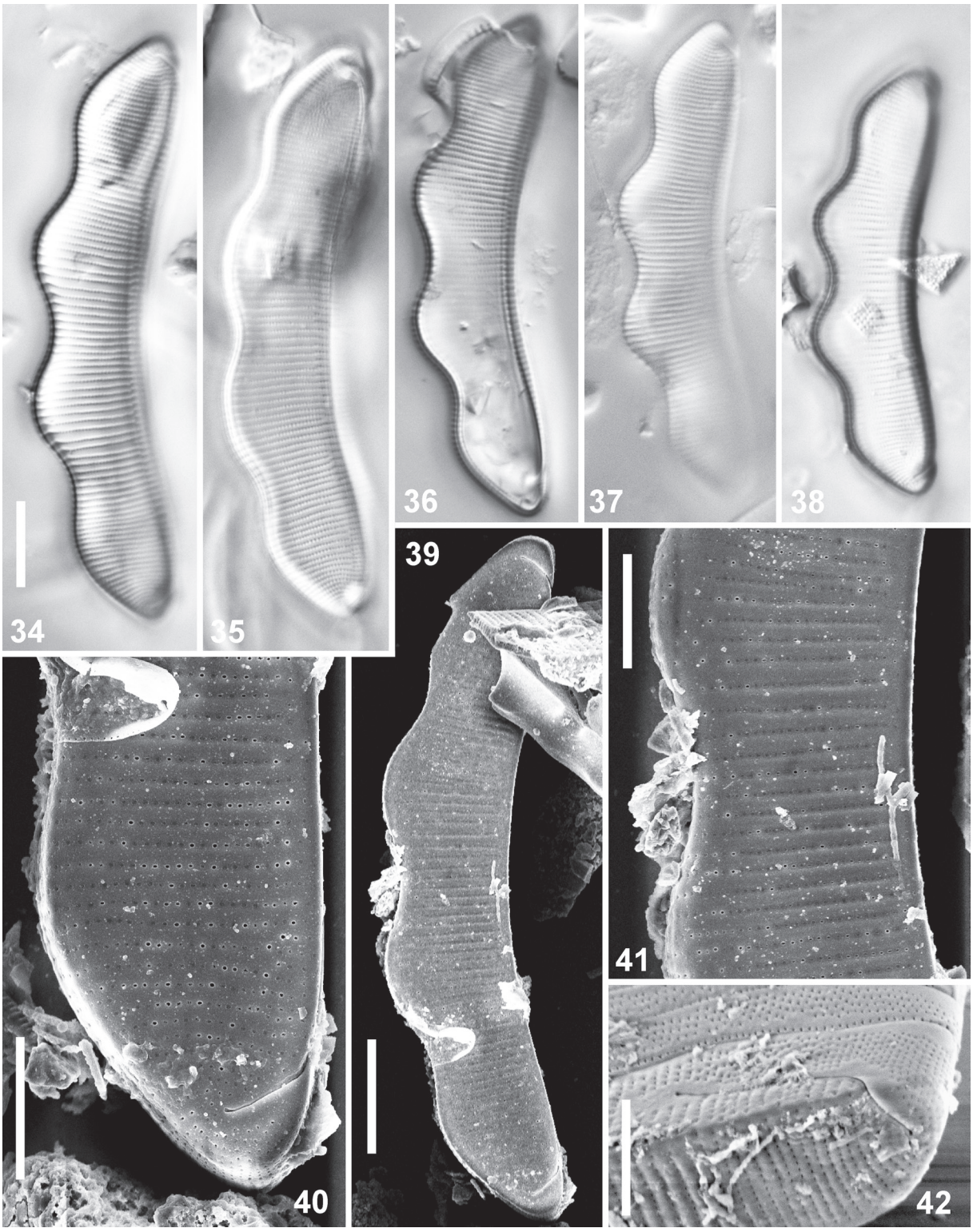
Remarks: The specimens of *Eunotia pseudoindica* (originally reported as *E. indica*) from Iberá can be clearly distinguished from those of *E. indica* by their valve outline, with apices distinctly cuneate rather than rounded and ventral margin concave, not swollen at the middle, thus supporting the distinction between both taxa made by Frenguelli (1941). The analysis with SEM also revealed that valves of *E. pseudoindica* have a dorsal ridge and apices with a distinct, conical spine, which are not revealed under LM. Since under SEM we found in the original material of *E. indica* only one valve in internal view, we could not confirm the



