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### **► To cite this version:**

Catherine Riaux-Gobin, Andrzej Witkowski, Yenny Risjani, Yunianta Yunianta, Véronique Berteaux-Lecellier, et al.. Upsilococoneis dapalistriata gen. nov. & comb. nov. (Bacillariophyta) – a pantropical marine member of Cocconeidaceae. Oceanological and Hydrobiological Studies, 2022, 51 (1), pp.23-31. 10.26881/oahs-2022.1.03 . hal-03839225

**HAL Id: hal-03839225**

**<https://univ-perp.hal.science/hal-03839225>**

Submitted on 4 Nov 2022

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## *Upsilococconeis dapalistriata* gen. nov. & comb. nov. (Bacillariophyta) – a pantropical marine member of Cocconeidaceae

by

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DOI: <https://doi.org/10.26881/oahs-2022.1.03>

Category: **Original research paper**

Received: **June 15, 2021**

Accepted: **July 5, 2021**

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### Abstract

*Cocconeis dapalistriata*, first described as a member of the genus *Cocconeis*, is re-examined due to its unique ultrastructure. Both valvocopulae of this taxon show significant differences compared to those found in the genus *Cocconeis*. They are expanded and show some similarities with those found in *Amphicocconeis*. On the other hand, terminal parts of the raphe valve (RV) in *C. dapalistriata* are simple and the raphe valve (RV) striae are composed of small round areolae with a hymenate occlusion with radial slits, similar to those observed in *Cocconeis*. *Campyloneis* and *Xenococconeis* also have expanded valvocopulae but with numerous morphological differences compared to those found in *C. dapalistriata*. Furthermore, the areolae of the sternum valve (SV) in *C. dapalistriata* are occluded by a concave velum with no apparent internal slits, and externally ornamented with irregular silica crystals. *Upsilococconeis* Riaux-Gobin, Witkowski & Risjani gen. nov. is proposed to accommodate the latter taxon. First described from the Western Indian Ocean (Mascarenes), it was subsequently listed from the Western Pacific Ocean (Guam), the South Pacific Ocean (French Polynesia and New Caledonia) and from the Eastern Indian Ocean (Indonesia), and thus may qualify as pantropical.

**Key words:** diatoms, benthic, pantropical, *Upsilococconeis* gen. nov., *Upsilococconeis dapalistriata* comb. nov.

## 1. Introduction

The order Achnanthes (Bacillariophyceae) comprises several genera with a complex system of valvocopulae ensuring the cohesion of the frustule, which probably plays a major role. These valvocopulae show great morphological diversity and, following Holmes et al. (1982), the “morphology of the fimbriate valvocopulae varies and is diagnostic of each taxon”. Among the achnantheid genera, *Cocconeis* Ehrenberg is the most diverse, with at least 560 species and 293 infraspecific names, 204 of which are accepted names (Guiry & Guiry 2021). Several *Cocconeis* species have complex valvocopulae that never extend across the entire valve. Several other genera, *Campyloneis* Grunow, *Amphicocconeis* De Stefano & Marino and *Xenococconeis* Riaux-Gobin also have complex and expanded valvocopula systems.

*Cocconeis dapalistriata* was originally described from marine benthic tropical habitats of coral reefs in the Western Indian Ocean (the Mascarene Islands; Riaux-Gobin et al. 2011). It was later reported from Guam Island in the Western Pacific Ocean by Lobban (2015), NW Madagascar (Western Indian Ocean), misidentified as *Amphicocconeis* (A. Kryk, personal communications), and the coasts of the Indonesian islands (Borneo, Komodo, Flores and East Java) of the Western Pacific Ocean and the Eastern Indian Ocean (Risjani et al. 2021). The species has also been recorded in the South Pacific Ocean (French Polynesia and Melanesia, New Caledonia; Riaux-Gobin, unpublished observations). This taxon, previously considered as a *Cocconeis* member, has enough unique morphological features to justify the creation of a new genus and a new combination. This paper provides details on the ultrastructure of its frustule, which justifies the establishment of the new diatom genus *Upsilococconeis*.

## 2. Materials and methods

### 2.1. Diatom materials

The material studied comes from several locations: 1) Réunion and Rodrigues islands (Mascarenes, Western Indian Ocean) with several sites, including one close to St Leu, Réunion (21°09'S; 55°18'E); 2) French Polynesia (South Pacific), Raivavae Island (the Austral Islands; RAI 20, 23°51.274'S; 147°39.595'W), and Moorea (Society Archipelago; Papetoai, 17°29.873'S; 149°54.794'W and Afareaitu, 17°33.244'S; 149°47.353'W); 3) South Province, New Caledonia (South Pacific), Anse Vata (sample NC30, 22°18.495'S; 166°26.898'E, sampling

permit n°21346-2019/2-REP/DENV); 4) Komodo islands (Indonesia, Flores Sea, Eastern Indian Ocean; sample Labuan Bajo 2, 8°30'1"S; 119°52'40"E).

