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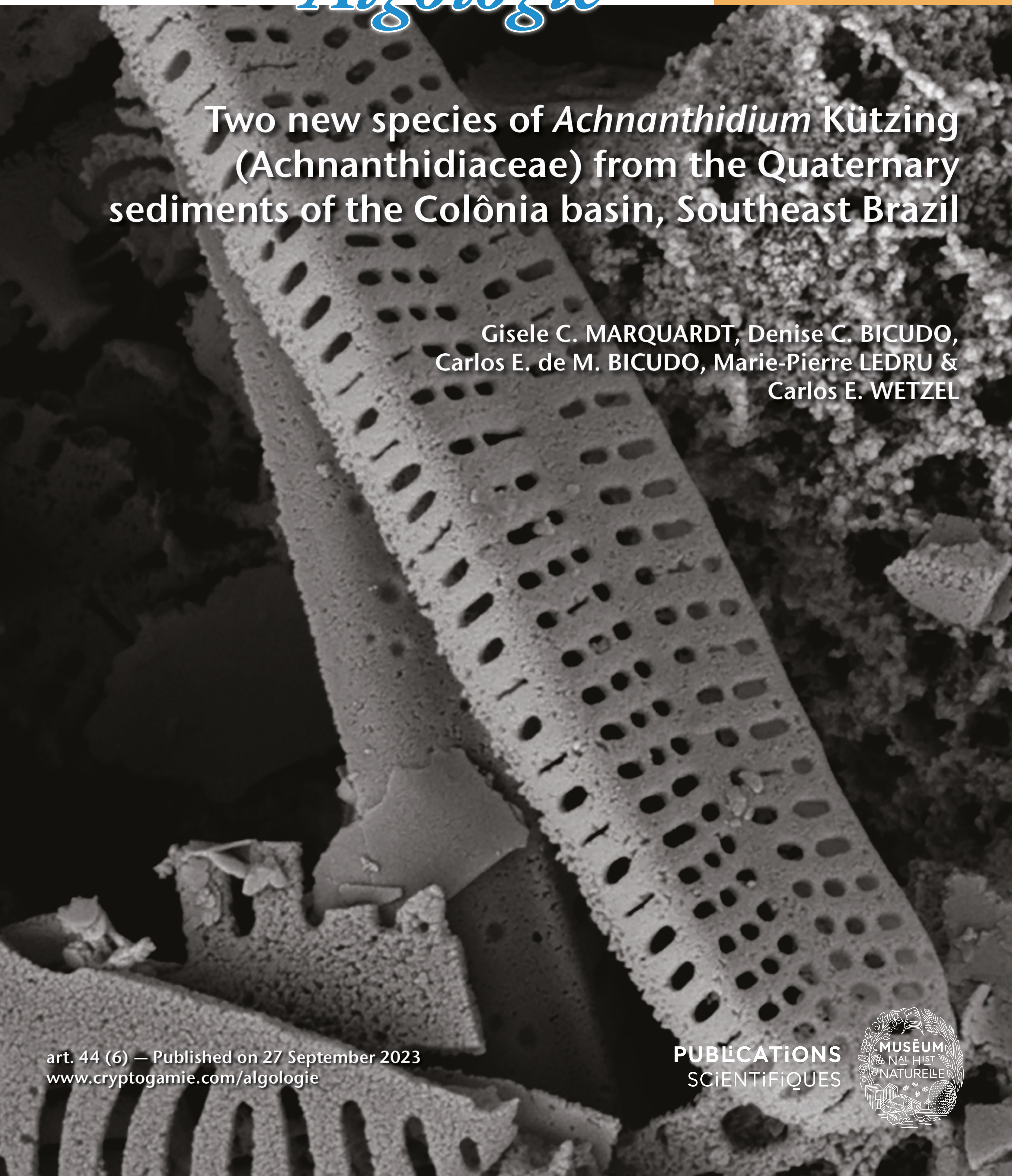

Two new species of *Achnanthidium* Kützing (Achnanthidiaceae) from the Quaternary sediments of the Colônia basin, Southeast Brazil

Gisele C. MARQUARDT, Denise C. BICUDO, Carlos E. de M. BICUDO, Marie-Pierre LEDRU & Carlos E. WETZEL

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Two new species of *Achnanthidium* Kützing (Achnanthidiaceae) from the Quaternary sediments of the Colônia basin, Southeast Brazil

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ABSTRACT

This research uses the techniques of light and scanning electron microscopy to observe two species of *Achnanthidium* Kützing belonging to the *A. minutissimum* '*sensu lato*' complex, collected from the Pleistocene sediments of the Colônia basin, Southeast Brazil. We compared *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. and *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. to their morphologically closest species, revealing different valve outlines, valve apices shapes, central areas, and raphe structures. Our results help to enlarge the taxonomic knowledge on the genus in South America, which is fundamental for a better understanding of the diatom distribution and diversity patterns in poorly studied areas. Our research also improves the current knowledge on the evolution of the paleolake in the Colônia basin (São Paulo) since the early Pleistocene.

KEY WORDS
Brazil,
diatoms,
Bacillariophyceae,
Achnanthidium,
morphology,
ultrastructure,
new species.

RÉSUMÉ
*Deux nouvelles espèces d'*Achnanthidium *Kützing (Achnanthidiaceae) provenant des sédiments quaternaires du bassin de Colônia, sud-est du Brésil.*
Cette recherche utilise des techniques de microscopie optique et de microscopie électronique à balayage pour observer deux espèces d'*Achnanthidium* Kützing appartenant au complexe *A. minutissimum* '*sensu lato*', prélevées dans des sédiments pléistocènes du bassin de Colônia, dans le sud-est du Brésil. Nous avons comparé *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. et *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. avec leurs espèces morphologiquement les plus proches, révélant des contours de valves, des formes d'apex de valves, des zones centrales et des structures de raphé différents. Nos résultats permettent d'élargir les connaissances taxonomiques du genre en Amérique du Sud, ce qui est fondamental pour mieux comprendre les schémas de distribution et de diversité des diatomées dans les régions peu étudiées. Nos recherches améliorent également les connaissances actuelles sur l'évolution du paléolac dans le bassin de Colônia (São Paulo) depuis le début du Pléistocène.

MOTS CLÉS
Brésil,
diatomées,
Bacillariophyceae,
Achnanthidium,
morphologie,
ultrastructure,
espèces nouvelles.

INTRODUCTION

Kützing (1844: 75) proposed *Achnanthidium* as "Individua singularia vel binata, libera (nec adnata), a latere primario linearia genuflexa". Kützing described simultaneously the following two species: *A. microcephalum* Kützing and *A. delicatulum* Kützing, without designating a generitype. *Achnanthidium microcephalum* is currently considered the generitype of the genus *Achnanthidium* (Ross *in* Farr *et al.* 1979; Farr & Zijlstra 2013). Round & Bukhtiyarova (1996) redefined *Achnanthidium* considered a narrower concept of the genus according to some morphological aspects, such as V-shaped cells in girdle view, striae with simple rows of areolae, either interrupted or shorter, and less close to the center, simple raphe fissures with straight or sometimes turned distal ends on the valve plan and a separate row of areolae on the mantle (Monnier *et al.* 2004). Currently, *Achnanthidium* covers monoraphid species having the following features: linear to lanceolate-elliptic valve outlines, uniseriate striae that are spaced wider in the center and denser toward the valve apices, a straight central raphe hardly expanded at the center and straight or turned to one side at the apex and a row of elongate areolae on the mantle (Round & Bukhtiyarova 1996). Nevertheless, several of these features cannot be easily observed under light microscopy (LM), often hampering identification and preventing the valve ultrastructure from being clearly examined (Al-Handal *et al.* 2021).

