Cocconeis napukensis sp. nov. (Bacillariophyceae) from Napuka Atoll (South Pacific) and lectotypification of Cocconeis subtilissima Meister

Catherine Riaux–Gobin1,2*, Pierre Compère3, Michel Coste4, François Straub5 & Lukas Taxböck6

1 CRIOBE–USR 3278 CNRS–EPHE–UPVD, 2 Laboratoire d’Excellence ‘CORAIL’, Perpignan, France; *Corresponding author e–mail catherine.gobin@univ–perp.fr, 3 Botanic Garden Meise, Domein van Bouchout, 1860 Meise, Belgium; e–mail: pierre.compere@br.fgov.be 4 IRSTEA, 50 avenue de Verdun, 33612 Cestas, France; e–mail: michel.coste@irstea.fr 5 PhycoEco, Rue des XXII–Cantons 39, La Chaux–de–Fonds, Suisse; e–mail: fstraub@phyeco.ch 6 Institute of Systematic Botany, University of Zürich, Zürich, Switzerland; e–mail: lukas.taxboeck@systbot.uzh.ch

Abstract: A 2012 microphytobenthos survey from coral reef environment at Napuka Atoll (Tuamotu Archipelago, South Pacific) focussed on diatom assemblages. Atolls are tropical carbonate, productive ecosystems, with a fast turnover, from which benthic diatom floras are poorly known. When compared to younger volcanic islands from the same area, Napuka shows a poor colonisation by benthic diatoms. Although normally rare, Achnanthales occur in the assemblages from Napuka. In the tidal zone, marine debris of sponge origin were colonized by several taxa, among others a small–celled Cocconeis here described as C. napukensis sp. nov. The new taxon has some likeness to Cocconeis subtilissima Meister and to C. vairaensis Ricard. Original drawings and type material are examined when available. A lectotypification and an emended description of Cocconeis subtilissima are proposed, along with the description of Cocconeis suzukii sp. nov. and Cocconeis meisteri sp. nov. from Meister type material. The morphological features of C. napukensis are investigated with scanning electron microscope (SEM) and light microscope (LM). Until now C. napukensis has not been found in the other investigated sites of Tuamotu and Society Archipelagos.

Key words: Cocconeis spp., Cocconeis subtilissima Meister typification, Napuka Atoll, South Pacific


INTRODUCTION

The atolls of Napuka (14°10′7″S, 141°13′56″W; 12 km², Fig. 1) and Tepoto North (14°08′S; 141° 24′W; 2 km²) are located in North Tuamotu (Fig. 1), 450 km South of Marquises Islands. The latter atolls are isolated in a vast oceanic zone, justifying the name ‘Îles de la Désolation’ or ‘Îles du Désappointement’, with their only accompaniment Puka Puka, lying 272 km southeastwards. The westerly South Equatorial Current (SEC) (Tabata 1975; Rougerie et al. 1997) prevents Napuka from being directly influenced by other islands and reinforces its geographic isolation. Ornithological studies report Acrocephalus atypus flavidus Cibois & Thibault (2005) to be endemic to Napuka. Neither hydrological studies nor taxonomical surveys of microalgae are available for Napuka, while the hydrology and phytoplankton at Takapoto, a nearby atoll of West Tuamotu (Fig. 1), are documented (Sournia & Ricard 1975, 1976; Magnier & Wauthy 1976; Ricard et al. 1979). Napuka and Tepoto North have no direct communication with the ocean, with several ‘hoa’ (shallow channels between ‘motus’ – coral sand islands–) permitting intermittent exchange with the open ocean. An endo–upwelling theory explaining the apparent contradiction between the high productivity of South Pacific atolls and the oligotrophy of the surrounding ocean was formulated by Rougerie & Wauthy (1986): the atoll’s lagoon is fed by deep interstitial waters enriched with nutrients. Subsequent studies (Charpy–Roubaud et al. 1990; Leclerc 1998; Charpy 2001) support a different theory: the advective supply of nutrients by the ocean, combined with a high turnover, explains the nutrient status of the atoll’s lagoon. Organic matter i.e., aggregates, were also shown to constitute a substantial contribution to the trophic systems within the atoll’s lagoon (Marshall 1965). Nevertheless, the Chlorophyll a concentration
is higher in the lagoon’s phytoplankton than in the adjacent ocean (Krausnick 1973; Sournia & Richard 1975; Richard et al. 1979 and references therein, Hatcher 1997). The gross primary production of atolls is high (Sournia & Richard 1975; Sournia 1977 and references therein) but with diatoms playing a minor role among microalgae (Richard et al. 1979). At Napuka (Tuamotu) and Tetiaroa (Society) the marine benthic diatoms are relatively rare while they are abundant in high volcanic islands such as Tahiti and Moorea (pers. obs.). On the other hand, dinoflagellates (Stancia et al. 2013) and Coccolithophoridae are dominant on atolls among microalgae, even if less diversified than diatoms (Richard 1979, and pers. obs.). In the South Pacific Ocean the benthic diatoms (linked to sediments and macroalgae) from atoll’s lagoon are dominant versus typically planktonic ones (Richard 1979, and refs therein).

