



Cocconeis vaiamanuensis sp. nov. (Bacillariophyceae) from Raivavae (South Pacific) and allied taxa: ultrastructural specificities and remarks about the polyphyletic genus *Cocconeis* Ehrenberg

Catherine Riaux-Gobin^{1,2} · Pablo Saenz-Agudelo³ · Ewa Górecka⁴ · Andrzej Witkowski⁴ ·
Genowefa Daniszewska-Kowalczyk⁴ · Luc Ector⁵

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Abstract

A small marine monoraphid diatom with a linear-elliptic shape and simple terminal raphe endings was present on Raivavae (South Pacific). Particularly due to its different stria structure on both valves, this taxon is here classified as *Cocconeis*. The new species was present on the rocky intertidal shore of the coral-reef lagoon, as an epiphyte on a turf. *Cocconeis vaiamanuensis* sp. nov. can be compared to some other monoraphids with a simple raphe system and a rod-like shape. The new taxon has small marginal processes on the sternum valve (SV) mantle, as previously reported for *Cocconeis peltooides*. Such processes were also previously observed in *Platessa* and *Psammothidium*. A cladistic analysis based on ultrastructure shows an affiliation between several close-by taxa. *Cocconeis* of the *C. peltooides* section are close to *Psammothidium*, whereas other *Cocconeis* without processes are closer to *Platessa* and *Achnantheidium*. A clone of *Cocconeis* cf. *sigillata* (SZCZCH1200) allowed for a molecular phylogeny to be reconstructed. The molecular signature of *Cocconeis* cf. *sigillata* is close to that of *Lemnicola hungarica*. *Cocconeis* is a genus with different and complex morphologies that may be split into independent clades (genera). The SV processes may be a vestigial character reminiscent of an ancestral state.

Keywords Ancestral character · Cladistic analysis · Marginal processes · Phylogenetic analysis · *rbcL* · Shape convergence

Introduction

Raivavae (in Tahitian: Ra'ivāvae), part of the Austral Islands, also referred to as the Tupua'i Islands (South Pacific, Fig. 1), was first mentioned by Europeans in 1775, i.e., by the Spanish naval officer Tomas Gayagos, who was the commander on-board the frigate Aguila. Raivavae is a volcanic island (high island, erected between 10.6 and 5.4 Ma BP, Montaggioni 2015) with a large lagoon delineated by a coral-reef barrier with several motu (low coral islands), among which motu Vaiamanu (Fig. 1). Raivavae has a rocky shore and sheltered small bays with sandy beaches of coral sand. Ancestral marae are present on several parts of the island, witness to a rich culture and cultural past. The intertidal habitats of the lagoon were investigated in October 2018 to study monoraphid benthic diatoms. Several areas were sampled, in particular the fringe of Ruataru rock ("Rocher de l'Homme," name referring to a Tahitian legend) (Fig. 1). Other sediments and seaweeds were also sampled

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✉ Catherine Riaux-Gobin
catherine.gobin@univ-perp.fr

¹ PSL Research University: CNRS-UPVD-EPHE, USR3278
CRIOBE, University of Perpignan, Perpignan, France

² Laboratoire d'Excellence 'CORAIL', University of Perpignan,
Perpignan, France

³ Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral
de Chile, Valdivia, Region de Los Rios, Chile

⁴ Institute of Marine and Environmental Sciences, University of
Szczecin, Szczecin, Poland

⁵ Environmental Research and Innovation Department (ERIN),
Luxembourg Institute of Science and Technology (LIST),
Belvaux, Luxembourg



Fig. 1 Raivavae location in the Austral Archipelago (South Pacific), with location of Ruatara rock and motu Vaiamanu

on the North coast of Raivavae. The monoraphid diatoms in Raivavae include several genera (Table 1), upon which *Achnanthisidium* Kützing, 1844, *Amphicocconeis* De Stefano & D Marino, 2003, *Astartiella* Witkowski, Lange-Bertalot & Metzeltin, in Moser et al. 1998, *Cocconeis* Ehrenberg, 1837, *Madinithidium* Desrosiers, Witkowski & Riaux-Gobin, in Desrosiers et al. 2014, *Planothidium* Round & Bukhtiyarova, 1996, *Pseudachnanthisidium* Riaux-Gobin, in Riaux-Gobin and Witkowski 2015 and *Scalariella* Riaux-Gobin, in Riaux-Gobin et al. 2012 (Table 1). Among these genera, *Cocconeis* and

Amphicocconeis had the most remarkable species diversity. Several new *Amphicocconeis* will be detailed elsewhere (C Riaux-Gobin pers. comm.). We here focus on a small linear-elliptical monoraphid taxon described as new: *Cocconeis vaiamanuensis* sp. nov. The new taxon is detailed with LM (light microscope) and SEM (scanning electron microscope) and compared with allied taxa. Some characters of the taxon, such as its valve shape and presence of small processes on the SV mantle (see description below), prompted us to establish a cladistic analysis, based on ultrastructure, giving some light about a possible connection among several genera such as: *Psammothidium* Bukhtiyarova & Round, 1996, *Platessa* Lange-Bertalot in Krammer & Lange-Bertalot, 2004, *Lemnicola* Round & Basson, 1997, *Pauliella* Round & Basson, 1997, *Achnanthisidium*, *Karayevia* Round & Bukhtiyarova ex Round, 1998, *Rossithidium* Round & Bukhtiyarova, 1996 and *Cocconeis*. It can be first noted that, except for *Cocconeis*, the previously cited genera are mostly associated with freshwater, while the new taxon is a priori strictly marine. The morphological limits between some of the latter genera are particularly blurred, with incertitude about the particular position of several of them (see below). The use of SEM is often decisive in delineating taxa, and therefore strengthening the results of morphological cladistic analyses that permit to sort them. In the same manner, concerning the molecular phylogeny, without direct observation of cells under a microscope, it can be challenging to predict the identity of some diatoms as belonging to a particular genus, solely on their position in the molecular phylogeny (Frankovich et al. 2018).

The genus *Cocconeis* is diverse in valve shape, ornamentation, and copula structure, allowing for several sub-groups to be identified, such as the Section *Alveolatae* De Stefano & OE Romero (De Stefano and Romero 2005) characterized by a bilayered complex SV, and the Section characterized by a marginal row of simple SV processes and complex RV striation (Riaux-Gobin et al. 2015), comprising *Cocconeis peltoides* Hustedt, 1939. The present study particularly seeks to provide insights into the phylogenetic and cladistic position of members of *Cocconeis* with or without processes. Such processes were named “poroids” in Tudesque et al. (2016) for some *Platessa* species, with the comment: “This type of ‘poroid’ requires further investigation because it could be reminiscent of an ancestral portula.” These structures were named “rimoportula” in Romero & Riaux-Gobin (2014) for *Cocconeis pseudograta* Hustedt, 1939. Here we prefer to use the term “simple process”, because these structures (that open externally via a tiny pore on the SV mantle and closed internally by a sort of polymorph domed hymen, see Riaux-Gobin et al. 2015) differ from true rimoportulae that are characterized by pair of lips in internal valve face, and simple pore or often more or less long tubes in external valve face, as illustrated in Round et al. (1990). Nevertheless, the difference in the complexity of these processes may be phenotypic differentiation among diatom Classes. SV processes were also

Table 1 Assemblage of Achnanthisales from Raivavae (South Pacific)

<i>Achnanthisidium</i> sp.
<i>Achnanthisidium glyphos</i> Riaux-Gobin, Witkowski & Compère
<i>Amphicocconeis</i> cf. <i>discrepans</i> (AWF Schmidt) Riaux-Gobin, Witkowski, Ector & Igersheim
<i>Amphicocconeis</i> cf. <i>rodriguensis</i> Riaux-Gobin & Al-Handal
<i>Amphicocconeis</i> spp. (several species)
<i>Astartiella</i> sp.
<i>Cocconeis</i> cf. <i>borbonica</i> Riaux-Gobin & Compère
<i>C. carinata</i> Riaux-Gobin, Ector & Witkowski
<i>C. convexa</i> MH Giffen
<i>C. coralliensis</i> Riaux-Gobin & Compère
<i>C. coronatoides</i> Riaux-Gobin & Romero
<i>C. cupulifera</i> Riaux-Gobin, OE Romero Compère & Al-Handal
<i>C. dapalstriata</i> Riaux-Gobin, OE Romero, Compère & Al-Handal
<i>C.</i> cf. <i>dirupta</i> W Gregory
<i>C. distans</i> W Gregory
<i>C. geometrica</i> Riaux-Gobin, OE Romero, Compère & Al-Handal
<i>C. guttata</i> Hustedt & Aleem
<i>C. margaritata</i> Riaux-Gobin & Al-Handal
<i>C. mascarenica</i> Riaux-Gobin & Compère
<i>C.</i> cf. <i>mascarenica</i> Riaux-Gobin & Compère
<i>C.</i> cf. <i>meisteri</i> Riaux-Gobin, Compère, M Coste, Straub & Taxböck
<i>C. molesta</i> Kützing
<i>C.</i> cf. <i>molesta</i> Kützing
<i>C. paucistriata</i> Riaux-Gobin, OE Romero, Compère & Al-Handal
<i>C. peltoides</i> Hustedt
<i>C.</i> cf. <i>pseudograta</i> Hustedt
<i>C. pseudomarginata</i> W Gregory
<i>C. scutellum</i> Ehrenberg
<i>C. sigillata</i> Riaux-Gobin & Al-Handal
<i>C. vaiamanuensis</i> sp. nov.
<i>C.</i> sp. 1
<i>Madinithidium flexuistriatum</i> (Riaux-Gobin, Compère & Witkowski) Witkowski, Riaux-Gobin & Desrosiers
<i>Planothidium</i> cf. <i>mathurinense</i> Riaux-Gobin & Al-Handal
<i>Planothidium</i> spp. (several species)
<i>Planothidium rodriguense</i> Riaux-Gobin & Compère
<i>Pseudachnanthisidium</i> sp.
<i>Scalariella</i> sp.

observed in several *Platessa* (Romero 2016; Wetzel et al. 2017), *Psammothidium* (Potapova 2012; Blanco et al. 2017), *Lemnicola* (Shi et al. 2018), *Rossithidium* (Potapova 2012), *Pauliella* (Round and Basson 1997), *Achnantheidium* (Jüttner et al. 2020), and *Karayevia* (Spaulding and Edlund 2008).

On the other hand, recent increases in the number of phylogenetic analyses have provided important clues allowing us to propose genetic affiliations. A *rbcL* molecular analysis of a clone of *Cocconeis* cf. *sigillata* SZCZCH1200 (collected in Laoshan Shangquan coastal area, China) (see *C. sigillata* Riaux-Gobin & Al-Handal, in Riaux-Gobin et al. 2011a), a taxon similar to *C. peltooides*, with marginal SV processes, allowed for the illustration of the complex and diverse relationships of *Cocconeis* (currently called *Cocconeis*) with other genera. Our results add to those of other recent phylogenetic investigations (i.e., Nakov 2014; Kulikovskiy et al. 2016, 2019; Thomas et al. 2016; Witkowski et al. 2016; Shi et al. 2018).

A polyphyletic position of the genus *Cocconeis* is considered, and the term Achnanthes (Order Achnanthes Silva, 1962), up to now treated as homogenous (De Stefano and Marino 2003; Le Cohu 2005) is here reconsidered, as previously addressed in several other studies (i.e., Cox 2006; Cox and Williams 2006; Kulikovskiy et al. 2016; Davidovich et al. 2017).

Material and methods

Diatom materials

Marine materials (sediments, seaweeds, diverse scrapings) collected in October 2018 from Raivavae (Austral Archipelago) were observed with LM and SEM, and are here illustrated and discussed. A strain of *Cocconeis* cf. *sigillata* was isolated and cultured by Chunlian Li at SZCZ (Szczecin University) from a sand beach in Laoshan Shangquan coastal area, China (36.092 N; 120.469 E), isolate SZCZCH1200; 101 stored in the Szczecin Diatom Culture Collection (SZCZ), University of Szczecin, collectors: Yu Shu-xian, Wang Yin-chu, Wang Xiu-jing, and Witkowski Andrzej, sampled in June 2015, Witkowski Lab Voucher SZCZCH1200. The molecular marker analysis was performed (see below), along with LM and SEM examination at SZCZ, Szczecin University.

Sample preparation and examination

Materials (preserved in methanol) were washed with distilled water to remove salts (sedimentation method), treated with 30% H₂O₂ 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. Diatom slides were examined with a Zeiss Axiophot 200, with phase contrast and differential interference contrast (Nomarski interference contrast) optics and photographed with a Canon PowerShot G6 digital camera

(CRIOBE-USR 3278, Perpignan, France). For SEM examination, drops of cleaned or raw material were filtered with a syringe-filter, through 1 µm Nuclepore® filters and rinsed twice with deionized (Milli-Q) water to remove salts. Filters were mounted onto aluminum stubs and air-dried before coating with gold-palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi S-4500 SEM operated at 5 kV, calibrated with a Silicon grating TGX01 (C2M, Perpignan, France). Images kept in the authors' collection and handled with Photoshop and Adobe-illustrator. Measurements were performed using SEM images (60 individuals of *Cocconeis vaiamanuensis* sp. nov. were measured).

Cladistic analysis method

A morphological cladistic analysis (ultrastructural characters) was applied to the taxa, including 16 characters (Table 2) and 34 taxa from 9 genera (Table 3). Taxa were selected following the accuracy of their SEM description, permitting or not to detail SV processes, RV transapical marginal poroids, and characteristics of the terminal raphe endings. The chosen characters consist of ultrastructural details allowing to define each of the nine genera included in the analysis: the shape of the valve, particular structures such as the mantle SV processes, valvocopula structure, stria pattern. For the outgroup, we selected a *Planothidium* (*Planothidium juandenovense* Riaux-Gobin & Witkowski in Riaux-Gobin et al. 2018). We used the software PAUP*4.0a165 (Swofford 2003). We ran a Bootstrap method with a heuristic search algorithm to search for the most parsimonious trees (100 bootstraps). Characters were analyzed as unordered and unweighted. The resulting 100 most parsimonious trees were then used to build a 50% Majority-rule consensus tree, which is presented in Figure 8.

