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## *Cocconeis neuquina* Frenguelli (Bacillariophyta): emended description, lectotypification, ecology, and geographical distribution

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In this article, we examine the type material of *Cocconeis neuquina* Frenguelli from the type locality in Neuquén province and other samples in southern Santa Cruz province (Patagonia, Argentina). *Cocconeis neuquina* is a small species with an oval-subcircular to broadly elliptical valve outline. The sternum valve is externally convex, striae are radiate and uniseriate, and areolae are rounded towards the mantle. The raphe valve is externally concave, the raphe is straight and filiform, striae are uniseriate, slightly radiate, and the first areola close to the mantle is drop-shaped. With this contribution we aim to clarify the morphology of this species, provide a more detailed description of valve ultrastructure, present its lectotypification and extend its geographical distribution.

**Keywords:** Bacillariophyceae, Cocconeis, diatoms, freshwater, Patagonia, South America

### Introduction

The genus *Cocconeis* Ehrenberg contains benthic, monoraphid diatoms with intricately ornamented valves and elaborate, functionally complex girdle bands (Kobayasi and Nagumo 1985, Round et al. 1990, De Stefano & De Stefano 2005, De Stefano & Romero 2005). The identification of monoraphid diatoms like *Cocconeis* is challenging. Over the past 20 years many new taxa have been described from different regions (e.g. Al-Handal et al. 2010, Riaux et al. 2010, Romero & Riaux-Gobin 2014). However, few studies have re-examined the type material of species and varieties of *Cocconeis*, and most of these have been published recently (Jahn et al. 2009, Romero & Riaux-Gobin, 2014, Riaux et al. 2016). Nevertheless, there is still a lot of work to be done on revising species and varieties of *Cocconeis*, which also applies to *C. neuquina* Frenguelli.

Joaquín Frenguelli (1883–1958) was the first scientist methodically and rigorously researching diatoms in Argentina, publishing 64 works, geographically distributed throughout the country. Between 1918 and 1953, he described 421 new taxa (2 genera, 183 species, 211 varieties, and 25 formae) in 38 papers (see Sar et al. 2009). Frenguelli's diatom collection is hosted at the Facultad de Ciencias Naturales y Museo (La Plata, Argentina), and can be considered the starting point for studying the diatom flora from the southern South America.

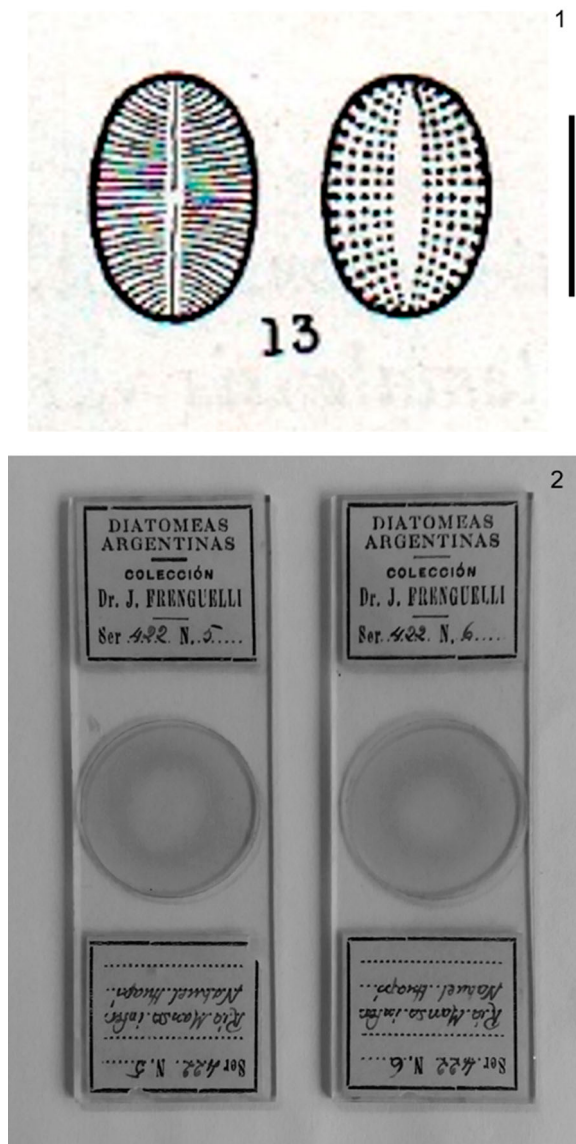
Frenguelli (1942: 97, plate 1, Fig. 13) reported three *Cocconeis* taxa (*Cocconeis placentula* Ehrenberg, *C. placentula* var. *euglypta* (Ehrenberg) Cleve and the new species *C. neuquina*) growing on the aquatic plant *Myriophyllum* sp. (Saxifragales, Haloragaceae) and mosses in the Manso River waterfall (circa 41° 22' S, 71° 44' W, Neuquén Province, near the southern shore of Lake Mascardi). He mentioned that this small *Cocconeis* species occurs in one of the two sites he sampled (Lake Mascardi and a meltwater spring from a snowdrift near the Copahué volcano), in which he found the majority of the new species he described from Neuquén.