Figures 27–33. *Eunotia pseudoindica* Frenguelli. SEM. Specimens of type population. **(27–30, 32–33)** External views. **(27)** Entire valve. **(28)** Detail of mid-valve showing striae and dorsal marginal ridge. **(29)** Detail of valve apex showing distal raphe ending and spine. **(30)** Tilted view of the valve apex showing spine. Note longitudinal external opening of the rimoportula (arrow). **(31)** Internal view of an entire valve. **(32)**. Dorsal girdle view of a frustule. **(33)** Detail of the frustule apex in girdle view showing the mantle raphe branches, spine and girdle bands. Scale bar 10 µm (27, 31–32); 5 µm (28–30, 33).

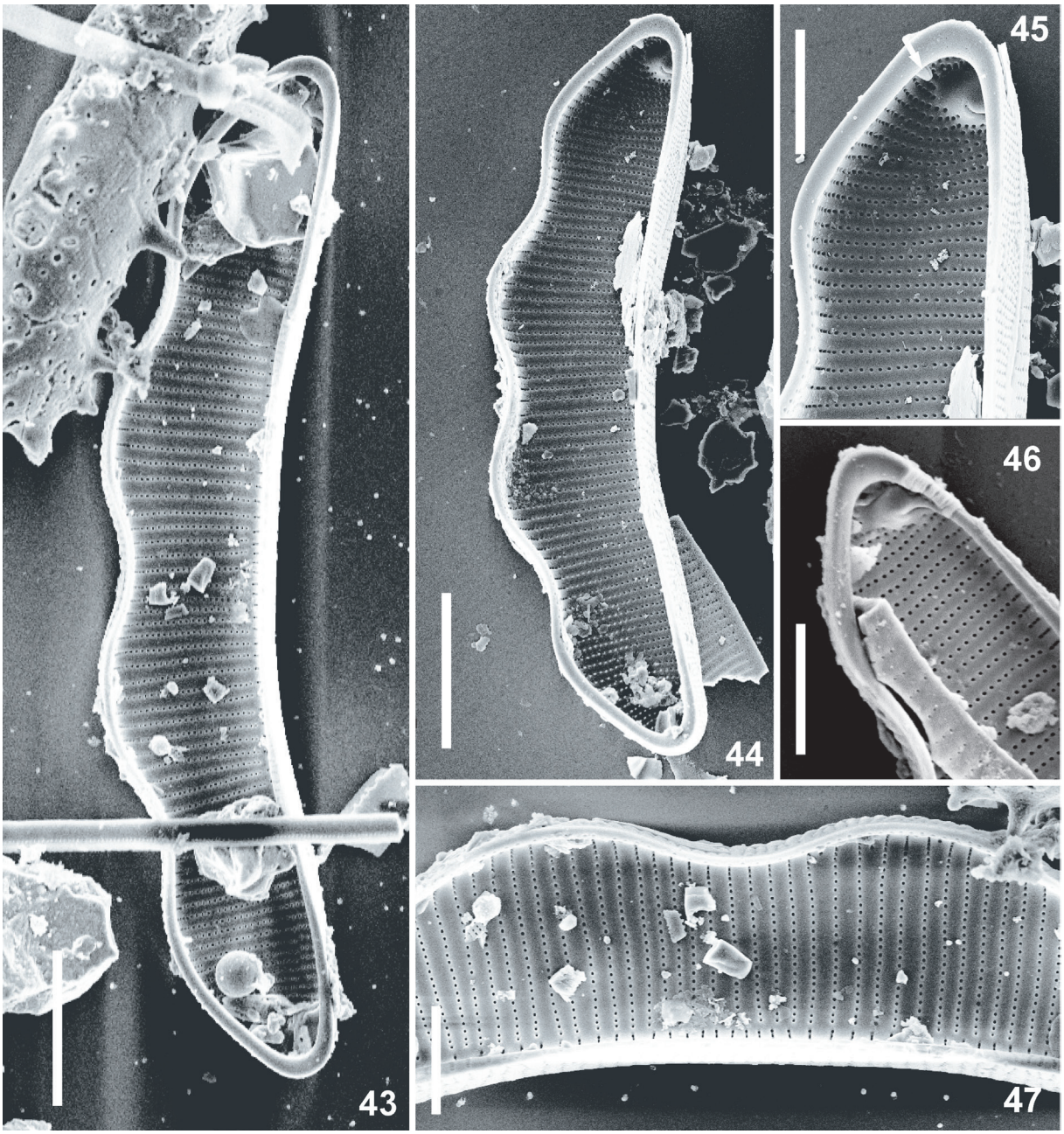
presence/absence of such features in the latter species. However, the presence of pseudosepta in *E. indica* and the lack of this structure in *E. pseudoindica* allow a further differentiation of both taxa.

