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Cocconeis subantarctica sp. nov. from Kerguelen Archipelago (Austral Ocean) and comparison with *Cocconeis stauroneiformis* (W.Smith) Okuno

by

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Abstract

Cocconeis subantarctica sp. nov., a small monoraphid marine diatom, previously described as C. scutellum cf. var. *parva* Grunow, is reported from the Kerguelen Archipelago. Based on the careful re-examination of the material using SEM (scanning electron microscopy), both valves and the cingulum were described, which enabled a better classification of this small Subantarctic taxon. The shape of the frustule is widely rounded to subdiscoid, with uniseriate and radiate striae on both valves. The SV (sternum valve) areolae have rota-like hymenate pore occlusions, with larger marginal areolae separated by a hyaline rim. The RV (raphe valve) areolae are more complex than those of the SV, with several reniform concentric hymenate occlusions. This taxon has no real stauros, only one virga, which is larger on one side of each valve. The species is not a member of the *Cocconeis scutellum* 'complex', but is closely related to C. stauroneiformis despite several morphological differences.

Key words: *Cocconeis*, ultrastructure, SEM, Austral Ocean

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Introduction

Several sampling campaigns (TAAF-Terres Australes & Antarctiques Françaises, 'MicrophytoKer' 1985-1992 programs) in Kerguelen Main Island (49°31'S, 69°55'E, Austral Ocean) gave us the opportunity to sample benthic marine diatoms representing the Achnanthales order, from which several new species were described (Riaux-Gobin & Compère 1996; Riaux-Gobin & Romero 2003; Riaux-Gobin et al. 2007; Riaux-Gobin et al. 2009; Witowski et al. 2012), as well as new species from other orders (Riaux-Gobin & Compère 2004; Witkowski et al. 2010a,b).

This small taxon was previously identified and described as *C. scutellum* cf. var. *parva in* Riaux-Gobin & Romero based on the sternum valve (SV) only (2003: pl. 30, figs 1-5). The SEM re-examination of the material enabled us to redefine this taxon and to classify it more adequately. Despite certain similarities with *C. stauroneiformis* (W.Smith) Okuno 1957 (Basionym: *C. scutellum* var. *stauroneiformis* W.Smith), the taxon shows noticeable morphological differences that have been addressed in the present report.

Several varieties of *C. scutellum* Ehrenberg, mentioned by Cleve (1895), were later recombined, such as *C. stauroneiformis*. This shows the ambiguity concerning the concept of variety versus species, and the difficulties in defining these concepts.

Some taxa characteristic of Antarctic and Subantarctic floras (particularly from continental environments) are suspected to have a restricted biogeography (Vyverman et al. 2010; Kopalová et al. 2015) and several marine Cocconeidaceae also seem to be restricted to polar regions (see Riaux-Gobin & Romero 2003: p. 18-19). Our objective was also to clarify the exact classification of the above-mentioned small Subantarctic taxon, which may have the same geographical constraints.

In this paper, we describe *Cocconeis* subantarctica sp. nov. and compare its structure with that of two allied taxa. In particular, we focus on the intricate history and taxonomic specificities of *Cocconeis stauroneiformis*, which shares several similarities with the new species.

Materials and methods

Materials used in this study are derived from the Kerguelen Archipelago [samples from Mayès Island, January 20 1991 (49°28'20"S, 69°55'55"E) and Pointe Bizet (49°31'12"S, 69°54'36"E), January 18 1991, Table 1]. Samples were preserved in formalin (10% final concentration); they represent a subsample from the previous survey (see Riaux-Gobin & Romero 2003).

Before the light microscope (LM) examination, samples were washed with distilled water to remove salts, 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 under a Zeiss Axiophot 200 with differential interference contrast (DIC) optics and photographed with a Canon PowerShot G6 digital camera (CRIOBE-USR 3278, Perpignan, France). Before the SEM examination, 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 using Hitachi S-4500 SEM operated at 5 kV, calibrated with a Silicon grating TGX01 (C2M, Perpignan, France).

The LM illustrations do not give a perfect overview of the taxon described in this report, particularly in terms of the structure of areolae, which required SEM for an accurate description. Therefore, according to Article 40.4 of the International Code of Botanical Nomenclature (McNeill et al. 2012), and recognizing that it is a challenge to permanently preserve specimens on a stub, we identified the holotype as a specimen on the SEM stub, thus enabling the best diagnostic features of the new taxon to be clearly viewed.

