Phytotaxa 227 (2): 101–119
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.227.2.1

Achnanthes citronella, *A. trachyderma comb. nov.* (Bacillariophyta) and allied taxa pertaining to the same morphological group

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Abstract

Several diatoms in the family Achnanthaceae (Bacillariophyta), mainly from marine environments, have species with strongly apiculate, lemon-shaped valves. Some of them originally described under the genus *Cocconeis* (*i.e*., *C. trachyderma* or *C. citronella*), while others were first described as *Stauroneis* species [*i.e. Stauroneis apiculata* or *S.*(?) *obesa*]. Afterwards, *Cocconeis citronella* has been recombined within *Achnanthes* by Hustedt. The type material of *C. citronella* from Albert Mann's collection, housed in the Smithsonian Institution (US), has been examined with light microscope; some ambiguities are pointed out and new details added to the original description. The intricate history of the latter taxon is redrawn and comparison with allied taxa are tentatively addressed. *Cocconeis trachyderma* is lectotypified and recombined as *Achnanthes trachyderma comb. nov*. *Stauroneis apiculata* and *S.*(?) *obesa* are recombined as *Achnanthes apiculata comb. nov.* and *Achnanthes obesa comb. nov*. respectively. The examination with light and scanning electron microscope of several marine samples from the Society Archipelago details the unique morphology of *Achnanthes trachyderma* which, until recently, has been often misidentified as *Achnanthes citronella* due to certain similarities between both taxa.

Key words: *Achnanthes citronella*, *A. trachyderma comb. nov*., Achnanthales, morphology, Indo-Pacific Basin, SEM

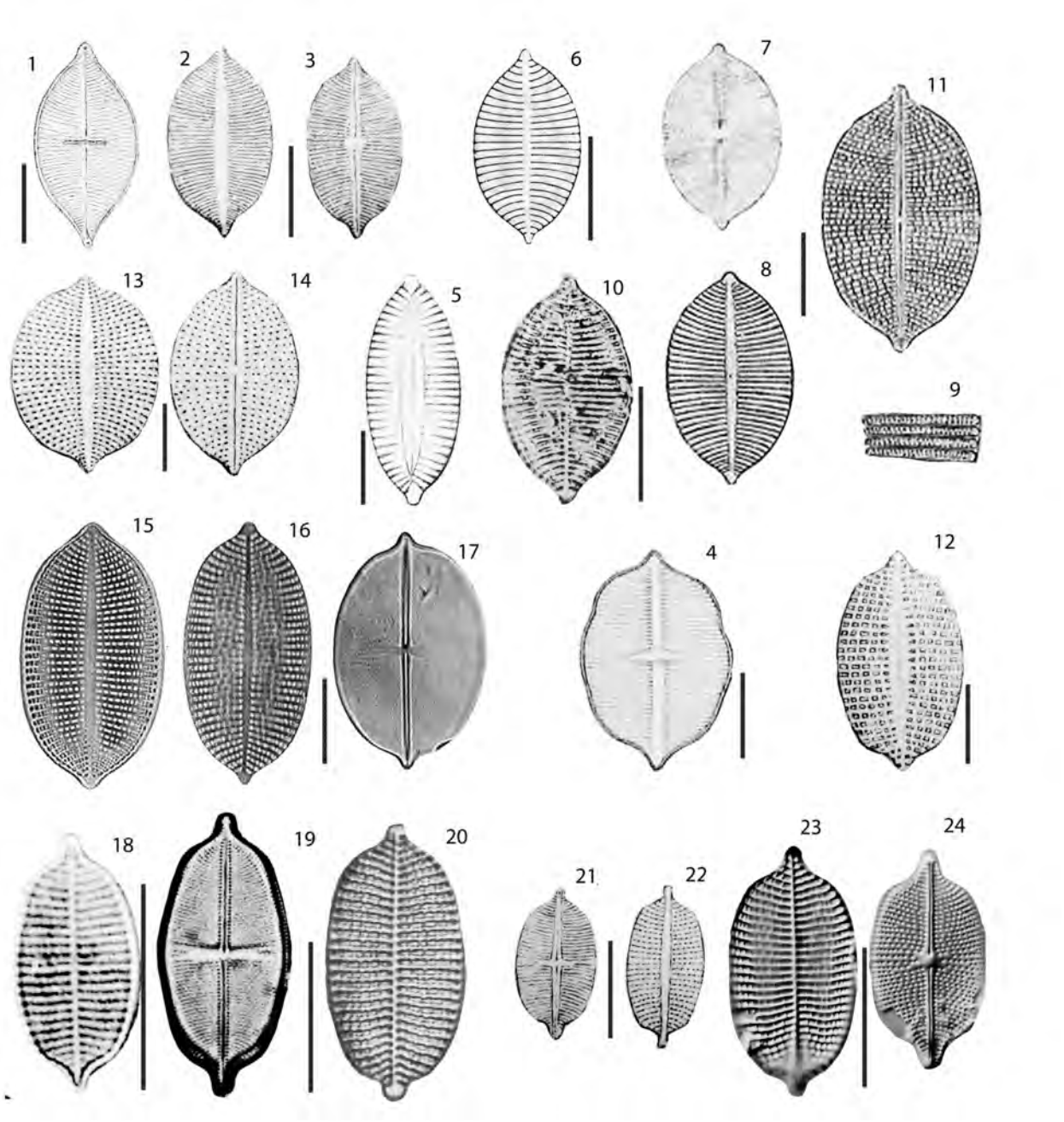
Introduction

Some benthic marine diatoms species in the order Achnanthales (Bacillariophyta) present valves of a characteristic apiculate or lemon shape (Figs 1–24). Several of them were first described as species of *Cocconeis* [*i.e. Cocconeis citronella* A.Mann (1925: pl. 13, figs 3–6, reproduced here as Figs 15–17), *C. trachyderma* F.Meister (1935: figs 63, 64, reproduced here as Figs 19, 20)] while some others, bearing some similarity with the latter, were first described amongst the biraphids, such as *Stauroneis*(?) *obesa* Greville (1866: pl. 3, fig. 12, here reproduced as Fig. 4) or *Stauroneis apiculata* Greville (1859: pl. 4, fig. 8, here reproduced as Fig. 1), when they are actually monoraphid diatoms. Some of these taxa, probably pertaining to the same morphological group, have been later transferred to *Achnanthes*, several of them having an intricate taxonomic history resulting in some taxonomic confusions.

Some papers illustrate diatoms identified as *Achnanthes citronella* (A.Mann) Hustedt in Schmidt *et al*. (1937: pl. 415, figs 3–8) with light (LM), scanning electron (SEM) and transmission electron (TEM) microscope, *e.g*. Meister (1935: 98, pl. 6, fig. 53), Foged (1975: 7, pl. 9, fig. 13), Gerloff & Helmcke (1977: pls 939–945), Foged (1984: 12, pl. 32, fig. 10); Podzorski & Håkansson (1987: 41, pl. 12, fig. 1), Navarro *et al*. (2000: pl. 14, figs 5–7), Riaux-Gobin *et al*. (2011: 13, pl. 1, fig. 6; pl. 8, figs 1–3), Lobban *et al*. (2012: 285, pl. 38, figs 5, 6), Stidolph *et al*. (2012: pl. 21, fig. 12) and Wisshak *et al*. (2014: 115, fig. 3F). All the latter works refer to taxa with diverse morphologies, sometimes without illustrating both valves (sternum valve, SV and raphe valve, RV).

On the other hand, Montgomery (1978: pl. 72, figs C–G, SEM) illustrated diatom specimens as *Cocconeis trachyderma* F.Meister (1935: 99, figs 63, 64) with features very close to those of *Achnanthes citronella*.

Accepted by Saúl Blanco Lanza: 4 Sept. 2015; published: 23 Sept. 2015



FIGURES 1–24. 1. *Stauroneis apiculata*. 2, 3. *Cocconeis apiculata*. 4. *Stauroneis*(?) *obesa*. 5. *Cocconeis robusta*. 6. *Rhaphoneis mammalis*. 7–9. *Achnanthes mammalis*. 10. *Achnanthes mammalis* var. *reticulata* according to Foged (see text, reproduced with permission of E. Schweizerbart). 11. *Achnanthes* (*Actinoneis*) *mammalis* var. *reticulata*. 12. Unnamed individual in Schmidt *et al*. (1895, pl. 198, fig. 40). 13, 14. *Cocconeis citrina*. 15–17. *Cocconeis citronella*. 18. *Cocconeis sabangi*. 19, 20. *Cocconeis trachyderma*. 21, 22. *Achnanthes schmidtii*. 23, 24 *Achnanthes schmidtii* (reproduced with permission of E. Schweizerbart). Scale bars = 20 µm.

The above remarks point that several taxa from the *Achnanthes citronella* group are difficult to discriminate and define clearly. We here i) clarify the nomenclatural history of *Achnanthes citronella*, ii) propose a new synonym to the latter, iii) detail the SEM morphology of the close taxon first described as *Cocconeis trachyderma*, iv) propose several new combinations concerning some allied taxa, and v) propose a tentative identification key mainly based on LM examinations.

Materials and Methods

Materials used in this study are derived from several sources (Table 1):

TABLE 1. Type slides examined. Slides cited or labelled by the author to contain this species. * in Riaux-Gobin *et al.* (2014). US = Smithsonian Institute. Z = Zurich University Herbarium. BR = Natural History Museum. - = no data.