When describing *E. pseudoindica*, Frenguelli (1941) linked this diatom to the complex of varieties within *E. zygodon,* a species described by Ehrenberg (1843) from French Guiana. Comparing to the LM image of the lectotype specimen illustrated in Reichardt (1995, pl. 1, Figure 16), both taxa have similar shape



Figures 34–42. *Eunotia zygodon* Ehrenberg (=*Eunotia indica* var. *bigibba* Frenguelli). **(34–38)** LM. Size decreasing series. Specimens of Series 265. **(34–38)** LM. Size decreasing series. **(39–42)** SEM. External views. **(39)** Entire valve. **(40)** Detail of valve apex showing striae and distal raphe ending. **(41)** Detail of mid-valve. **(42)** Tilted view of a frustule apex showing raphe and mantle areolation. Scale bar 10 µm (34–39); 5 µm (40–42).

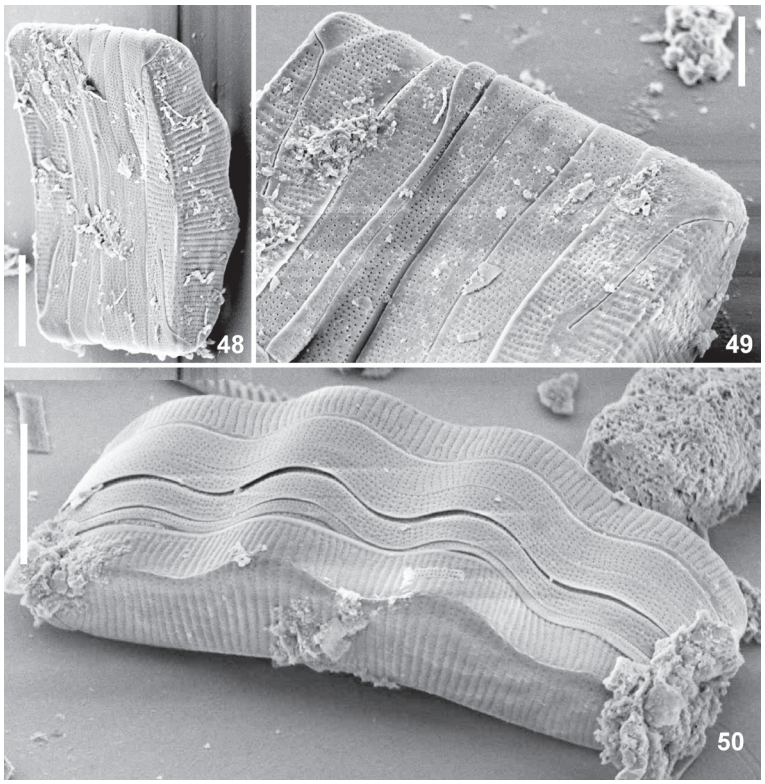
of valve apices and striation pattern, but they differ in valve outline since *E. zygodon* has two prominent humps in the dorsal margin. Lange-Bertalot (1993, pl. 25, Figures 1–3) examined with SEM specimens of *E. zygodon* found in fossil materials from Florida (USA); compared to the type specimens of *E. pseudoindica* both taxa have similar distal raphe endings but beyond the different valve outline, the former species lacks conical spines at valve apices, its valve margin is not ornamented with an irregular ridge and interstriae are