Frustule length and width are expressed as a mean (in μ m) \pm standard deviation (SD = σ , quantifying the dispersion), minimum-maximum (μ m) and the number of examined specimens (n). The length/width ratio (L/W $\pm \sigma$) quantifies the degree of elongation of the valve. The striae density in 10 μ m is expressed as a mean ($\pm \sigma$) and minimum-maximum.

Table 1

List of materials examined, including locality, geographical coordinates								
Locality	Island	Date	Material	Zonation	Latitude	Longitude		
Mayès I.	Kerguelen	20.01.1991	sediment	20 m deep	49°28′20″S	69°55′55″E		
Pointe Bizet		18.01.1991		intertidal	49°31′12″S	69°54′36″E		



The general terminology used for diatom frustules follows Anonymous (1975), Ross et al. (1979) and Round et al. (1990). As previously proposed, especially by Riaux-Gobin et al. (2013), we have defined the valve with a raphe as the raphe valve (RV) and the valve without a raphe as the sternum valve (SV). This study used typification rules as established by McNeill et al. (2012) and Blanco (2016).

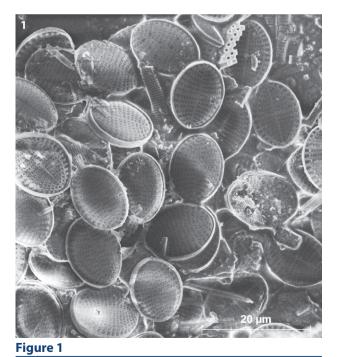
Results

Cocconeis subantarctica Riaux-Gobin & Witkowski sp. nov. SEM, Figs 1, 3a-g, 4a-d, 5a-e, 6a-d. LM, Fig. 2a-i.

The re-examination of two samples from Kerguelen Is. with SEM enabled us to examine several isolated specimens, as well as a large monospecific aggregate (clump) of this species (Fig. 1, possibly a fecal pellet of meiofauna, with diverse diatom debris and no macroalgae which would indicate that these specimens are epiphytic).

LM description

The frustules are round-elliptic to subdiscoid (Fig. 2a-b, d-e) and oblong-elliptical in rare, smaller specimens (Fig. 2c, f, i). Valves small (12-18 μm in



Cocconeis subantarctica. SEM. monospecific clump (possibly in a fecal pellet). Scale bar: 20 µm

length, 8-15 μ m in width, 12-14 RV striae in 10 μ m, 11-14 SV striae in 10 μ m, LM and SEM, n = 80, Table 2). SV sternum (axial area) narrow and straight. SV and RV striae with more or less the same stria density. Striae equidistant and radiate. No real stauros present (only one virga larger on one side of both valves (Fig. 2d-e, h arrowheads). SV areolae are not arranged along axial rows (Fig. 2d-e, Fig. 3a), while the RV areolae are often arranged along axial rows (Fig. 2g-h). Note a marginal row of larger SV areolae with a narrow hyaline marginal rim (Fig. 2c-f).

SEM description

SV: Slightly convex (Fig. 3c), regularly spaced striae (except one mid-valve virga often larger on one side, Fig. 3a, e arrowheads), uniseriate and radiate. Areolae (ca. 21.6 in 10 µm) with complex hymenate pore occlusions (appearing as a pierced rota in the more simple cases, but with hymenes, Fig. 3f arrowhead): one or two round openings are surrounded by two or more reniform openings (Fig. 3f), and all of these openings are closed by internal hymenes with radiate slits (Fig. 4d arrowhead). Each stria ends marginally by a transapically-elongate and more complex areola (Fig. 3g), often separated from the rest of the stria by a marginal hyaline area (Fig. 3b-c arrows). The occlusions appear similar internally and externally (Fig. 4b, d). In the internal view, the virgae are weakly silicified (Fig. 4 d arrow; see also pl. 30, fig. 3 in Riaux-Gobin & Romero 2003). No areolae on apices (Fig. 3a-b, e). Sternum straight and relatively narrow, externally not depressed (Fig. 3c). Sternum valve valvocopula (SVVC) possibly open on both apices (Fig. 3b arrowheads), with low edge's undulations but no real fimbriae (Fig. 4c arrowhead). Wide cingulum composed of two open valvocopulae and one or two supplementary open bands with ligulae (Fig. 3d arrowhead).