Species	Type	Slide	Collection	Housed	Guide n°	Fig.
Cocconeis citronella	+	Cat. # 43609	A. Mann	US	D2312	44
Cocconeis citronella	-	2202	A. Mann	US	D2314	52
Cocconeis citronella	-	3905	A. Mann	US	D4518	54
Cocconeis citronella	-	2201	H.W. Henshaw	US	D2313	53
Cocconeis trachyderma	-	Nagasaki 3409000	F. Meister	Z	-	*fig. 1
Cocconeis trachyderma	-	Nagasaki 3409001	F. Meister	Z	-	*fig. 1
Cocconeis trachyderma	-	Nagasaki 3409003	F. Meister	Z	-	*fig. 1
Cocconeis trachyderma	-	Nagasaki 3409008	F. Meister	Z	-	-
Cocconeis trachyderma	-	Nagasaki 3409010	F. Meister	Z	-	-
Cocconeis trachyderma	-	Nagasaki 3409011	F. Meister	Z	-	-
Cocconeis trachyderma	-	Nagasaki 3409017	F. Meister	Z	-	-
Cocconeis trachyderma	-	Nagasaki off shells 22045	M. Voigt	Eawag, Dübendorf	-	-
Cocconeis trachyderma	-	Nagasaki off shells 22046	M. Voigt	Eawag, Dübendorf	-	-
Cocconeis trachyderma	-	Nagasaki off shells 22047	M. Voigt	Eawag, Dübendorf	-	-
Stauroneis apiculata	-	Patos guano	R.K. Greville	BR	BM 1753	-
Stauroneis(?) *obesa*	+	Curteis Straits Queensland	R.K. Greville	BR	BM 2736	-
Stauroneis obesa	-	-	R.K. Greville	BR	BM 2593	-
?*Achnanthes mammalis*	-	-	R.K. Greville	BR	BM 2887	-

a) Albert Mann's slide collection: Type slide Cat. # 43609. Labelled '*C. citronella* A.Mann'. Holotype: From Philippines (Jolo Jolo, Sulu Island) 3–17. Slide 2202, from Philippine Islands, labelled '*C. citronella* Mann nom. nov'. Slide 3905, Mann Phil. Diat., from Laysan Island #1 4/11/23, labelled '*C. citronella* Mann'. These slides are housed in the Smithsonian Institute, Washington (US).

b) Henry Wetherbee Henshaw's collection: slide 2201 from Jolo, Sulu Island 3-4-17. Labelled '*C. citronella* Mann nom. nov.'. This slide is housed in US.

c) Friedrich Meister's type material: F. Meister's slides are housed in the Zurich University Herbarium (Z). The slides 'Nagasaki 3409000'– '01', '03'– '08', '10'– '11'– '17' have been examined. F. Meister's handwritten notes assign these slides to the shell of a marine snail from Nagasaki (Japan), material collected by M. Voigt (Meister 1935: 96). These slides are supposed to contain *Cocconeis trachyderma*. Some Meister's notes roughly indicate the position of remarkable taxa on the slides, but no indication concerns *Cocconeis trachyderma*.

d) Manfred Voigt's slide collection: Several M. Voigt's slides have been prepared from the same sample than those from F. Meister (see above, 'Nagasaki off shells', 22045-46-47). The slide 22045 was pointed out, in M. Voigt's hand notes, to contain *Cocconeis trachyderma*. These slides are housed in the Swiss Federal Institute of Aquatic Science and Technology, Dübendorf.

e) Robert Kaye Greville's slide collection: Patos guano, BM 1753 containing *Stauroneis apiculata* Greville (1859: 30). Curteis Straits Queensland, coll. Dr. Roberts, BM 2736, holotype of *Stauroneis*(?) *obesa* Greville (1866: 237). Also from R.K. Greville's slide collection: BM 2593 and BM 2887. These slides are housed in the Natural History Museum, London (BM).

f) Society Archipelago material and preparation: The marine benthic samples were collected in Tahiti and Moorea Islands (from intertidal surface sediment, coral debris and lagoon macroalgae) and preserved in formaldehyde (10%

final concentration). For SEM examination, the samples were filtered through 1 µm Nuclepore filters and rinsed twice with deionised (milliQ) water to remove salts. Filters were air-dried and mounted onto aluminum stubs before coating with gold-palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi S-4500 SEM operated at 5 kV (C2M, Perpignan University, France). For LM examination, the sample was washed with distilled water to remove salts, treated with 30% H_2O_2 for 2 h at 70 °C to remove organic matter, rinsed several times in distilled water, alcohol-desiccated and mounted on glass slides using Naphrax® (Oscar E. Romero, pers. com.). Diatom slides were examined with a Zeiss Axiophot 200, with differential interference contrast (DIC) optics and photographed with a Canon PowerShot G6 digital camera (CRIOBE, France).

For the description of the frustule, terminology follows Anonymous (1975), Ross *et al*. (1979) and Round *et al*. (1990). As previously proposed, in particular by Riaux-Gobin *et al*. (2013), we designate the valve with a raphe as the raphe valve (RV) and the valve without a raphe as the sternum valve (SV).

Results

Achnanthes citronella has been more or less recently illustrated with different morphologies (see above). The examination of the type slide 43609 (D 2312 in US) allowed us to amend the original description and raise some ambiguities. Several taxa similar to *Achnanthes citronella* are detailed in Table 2, briefly described below or more extensively described and illustrated (*i.e*., *Cocconeis trachyderma*). Along their somewhat taxonomic intricate history, several of these allied taxa were previously proposed as synonyms. A tentative morphological identification key is proposed.

Achnanthes citronella (A.Mann) Hustedt in Schmidt *et al*. (1937: pl. 415, figs 3–8) (Table 2) *emend*. Riaux-Gobin (Figs 15–17, 25, 26, 33, 35–38).

Basionym: *Cocconeis citronella* A.Mann (1925: pl. 13, figs 3–6, reproduced here as Figs 15–17).

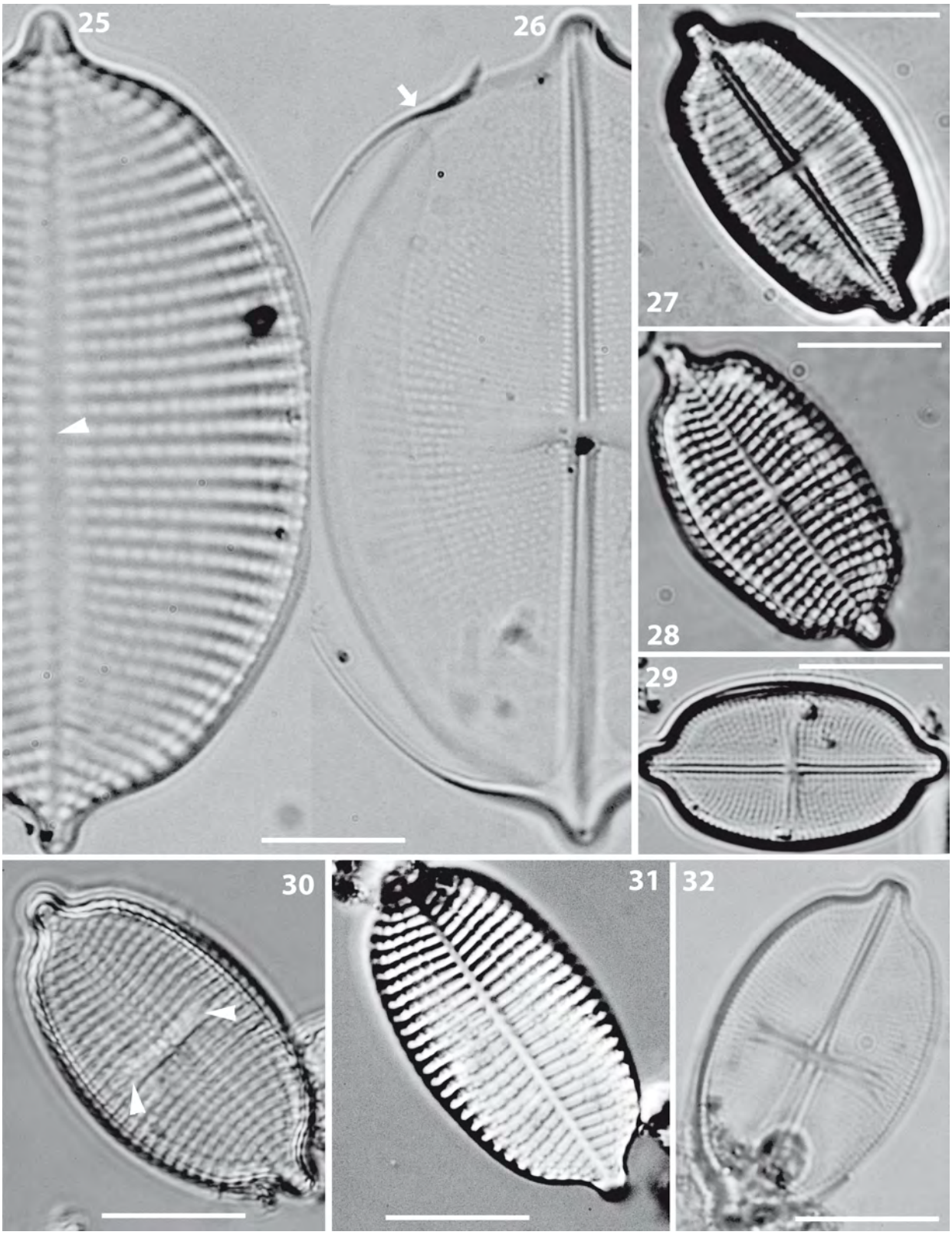
Heterotypic synonym: *Achnanthes mammalis* var. *reticulata* Cleve (1895: 187), *syn*. *nov*. As stated by Mann (1925: 'Cleve's form' [actually a variety] seems to be the same as […] in Schmidt's Atlas: plate 198, figs 35, 36, 40' (fig. 40 reproduced here as Fig. 12). *Achnanthes mammalis* var. *reticulata* (Fig. 11) is proposed to be a synonym of *Achnanthes citronella* since the morphology of the SV by Cleve fits that by A. Mann (Fig. 15), and because *Achnanthes mammalis* var. *reticulata* lacks the double striation present in *Achnanthes mammalis sensu* Cleve (Figs 8, 9, see description below).