Figures 43–47. *Eunotia zygodon* Ehrenberg (=*Eunotia indica* var. *bigibba* Frenguelli). SEM. Internal views. **(43–45, 47)** Specimen of Series 264. **(46)** Specimen of Series 260. **(43–44)** Entire valves. **(45–46)** Details of valve apex showing the helictoglossae. Note internal opening of the rimoportula in Figure 45 (arrow). **(47)** Detail of mid-valve showing striation pattern. Scale bar 10 µm (43–44); 5 µm (45–47).

not elevated. These differences allow us to conclude that both taxa are not conspecific. *Eunotia pseudoindica* shows resemblance to several species described from tropical or subtropical American environments (the comparison of morphometric data of all these allied taxa are summarized in Table 1). *E. xystriformis* Manguin (in Bourrelly & Manguin, 1952, p. 49) reported from Brazil (Costa *et al.*, 2017) closely resembles *E. pseudoindica* morphometrics and presence of apical spines but they differ in overall valve shape, mainly in the outline of the valve apices, which are round instead of cuneate in the former species. These differences are more pronounced when compared with the original specimens from Guadeloupe illustrated in Metzeltin & Lange-Bertalot (2007, Figures. 64: 1–7), including one of the original illustrations of Bourrelly & Manguin (1952).

Other *Eunotia* species bearing apical spines are *E. platyvalva* Burliga et Kociolek (2012, p. 63) and *E. helodesiana* Kociolek *et* Burliga (in Burliga & Kociolek, 2012, p. 65), both described from Brazilian Amazonia. Compared to *E. pseudoindica*, valves of *E. platyvalva* are generally longer, with apices rounded and more protracted, and with higher stria and areola densities. *E. helodesiana* differs from *E. pseudoindica* in its valve outline, apices rounded and higher stria



Figures 48–50. *Eunotia zygodon* Ehrenberg (= *Eunotia indica* var *bigibba* Frenguelli). SEM. External girdle views. Specimens of Series 260. SEM. External girdle views. **(48, 50)** Entire frustules. **(49)** Detail of the apex showing mantle raphe branches and girdle bands ornamented with parallel rows of small poroids. Scale bar 10 µm (48, 50); 5 µm (49).

density at mid-valve. Valves of *E. monodontiforma* Lange-Bertalot et Nörpel-Schempp (Rumrich *et al.*, 2000, p. 121), described from Laguna Negra (Venezuela), shows similar ranges of morphometric parameters to those of *E. pseudoindica*, and also have raised interstriae and a somewhat spiny ridge at the dorsal margin; however, in the former species apices are rounded instead of cuneate, apical spines are lacking and distal raphe fissures reach the dorsal margin whereas in *E. pseudoindica* they terminate in a pore half-way between the dorsal and ventral margins.