During the CORal reef DIAatoms (CORDIA) 2012 project, the Achnanthales flora of Napuka was investigated with a particular focus on Cocconeis, a genus pertaining to this order. A small–celled Cocconeis taxon first caught our attention and is here described as new: Cocconeis napukensis sp. nov. The latter taxon is compared to C. subtilissima Meister (1935), from which several later on definitions seem contradictory.

**Materials and Methods**

Materials used in this study are derived from three sources: 1) Friedrich Meister’s type material from Nagasaki, Japan (Fig. 1), 2) M. Voigt’s slide collection labelled ‘Nagasaki off shells’ and 3) a recent marine sample from Napuka Atoll, South Pacific, Tuamotu Archipelago.

Meister’s type material: F. Meister’s slides are housed in Herbarium of the University of Zürich (Switzerland). The slides ‘Nagasaki 3409000’ to ‘01’, ‘03’ to ‘08’, ‘10’ to ‘11’ to ‘17’ have been examined (Fig. 1). According to notes accompanying the sample preparation by F. Meister, the first numbers assign the year of preparation, the third and fourth number the month, and the last three numbers are sequential numbers. F. Meister’s hand written notes assign these slides to the shell of a marine snail from Nagasaki (‘Nagasaki, Japan, auf Meeresschnecken. verunreinigt mit Süßwasserformen’, ‘Nagasaki, Japan, on marine snail, contaminated with fresh water forms’). These slides are supposed to contain Cocconeis subtilissima Meister (see Meister 1935). Some Meister’s notes roughly indicate the position of remarkable taxa on the slides. Unfortunately no indication concerning Cocconeis subtilissima, but a new Cocconeis is indicated as present on the sector ‘c’ of the slide 3409000 (‘Cocconeis n. sp.’).

Voigt’s slide collection: Several of M. Voigt’s slides have been prepared from the same sample (‘Nagasaki off shells’, 22045–46–47) and some other slides [‘Nagasaki on shells’, 22072(35)–77(35), 22074(35) have probably been prepared in 1935, and most probably from the same sample]. These slides are housed in Dübendorf (Switzerland) and they have been studied. Hand notes by M. Voigt indicate which taxon was found in which slide. Here again, there was no Cocconeis subtilissima. Nevertheless, the slide 22045 was examined with particular attention, since it was pointed out by M. Voigt to contain Cocconeis trachyderma F. Meister, a new species appearing together with Cocconeis subtilissima (see Meister 1935).

Napuka Atoll material (South Pacific, Tuamotu Archipelago): During a 2012 expedition (CORDIA) at Napuka (12 km²) several marine and lagoon sites were sampled, particularly tidal debris of sponge origin (15NPK7–2, 14°10.702S, 141°15.949W) collected from the intertidal bed rock, close to the Napuka airstrip.

Napuka Atoll material preparation: The sample was preserved in formaldehyde (10% final concentration). For scanning electron microscope (SEM) examination, the sample was filtered through 1 µm Nuclepore filters and rinsed twice with deionised (miliQ) water to remove salts. Filters were air-dried and mounted onto aluminum stubs before coating with gold–palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi S–4500 SEM operated at 5 kV (C2M, Perpignan University, France). For light microscope (LM) examination, the sample was 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 Hyrax® (O. Romero pers. com.). Diatom slides were examined with a Zeiss Axioskop 200, with differential interference contrast (DIC) optics and photographed with a Canon PowerShot G6 digital camera (CRIOBÉ–Perpignan University, France).

The LM illustration of the new taxon from Napuka does not give a complete overview of its particular features, i.e., the sternum valve (SV) striation, the exact pattern and number of axial rows of alveoli and the valvocopulae. Therefore, according to Article 40.2 of the International Code of Nomenclature (McNeill et al. 2012) we designated the SEM stub as the holotype showing the best diagnostic features of the new species. Although it is a challenge to
permanently preserve specimens on stubs, they are referenced and kept in an air–dried container at CRIOBE–Perpignan University, France. Isotypes are designated from slides made from the same sample in which the new taxon was observed. All morphometric data are presented in Table 1.