Original diagnosis:—'Valves broadly oval with apiculate apices; lower valve with delicate radiating beaded lines closely set, slightly more evident in a band near each margin, otherwise very obscure and misty; almost reaching the raphe but lacking on either side of the central nodule, so that a hyaline stauros is produced which is about one-fifth the width of the valve; upper valve with widely set rows of coarse rectangular beads radially arranged and slightly curved toward the two apices, the outer beads of these rows next to the margins of the valve being plainly larger than the others; a hyaline median line corresponding to the raphe line of the lower valve. Length of valve 0.062–0.070; width of valve 0.034–0.039; lines on upper valve 6.5 in 0.01 mm.; lines on lower valve 21–25 in 0.01 mm (Mann 1925: 61).

Type:—PHILIPPINE ISLANDS. Sulu: Jolo Jolo (holotype: slide 43609, US! D 3212, here illustrated as Fig. 34, see Table 1).

Type observation and amended description:—The shape of the valves (Figs 25, 26) is broad-elliptical with apiculate apices (lemon-shaped), with no clearly-marked shoulders near the apices. The SV striae are composed of quadrangular areolae (with no axial arrangement, Figs 25, 33), radiate on all valve long and marginally curved at the apices (Fig. 38). The SV apices lack areolae (Fig. 38). The SV sternum is slightly elliptical and larger on the centre of the valve (Fig. 25, arrowhead). The SV stria density is 6.5–7.5 in 10 µm. The two published RV valves (figs 5, 6, *op*. *cit*.) are the same one oriented in opposite ways: they correspond to the RV mounted on the type slide. The RV valcocopula (RVVC) is open and lacks fimbriae (Fig. 26, arrow). The RV (Figs 35–37) stria density is 13.5–17.0 in 10 µm in mid-hemivalve, 17.5–18.0 along the raphe, 21–24 on the extreme margin (Fig. 36, arrowhead), *vs*. 21–25 in the original diagnosis. The central area is enlarged in a butterfly-shaped stauros (Fig. 35), relatively high and reaching not more than half-hemivalve (Fig. 35, arrowheads).

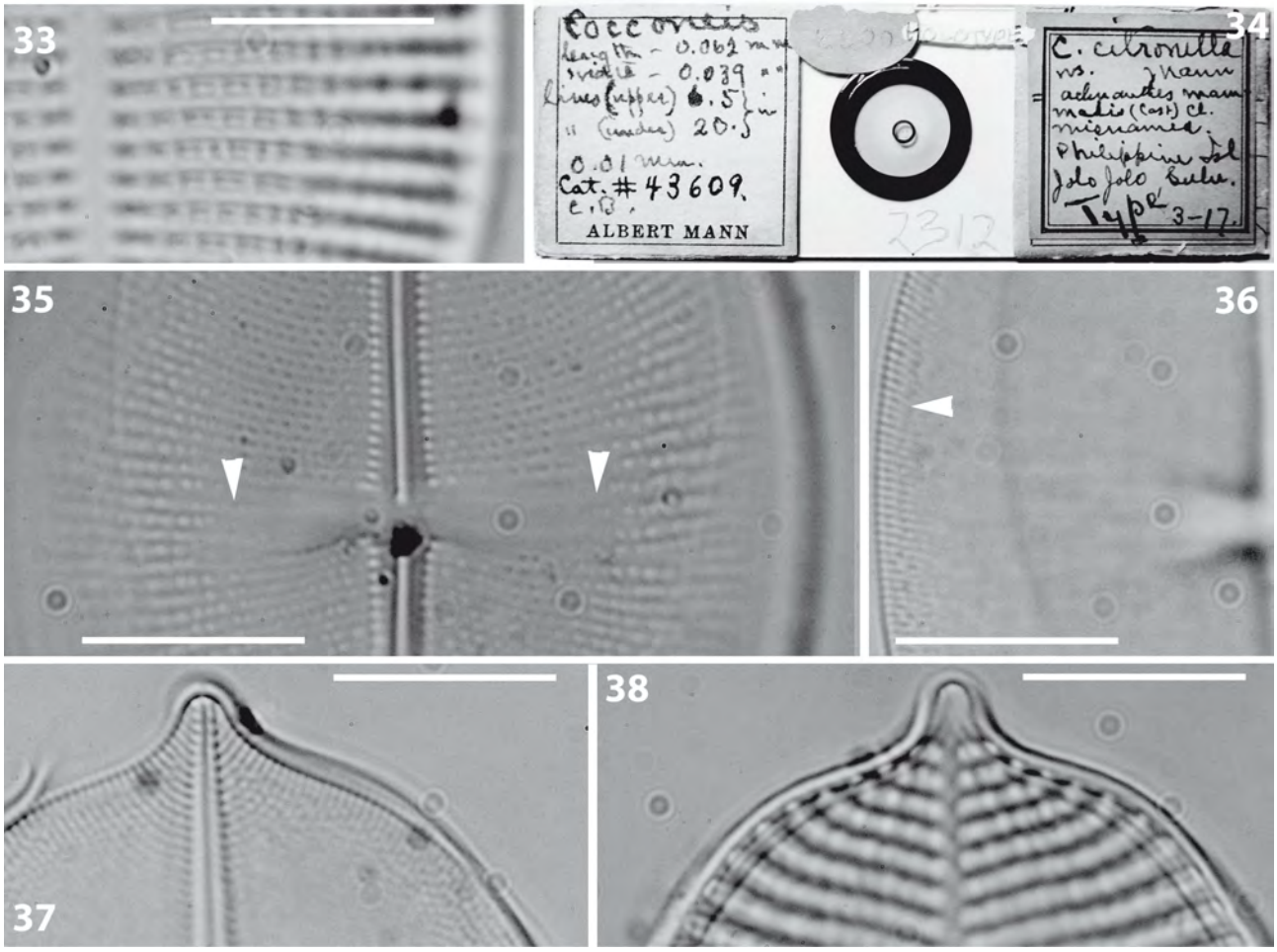
Remarks and ambiguities:—Hustedt in Schmidt *et al*. (1937: pl. 415, figs 3–8) established the combination *Achnanthes citronella* (A.Mann) Hustedt with *Cocconeis citronella* A.Mann (1925: 61) as basionym, *Cocconeis sabangi* F.Meister (1932: 12) as a probable synonym and rejecting *Achnanthes mammalis* (Castracane 1886: 48) Cleve (1895: 187) as synonym, 'since Castracane showed only one valve that could belong to different species'.



FIGURES 25–32. 25, 26. *Achnanthes citronella*. Individuals from type slide 43609, labelled as 'Jolo Jolo, Sulu, Philippine Islands, 3-17' (see Fig. 34), A. Mann's collection, housed in US. Lemon-shaped SV with an elliptic SV sternum (Fig. 25, arrowhead) and rectangular areolae without axial arrangement, RV finely striated, detached open valvocopula without fimbriae (Fig. 26, arrow) and a short butterfly-shaped stauros. 27–32. *Achnanthes trachyderma*. 27–29. Individuals from Meister's slides collection, housed in Z. Frustule from slide 3409001 showing a large RV stauros and fine RV striae (Fig. 27), and SV coarse striation (Fig. 28). 29. Illustration of the lectotype. A RV from slide 309008, with a fine striation and a narrow extended stauros. 30–32. *Achnanthes trachyderma*. Individuals from Society Archipelago, South Pacific, with relatively large stauros (Fig. 30, arrowheads), SV striae parallel, only slightly radiate at the apices, narrow sternum (Fig. 31). 32. RV with fine striae and large and thin stauros. Scale bars = 10 µm.

TABLE 2. *Achnanthes* and *Cocconeis* taxa discussed in the text: morphological comparison. nd = no data. ( ) = following illustration.

	Achnanthes trachyderma (F.Meister) *comb. nov.*	*Achnanthes apiculata* (Greville) *comb. nov.*	*Achnanthes obesa* (Greville) *comb. nov.*	*Achnanthes mammalis* (Castracane) Cleve var. *mammallis*	*Achnanthes mammalis* var. *reticulata* Cleve	*Achnanthes citrina* (Schmidt in Schmidt *et al.*) Peragallo	*Achnanthes citronella* (A.Mann) Hustedt	*Achnanthes schmidtii* Heiden	*Cocconeis sabangi* F.Meister
Ref.	This study	This study	This study	Cleve (1895)	Cleve (1895)	Peragallo (1897)	Hustedt in Schmidt *et al.* (1874–1959)	Heiden & Kolbe (1928)	Meister (1932)
Basionym/ Synonyms	*Cocconeis trachyderma*	*Stauroneis apiculata*	*Stauroneis*(?) *obesa*	*Rhaphoneis mammalis*, Synonyms: *Stauroneis apiculata*, *Stauroneis*(?) *obesa*, ?*Stauroneis thaitiana*		*Cocconeis citrina*	*Cocconeis citronella* as new species? or new name	*Achnanthes neokisselevii* VanLandingham (1969: 1482) replaced name for *Eucocconeis schmidtii* Kisselev (1931: 99, 115) (priority for *Achnanthes schmidtii*)	
	Figs 30–32, 45–57	Fig. 1, reproduced from Greville (1859)	Fig. 4, reproduced from Greville (1866)	Fig. 4, reproduced from Greville (1866); Fig. 6, reproduced from Castracane (1886); Figs 7–9, reproduced from Cleve (1895)	Fig. 11, reproduced from Cleve (1895)	Figs 13, 14, reproduced from Schmidt in Schmidt *et al*. (1874–1959)	Figs 15–17, reproduced from Mann (1925)	Figs 21, 22, reproduced from Schmidt in Schmidt *et al*. (1874–1959); Figs. 23, 24, reproduced from Simonsen (1992)	Fig. 18, reproduced from Meister (1932)
Valve shape	elliptic to oblong-elliptic, apiculate	elliptic, apiculate	broad elliptic with 3 lateral gibbosities	elliptic, apiculate	elliptic, apiculate	elliptic to almost orbicular, apiculate	broadly oval, strongly apiculate	broadly oval, strongly apiculate	elliptic, apiculate
Length (µm)	24.1–31.5 ($\bar{x}$: 28.2 ± 2.7)	50.8 (Greville 1859)	43	45–63	see type	40–57	62–70	25–46	20–33
Width (µm)	11.5–17.5 ($\bar{x}$: 14.4 ± 1.4)	25.4 (Greville 1859)	(30)	20–38	see type	25–40	34–39	13–22	11–17
SV striae: density in 10 µm and aspect	9.8–12.1 ($\bar{x}$: 10.9 ± 0.7)	13.4, fine (Greville 1859)	13 (only slightly oblique on apices, composed of oblong rectangular areolae)	6, slightly radiate costae alternating with double rows of small puncta	see type. Without rows of puncta between the costae, but connected by longitudinal costae, forming an irregular reticulum	7–8 (strongly radiate on apices, composed of oblong areolae, in longitudinal zig-zag rows)	6.5	8.5–10	12, subradiate
SV sternum shape	narrow	nd	(linear, narrow)	linear, narrow	(slightly elliptic)	(elliptical, relatively large)	(slightly elliptic, narrow to slightly enlarged)	linear, narrow	(linear, narrow)
RV striae: density in 10 µm and aspect	22.9–26.4 ($\bar{x}$: 24.3 ± 1.1) striae delicate, radiate	nd	(21) (striae delicate, strongly radiate)	21 (middle) to 25 (ends) In the middle alternately longer and shorter, finely punctate	see type nd	15–16 (coarsely punctuate)	21–25 delicate radiating beaded numerous lines, obscure, almost reaching the raphe	5–6 (coarsely punctuated, *cf.* Simonsen 1992, pl. 30, fig. 6)	30 subradiate