### 2.2. Sample preparation and examination

The material (preserved in methanol or formalin) was washed with distilled water to remove salt, treated with 10% HCl to remove carbonates and H<sub>2</sub>O<sub>2</sub> to remove organic matter, and rinsed again in distilled water. For light microscope (LM) observations, diatom slides were examined with a Zeiss Axio Imager M2 (Carl Zeiss, Jena, Germany) using a x100 Plan Apochromat oil immersion objective (NA = 1.46) equipped with DIC (University of Szczecin, Institute of Marine and Environmental Sciences, Szczecin, Poland). For scanning electron microscopy (SEM) observations, drops of raw or cleaned material were filtered through 1 µm Nuclepore® filters and rinsed with deionized milliQ. Filters were air-dried and mounted on aluminum stubs before being coated with a gold palladium alloy (EMSCOP SC 500 sputter coater) and examined under a Hitachi SU 8010 SEM unit (University of Rzeszów, Poland), and a Hitachi S-4500 SEM operated at 5 kV, calibrated with Silicon grating TGX01 (C2M, Perpignan, France). Stria density was determined on the mid half-valve.

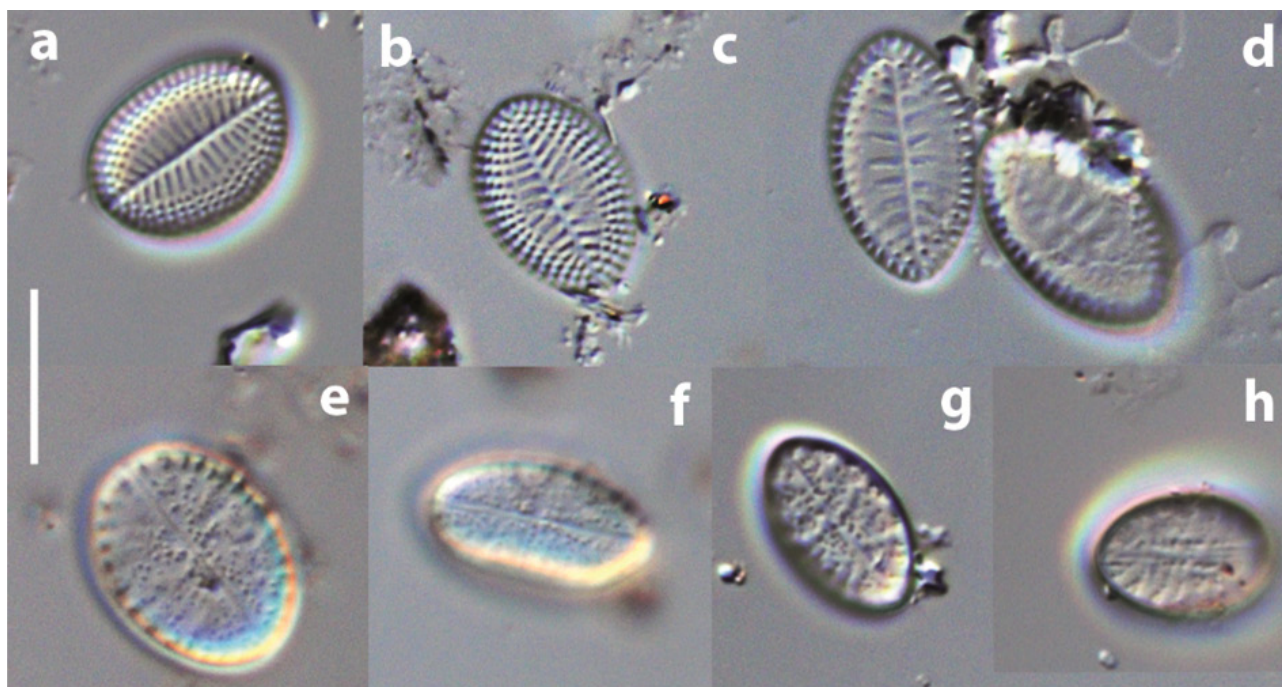
We name the raphe valve (RV) valvocopula as RVVC and the sternum valve (SV) valvocopula as SVVC.