Phylogenetic analysis method (DNA extraction, PCR, and molecular analysis)

Several clones, or strains, of *Cocconeis* and other genera, were cultured in SZCZ (Szczecin University), and molecular analyses were compared to data from GenBank®. Particularly, a clone of *Cocconeis* cf. *sigillata* SZCZCH1200 [see above details] was cultured and analyzed. Two strains of *Triparma pacifica* (Guillou & Chrétiennot-Dinet) Ichinomiya & Lopes dos Santos in Ichinomiya et al. (2016), p. 1432; Basionym: *Bolidomonas pacifica* Guillou & Chrétiennot-Dinet in Guillou et al. 1999, p. 371) were chosen as an outgroup. The final *rbcL* gene trees are available in Fig. 8. The full list of sequences used in phylogenetic analyses along with GenBank® accession numbers is available (Table 4).

DNA extraction using Chelex® 100 resin (Bio-Rad, cat. no. 142-2842-MSDS) followed the method described in Kryk et al. (2020). The molecular marker *rbcL* was amplified using primer and PCR protocol as described in Dąbek et al. (2017). The

sequencing of the PCR products was performed using BigDye Terminator v.3.1 chemistry and ABI3730 xl sequencer by the oligo.pl DNA Sequencing Laboratory at the Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw, Poland. For sequence assembling, BioEdit ver. 7.2.5 (Hall 1999) was used. For maximum likelihood (ML) estimation, phylogenetic tree was inferred with 1000 bootstrap replicates using rapid bootstrap analysis in RAxML v.8.1 (Stamatakis 2014). The best score for ML tree was chosen as the final tree, and bootstrap support values (bv) were added at nodes. For Bayesian Interference, the tree was carried out using MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001). The data was partitioned as three different codon positions. Two Bayesian inference analyses each with four chains (one cold and three heated) were run using GTR + G + I model. During this procedure, the standard deviation of split frequencies was around 0.01 when it reached 150,000,000 generations, which were run per analysis with sampling every 1000th iteration, generating in total of 150,000 samples. 25% of the samples were discarded, then the rest were used to get a majority rule consensus tree and obtain posterior probabilities for nodes.

Results

Marine Achnanthes assemblage from Raivavae (Table 1)

The microphytobenthos from the intertidal environments of Raivavae is highly diversified (in term of species number), particularly within the monoraphids (Table 1). We note the presence of several pantropical taxa, from which several were previously reported from the Indian Ocean. Some taxa belonging to *Olifantiella* Riaux-Gobin & Compère, 2009, and *Amicula* Witkowski, Lange-Bertalot & Metzeltin, 2000, were also present. Most monoraphids (Table 1) are present in several other places in the South Pacific. In contrast, *Cocconeis vaiamanuensis* sp. nov. may be a local endemic, since it has never been cited from elsewhere. During several sampling campaigns in the South Pacific, we noticed different productivity and species diversity of benthic diatoms, particularly concerning the monoraphids, as a function of the geomorphology of the site: atolls (carbonate environments) versus high volcanic islands (siliceous environments, see remarks in Riaux-Gobin et al. 2014). More than 37 monoraphid taxa were reported from Raivavae, upon which 25 *Cocconeis* (Table 1). *Amphicocconeis*, with several taxa, is detailed elsewhere.

Cocconeis vaiamanuensis Riaux-Gobin, Witkowski & Ector sp. nov. (Table 2; LM Fig. 2 a–p; SEM Figs. 3, 4, 5, 6)

Class: Bacillariophyceae Haeckel, 1878

Order: Achnanthes Silva, 1962

Family: Cocconeidaceae Kützing, 1844

Genus: *Cocconeis* Ehrenberg, 1837

Description

Frustule solitary, valve oblong-elliptic to linear in the larger specimens (SEM, $n = 60$, length 7–15 μm , width 3–5 μm , L/W 2.2), with round apices. Never observed in girdle view during this survey.

Sternum valve (SV) slightly concave (Fig. 3), with a narrow, flat and straight sternum. Small round areolae (ca. eight per stria; 4–5 in 1 μm). SV striae uniseriate ($n = 32$, 16–22, \bar{x} 19.6 \pm 1.3 in 10 μm), parallel in mid-valve to radiate and slightly denser on apices. Striae composed of tiny areolae, more or less in zig-zag, internally closed by strongly convex hymenes without obvious slits or punctuations (Fig. 4b, c). Running all over the valve, a marginal embossed apical and hyaline area similar to a *crista marginalis* (Fig. 3, arrow). Mantle narrow with one row of small pores providing access to a process (Fig. 3f, arrows). This small process is internally closed by a hemispheric plug or hymen, slightly different and smaller in size than that of the SV areolae (Fig. 4d, arrowhead). One process regularly faces each stria (Fig. 4b, arrowheads). Strong virgae, externally embossed on their most marginal part (Fig. 3d, arrowheads). Relatively high cingulum composed of several open and large and thin cingulae devoid of ornamentation (Fig. 3, arrowhead, c, e). SVVC apparently with no fimbriae (Fig. 4c, arrowhead and ellipse). SV valve possibly bi-layered (Fig. 4d, framed arrowheads).

Raphe valve (RV) strongly convex (Fig. 5c). Striae radiate, slightly denser on apices ($n = 30$, 20–24, \bar{x} 21.3 \pm 1.2 in 10 μm), composed of small areolae, biseriate near the axial area, uniseriate on a short median section, and up to quadriseriate near the margin. On rare specimens (one observed, see supplementary Fig. 11), the RV striae are distinctly biseriate, with alternate areolae. RV areola hymenes internally convex with a crenulated border giving it a star-like shape (Fig. 6d, e, arrowheads). A marginal row of dense and apically elongate-oblong poroids (60–72, \bar{x} 65.2 \pm 3.5 in 10 μm , Fig. 5, black arrowhead), separated from the rest of the valve by a large hyaline apical area (Fig. 5, white arrowhead), corresponding to an internal flat unraised rim (Fig. 6). Central area reduced to absent (no evident fascia, Fig. 5, or short hemi-fascia on some specimens). Raphe filiform, straight. Proximal raphe endings externally close to each other (slightly bent on the same side, Fig. 5e) and internally bent in opposite directions (Fig. 6b). Terminal raphe endings simple, close to the margin (Fig. 5b, arrowhead), apically surrounded by an anchor-like silica fold (Fig. 5d, arrowhead) with no connection to the interior of the valve. No RV areolae on apices (Fig. 5b, ellipse). RVVC taking place on the border of the RV, with no fimbria (Fig. 6, arrowhead), or a slightly undulated edge (Fig. 6f, framed

Table 2 Characters, state, and coding used in the Cladistic Analysis. *See definition in the text

N°	Definition	States	Coding
1	Frustule bent along apical axis	Not bent	0
		Bent	1
		Not detailed	2
2	Raphe terminal endings	Simple	0
		Simple with groove	1
		Short fissure slightly deflected	2
		Large fissure	3
		Elliptic	0
3	Valve shape	Subrostrate	1
		Round-elliptic	2
		Linear	3
		Oblong-elliptic	4
		Flat	0
4	SV curvature	Concave	1
		Convex or flat with a concave sternum	2
		Convex	3
		Flat	0
5	RV curvature	Concave	1
		Convex	2
		No Fascia	0
6	Fascia	Fascia on SV	1
		Fascia on RV	2
		Fascia on both valves	3
		Absent	0
7	<i>SV crista marginalis</i>	Present	1
		Regularly spaced	0
8	Stria spacing	Slightly denser on apices	1
		Markedly denser on apices	2
		Parallel to almost parallel	0
9	RV stria orientation	Radiate	1
		Only strongly radiate on apices	2
		Similar	0
10	SV & RV structure	Closely similar	1
		Dissimilar	2
		Uniseriate	0
11	SV striae	Uni to biseriate	1
		Regularly biseriate (or triseriate)	2
		Marginally multiseriate	3
		Multiseriate (>3)	4
		Uniseriate	0
12	RV striae	Uni to biseriate	1
		Regularly biseriate (or triseriate)	2
		Multiseriate (>3)	3
		Similar	0
13	SV & RV stria density	Closely similar	1
		Dissimilar	2
		Apparently absent	0
14	SV one row of processes on mantle*	Present tiny, one per stria	1
		Denser than striae	2
		Slit-like, one per stria	3
		Slit-like, denser than striae	4
		Apparently absent	0
15	RV one row of oblong poroids on mantle*	Present tiny, one per stria	1
		Denser than striae	2
		Slit-like, one per stria	3
		Slit-like, denser than striae	4
		Apparently with straight to simply undulated edge	0
16	Valvocopulae	Fimbriae more or less complex	1
		Not detailed	2

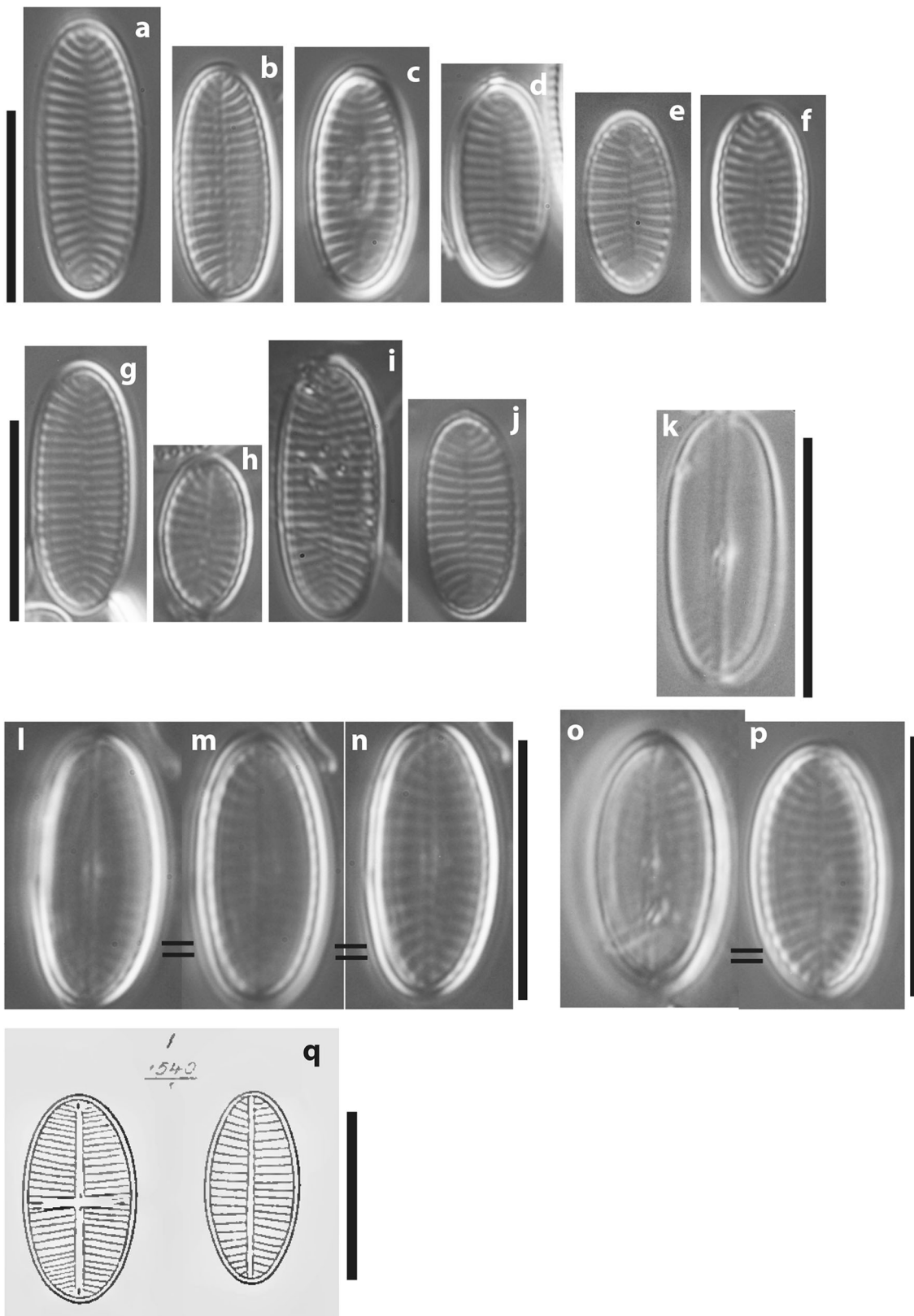
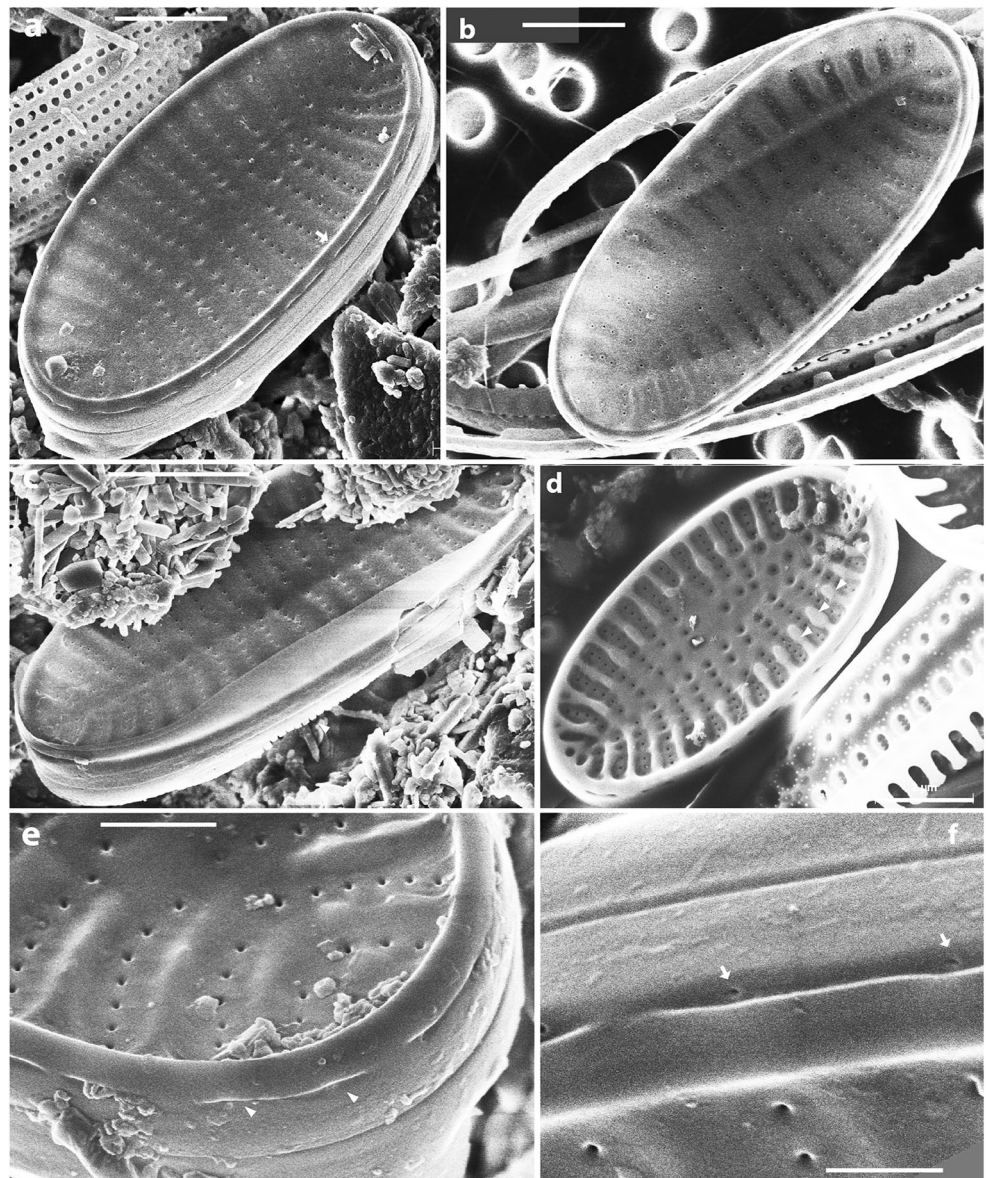


Fig. 2 *Cocconeis vaiamanuensis* sp. nov. LM (Raivavae, Ruatara rock). **a–j** SV with linear-elliptical shape, round apices and regularly spaced striae; **k** RV with almost invisible striae; **l–p** complete frustules at different foci allowing for the RV and SV of each specimen to be

delineated and visualized. Scale bars = 10 μm (Nomarski interference contrast); **q** *Cocconeis finmarchica* Grunow in Cleve & Grunow. Original drawings. Note the marginal hyaline area on both valves, and the RV fascia. Scale bar = 10 μm.