FIGURES 33–38. *Achnanthes citronella*. 33. Details of the SV striation. 34. Type slide 43609. 35. RV central area with the short and high/thick stauros (arrowheads). 36. Marginal dense RV striae (arrowhead). 37. RV apex with curved striae regularly spaced. 38. SV apex lacking areolae. Scale bars = 10 µm.

Surprisingly, Mann (1925: pl. 13, figs 3–4) did not illustrate the SV selected by himself as type material (see Fig. 25), but two other SVs that are narrower (elongate to linear-elliptical), with a larger sternum and a low stria density (Figs 15, 16). It would have been interesting to search for more valves in the original raw material (Jolo Jolo, Philippines), but neither the slides made from the raw type material, nor other mounted *C. citronella* RVs are available from A. Mann's collection. On the other hand, three slides labelled as '*C. citronella* Mann *nom. nov.*', housed in US, only contain each one isolated SV valve of the species: 1) Fig. 39, from slide 2202 (Fig. 42), upper valve, from Philippine Islands, Albert Mann collection, annotated: '0.070x0.034 mm, Sch. At. 198, 40, no name?', 2) Fig. 40, from slide 2201 (Fig. 43), from Jolo, Sulu Td. 3-4-17, H.W. Henshaw collection, annotated: '0.070x0.037 mm upper valve' and 3) Fig. 41, from slide 3905 (Fig. 44), Laysaw Is. #1, wash from algae in 3 ft. of water onshore reef. 4/11/23, Albert Mann collection, annotated: 'length 0.033 1/2 normal size, Mann Phil. Diat. Styrax 6/24'. The individuals illustrated in Figs 39, 40 have a large size, a large SV sternum and a low SV stria density (< 6 in 10 µm), while the individual illustrated in Fig. 41 has a small length, a narrow SV sternum, areolae present on apices and dense SV striae (*ca*. 12 in 10 µm). The latter individual (as annotated on the label) does not fit the original diagnosis of *Achnanthes citronella* and probably pertains to *Achnanthes trachyderma* (see below).

Meister (1935) showed some doubts concerning the correspondence of the RV valve of *Cocconeis citronella* illustrated by Mann (1925: figs 5, 6, reproduced here as Fig. 17) to the SV illustrated in figs 3, 4 (*op. cit.*, reproduced here as Figs 15, 16). The shape of the unpublished SV from the type slide material (Fig. 25) obviously pertains to a different taxon than the one corresponding to the published SVs (Figs 15, 16). Unfortunately, Mann (1925) provides only one RV image (Figs 17, 26), so, it is difficult to insure the correspondence of this RV to the published SVs. Our hypothesis is that Figs 25, 26 possiby refer to a new and true *Cocconeis* (*Achnanthes*) *citronella*, while Figs 15, 16 better fit in another taxon such as that illustrated in Fig. 11 (*Achnanthes mammalis* var. *reticulata*).

***Cocconeis citronella*—new species *vs*. new name:**—In the protologue, A. Mann showed some hesitation between 'replacement name' (*nom. nov*.) for *Achnanthes mammalis sensu* P.T. Cleve *non* (Castracane) Cleve, and name of a new species for his *Cocconeis citronella* [see the original diagnosis entitled: '*Cocconeis citronella*, new species?'; the annotation '*nom. nov*.' on several slides and 'new name' on captions (*op. cit*.: 178, pl. 13, figs 3–6); and the annotation on the type slide 43609 (see Fig. 34): '*C. citronella* ns Mann = *Achnanthes mammalis* (Cast.) Cl. misenamed']. Mann (1925: 61) obviously did not examine the type of *Rhaphoneis mammalis* and decided quite arbitrarily to describe his material as a new taxon. However, according to McNeill *et al*. (2012: art. 41.7, Note 3), *Cocconeis citronella* A.Mann is the name of a new species and cannot be a replacement name.

Allied taxa pertaining to the Achnanthes citronella *morphological group and doubtful taxa*

Achnanthes trachyderma* (F.Meister) *comb. nov. (Figs 19, 20, 27–29, Table 2)

Basionym: *Cocconeis trachyderma* F.Meister, *Berichte der Schweizerischen Botanischen Gesellschaft* 44: 99, figs 63, 64. 1935 (figures reproduced here as Figs 19, 20).

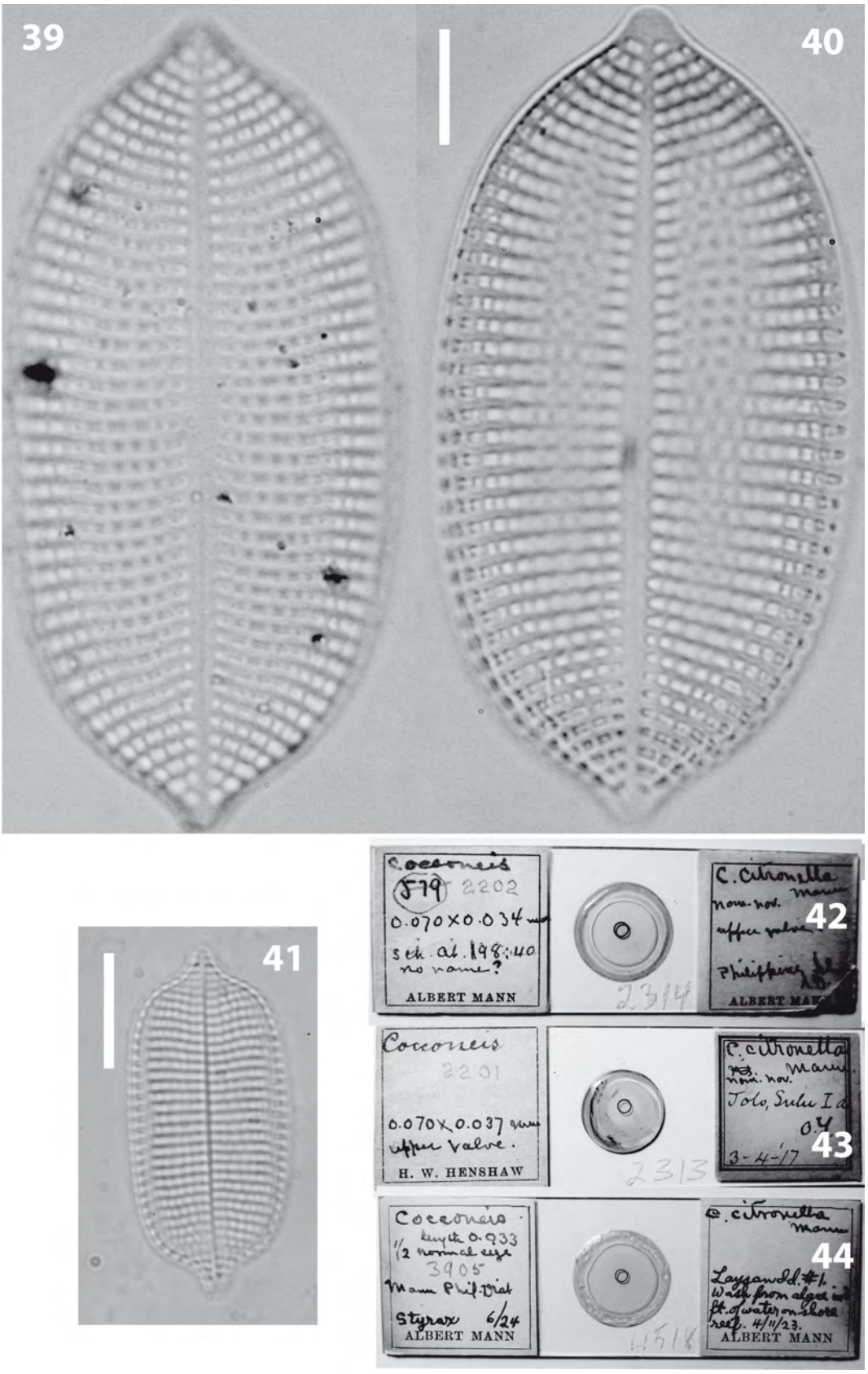
Translation of the original diagnosis:—'Valves elliptical with elongate, capitate endings, 29 to 32 µm long, 14 to 15 µm wide. Raphe valve with 26 radiate, punctuate-dotted striae and a stauroid central area, which extends beyond the midline of the half valve. Rapheless valve with a very narrow pseudoraphe and 9 to 11 coarsely punctate striae in 10 µm. Not rare in Nagasaki'.