## 3. Results

### 3.1. New morphological observations of *Cocconeis dapalistriata* Riaux-Gobin, Romero, Compère & Al-Handal

Several new ultrastructural features allow us to emend the original description of *Cocconeis dapalistriata* Riaux-Gobin, Romero, Compère & Al-Handal (Riaux-Gobin et al. 2011). The SVVC was originally described as having irregularly chiseled digitate fimbriae (ref. cit., pl. 39, Fig. 6). The subsequent detailed examination of the material from different oceanic basins (see Introduction, Figs 1–7 and Table 1) proved, in particular, that the SVVC is closed and composed of arborescent and coalescent extended fimbriae, overlying the SV areola hymenes and virgae. Small irregular pores are present on the SVVC, framing and surrounding the underlying SV areolae, and possibly allowing the exchange with the inner part of the cell. This complex SVVC can be relatively narrow (Fig. 4a,b) with an irregular edge, or can extend over 1/4 of the internal valve face (Fig. 4d) up to covering



**Figure 1a – h**

*Upsilococoneis dapaistrata*. LM. Specimens from Komodo (Fig. 1a, from the paratype slide SZCZ26223). SV (a–d), SVVC (e–h). Scale bar: 10  $\mu$ m.

the entire valve face (Fig. 5a,b). In the latter case, there is an open and restricted central area with an indented border (Fig. 5a,b, arrowheads). This SVVC may appear as 'dots of leopard skin' visible as plated on the SV areola hymenes (Fig. 6c, arrowhead). There is no geographical delineation as to the extent of the SVVC (from narrow to extended). The RV in *Cocconeis dapaistrata* has features similar to those in *Cocconeis*, with RV areola hymenes bearing radial slits (Fig. 6b) and simple raphe endings (Fig. 6b) near the margin. Note that the RV areolae are round and not elongate, as erroneously illustrated in Riaux-Gobin et al. (2011,

pl. 40, Fig. 3). The RV mantle is narrow. The RV central area is small and elliptic (Fig. 6d). Helictoglossae are discrete (Fig. 6e). Regardless of the sampling area (South Pacific Ocean, Eastern Indian Ocean), the RVVC is expanded and closed, internally covering the entire RV valve surface (Fig. 7a,b). In advalvar view, the RVVC is largely convex, with radiate furrows patterned on the underlying RV striae. Small irregular pores are scattered over the latter furrows. The axial area of the RVVC shows two grooves framing the raphe present on the underlying RV. The margin of the RVVC features a type of groove with a row of small irregular beads

**Table 1**

Biometrics and main features of *Upsilococoneis dapaistrata* comb. nov. from Komodo Island (Eastern Indian Ocean), Mascarenes (Western Indian Ocean), French Polynesia & New Caledonia (South Pacific).

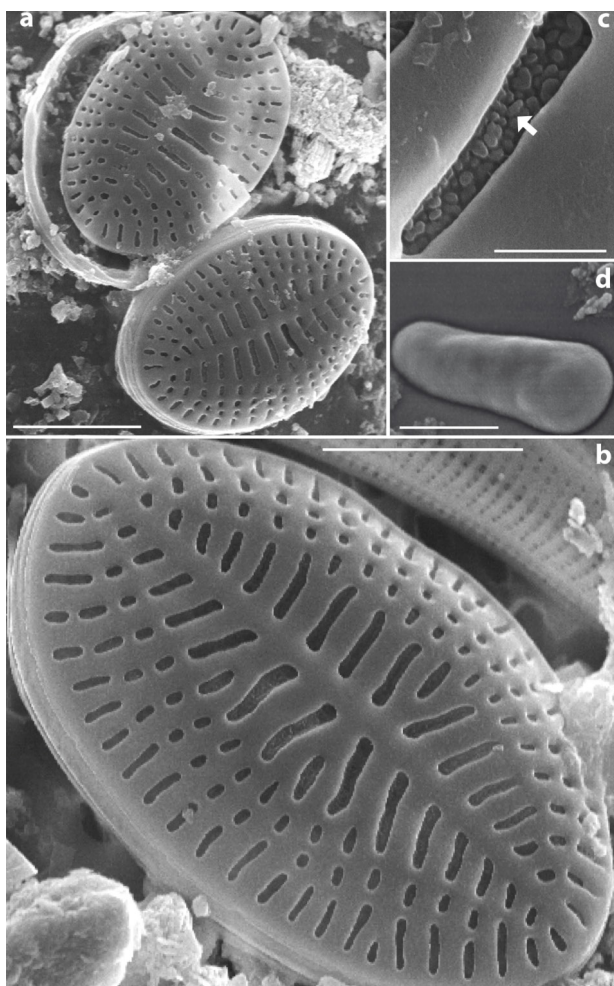
| <i>Upsilococoneis dapaistrata</i> |  |                       |                     |                       |                       |                       |                       |
|-----------------------------------|--|-----------------------|---------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| n (SEM)                           | Oceanic basin                                    | length                | width               | SV str.               | SVVC rows of pores    | RV str.               | RVVC rows of pores    |
| 15                                | Komodo Island (Eastern Indian Ocean)             | 8 – 16<br>11 $\pm$ 3  | 5 – 10<br>7 $\pm$ 1 | 11 – 14<br>12 $\pm$ 1 | 11 – 18<br>13 $\pm$ 3 | 38                    | 36 – 45<br>40 $\pm$ 4 |
| 13                                | Mascarenes (Western Indian Ocean)                | 12 – 15<br>13 $\pm$ 1 | 7 – 10<br>8 $\pm$ 1 | 11 – 16<br>14 $\pm$ 2 | -                     | 40                    | -                     |
| 12                                | French Polynesia & New Caledonia (South Pacific) | 8 – 13<br>12 $\pm$ 2  | 4 – 10<br>7 $\pm$ 1 | 12 – 20<br>14 $\pm$ 3 | 12 – 13<br>12 $\pm$ 1 | 38 – 52<br>43 $\pm$ 8 | 43                    |