RV: Thin, flat to concave, striae uniseriate (mean 12.9 in 10 µm, n=16), regularly spaced, except for the two median striae, slightly more distant (one virga larger), but often only on one side of the valve (Fig. 5a-b arrowhead), so that there is no real stauros or fascia (see LM, Fig. 2g-i). RV areolae (ca. 21.3 in 10 µm) with a structure slightly more complex than that of the SV (Fig. 5c), with several reniform concentric hymenate occlusions with slits. The marginal row of elongate and complex areolae (complex hymenate perforated plates with marginal pegs, Fig. 5d arrowhead), separated from the rest of the stria by a well-marked hyaline rim (Fig. 5b). In the internal view, the rim has no bumps (Fig. 6a). Areolae are roughly arranged along axial rows (Fig. 6c). No areolae on apices (Fig. 5c framed arrow). Raphe filiform and straight. External proximal raphe





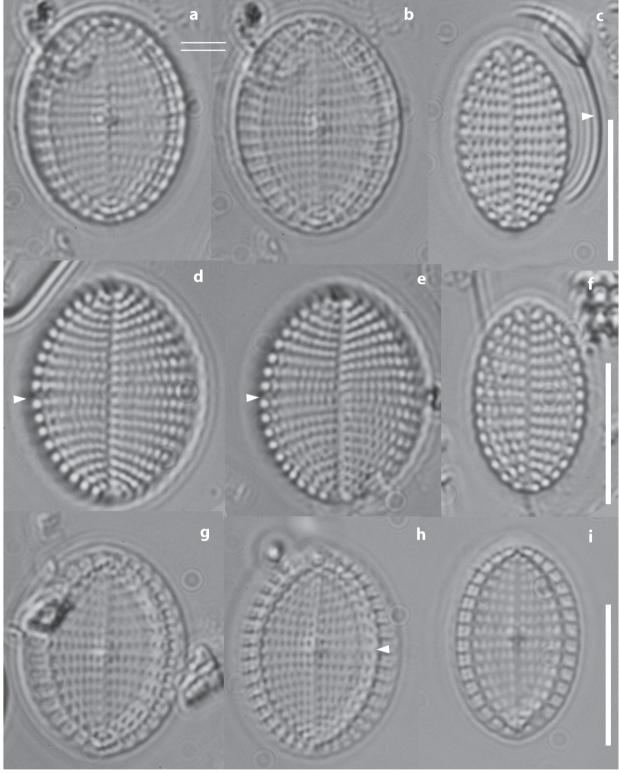


Figure 2a-i

Cocconei subantarctica. LM (Pointe Bizet, Kerguelen Main Island). Complete frustule (a-b); often subdiscoid (d-e, g); elliptic small specimen with SVVC without fimbriae (c arrowhead); SVs with one virga slightly larger on one side of the valve (d-e arrowheads), SV areolae are not arranged in a regular axial pattern (d-e); small elliptic SV with pearl-like marginal areolae (f); RVs (g-i) with one virga slightly larger on one side (h arrowhead), and RV areolae arranged along axial rows. Note the marginal hyaline rim and large marginal areolae. **Scale bar: 10 µm**

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Table 2

Morphometrics and features of 1) C. subantarctica sp. nov. (Kerguelen Is., present study), 2) C. stauroneiformis (cf. Riaux-Gobin & Romero 2003, Kerguelen Is.) and 3) C. stauroneiformis sensu Romero (1996, diverse origin)