Eunotia zygodon Ehrenberg (Figures 34–50)

Synonym: *Eunotia indica* var. *bigibba* Frenguelli 1933
= *Eunotia pseudoindica* var. *bigibba* (Frenguelli) Luchini *et* Verona 1972

Description

LM (Figures 34–38): Valves asymmetrical to the apical axis, ventral margin concave and dorsal margin convex and 4-undulated. Ends subcapitate, clearly differentiated from the main body of the valve by a constriction of the dorsal margin, apices cuneate. Striae uniseriate and irregularly spaced, parallel over almost the entire length of the valve; near the apices striae become radiate, more densely arranged and curved around the distal end of the raphe. Areolae round, distinguishable with LM.

SEM (Figures 39–50): Frustules rectangular in girdle view. Valve face flat. Striae composed of round areolae. Interstriae raised and thickened. Raphe branches short, mostly positioned on the ventral mantle; distal raphe endings simple, slightly expanded and without terminal fissure, located onto the valve face near the apices. Internally the raphe terminates in small helictoglossae. One rimoportula per valve located at the apex, the internal opening is located on the dorsal mantle; the external opening was not observed. Mantle striae parallel, intercalated with shorter striae near the valve margin; striae beneath the raphe and around the apices more densely arranged and composed of smaller areolae. At least 4 open girdle bands, ornamented with parallel rows of small poroids.

Morphometric data (n= 45): length: 35.5–89.5 µm; width: 8.0–11.5 µm (at mid-valve); 9.5–13 µm (at humps); striae in 10 µm: 12–16 (at mid-valve), 14–18 (near the apices); areolae in 10 µm: 24–28; poroids on girdle bands: 20–24 in 10 µm. The specimens were found in series 261, 263, 264 and 265.

Lectotype of *Eunotia indica* var. *bigibba* Frenguelli 1933 (here designated): LPC Frenguelli Collection (Museo de La Plata, Buenos Aires, Argentina) Slide 265(3), represented by the specimen in Figure 34 (Finder N/40-1).

Remarks: In the original description of *Eunotia pseudoindica* var. *bigibba* Frenguelli (1933) distinguished it from the nominate variety mainly by its valve outline, characterized by the presence of two humps on the dorsal margin, and by the apices less distinctly cuneate. SEM images obtained in this study also revealed differences in their fine morphology such as the lack of spines at the apices, lack of marginal costae and lower density of poroids on girdle bands. On the other hand, valves of this variety are strongly reminiscent of that of

the lectotype specimen of *E. zygodon* illustrated in Reichardt (1995, pl. 1, Figure 16), a species described by Ehrenberg (1843) from French Guiana. Both taxa are similar in valve outline and dimensions (Table 2) and only differ slightly in the stria density: 10–11 in 10 µm in *E. zygodon* vs 12–16 µm in var. *bigibba* (according to our measurements, although Frenguelli reports for the latter 9–10 striae in µm). Despite the subtle difference in stria count between Frenguelli's variety and the lectotype of *E. zygodon*, it is not possible to separate both taxa and therefore we propose they are conspecific. Reinforcing this idea, Frenguelli's materials also agree in valve outline and morphometrics with those specimens from Amazonia reported as *E. zygodon sensu stricto* by Metzeltin & Lange-Bertalot (1998, pl. 37, Figures 1–4) (Table 2), who explicitly mentioned that they compared their specimens with the lectotype image in Reichardt (1995).

***Eunotia hustedtii nom. nov. et stat. nov.* Guerrero *et* Vouilloud (Figures 51–56)**

Synonym: *Eunotia zygodon* var *gracilis* Hustedt in Schmidt 1913, pl. 287, Figure 10 ex Simonsen 1987