Regarding diatom biodiversity, the Patagonian province of Santa Cruz remains a poorly known territory, with few studies combining the study of diatom assemblage composition and environmental characteristics. There are several works on its modern and fossil diatom floras (e.g. Krasske 1949, Luchini 1976, Maidana et al. 2005, Messyasz et al. 2007, and Recasens et al. 2010) but none of these studies from Santa Cruz mention Frenguelli's *C. neuquina* as part of the diatom communities. However, it has been reported for other provinces in Argentina: Chubut (Luchini 1974), San Luis (Maidana 1994a), and Río Negro (Luchini 1973, Maidana 1994b).

While analysing lacustrine surface sediments of southern Santa Cruz for ongoing palaeolimnological studies,

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**Figs 1–2.** *Cocconeis neuquina* Frenguelli in Frenguelli (1942, plate 1, Fig. 13). Fig. 1. Original drawings of RV and SV by J. Frenguelli. Scale bar = 10  $\mu\text{m}$ . Fig. 2. Slides n° 5 and 6, Series 422, from the Frenguelli Collection, Rio Manso, Neuquén, Argentina.

*C. neuquina* was found in the shallow lake Laguna Huergo. Using light (LM) and scanning electron microscope (SEM), we examined the population from Laguna Huergo and materials containing *C. neuquina* (Figs 1, 2) held in Frenguelli's collection to corroborate our preliminary identification. Our results allowed us to corroborate the taxonomic status of *C. neuquina*, provide an emended description of the species, and extend its biogeography. As Frenguelli only provided a brief description and an iconotype (1942: 97; plate 1, fig. 13), but no specific accessioned slides or material, a lectotype is also proposed.

## Materials and methods

Studied samples are: (a) Slides n° 5 and 6, and dry oxidized material of Series 422 (Manso River, Neuquén province, Argentina) deposited in the Frenguelli collection (Museo de Ciencias Naturales, La Plata, Argentina) and (b) LPC 15255 surface sediments from Laguna Huergo (Santa Cruz, Argentina, 51° 44' 38" S, 72° 4' 2" W) collected by dragging in 2013.

The sediment sample from Laguna Huergo was dried at 80°C, then oxidized with H<sub>2</sub>O<sub>2</sub> (30%, 100 Vol.), heating in a microwave oven for two minutes, in order to eliminate organic matter. Afterwards, samples were rinsed repeatedly with distilled water to neutrality. Permanent slides, labelled as HUE-2013, were mounted using Naphrax® and deposited in the Frenguelli collection (LPC 15255, Museo de Ciencias Naturales, La Plata, Argentina).

LM observations were performed at Laboratorio de Diatomeas continentales, using a Reichert-Jung Polivar binocular light microscope equipped with a PlanApo 100X, NA 1.32, immersion objective, DIC optics, and a Canon EOS 600D digital camera. For SEM observations, aliquots of the cleaned material were dried on aluminium stubs at room temperature before being coated with gold (20 nm thickness) and examined using a Carl Zeiss SUPRA 40 (15 kv) at the Centro de Microscopías Avanzadas (CMA) (FCEyN, Universidad de Buenos Aires, Argentina).

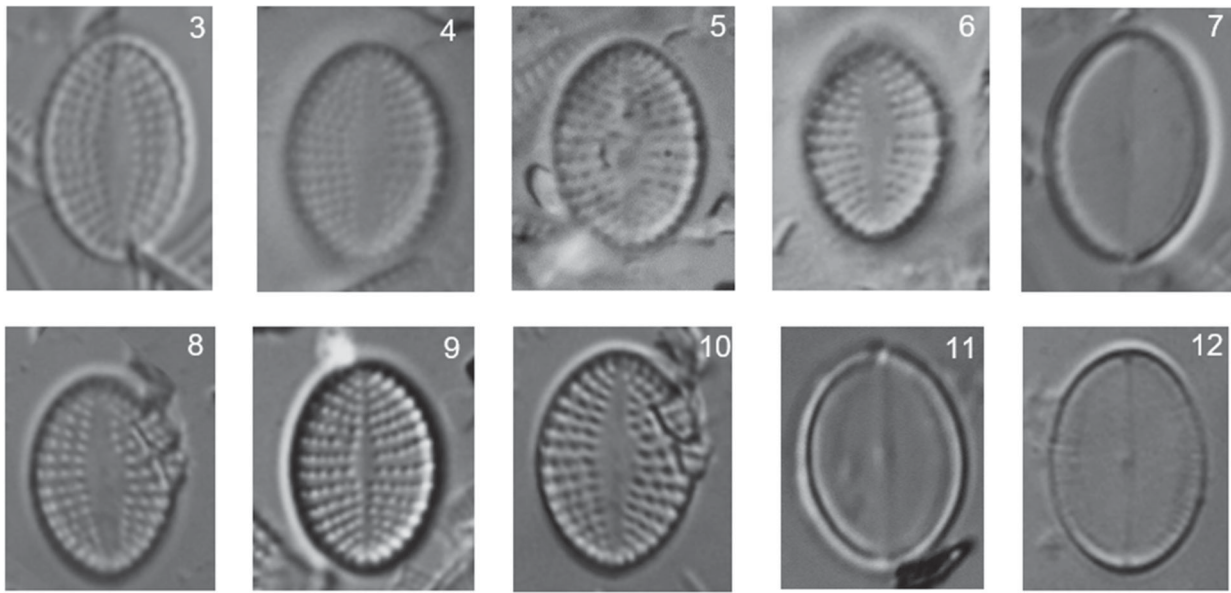
The general terminology used for the frustule description followed that of Anonymous (1975) and Ross et al. (1979). We followed the terminology proposed by Riaux-Gobin et al. (2016) to designate the valve with a raphe as the raphe valve (RV) and the valve without a raphe as the sternum valve (SV).