	Cocconeis subantarctica sp. nov. present study n = 80	Cocconeis stauroneiformis (W.Smith) Okuno sensu Riaux-Gobin & Romero (2003)	<i>Cocconeis stauroneiformis</i> (Rabenh.) Okuno <i>sensu</i> Romero (1996)	Cocconeis scutellum var. posidoniae M.De Stefano, D.Marino & L.Mazzella (2000)
Valve face	subround to elliptic	elliptic	elliptic to elliptic-lanceolate	elliptic
Length (µm) min-max	12-18 14.6 ± 1.0	15-32	9.6-36	-
Width (µm) min-max	8-15 10.3 ± 1.3	8-21	5.5-27	-
SV stria density min-max	11-14 12.6 ± 0.9 uniseriate, rotate and reniform hymenate occlusions	8-9 wavy transapical rows, externally complex, internally uniseriate	6-11 externally tetra- to pentaseriate, internally uniseriate	12-14 uniseriate, transapical rows of areolae with axial bar, rotate or not
RV stria density min-max	12-14 13 ± 0.6 uniseriate, hymenate reniform occlusions	8-10 biseriate in mid-valve, complex on the margin	6-12 biseriate, tetra- to pentaseriate at the margin	18-23 uniseriate
SV sternum	straight, relatively large	straight, narrow, externally depressed (thickened internally)	straight, narrow, concave	straight, narrow
SV fascia	one virga larger on one side	absent	absent	absent
Marginal SV areolae	transapical to quadrangular group of hymenate reniform occlusions	undifferentiated from the other areolae	-	biseriate to triseriate occlusions
SV marginal rim	often present	absent	absent	absent
SV internal virgae	large, flat	thickened	elevated	narrow, not elevated
SVVC	with short undulations, possibly open at both ends	short fimbriae	reduced fimbriae, open at both ends	digit fimbriae
RV fascia	often assymetrical	more or less wide	present	absent
RV marginal rim	present	robust	present	present
Marginal RV areolae	transapical and complex large group of concentric hymenate reniform occlusions	apically elongated group of hymenate reniform occlusions	group of hymenate reniform occlusions	striae biseriate on the mantle
RVVC	open, without fimbriae	-	short fimbriae, open at one apex	fused fimbriae
Biogeography	Kerguelen Is.	Kerguelen Is.	diverse origin	Ischia I. (Italy)

- (not specified)

endings relatively close to each other and straight (Fig. 5c arrowhead), internally deflected on opposite sides (Fig. 6b arrowheads). Terminal raphe endings well distant from the margin (Fig. 5b), internally terminating in subtle and straight helictogossae (Fig. 6a arrowhead, d). Axial area narrow. Raphe valve valvocopula (RVVC) narrow, open (Fig. 6d arrows) and lacking fimbriae (Fig. 6a twin arrowheads).

Holotype: Specimen on stub '180915-1' sent to NHM (BM 101 806 material). Holotype illustration: SEM Fig. 3a.

Isotypes: Slides mounted with the same material as the stub: BM 101 806 (National History Museum, London, UK), slide SZCZ 16662(10) in the collection of A. Witkowski (the Faculty of Geosciences,

Szczecin, Poland) and slide KER11 in the collection of C. Riaux-Gobin (CRIOBE-CNRS, USR 3278, Perpignan, France).

Type locality: 'Pointe Bizet' (Île Longue, Kerguelen Main Island). Collector C. R.-G., January 18 1991.

Biogeography: intertidal to subtidal sheltered muddy Subantarctic environment.

Etymology: The specific epithet refers to the Subantarctic zone, which comprises the Kerguelen Archipelago.

Taxonomic remarks: The SV of Cocconeis subantarctica sp. nov. shares some similarities with that of Cocconeis scutellum var. posidoniae M.De Stefano, D.Marino



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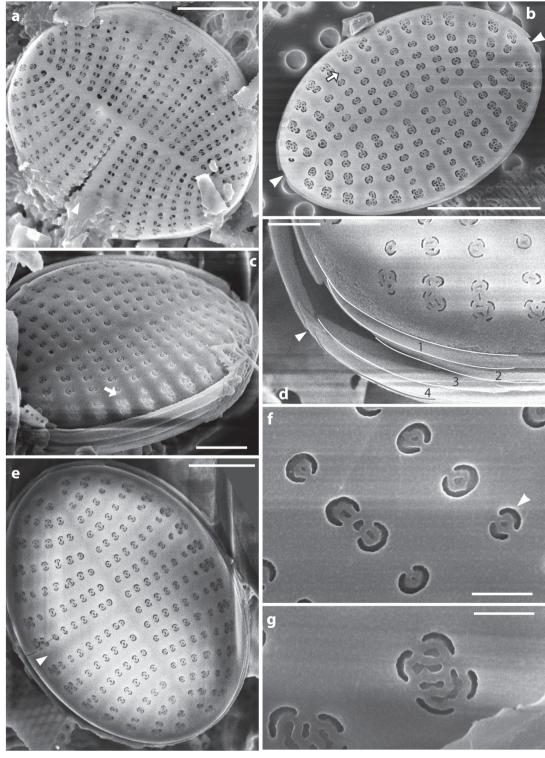