Fig. 3 *Cocconeis vaiamanuensis* sp. nov. SEM (Raivavae, Ruatara rock). **a–b** SV in external view. Slightly concave, with regularly spaced striae. Note the marginal *crista marginalis* (arrow). Cingulum composed of several large copulae (arrowhead); **c** dense marginal striation of the RV (arrowhead); **d** marginal raised portion of the SV virgae (multiple arrowheads); **e–f** position of the small aperture of each process on the SV mantle (twin arrowheads, twin arrows). Scale bars = 3 μ m (c), 2 μ m (a–b, d), 700 nm (e), 300 nm (f)



arrowheads). Central area almost absent (Fig. 5). Helictoglossa straight and low (Fig. 6g).

Holotype:

Whole slide from the sample RAI 20, deposited at NHM (BM 81917 material). Holotype illustrated in Fig. 5.

Type locality:

Ruatara rock (Rocher de l'Homme), Raivavae (Austral Islands, South Pacific), RAI 20 (intertidal red macroalgal turf on small fissures of the rock). Geo localization: S 23° 51.274'; W 147° 39.595'; T°C 23°.7, salinity < 40‰. Sampled by C. Riaux-Gobin on 08 10 2018.

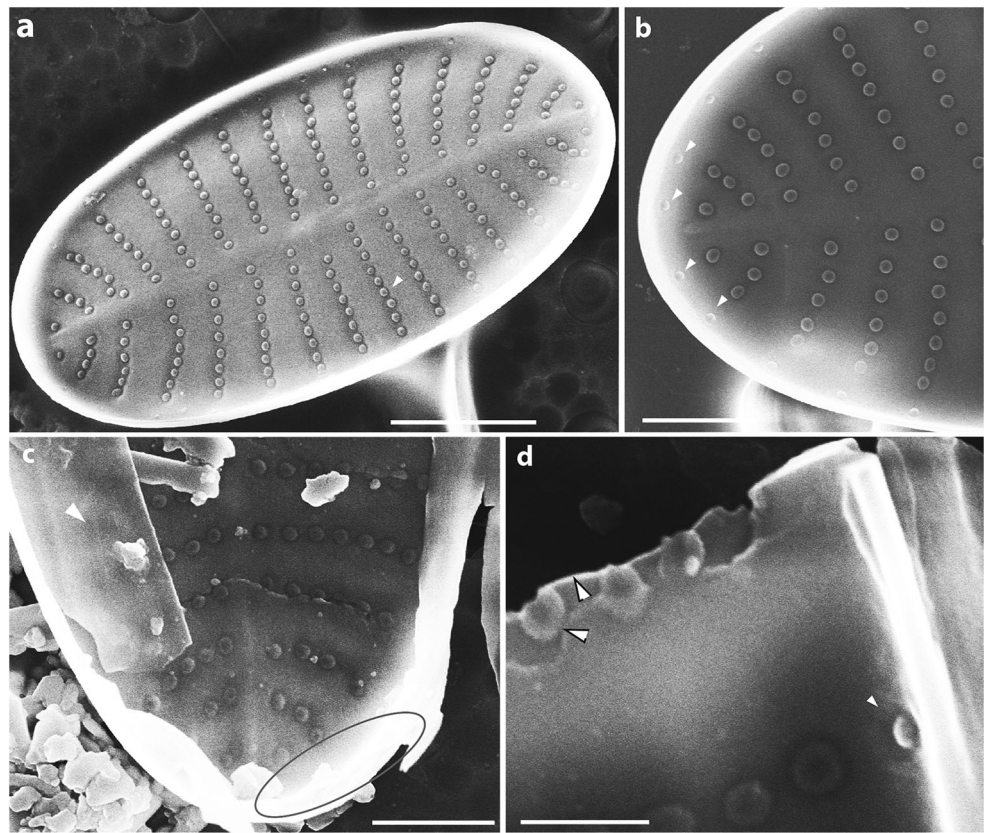
Ecology:

Relatively rare, marine intertidal taxon, living on rocky shore covered by turf. The new taxon was present in RAI 20 (see above) but also, in lower densities, on RAI 18 (same GPS position-geo localization, on red-dark short algae), and RAI 21 (same geo-localization, red-brown algae, longer than those in RAI 18). Taxonomy of the varied short macroalgae (turf) not available.

Etymology:

The epithet *vaiamanuensis* refers to the most famous motu from Raivavae, the motu Vaiamanu (in Tahitian “the place where there are birds”), also named “motu Piscine.”

Fig. 4 *Cocconeis vaiamanuensis* sp. nov. SEM (Raivavae, Ruatara rock). **a** SV in internal view. Regular arrangement of striae composed of small round areolae with convex hymenes. Areolae near the sternum less dense than on the margin (arrowhead); **a** narrow and straight SV sternum; **b** SV processes, facing each stria, smaller than the areolae (multiple arrowheads); **c** broken SV with a large copula (arrowhead), SVVC still attached to the SV, with no fimbriae (ellipse); **d** Detail of the SV processes (arrowhead), note that the SV is possibly bi-layered (framed arrowheads). Scale bars = 2 μm (**a**), 1 μm (**b–c**), 300 nm (**d**)



Distribution:

Until now only found on Raivavae, as a possible local endemic [i.e., to the best of our knowledge, absent in Rapa (Austral Islands), as well as in the other visited Polynesian Archipelagos. Also absent from Mascarenes and Scattered Islands (Indian Ocean), and other tropical locations referenced, i.e., in Riaux-Gobin et al. (2011c, p. 7).

Remarks:

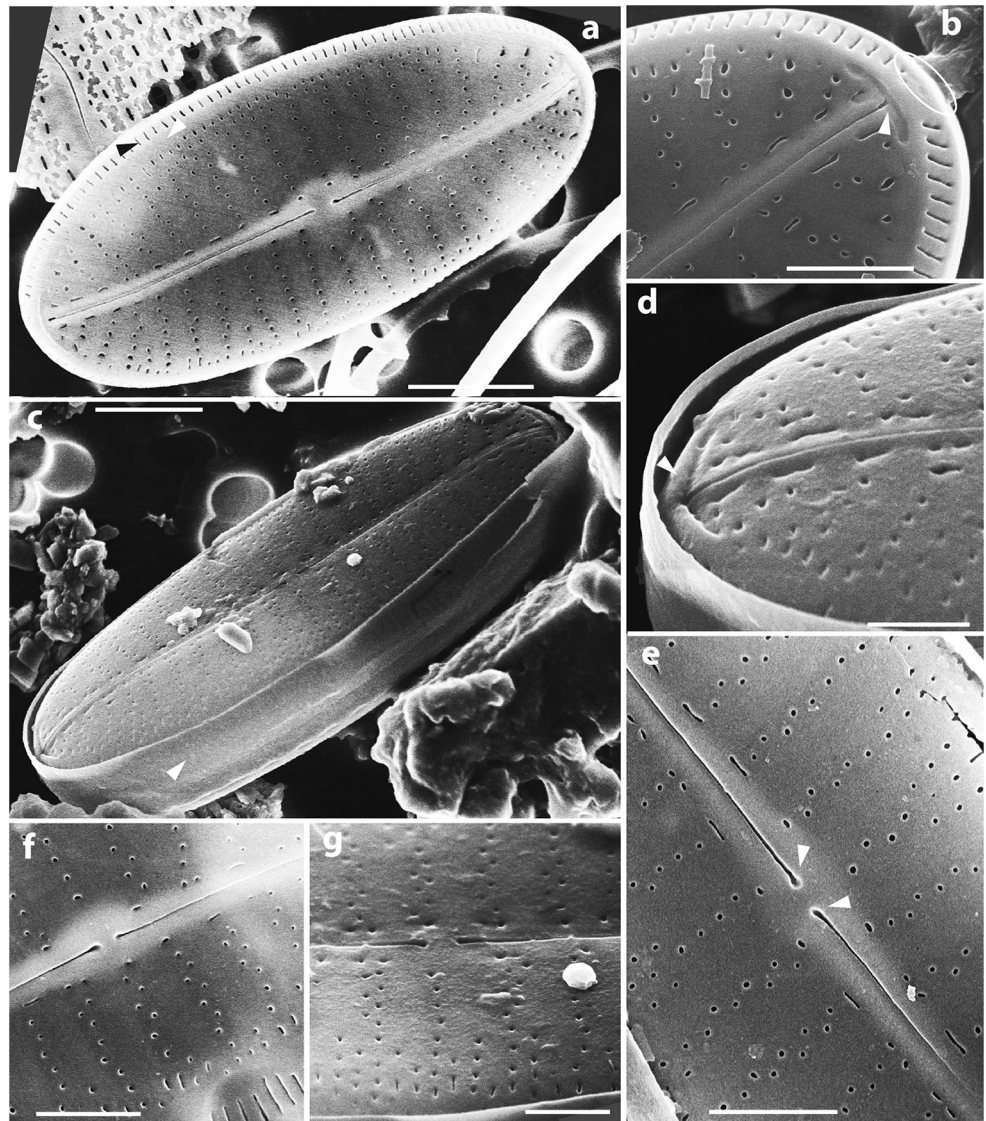
Relatively rare taxon (< 5% of the all benthic diatom assemblage in RAI 20; occasionally present only on three samples in the vicinity of Ruatara). Some dissimilarity concerning the ultrastructure of the valves with *Cocconeis nugalas* MH Hohn & Hellerman (Hohn and Hellerman 1966) [synonym *C. hauniensis* Witkowski (Witkowski 1993; Desianti et al. 2015; see also SEM in Riaux-Gobin and Romero 2003, pl. 41–43)]. The SV sternum is elliptical and slightly concave in *C. nugalas* while narrow-linear and flat in the new taxon. *Cocconeis nugalas* has no *crista marginalis*. The SV virgae are more significantly embossed in the new taxon than in *C. nugalas*. Furthermore, on *C. vaiamanensis* the RV striae are biseriate on a part of their length and composed of tiny areolae, while bigger and uniseriate on *C. nugalas*

(Riaux-Gobin and Romero 2003: pl. 43, Fig. 3). The RV of *C. vaiamanuensis* has a margin with almost four oblong poroids between each stria, seemingly more complex than in *C. nugalas* where there is only one marginal oblong poroid between each stria. The hyaline marginal area is narrower in *C. nugalas*. Furthermore, the valve shape is different between the two taxa: elliptical in *C. nugalas* and linear-elliptical to rod-like in the new taxon. The two taxa are thus significantly dissimilar.

Based on LM, similarities also exist with *Cocconeis finmarchica* Grunow in Cleve & Grunow (Cleve and Grunow 1880, p. 16, pl. 1, Fig. 1; illustrated here in Fig. 2q), also a small taxon, with a narrow and straight SV sternum and a SV hyaline marginal area (possibly a *crista marginalis*), and an RV hyaline margin. The RV of the latter has a slightly denser RV striation than the SV (24 in 10 μm , 20 in 10 μm in the SV) and radiate RV striae, such as in the new taxon. The only points that do not match the new taxon are the narrow and long fascia on the RV in *C. finmarchica*, and the shape of the frustule that is ellipsoid. No recent bibliography offers SEM for *C. finmarchica*.

For *Cocconeis* with SV processes, and concerning the taxonomic key presented in Riaux-Gobin et al. (2015), the addition of a supplementary group would be necessary to identify the new taxon: i.e., “Group 5 with SV striae composed of numerous areolae, with no partition, and with a narrow

Fig. 5 *Cocconeis vaiamanuensis* sp. nov. SEM (Raivavae, Ruatara rock). **a** RV in external view. Whole valve with radiate striae, marginal hyaline area (white arrowhead), one row of marginal elongate poroids, denser than the striae (black arrowhead); **b** simple terminal raphe ending (arrowhead), absence of elongate poroids on apex (ellipse); **c** high cingulum (arrowhead); **d** anchor-like and raised fold around the simple terminal raphe ending (arrowhead); **e** proximal raphe endings small and bent on primary side (twin arrowheads); **f** RV striae with small areolae in quincunx ending in a pyramidal shape before the marginal hyaline area; **g** central area absent-missing. Scale bars = 2 μ m (a, c), 1 μ m (b, e–f), 700 nm (g), 600 nm (d)



sternum void of areolae.” This key would clearly benefit from references to the structure of the RV when available. However, neither *C. inaequalistriata* Riaux-Gobin, OE Romero, Compère & Al-Handal (Riaux-Gobin et al. 2011c, p. 28–29, pl. 48, Figs. 1–6; Riaux-Gobin et al. 2015, Fig. 13), nor *C. sp4* in Riaux-Gobin et al. (2015), Figs. 12, 30–32; also illustrated in Riaux-Gobin et al. 2011c,? *Cocconeis* sp. 1, p. 41, pl. 85, Figs. 1–4) match the new taxon.