Measurements expressed as min. – max. and mean  $\pm$  SD ( $\mu$ m), without decimals. SD = standard deviation ( $\sigma$ ).

Stria density and valvocopula rows of ornamentalations expressed in 10  $\mu$ m.

n = SEM observed specimens.





**Figure 2a – d**

*Upsilonococconeis dapalistriata*. SEM. SV. Specimens from Réunion (a–c), specimen from Komodo (d). Figs 2a–b. SV, epipsammic specimens with characteristic large SV areola pattern. Fig. 2c. External view of SV areola occlusion with silica crystal-like ornamentation (arrow). Fig. 2d. Internal view of SV areola hymenes. Scale bars: 5  $\mu\text{m}$  (Fig. 2a), 4  $\mu\text{m}$  (Fig. 2b), 600 nm (Fig. 2c), 500 nm (Fig. 2d).

that may serve as anchorage in the RV (Fig. 7b, twin arrowheads). Furthermore, the SV areolae in *Cocconeis dapalistriata* are occluded by a concave velum, having neither slits nor visible pores (Fig. 2d), and externally ornamented with irregular silica structures (Fig. 2c, arrow). At least one additional open cingular band is observed (Fig. 7a, black ellipse), rendering an eventual anchorage between both valvocopulae impossible. Neither papillae nor anchorage marks are visible on the valvocopulae or on the inner parts of the valves.

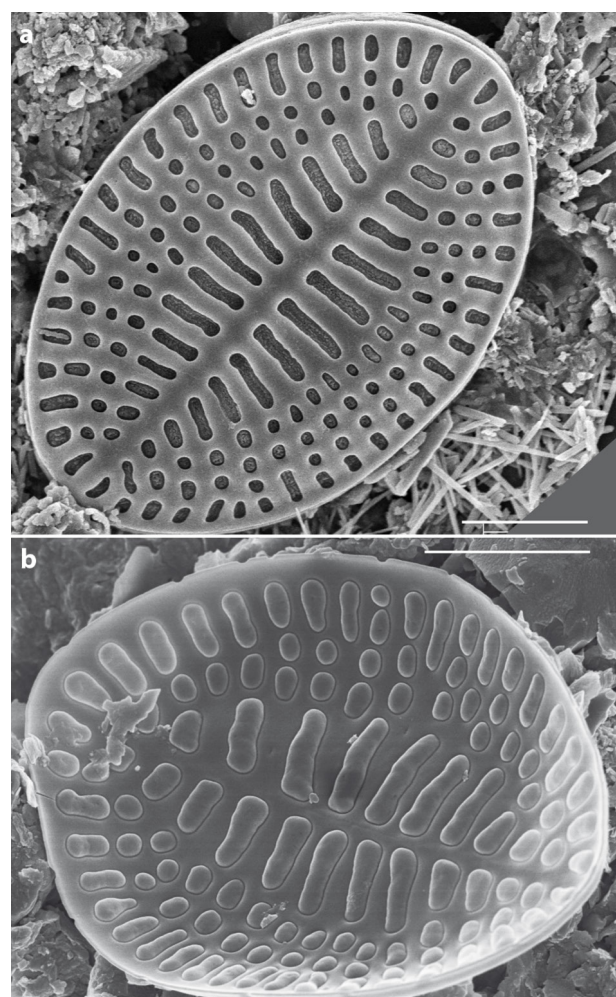
### 3.2. Proposal to create *Upsilonococconeis* gen. nov. to allocate *U. dapalistriata* comb. nov.

The morphology of both valvocopulae in *Cocconeis dapalistriata* is unique and cannot be attributed to the genus *Cocconeis*. *Upsilonococconeis* Riaux-Gobin, Witkowski & Risjani gen. nov. is proposed to accommodate *Upsilonococconeis dapalistriata* comb. nov. (synonym *Cocconeis dapalistriata*).