Figure 3a-g

Cocconeis subantarctica. SEM (Pointe Bizet, Kerguelen Is.). SV in the external view, note the subround shape (an illustration of the holotype); small elliptic SV with oblong complex marginal areolae separated from the rest of the stria by a hyaline rim (b framed arrow), and SVVC possibly open at both apices (b arrowheads); SV convex and flat (c); SV apex with 4 cingular bands (numbered 1-4), from which several are open; note a ligula (d arrowhead); one SV virga larger on one side (e arrowhead); detail of SV ornamentation with a kind of hymenate pierced rotae (f arrowhead), detail of the marginal complex and larger areolae (g). **Scale bars: 5 µm (a-b), 3 µm (e), 2 µm (c), 500 nm (f), 400 nm (g)**

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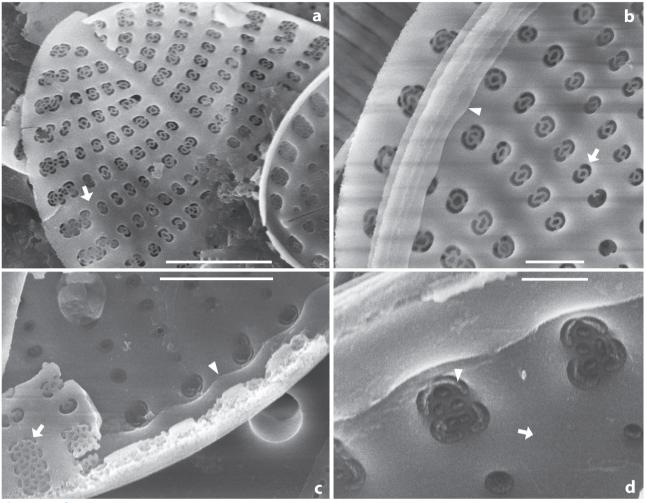


Figure 4a-d

Cocconeis subantarctica. SEM (Pointe Bizet, Kerguelen Is.). SV in the internal view. Eroded SV in the internal view with flat virgae (a arrow); SVVC with undulating edge (b arrowhead), flat virgae, and SV areolae with a kind of pierced rota (b arrow); broken frustule showing RV marginal large and complex areolae (c arrow), SVVC still in place, with undulating short fimbriae (c arrowhead); detail of marginal complex areolae with domed hymenes still in place (d arrowhead) and low virgae (d arrow). Scale bars: 3 µm (a), 1 µm (b), 500 nm (c-d)

& L.Mazzella (De Stefano et al. 2000: figs 72-79), but the marginal areolae of the latter are multiseriate as in *C. scutellum* var. *scutellum*, with no hyaline rim. In our taxon, the marginal areolae are a complex arrangement of hymenate reniform structures, often delineated by a hyaline rim (see description). Furthermore, the RV structure of our taxon is different from that of *C. scutellum* var. *posidoniae* (see De Stefano et al. 2000: figs 80-86). The re-examination of the Kerguelen material enabled the RV of our new taxon to be described and revealed a high degree of similarity with *Cocconeis stauroneiformis* (W.Smith) Okuno (see below, history and detailed comparison with *C. subantarctica* sp. nov.)

History and taxonomic remarks on *Cocconeis* stauroneiformis (W.Smith) Okuno

Cocconeis scutellum var. stauroneiformis W.Smith (1853/1852: p. 22, ' β Nodule dilated into a stauros, Supp. Pl. 30. fig. 34 β ', reproduced in Fig. 7a; no type, no locality) is the basionym of *C. stauroneiformis* (W.Smith) Okuno. For comparison, Fig. 7b refers to *Cocconeis scutellum* Ehrenberg, as illustrated *in* Smith (1852: pl. 3, fig. 34). Even if the above-mentioned variety β is not implicitly named and if the diagnosis is reduced to the notification of the presence of a stauros, the illustration (Ref. cit. fig. 34 β , Fig. 7a) is considered the holotype (McNeill et al. 2012: art. 8.1). The original nomenclatural name *C. scutellum* var.