Type:—JAPAN. Nagasaki, 'shell of a marine snail from Nagasaki', see Materials & Methods (lectotype here designated among the numerous slides from Nagasaki studied by Meister and containing this species: Z!, slide 3409008 in coll. F. Meister's, illustrated here as Fig. 29. See Table 1).

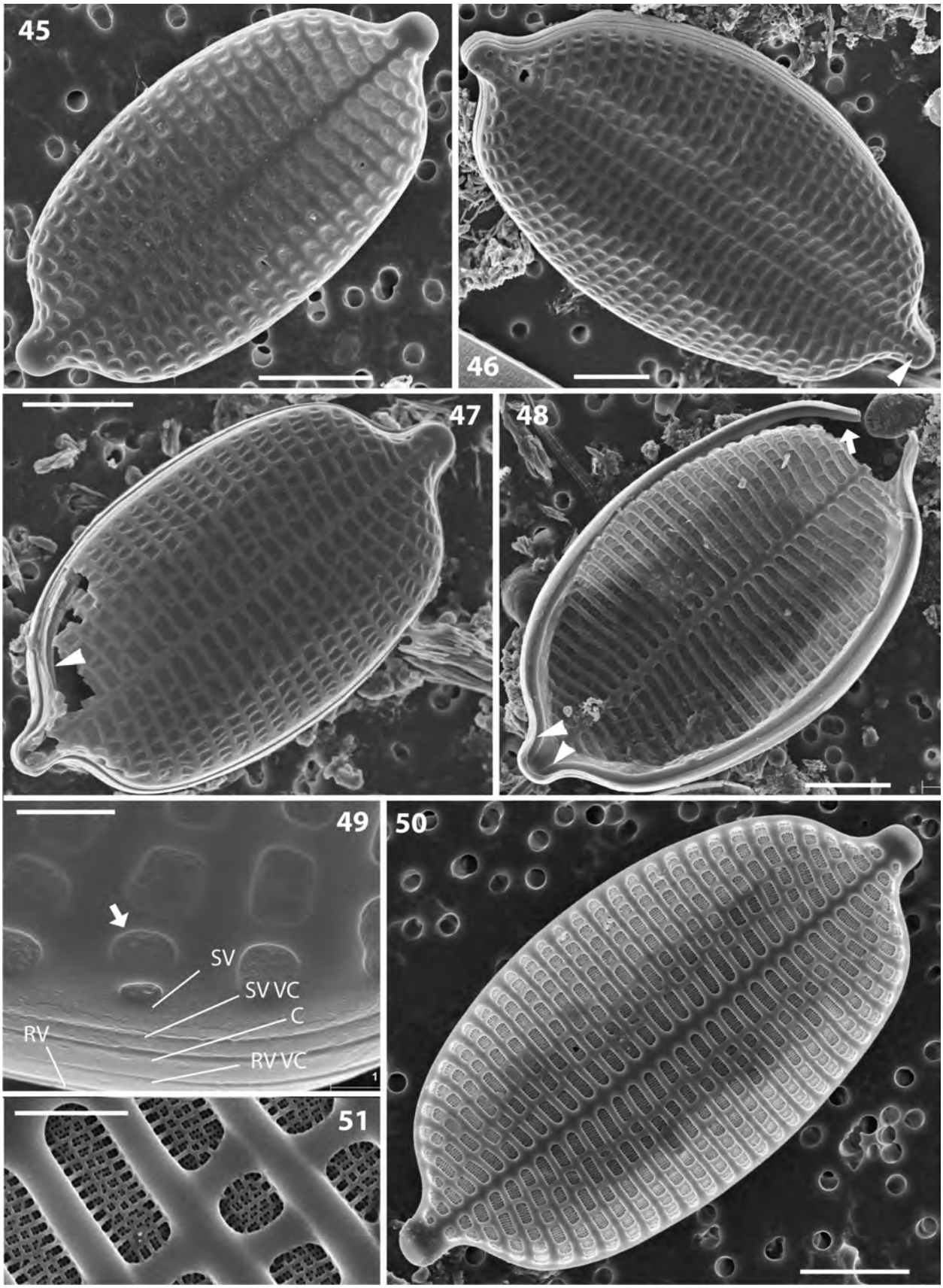
Type observation:—The taxon is rare in F. Meister's and M. Voigt's slides. The individuals are small (*ca*. 25.6 µm long, 13.2 µm wide; *ca*. 11.5 SV striae in 10 µm and 25.5 RV striae in 10 µm), relatively narrow (L/W: 1.94), with well-marked shoulders near the apices. The RV stauros is wide-ranging and thin, reaching almost the margins (Fig. 29). It can be remarked that the Nagasaki material also contains individuals slightly bigger (*ca*. 33.1 µm long, 17.4 µm large, 10.2 SV striae in 10 µm and 21.3 RV striae in 10 µm) but with an extended stauros as in the smaller individuals.

Remarks:—M. Voigt, in his hand notes about '*Cocconeis trachyderma* v. *elliptica* Mfrd. Vgt.' (an undescribed variety marked from slide 22045, Nagasaki: 'similar Meister's type') refers to '*Achnanthes*?' as a remark, proving his doubts about its belonging to *Cocconeis*. Meister (1935: 99) also illustrated a SV of *Cocconeis citronella* from his Nagasaki material, with the remark that the latter has a lanceolate pseudoraphe, being narrow in *Cocconeis trachyderma*. Furthermore, Meister (1935: 99) specified that the central area is much shorter in *Cocconeis citronella* than in *C. trachyderma*.

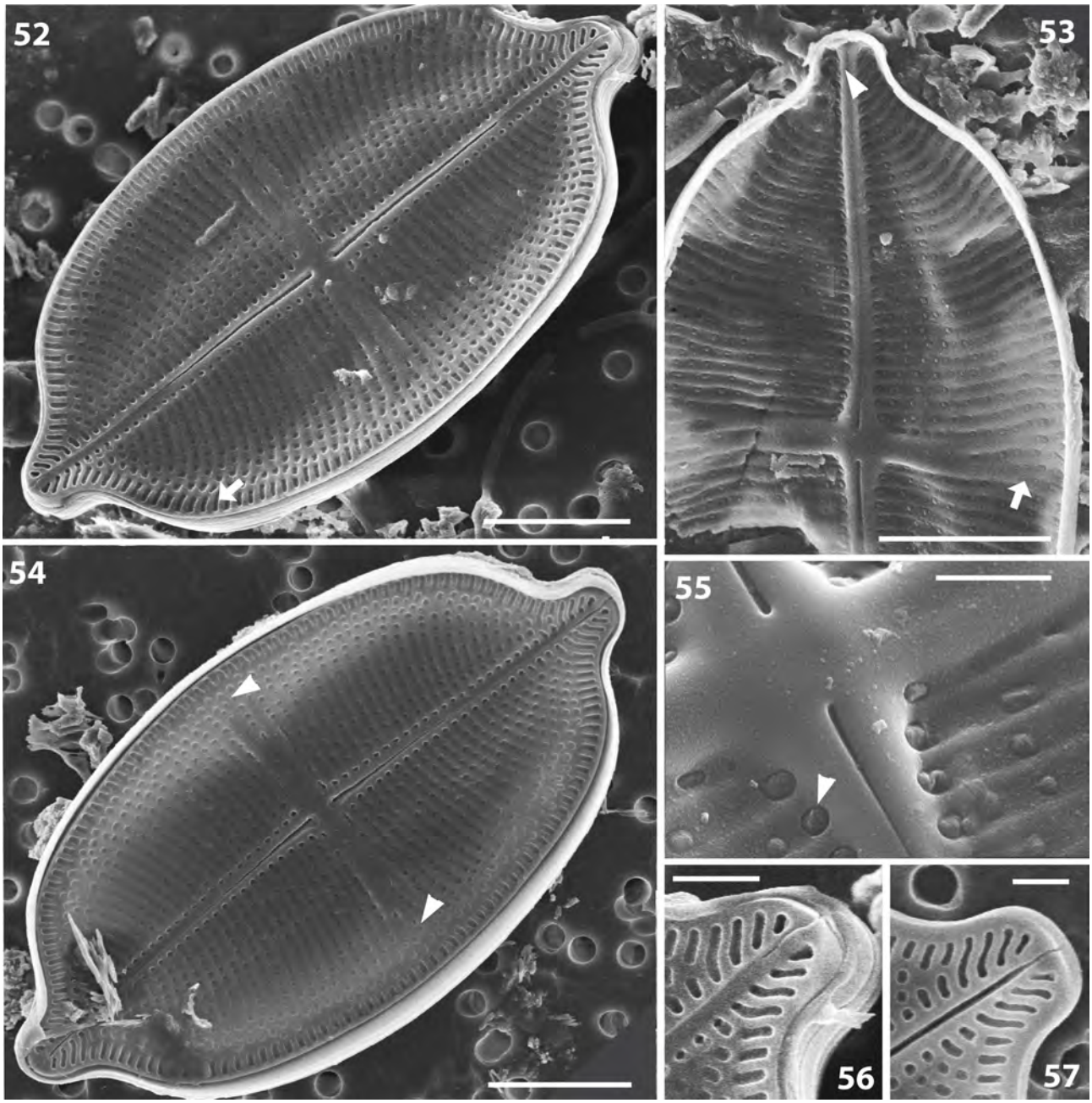
Material from Society Archipelago (South Pacific):—(LM: n=3, Figs 30–32; SEM, n=21, Figs 45–57). The individuals from the Society Archipelago are always small (25.6 + 2.9 µm long; 13.2 ± 0.9 µm wide), the SV stria density is higher than in *A. citronella* (Table 1) and the stauros is extended; the SV sternum is narrow. This taxon is frequent in Tahiti and Moorea Islands. The morphology of the South Pacific taxon (Figs 30–32) roughly matches that of *Achnanthes trachyderma comb. nov*. The SEM examination allows to add some details to the diagnosis: the SV is strongly convex, one row of SV large areolae lies on each side of the narrow sternum (Figs 45–47), the SV apices are void of areolae except in rare cases (Fig. 46, arrowhead), the valvocopula system lacks fimbriae (Fig. 47, arrowhead). The SV areolae hymenes are externally smooth (with no apparent perforations or slits, Fig. 49), and lying under the valve face (Fig. 49, arrow); in internal view they show a complex structure with a grid pattern (Figs 48, 50, 51). The cingulum is composed of the valvocopulae and an additional copula (C in Fig. 49). The SV striae (11.5 ± 0.7 striae in 10 µm) are parallel in mid-valve to only slightly radiate at the apices (Fig. 50). The RV is slightly concave (Fig. 52), finely striated (25.5 ± 1 striae in 10 µm), with striae strongly radiate and composed of small areolae internally closed by domed hymenes (Fig. 55, arrowhead), with one row of longer areolae near the margin (Fig. 52, arrow). The raphe is filiform and straight, the axial area narrow, the central raphe endings straight and close to each other, the terminal raphe fissures very slightly undulating and continuing on the mantle (Figs 56, 57). The central area is enlarged in a narrow but extended stauros delineated on the margins by short striae (Fig. 53, arrow; Fig. 54, arrowheads). Helictoglossae are low (Fig. 53, arrowhead).