Achnanthidium species are usually assigned to either one of the two following groups of species: 1) *A. minutissimum* (Kützing) Czarnecki species complex (straight terminal raphe endings, and round to elliptical areolae); and 2) *A. pyrenaicum* (Hustedt) Kobayasi species complex (external terminal raphe fissures deflected in the same direction, and with lineate areolae (Novais *et al.* 2015). More recently, a third group has been reviewed and described as a new genus. Czarnecki (1994) transferred *Achnanthes exigua* Grunow to *Achnanthidium exiguum* (Grunow) Czarnecki but did not justify the new combination. Later, the taxon was transferred to *Lemnicola exigua* (Grunow) Kulikovskiy, Witkowski & Plinski in Plinski & Witkowski (2011) and finally assigned to the genus *Gogorevia* Kulikovskiy, Glushchenko, Maltsev & Kociolek in Kulikovskiy *et al.* (2020) based on molecular and morphological features. Other studies have addressed the morphology of *Achnanthidium* taxa and helped solving some of the above-mentioned complexes of species, thus enlarging the knowledge on the ecological importance of the genus and the biogeography of different species (e.g. Lange-Bertalot & Ruppel 1980; Potapova & Hamilton 2007; Wojtal *et al.* 2011; Marquardt *et al.* 2017). Furthermore, over the past 20 years, several new *Achnanthidium* species have been described worldwide (e.g. Krammer & Lange-Bertalot 2004; Potapova & Ponader 2004; Monnier *et al.* 2004; Potapova 2006; Cantonati & Lange-Bertalot 2006; Ivanov & Ector 2006; Zidarova *et al.* 2009; Novais *et al.* 2011; Wojtal *et al.* 2011; Witkowski *et al.* 2012; Van de Vijver & Kopalová 2014; Pérès *et al.* 2014; Liu *et al.* 2016; Karthick *et al.* 2017; Krahn *et al.* 2018; Wetzel *et al.* 2019; Miao *et al.* 2020; Liu *et al.* 2021; Ge *et al.* 2022; Kapustin *et al.* 2022; Solak *et al.* 2022; Yu *et al.* 2022). Some of these species were identified not only through morphological but also molecular analyses (Pinseel *et al.* 2017; Miao *et al.* 2020; Tseplik *et al.* 2021).

Achnanthidium is considered one of the most abundant and common diatom genera in freshwater ecosystems worldwide (Wetzel *et al.* 2019). To date, there are 145 taxonomically accepted names listed, including species and infraspecific taxa belonging to the *Achnanthidium* (Guiry & Guiry 2022). The presence of *Achnanthidium* representatives was also reported in Pleistocene sediments around the world, including Argentina, Ethiopia, Japan, United States, and Mexico, to mention a few (e.g. Auer 1959; Stoermer 1963; O'Brien 1968; Gasse 1980; Van Landingham 2000; Tanaka & Nagumo 2000; Yasui & Kobayashi 2001; Spaulding *et al.* 2020). Kulikovskiy *et al.* (2011) reported the presence of the species *A. sibiricum* Kulikovskiy, Lange-Bertalot, Witkowski & Khursevich in fossil deposits extending back to the Pliocene sediments of the Lake Baikal.

Despite being widespread in the Brazilian ecosystems, very few studies have addressed the ecological aspects of the genus (e.g. Lobo *et al.* 2004; Bartozek *et al.* 2018), and only three have focused on its palaeoecological significance (e.g. Ruwer &

Rodrigues 2018, 2021; Ruwer *et al.* 2021). In fact, the lack of taxonomic precision due to the unclear definition of species boundaries often leads the name *Achnantidium minutissimum* to refer to a species with broad tolerance ranges, successfully occurring from oligotrophic to eutrophic environments. More recently, some taxonomic studies analyzing material collected from the State of São Paulo, Southeast Brazil, have been published (e.g. Marquardt *et al.* 2017; Costa *et al.* 2022). Their research objective was to show the ecological patterns with a fine-grained taxonomy to reveal the ecological preferences of some key groups in Brazilian reservoirs, for example. *Achnanthidium minutissimum* is considered in Southern Brazil a species with low tolerance to eutrophication (Lobo *et al.* 2015).

Achnanthidium are often reported as periphytic species, although planktonic representatives have also been described (Marquardt *et al.* 2017). Species belonging to the genus are reported to thrive in running water (Peterson & Stevenson 1992), responding differently to the water chemistry, ranging from oligotrophic to eutrophic and from alkaline to acidic environments (Krammer & Lange-Bertalot 1991; Krahn *et al.* 2018). In Kingston (2003), Cholnoky (1968) considered some species to be "oxygen loving" since they were found in turbulent, well-oxygenated water. *Achnanthidium* species can live on high plants' stalks above the dense prostrate masses of other algal species, where they can benefit from a faster replenishment of the flowing host's chemical constituents (Kingston 2003).

Herein, we describe two new *Achnanthidium* species based on LM and SEM observations. We also compared both species with other similar species based on the available literature. This study is part of an interdisciplinary palaeoecological project conducted in the Colônia basin, Brazilian Coastal Plain, Atlantic Forest, São Paulo Metropolitan Region (SPMR), following multiproxy analyses of the Quaternary sediment deposits (Simon *et al.* 2020). In this framework, we aimed to enlarge the knowledge on both the diversity and distribution of diatoms in South America, which is fundamental for a better understanding of the diatom distribution and diversity patterns in poorly studied areas. Our research also reveals that the studied biota had an important role in the history of the Colônia basin. In this way, the detailed descriptions of the *Achnanthidium* species help to improve the current knowledge on the evolution of the paleolake in the Colônia basin (São Paulo) since the early Pleistocene. This site became a reference for tropical palaeoecological research in the Southern hemisphere due to its continuous sedimentary infill, more particularly, regarding the Atlantic rainforest evolution (Ledru *et al.* 2015). Thereby, we also aimed to provide information on both the climatic and ecological variability for the period recorded.

MATERIAL AND METHODS

The Colônia basin is a 3.6 km wide circular structure with an outer rim elevated by up to 125 m, whose origin has been debated since the early 1960s. The crater-like structure is located on the southern outskirts of the city of São Paulo, Brazil, near the Atlantic Mountain range. Riccomini *et al.* (2011) described that the depression was filled with organic-rich sediments from the Quaternary age. Additionally, its northern area has been urbanized in recent years, whereas the central area is now a swamp, partially drained by the Vargem Grande stream, which exhibits a peculiar radial centripetal pattern with a single outlet through the eastern rim of the structure (Riccomini *et al.* 2011). Other studies in the area estimated the age of the basin's formation between 5.3 and 11.2 Ma (Simon *et al.* 2020).

In August 2017, the International Consortium (Colônia Deep Drilling Project: TROPICOL) collected a 5200 cm long sediment core (COL17-3, sampling resolution 1 cm) from the area. The collection was performed using a built-in pushing corer with rotary tubing mounted on a 6T Caterpillar drilling rig, with posterior subsampling every 3 cm for diatom analysis. The age model based on radiocarbon dates, OSL authigenic 10Be/9 Be, and paleomagnetism indicated an age of 1.5 Ma at the base of the core (Simon *et al.* 2020). See Marquardt *et al.* (2021a, b) for detailed information on the study area.

For this study, we selected two samples (liner depth: 4268-69 cm and 4376-77 cm; respective composite depths: 4311 cm and 4471 cm) from the sediment core with the highest abundances of *Achnanthidium* species. According to Simon *et al.* (2020), these samples are aged 1.37 and 1.41 Ma, respectively.

The procedure for slide preparation was adapted from standard methods (Battarbee 1986). The volume of 0.5 g wet sediment was treated with 37% HCl and 30% H_2O_2 and heated at 80°C for approximately six hours. The samples were washed with distilled water for the removal of acid and peroxide to the neutrality. Permanent slides for LM analyses were prepared using Naphrax® (RI = 1.73) as the mounting medium. The slides were examined using an Axioscop Imager A2 equipped with Differential Interference Contrast, under oil immersion at ×1000 magnification equipped with a digital camera AxioCamMR5. Relative abundance was estimated by counting a minimum of 400 valves with an efficiency count of at least 90% (Pappas & Stoermer 1996).