The genera *Psammothidium* and *Platessa* also have simple terminal raphe endings, but none correspond to our marine taxon. A cladistic analysis, based on ultrastructural characters (see below and Fig. 7), allows us better to understand the degree of proximity of genera and taxa. A phylogenetic tree including a taxon pertaining to the *Cocconeis peltoides* group also allows for some remarks to be made (see below and Fig. 8).

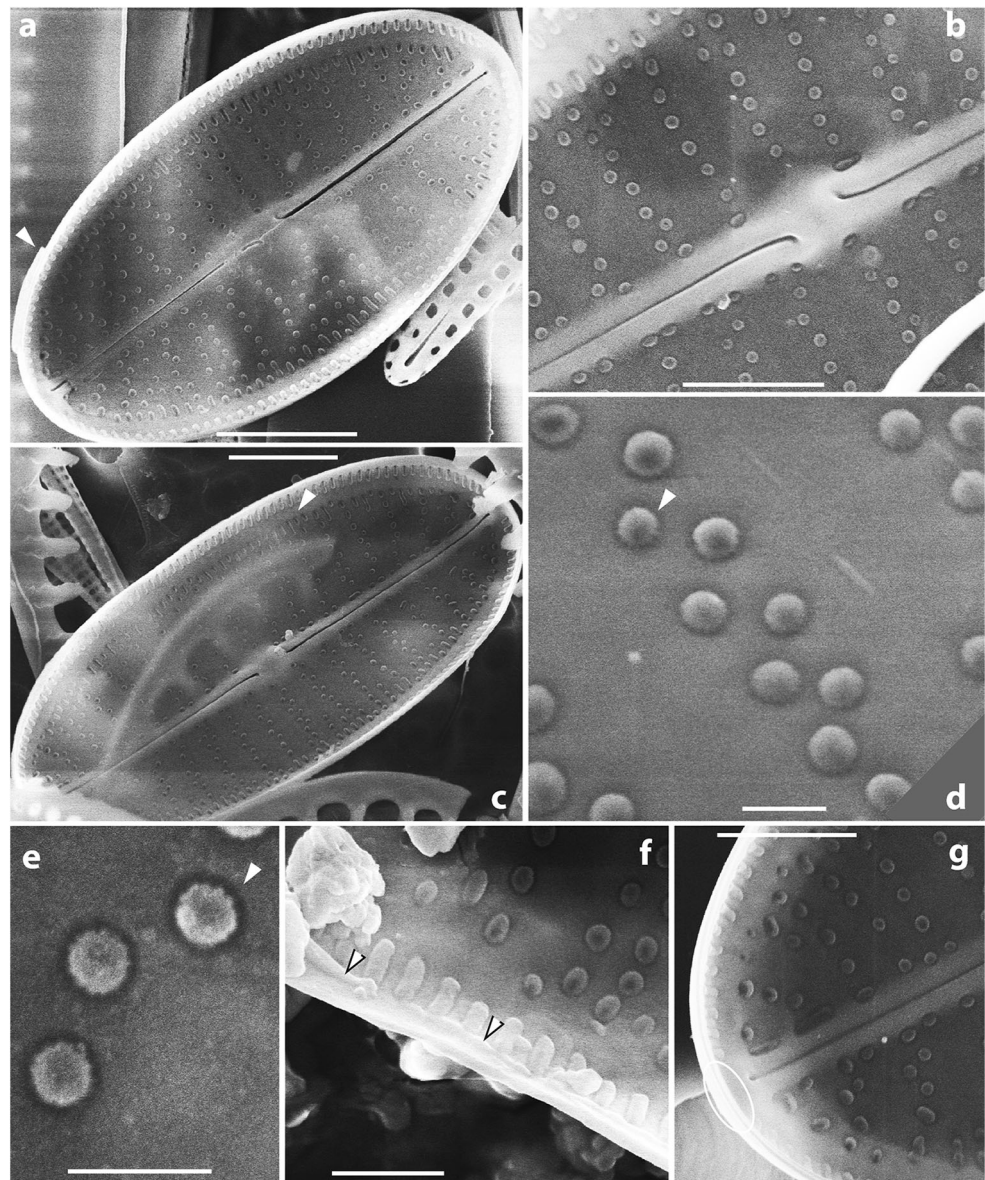
Cladistic analysis based on ultrastructure (Tables 3, 4, Fig. 7)

It can be first pointed that several selected characters (Table 3) may appear as blurry, such as the valve shape (difficult to define accurately) or curvature of the frustule in cingular view (along the apical axis), a major-determinant character often neglected in descriptions. The morphology of the valvocopulae (with or without fimbriae), also an important character, is not often detailed.

Planothidium juandenovense is the outgroup, with groups of areolae with a multiseriate arrangement on the SV mantle and terminal raphe fissures strongly bent.

Platessa bahlsii Potapova (Potapova 2012) is the only taxon in the analysis showing multiseriate striae, seemingly belonging to *Planothidium* but with simple terminal raphe endings.

Fig. 6 *Cocconeis vaiamanuensis* sp. nov. SEM (Raivavae, Ruatara rock). **a** RV in internal view. Whole valve with a small portion of the RVVC, apparently with no fimbriae (arrowhead), low helictoglossa; **b** proximal raphe endings curved in opposite sides; **c** unraised marginal hyaline area (arrowhead); **d** domed RV areolae, in quincunx (arrowhead); **e** crenulated periphery of the RV hymenes (arrowhead); **f** probable edge of the RVVC slightly undulated, with no fimbriae (framed arrowheads); **g** detail of apex without poroids (ellipse). Scale bars = 2 μm (**a**, **c**), 1 μm (**b**, **g**), 600 nm (**f**), 200 nm (**d–e**)



Platessa bahlsii appears as an independent taxon (monophyletic). It would be recommended to culture such a taxon and to do molecular analyses to evaluate its degree of affiliation (proximity) to *Planothidium*. Kulikovskiy et al. (2020) recently suggested that “*P. bahlsii* belongs to the group of species without sinus or cavum in the genus *Planothidium*”, and proposed the new combination *Planothidium bahlsii* (Potapova) Kulikovskiy, Glushchenko & Kociolek, in Kulikovskiy et al. (2020).

The cladistic analysis (Fig. 7) roughly has two poles: (1) Group I composed of taxa pertaining to *Platessa*, *Cocconeis* without SV processes and *Achnanthisidium* and (2) Group II composed of *Psammothidium*, *Cocconeis* with SV processes and other atypic taxa upon which *Rossithidium* that is not accepted as different from

Psammothidium by various authors (see Kulikovskiy et al. 2016; Jüttner et al. 2020).

Illustrating the difficulty of establishing limits between *Achnanthes* Bory, 1822, *Psammothidium*, *Platessa* and *Cocconeis*, we can cite the intricate taxonomic history of *Cocconeis therezienii* Le Cohu & R.Maillard ex Van de Vijver & Le Cohu (Van de Vijver and Le Cohu 2019). The interpretative analysis of a taxon by different authors may illustrate the difficulty of defining it correctly. For example, *Platessa oblongella* (Østrup) CE Wetzel, Lange-Bertalot & Ector (Wetzel et al. 2017) and its synonym *Karayevia oblongella* (Østrup) Aboal, in Aboal et al. (2003), do not appear at the same level in the cladistic analysis (Fig. 7), due to SEM observations that do not exactly match.

Majority-rule consensus tree

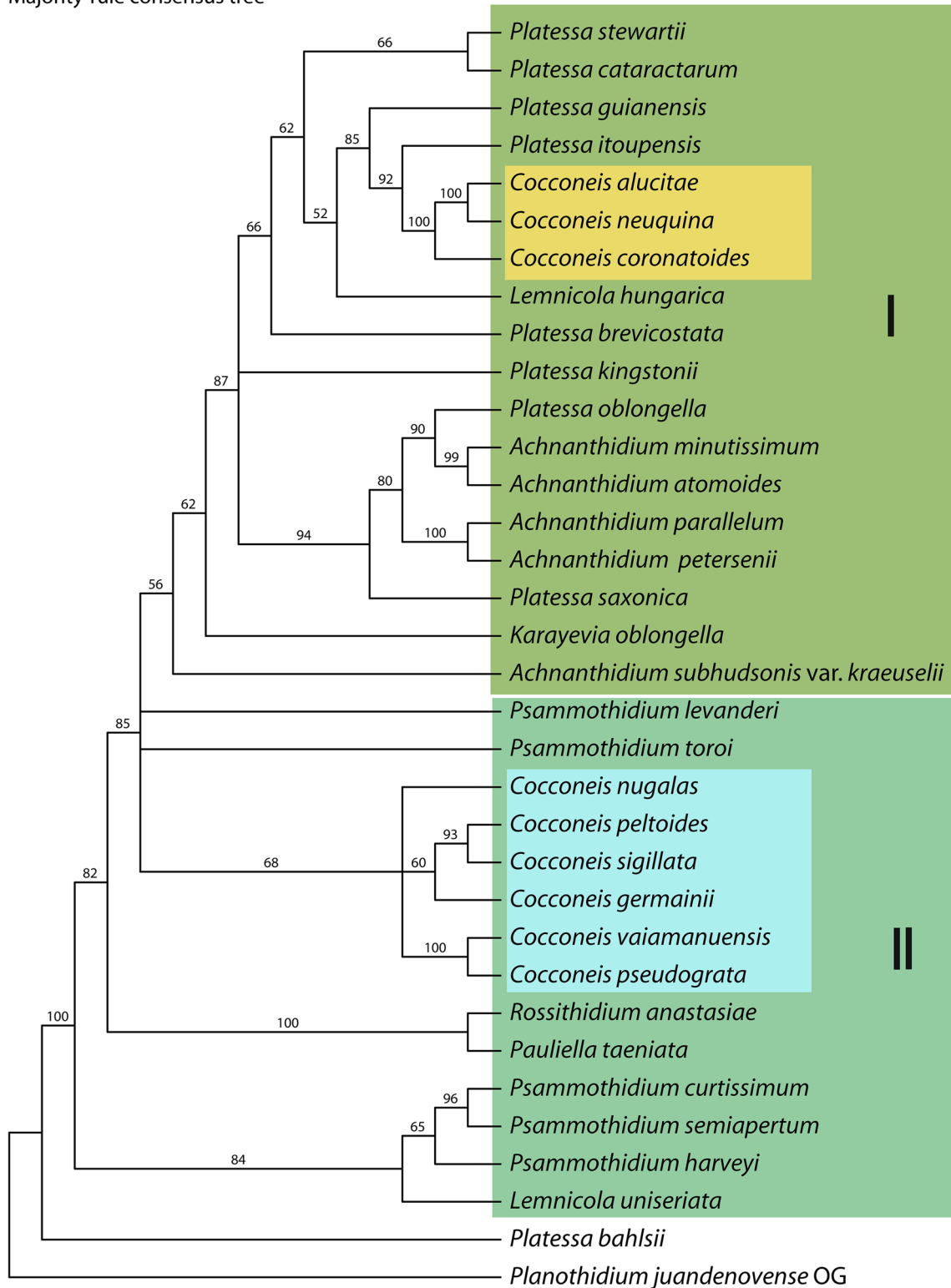


Fig. 7 Cladistic Analysis based on ultrastructure. OG = out group. See comments in the text



Fig. 8 Phylogenetic tree, showing the position of different groups of *Cocconeis*. See comments in the text

Table 3 Taxa (34 species), character coding (16 ultrastructural characters), author and year, where can be found the SEM documents referring to each taxon). OG = out group

n°	Taxon name, authorities	Character number																Authors - year, SEM documents
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	<i>Achnanthydium atomoides</i> O Monnier, Lange-Bertalot & Ector	1	0	4	3	1	2	0	2	2	2	0	0	2	1	1	2	Monnier et al. 2004
2	<i>Achnanthydium minutissimum</i> (Kützing) Czarnecki	1	2	3	3	1	2	0	2	2	0	0	0	1	3	1	0	Czarnecki 1994, Potapova 2009
3	<i>Achnanthydium parallelum</i> JR Carter ex Jüttner, DM Williams, Ector & CE Wetzel	1	0	3	2	1	2	0	0	0	1	0	0	1	3	3	0	Jüttner et al. 2020
4	<i>Achnanthydium peterseii</i> (Hustedt) CE Wetzel, Ector, DM Williams & Jüttner (<i>Rossthydium</i>)	2	0	4	2	1	2	0	0	1	1	0	0	1	3	3	0	Jüttner et al. 2020
5	<i>Achnanthydium subhudsonis</i> var. <i>krauselii</i> (Cholnoky) Cantonati & Lange-Bertalot	1	3	4	1	2	0	0	2	1	2	0	0	2	1	1	2	Kusber et al. 2017, Spaulding and Potapova 2014
6	<i>Cocconeis alucitae</i> Riaux-Gobin & Compère	0	0	2	3	0	0	0	0	1	2	3	1	1	0	0	1	Riaux-Gobin and Compère 2008
7	<i>Cocconeis coronatoides</i> Riaux-Gobin & Romero	0	0	0	3	1	0	1	0	1	2	1	0	2	0	0	1	Riaux-Gobin et al. 2010, 2011b
8	<i>Cocconeis germainii</i> Riaux-Gobin, Witkowski & OE Romero	0	0	0	2	0	0	0	0	1	2	0	0	2	1	4	0	Riaux-Gobin et al. 2007
9	<i>Cocconeis neuquina</i> Frenguelli	0	0	2	3	0	0	0	0	1	2	0	0	2	0	0	1	Frenguelli 1942, García et al. 2018
10	<i>Cocconeis nugalas</i> MH Hohn & Hellerman	0	0	2	2	0	0	0	0	1	2	0	0	0	1	4	0	Hohn and Hellerman 1966, Riaux-Gobin et al. 2015
11	<i>Cocconeis peltoides</i> Hustedt	0	0	0	2	1	0	1	0	1	2	0	0	2	1	4	0	Hustedt 1939, Riaux-Gobin et al. 2011a
12	<i>Cocconeis pseudograta</i> Hustedt	0	1	2	1	2	0	1	0	1	2	0	0	2	1	4	0	Hustedt 1939, Romero and Riaux-Gobin 2014
13	<i>Cocconeis sigillata</i> Riaux-Gobin & Al-Handal	0	0	0	2	1	0	1	0	1	2	2	0	2	1	4	0	Riaux-Gobin et al. 2011a
14	<i>Cocconeis vaiamanuensis</i> Riaux-Gobin, Witkowski & Ector	0	1	4	1	2	0	1	0	1	2	0	1	0	1	4	0	present paper
15	<i>Karayevia oblongella</i> (Østrup) Aboal	0	0	4	0	2	2	0	0	1	2	0	0	2	1	1	2	Aboal et al. 2003
16	<i>Lemnicola hungarica</i> (Grunow) Round & Basson	0	3	1	3	1	2	0	0	0	2	2	2	0	1	1	0	Round and Basson 1997, Shi et al. 2018
17	<i>Lemnicola uniseriata</i> Y Shi & B-H Kim	0	3	0	3	3	3	0	0	1	0	0	0	0	1	1	2	Shi et al. 2018
18	<i>Pauliella taeniata</i> (Grunow) Round & Basson	2	0	3	0	0	0	0	0	0	0	0	0	0	3	3	2	Round and Basson 1997
19	<i>Planothydium juandenovense</i> Riaux-Gobin & Witkowski (OG)	0	3	0	2	2	0	1	0	1	0	4	3	0	0	0	2	Riaux-Gobin et al. 2018
20	<i>Platessa bahlsii</i> Potapova	0	0	0	2	2	0	0	0	1	0	4	3	0	0	0	2	Potapova 2012
21	<i>Platessa brevicostata</i> (Hustedt) Lange-Bertalot	0	0	4	0	1	0	0	0	1	1	2	2	0	1	1	0	Krammer and Lange-Bertalot 2004, Romero 2016
22	<i>Platessa cataractarum</i> (Hustedt) Lange-Bertalot	0	0	0	1	0	2	0	0	1	2	1	1	0	1	1	0	Krammer and Lange-Bertalot 2004, Romero 2016
23	<i>Platessa guianensis</i> Le Cohu, Tudesque & CE Wetzel	1	0	0	3	1	2	0	0	1	2	2	2	1	3	1	0	Tudesque et al. 2016
24	<i>Platessa itoupensis</i> Tudesque, Le Cohu & CE Wetzel	0	1	0	3	1	0	0	1	1	1	2	2	1	0	0	0	Tudesque et al. 2016
25	<i>Platessa kingstonii</i> Potapova	0	0	4	0	0	2	0	0	1	2	2	0	2	0	1	0	Potapova 2012
26	<i>Platessa oblongella</i> (Østrup) CE Wetzel, Lange-Bertalot & Ector	1	0	0	3	1	2	0	0	1	2	1	0	2	1	2	0	Wetzel et al. 2017, Potapova 2011