FIGURES 39–44. *Achnanthes citronella*. 39, 40. Large oblong-elliptic individuals with coarse SV striation. 41. Small-celled individual with dense SV striation (see text). 42. Slide 2202 from A. Mann collection labelled as '*C. citronella* Mann nom. nov.'. 43. Slide 2201 from H.W. Henshaw collection labelled as '*C. citronella* Mann nom. nov.'. 44. Slide 3905 from A. Mann collection labelled as '*C. citronella* Mann 1/2 normal size'. Scale bars = 10 µm.



FIGURES 45–51. *Achnanthes trachyderma*. Individuals from Society Archipelago, SEM. 45. SV external side, with narrow sternum. 46. Apices with areolae (arrowhead). 47. Valvocopulae system lacking fimbriae (arrowhead). 48. SV internal side, with open SVVC (arrow) and no fimbriae (arrowheads). 50. Internal SV areolae pattern and no areolae on apices. 49. Detail of the cingulum composed of the two valvocopulae (SVVC and RVVC) and a supplementary copula (C). 51. Detail of the internal structure of the SV areolae. Scale bars = 5 µm (Figs 45–48, 50); 1 µm (Figs 49, 51).



FIGURES 52–57. *Achnanthes trachyderma*. Individuals from Society Archipelago, SEM. 52. RV external side with laciniate stauros reaching almost the margin. 53. RV internal side with the stauros marginally delineated by very short striae (arrow), low helictoglossa (arrowhead). 54. RV external side with large stauros (arrowheads). 55. Detail of the central area in internal side, with areola domed hymenes (arrowhead). 56. RV apex with strongly bent striae with a marginal row of larger areolae. 57. Terminal raphe fissure continuing on the mantle. Scale bars = 5 µm (Figs 52–54); 1 µm (Figs 55–57).

Achnanthes apiculata* (Greville) *comb. nov. (Figs 1, 58–61, Table 2)

Basionym: *Stauroneis apiculata* Greville, *Edinburgh New Philosophical Journal, New Series* 10: 30, pl. 4, fig. 8. 1859 (figure reproduced here as Fig. 1).

Description:—From David M. Williams's photographs (Williams 1988: 47, pl. 54, figs 2, 3), it can be stated that it has an elliptic-apiculate shape, 12.5–13.0 striae in 10 µm, with an extended but thin stauros clearly present. Individual length 45 µm. These images do not permit to determine if the taxon is a biraphid as supposed by R.K. Greville. Our type examination (Figs 58–61) shows that it is a monoraphid diatom, even if the RV striation is difficult to focus on (Figs 60, 61). The stauros extends to the half of the valve width. The SV striae, slightly radiate and present at the apices (Fig. 59, arrow), are composed of rectangular-oblong areolae, the SV sternum is narrow (Fig. 58).

Type:—UNITED STATES. California, Patos guano (slide BM 1753, *cf*. Williams 1988). Figs 58–61.

Remarks:—Since *Achnanthes apicultat*a (R.M. Patrick 1945: 167, pl. 1, figs 4–5) R.A. Matthews (1982: 193) is an invalid name, it cannot prevent the use of this name for a new combination. *Stauroneis apiculata* is cited by P.T. Cleve as a synonym of *Achnanthes mammalis* (Castracane) Cleve (1895). See the discussion in Mann (1925). Stidolph *et al*. (2012: pl. 22, fig. 22) illustrate an individual (with both valves and apparently uniseriate striae) as *Cocconeis apiculata*, with a RV stauros and no shoulders near apices, stating that 'this species will be transferred to the genus *Schizostauron* Grunow (1867: 28)' (A. Witkowski *in litt*. 2012).

Achnanthes mammalis (Castracane) Cleve (1895: 187, pl. 3, figs 13–15) (Figs 7–9, Table 2)

Basionym: *Rhaphoneis mammalis* Castracane (1886: 48, pl. 26, fig. 3, upper valve reproduced here as Fig. 6).

Homotypic synonyms: *Actinoneis mammalis* (Castracane) Cleve (1895: 187), *Cocconeis mammalis* (Castracane) F.W.Mills (1933: 426, 435), *Nematoplata mammalis* (Castracane) Kuntze (1898: 146) (Fourtanier & Kociolek 2009, 2011).

Type:—THAITI. Challenger material from the harbor of Tahiti, not found in BM.

Remarks:—Among P.T. Cleve's figures 13–15 (1895: pl. 3), the SV illustrated in figs 14, 15 (reproduced here as Figs 8, 9) can be attributed to *Raphoneis mammalis*, but with a detail absent in the original description: the presence of a double row of small puncta per stria (Fig. 9). The fig. 14 (reproduced here as Fig. 7) illustrates a RV that may be identified either as *Stauroneis thaitiana* or as *Stauroneis apiculata* (Fig. 1), seeming very close to each other. Unfortunately, no Castracane slide housed in BM is labelled as *Stauroneis thaitiana*. Concerning *Stauroneis*(?) *obesa* Greville, the type examination by Williams (1988: 47, pl. 54, figs 5, 6) and our own observations (see below) definitively establish its belonging to the Achnanthales, with particular characters (see below).

According to Foged (1978: 28, pl. 13, fig. 6 reproduced here as Fig. 10 with permission of E. Schweizerbart), Fig. 10 would illustrate *Achnanthes mammalis* var. *reticulata* with apparently a double row of puncta per stria, and without the reticulate aspect shown in the original illustration of *Achnanthes mammalis* var. *reticulata* Cleve (1895: 187, pl. 3, fig. 16, reproduced here as Fig. 11). Furthermore, the smooth lemon shape (without shoulders) of the valve illustrated by Foged (1978) would be closer to *Achnanthes mammalis* var. *mammalis* than to *Achnanthes mammalis* var. *reticulata*.

In slide BM 2887 (R.K. Greville's collection), an individual with biseriate SV striae (Figs 62–64) and lemon-shaped valves (without shoulders) may be close to *Achnanthes mammalis*. This taxon has a butterfly-shaped large RV stauros (Fig. 64) permitting to differentiate it from *Achnanthes meisteri* Hustedt in Schmidt *et al*. (1937: pl. 415, figs 19, 20). Note that BM 2887 is labelled as *Stauroneis obesa* but modern microscopy permits to resolve the unique biseriate structure of the SV striae (Figs 62, 63).

Achnanthes obesa* (Greville) *comb. nov. (Figs 4, 65–67, Table 2)

Basionym: *Stauroneis*(?) *obesa* Greville, *Transactions of the Botanical Society of Edinburgh* 8: 237, pl. 3, fig. 12. 1866 (figure reproduced here as Fig. 4).