The SEM analyses were performed in different places and using different methods. For such a purpose, we deposited subsamples of the oxidized material on aluminum stubs coated with gold at 1 kV for five minutes in a Balzers Sputtering/SDC030 sputter coater at the Instituto de Pesquisas Ambientais (IPA). A microscope Jeol-JSM 7401F (FEG) operated at 5 kV was used for analyses (Instituto de Química, Universidade de São Paulo). Immediately after, the material was coated with gold using an Emitech Coating System for 270 seconds at 15 mA. A high vacuum scanning electron microscope LEO440i (LEO Electron Microscopy Ltd, England) operated at 20 kV, 5 mm work distance, with 15 pA of emission current (Instituto de Geociências, USP). Additionally, preparation was filtered, and parts of the oxidized suspensions were rinsed with additional deionized water through a 3 µm Styrofoam polycarbonate membrane filter (Merck Millipore), mounted on aluminum stubs and coated with platinum using a BAL-TEC MED 020 Modular High Vacuum Coating System for 30 seconds at 100 mA. The analyses were carried out using a Hitachi SU-70 ultra-high-resolution analytical field emission (FE) scanning electron microscope (Hitachi High-Technologies Corporation, Tokyo, Japan) operated at 5 kV and 10 mm distance

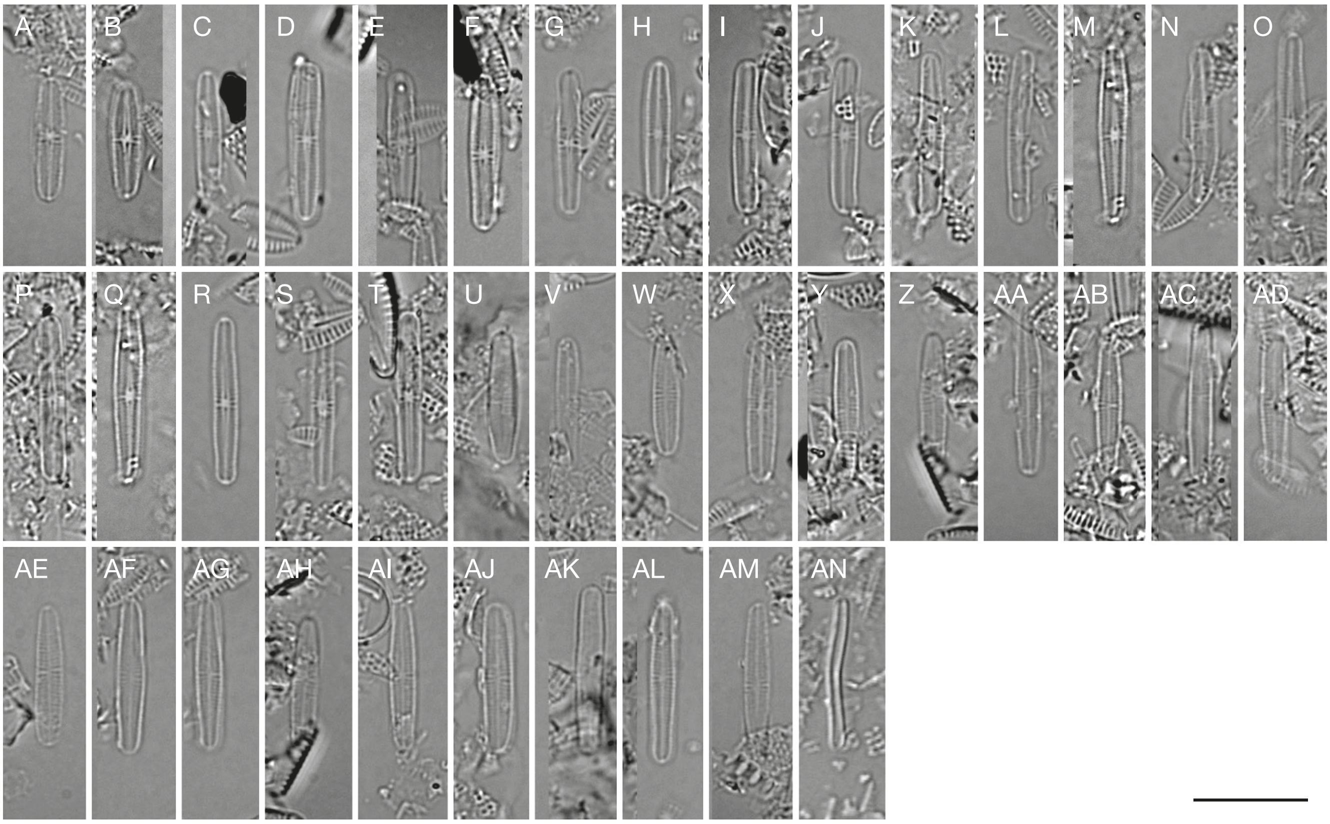

FIG. 1. — *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. LM micrographs, size diminution series: **A**-**T**, raphe valve; **U**-**AM**, raphless valve; **AN**, frustules in girdle view. Scale bar: 10 µm.

(Luxembourg Institute of Science and Technology). The SEM images were taken using the lower (SE-L) detector signal.

The micrographs were digitally manipulated and the plates containing the LM and SEM images were prepared on Corel Draw 2021. The morphological terminology adopted was based on Barber & Haworth (1981) and Round *et al.* (1990).

Holotype permanent slides and clean samples are deposited at the “Herbário Científico do Estado Maria Eneyda P. Kauffmann Fidalgo” (SP), São Paulo State Department of Environment, Infrastructure and Technology, Brazil. The isotype slide is deposited at BR, Meise Botanic Garden, Belgium.

RESULTS

Class BACILLARIOPHYCEAE Haeckel
Subclass BACILLARIOPHYCIDAE D.G.Mann
Order ACHNANTHALES P.C.Silva
Family ACHNANTHIDIACEAE D.G.Mann
Genus *Achnanthidium* Kützing

Achnanthidium ectorianum
Marquardt & C.E.Wetzel, sp. nov.
(Figs 1-4)

HOLOTYPE. — **Brazil**. São Paulo, SP, Parelheiros District, Colônia crater, 23°52’S, 46°42’20”W, 900 m a.s.l., from sample 4268-69 cm liner depth (*c.* 1.37 Ma; 4311 composite depth) of the COL17-3 sediment core, VIII.2017, M.-P. Ledru & A.O. Sawakuchi (SP[SP365.548]!).

ISOTYPE. — Same data as holotype (BR[BR4582]!).

TYPE LOCALITY. — **Brazil**. São Paulo, SP, Parelheiros District, Colônia crater, 23°52’S, 46°42’20”W, 900 m a.s.l.

ETYMOLOGY. — The species is dedicated in honor of our mentor, friend, and colleague Luc Ector (1962-2022), who taught us much about *Achnanthidium* and its features.

ECOLOGY AND DISTRIBUTION. — *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. was frequently observed in the core (11.1% relative abundance). Accompanying taxa included an undetermined diatom genus (43%), *Staurosira* sp. 1 (20%), *Pseudostaurosira crateri* Marquardt & C.E.Wetzel (10%), *Aulacoseira ambigua* (Grunow) Simonsen (3.8%), and *Planothidium scrobiculatum* Marquardt & C.E.Wetzel (3.7%).

DESCRIPTION

LM observations (Fig. 1)

Frustule in girdle view is narrow, rectangular, and bent with weakly recurved apices (Fig. 1AN). Linear-elliptical valves, with almost parallel margins, are very delicate and difficult to observe. Broadly rounded to subrostrate apices (Fig. 1A-AM), sometimes slightly curved to the same side (Fig. 1I-L); 10.5-15.5 µm long, 2.5-3.0 µm wide. Raphe valve: very narrow axial area, linear to linear-lanceolate; central area composed of 1-3 shortened striae on both sides of the valve, resembling an X-shape (Fig. 1D-G). Raphe filiform, straight. Transapical