Table 3 (continued)

n°	Taxon name, authorities	Character number																Authors - year, SEM documents
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
27	<i>Platessa saxonica</i> (Kraske ex Hustedt) CE Wetzel, Lange-Bertalot & Ector	1	0	4	2	1	2	0	0	1	2	2	0	2	1	1	0	Wetzel et al. 2017
28	<i>Platessa stewartii</i> (RM Patrick) Potapova	0	0	0	2	0	3	0	0	1	0	2	2	0	1	1	0	Potapova 2012
29	<i>Psammothidium curtissimum</i> (JR Carter) Aboal	0	0	0	0	0	3	0	0	1	0	0	0	0	2	2	0	Aboal et al. 2003, Potapova 2010, Blanco 2016
30	<i>Psammothidium harveyi</i> (Reimer) Potapova	0	2	1	1	2	3	0	0	1	0	0	0	0	1	1	0	Potapova 2012
31	<i>Psammothidium levanderi</i> (Hustedt) Bukhtiyarova & Round	0	0	0	1	0	0	0	0	1	2	0	0	0	3	1	2	Bukhtiyarova and Round 1996, Blanco et al. 2017
32	<i>Psammothidium semiapertura</i> (Hustedt) Aboal	0	0	0	2	2	3	0	0	1	0	0	0	0	2	2	2	Aboal et al. 2003, Potapova 2012
33	<i>Psammothidium toroi</i> S Blanco, Pla-Rabes, CE Wetzel & I Granados	0	0	0	1	2	0	0	0	1	2	0	0	0	2	2	2	Blanco et al. 2017
34	<i>Rossithidium anastasiae</i> (Kaczmarek) Potapova	0	0	3	0	0	0	0	0	0	0	0	0	0	1	1	2	Potapova 2012

Molecular phylogenetic position of *Cocconeis* cf. *sigillata* SZCZCH1200 and some other *Cocconeis* (Figs. 8, 9)

Our rbcL-based phylogenetic trees recover monoraphid diatoms as polyphyletic and spreads them over two diatoms clades: *Achnanthes* + Bacillariaceae sister to Cocconeidae + other monoraphid and raphid diatoms (100% ML bootstrap, 0.5536 BI posterior probability), although the support of some branches within the two clades is very low.

As mentioned, *Achnanthes* as representative of Achnantheaceae is placed within the large clade together within Bacillariaceae family as sister to *Nitzschia* Hassall, 1845, *Psammodictyon* DG Mann, in Round et al. 1990 and *Tryblionella* W Smith, 1853, however, with a low support (< 50% ML bootstrap, 0.5035 BI posterior probability). This position of *Achnanthes* spp. is stable on either single gene (Mann et al. 2020), three genes (Theriot et al. 2015; Ashworth et al. 2017) or in multigene (Theriot et al. 2010; Nakov et al. 2018a, b) trees.

Cocconeidae, represented in our phylogeny by several strains of *Cocconeis* Ehrenberg, are spread over a few groups and are seemingly polyphyletic. The major *Cocconeis*-bearing clade is recovered fairly isolated and is positioned at the base of the clade containing all monoraphids and raphids, excluding Bacillariaceae. Here, *Cocconeis pediculus* Ehrenberg, 1838, and *C. placentula* Ehrenberg, 1838, create a fairly distant and monophyletic group, which is in a sister relationship to *Cocconeis* sp. KC309551 (strain name MPA2013ECT3901, see Table 4) (81% ML bootstrap, 1 BI posterior probability),

and together they are grading into a smaller group composed of *Berkeleya hyalina* (Round & ME Brooks) EJ Cox, 1975 (< 50% ML bootstrap) and two *Planothidium* and *Cocconeis* cf. *cupulifera* Riaux-Gobin, OE Romero, Compère & Al-Handal, 2011c, KT943680 (strain name SZCZCH662) (< 50% ML bootstrap). The relationship of the latter taxon to *Planothidium* spp. is moderate (65% ML bootstrap, 1 BI posterior probability).

Psammothidium, *Rossithidium* and some *Achnantheidium* form a paraphyletic group with low support at the nodes but usually moderate to high (> 60% ML bootstrap, > 0.68 BI posterior probability) in the particular clades. This clade is grading further into a monophyletic branch composed of *Achnantheidium* (10 species), and another clade of *Pauliella taeniata* (Grunow) Round & Basson, 1997, both with moderate to high support. *Cocconeis* cf. *sigillata* MT015687 (strain name SZCZCH1200) and *C. cf. mascarenica* Riaux-Gobin & Compère, 2008 KT943679 (strain name SZCZCH283) (73% ML bootstrap, 0.9999 BI posterior probability) are nested within this clade (though, with low bv), with unresolved trichotomy including *Lemnicola hungarica* (Grunow) Round & Basson, 1997, and *Cocconeis* sp. KT943614 (strain name SZCZP67) (here with also very low bv). Sister to the above monoraphid clades is *Planothidium* related to the clade of Cymbellales, however, with a low support (54% ML bootstrap, 0.9812 BI posterior probability).

Cocconeis stauroneiformis Okuno, 1957, AB430694 (strain name s0230) is positioned within Surirellales and hence fairly distant from the above monoraphids

Table 4 All strains used for the phylogenetic analysis, including the taxon name, strain ID, and accession number (*rbc L*) in genbank

Taxon	Strain ID	Assession number (<i>rbcL</i>)	Taxon	Strain ID	Assession number (<i>rbcL</i>)
<i>Achnanthes coarctata</i>	UTEX FD185	HQ912458	<i>Fragilariopsis cylindrus</i>	E8C2	EF423499
<i>Achnanthes</i> sp.	SZCZCH113	KT943615	<i>Fragilariopsis kerguelensis</i>	E13B2	EF423500
<i>Achnanthes</i> sp.	MPA-2013	KC309545	<i>Geissleria decussis</i>	FD50	KJ011830
	SanNic1Achnan				
<i>Achnanthes</i> sp.	MPA-2013	KC309547	<i>Hantzschia amphioxys</i> var.	A4	HQ912390
	ECT3911Achnan		<i>major</i>		
<i>Achnanthes</i> sp.	SZCZM119	KT943616	<i>Karayevia ploenensis</i> var.	D03_034	KM084931
			<i>gessneri</i>		
<i>Achnanthes</i> sp.	MPA-2013	KC309546	<i>Kolbesia sinica</i>	SZCZM123	KT943677
	ECT3883Achnan				
<i>Achnantheidium catenatum</i>	TCC849	KY799133	<i>Lemnicola hungarica</i>	UTEX FD456	HQ912490
<i>Achnantheidium</i> cf. <i>lineare</i>	NA-2016 strain B397	KR709273	<i>Lemnicola hungarica</i>	Lemn1	KJ658388
<i>Achnantheidium coarctatum</i>	UTEXFD185	HQ912458	<i>Madinithidium vietnamica</i>	SVN252	MH231749
<i>Achnantheidium daonense</i>	PS3	KJ658395	<i>Mastogloia aquilegiae</i>	KSA2015-49 Masto-B1	MH064100
<i>Achnantheidium digitatum</i>	SPITS_EBA-A_22	KU687461	<i>Mastogloia</i> sp.	29×07-6B	HQ912496
<i>Achnantheidium digitatum</i>	SPITS_M2AplusB_32	KU687471	<i>Mastogloia</i> sp.	SA17 Masto-C1	MH064101
<i>Achnantheidium kranzii</i>	A100r	KJ658379	<i>Mastogloia</i> sp.	KSA2016-44 Masto-A37	MH064102
<i>Achnantheidium</i>	TCC746	KF959649	<i>Navicula cryptocephala</i>	UTEX FD109	HQ912467
<i>minutissimum</i>					
<i>Achnantheidium</i>	TCC748	KY799134	<i>Navicula flagellifera</i>	TA105	KY320296
<i>minutissimum</i>					
<i>Achnantheidium</i>	TCC564	KY863481	<i>Navicula gregaria</i>	TA289	KY320297
<i>minutissimum</i>					
<i>Achnantheidium pyrenaicum</i>	TCC832	KY799135	<i>Navicula perminuta</i>	TA413	KY320299
<i>Achnantheidium reimeri</i>	Arei2	KJ658387	<i>Navicula tripunctata</i>	TCC580	KT072925
<i>Achnantheidium rivulare</i>	Ariv2	KJ658390	<i>Neidium affine</i>	UTEX FD127	HQ912447
<i>Achnantheidium</i>	TCC831	KY799136	<i>Nitzschia aurariae</i>	SZCZCH966	KT943663
<i>straubianum</i>					
<i>Achnantheidium</i>	TCC833	KY799137	<i>Nitzschia</i> cf. <i>dubiiiformis</i>	SZCZCH970	KT943666
<i>straubianum</i>					
<i>Aneumastus albanicus</i>	voucher 24426	MH756650	<i>Nitzschia filiformis</i>	UTEX FD267	HQ912453
<i>Aneumastus stroesei</i>	voucher 23685	MH756663	<i>Nitzschia frustulum</i>	CCMP558	EF423498
<i>Aneumastus subapiculatus</i>	voucher 24434	MH756665	<i>Nitzschia longissima</i>	KSA2015-9	MH064112
			Nitz.longi-ED		
<i>Astartiella</i> sp.	SZCZCH151	KT943613	<i>Parlibellus berkeleyi</i>	SEH015	JX905679
<i>Auricula complexa</i>	26vi08.1 J.1	KX120569	<i>Parlibellus delognei</i> f.	TA387	KY320291
			<i>ellipticus</i>		
<i>Auricula mirabilis</i>	4vi08.1cA	KX120567	<i>Parlibellus hamulifer</i>	GU44AK-4	KJ577903
<i>Bacillaria paxillifer</i>	UTEX FD468	HQ912491	<i>Parlibellus hamulifer</i>	SantaRosa cor.green	KU179122
			“Trachy-1”		
<i>Berkeleya hyalina</i>	ECT3614Bhya	KJ577882	<i>Parlibellus harffianus</i>	SZCZCH75	KT943686
<i>Berkeleya rutilans</i>	ECT3616	HQ912501	<i>Pauliella taeniata</i>	CCMP1115	KJ658391
<i>Bolidomonas pacifica</i>	p380	AB430698	<i>Pauliella taeniata</i>	C124	FJ002105
<i>Bolidomonas pacifica</i>	CCMP1866	HQ912421	<i>Phaeodactylum</i>	CCMP2561	HQ912420
			<i>tricornutum</i>		
<i>Caloneis</i> cf. <i>westii</i>	SZCZCH1002	KT943654	<i>Pinnularia brebissonii</i>	UTEX FD274	HQ912468
<i>Caloneis lewisii</i>	UTEX FD54	HQ912444	<i>Pinnularia termitina</i>	UTEX FD484	HQ912465
<i>Campylodiscus clypeus</i>	nycCA2	KX120583	<i>Placoneis clementis</i>	FD419	KJ011851
<i>Campylodiscus levanderi</i>	3637.C10.100	KX120602	<i>Placoneis elginensis</i>	UTEX FD416	HQ912471
<i>Climaconeis riddleae</i>	ECT3724	HQ912508	<i>Planothidium caputium</i>	D06_113	KY650812
<i>Cocconeis</i> cf. <i>cupulifera</i>	SZCZCH662	KT943680	<i>Planothidium caputium</i>	B086-3	KY650806
<i>Cocconeis</i> cf. <i>mascarenica</i>	SZCZCH283	KT943679	<i>Planothidium</i> cf.	D17_002	KY650822
			<i>subantarcticum</i>		
<i>Cocconeis</i> cf. <i>sigillata</i>	SZCZCH1200	MT015687	<i>Planothidium</i>	D108_021	KY650818
			<i>cryptolanceolatum</i>		
<i>Cocconeis pediculus</i>	SpC01	KM084991	<i>Planothidium</i>	D21_002	KY650823
			<i>cryptolanceolatum</i>		
<i>Cocconeis pediculus</i>	D36_020	KM084977	<i>Planothidium</i>	D26_014	KY650826
			<i>cryptolanceolatum</i>		