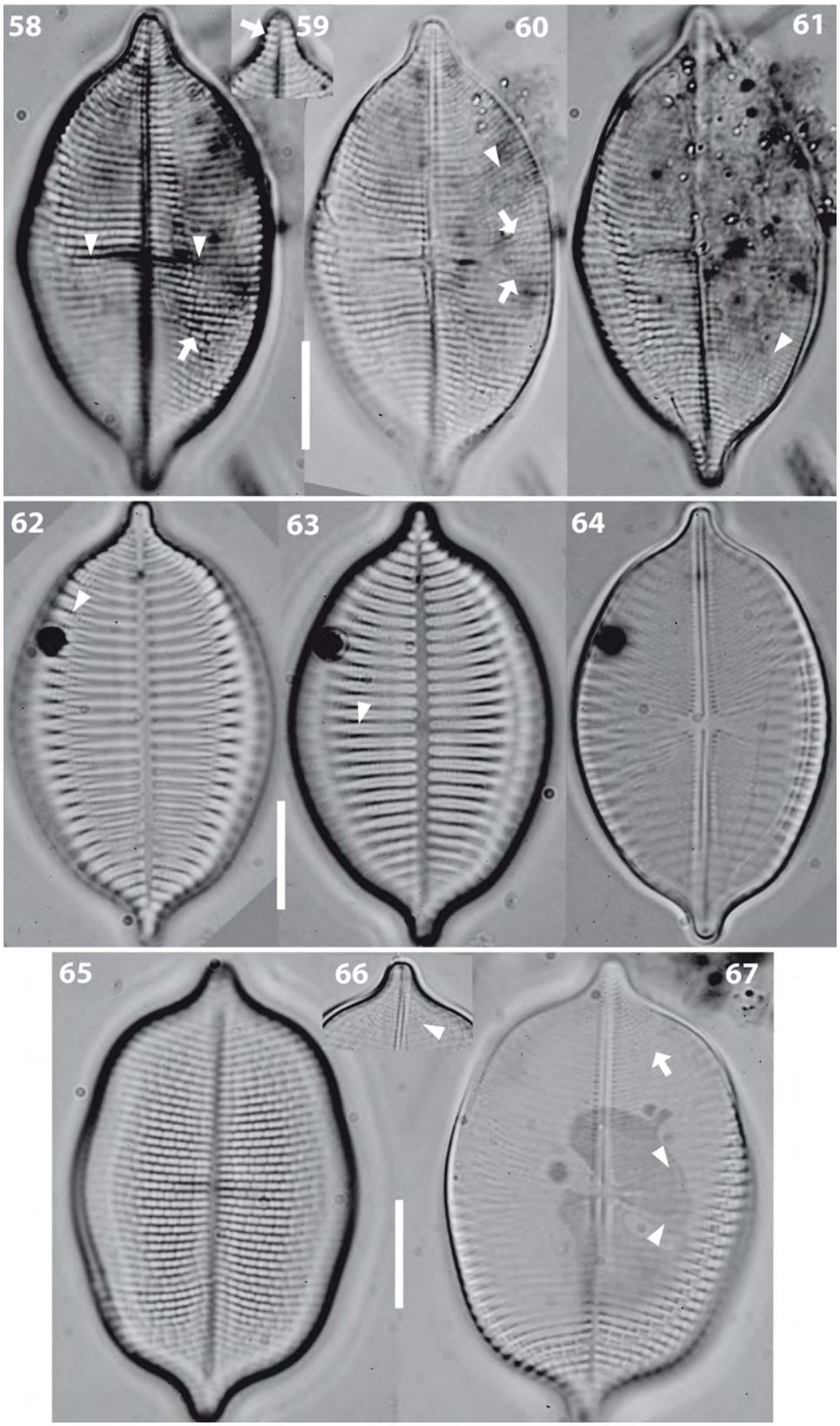
Synonym: *Navicula obesa* (Greville) A.Mann, *pro parte typica*.

Type:—AUSTRALIA. Queensland: Curteis Straits (slide BM 2736, *cf*. Williams 1988: 47, pl. 54, figs 5, 6).

Remarks:—From D.M. Williams's type photographs (Williams 1988): individual length 43 µm, SV with 13 striae in 10 µm, valve broad elliptic with three lateral gibbosities per hemivalve. Presence of a short stauros in fig. 5, while absent in fig. 6. The last remark implies that this taxon belongs to order Achnanthales and that the question mark by R.K. Greville probably denotes his hesitating about classifying this taxon.

Two individuals were observed in slide BM 2736 and one in BM 2593 (isotype slide also labelled as *Stauroneis obesa*) (Figs 65–67). The individuals have undulated lateral margins, large width, narrow SV sternum, dense and parallel SV striae (13 in 10 µm), only slightly oblique at apices, RV finely striated (*ca*. 21 striae in 10 µm, Figs 66, 67) and a high butterfly-like stauros (Fig. 67, arrowheads). In view of his unique morphology and the specific epithet, we propose *Achnanthes obesa* to be restricted to the individuals with broad valves and lateral gibbosities.

In slide BM 2593 we observed an individual without lateral gibbosities (length 39 µm, width 20 µm, 11 SV striae in 10 µm, *ca*. 23 RV striae, not illustrated here) but its length/width is high (2.0 versus 1.7 for the individuals with gibbosities). The latter narrow individual can hardly be defined as '*obesa*' and may probably pertain to *Achnanthes trachyderma* (see above).



FIGURES 58–67. 58–61. *Achnanthes apiculata comb. nov*. 62–64. *Achnanthes* cf. *mammalis*. 65–67. *Achnanthes obesa comb. nov*. 58. Individual from BM 1753, note the SV oblong rectangular areolae (arrow) and the position of the underlying RV extended and narrow stauros (arrowheads). 59. Apical areolae (arrow). 60. Laciniate marginal striae around the stauros (arrows). 60, 61. RV strongly radiate striae (arrowheads). 62, 63. Individual from BM 2887 with biseriate SV striae (arrowheads). 62. Apices free of areolae. 64. RV striae strongly radiate, stauros extended and high, reaching half valve width. 65, 66. Individual from BM 2593. 67. Individual from BM 2736, note the lateral gibbosities. 65. SV rectangular areolae. 66. RV striae strongly bent on apices (arrowhead). 67. Butterfly RV stauros (arrowheads) and striae radiate and thin (arrow). Scale bars = 10 µm.

Observations:—*Stauroneis obesa* was cited by Cleve (1895) as a synonym of *Achnanthes mammalis*. Mann (1925) recombined the first taxon as *Navicula obesa* (Greville) A.Mann, but on his illustrations (pl. 23, fig. 6 and pl. 24, fig. 1, *op. cit*.) the striae are strongly radiate and curved, while they are straight and only radiate at the apices in *Stauroneis obesa* (Williams 1988: pl. 54, figs 5, 6, reproduced here as Figs 65–67). The outline of *Navicula obesa* (see above) does not match the illustration by Greville (1866: pl. 3, fig. 12, reproduced in Fig. 4); however, the type of *Navicula obesa* remains that of its basionym, *Stauroneis*(?) *obesa* (see McNeill *et al*. 2012, art. 7.3) and *Navicula obesa* is a synonym of *Achnanthes obesa*. On the other hand, the biraphid diatom observed and illustrated by A. Mann under this name belongs to an indeterminate taxon of the order Naviculales.

Achnanthes schmidtii Heiden in Heiden & Kolbe (1928: 581) (Figs 21, 22, Table 2)

Type:—pl. 198, figs 37, 38 in Schmidt *et al*. (1895) (designated by Simonsen 1992: 31), reproduced here as Figs 21, 22.

Remarks:—The individuals are relatively small (25–46 µm long, 13–22 µm wide, with 8.5–10.0 SV striae in 10 µm). Following Simonsen (1992: pl. 30, figs 6–9; fig. 7 reproduced here as Fig. 23 and fig. 6 reproduced here as Fig. 24 with permission of E. Schweizerbart), *Achnanthes schmidtii* is a synonym of *Achnanthes citronella*. Nevertheless, the RV of *Achnanthes schmidtii* (Fig. 24) has coarse areolae and a very reduced stauros, therefore it may be considered a separated entity.

Achnanthes citrina (A.Schmidt) Peragallo (1897: 4) (Figs 13, 14)
Basionym: *Cocconeis citrina* A.Schmidt in Schmidt *et al.* (1895: pl. 198, figs 28–30, reproduced here as Figs 13, 14).

Remarks:—The outline of this taxon is almost discoid with apiculate apices (length 39–58 µm, width 24–49 µm). The RV and SV have a low density of striae (*ca*. 8 in 10 µm); the RV striae are composed of a limited number of areolae, and there is no stauros (Fig. 14). Mann (1925: 61) evoked a certain similarity of the latter taxon with that in Schmidt's Atlas: pl. 198, figs 35, 36, 40, 'except that the lower valve […] is very different'. A SV of this taxon has been illustrated by Desikachary (1988: vol. 5, pl. 402, fig. 7), but without a recent description or illustration of the RV, we prefer not to include this taxon in the key.

Cocconeis sabangi F.Meister (1932: 28, pl. 9, fig. 63) (Fig. 18)

Remarks:—Small taxon (23–33 µm long, 11–17 µm wide), with 12 SV striae in 10 µm and 30 RV striae in 10 µm. Meister (1932) did not illustrate the RV of his new taxon, but referred to figs 33–41 in Schmidt's Atlas (pl. 198) with a remark about the incorrect striation in Schmidt's figures where the fine striation of the RV is hidden by the rough structure of the SV. Hustedt in Schmidt *et al*. (1937) suggests *Cocconeis sabangi* to be a synonym of his new combination *Achnanthes citronella*. Foged (1984) also indicates *Cocconeis sabangi* to be a synonym of *Achnanthes citronella*, but he also proposed *Cocconeis sabangi* to be a synonym of *Cocconeis apiculata*. This doubtful taxon is not included in the identification key.

Cocconeis apiculata A.Schmidt in Schmidt *et al*. (1895: pl. 198, figs 31–32) (Figs 2, 3)

Annotation in caption by A. Schmidt: '*Cocconeis apiculata* A.Schmidt, following Grove = *Cocconeis robusta* Leud. Fortm.'

Type:—Schmidt's type material from the Cape of Good Hope has not been found, therefore Schmidt's figures 31–32 are considered as types.

Description:—Following Schmidt's figures: length 36–42 µm, width 19–23 µm, *ca*. 10–12 SV striae in 10 µm. No stauros. *Cocconeis robusta* Leuduger-Fortmorel (1879: 11, pl. 1, fig. 1 reproduced here as Fig. 5), cited by A. Schmidt as similar to his *Cocconeis apiculata*, shows apiculate apices that may be similar to *C. apiculata*, while all other features are different: in *C. robusta* the striae are short and robust, radiate but not curved, the axial area is wide-elliptical, devoid of structures, the valve shape is elongate. *Cocconeis robusta* may be close to *Stauroneis australis* Greville (1863: 579, pl. 15, fig. 13). *Stauroneis australis* was typified by Williams (1988: BM 2678, holotype, pl. 54, fig. 7, individual length 110 µm). From D.M. Williams's photograph, SV has 9 striae in 10 µm, with striae coarser near the margin and irregularly spaced, and presents a short, well-identifiable stauros.