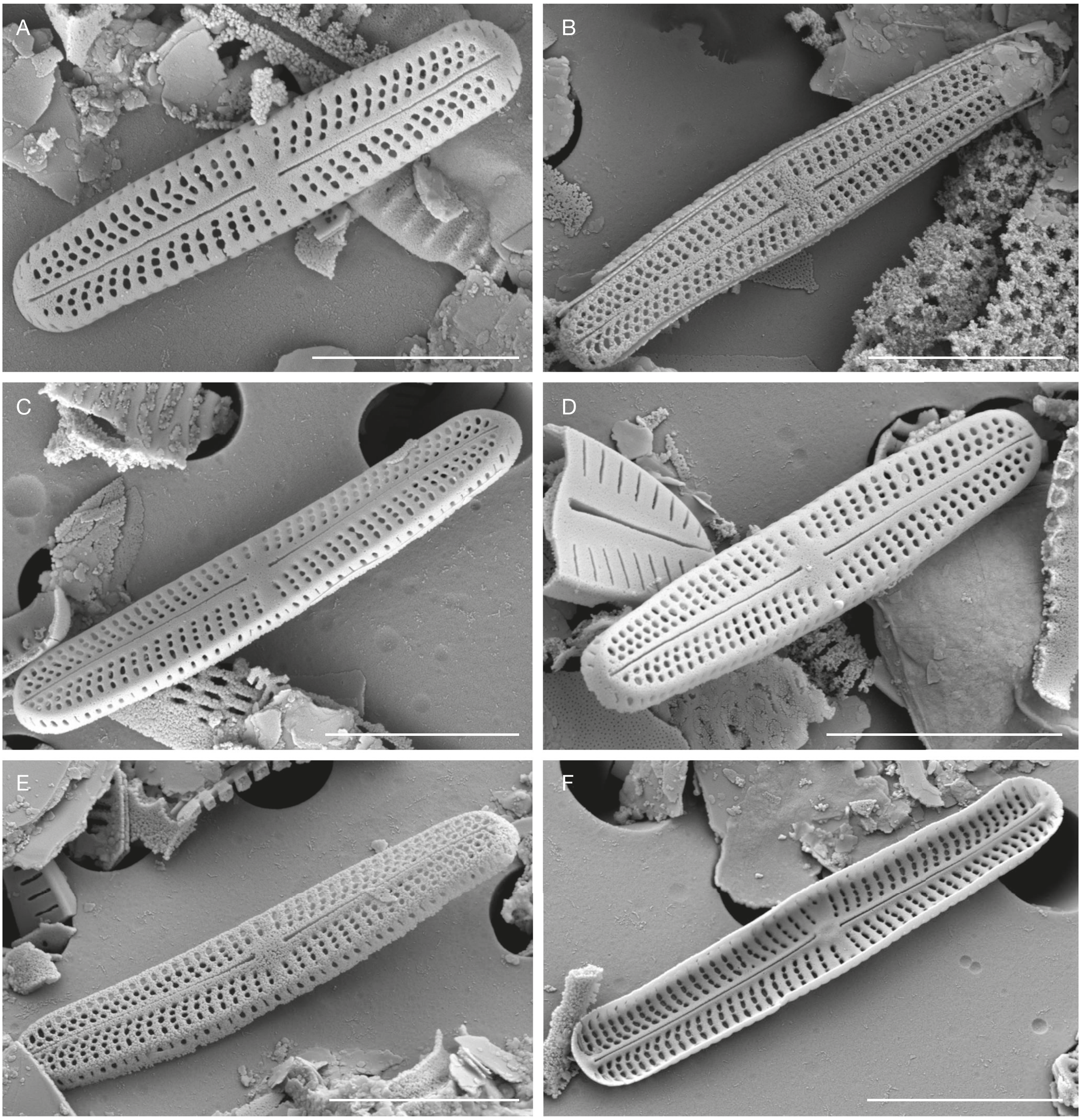

FIG. 2. — *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: **A**-**E**, external views, raphe valve; **F**, internal view, raphe valve. Scale bars: A, 4 µm; B-F, 5 µm.

striae not discernible. Rapheless valve: narrow and linear axial area (Fig. 1U-AM). Transapical striae not discernible. The girdle view is narrow, rectangular, and arcuate, with pointed apices faintly curved to the rapheless valve (Fig. 1AN).

SEM observations (Figs 2-4)
Raphe valve: raphe prolonged after the striae, terminating on the border between the valve face and mantle (Fig. 2A-D). Straight central and terminal raphe fissures (Fig. 2A-E). Striae (30-38) are mainly composed of 2-3, rarely 4, that are rounded areolae, curved close to the apices (Fig. 2A-E). Internally, proximal raphe endings slightly deflected in opposite directions, distal endings terminating in small helictoglossae (Fig. 2F). Rapheless valve: very narrow axial area, slightly depressed below the valve surface (Figs 3D, F; 4C, F). Striae (32-36 in 10 µm) are mainly composed of 2-4 rounded to elongate areolae (Figs 3A-F; 4A-C). At times, the areolae fuse forming a slit (Figs 3A; 4A, E). Mantle with one row of slit-like transapically orientated areolae (Figs 3B, D; 4A-C, F).

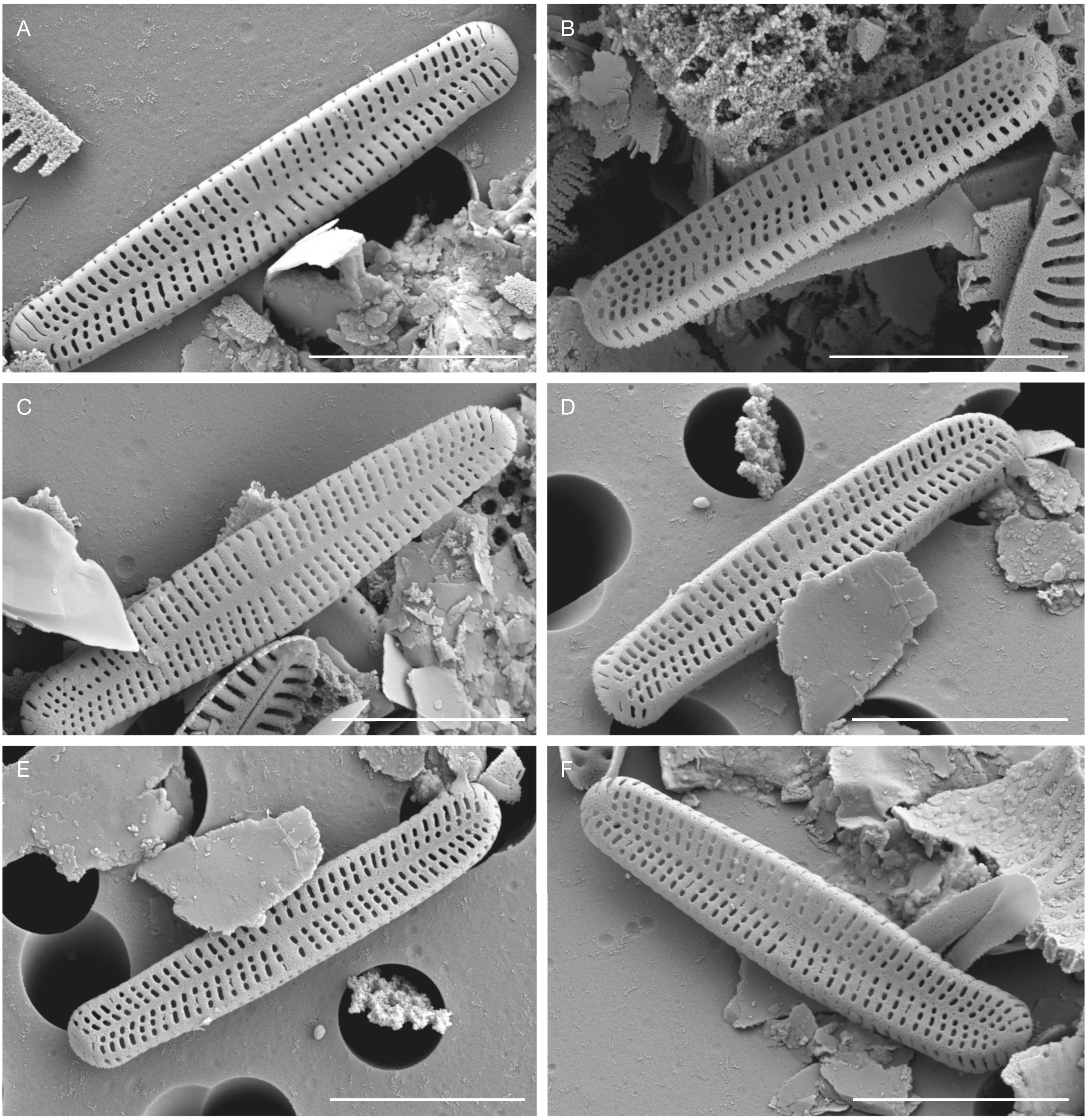

FIG. 3. — *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: external views, rapheless valve. Scale bars: 5 μm.

Achnanthidium craterianum Marquardt & C.E.Wetzel, sp. nov. (Figs 5-8)

HOLOTYPE. — **Brazil**. São Paulo, SP, Parelheiros District, Colônia crater, 23°52'S, 46°42'20"W, 900 m a.s.l., from sample 4268-69 cm liner depth (*c.* 1.37 Ma; 4311 composite depth) of the COL17-3 sediment core, VIII.2017, M.-P. Ledru & A.O. Sawakuchi (SP[SP514.067]!).

ISOTYPE. — Same data as holotype (BR[BR4737]!).

TYPE LOCALITY. — **Brazil**. São Paulo, SP, Parelheiros District, Colônia crater, 23°52'S, 46°42'20"W, 900 m a.s.l.

ETYMOLOGY. — The Latin name *craterianum* refers to the Colônia Basin geomorphological structure where the sample was collected.

ECOLOGY AND DISTRIBUTION. — *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. was abundant in the core (60% relative abundance). Accompanying taxa included mainly *Aulacoseira ambigua* (28%) and *Staurosira* sp. 1 (5%) as dominant species.