***Upsilonococconeis* Riaux-Gobin, Witkowski & Risjani gen. nov.**

**Order:** Achnanthes

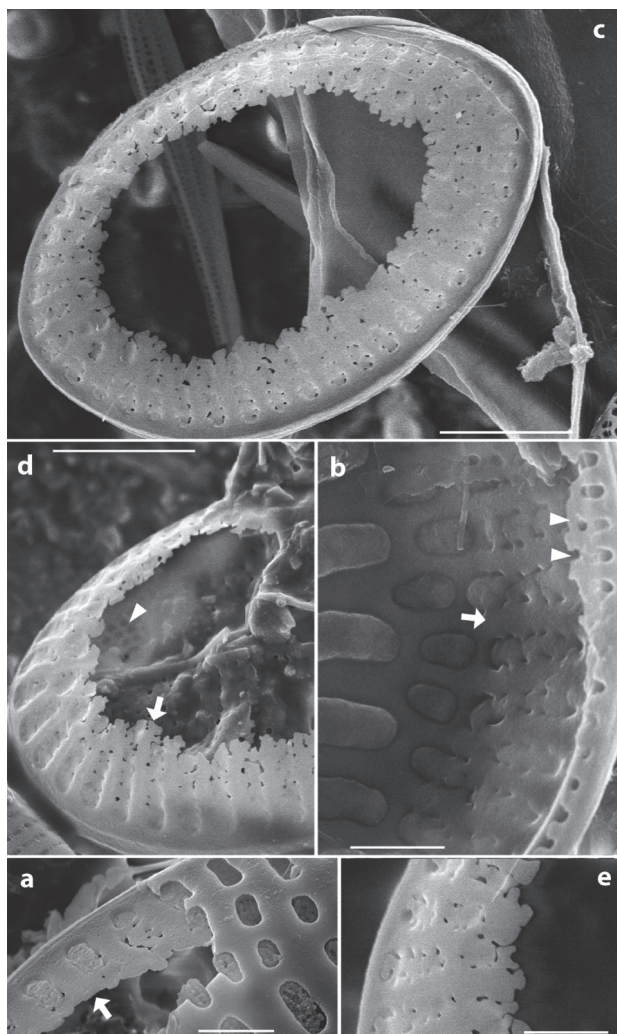
**Family:** Cocconeidaceae



**Figure 3a – b**

*Upsilonococconeis dapalistriata*. SEM. SV. Fig. 3a, external view (specimen from French Polynesia). Fig. 3b, internal view (specimen from Komodo). Scale bars: 3  $\mu\text{m}$  (Figs 3a–b).



**Figure 4a – e**

*Upsilococoneis dapaistrata*. SEM. SVVC. Specimens from New Caledonia. Fig. 4a–b, SVVC narrow (arrows). Fig. 4b, RV margin (twin arrowheads). Fig. 4c–e, SVVC  $\frac{1}{4}$  of the valve, with underlying RV striation (Fig. 4d, arrowhead), SVVC arborescent fimbria edge (Fig. 4e). Scale bars: 3  $\mu$ m (Figs 4c–d), 1  $\mu$ m (Figs 4a–b, e).

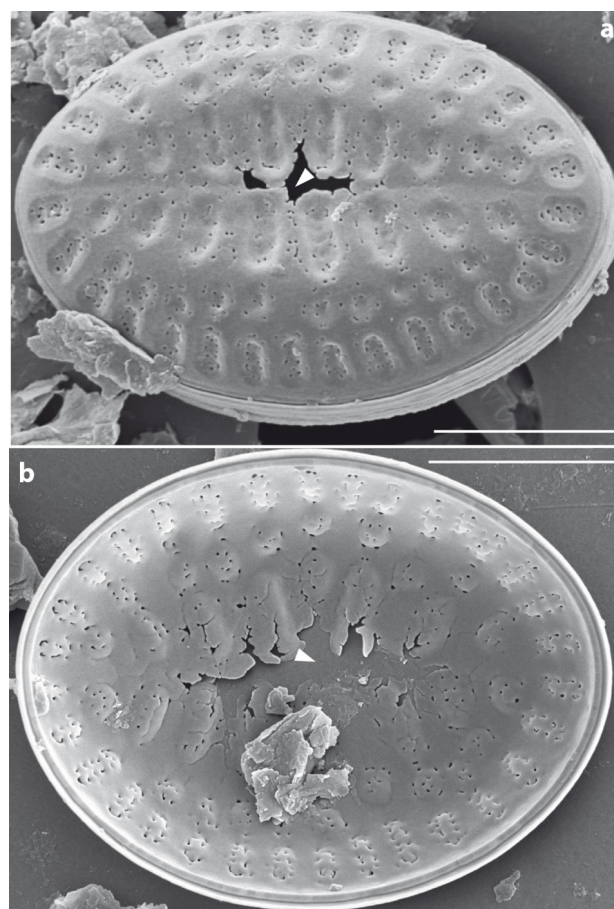
**Description:** SV elliptic to subcircular, coarse, with strong and radiate areolae denser at the margin, externally closed by concave hymenes without visible slits, presence of irregular siliceous ‘crystal-like’ ornamentation. SVVC narrow to expanded, composed of arborescent and coalescent fimbriae. RV thin, with radiate and equidistant dense striae, composed of round areolae occluded by hymenes with radiate slits, no marginal axial areas, raphe straight, central area elliptic and narrow, proximal raphe endings discrete and close to each other, terminal raphe endings