Remarks:—A. Schmidt in Schmidt *et al*. (1895) did not refer directly or indirectly to *Stauroneis apiculata* (Fig.

1); therefore, this name cannot be the basionym of his *Cocconeis apiculata* which thus is clearly the name of a new species. In fact, the stauros present in *Stauroneis apiculata* (Williams 1988, pl. 54, figs 2, 3; and our Figs 1, 58, 60, 61) is not illustrated in *Cocconeis apiculata* A.Schmidt in Schmidt *et al*. (Figs 2, 3). Following these remarks, we can note that Mann (1925: 61, 62) probably improperly stated that 'Schmidt'…'makes *Cocconeis apiculata* (Greville) A.Schmidt and illustrates in the latter's Atlas, plate 198, figures 31, 32'. Mann (1925: 60) also proposed Schmidt Atlas's fig. 38 (unnamed in pl. 198) to be the same *Cocconeis apiculata* as fig. 31, with the following remark: 'it may be synonymous with *Raphoneis mammalis* Castracane' [here reproduced as Fig. 6] […] and if it is the case, Castracane's name would have priority against Schmidt's one'. Finally, A. Mann concluded 'see a discussion of these forms under *C. citronella*, new species'. It can be noted that Mann (1925: 62) also states that 'it may be here added that Castracane's *Rhaphoneis mammalis* is probably a synonym of *Cocconeis robustus* Leuduger-Fortmorel' (see above the note about *Cocconeis robusta*).

Foged (1984: 28) states that '*Cocconeis apiculata* and *Achnanthes citronella* are difficult to separate, they may belong to the same species'.

From A. Schmidt's illustrations, ascription of this species to *Achnanthes* rather than to *Cocconeis* is not possible. An examination of the original material from the Cape of Good Hope would be necessary to ascertain its taxonomical position. As it differs from most of the taxa here treated by the small rounded central area, not prolonged transversally in a stauros, we prefer not to include this doubtful taxon in the identification key.

Tentative identification key based on LM observations

1. Protracted apices, neither discontinuity nor shoulders near apices 2
- Striae biseriate, radiate, RV with a stauros ..... *Achnanthes mammalis sensu* Cleve

2. SV striae uniseriate, strongly radiate, RV with a stauros, fine SV areolae, long apices with presence of SV areolae..... *Achnanthes apiculata*
- Protracted apices, shoulders, SV striae uniseriate only radiate on apices, coarse SV areolae, reticulum-like..... 3

3. Length > 45 µm, SV stria density < 7 in 10 µm, short RV stauros ..... *Achnanthes citronella*
- Length < 45 µm, SV stria density > 7 in 10 µm, RV stauros more or less wide 4

4. Undulated margins, high L/W ratio ..... *Achnanthes obesa*
- Oblong to linear valve shape, wide RV stauros ..... *Achnanthes trachyderma*
- Short RV stauros, coarse RV striation ..... *Achnanthes schmidtii*

Conclusion

The taxonomic history of *Achnanthes citronella* seems to be intricate, unclear and sometimes confused. The lack of reliable illustrations concerning the older descriptions makes difficult the comparisons. The numerous hesitancies by A. Mann in the original description ('new name' *vs*. 'news species') and material labelling, the remarks by Meister (1935) about the ambiguities in the original illustration and, finally, the contradictory recent descriptions (see references in the Introduction) motivated these taxonomic notes.

Nevertheless, *Achnanthes mammalis* var. *reticulata* seems to have high similarity with *Achnanthes citronella*. *Cocconeis sabangi*, *Achnanthes schmidtii* and *Achnanthes trachyderma comb. nov*. share also some similarities among them and with the latter, but with a denser SV striation, a narrower and more linear frustule shape and a smaller length (Table 2). For these reasons, *Achnanthes trachyderma* has probably been often misidentified as *A. citronella*.

If all the bibliography available about *Achnanthes citronella* (Table 3) is examined, it can be noted that only Mann (1925), Meister (1935) and Wisshak *et al*. (2014) showed large individuals (> 45 µm long): these individuals have lemon-shaped valves, with a SV sternum enlarged, a low SV stria density [6.5 in 10 µm in Mann (1925) and Meister (1935), up to 10.5 in Wisshak *et al*. (2014)] and a relatively short RV stauros. These taxa may all refer to *A. citronella* (synonym: *A. mammalis* var. *reticulata* Cleve). All the other references from Table 3 refer to smaller individuals (< 45 µm long and often < 30 µm), with narrow-shaped valves, a dense SV striation (> 11 striae in 10 µm) and with a wide RV stauros: they may all refer to *Achnanthes trachyderma comb. nov*.

TABLE 3. *Cocconeis trachyderma* and *Achnanthes citronella* features from photographic documents (in chronologic order). nd = no data. ( ) = from illustration.

Name	Reference	Length (µm)	Width (µm)	Frustule shape	SV striae in 10 µm	SV sternum	RV stauros	RV striae in 10 µm
Cocconeis citronella	Mann (1925)	62–70	34–39	broadly oval with apiculate apices	6.5	(elliptic, enlarged in mid-valve)	hyaline stauros 1/5 of the valve width	21–25
Cocconeis citronella	Meister (1935)	(78)	(44.6)	(lemon-shaped, with shoulders)	(6.5)	(elliptic, enlarged in mid-valve)	nd	nd
Cocconeis trachyderma	Meister (1935)	29–32	14–15	elliptic with elongate-capitate endings	9–11	thin pseudoraphe	stauroid central area reaching 1/2 valve width	26
Achnanthes citronella	Gerloff & Helmcke (1977)	(19–28.6)	(11.2–13.9)	(narrow-elliptic, apiculate, with shoulders)	(9–14)	(narrow to enlarged in mid-valve)	(narrow, 1/2 valve width)	(24–26)
Cocconeis trachyderma	Montgomery (1978)	23–35	(10.6–20.1)	(lemon-shaped to oblong-elliptic, with shoulders)	(9.3–13.0)	(narrow to slightly enlarged)	(narrow, < 1/2 valve width)	24
Achnanthes citronella	Podozorski & Håkansson (1987)	30.3	15.3	(narrowly elliptic, apiculate, with shoulders)	nd	nd	(narrow, 2/3 valve width)	(dense)
Achnanthes citronella	Navarro *et al.* (2000)	(22–24)	(10.5–11.3)	(narrowly elliptic, apiculate, with shoulders)	(12)	(narrow)	nd	nd
Achnanthes citronella	Riaux-Gobin *et al*. (2011)	33–34	18.6–19	(lemon-shaped, to oblong-elliptic, with shoulders)	11–11.4	(slightly enlarged in mid-valve)	nd	nd
Achnanthes citronella	Stidolph *et al*. (2012)	(22.9)	(10.5)	(narrow-elliptic, apiculate, with shoulders)	(ca. 14.3 only radiate on apices)	(narrow)	nd	nd
Achnanthes citronella	Lobban *et al*. (2012)	28–30	13	lemon-shaped (to oblong-elliptic, with shoulders)	11–12, mostly parallel	(narrow)	(narrow, 1/2 valve width)	26, radiate
Achnanthes citronella	Wisshak *et al.* (2014)	(41.3)	(24.6)	(lemon-shaped, with shoulders)	(10.5)	(elliptic, enlarged in mid-valve)	(narrow, < 1/2 valve width)	(17–19)

If the SV stria density seems to be a good criterion to split *A. citronella* from *A. trachyderma comb. nov*., the SV sternum shape and width may be a less strong criterion (see the large morphological variability in the individuals illustrated in Gerloff & Helmcke 1977).

It can be noted that, except for *Cocconeis apiculata* (even if no LM or SEM illustrations are available), every taxon here commented shows a RV stauros (or fascia) delineated by short marginal striae: this particular stauros has a marginally laciniate aspect. *Stauroneis apiculata* reported (probably wrongly) by Stidolph *et al*. (2012) as *Cocconeis apiculata*, is mentioned as being soon transferred to the genus *Schizostauron* by A. Witkowski (A. Witkowski, *in litt*. 2012).

The commented taxa from the present report belong mainly to the order Achnanthales, with a marginally bifurcate or laciniate RV stauros: they may pertain to a separate group for which the correct genus name could be *Schizostauron*. Nevertheless, we prefer here to follow Ross (1963: 66–84) who includes the type of *Schizostauron* in *Achnanthes*.

Acknowledgments

Many thanks are due to David G. Mann and Leonie Paterson (Royal Botanic Garden Edinburgh, Edinburgh) for bibliographic help. Rusty Russel, Stan Yankowski, John Boggan, Meghann Toner and Melinda Peters from the Smithsonian Institute United States National Herbarium (Dept. of Botany, National Museum of Natural History Smithsonian Institution, Washington, DC) helped about *Cocconeis citronella* type slide localization and loan. We warmly thank François Straub, Lukas Taxböck and Regula Illi (M. Voigt Collection Curator, Eawag, Dübendorf, Switzerland) for their help on localization of type material from Zurich University Herbarium (Switzerland) and Dübendorf and the loan of original material. We acknowledge NHM for the loan of slides from Robert Kaye Greville's slide collection. Thanks are also due to Bank Beszteri (Alfred Wegener Institut für Polar- und Meeresforschung in der Helmholtz Gemeinschaft, Bremerhaven) and Maggy Nugues (CRIOBE-USR 3278, Laboratoire d'Excellence 'CORAIL', Perpignan) for their help in German translation. E. Schweizerbart (www.schweizerbart.de) the distributor for J. Cramer/Gebrueder Borntraeger in Stuttgart is acknowledged for giving permission to reproduce several illustrations from *Bibliotheca Diatomologica* 24 and *Bibliotheca Phycologica* 41. Two anonymous reviewers and Saúl Blanco Lanza are greatly thanked for their constructive comments. CNRS-USR 3278-Labex CORAIL funded the CORDIA projects.

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