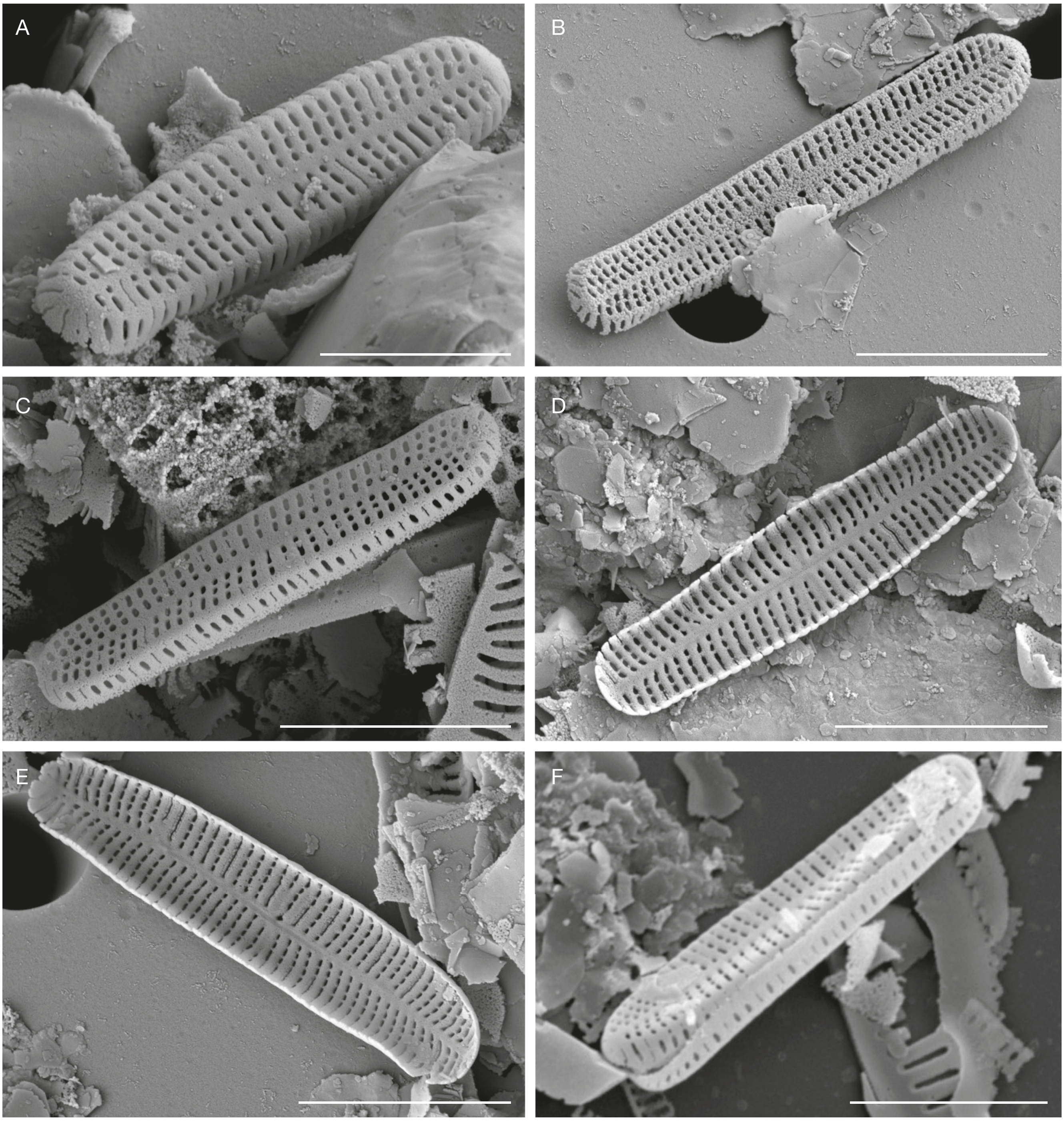

Fig. 4. — *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: **A**-**C**, external views, rapheless valve; **D**-**E**, internal views, rapheless valve; **F**, girdle view. Scale bars: A, 3 µm; B-F, 5 µm.

Description

LM observations (Fig. 5)

Frustule girdle in view is rectangularly arched, with pointed apices slightly curved (Fig. 5AI, AJ). Valves linear to linear-lanceolate, with margins almost parallel to only slightly widening toward the central area. Sub-capitate to capitate apices, protracted (Fig. 5A-AH), facing opposite directions (Fig. 5B-O, R-AH); 8.5-19.0 µm long, 2.0-2.5 µm wide. Raphe valve: narrow to faintly lanceolate axial area toward the central area; rounded central area, with 2-4 shortened striae on both sides of the valve (Fig. 5A-U). Straight raphe filiform. Transapical striae slightly radiating throughout the entire valve, more spaced in the central area, becoming denser and more strongly radiating toward the apices (Fig. 5A-U); 32-33 in 10 µm. Rapheless valve: narrow, linear axial area, sometimes faintly lanceolate toward the central area; absent central area or narrow lanceolate (Fig. 5V-AH). Transapical striae slightly radiate throughout the entire valve, more spaced in the central area, becoming denser towards the

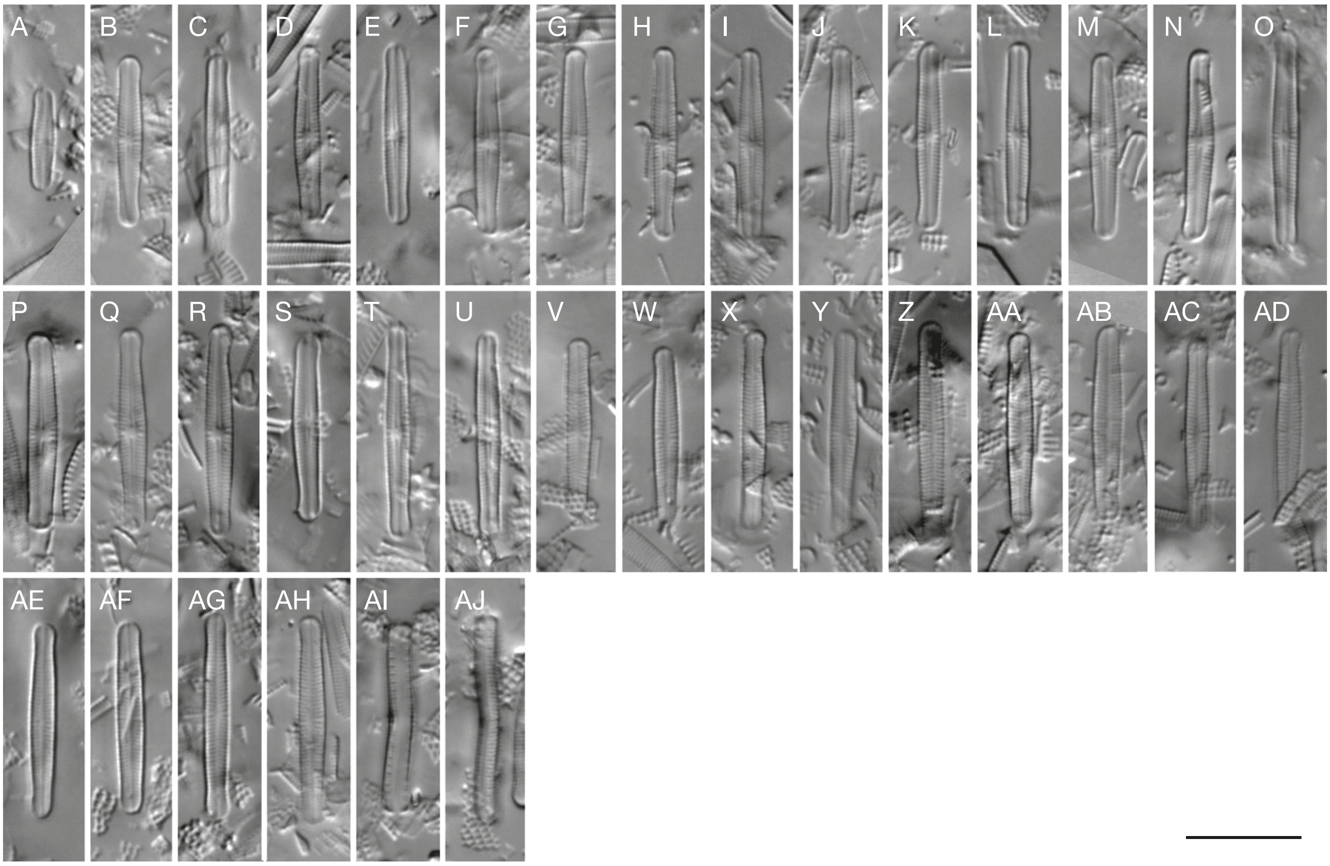

FIG. 5. — *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. LM micrographs, size diminution series: **A**-**U**, raphe valve; **V**-**AH**, raphless valve; **AI**-**AJ**, frustules in girdle view. Scale bar: 10 µm.

apices; 40-42 in 10 µm. Rectangular arcuate girdle view, with pointed apices slightly recurved to the rapheless valve (Fig. 5AI-AJ).