Terminology and abbreviations: Various terminologies have been proposed for the order Achnanthales Silva. As previously proposed, in particular by Riaux–Gobin et al. (2013), and following the Greek origin of the word ‘sternum’, it is proposed to designate the valve with a raphe as the raphe valve (RV) and the valve without a raphe as the sternum valve (SV). For the description of the frustule and its parts, terminology follows Anonymous (1975), Ross et al. (1979) and Round et al. (1990).

RESULTS

Even if quantitatively rare, some Achnanthales are present in marine environments of Napuka, particularly in 15NPK7–2, with several species shared with the assemblages of Tahiti and Moorea Islands. The complete Cocconeis assemblage from Napuka, with several unique taxa, will be detailed elsewhere sensu its parts, terminology follows Anonymous (1975), sternum valve (SV). For the description of the frustule and ‘sternum’, it is proposed to designate the valve with a raphe.

As previously proposed, in particular by F. Meister (1935, p. 99, figs 61–62, reproduced in our Figs 6–7), LM (Figs 13–20, Table 1)

Lectotype (designated here): F. Meister’s slide ‘Nagasaki 3409003’ (Fig. 1) housed in Herbarium of the University of Zürich (Switzerland). Lectotype specimen illustrated in Figs 13 (RV)–14 (SV).

Lectotype remarks: None of F. Meister’s slides is annotated as containing Cocconeis subtilissima. Nevertheless as indicated by Meister (1935), the sample and the corresponding labelled slides ‘Nagasaki off shells’ from 1934 might contain Cocconeis subtilissima. The notes about the slide 3409000 refer to a Cocconeis n. sp. from sector ‘c’, but the C. subtilissima specimen found on this slide (and not from sector ‘c’) is inconclusive because of the SV. On the other hand, Figs 13–14 illustrate a specimen of C. subtilissima showing both valves relatively accurately.

Lectotype locality: Nagasaki, Japan (from the shell of a marine snail).

Translation of the original German diagnosis: Valve elliptical, 28 µm long, 14 µm wide. Raphe valve with 23 radial transapical striae in 10 µm, raphe markedly sigmoid, axial area very narrow, central area roundish, small. Rapheless valve with 34 slightly radial transapical striae, interrupted by an apical hyaline band in the mid–hemivalve. This band is irregularly defined. Axial area narrow, more or less thin, narrower in mid–valve. fig. 61–62. Nagasaki, very scarce.

Our examinations (LM, n=11): 27.7±1.9 µm long; 12±0.8 µm wide
Stria densities: >35 (difficult to discern) SV str. in 10 µm; 26.18±1.17 RV str. in 10 µm
L/W: 2.1±0.1

Emended description: Valve oblong–elliptical to linear–elliptical, with round to blunt apices, RV striae dense, equidistant, radiate in the last third of the valve. Raphe sigmoid particularly clearly at apices, terminal raphe fissures close to the margin distinctly bent in opposite directions, central raphe endings close to each other (Figs 16, 18). Axial area narrow, central area transapically elongated into a short fascia. SV densely striated, each hemivalve has a hyaline apically elongated area splitting the striae in two parts. Axial area relatively large, with almost no constriction in mid–valve.

Remarks: The taxon is relatively rare in the Meister type slides, on the eight Meister’s slides observed only 22 specimens were encountered, and only a SV on the two Voigt’s slides prepared with the same material. Only 11 specimens were clean enough concerning the RV stria densities (Table 1). The SV striae were almost indiscernible, even with interferential contrast, while F. Meister succeeded in counting 34 str. in 10 µm. The RV fascia described as a small and round central area by Meister (1935) is well identifiable in his figure 61 as a black oblong mark.

Cocconeis meisteri Riaux–Gobin et al. sp. nov. (LM, Figs 21–23, Table 1)

Description: Valve small, elliptical with round apices, RV striae equidistant and radiate. Raphe very slightly sigmoid, terminal raphe fissures close to the margin and slightly bent in opposite directions, central raphe endings robust, relatively close to each other. Axial area narrow, small central area. SV densely striated, each hemivalve shows a hyaline apically elongate area dividing the striae in two parts. Sternum large, clearly constricted in mid–valve (Fig. 22, arrows).

Morphometrics (LM, n=17): 20.7±3.2 µm long; 12.7±2.2 µm wide
Stria densities: 34±3.8 SV str. in 10 µm; 25.7±1.7 RV str. in 10 µm
Table 1. Features of the commented or described *Cocconeis* species [(*) measurements performed on the original photographs; (nd) no data; (in bold) average ± standard deviation; (SV) sternum valve; (RV) raphe valve].