## Results

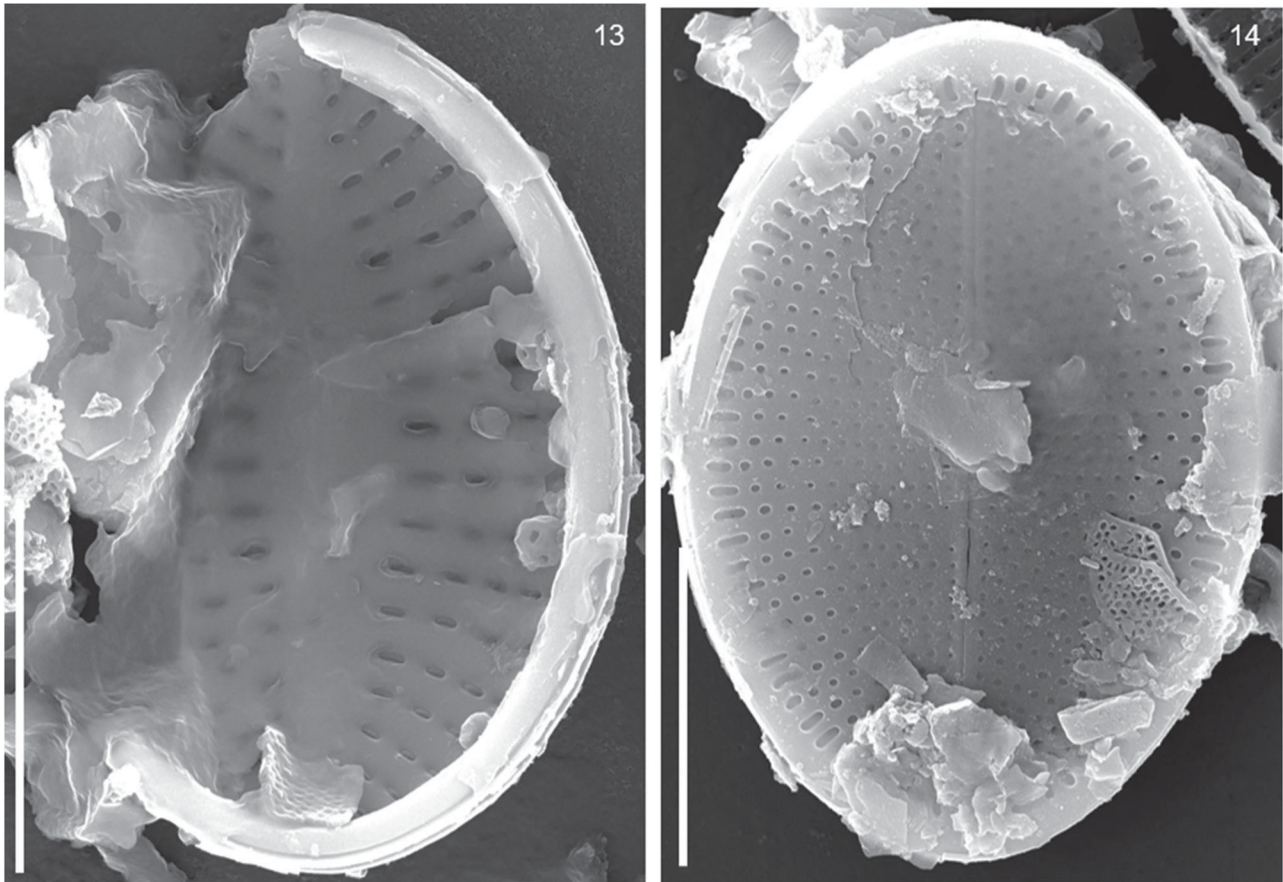
In his original publication, Frenguelli (1942: 97; plate 1, fig. 13, here reproduced in Fig. 1) provided a brief Latin diagnosis and drawings of both RV and SV:

Parva; valvis ovalibus, 13–16  $\mu$  longis et 9–11  $\mu$  latis; valve superiori striis 12–13 in 10  $\mu$ , grosse granulates, ad marginem validioribus, pseudorhaphae lineari-lanceolata; valve inferiori striis 20–22 in 10  $\mu$ , delicatas, raphae filiformi recta, area longitudinali anguste lineari circa nodulum centrali haud dilatata.