SEM observations (Figs 6-8)
Raphe valve: raphe prolonged after the striae, terminating on the border between the valve face and mantle (Fig. 6A-C). Central and terminal raphe fissures are straight and slightly expanded at the endings (Fig. 6A-D). Striae composed of 2-3 rounded areolae, becoming denser toward the apices (Fig. 6A-C). Internally, proximal raphe endings slightly deflected in opposite directions, distal endings terminating in small helictoglossae (Fig. 6A-C). Rapheless valve: very narrow axial area, lanceolate towards the central area (Figs 6E, F; 7D). Striae composed of 2-3 rounded to slit-like areolae (Fig. 6E, F). Mantle with one row of slit-like transapically orientated areolae (Figs 6F; 8A-C).

DISCUSSION

Our study proposes two new *Achnanthidium* species from the Colônia paleolake based on a set of morphological features, including valve outline, the shape of apices, central area, and raphe structure. Furthermore, features such as stria and areola density provided additional information to identify both species. Both species are characterized by a valve outline with almost parallel sides. *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. has delicate valves that appear faded under the LM. The species is broadly rounded, with subrostrate apices and a central area in raphe valves resembling an 'X-shape'; in addition to raphe fissures prolonged after the striae terminating on the junction of the valve face and the mantle. *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. is distinguished by sub-capitate to capitate valve apices, which are protracted and faced opposite directions under the LM, in addition to the raphe structure. Table 1 for *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. and Table 2 for *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. synthetize the main features of the new species, as well as similar species, based on the literature.

The *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. has different valve dimensions almost parallel valve margins and broadly rounded to subrostrate apices. However, it resembles the *Achnanthidium neotropicum* K.J.Krahn & C.E.Wetzel described based on modern and subfossil sediments from Lake Apastepeque, El Salvador (Krahn *et al.* 2018). Nevertheless, valves of *A. neotropicum* are sometimes constricted in the center, especially in longer specimens, which has not been observed in *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. Regarding the characteristics of the central area, *A. neotropicum* often presents a rectangular

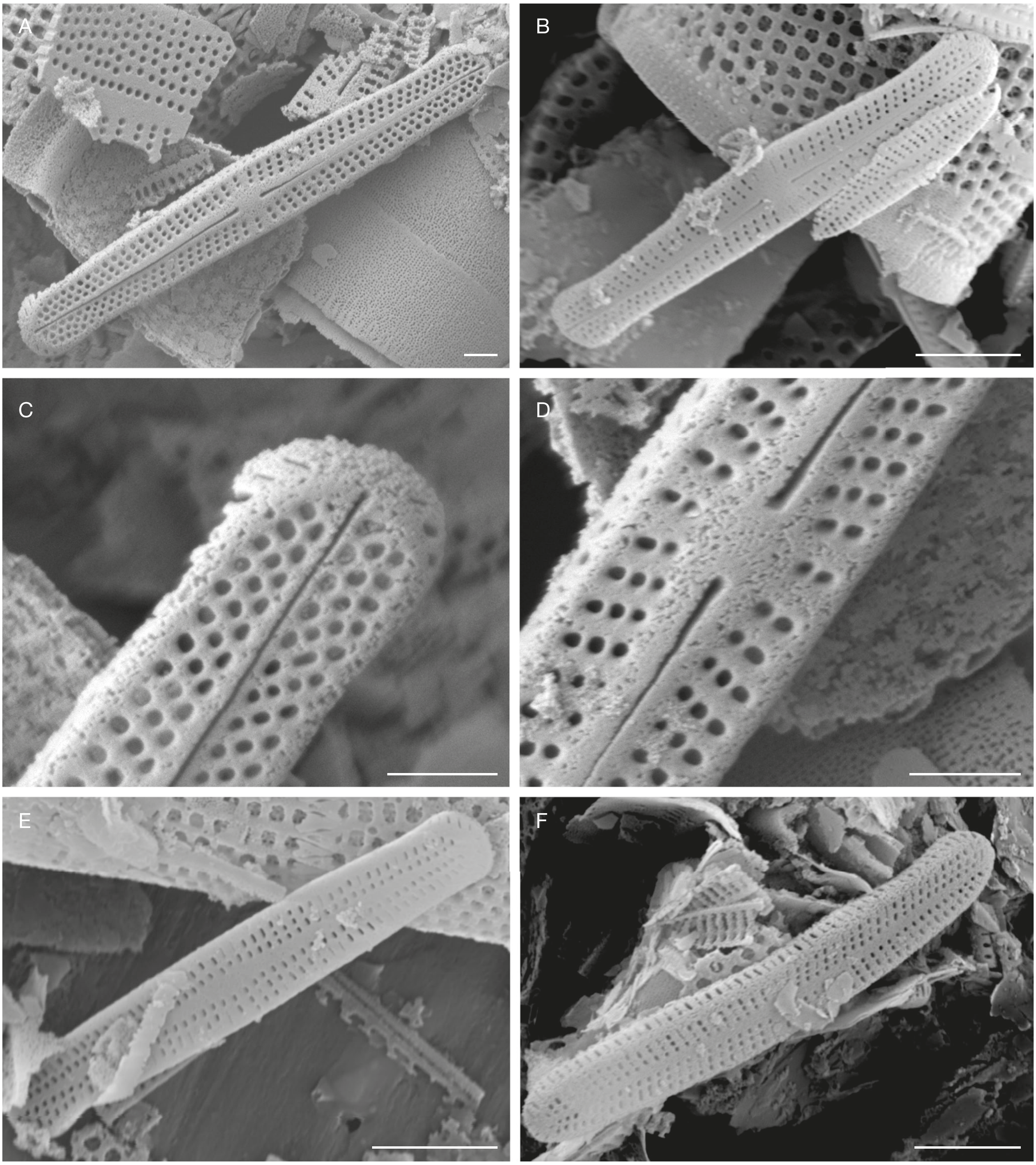

Fig. 6. — *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: **A**-**D**, external views, raphe valve; **C**, detail of terminal raphe fissure and areolae; **D**, detail of central raphe fissures and central area; **E**, **F**, external views, rapheless valve. Scale bars: A, C, D, 1 µm; B, E, F, 3 µm.

fascia, whereas the central area of *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. is always small, resembling an 'X-shape'.

The valve outline in *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. also resembles the *A. lailae* van de Vijver, found living on the sediment of several lakes at James Ross Island (Van de Vijver & Kopalová 2014). However, the species can be easily distinguished by their central area features, which forms a typical rectangular fascia reaching valve margins in *A. lailae*. Additionally, terminal raphe fissures are weakly deflected in *A. lailae*, whereas the *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. has a small central area, resembling an 'X-shape', and straight terminal raphe fissures.