= *Eunotia pseudoindica* var. *gracilis* (Frenguelli) Frenguelli 1941

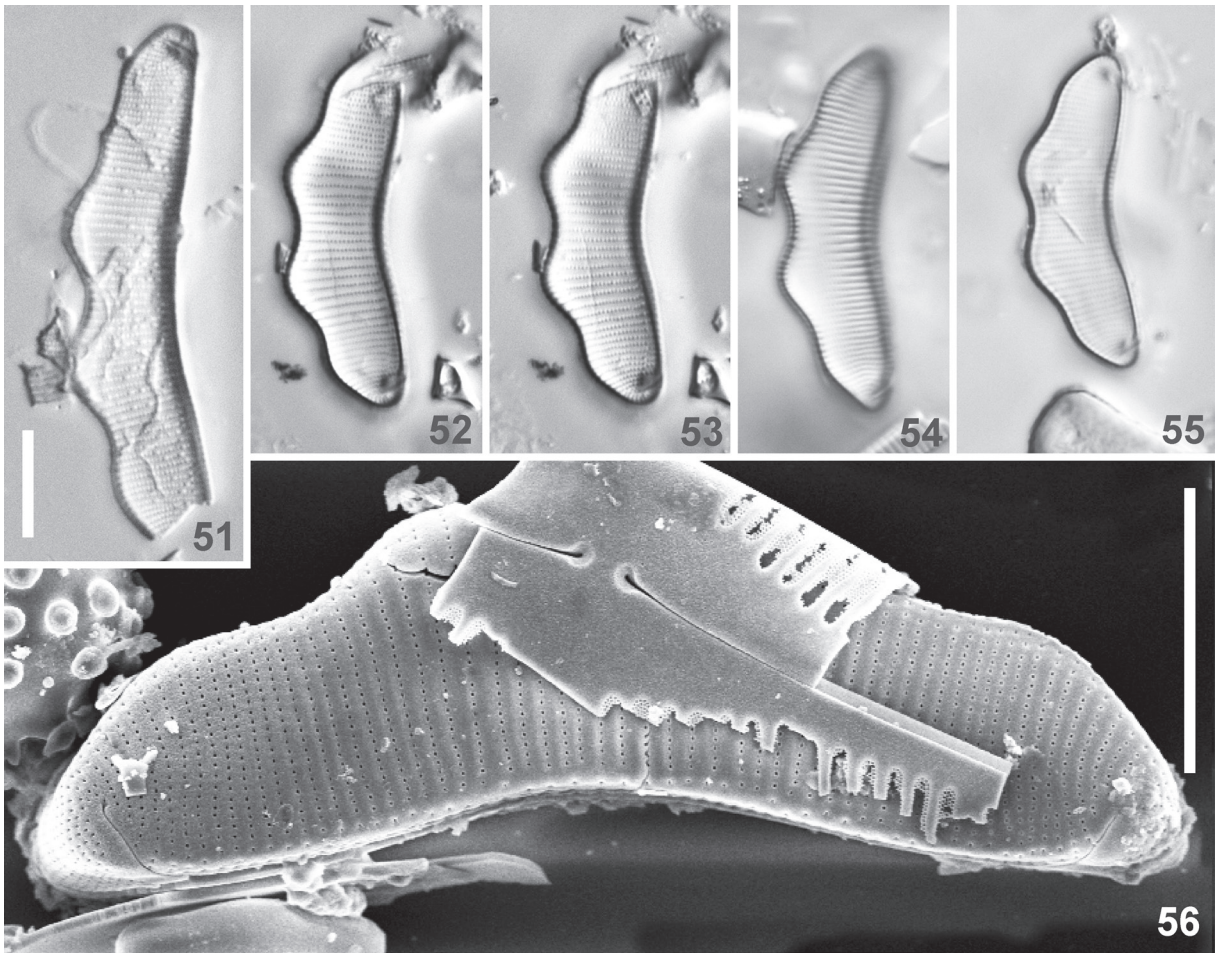
= *Eunotia indica* var. *gracilis* Frenguelli 1933

Description

LM (Figures 51–55): Valves asymmetrical to the apical axis, ventral margin concave and dorsal margin convex and undulated, with two humps. Ends protracted, slightly differentiated from the main body of the valve by a subtle constriction of the dorsal margin. Apices rounded to cuneate. Striae uniseriate and regularly spaced, parallel over almost the entire length of the valve; near the apices striae become radiate, more densely arranged and curved around the distal end of the raphe. Areola round, distinct in LM.