<table>
<thead>
<tr>
<th>C. napukensis sp. nov.</th>
<th>C. subtilissima</th>
</tr>
</thead>
<tbody>
<tr>
<td>present paper</td>
<td>original description by Meister (1935)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>C. subtilissima</th>
<th>C. suzukii sp. nov.</th>
<th>C. vairaensis</th>
<th>C. meisteri sp. nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>from F. Meister type slides</td>
<td>present paper</td>
<td>from F. Meister type slides</td>
<td>present paper</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Valve shape</th>
<th>elliptic to oblong–elliptic in larger specimens</th>
<th>elliptic</th>
<th>linear–elliptic</th>
<th>elliptic</th>
<th>elliptic</th>
<th>elliptic</th>
<th>elliptic</th>
<th>elliptic to oblong–elliptic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lenght (μm)</td>
<td>6.3–22.8 (14.3±4.3)</td>
<td>23.8–30 (25.7±1.9)</td>
<td>14–32</td>
<td>14–45</td>
<td>18–24.8 (21.1±2.2)</td>
<td>18–28</td>
<td>16.7–27.9 (20.7±3.2)</td>
<td></td>
</tr>
<tr>
<td>Width (μm)</td>
<td>3.7–11.8 (8.1±2.5)</td>
<td>11–13.4 (12±0.8)</td>
<td>9–23.5</td>
<td>8.5–39.0</td>
<td>10.5–15.6 (13.8±1.6)</td>
<td>9–14</td>
<td>9.5–15.7 (12.7±2.2)</td>
<td></td>
</tr>
<tr>
<td>Length/Width</td>
<td>1.6–2.6 (1.8±0.2)</td>
<td>2–2.3 (2.1±0.1)</td>
<td>(1.6*)</td>
<td>(1.5*)</td>
<td>1.39–1.71 (1.5±0.1)</td>
<td>(1.7*)</td>
<td>1.47–1.9 (1.6±0.1)</td>
<td></td>
</tr>
<tr>
<td>SV sternum shape and width</td>
<td>relatively large, almost straight, concave, strongly constricted in mid–valve</td>
<td>narrow, more or less thin, constricted in mid–valve</td>
<td>slightly sigmoid, relatively large, not constricted in mid–valve</td>
<td>clearly sigmoid, relatively narrow, regular, no constriction</td>
<td>clearly sigmoid, narrow, shallow, regular, no constriction</td>
<td>clearly sigmoid, narrow, shallow, regular, no constriction, one stria shorter on one side</td>
<td>sigmoid, relatively large, slight constriction in mid–valve</td>
<td>slightly sigmoid, relatively large, constriction in mid–valve</td>
</tr>
<tr>
<td>SV alveoli per hemivalve (per stria)</td>
<td>two (up to three)</td>
<td>two</td>
<td>two</td>
<td>two to &gt;three</td>
<td>two</td>
<td>two</td>
<td>two</td>
<td></td>
</tr>
<tr>
<td>SV Striae in 10 μm</td>
<td>33.5–44.9 (38.5±2.6)</td>
<td>&gt;35 difficult to discern in LM</td>
<td>32–34</td>
<td>28–30</td>
<td>25–31.6 (28.7±1.6)</td>
<td>22–23</td>
<td>28.3–40 (34±3.8)</td>
<td></td>
</tr>
<tr>
<td>Raphe shape</td>
<td>gently sigmoid</td>
<td>markedly sigmoid</td>
<td>sigmoid at apices, strong,</td>
<td>sigmoid</td>
<td>sigmoid</td>
<td>robust, sigmoid</td>
<td>sigmoid</td>
<td>slightly sigmoid,</td>
</tr>
</tbody>
</table>

Riaux-Guin & et al.: *Cocconeis napukensis* and allied taxa
<table>
<thead>
<tr>
<th>Position of the terminal raphe endings</th>
<th>Helictoglossae</th>
<th>RV apical area</th>
<th>L/W: 1.6±0.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>(20.3±2.2)</td>
<td></td>
</tr>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>27.9±3.2</td>
<td></td>
</tr>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>25–28.6</td>
<td></td>
</tr>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>(26.2±1.2)</td>
<td></td>
</tr>
<tr>
<td>close to the margin</td>
<td>nd</td>
<td>24–28</td>
<td></td>
</tr>
<tr>
<td>far from the margin</td>
<td>nd</td>
<td>24–27</td>
<td>(25.7±1.7)</td>
</tr>
<tr>
<td>far from the margin</td>
<td>nd</td>
<td>22–23</td>
<td>(26.2±1.2)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>26–28</td>
<td>(26.2±1.2)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>24–28</td>
<td></td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>24–27</td>
<td>(25.7±1.7)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>22–23</td>
<td>(26.2±1.2)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>26–28</td>
<td>(26.2±1.2)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>24–27</td>
<td>(25.7±1.7)</td>
</tr>
<tr>
<td>well apart from the margin</td>
<td>nd</td>
<td>22–23</td>
<td>(26.2±1.2)</td>
</tr>
<tr>
<td>far from the margin</td>
<td>nd</td>
<td>26–28</td>
<td>(26.2±1.2)</td>
</tr>
</tbody>
</table>