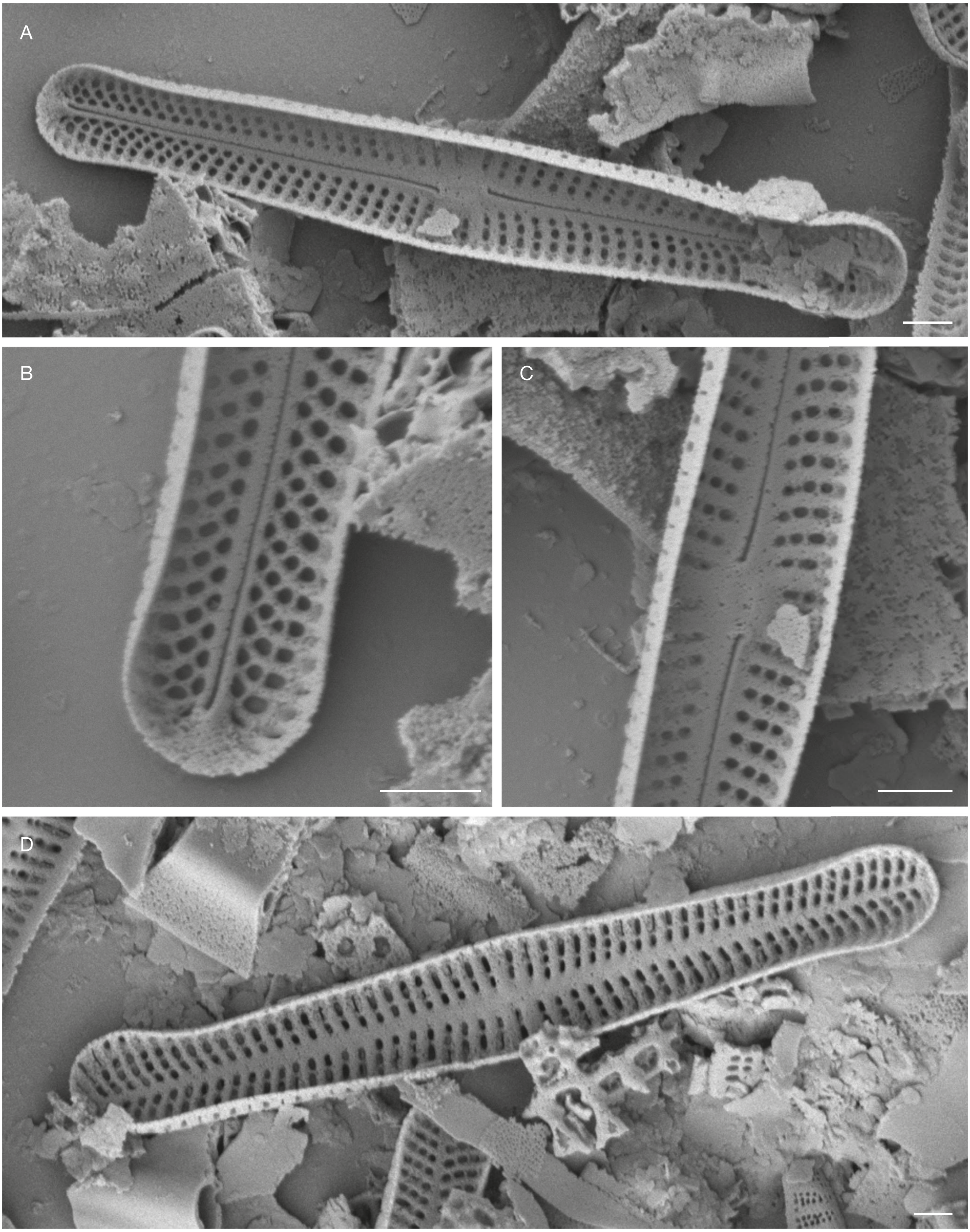

Fig. 7. — *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: **A**-**D**, internal views; **A**-**C**, raphe valve; **B**, detail of helictoglossa, apical striae, and areolae; **C**, detail of the central area and transapical striae; **D**, rapheless valve. Scale bars: 1 μm.

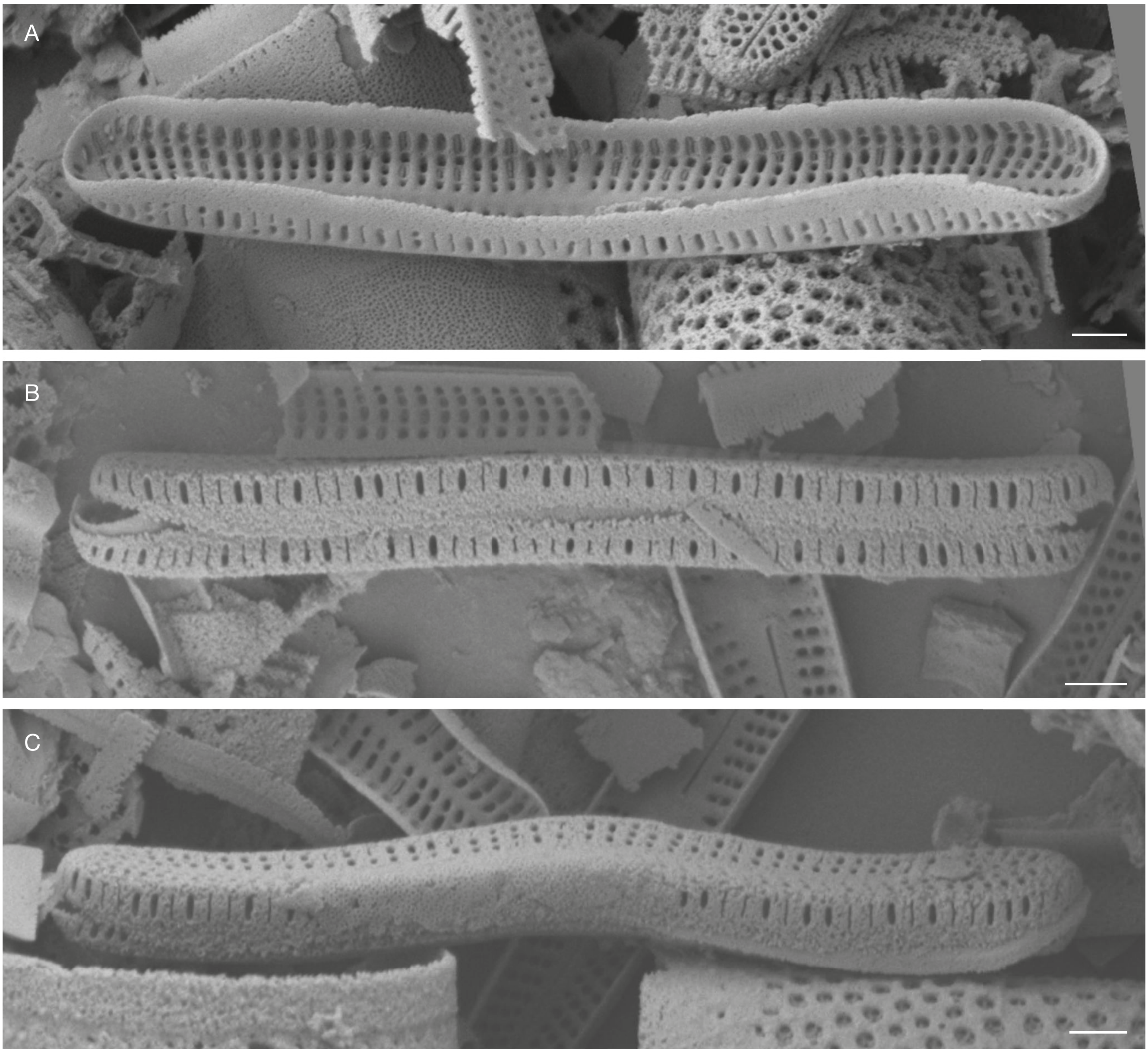

Fig. 8. — *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. Population from the type locality. SEM: **A**-**C**, girdle views. Scale bars: 1 µm.

Finally, *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. resembles *A. anatolicum* C.N.Solak, Wojtal, S.Blanco, Peszek & M.Rybak, as described by Solak *et al.* (2022) from a deep soda lake, Lake Salda, southwest Anatolia, Turkey. According to the authors, the flat valve is the most typical feature of *A. anatolicum* since most *Achnanthidium* species typically have more or less arched valves. Even though the SEM images could not reveal the arched appearance of the valves of *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov., the LM observations show it clearly. Unfortunately, *A. anatolicum* could not have girdle view LM images generated. However, the apices in *A. anatolicum* are sub-capitate are clearly detached from the de valve. In turn, the apices are broadly rounded and subrostrate in the new species. Additionally, the two species present different values of valve dimensions, stria density, and areola number (Table 1).

Achnanthidium sieminskae Witkowski, Kulikovskiy & Riaux-Gobin in Witkowski *et al.* (2012) is one of the species that most closely resembles *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. However, *A. sieminskae* has protracted and slightly capitate apices, but some representatives pressent rostrate apices (Van de Vijver & Kopalová 2014). According to Van de Vijver & Kopalová (2014), the presence of clear rostrate to capitate apices is considered one of the main features to distinguish *A. sieminskae* from other similar species. Thus, LM images show the valve apices in *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. facing in opposite directions. Another important distinctive feature are the distal raphe fissures weakly deflected and extending slightly beyond the last stria, terminating on the valve face/mantle junction in *A. sieminskae*. Nevertheless, *A. craterianum* Marquardt & C.E.Wetzel,

Table 1. — Morphometric data from *Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov. populations found in the Colônia basin, São Paulo, Brazil, and the most similar taxa belonging to the *A. minutissimum* complex.