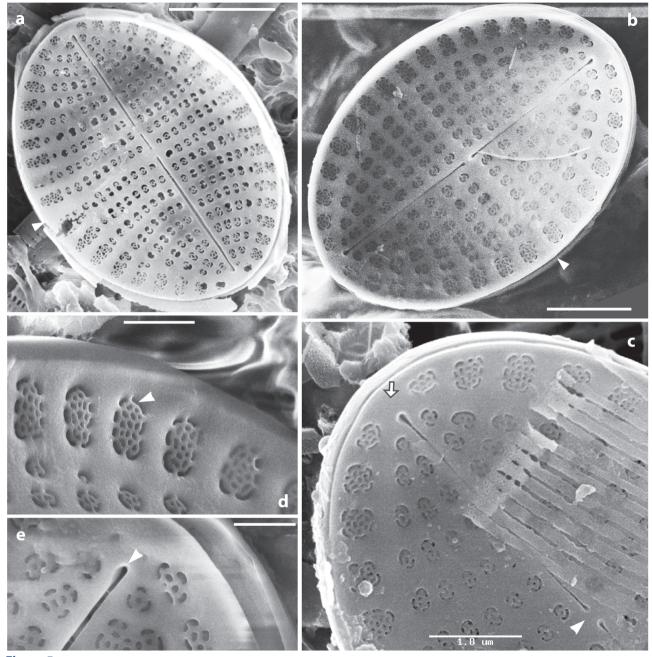


Figure 5a-e

Cocconeis subantarctica. SEM (Pointe Bizet, Kerguelen Is.). RV in the external view, note the round shape (a) with oblong complex marginal areolae and the presence of a larger asymmetrical virga (a-b arrowheads); detail of the marginal row of complex areolae with a kind of pegs (d arrowhead); apex void of areolae (c framed arrow), and close proximal raphe endings (c arrowhead); detail of a terminal raphe ending (e arrowhead). Scale bars: 5 µm (a), 3 µm (b), 1.8 µm (c), 1 µm (d), 700 nm (e)

stauroneiformis W.Smith is used in Van Heurck (1880: pl. 29, figs 10-11, reproduced in Fig. 7 c, clearly referring to W. Smith, thus not as a homotypic synonym), Cleve (1895), Peragallo & Peragallo (1897-1908: pl. 4, fig. 4, reproduced in Fig. 7d), Hustedt (1933-1959: fig. 792). The name afterwards transferred to *C. stauroneiformis* (W.Smith) Okuno (1957: p. 217-221, figs 2a-c), used in Witkowski et al. (2000), Riaux-Gobin & Romero (2003) and Lee et al. (2012), while e.g., Rivera (1974), Romero (1996), De Stefano et al. (2000) and Sar et al. (2003) erroneously refer to *C. staurone-iformis* (Rabenhorst) Okuno. Hustedt (1933-1959),



and afterward VanLandingham (1967-1979) erroneously refer to *C. paniformis* J.-J.Brun. as a synonym of *C. scutellum* var. *stauroneiformis* W.Smith [Schmidt et al. 1874-1959: pl. 189, figs 16-20, reproduced in Fig. 7e; Schmidt's caption refers to *C. panifomis* Brun and only mentions that for several of these illustrations (ref. cit.: figs 16-19), a stauros is clearly indicated, but the name *C. scutellum* var. stauroneiformis is not mentioned]. See the illustration in Montgomery (1978: pl. 62, figs E-H; pl. 63, figs 4A-B) and illustration of *C. caribensis* Romero et Navarro (1999), but *C. paniformis* remains a valid taxon with priority over *C. caribensis*. It can be noted that *C. tuamotuana* Riaux-Gobin, Compère & W.Jordan (2015) has no stauros but belongs to the same group as the above-mentioned tropical diatoms. In addition,

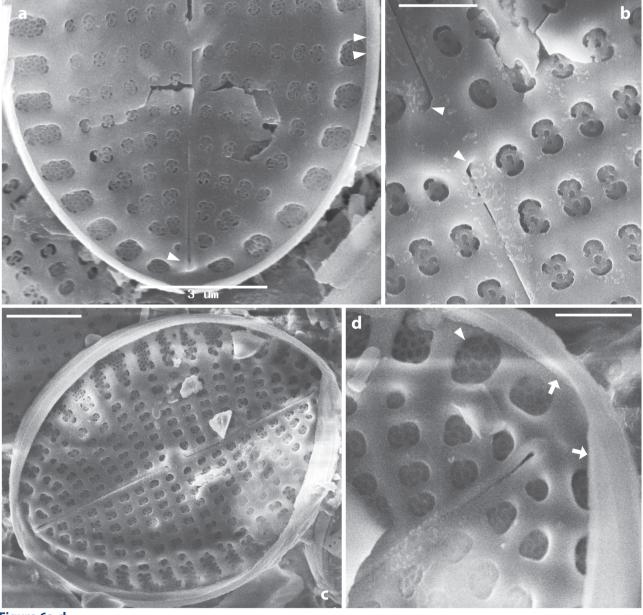


Figure 6a-d

Cocconeis subantarctica. SEM (Pointe Bizet, Kerguelen Is.). RV in the internal view. Marginal rim and subtle helictoglossa (6 arrowheads) and narrow RVVC with no fimbriae (a twin arrowheads); central area, with proximal raphe endings bent in opposite directions (b arrowheads). Entire valve with the cingulum, note the axial rows of areolae (c); detail of an apex with subtle helictoglossa, complex marginal areolae (d arrowhead) and open copula (d arrows). Scale bars: 3 µm (a, c), 1 µm (b, d)