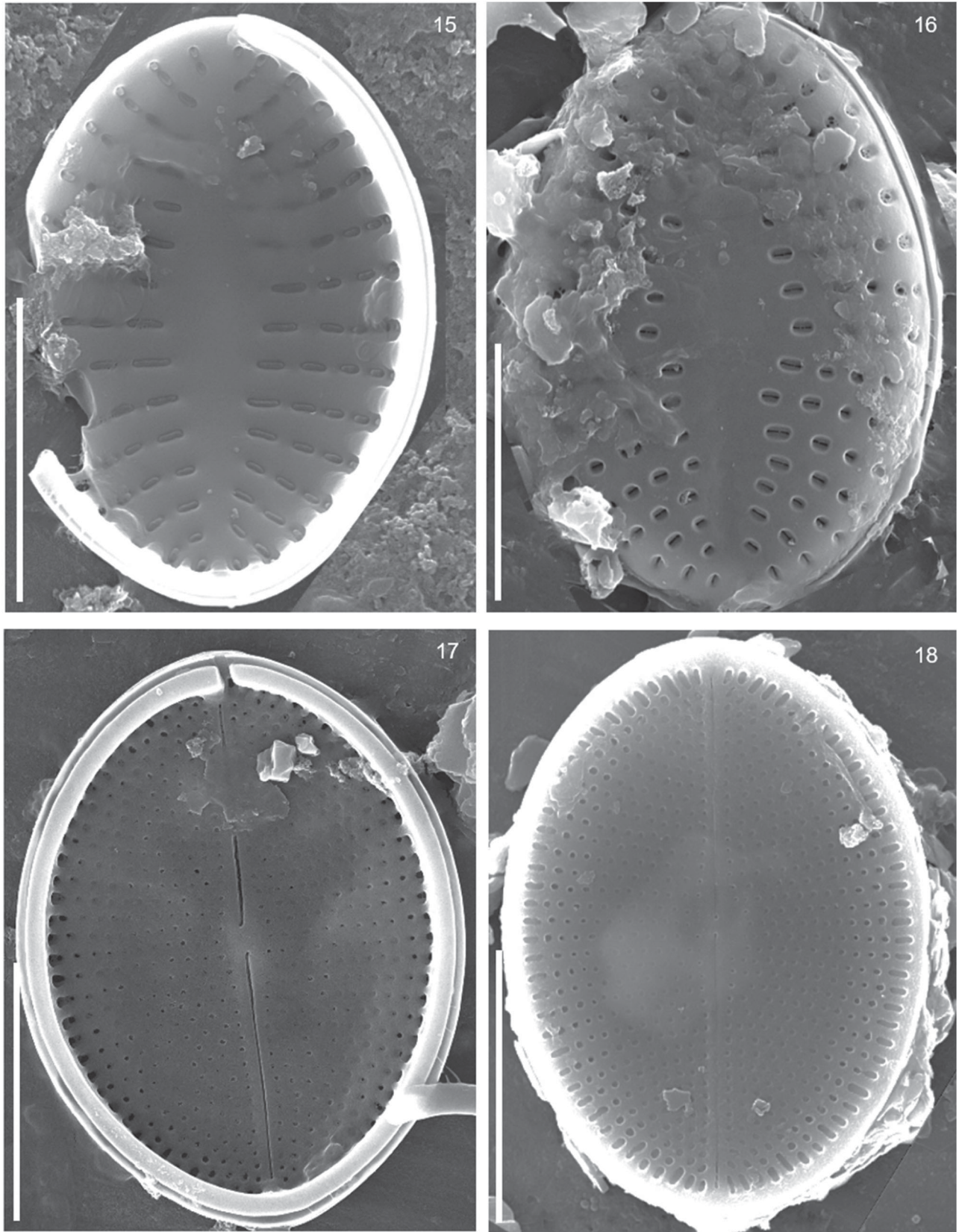
This can be translated as: Small; oval valves, 13–16  $\mu\text{m}$  long and 9–11  $\mu\text{m}$  wide; striae in the upper valve (= SV) 12–13 in 10  $\mu\text{m}$ , coarsely granulated, larger at the margins, pseudoraphe linear-lanceolate; striae in the lower valve (= RV) 20–22 in 10  $\mu\text{m}$ , delicate; straight and filiform raphe, narrow linear axial area, quite large around the central nodule.



**Figs 3–12.** LM images of *Cocconeis neuquina* Frenguelli. Figs 3–7. Valves found in slides n° 5 and 6, Series 422, from the Frenguelli Collection. Figs 3–6. Sternum valves (Fig. 3. Lectotype, Slide n° 6, Series 422). Fig. 7. Raphe valve Lectotype (Slides n° 6, Series 422). Figs 8–12. Valves found in Laguna Huergo (Acc. No. LPC 15255) Figs 8–10. Sternum valves. Figs 11–12. Raphe valves. Scale bar = 10  $\mu$ m.