simple and close to the margin. RVVC wide, covering the entire valve face, with furrows corresponding to each of the underlying RV striae. Two median furrows indicate the presence of the raphe occurring on the underlying RV.

***Upsilococoneis dapaistrata* (Riaux-Gobin, Romero, Compère & Al-Handal) Riaux-Gobin, Witkowski & Risjani comb. nov.**

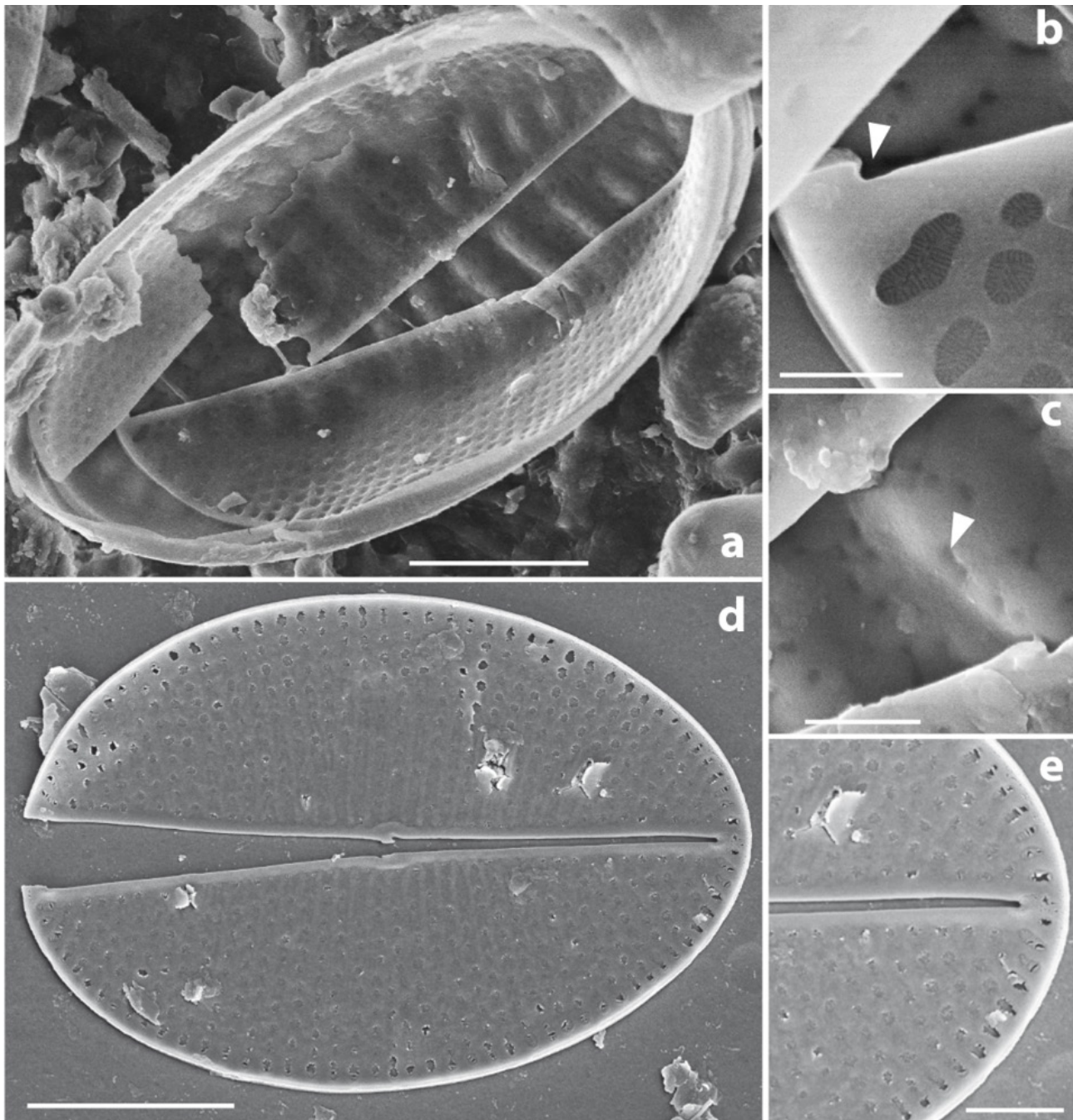
**Description:** See genus description.