Table 4 (continued)

Taxon	Strain ID	Assession number (<i>rbcL</i>)	Taxon	Strain ID	Assession number (<i>rbcL</i>)
<i>Cocconeis pediculus</i>	Coco1	KM084929	<i>Planothidium</i>	PF1	KJ658392
<i>Cocconeis placentula</i>	UTEX FD23	HQ912456	<i>frequentissimum</i>	D06_117b	KY650813
<i>Cocconeis placentula</i>	D36_012	KM084976	<i>Planothidium</i>		
<i>Cocconeis placentula</i> var. <i>euglypta</i>	TCC449	KT072907	<i>frequentissimum</i>		
<i>Cocconeis</i> sp.	SZCZP67	KT943614	<i>Planothidium lanceolatum</i>	PL2	KJ658393
<i>Cocconeis</i> sp.	MPA-2013 ECT3901cocconeid	KC309551	<i>Planothidium lanceolatum</i>	PL3	KJ658389
<i>Cocconeis stauroneiformis</i>	s0230	AB430694	<i>Planothidium</i>	Ko0408	KY650831
<i>Craspedostauros alyoubii</i>	UTKSA0083	KX981814	<i>suncheonmanense</i>		
<i>Craspedostauros</i>	CCMP797	KX981815	<i>Planothidium taeansa</i>	D26_002	KY650825
<i>amphoroides</i>			<i>Prestauroneis integra</i>	AT-177.13	AM710492
<i>Craspedostauros</i> cf. <i>neoconstrictus</i>	CCMP1120	KX981817	<i>Psammodictyon</i>	GU7X-7 peanut5	KX981830
<i>Craspedostauros paradoxa</i>	GU44BK-1 keeledHcpA25	KX981816	<i>constrictum</i>		
<i>Craticula accomoda</i>	TCC107	KF959638	<i>Psammodictyon</i>	KSA2015-38 FORAM	MH064134
<i>Craticula ambigua</i>	B060	MH231744	<i>pustulatum</i>		
<i>Craticula cuspidata</i>	UTEX FD35	HQ912445	<i>Psammothidium abundans</i>	MIC5_40b	KU687468
			<i>Psammothidium papilio</i>	SHIR_Kbis7	KU687473
<i>Craticula cuspidata</i>	Navi4	KM084985	<i>Psammothidium</i>	B422	KR709269
			<i>subatomoides</i>		
<i>Craticula cuspidata</i>	Ind367	MH231745	<i>Psammothidium</i>	B356	KR709270
			<i>subatomoides</i>		
<i>Craticula importuna</i>	AT-70Gel14a	AM710444	<i>Psammothidium</i>	B352	KR709276
			<i>subatomoides</i>		
<i>Craticula molestiformis</i>	AT-5Nav02	AM710443	<i>Pseudo-nitzschia</i>	FBJun06.6	EF423504
			<i>americana</i>		
<i>Cylindrotheca closterium</i>	CCMP1855	HQ912509	<i>Pseudo-nitzschia</i>	BB19	EF423503
<i>Cylindrotheca</i> sp.	UTKSA0079	KX981826	<i>fraudulenta</i>		
<i>Cymatopleura elliptica</i>	L1333	HQ912523	<i>Rhopalodia contorta</i>	L1299	HQ912392
<i>Cymatopleura solea</i>	27A	KX120605	<i>Rhopalodia gibba</i>	CH155	HQ912393
<i>Cymbopleura</i>	22vi092D	KJ011815	<i>Rossithidium anastasiae</i>	Ros1	KJ658396
<i>naviculiformis</i>			<i>Rossithidium petersenii</i>	B354	KR709275
<i>Cymbopleura</i> sp.	TN-2014 CH254	KJ011817	<i>Schizostauron</i>	SZCZP39	KT943604
<i>Denticula kuetzingii</i>	UTEX FD135	HQ912474	<i>davidovichiorum</i>		
<i>Dorofeyukea indokotschyi</i>	Ind313	MH231746	<i>Schizostauron</i> sp.	SZCZE421	KT943610
<i>Dorofeyukea indokotschyi</i>	Ind365	MH231747	<i>Schizostauron</i> sp.	SZCZE399	KT943609
<i>Dorofeyukea kotschyi</i>	Ind381	MH231748	<i>Simonsenia aveniformis</i>		KR048205
			<i>Stauroneis acuta</i>	UTEX FD51	HQ912443
<i>Entomoneis pusilla</i>	PMFBIOPI1	MF000640	<i>Stauroneis</i> cf. <i>anceps</i>	KEL-2015 JAR44_ 3BRUN6	KM999047
			<i>Stauroneis</i> cf. <i>gracilis</i>	KEL-2015 JAR44_ 5ARun6	KM999046
<i>Entomoneis vilicicii</i>	PMFBION4A	MF000637	<i>Stauroneis</i> cf. <i>gracilis</i>	B375	MH231750
<i>Epithemia argus</i>	CH211	HQ912394	<i>Stauroneis gracilis</i>	B540	MH231751
<i>Epithemia turgida</i>	CH154	HQ912396	<i>Stauroneis gracilis</i>	B651	MH231754
<i>Eunotia bilunaris</i>	UTEX FD412	HQ912463	<i>Stauroneis heinii</i>	B644	MH231752
<i>Eunotia glacialis</i>	UTEX FD46	HQ912450	<i>Stauroneis phoenicenteron</i>	AT-182.07	AM710498
<i>Fistulifera pelliculosa</i>	CCMP:543	HQ337547	<i>Stauroneis subgracilis</i>	B376	MH231753
<i>Fistulifera pelliculosa</i>	IK_MTA116	JN162792	<i>Stenopterobia curvula</i>	L541	HQ912402
<i>Fistulifera saprophila</i>	TCC535	KF959644	<i>Surirella minuta</i>	UTEX FD320	HQ912522
<i>Fistulifera saprophila</i>	LCR-S-20-3	JQ610165	<i>Surirella splendida</i>	19C	HQ912401
<i>Fistulifera saprophila</i>	TCC508	KC736593	<i>Tryblionella apiculata</i>	UTEX FD465	HQ912464
<i>Fistulifera saprophila</i>	TCC557	KT072923	<i>Tryblionella gaoana</i>	SZCZCH97	KT943683

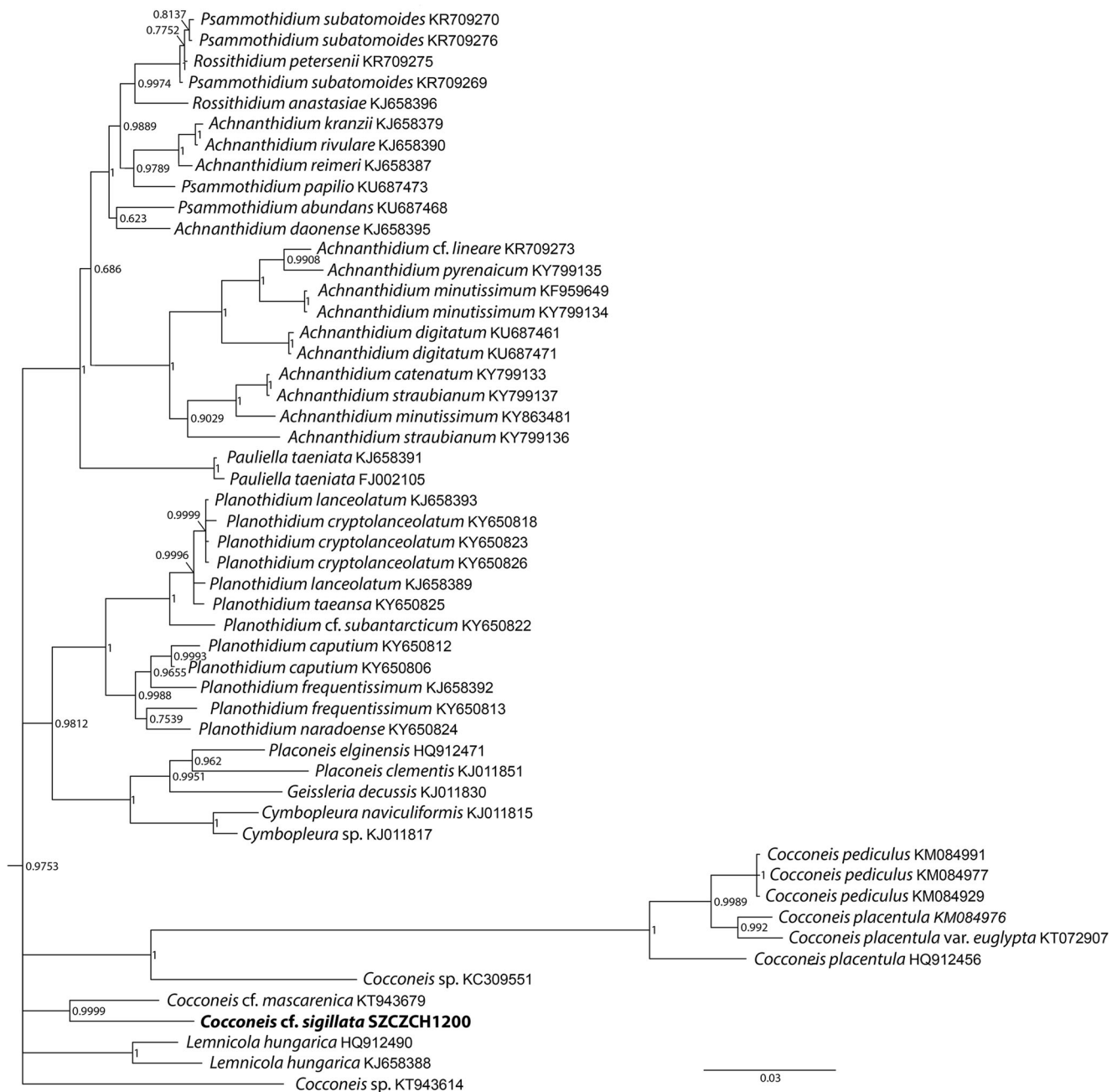


Fig. 9 Detail of the position of *Cocconeis cf. sigillata* MT015687 (SZCZCH1200) in the phylogenetic tree (Fig. 8). See comments on the text

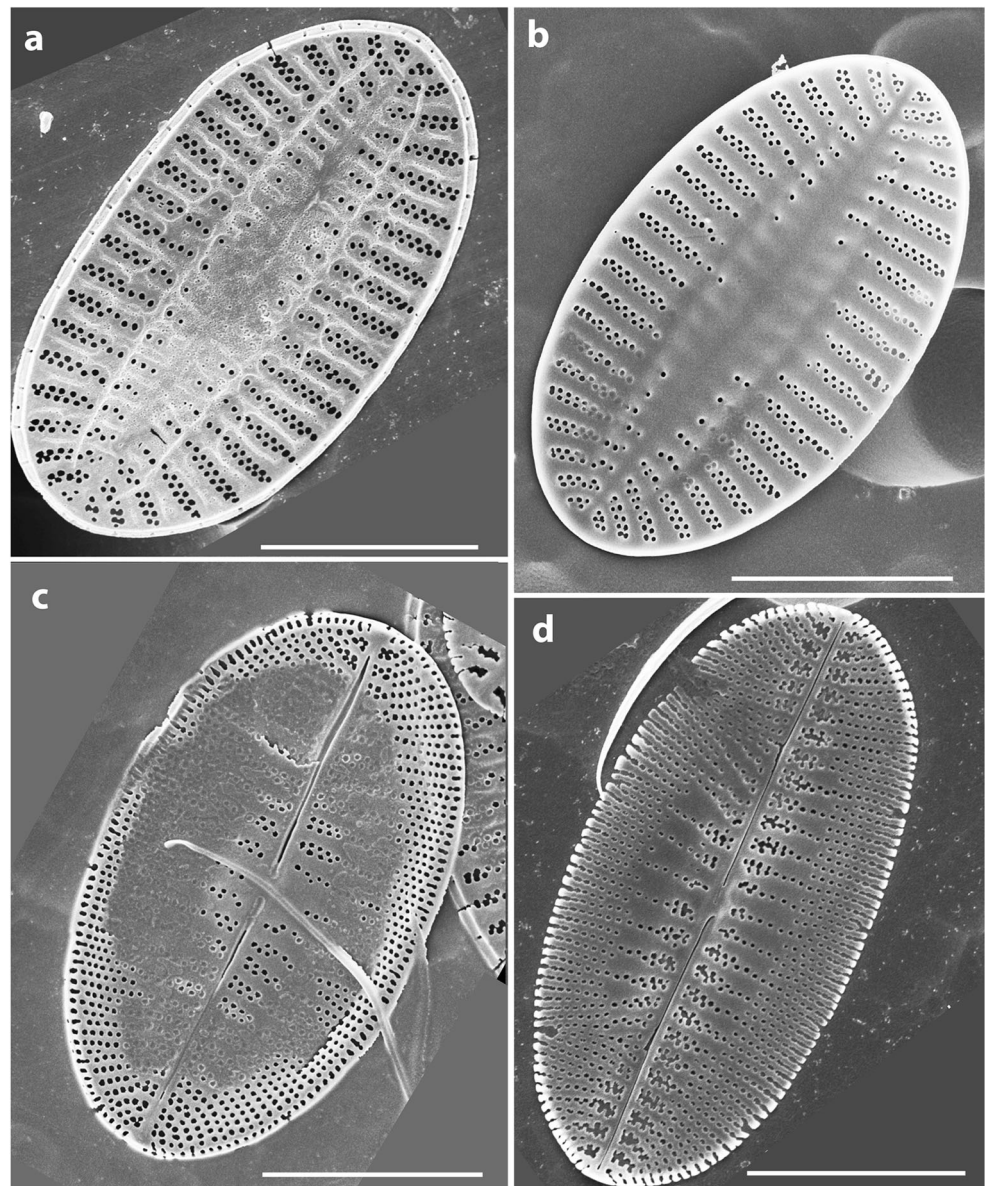
and the major *Cocconeis* clades. Although, the relationship is weakly supported (< 50% ML bootstrap, 0.7763 BI posterior probability).

Finally, *Schizostauron* Grunow, 1867, *Astartiella* Witkowski, Lange-Bertalot & Metzeltin in Moser et al. 1998, *Madinithidium* Desrosiers, Witkowski & Riaux-Gobin, in Desrosiers et al. 2014, *Karayevia* and *Kolbesia* Round & Bukhtiyarova ex Round, 1998, belong in a monophyletic clade together with Stauroneidaceae as well as *Parlibellus* EJ Cox, 1998 and *Fistulifera* Lange-Bertalot, 1997.