**Figs 13–14.** SEM images of *Cocconeis neuquina* Frenguelli (type, dry oxidized, material of Series 422). Fig. 13. Internal view of the SV. Fig. 14. External view of the RV. Scale bar = 5  $\mu$ m.



**Figs 15–18.** SEM images of valves of *Cocconeis neuquina* found in Laguna Huergo, Santa Cruz, Argentina (Acc. No. LPC 15255). Fig. 15. Internal view of SV. Figs 16. External view of SV. Fig. 17. Internal view of RV, with an open valvocopula. Fig. 18. External view of RV. Scale bars = 5  $\mu$ m.

**Examination of *C. neuquina* (type material)**

**LM:** Figs 3–7. Valves ( $n = 16$ , means  $\pm$  SD) are 9.8–12.5 ( $11.1 \pm 0.7$ )  $\mu\text{m}$  long, 7.4–8.6 ( $7.5 \pm 0.4$ )  $\mu\text{m}$  wide, with 10–16 ( $12 \pm 1.5$ ) SV striae in 10  $\mu\text{m}$ , and 28–30 ( $29 \pm 1.4$ ) RV striae in 10  $\mu\text{m}$ . Valves delicate, oval-elliptical. SV is recognizable by the prominent areolae, axial area is linear-lanceolate. RV was rare, its areolae are not distinguishable under LM, raphe is straight.

**SEM:** Figs 13–14, 19. Diatoms are very abundant in the studied type material, although it was difficult to find *C. neuquina* since their valves are small, and no unbroken and/or clean valves were found. The few valves found showed that SV areolae are transapically elongate, RV areolae are rounded almost throughout the striae, while the areolae closest to the margin are drop-shaped.

**Examination of *C. neuquina* (Laguna Huergo)**

**LM:** Figs 8–12. Valves ( $n = 56$ ) are 8.54–14 ( $10.6 \pm 0.6$ )  $\mu\text{m}$  long, 6.2–10.2 ( $7.8 \pm 0.6$ )  $\mu\text{m}$  wide, with 10–20 ( $12 \pm 2.2$ ) SV striae in 10  $\mu\text{m}$ , and 26–34 ( $30 \pm 4.8$ ) RV striae in 10  $\mu\text{m}$ . Valves oval-elliptical. SV with prominent areolae, axial area varies from linear to lanceolate. RV very delicate, raphe is straight. The short advalvar fimbriae of both RV and SV valvocopulae are indistinguishable with LM.

**SEM:** Figs 15–18, 20–26. SV areolae are internally occluded with perforations and transapically elongated. The RV areolae are rounded to subcircular, the first areola next to the mantle is drop-shaped. Internal raphe proximal endings are slightly deflected in opposite directions while externally they are drop-shaped. The terminal raphe endings are straight with subtle helictoglossae. The valvocopulae of both RV and SV are open and possess short advalvar fimbriae.

Diatom abundance in Frenguelli's material from lake Mascardi (Series 422, slides n° 5 and 6° and dry material) is very high. However, *C. neuquina* is scarce (mentioned as rare by Frenguelli 1942: 77). We were able to obtain only a few images with LM and SEM. Under LM and SEM the specimens found in Laguna Huergo were identical to those found in Frenguelli's collection. Based on this morphological similarity, we use the Laguna Huergo material to illustrate details such as the proximal and terminal endings, areolae, and the open fimbriate valvocopulae. As shown in Table 1, the morphometric data of both populations overlap. We propose that the smaller specimens found in Laguna Huergo (8.5–14  $\mu\text{m}$  in length  $\times$  6.2–10.2  $\mu\text{m}$  in width) represent the lower part of the size variation. Based on this observation, therefore, we broaden the size range of *C. neuquina* valves to 8.5–16  $\mu\text{m}$  in length, 6.2–11  $\mu\text{m}$  in width.

Since no specimen was designated as holotype by Frenguelli, we selected an SV and RV specimen of *C.*

*neuquina* in one of the Frenguelli's slides as the lectotype (SV Fig. 3 and RV Fig. 7). The valves from Laguna Huergo are morphologically closest to the description and illustrations given by Frenguelli (1942, plate 1, fig. 13) and identical to *C. neuquina* once analysed with electron microscopy. Therefore, we propose the Laguna Huergo material as paralectotype of *C. neuquina*.

**Emended diagnosis of *C. neuquina***

*Cocconeis neuquina* Frenguelli Figs 3–12 (LM); Figs 13–26 (SEM)

**Iconotype:** Frenguelli (1942): XVII Contribución de las diatomeas argentinas. Diatomeas del Neuquén (Patagonia), plate 1, fig. 13. Revista del Museo de La Plata (n. s.) 5, Botánica 20: 73–219.

**Lectotype (designated here):** Manso River, Neuquén province, Argentina, Frenguelli's collection (Museo de Ciencias Naturales, La Plata, Argentina), Slide n°6, Series 422, here represented by Figs 3, 7).