**Habitat Ecology:** A relatively rare taxon at all analyzed sites except for samples collected from Komodo National Park (sand) and Tiga Warna Beach on the south coast (sand) of East Java Island (Risjani et al. 2021). Its relative abundance in sample SZCZ 26223 was

**Figure 5a – b**

*Upsilococoneis dapaistrata*. SEM. Extended SVVC. Specimens from Komodo. Fig. 5a, SVVC extended in advalvar view. Note the central void area (arrowheads). Fig. 5b, SVVC extended in abvalvar view. Note the central void area. Scale bars: 3  $\mu$ m (Figs 5a–b).





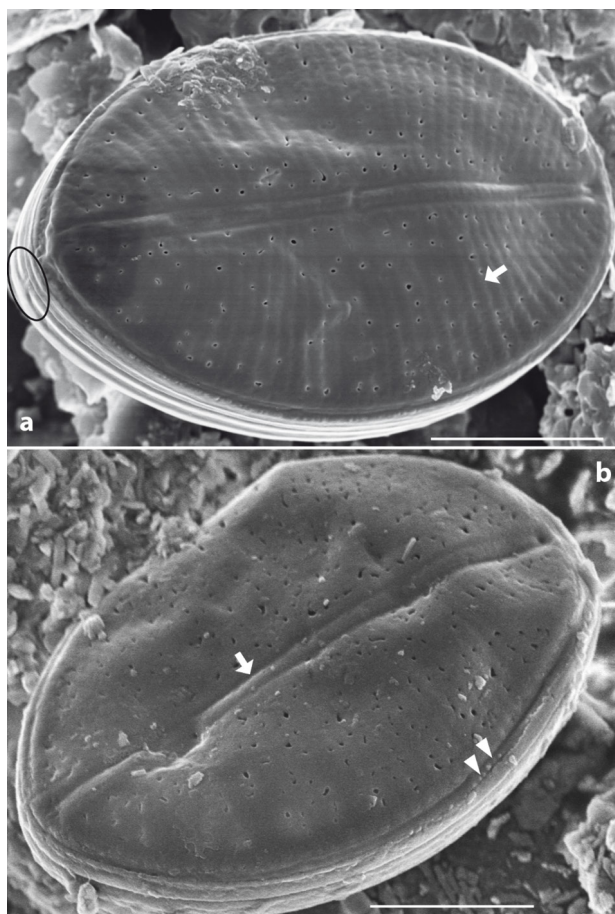
**Figure 6a – e**

*Upsilonococconeis dapalistriata*. SEM. RV. (Fig. 6a–c, specimen from New Caledonia; Figs 6d–e, specimen from Komodo). Fig. 6a, RV in external view. Fig. 6b, simple terminal raphe ending (arrowhead) and RV areola occlusion with radiate slits. Fig. 6c, leopard-like dots indicating the SVVC (arrowhead). Fig. 6d, RV in internal view, with low helictoglossae and small central area. Fig. 6e, helictoglossa. Scale bars: 3  $\mu$ m (Figs 6a,d), 1  $\mu$ m (Fig. 6e), 500 nm (Fig. 6c), 400 nm (Fig. 6b).

ca. 10%. The species appears to be either epiphytic or epipsammic on different marine tropical substrates throughout the Indo-Pacific Basin.

**Basionym:** *Cocconeis dapalistriata* Riaux-Gobin, Romero Compère & Al-Handal





**Figure 7a – b**

*Upsilonococconeis dapaistrata*. SEM. Extended RVVC in advalvar view. (Fig. 19, specimen from Komodo; Fig. 20, specimen from New Caledonia). Fig. 19, Note the radiate furrows corresponding to the underlying RV striae (arrow). Note the open additional cingular band (black ellipse). Fig. 20, Note the axial furrows indicating the underlying RV raphe (arrow). Note the marginal furrow with small structures (twin arrowheads). Scale bars: 3  $\mu$ m (Figs 19–20).

**Holotype:** SEM (Riaux-Gobin et al. 2011, pl. 39, fig. 2; SEM 130508-45), stub No. 2 29/04/2008, from sample 'St Leu U3 bis'. Sample, original picture and stub in collection C. Riaux-Gobin (USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, France).