	***Achnanthidium ectorianum* Marquardt & C.E.Wetzel, sp. nov.**	***A. neotropicum* K.J.Krahn & C.E.Wetzel**	***A. lailae* van de Vijver**	***A. anatolicum* C.N.Solak, Wojtal, S.Blanco, Peszek & M.Rybak**
Reference	this study	Krahn *et al.* (2018)	Van de Vijver & Kopalová (2014)	Solak *et al.* (2022)
Valve outline	linear-elliptical, with almost parallel margins	linear to linear-lanceolate, parallel margins, partially constricted	linear to very slightly linear-lanceolate	linear
Valve apices	broadly rounded, subrostrate	broadly rounded, subrostrate	non-protracted, broadly rounded, never rostrate or capitate	subcapitate
Length (µm)	10.5-15.5	6.7-23.4	10-14	11.5-23.0
Width (µm)	2.5-3.0	2.0-3.0	1.8-2.5	2.5-3.5
Girdle view	narrow, rectangular, bent with weakly recurved apices	rectangular, bent with recurved apices	narrow, rectangular, bent with weakly recurved apices	unbent
Raphe valve				
Axial area	narrow and linear to linear-lanceolate	narrow, slightly widening towards the central area	linear to linear-lanceolate widening towards the central area	very narrow, slightly widening towards the central area
Central area	'X' appearance	rectangular fascia or shortened, more widely spaced striae	rectangular fascia	small bordered by 3-4 widely spaced stria both sides
Terminal raphe fissures	straight, terminating after the last striae	almost straight, small and drop shaped, terminating after the last striae	weakly deflected, terminating after the last striae	
Stria density (in 10 µm)	30-38	30-36	30-33	26-28
Areolae opening	rounded	rounded to elongated areolae, sometimes slit-like near the margins	rounded to slit-like	rounded to elongated
Areolae number (at the center)	2-3, rarely 4	3-4, rarely 2 in constricted valves	2-3	4 (5, rarely 2-3 at apices)
Rapheless valve				
Axial area	narrow and linear	linear to weakly lanceolate	lanceolate axial area, widening near the valve center	narrow and linear
Central area	absent	almost absent or irregular with shortened, more widely spaced striae	elongated, rhombic lanceolate with longer marginal striae	almost absent
Stria density (in 10 µm)	32-36	30-36	28-30	27-29
Areolae opening	rounded to elongated, sometimes fused, forming a slit	rounded to slit-like near the margins	rounded to slit-like	rounded to elongated
Areolae number (at the center)	2-3, rarely 4	3-4	2-3	4-5 (rarely 2, 3 at apices)

sp. nov. has straight external raphe branches, with drop-like expanded proximal and distal raphe fissures, which prolong after the striae terminate on the border of the valve face and mantle. It is worth noting that *A. sieminskae* shows the valve central portion larger than the constriction before the apices, and sometimes larger than the apices. Such a feature was not observed in the Brazilian species, whose valve width and outline are almost continuous and parallel from the center to the apices. Finally, the girdle view shows *A. sieminskae* frustules bent around the transapical axis, with clearly recurved apices, whereas they are less arcuate in *A. craterianum* Marquardt & C.E.Wetzel, sp. nov., with pointed apices only slightly recurved to the rapheless valve. Finally, *A. sieminskae* distribution seems to be limited to the Sub Antarctic Islands (Witkowski *et al.* 2012), in both the Indian and Atlantic Oceans (Van de Vijver & Kopalová 2014).

Furthermore, it is possible to compare *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. and *A. caledonicum* (Lange-Bertalot) Lange-Bertalot. *Achnanthidium caledonicum* has a complex taxonomic history and can be characterized by a slightly swollen valve mid-region. In addition, larger specimens of *A. caledonicum* have strongly capitate apices (Slate & Stevenson 2007). *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. shows protracted, sub-capitate

Table 2. — Morphometric data from *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov. populations found in the Colônia basin, São Paulo, Brazil, and the most similar taxa belonging to the *A. minutissimum* complex. **ND**, no data.

	***Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov.**	***A. sieminskae* Witkowski, Kulikovskiy & Riaux-Gobin**	***A. caledonicum* (Lange-Bertalot) Lange-Bertalot**	***A. digitatum* Pinseel, Vanormelingen, Hamilton & van de Vijver**
Reference	this study	Van de Vijver & Kopalová (2014)	Wojtal *et al.* (2011)	Pinseel *et al.* (2017)
Valve outline	linear to linear-lanceolate with almost parallel margins	linear to narrowly linear-lanceolate with almost parallel to slightly convex margins	linear to linear-lanceolate	linear to slightly linear-lanceolate with almost parallel margins
Valve apices	subcapitate to capitate, protracted and faced to opposite directions	clearly protracted, rostrate to capitate apices	capitate	protracted, (slightly) subrostrate to broadly rounded, not protracted, in smaller specimens
Length (µm)	8.5-19.0	9.5-18.0	14.2-38.0	8.6-19.1
Width (µm)	2.0-2.5	1.9-3.1	2.3-3.2	1.8-2.3
Girdle view	rectangular arched, with pointed apices slightly curved	clearly bent around the transapical axis and with clearly recurved apices	ND	rectangular arched
Raphe valve				
Axial area	axial area narrow to faintly lanceolate towards the central area	narrow linear	linear, becoming weakly lanceolate towards the central area	narrow, linear, only slightly widening towards central area; almost absent near the apices
Central area	small, rounded	elliptical to rounded, very small, almost indistinct	rhombic	small, rounded or forming a clear rectangular fascia
Terminal raphe fissures	straight, terminating after the last striae	weakly deflected, terminating on the valve face/mantle junction	straight, terminating after the last striae	straight, terminating after the last striae
Stria density (in 10 µm)	32-33	32-34	30-35	31-36
Areolae opening	rounded	round to slit-like	round, elongated or slit-like	rounded or broadly transapically elongated
Areolae number (at the center)	2-3	2-3	2-4	2, rarely 3
Rapheless valve				
Axial area	narrow and linear to weakly lanceolate towards the central area	narrow and linear	linear, weakly lanceolate towards the central area	narrow linear, slightly widening towards the central area
Central area	absent or narrow lanceolate	absent	absent	almost non-existent, never forming a fascia or subfascia
Stria density (in 10 µm)	40-42	34-36	ND	31-36
Areolae opening	rounded to elongated	round to slit-like	round, elongated or slit-like	rounded or broadly transapically elongated
Areolae number (at the center)	2-3	2-5	ND	2, rarely 3

to capitate apices, and the mid-region sides of their valves are almost parallel. However, the Brazilian species resembles the *A. caledonicum* illustrated by Wojtal *et al.* (2011), which does not have a swollen middle area. Notwithstanding, the species described by Wojtal's has a larger central portion than the constriction before the apices, and sometimes larger than the apices. Such a constriction has never been observed in *Achnanthidium craterianum* Marquardt & C.E.Wetzel, sp. nov., whose valve width is more or less similar from the center to the apices beginning.

Achnanthidium craterianum Marquardt & C.E.Wetzel, sp. nov. also resembles *A. digitatum* Pinseel, Vanormelingen, Hamilton & van de Vijver. Nonetheless, the latter has subrostrate to broadly rounded, and apices that are never protracted. Areola margins are also narrow and mostly slit-like in *A. digitatum*, and the central area usually forms a clear rectangular fascia, opposite to the small, rounded central area in *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. Furthermore, the number of striae may provide additional support for distinguishing the two taxa since in *A. digitatum* striae are composed of two, and only rarely three, areolae, opposite to *A. craterianum* Marquardt & C.E.Wetzel, sp. nov., in which striae are composed of two, mainly three, areolae.

Achnanthidium ectorianum Marquardt & C.E.Wetzel, sp. nov. and *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. were found at high concentration and good preservation in the sediment over a long period of *c.* 40.000 years between *c.* 1.41 and 1.37 Ma. Ongoing analyses on associated flora revealed that *A. ectorianum* Marquardt & C.E.Wetzel, sp. nov. is accompanied by low abundances of planktonic species and higher abundances of an unidentified diatom genus (currently named genus 1), which is likely benthic. Genus 1, the most abundant diatom of this section, appeared in Amazonian records (Xingu basin) associated with higher insolation and dryer episodes during a low-productivity oligotrophic interval. In contrast, *A. craterianum* Marquardt & C.E.Wetzel, sp. nov. has been reported in a zone consistently dominated by planktonic taxa. Such a successional increase is followed by a reversed successional decrease of both genus 1 and *Pseudostaurosira crateri*. The diatom assemblage turnovers as periphytic and planktonic dominance changes, highlighting significant shifts in environmental and water parameters, especially water level, in the paleolake of the Colônia during the early Pleistocene, as shown in Rodríguez-Zorro *et al.* (2022).

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