**Holotype**: Permanent slide ‘Nagasaki off shells 22046’, from Voigt’s slide collection housed in Dübendorf (Switzerland). Holotype specimen illustrated in Figs 21 (RV), 22 (SV).

**Type locality**: Nagasaki, Japan.

**Etymology**: Named in honor of Friedrich Meister.

**Remarks**: Cocconeis meisteri is not rare in the M. Voigt’s slides. We first misidentified these specimens as C. subtilissima, due to the constriction of their SV sternum and referring to the German diagnose of the latter (‘in der Schalenmitte enger’). Nevertheless, the valve shape and the RV features of C. meisteri differ completely from those of C. subtilissima.

**Cocconeis suzukii Riaux–Gobin et al. sp. nov. (LM, Figs 24–28, Table 1)**

**Synonym**: Cocconeis subtilissima Meister sensu Suzuki et al. [2000, figs 3 (RV), 4 (SV)].

**Description**: Valve elliptical with round apices, RV striae equidistant and radiate. Raphe robust, clearly sigmoid, terminal raphe fissures far from the margin and bent to opposite directions, central raphe endings robust, relatively close to each other. Axial area narrow, central area not expanded. SV striation easily discernible, each hemivalve carries a hyaline apically elongate area splitting the striae in two parts. Sternum large, elliptical and sigmoid, not constricted in mid–valve, one mid–valve stria shorter on one side (Figs 26–27, arrows).

**Morphometrics** (LM, n=18): 21.1±2.2 µm long; 13.8±1.6 µm wide
Stria densities: 28.7±1.6 SV str. in 10 µm; 25.9±1.3 RV str. in 10 µm
L/W: 1.5±0.1

**Holotype**: F. Meister’s type slide ‘Nagasaki 3409001’ housed in Herbarium of the University of Zürich. Holotype illustration: Figs 24 (RV), 25 (SV).

**Holotype locality**: Nagasaki, Japan (from the shell of a marine snail).

**Etymology**: This taxon is dedicated to DrHidekazu Suzuki who first illustrated it from a Japanese area.

**Remarks**: This taxon is not rare on F. Meister’s and M. Voigt’s slides. Its shape is rarely elongate, and the SV striation is coarser than in C. meisteri and C. subtilissima. Furthermore, the sigmoid SV sternum is different from that of C. meisteri. This taxon is similar to C. subtilissima Meister sensu Suzuki et al. (2000). For this reason we propose the new species Cocconeis suzukii sp. nov.
Material from Napuka Atoll (Tuamotu Archipelago, South Pacific Ocean)

*Cocconeis napukensis* **Riaux–Gobin et al.** sp. nov. (LM, Figs 29–37; SEM, Figs 38–65; Table 1)

**Description:** Small–celled, elliptic to linear–elliptic with round apices (Figs 29–43).

**Sternum valve (SV):** Valve face externally strongly convex (Figs 38–41), bi–layered and strongly silicified, with two longitudinal rows of alveoli (up to three in larger specimens, i.e., Fig. 43), sternum almost straight to very slightly sigmoid, widely lanceolate, with no fascia, externally strongly constricted and concave in its mid–part (Figs 38–41). In the biggest specimens, the constricted part of the sternum may be a narrow straight band (Figs 40, 43). Striae uniseriate, dense, difficult to discern in LM (Figs 29–34). Alveoli regularly radiate, externally open by an oblong lumen interrupted by
one (or two in the bigger specimens) hyaline and thin longitudinal line (Figs 41, 43, arrows). Apical alveoli short and deflected in opposite directions from one pole to the other. Internally, each alveolus opens to a small round pore, arranged along a regular apical line (Figs 44, 45, arrows). SV valvocopula (SVVC) robust (Fig. 48) and open (Fig. 49), with an irregular thin edge without fimbriae (Fig. 44, arrows; Fig. 49, arrow). The abvalvar (Fig. 49) and advalvar sides of the SVVC have no ornamentation (Fig. 43).