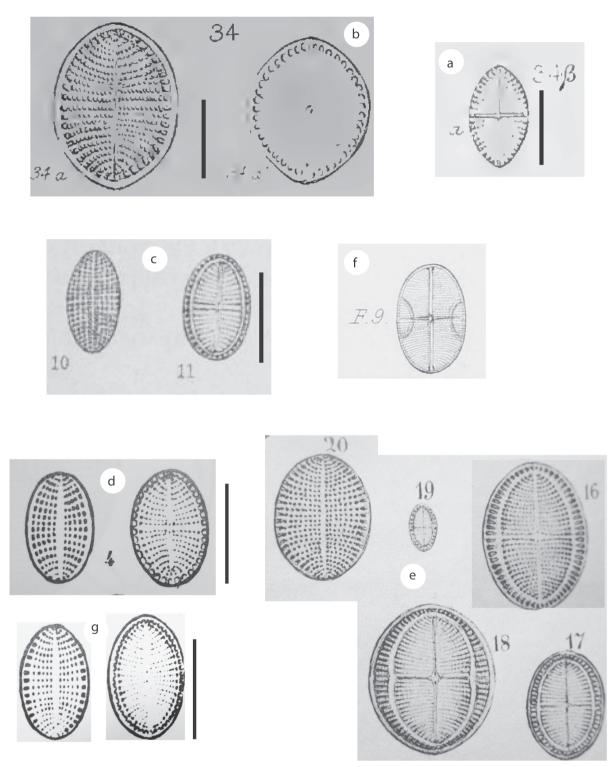


Figure 7a-g

Cocconeis scutellum var. *stauroneiformis* W.Smith (1852: Supp. Pl. 30, fig. 34 β) (a). *Cocconeis scutellum* Ehrenberg *in* Smith (1852: pl. 3, fig. 34) (b). *Cocconeis scutellum* var. *stauroneiformis* W.Smith *in* Van Heurck (1880: figs 10-11) (c). *Cocconeis scutellum* var. *stauroneiformis* Sm. *in* Peragallo & Peragallo (1897-1908: pl. 4, fig. 4) (d). *Cocconeis paniformis* Brun and allied, *in* Schmidt et al. (1874-1959: pl. 189, figs 16-20, see text) (e). *Cocconeis scutellum* var. *y in* Roper (1858: pl. 3, fig. 9) (f). *Cocconeis scutellum* Ehrenberg f. *parva in* Peragallo & Peragallo (1897-1908: pl. 4, fig. 3) (g). Scale bars: 20 µm. Refer to Roper (1858) and Schmidt et al. (1874-1959) for other illustrations.



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Cocconeis scutellum var. stauroneiformis Rabenhorst (1864: p. 101) is a heterotypic synonym, with a short diagnosis (no iconography, no measurements, no locality) referring to Roper (1858: pl. III, fig. 9, C. scutellum var. y, reproduced in Fig. 7f). Following Roper (ref. cit.)... 'I think it better to consider it as a variety, though (...) it should be classed as a distinct species'. The latter taxon was later described as C. binotata Grunow (1863: p. 145, pl. 4, fig. 13a,b), Orthoneis binotata (Grunow) Grunow (1867: p. 15) and finally transferred to Mastogloia binotata (Grunow) Cleve [1895: 148, Orthoneis (Stictoneis) binotata Grunow 1863]. Illustrated in Van Heurck (1880-1885: pl. 28, fig. 7) as Orthoneis binotata Grunow, annotated as C. scutellum var. y Roper. The latter taxon is not a Cocconeis.