Discussion

It can be noted that among the morphological characters chosen to delineate groups of taxa in our ultrastructural cladistics analysis (Table 3, Fig. 7), the absence of SV processes (i.e., in *Platessa bahlsii* Potapova, 2012, *P. itoupensis* Tudesque, Le Cohu & CE Wetzel, 2016, *P. kingstonii* Potapova, 2012, *Cocconeis alucitata* Riaux-Gobin & Compère, 2008, *C. neuquina* Frenguelli, 1942, *C. coronatoides* Riaux-Gobin & OE Romero, in Riaux-Gobin et al. 2011b) does not tightly group the latter taxa. Thus, it proves

Fig. 10 *Cocconeis* cf. *sigillata* MT015687 (SZCZCH1200). **a** SV in external view, with biseriate striae, *crista marginalis* and SV processes on the mantle; **b** SV in internal view, with an elliptic SV stemum void of areolae; **c** RV in external view; **d** RV in internal view with two shorter striae between each stria. Striae biseriate near the raphe. Note the Voigt discontinuities (**d**). Scale bars = 5 μ m



that a more determinant character (than the absence of SV processes), or a combination of characters, better drives the analysis. In the same manner, the terminal raphe endings (simple or showing either more or less large and bent fissures) do not seem determinant to group or individualize taxa.

Following this cladistic analysis, *Cocconeis peltoides* and affiliated taxa (with SV processes), are close to *Psammothidium levanderi* (Hustedt) Bukhtiyarova & Round, 1996 and *P. toroi* S Blanco, Pla-Rabès, CE Wetzel & I Granados, 2017. In contrast, *Cocconeis* taxa without SV processes (such as *C. alucitae*, *C. neuquina* and *C. coronatoides*) are part of another clade, close to several *Platessa* and far from *Achnanthisdium*.

Our phylogenetic tree (Fig. 8) suggests that the genus *Cocconeis* is not monophyletic. Surprisingly *C. cf. cupulifera* SZCZCH662 (see Riaux-Gobin et al. 2011c, p. 24) has no genetic affiliation to *C. cf. sigillata* SZCZCH1200. In

contrast, they both have SV processes and pertain to the same morphological group. Also surprising is the place of *C. cf. mascarenica* SZCZCH283 (a taxon without SV processes, cf. Riaux-Gobin and Compère 2008) that locates as a sister of *C. cf. sigillata* (Fig. 8). Several previous investigations (Nakov 2014; Kulikovskiy et al. 2016, 2019; Thomas et al. 2016; Witkowski et al. 2016; Shi et al. 2018) also showed that *C. placentula* Ehrenberg, 1838 and *C. pediculus* Ehrenberg, 1838 group together and that *C. stauroneiformis* Okuno, 1957 pertains to another clade. Finally, and as previously stated by, i.e., Kulikovskiy et al. (2016), the Order Achnanthes arbitrarily groups numerous genera that are not genetically inter-connected, and is thus a polyphyletic group. In more general terms, in support of Thomas et al. (2016), “the monoraphid diatoms are not a natural group.” Shape convergence strongly influenced past

taxonomy, which needs to be revisited in light of genetic approaches. Nevertheless, genetic and morphological approaches (Figs. 7, 10) may complement each other, since the cultivation, followed by sequencing of numerous taxa (i.e., small marine taxa, particularly monoraphid ones) has up to now been impossible (no entries in GenBank), yet essential to clarify their phylogenetic position. Therefore, as a first step, the cladistic analyses based on ultrastructure can help to provide preliminary keys.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All samplings were done in French Polynesia, under the agreement of CRILOBE (CNRS–USR 3278, France). Diatoms are not protected organisms.

Data availability The datasets generated during and/or analyzed during the current study, particularly all SEM images, are available from the corresponding author on reasonable request. No citations of other datasets.

Author contribution CR-G, AW, and EG conceived and designed research, and analyzed data. CR-G conducted the sampling and ultrastructural description of the new taxon. EG and AW conducted the genetic analysis of a close taxon. PS-A conducted the cladistic analysis on ultrastructural characters. LE managed bibliographic research. GD-K conducted the technical assistance. CR-G wrote the manuscript with help of EG and all co-authors. All authors read and approved the manuscript.

References

- Aboal M, Álvarez Cobelas M, Cambra J, Ector L (2003) Floristic list of non-marine diatoms (*Bacillariophyceae*) of Iberian Peninsula, Balearic Islands and Canary Islands. Updated taxonomy and bibliography. *Diatom Monographs* 4:1–639
- Ashworth MP, Lobban CS, Witkowski A, Theriot EC, Sabir MJ, Baeshen MN, Hajarrah NH, Baeshen NA, Sabir JS, Jansen RK (2017) Molecular and morphological investigations of the stauros-bearing, raphid pennate diatoms (*Bacillariophyceae*): *Craspedostauros* E.J. Cox, and *Staurotropis* TBB Paddock, and their relationship to the rest of the Mastogloiales. *Protist* 168:48–70. <https://doi.org/10.1016/j.protis.2016.11.001>
- Blanco S (2016) A nomenclatural note on two species of the Achnanthesiaceae (*Bacillariophyta*). *Notul Alg* 4:1–2
- Blanco S, Pla-Rabès S, Wetzel CE, Granados I (2017) A new *Psammothidium* species (*Bacillariophyta*, *Achnanthesiaceae*) from Cimera Lake (Gredos mountain range), Central Spain. *Cryptogam Algal* 38:17–29. <https://doi.org/10.7872/crya/v38.iss1.2017.17>
- Bory de Saint-Vincent JBG (1822) *Achnanthes*. *Achnanthes*. In: Audouin I et al (eds) *Dictionnaire Classique d'Histoire Naturelle*, vol 1, Paris, pp 79–80
- Bukhtiyarova L, Round FE (1996) Revision of the genus *Achnanthes sensu lato*. *Psammothidium*, a new genus based on *Achnantheidium marginulatum*. *Diatom Res* 11(1):1–30. <https://doi.org/10.1080/0269249X.1996.9705361>
- Cleve PT, Grunow A (1880) Beiträge zur Kenntniss der arctischen Diatomeen. *Kunl. Svenska Vetenskapsakad Handl* 17:121 pp., 7 pls
- Cox EJ (1975) Further studies on the genus *Berkeleya* Grev. *Br Phycol J* 10:205–217. <https://doi.org/10.1080/00071617500650191>
- Cox EJ (1988) Taxonomic studies on the diatom genus *Navicula* V. The establishment of *Parlibellus* gen. nov. for some members of *Navicula* sect. *Microstigmatae*. *Diatom Res* 3:9–38. <https://doi.org/10.1080/0269249X.1988.9705014>
- Cox EJ (2006) *Achnanthes sensu stricto* belongs with genera of the Mastogloiales rather than with other monoraphid diatoms (*Bacillariophyta*). *Eur J Phycol* 41:67–81. <https://doi.org/10.1080/09670260500491543>
- Cox EJ, Williams DM (2006) Systematics of naviculoid diatoms (*Bacillariophyta*): a preliminary analysis of protoplast and frustule characters for family and order level classification. *Syst Biodivers* 4: 385–399. <https://doi.org/10.1017/S1477200006001940>
- Czarniecki DB (1994) The freshwater diatom culture collection at Loras College, Dubuque, Iowa. In: *Proceedings of the 11th International Diatom Symposium San Francisco, California 12–17 August 1990* (Kociolek JP, ed.). *Mem Calif Acad Sci* 17:155–174
- Dąbek P, Ashworth MP, Witkowski A, Li C, Bommman TG, Gonçalves V, Park J, Kim JS (2017) Towards a multigene phylogeny of the Cymatosiraceae (*Bacillariophyta*, *Mediophyceae*) I: novel taxa within the subfamily Cymatosiroideae based on molecular and morphological data. *J Phycol* 53:342–360. <https://doi.org/10.1111/jpy.12501>
- Davidovich NA, Davidovich OI, Witkowski A, Li C, Dąbek P, Mann DG, Zgłobicka I, Kurzydłowski KJ, Gusev E, Górecka E, Krzywda M (2017) Sexual reproduction in *Schizostauron* (*Bacillariophyta*) and a preliminary phylogeny of the genus. *Phycologia* 56:77–93. <https://doi.org/10.2216/16-29.1>
- De Stefano M, Marino D (2003) Morphology and taxonomy of *Amphicocconeis* gen. nov. (*Achnanthes*, *Bacillariophyceae*, *Bacillariophyta*) with considerations on its relationship to other monoraphid diatom genera. *Eur J Phycol* 38:361–370. <https://doi.org/10.1080/09670260310001612646>
- De Stefano M, Romero O (2005) A survey of alveolate species of the diatom genus *Cocconeis* (Ehr.) with remarks on the new section *Alveolatae*. *Bibl Diatomol* 52:1–133
- Desianti N, Potapova M, Beals J (2015) Examination of the type materials of diatoms described by Hohn and Hellerman from the Atlantic Coast of the USA. *Diatom Res* 30:93–116. <https://doi.org/10.1080/0269249X.2014.1000020>

- Desrosiers C, Witkowski A, Riaux-Gobin C, Zgłobicka I, Kurzydłowski KJ, Eulin A, Leflaive J, Ten-Hage L (2014) *Madinithidium gen. nov.* (Bacillariophyceae), a new monoraphid diatom genus from the tropical marine coastal zone. *Phycologia* 53:583–592. <https://doi.org/10.2216/14-21R2>
- Ehrenberg CG (1837) Zusätze zur Erkenntniss grosser organischer Ausbildung in den kleinsten thierischen Organismen. *Abh Königl Akad Wiss Berlin* 1835:151–180
- Ehrenberg CG (1838) *Die Infusionsthierchen als vollkommene Organismen. Ein Blick in das tiefere organische Leben der Natur.* Leipzig: Verlag von Leopold Voss. pp. 1–xvii, 1–548, pls 1–64 [two volumes: Text, Atlas]
- Frankovich TA, Ashworth MP, Sullivan MJ, Theriot EC, Stacy NI (2018) Epizoic and apochlorotic *Tursiocola* species (Bacillariophyta) from the skin of Florida Manatees (*Trichechus manatus latirostris*). *Protist* 169:539–568. <https://doi.org/10.1016/j.protis.2018.04.002>
- Freguelli J (1942) XVII Contribución al conocimiento de las diatomeas Argentinas. Diatomeas del Neuquén (Patagonia). *Rev Mus La Plata (Nueva Serie), Sección Botánica* 20, 5:73–219, 12 pls
- García ML, Echazú DM, Romero OE, Maidana NI (2018) *Cocconeis neuquina* Freguelli (Bacillariophyta): emended description, lectotypification, ecology, and geographical distribution. *Diatom Res* 33:219–228. <https://doi.org/10.1080/0269249X.2018.1485596>
- Grunow A (1867) Diatomeen auf *Sargassum* von Honduras gesammelt von Linbig. *Hedwigia* 6(1–3):1–8 17–32, 33–37
- Guillou L, Chrétiennot-Dinet M-J, Medlin LK, Claustre H, Loiseaux-de Goër S, Vault D (1999) *Bolidomonas*: a new genus with two species belonging to a new algal class, the Bolidophyceae (Heterokonta). *J Phycol* 35:368–381. <https://doi.org/10.1046/j.1529-8817.1999.3520368.x>
- Haeckel E. (1878) *Das Protistenreich. Eine populäre uebersicht über das Formengebiet der niedersten Lebewesen. Mit einem wissenschaftlichen Anhänge: System der Protisten.* Leipzig: Ernst Günther's Verlag. pp. 1–104, 58 figs <https://doi.org/10.5962/bhl.title.58542>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp Ser* 41:95–98
- Hassall AH (1845) *A history of the British freshwater algae, including descriptions of the Desmidiaceae and Diatomaceae.* With upwards of one hundred plates, illustrating the various species. Vol. I. pp. [i]–viii, [j]–462, [i], err.]. London, Edinburgh, Paris & Leipzig: S. Highley, H. Baillière; Sunderland & Knox; J.B. Baillière; T.O. Weigel
- Hohn MH, Hellerman J (1966) New diatoms from the Lewes-Rehoboth Canal, Delaware and Chesapeake Bay Area of Baltimore. *Maryland Tran Am Microsc Soc* 85:115–130. <https://doi.org/10.2307/3224781>
- Hustedt F (1939) Die Diatomeenflora des Küstengebietes der Nordsee vom Dollart bis zur Elbemündung. I. Die Diatomeenflora in den Sedimenten der unteren Ems sowie auf den Watten in der Leybucht, des Memmert und bei der Insel Juist. *Adh Naturwiss Ver Bremen* 31(2/3):571–677
- Ichinomiya M, Lopes dos Santos A, Gourvil P, Yoshikawa S, Kamiya M, Ohki K, Audic S, de Vargas C, Noël M-H, Vault D, Kuwata A (2016) Diversity and oceanic distribution of the Parmales (Bolidophyceae), a picoplanktonic group closely related to diatoms. *ISME J* 10:2419–2434. <https://doi.org/10.1038/ismej.2016.38>
- Jüttner I, Wetzel CE, Williams DM, Ector L (2020) Investigations of the type materials of *Achnanthes parallela* J.R.Carter and *Achnanthes petersenii* Hustedt (Bacillariophyceae) with comments on the genus *Rossethidium* Round & Bukhtiyarova. *Bot Lett* 167:57–69. <https://doi.org/10.1080/23818107.2019.1668297>
- Krammer K, Lange-Bertalot H (2004) Bacillariophyceae 4. Teil: Achnanthaceae, Kritische Ergänzungen zu *Achnanthes* s. 1., *Navicula* s. str., *Gomphonema*. *Gesamtliteraturverzeichnis Teil 1–4* [second revised edition] [With "Ergänzungen und Revisionen" by H. Lange Bertalot]. In: *Süßwasserflora von Mitteleuropa.* (Ettl, H. et al. Eds) Vol. 2, pp. 1–468. Heidelberg: Spektrum Akademischer Verlag
- Kryk A, Bağ M, Górecka E, Riaux-Gobin C, Bemiasa J, Bemanaja E, Li C, Dąbek P, Witkowski A (2020) Marine diatom assemblages of the Nosy Be Island coasts, NW Madagascar: species composition and biodiversity using molecular and morphological taxonomy. *Syst Biodivers* 18:161–180. <https://doi.org/10.1080/14772000.2019.1696420>
- Kulikovskiy MS, Andreeva SA, Gusev ES, Kuznetsova IV, Annenkova NV (2016) Molecular phylogeny of monoraphid diatoms and raphe significance in evolution and taxonomy. *Biol Bull* 43:398–407. <https://doi.org/10.1134/S1062359016050046>
- Kulikovskiy M, Maltsev Y, Andreeva S, Glushchenko A, Gusev E, Podunay Y, Ludwig TV, Tusset E, Kociolek JP (2019) Description of a new diatom genus *Dorofeyukea* gen. nov. with remarks on phylogeny of the family Stauroneidaceae. *J Phycol* 55: 173–185. <https://doi.org/10.1111/jpy.12810>
- Kulikovskiy MS, Glushchenko AM, Genkal SI, Kuznetsova IV, Kociolek JP (2020) *Platebaikalica* – a new monoraphid diatom genus from ancient Lake Baikal with comments on the genus *Platessa*. *Fottea* 20:58–67. <https://doi.org/10.5507/fof.2019.014>
- Kusber W-H, Cantonati M, Lange-Bertalot H (2017) Validation of five diatom novelties published in "Freshwater Benthic Diatoms of Central Europe" and taxonomic treatment of the neglected species *Tryblionella hantzschiana*. *Phytotaxa* 328:90–94. <https://doi.org/10.11646/phytotaxa.328.1.6>
- Kützing FT (1844) *Die Kieselschaligen Bacillarien oder Diatomeen.* pp. [i–viii], [1]–152, pls 1–30. Nordhausen: zu finden bei W. Köhne <https://doi.org/10.5962/bhl.title.64360>
- Lange-Bertalot H (1997) *Frankophila, Mayamaea* und *Fistulifera*: drei neue Gattungen der Klasse Bacillariophyceae. *Arch Protistenkd* 148:65–76. [https://doi.org/10.1016/S0003-9365\(97\)80037-1](https://doi.org/10.1016/S0003-9365(97)80037-1)
- Le Cohu R (2005) Révision des principales espèces dulçaquicoles d'Achnanthales (Bacillariophyta) des îles subantarctiques de Kerguelen. *Algol Stud* 116:79–114. <https://doi.org/10.1127/1864-1318/2005/0116-0079>
- Mann DG, Trobajo R, Sato S, Li C, Witkowski A, Rimet F, Ashworth MP, Hollands RM, Theriot EC (2020) Ripe for reassessment: a synthesis of available molecular data for the speciose diatom family Bacillariaceae. *Mol Phylogenet Evol.* <https://doi.org/10.1016/j.ympev.2020.106985>
- Monnier O, Lange-Bertalot H, Rimet F, Hoffman L, Ector L (2004) *Achnantheidium atomoides* sp. nov., a new diatom from the Grand-Duchy of Luxembourg. *Vie Milieu* 54:127–136
- Montaggioni L (2015) Naissance et évolution géologique des Iles Australes. In: Salvat B, Bambridge T, Tanret D, Petit J (eds) *Environnement marin des Iles Australes, Polynésie Française.* Institut Récifs Coralliens Pacifique CRIOBE, Pew Charitable Trusts, Polynésie Française, pp 28–39
- Moser G, Lange-Bertalot H, Metzeltin D (1998) Insel der Endemiten. Geobotanisches Phänomen Neukaledonien. [Island of endemics. New Caledonia - a geobotanical phenomenon]. *Biblioth Diatomol* 38:[1]–464
- Nakov T (2014) Studies of phylogenetic relationships and evolution of functional traits in diatoms. PhD thesis, The University of Texas at Austin
- Nakov T, Beaulieu JM, Alverson AJ (2018a) Insights into global planktonic diatom diversity: the importance of comparisons between phylogenetically equivalent units that account for time. *ISME J* 12: 2807–2810. <https://doi.org/10.1038/s41396-018-0221-y>
- Nakov T, Beaulieu JM, Alverson AJ (2018b) Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (diatoms, Bacillariophyta). *New Phytol* 219: 462–473. <https://doi.org/10.1111/nph.15137>