SEM (Figure 56): Valve face flat. Striae composed of round areolae. Raphe branches short, mostly positioned on the ventral mantle; distal raphe endings simple, slightly expanded and without terminal fissure, located onto the valve face near the apices. No internal valve views could be obtained.

Morphometric data (n= 9): length: 29.5–52.5 µm; width: 7.5–8.5 µm (at mid-valve); 8.5–10.5 µm (at humps); striae in 10 µm: 13–16 (at mid-valve); 16–20 (near the apices); areolae in 10 µm: 24–28. The specimens were found in series 261, 263, 264 and 265.



Figures 51–56. *Eunotia hustedtii nom. nov. et stat. nov.* Guerrero & Vouilloud (= *Eunotia indica* var *gracilis* Frenguelli). **(51–55)** LM. Size decreasing series. **(51)** Specimen of Series 263. **(52–54)** Specimens of Series 265 (type population). **(55)** Specimen of Series 261. Specimen in Figure 54 represents the lectotype. **(56)** SEM. External view of an entire valve. Specimen of Series 265 (type population). Scale bar 10 µm.

Lectotype (here designated): LPC Frenguelli Collection (Museo de La Plata, Buenos Aires, Argentina) Slide 265(3), represented by the specimen in Figure 54 (Finder N/38-1).

Remarks: Simonsen (1987) provided a Latin diagnosis to validate Hustedt's variety. According to the original description by Frenguelli (1933), valves of *Eunotia indica* var. *gracilis* are smaller and slender and have humps relatively more prominent than var. *bigibba*. Later, Frenguelli (1941) introduced the new combination *E. pseudoindica* var. *gracilis* and proposed *Eunotia zygodon* var. *gracilis* described by Hustedt (in Schmidt 1913) from Guyana to be a synonym. In their study of the tropical diatoms from South America, Metzeltin & Lange-Bertalot (1998) considered *E. zygodon* var. *gracilis* and *E. pseudoindica* var. *gracilis* as synonyms of *E. zygodon*. Even though we agree that both varieties should be considered the same taxon, the presence of two central humps more clearly differentiated contrasting the rather 4-undulate dorsal margin in *E. zygodon*, leads us to propose the elevation of var. *gracilis* to the rank of species. Since the epithet "*gracilis*" is not available, we named the species in honor of the German diatomist Friedrich Hustedt (1886–1968).

Discussion

Of the four taxa examinated in this study, only *E. indica* is not present in Iberá. This species was originally described from South Asia (Indonesia) and considered cosmopolitan. Reports from other regions of the world including Argentina are doubtful and consequently should be viewed with caution.

Eunotia pseudoindica has been reported exclusively from different regions of South America having a neotropical distribution. Besides the records from Argentina (type locality and Río de la Plata estuary), *E. pseudoindica* has been found in Colombia (Sala *et al.* 2002) and has been frequently reported from Brazil (Bicca, 2007; Bicca *et al.*, 2011; Canani *et al.*, 2011; Costa *et al.*, 2017; Souza-Mousiman *et al.*, 2011; Tremarin *et al.*, 2008; Wetzel, 2011).

Eunotia hustedtii has been recorded -as *E. zygodon* var. *gracilis*- at several sites in Argentina and Brazil.

Eunotia zygodon is a worldwide reported species (Guiry & Guiry, 2025) which shows a wide range of valve dimension and outline (Costa *et al.*, 2017; Taylor *et al.*, 2016; Wetzel, 2011; among others). Even Frenguelli (1933) reported this taxon from Iberá but these specimens do not match the type material shown in Reichardt (1995). All the above mentioned suggest the need of a critical revision of this purported cosmopolitan taxon.

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