**Isolectotype:** Manso River, Neuquén province, Argentina, Frenguelli's collection (Museo de Ciencias Naturales, La Plata, Argentina), Slide n° 5.

**Paralectotype:** Laguna Huergo, Santa Cruz province, Argentina, Frenguelli's collection (Museo de Ciencias Naturales, La Plata, Argentina), Acc. No. LPC 15255.

**Type locality:** Rio Manso, Neuquén province, Argentina

**Description**

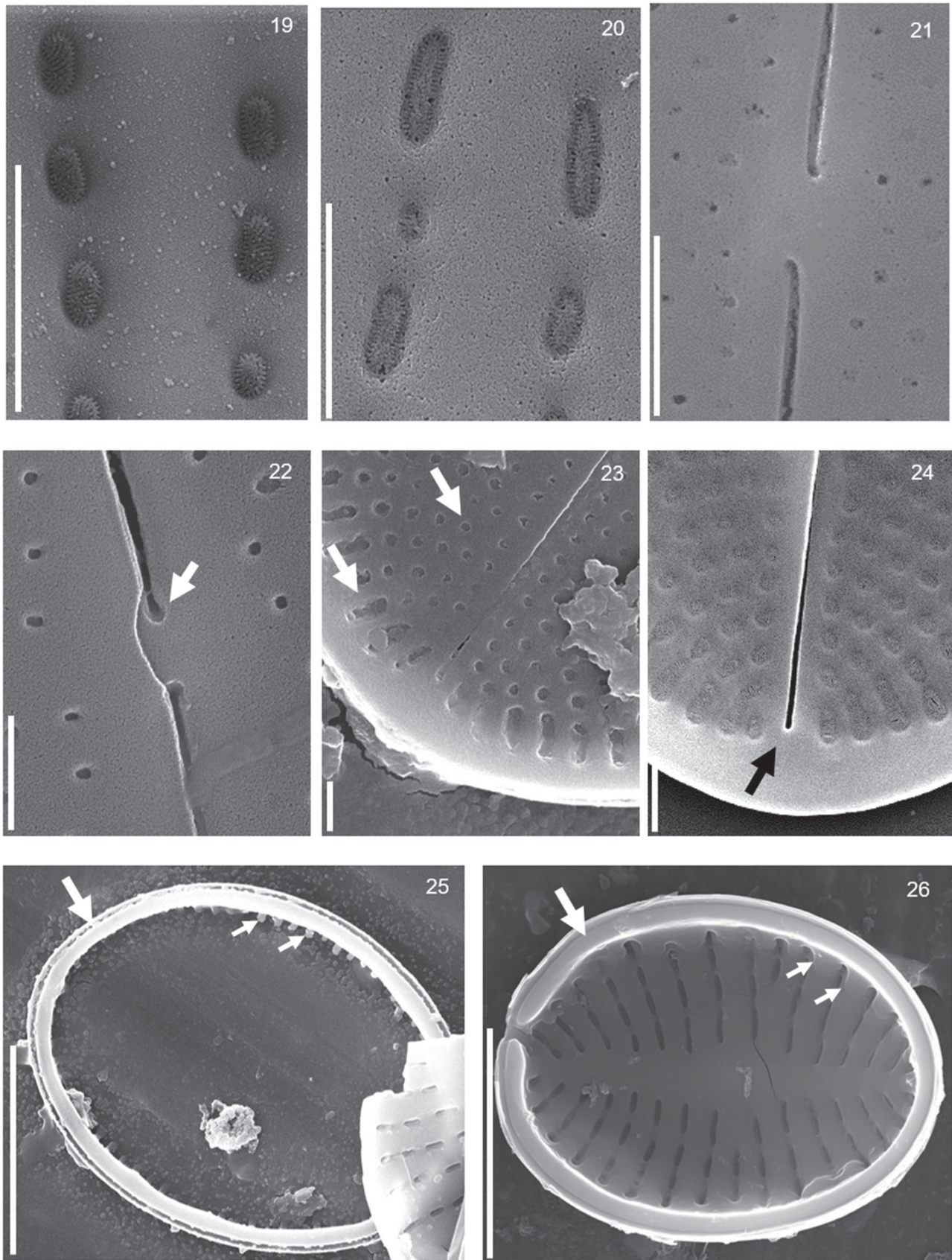
Valve outline ranges from oval-subcircular to broadly elliptical (Figs 3–12). SV externally convex (Figs 13, 15–16). Striae radiate and uniseriate, more distant around the central area in some specimens. Areolae are internally occluded by hymenes with linear perforations (Figs 19–20), more rounded towards the mantle and transapically elongated towards the sternum, with two to five areolae on each hemi-valve, easily distinguishable in LM (Figs 3–6, 8–10). Axial area is linear-lanceolate. The RV is externally concave, with a straight, filiform raphe (Figs 14, 18). Internally, the proximal raphe fissures are slightly deflected in opposite directions (Fig. 21) and externally they are drop-shaped (Fig. 22). Distal raphe endings are straight, distant from the margin (Fig. 23), with subtle helictoglossae (Fig. 24). Striae are uniseriate, slightly radiate, with the first areola close to the mantle drop-shaped, and circular to subcircular towards the valve centre (Figs 14, 18, 23). Both valves have open valvocopulae with short advalvar fimbriae (Figs 25, 26).