None of the available descriptions of Cocconeis stauroneiformis (from the oldest to the most recent one, see below) include observations of a type, instead they all refer to personal materials. The older illustrations refer to small and oblong-elliptical valves (e.g., Van Heurck 1880-1885: pl. 29, figs 10-11, reproduced in Fig. 7c and Peragallo & Peragallo 1897-1908: pl. 4, fig. 4, reproduced in Fig. 7d), with an SV showing axial rows of large guadrangular areolae, and an RV with a well-developed stauros, a marginal rim and a marginal row of larger structures. Several recent studies contributed to a better understanding of C. stauroneiformis, due to SEM examinations: the SV structure is unique with complex areolae, composed of three-dimensional structures (named 'loculi' by Okuno 1957: pl. 6, fig. 2b-c). These 'loculi' show reniform apertures closed by hymenes. These complex SV areolae open externally by multiple small pores, roughly grouped in quadrats arranged along axial rows (Romero 1996: fig. 29; De Stefano et al. 2000: fig. 88), while internally via quadrangular openings, with each stria bordered by strong virgae (Romero 1996: fig. 28; Riaux-Gobin & Romero 2003: pl. 15, fig. 1; Sar et al. 2003: fig. 54). The RV striae, described by Romero (1996) as biseriate, are composed of complex sub-guadratic areolae with reniform apertures closed by hymenes (Romero 1996: fig. 36; Lee et al. 2012: fig. 37; De Stefano et al. 2000: fig. 92). A stauros is well marked only on the RV (see all quoted references).

Comparison of C. *subantarctica* sp. nov. with C. *stauroneiformis* (Table 2)

Although the ultrastructure of *C. subantarctica* RV has some similarities with that of *C. stauroneiformis*, there are several important differences. For example, the RV striae in *C. stauroneiformis* are biseriate (cf. Romero 1996: table 3, figs 34-35, 37; Table 2) with

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complex areolae, while in the new taxon, uniseriate and externally less finely ornamented. A fascia is well marked in *C. stauroneiformis*, while more discrete or asymmetric in *C. subantarctica*. In *C. stauroneiformis*, there are always RV areolae on apices (e.g., *in* De Stefano et al. 2000: fig 91; Lee et al. 2012: fig. 37), while the apical areas in *C. subantarctica* are void. In *C. stauroneiformis*, the marginal complex RV areolae, separated from the rest of the stria by a hyaline rim, are short and more or less axially elongate (Romero 1996: fig 36; De Stefano et al. 2000: fig 92), while they are large and transapically elongate in the new taxon.

The most significant difference between the two taxa is their external SV ultrastructure: C. stauroneiformis shows a complex net of small poroids (e.g., Riaux-Gobin & Romero 2003: pl. 16, fig. 2), grouped along a guadratic pattern (Romero 1996: fig. 26; De Stefano et al. 2000: fig. 88; Riaux-Gobin & Romero 2003: pl. 15, fig. 1, 4), with virgae that are almost undifferentiated. The marginal SV areolae are not visibly different from other areolae on the valve. These quadrangular complex areolae are axially arranged and are internally uniseriate. In C. subantarctica, the SV ornamentation (particularly for the external view) is less complex than in C. stauroneiformis: the striae show areolae with more or less simple reniform poroids, as a kind of pierced hymenate rotae (Fig. 3f arrowhead). In C. subantarctica, the virgae are large and unornamented, and the marginal SV areolae are composed of a more complex arrangement of reniform poroids than in C. stauroneiformis. In C. subantarctica, a marginal SV hyaline area (or marginal rim), often clearly identifiable, separates the large and complex proximal areola from the rest of the stria (while this feature is not observed in C. stauroneiformis).

Another distinctive feature between the two latter taxa is the presence of strong and elevated internal SV virgae in *C. stauroneiformis* (Romero 1996: fig. 28), while in *C. subantarctica*, the virgae are large and flat (Fig. 4a-b, Table 2). It can also be noted that this taxon is basically smaller than *C. stauroneiformis* and the stria densities in both valves are higher on *C. subantarctica* than in *C. stauroneiformis* (Table 2). Finally, a large percentage of larger *C. subantarctica* specimens is characterized by subdiscoid shape (Fig. 2a-b, d-e).

Cocconeis subantarctica sp. nov. does not belong to the *C. scutellum* 'complex'. Although there are some similarities for smaller and most elliptical specimens, as shown in the illustration of *Cocconeis scutellum* Ehrenberg f. *parva in* Peragallo & Peragallo (1897-1908: pl. 4, fig. 3, reproduced in Fig. 7g), the SV sternum is more elliptical in the latter taxon. This observation reflects the important role of SEM in the study of small diatoms. To date, *Cocconeis subantarctica* sp. nov. has



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only been found in the type locality (Kerguelen Is.), and further studies are needed to clarify the biogeography of this taxon.

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