**Raphe valve (RV):** Externally flat to slightly concave. No fascia or marginal rim. Striae dense, uniseriate, regularly spaced and radiate (Figs 50–53), slightly denser close to apices. Central area reduced and round
Figs 21–28. (21–23) *Cocconeis meisteri* sp. nov. from F. Meister slides (LM), (21–22) complete valve at two different foci (raphe valve (RV) on the left with a slightly sigmoid raphe, sterna valve (SV) on the right with a constricted sterna, arrows), (23) SV showing the hyaline areas on each hemivalve; (24–28) *Cocconeis suzukii* sp. nov. from F. Meister slides (LM), (24–25) illustration of the holotype (Type slide n° 3409001), complete valve at two different foci (RV on the left with a strong raphe and terminal raphe fissures far from the margin; SV on the right with a sigmoid large sterna, with one stria shorter, arrow), (26) SV with a sigmoid sterna, with one stria shorter on one side, arrow, (27–28) complete valve at two different foci (RV on the right with a strong sigmoid raphe; SV on the left with a sigmoid large sterna, with one stria shorter, arrow). Scale bars 10 µm.

(Fig. 50). Areolae small, round and regular, occluded by depressed hymenes, with marginally and radially arranged short slits (Fig. 54). One marginal row of areolae occasionally slightly oblong. Small apical area devoid of areolae (Fig. 50, arrow). Axial area narrow. Raphe filiform, slightly sigmoid, with proximal raphe endings close to each other and distal raphe fissures simple and close to the margin (Figs 50, 51, 53).

Internally, the raphe is bordered by slightly raised ribs (Fig. 55). Helicoglossae short, raised and curved in opposite directions (Figs 56, arrow; 57). Complex and high cingulum composed of the two open valvocopulae and several additional open connecting bands (Figs 60–65). RV valvocopula (RVVC) thick, open, with the advalvar edge slightly crenelated (Fig. 58, short white arrows; 63, white arrow).
**Morphometrics** \( (n=50) \): 6.3–22.8 \((14.3\pm4.3)\) µm long; 3.7–11.8 \((8\pm2.5)\) µm wide  
Stria densities: 33.5–44.9 \((39.4\pm2.6)\) SV str. in 10 µm; 27.9–32.6 \((30.3\pm2)\) RV str. in 10 µm  
L/W: 1.8±0.2

**Holotype:** SEM stub no. 1 15NPK 7–2 12/07/2013 stored in C. Riaux–Gobin collection at CRIOBE–Université de Perpignan, France, Holotype specimen illustrated in Fig. 43.

**Isotypes:** from sample 15NPK7–2, sampled in 25 september 2012, slide BM101713 deposited in the Natural History Museum (London, UK) and slide NPK1 in collection C. Riaux–Gobin.


**Habitat:** Until now only found on Napuka Atoll (Tuamotu).

**Etymology:** The epithet refers to Napuka Atoll where
Figs 38–43. Cocconeis napukensis sp. nov. from Napuka (SEM). External views of the sternum valve (SV): (38) cingular view, note the two strongly concave constricted parts of the sternum (arrows); (39, 40) specimens with two alveoli. The arrow show the thin hyaline area externally delineating the alveoli; (41, 43) Holotype, larger specimens with three alveoli and two hyaline areas (arrows); sternum valve valvocopula (SVVC) open (Fig. 43, framed arrow) with smooth edge; (42) focus on the lumen of the alveoli, with a row of pores giving access to the interior of the cell (arrow). Scale bars 4 µm (29); 3 µm (24–27); 1 µm (28).

Remarks: Cocconeis napukensis SV has some similarities with the SV illustrated in Schmidt (1894) pl. 196, fig 8 (specimen on the right) under Cocconeis vetusta A. Schmidt. But the illustrated RV of the latter (left specimen in fig. 8, ref. cit.) has a transverse hyaline fascia much larger than in C. napukensis. Also some similarities with the SV illustrated in Schmidt (1894) pl. 192, fig 2 (reproduced in our Fig. 12), under Cocconeis comis A. Schmidt, but with a striation less dense than that in C. napukensis. C. comis RV
is not illustrated and not enough characteristics are mentioned for this taxon to permit a comparison with *C. napukensis*. *Cocconeis lorenziana* GRUNOW ‘formae minores’, in SCHMIDT (1894) pl. 191, figs 13–14, 24–27 (reproduced in our Figs 2–5, 8–9), illustrated by SEM in MONTGOMERY (1978, pl. 68, figs E, F), has some similarities with our taxon: i.e., presence of two rows of alveoli. But the valve of the latter is less elongate than in *C. napukensis*, and the SV sternum, even if irregular, is not constricted. Furthermore, the specimens of *C. lorenziana* GRUNOW ‘formae minores’ illustrated in SCHMIDT (ref. cit.) have a lower SV stria density than *C. napukensis*. It can be remarked that the SEM illustrations by MONTGOMERY (ref. cit.) somehow fit the illustrations of *C. subtilissima* MEISTER sensu SUZUKI et al. 2000, here described as *Cocconeis suzukii*.