**Dimensions:** Length: 8.5–16  $\mu\text{m}$ ; width: 6.2–11  $\mu\text{m}$ ; striae: SV: 10–20 in 10  $\mu\text{m}$ , RV: 20–34 in 10  $\mu\text{m}$ ; areolae: SV: 16–20 in 10  $\mu\text{m}$ , RV: 30–40 in 10  $\mu\text{m}$ .

**Table 1.** Morphometry and morphology of *Cocconeis neuquina* and comparison with some morphologically related *Cocconeis* species.

References		<i>C. neuquina</i> Frenguelli		<i>C. neothu-</i> <i>mensis</i>	<i>C. pseudothu-</i> <i>mensis</i>	<i>C.</i> <i>neodiminuta</i>
		This study	Frenguelli (1942)	Krammer & Lange-Bertalot (1991)	Reichardt (1982)	Krammer & Lange-Bertalot (1991)
Sternum valve	Length (µm)	8.5–14	13–16	6.5–13.0	11.5–13.5	8–18
	Width (µm)	6.2–10.2	9–11	4.0–8.3	8.2–9.5	6–9
	Valve outline	Oval-elliptical	Oval-elliptical	Elliptical-lanceolate	Broadly elliptical	Broadly elliptical
	Striae/10 µm	10–20	12–13	16–25	10–20	11–14
	Areolae	transapically elongated to rounded near the margin	transapically elongated to rounded near the margin	transapically elongated	transapically elongated	transapically elongated
	Areola occlusion	Internally occluded by hymenes with perforations	Internally occluded by hymenes with perforations	n.d	n.d	n.d
	Axial area	Narrow to lanceolate	Linear to lanceolate	Narrow to broadly lanceolate	Elliptic to lanceolate	Linear to lanceolate
Raphe valve	Central area	Not differentiated	Not differentiated	Not differentiated	Linear	Not differentiated
	Valvocopula	Open on one end	Open on one end	Absent	n.d	n.d
	Fimbriae	Advalvar, short	Advalvar, short	n.d	n.d	n.d
	Striae/10 µm	26–34	20–22	28–36	35–40	24–32
	Areolae/10 µm	35–40	30	34–37	10–20	25–32
	Raphe	Filiform straight	Filiform straight	Straight, filiform	Delicate, straight filiform	Straight, filiform
	Proximal raphe endings	Internal: slightly curved in opposite directions.External: drop-shaped	n.d	Delicate, closely located to each other	Closely located to each other	Small, closely located to each other
	Terminal raphe endings	Straight, well-separated from the margin, subtle helictoglossa	n.d	Small	n.d	Difficult to observe with LM
	Central area	Narrow, linear	Narrow, linear	Elliptical	Elliptical	Elliptical
	Valvocopula	Open on one end	n.d	Narrow	n.d	Narrow
Fimbriae	Advalvar, short	n.d	Short	n.d	n.d	
Ecology	Freshwater lakes, wetlands	Freshwater	Freshwater, lakes	Wet mosses, also fossil	Epyphytic, tycho- planktonic, lacustrine	
Distribution	Laguna Huergo, Santa Cruz, Argentina	Rio Manso, Neuquén, Argentina	Possibly cosmopolitan	France, Germany, Switzerland	Germany, Switzerland, Ireland	

Note: n.d = no data.



**Figs 19–26.** SEM details of the valves of *Cocconeis neuquina* Frenguelli. Fig. 19. Internal view. Detail of the SV areolae (type material, Serie 422). Figs 20–26. Specimens from Laguna Huergo (Acc. No. LPC 15255). Fig. 20. Internal view. Detail of the SV areolae. Fig. 21. Detail of the internal view of the proximal raphe ending, bent in opposite directions. Fig. 22. Detail of the external view of the drop-shaped, proximal raphe ending (arrow). Fig. 23. Detail of the external view of the terminal raphe ending and the different-shaped central and marginal areolae on the RV (arrows). Fig. 24. Detail of the internal view of the terminal raphe ending, with a low-raised helictoglossa (arrow). Fig. 25. RV valvocopula with short fimbriae (arrows). Fig. 26. Open valvocopula with short fimbriae (arrows) still attached to the SV. Scale bars = 500 nm (Figs 19–24); 5  $\mu$ m (Figs 25, 26).



### Ecology and distribution

*Cocconeis neuquina* was originally found growing on mosses in a waterfall, without any other environmental information. Nevertheless, Frenguelli (1942: 89) suggested this could be the habitat preferred by his new species.