- Okuno H (1957) Electron-microscopical study of the fine structures of diatom frustules XVI. Bot Mag (Tokyo) 70:216–222 <https://doi.org/10.15281/jplantres1887.70.216>
- Potapova M (2009) *Achnantheidium minutissimum*. In: Diatoms of North America. Retrieved January 23, 2020, from https://diatoms.org/species/achnantheidium_minutissimum
- Potapova M (2010) *Psammothidium microscopicum*. In: Diatoms of North America. Retrieved January 07, 2021, from https://diatoms.org/species/psammothidium_microscopicum
- Potapova M (2011) *Platessa oblongella*. In: Diatoms of North America. Retrieved January 07, 2021, from https://diatoms.org/species/platessa_oblongella
- Potapova MG (2012) New species and combinations in monoraphid diatoms (family Achnanthidiaceae) from North America. Diatom Res 27:29–42. <https://doi.org/10.1080/0269249X.2011.644636>
- Riaux-Gobin C, Compère P (2008) New *Cocconeis* taxa from coral sands off Réunion Island (Western Indian Ocean). Diatom Res 23:129–146. <https://doi.org/10.1080/0269249X.2008.9705742>
- Riaux-Gobin C, Compère P (2009) *Olifantiella mascarenica* gen. & sp. nov., a new genus of pennate diatom from Réunion Island, exhibiting a remarkable internal process. Phycol Res 57:178–185. <https://doi.org/10.1111/j.1440-1835.2009.00537.x>
- Riaux-Gobin C, Romero O (2003) Marine *Cocconeis* Ehrenberg (Bacillariophyceae) species and related taxa from Kerguelen's land (Austral Ocean, Indian sector). Bibl Diatomol 47:1–189
- Riaux-Gobin C, Witkowski A (2015) *Pseudachnantheidium megapteropsis* gen. nov. and sp. nov. (Bacillariophyta): a widespread Indo-Pacific elusive taxon. Cryptogam Algal 36:291–304. <https://doi.org/10.7872/crya/v36.iss3.2015.291>
- Riaux-Gobin C, Witkowski A, Romero OE (2007) *Cocconeis germainii* sp. nov. and a related taxon from Kerguelen archipelago (Austral Ocean, Indian sector). Diatom Res 22:329–340. <https://doi.org/10.1080/0269249X.2007.9705719>
- Riaux-Gobin C, Romero OE, Al-Handal AY, Compère P (2010) Two new *Cocconeis* taxa (Bacillariophyceae) from coral sands off the Mascarenes (Western Indian Ocean) and some related unidentified taxa. Eur J Phycol 45:278–292. <https://doi.org/10.1080/09670260903560076>
- Riaux-Gobin C, Compère P, Al-Handal AY (2011a) Species of the *Cocconeis peltoides* group with a marginal row of unusual processes (Mascarenes and Kerguelen Islands, Indian Ocean). Diatom Res 26:325–338. <https://doi.org/10.1080/0269249X.2011.639559>
- Riaux-Gobin C, Romero OE, Al-Handal AY, Compère P (2011b) Corrigendum. Eur J Phycol 46:88. <https://doi.org/10.1080/09670262.2011.552225>
- Riaux-Gobin C, Romero OE, Compère P, Al-Handal AY (2011c) Small-sized Achnanthes (Bacillariophyta) from coral sands off Mascarenes (Western Indian Ocean). Bibl Diatomol 57:1–234
- Riaux-Gobin C, Witkowski A, Ruppel M (2012) *Scalariella* a new genus of monoraphid diatom (Bacillariophyta) with a bipolar distribution. Fottea 12:13–25. <https://doi.org/10.5507/fot.2012.002>
- Riaux-Gobin C, Compère P, Coste M, Straub F, Taxböck L (2014) *Cocconeis napukensis* sp. nov. (Bacillariophyceae) from Napuka Atoll (South Pacific) and lectotypification of *Cocconeis subtilissima* Meister. Fottea 14:209–224. <https://doi.org/10.5507/fot.2014.016>
- Riaux-Gobin C, Witkowski A, Compère P, Romero OE (2015) *Cocconeis* Ehrenberg taxa (Bacillariophyta) with a marginal row of simple processes: relationship with the valvocopula system and distinctive features of related taxa. Fottea 15:139–154. <https://doi.org/10.5507/fot.2015.015>
- Riaux-Gobin C, Witkowski A, Igersheim A, Lobban CS, Al-Handal AY, Compère P (2018) *Planothidium juandenovense* sp. nov. (Bacillariophyta) from Juan de Nova (Scattered Islands, Mozambique Channel) and other tropical environments: a new addition to the *Planothidium delicatum* complex. Fottea 18:106–119. <https://doi.org/10.5507/fot.2017.019>
- Romero OE (2016) Study of the type material of two *Platessa* Lange-Bertalot species formerly *Cocconeis brevicostata* Hust. and *Cocconeis cataractarum* Hust. (Bacillariophyta). Diatom Res 31:63–75. <https://doi.org/10.1080/0269249X.2016.1143035>
- Romero OE, Riaux-Gobin C (2014) Two closely-related species of *Cocconeis* (Bacillariophyta): comparative study and typification. Plant Ecol Evol 147:426–438. <https://doi.org/10.5091/plecevo.2014.996>
- Round FE (1998) Validation of some previously published "achnantheid" genera. Diatom Res 13:181. <https://doi.org/10.1080/0269249X.1998.9705442>
- Round FE, Basson PW (1997) A new monoraphid diatom genus (*Pogoneis*) from Bahrain and the transfer of previously described species *A. hungarica* and *A. taeniata* to new genera. Diatom Res 12:71–81. <https://doi.org/10.1080/0269249X.1997.9705403>
- Round FE, Bukhtiyarova L (1996) Four new genera based on *Achnanthes* (*Achnantheidium*) together with a re-definition of *Achnantheidium*. Diatom Res 11:345–361. <https://doi.org/10.1080/0269249X.1996.9705389>
- Round FE, Crawford RM, Mann DG (1990) The diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge, pp 747
- Shi Y, Wang P, Kim H-K, Lee H, Han M-S, Kim B-H (2018) *Lemnicola hungarica* (Bacillariophyceae) and the new monoraphid diatom *Lemnicola uniseriata* sp. nov. (Bacillariophyceae) from South Korea. Diatom Res 33:69–87. <https://doi.org/10.1080/0269249X.2018.1465479>
- Silva PC (1962) Classification of algae. In: Lewin RA (ed) Physiology and biochemistry of algae. Academic Press, New York, pp 827–837
- Smith W (1853) *A synopsis of the British Diatomaceae*; with remarks on their structure, function and distribution; and instructions for collecting and preserving specimens. The plates by Tuffen West. In two volumes. Vol. 1. pp. [i]–xxxiii, 1–89, pls I–XXXI. London: John van Voorst, Paternoster Row <https://doi.org/10.5962/bhl.title.10706>
- Spaulding S, Edlund M (2008) *Karayevia*. In: Diatoms of North America. Retrieved January 07, 2021, from <https://diatoms.org/genera/karayevia>
- Spaulding S, Potapova M (2014) *Achnantheidium subhudsonis* var. *kraeuselii*. In: Diatoms of North America. Retrieved January 21, 2020, from https://diatoms.org/species/achnantheidium_subhudsonis_var_kraeuselii
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Swofford DL (2003) *PAUP*. Phylogenetic analysis using parsimony and other methods. Version 4*. Sinauer Associates, Sunderland, Massachusetts
- Theriot EC, Ashworth M, Ruck E, Nakov T, Jansen RK (2010) A preliminary multigene phylogeny of the diatoms (Bacillariophyta): challenges for future research. Plant Ecol Evol 143:278–296. <https://doi.org/10.5091/plecevo.2010.418>
- Theriot EC, Ashworth MP, Nakov T, Ruck E, Jansen RK (2015) Dissecting signal and noise in diatom chloroplast protein encoding genes with phylogenetic information profiling. Mol Phylogenet Evol 89:28–36. <https://doi.org/10.1016/j.ympev.2015.03.012>
- Thomas EW, Stepanek JG, Kociolek JP (2016) Historical and current perspectives on the systematics of the 'enigmatic' diatom genus *Rhoicosphenia* (Bacillariophyta), with single and multi-molecular marker and morphological analyses and discussion on the monophyly of 'monoraphid' diatoms. PLoS One 11:e0152797. <https://doi.org/10.1371/journal.pone.0152797>
- Tudesque L, Le Cohu R, Wetzel CE (2016) Two new *Platessa* (Bacillariophyceae) from Amazonia: *Platessa guianensis* spec. nov., and *P. itoupensis* spec. nov. Phytotaxa 267:237–255. <https://doi.org/10.11646/phytotaxa.267.4.1>

- Van de Vijver B, Le Cohu R (2019) Validation of “*Cocconeis therezienii* Le Cohu & Maillard”, a freshwater diatom species (*Cocconeidaceae*, Bacillariophyta) from the subantarctic îles Kerguelen. *Notul Alg* 86:1–4 <https://notulaealgarum.org/documents/Notulae%20algarum%20No.%2086.pdf>
- Wetzel CE, Lange-Bertalot H, Ector L (2017) Type analysis of *Achnanthes oblongella* Østrup and resurrection of *Achnanthes saxonica* Krasske (Bacillariophyta). *Nova Hedwigia Beih* 146: 209–227. <https://doi.org/10.1127/1438-9134/2017/209>
- Witkowski A (1993) *Cocconeis hauniensis* sp. nov., a new epipsammic diatom from Puck Bay (southern Baltic Sea). *Poland Nord J Bot* 13: 467–471. <https://doi.org/10.1111/j.1756-1051.1993.tb00083.x>
- Witkowski A, Lange-Bertalot H, Metzeltin D (2000) Diatom flora of marine coasts I. *Iconogr Diatomol* 7:1–925
- Witkowski A, Li C, Zgłobicka I, Yu SX, Ashworth M, Dąbek P, Qin S, Tang C, Krzywda M, Ruppel M, Theriot EC, Jansen RK, Car A, Płociński T, Wang YC, Sabir JSM, Daniszewska-Kowalczyk G, Kierzek A, Hajrah NH (2016) Multigene assessment of biodiversity of diatom (Bacillariophyceae) assemblages from the littoral zone of the Bohai and Yellow Seas in Yantai Region of Northeast China with some remarks on ubiquitous taxa. *J Coast Res* 74(sp1):166–195. <https://doi.org/10.2112/SI74-016.1>

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