Several features differentiate *C. napukensis* from *C. subtilissima* MEISTER sensu SUZUKI et al.
Figs 50–54. *Cocconeis napukensis* sp. nov. from Napuka (SEM). External views of the raphe valve (RV): (50, 52, 53) RV of different sizes, almost plane, with a slightly sigmoid raphe, regularly spaced and radial striae and narrow axial area; (51) detail showing the apical triangular area devoid of areolae and terminal raphe ending close to the margin; (54) detail of the areolae with hymenes showing short marginal slits. Scale bars 3 µm (50, 53); 2 µm (51, 52); 200 nm (54).

2000, here described as *Cocconeis suzukii* (see above, Discussion and Table 1): 1) a smaller length (on average 14.3 µm long versus 21.1, Table 1), 2) a different outline of the valve (oblong–elliptical to linear–elliptical in *C. napukensis*), 3) the SV sternum pattern, strongly constricted and straight in *C. napukensis*, while clearly sigmoid in *Cocconeis suzukii*, 4) if the RV is relatively similar on both taxa, the raphe terminal fissures in *C. napukensis* are close to the margin with valve apices completely free of areolae (Figs 50, 51, 53), while in *Cocconeis suzukii* they are far from the margin with some areolae present along the margin delineating a small arrow–head area devoid of areolae, 5) the helictoglossae are short and abruptly deflected in opposite directions in *C. napukensis* (Fig. 56), while long and sigmoid in *Cocconeis suzukii* (see *C. subtilissima* sensu SUZUKI et al. 2008, fig. 19, arrow), 6) the hyaline line externally delineating each alveolus is thin and regular in *C. napukensis* (Fig. 40–43) while larger in *Cocconeis suzukii*.

*C. napukensis* also has some similarities with *Cocconeis meisteri* sp. nov. found in the material of Meister (Figs 21–23), but with 1) smaller dimensions, 2) a more elongated shape (L/W 1.8 versus 1.6, Table 1), 3) three alveoli per stria on the bigger specimens versus two for *C. meisteri*, 4) stria densities higher on both valves, and 5) a more pronounced constriction of the SV sternum.

*Cocconeis vairaensis* RICARD (1975, pl. 2, fig. 21, reproduced in our Figs 10–11) (type slide and raw material not localized) has also some likeness with our new taxon, but is less elongate, has less dense striation and a same stria density on both valves (22–23 str. in 10 µm, Table 1), its SV sternum is irregular and only
very slightly constricted in the middle, and its RV is more deeply sigmoid than that of *C. napukensis*.

Finally, *C. napukensis* can be compared to *C. subtilissima Meister* (see above emended description). The two taxa differ by their shape (more oblong-linear and with blunt apices in *C. subtilissima*), by their RV stria pattern (presence of a short fascia in *C. subtilissima*), and by their SV pattern (no constriction of the SV sternum in *C. subtilissima*).

It can be remarked that *C. subtilissima* and *C. napukensis* concurrently possess a significantly denser striation on their SV, contrarily to *C. suzuki* and to *C. vairaensis* (Table 1).

**Discussion**

First discovered by *Meister* (1935) from a Japanese marine sample, *C. subtilissima* has been diversely interpreted by subsequent authors (i.e., *Suzuki* et al. 2000; *de Stefano & Romero* 2005; *Suzuki* et al. 2008; *Riaux-Gobin* et al. 2011; *Majewska* et al. 2013) entangling its real identity. But, following the original description and our examination of the type material, and except for some remarks by F. Meister that were erroneous (i.e., concerning the central area of the RV that is in fact a short fascia, and the SV sternum that is...
Figs 60–65. *Cocconeis napukensis* sp. nov. from Napuka (SEM). Detail of the cingular bands. The high and complex cingulum is composed of the two open valvocopulae (raphe valve valvocopula (RVVC) and sternum valve valvocopula (SVVC), two open copulae (C) and the mantle of each valve (VC, RV). (62, 63) particularly show the open RVVC in place (framed arrow, Fig. 63) and crenulated edge of the RVVC in advalvar side (white arrow, Fig. 63). Scale bars 1 µm (60, 61, 63, 64); 500 nm (62, 65).

not constricted), all other points fit exactly and the later interpretations were wrong.