In addition to the high abundance of *C. neuquina* in epibenthic samples of Laguna Huergo, this species was reported from other lakes and lagoons in the same area of Santa Cruz province (Lago del Desierto, Laguna Cóndor and Laguna Capri). Echazú (2012) reported specimens of this taxon as *Cocconeis* sp. 1 (Echazú 2012, fig. 3: 12–18; fig. 35: 5–6). In these shallow lakes, *Cocconeis* sp. 1 contributes between 3% and 18% of the entire diatom community. These shallow Patagonian lakes are characterized by circumneutral to alkaline pH (6.37–8.85), a wide range of temperatures and conductivity (1.7°–16.4°C; 37–1390  $\mu\text{S cm}^{-1}$ ). As noted by Frenguelli (1942) *Myriophyllum* sp. is also present in the shore area of all mentioned lakes.

The diatom flora of Laguna Huergo is dominated by *Amphora pediculus* (Kützing) Grunow, *Karayevia clevei* (Grunow) Bukhtiyarova, *Cyclotella ocellata* Pantocsek and small fragilarioid species. *C. neuquina* was also found in lake sediments (Maidana *et al.* 2005), where *Discostella stelligera* (Cleve & Grunow) Houk & Klee and *C. placentula* Ehrenberg were dominant species.

As it has already been reported for three Argentinian provinces (San Luis, Rio Negro, Chubut), we extend the geographical range of *C. neuquina* to the Santa Cruz province.

### Discussion

*Cocconeis neuquina* can be included in the group of small *Cocconeis* species (*Cocconeis neodiminuta* Krammer, *Cocconeis neothumensis* Krammer, and *Cocconeis pseudothumensis* Reichardt), which share similar overall morphology and show some overlap in their valve morphometry (Table 1).

Frenguelli (1942) noted that the SV of *C. neuquina* resembles that of *C. diminuta* Pantocsek (1902: 67, plate 7: fig. 181, plate 17: fig. 374, non Hustedt 1930) but is markedly different from the RV valve. Hustedt's (1930: 190, fig. 265) drawings of the diatom he identified as *C. diminuta* Pantocsek differ from those provided by Pantocsek (1902) and from *C. neuquina*, because the illustrated valves by Hustedt are more elliptical in outline. Krammer & Lange-Bertalot (2004, plate 56, figs 1–13, 18–32) illustrated *C. neodiminuta* Krammer (probably *C. diminuta*) and *C. disculus* (Schumann) Cleve, both clearly different from *C. neuquina*. The size of some specimens found in Laguna Huergo overlaps with that of *C. neodiminuta* and *C. neothumensis* (Table 1), however, the valve outline of *C. neuquina* is more elliptical, and the SV has a more linear axial area. In addition, *C. neodiminuta* has larger areolae

and higher areola density than the other species. *C. neothumensis* has crescent-shaped areolae, none of them similar to those of *C. neuquina* (Figs 19, 20)

Under LM, the general appearance of the SV and RV of *C. neuquina* is similar to those of *C. pseudothumensis* (Krammer & Lange-Bertalot 2004, fig. 56: 14–17, type material). However, the axial area of the SV of *C. pseudothumensis* is broader and elliptic-lanceolate (E. Reichardt, pers. comm), rather than linear-lanceolate as in *C. neuquina*. Romero & Van de Vijver (2011) stated that the striae of *C. pseudothumensis* are composed of only three areolae, which is not the case for *C. neuquina* (Figs 13–18). Additionally, SEM images of the SV of *C. pseudothumensis* in British rivers (provided by Round & Bukhtiyarova 1996, fig. 8) are completely different from *C. neuquina* (both the type material and the Laguna Huergo population). The striae of the *C. pseudothumensis* RV are only visible at the margins, as in *C. neuquina*. However, the RV of *C. neuquina* is more delicate and bears almost indistinguishable striae.

The valvocopula fimbriae of *Cocconeis* sensu lato are strongly variable in shape and insufficient observations have been published for the smallest *Cocconeis* species. Krammer & Lange-Bertalot (2004) observed that the RV valvocopula of *C. neodiminuta* has fimbriae with a row of poroids ('Porenreihe'), which are absent in *C. neuquina*. They also mentioned that *C. neothumensis* fimbriae are visible with LM (Krammer & Lange-Bertalot 2004), while fimbriae of *C. neuquina* are only visible with SEM (Figs 25, 26). Fimbriae of *C. pseudothumensis* are described as of the first order (typical elliptical outline and fimbriate margins, although no illustration was presented (Krammer & Lange-Bertalot 2004). Specimens of *C. neuquina* have open valvocopulae with simple, short, unornamented fimbriae in both valves (Figs 25–26).

The lack of observations on the valve ultrastructure of some small *Cocconeis* species makes it difficult to properly identify them. Although studying type material is time consuming, it is important to understand the actual concept of a taxon, in order to avoid misidentifications that lead to inaccurate ecological or palaeoecological interpretations. In conclusion, this study clarifies the taxonomy and morphology of the small, epiphytic *C. neuquina*, which is widely distributed in Patagonian lakes of Argentina.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.

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