**Holotype locality:** St Leu, coastal lagoon sediments, Réunion.

Paratypes: From sample 'St Leu U3 bis' slide REU7 in Collection C. Riaux-Gobin (USR 3278 CNRS-EPHE, CRIOBE-Université de Perpignan, France). Slide

SZCZ26223 from Komodo National Park (illustrated in Fig. 1a), in Collection A. Witkowski (Institute of Marine and Environmental Sciences, University of Szczecin, Poland).

**Etymology:** The genus name refers to *upsilon* (ὑψίλον), one of the last letters of the Greek alphabet, attesting to the distance between it and *Cocconeis*, the reference genus. The epithet (see Riaux-Gobin et al. 2011) refers 'to the remarkable and magnificent SV striation (from Latin *dapalis*, sumptuous)'.

## 4. Discussion

The complex valvocopula system in *Upsilonococconeis* can be compared to that in *Amphicocconeis*, *Cocconeis*, *Campyloneis* and *Xenococconeis*. The genus *Amphicocconeis* De Stefano & Marino is characterized by an RV with terminal raphe endings largely hooked on the mantle, and by RV striae composed of one to several macroareolae (De Stefano & Marino 2003; Riaux-Gobin et al. 2011; Riaux-Gobin et al. 2021). Our present taxon cannot be assigned to the latter genus. Furthermore, both valvocopulae in *Amphicocconeis*, often impressive, with rows of more or less complex pores, are open and never extend across the entire valves.

The genus *Cocconeis* exhibits valvocopulae with contrasted morphological characters, from open to closed, and from smooth to ornamented with more or less complex fimbriae. Note that this genus has been demonstrated to be polyphyletic, with several groups of taxa showing different morphologies, which can be divided into independent clades (Riaux-Gobin et al. 2021). *Cocconeis* species with the most unusual valvocopulae include *C. alucitae* (Riaux-Gobin et al. 2008), *C. scutellum* var. *gorensis* (De Stefano et al. 2008), *C. guttata* [Hustedt & Aleem 1951; Riaux-Gobin et al. 2011, pl. 46, figs 5–7, SVVC wide with arborescent fimbriae running around (rather than over) the SV areola hymenes, retaining large free holes], *C. spina-christi* Riaux-Gobin, Romero, Coste & Galzin (Riaux-Gobin et al. 2013), *C. pediculus* Ehrenberg (Ehrenberg 1938; Jahn et al. 2009, fig. 27, RVVC with fimbriae 'with frills', absent on poles), *C. antiqua* Tempère & Brun (Tempère & Brun 1889; De Stefano & Romero 2005, pl. 6, figs 10–11, RVVC with arborescent and not coalescent fimbriae), *C. delicata* A.W.F. Schmidt (in F. Meister's and M. Voigt's Nagasaki slides, cf. Riaux-Gobin et al. 2017, RVVC with not coalescent arborescent fimbriae, figs 35, 37) and *C. robusta* Jurilj (see Levlov et al. 2007, pl. 28, figs 3–4, arborescent RVVC fimbriae, absent on poles). Nevertheless, the



latter complex valvocopulae in *Cocconeis* (SVVC or RVVC) never extend over the entire valve face, as observed in *Upsilococoneis dapalistriata*.

The genus *Campyloneis* has complex and reticulate valvocopulae (Round et al. 1990; De Stefano et al. 2003) that are connected to each other via sophisticated papillae, and these reticulate valvocopulae are also connected to valves via anchorages. Such anchorages are absent in *Upsilococoneis dapalistriata*. Furthermore, the *Campyloneis* RV valve has a crenulate margin, which may be another unique feature in this genus.

Finally, the genus *Xenococconeis* also features complex valvocopulae with anchorages inter se, with some similarities but also many differences compared to those in *Campyloneis* (see Riaux-Gobin et al. 2014, i.e. table 2).

The valvocopulae in *Upsilococoneis* gen. nov. are unique and justify the creation of a new genus. Furthermore, although the RV in *U. dapalistriata* shows great similarities with what is observed in *Cocconeis*, the SV has unique features, particularly the external areola occlusion with silica outgrowths. *Cocconeis guttata* is one of the most related diatoms, but if the SVVC in *C. guttata* can be considered similar to that in *U. dapalistriata*, no expanded RVVC is reported in the latter species. The fact that the SVVC in *U. dapalistriata* can be narrow or completely covering the inner valve face may be related to different environmental factors (rough weather requiring stronger cohesion), or to the physiological state of the cell (close to duplication, or after reaching a resting stage).

## Acknowledgements

Yonko Gorand (C2M, University of Perpignan Via Domitia) is acknowledged for assistance with SEM, and the anonymous reviewer for constructive remarks.

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Yonko Gorand (C2M, University of Perpignan Via Domitia) is acknowledged for assistance with SEM, and the anonymous reviewer for constructive remarks.

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