In fact, De Stefano & Romero (2005, pls 32–33), Suzuki et al. (2008, figs 1–44), Riaux–Gobin et al. (2011, pl. 6/3–11, pls 73, 74) and Majewska et al. (2014, fig. 2, 31) roughly follow the definition by Suzuki et al. (2000). It can be noted that none of the above cited authors examined the original F. Meister type material. Furthermore, some errors can be pointed out: in De Stefano & Romero (2005) pl. 4 figs 1, 2 are the reproduction of pl. 4, figs 1, 2 of Suzuki et al. (2000) and were wrongly attributed to Meister (1935, figs 61, 62). The TEM images in Suzuki et al. (2000, figs 3, 4) are reproduced in Suzuki et al. (2008, figs 21,
26, with wrong scale bars: –10 µm instead of 5 µm–) while the rest of the description somehow differs from the first description by Suzuki et al. (2000) (see Table 1), i.e., the valves illustrated in Suzuki et al. (2008) are in major part largely elliptical and not oblong and the stria densities are significantly different. The SEM illustration in Majewska et al. (2013, fig. 2,31) is the exact reproduction of fig. 1, pl. 32 of De Stefano & Romero (2005) and not an illustration of their Mediterranean material.

In conclusion, Cocconeis subtilissima Meister differs from Cocconeis subtilissima sensu Suzuki et al. (2000), and it is the reason why we propose to define the new species Cocconeis suzuki sp. nov. All the taxa discussed in the present paper, including Cocconeis napukensis sp. nov., Cocconeis meisteri sp. nov. and Cocconeis vairaensis, differ from each other by several of their features (see Table 1 and key). These small–celled marine Cocconeis probably belong to the same group of species. Genetic data would be useful to show their taxonomic relationship.

The rich diversity of benthic diatoms from tropical and coral reef samples are up till now poorly documented (see introduction). Several new Achnanthes species and a new genus were recently described from the South Pacific (Riaux–Gobin et al. 2013, 2014a), while numerous other taxa are in common with the flora described from the Indian Ocean (i.e., Mascarenes, Riaux–Gobin et al. 2011). On the other hand, it is always time–consuming to explore the type collections (when they are found) but it is the only way to get a reliable concept of a taxon. In the case of C. subtilissima, the original photographs gave a good description that was later wrongly interpreted. In the same way, some reference books may give haphazard information if types are not checked (i.e., concerning Cocconeis pinnata Gregory and C. ornata Gregory in Hustedt 1931–1959, Riaux–Gobin et al. 2014b,c) that can induce subsequent misidentification.

Key to discriminate the discussed taxa

1. Elongated frustule, L/W >2, SV sternum almost straight, not constricted at mid–valve, short fascia on the RV................................. C. subtilissima
   Elliptical to oblong–elliptical frustule, L/W<2, no fascia on the RV................................................................. C. vairaensis
2. Low stria density, 22–23 in 10 µm, on both valves ......................................................................................... C. subtilissima
   Striae denser, often denser on the SV than on the RV................................................................. C. vairaensis
3. SV sternum not constricted at mid–valve, terminal raphe endings well apart from the margin................................. C. suzuki
   SV sternum constricted at mid–valve, terminal raphe endings close to the margin or unclear, high SV stria density................................................................. C. meisteri
4. Av. 34 SV striae in 10 µm, av. 26 RV striae, SV sternum slightly sigmoid, not strongly constricted at mid–valve, L/W 1.6……
   Smaller size, striae slightly denser on both valves, SV almost straight, strongly constricted at mid–valve, L/W 1.8…… C. napukensis

Acknowledgments

Jean Kape ‘Fasan Chong’, Remy Tchong and Marina Taki are warmly acknowledged for their hospitality and friendship during the stay of C. R.–G. in Napuka Atoll. René Galzin (CRIOBE–Moorea, French Polynesia) greatly helped in the logistic of the project. Thanks are also due to Oscar E. Romero (MARUM–Center for Marine Environmental Sciences, University of Bremen). We warmly acknowledge the anonymous reviewers and Aloisie Pouličková for improving the manuscript, and Friedel Hinz (BRM) and Regula Illi (M. Voigt Collection Curator, Eawag, Dübendorf, Schweiz) for the loan of original material, Dimitri Gorand (C2M, Perpignan University) for his assistance with the SEM and Margie Koster, Switzerland, for the English revision. Naturalia & Biologia and CNRS–USR 3278 funded the CORDIA 2012 project.

References


