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Marine Achnanthales and *Olifantiella* from the Gambier Archipelago (South Pacific)*

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Abstract— Mangareva, along with several other islets from the 'Gambier almost-atoll', are residual parts of a past volcano pertaining to the Gambier Archipelago (South Pacific). The islets are surrounded by a vast lagoon delineated by a partly subsided coral barrier reef. Benthic diatom assemblages from these marine environments included, among others, Achnanthales and species of the elusive genus *Olifantiella*, with *Cocconeis*, *Amphicocconeis* and *Planothidium* as the most diverse genera. Hao, a large Tuamotu atoll 830 km northwest of Gambier, was sampled at about the same time. A Non-Metric Multidimensional Scaling applied to data from Mangareva and Hao highlighted groups of locations and biotopes. A PERMANOVA analysis was applied to test for the effect of both biotope and location on the differences in community composition. The geologic history of the reef structure (from volcanic and silicic environments surrounded by a reef in Mangareva, to typically coral and calcic environments in Hao, with a much older geologic history) may have played a role in the degree of colonization by benthic diatoms. Some taxa and morphs were only observed in Mangareva, whereas some others, present in north Tuamotu, were apparently absent in Gambier, permitting some remarks on tropical diatom biogeography and possible endemism, taking into account that the Gambier sector is located to the south in the South Equatorial Current, and thus largely removed from the influence of other Polynesian islands.

Introduction

Polynesia, along with Micronesia and Melanesia, is a sub-region of Oceania (Fig. 1, South Pacific Ocean), comprising numerous archipelagos composed of volcanic islands and atolls of diverse ages and along different alignments, with more or less extended reef systems. The multiplicity in geologic origin and age for the South Pacific Archipelagos, persuaded us to give some geological details, that may influence the chemical environment of each island. These reef structures have witnessed a complex geologic past related to the movement of the Pacific plate (Hekinian et al. 2004, Clouard & Gerbault 2008, Delavault 2014, Pockalny et al. 2021). Several hot spots lasting from Paleocene (> 60 Ma BP) to sub-actual and actual, including the active volcano on Mehetia (Society Archipelago), have affected these impressive past structures. Ito et al. (1995) suggested that the northernmost Tuamotu Islands formed as late as 55–47 Ma. Following Buigues et al. (1993, in

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Rougerie 1995), if the age of the atolls is defined by the end of their volcanic activity, Rangiroa (Tuamotu atoll) can be ca. 50 Myr old, while Gambier can be 0.45 Ma and Mururoa 10 Ma respectively (ref. cit.), keeping in mind that the dating of the volcanic basement of Tuamotu is currently imprecise (Bonvallot 1993). Compared to the Tuamotu alignment, Easter Island (in the extreme East of Polynesia, Fig. 1) is a younger structure (Vezzoli & Acocella 2009), in relation to the Nazca plate. Following Haase et al. (1997), the oldest volcanic events in Easter Island are dated around 0.7–0.5 Ma (Kaneoka & Katsui 1985). Among all these islands, a wide range of geological state exists (from old Tuamotu atolls to very young to still active volcanoes). Today's oceanic currents circulate within these extended archipelagos, such as the South Equatorial Current (SEC) characterized by a north-westward flow.

Gambier Archipelago (Fig. 2, French Polynesia) is located at the southern end of the Tuamotu alignment and administratively includes Gambier almost-atoll (with several islets and coral motu), Temoe atoll, Portland Bank (Fig. 2) and Minerva and Bertero reefs. Duncan et al. (1974, in Stoffers et al. 1990) proposed that Pitcairn Island, Gambier, Mururoa and the Duke of Gloucester Islands were all part of a hot spot-generated island chain, and Stoffers et al. (ref. cit.) suggested that either the Pitcairn hotspot is only sporadically active, or that lithospheric tectonism controls the location of volcanism. Following Clouard & Bonneville (2005), the Gambier almost-atoll is 5.7–6.2 Myr old (much older than stated above), but still much younger than Fangataufa (13-96 Ma) and Mururoa (11.8-9.5 Ma) that may pertain to the same alignment (ref. cit.). Recently available hypotheses (see Stoffers et al. 1990, Hekinian et al. 2003, Cordier et al. 2021) attest to the complexity of the involved geologic events around the Pitcairn hot spot.

Following Rougerie (1995), Gambier is an almost-atoll ('quasi-atoll' or 'presqu'atoll'), the last step before the complete subsidence of the remaining volcanic parts and it becoming a 'true atoll'. The term almost-atoll is used when the surface of the lagoon becomes greater than the surface of the basaltic emerged island (Rougerie 1995). Clipperton (North Pacific Ocean, French territory originally named 'Île de la Passion'), as well as Fatu Huku (Marquesas Islands, north of Hiva Oa), are almost-atolls. Note that the Gambier coral barrier reef is in part flooded, so, it may partly escape the official definition of 'almost-atoll', and could be equally described as an 'island complex'.

The Gambier island complex (19°22.816 S, 138°43.133'W) comprises several volcanic islets enclosed in a broad lagoon (Fig. 2, insert), among which, Mangareva, the largest island, houses Rikitea, the chief village. All these remaining volcanic islets were once part of an ancient caldera. Gambier also comprises several motu, of which Totegegie houses an airport (Fig. 2). The Gambier barrier reef is extensive, ca. 65 km long, lying flush with the sea surface in the north, with its southern part flooded as a consequence of a differentially faster subsidence. This almost-atoll is ca. 24 km in diameter, with a lagoon up to ca. 21 m deep (Pirazzoli 1984), with remaining volcanic islands attesting to the impressive size of the past volcano.

From the Gambier complex no data are available on benthic marine diatoms, but some studies do concern the phytoplankton and primary production of its lagoon (Hulot 2019). From the Pitcairn sector (east of Gambier, Fig. 2), no diatom data are available, whereas from Easter Island (Fig. 1) studies on freshwater diatoms were published (Cocquyt 1991, Dumont et al. 1998), and some marine diatoms (*Florella pascuensis* Navarro 2002 and two new marine *Cocconeis*, Riaux-Gobin et al. 2025) were published.

The present report focuses on marine Achnanthales from Gambier (mostly members of the Family Cocconeidaceae) and *Olifantiella* Riaux-Gobin & Compère taxa from Mangareva. The scanning electron microscope (SEM) was the favored instrument for the fine study of these mostly small taxa. Morphological details, such as the ultrastructure of both valvocopulae, only permit to separate close taxa and morphs (or formae). Light microscope (LM) illustrations of several of these Cocconeidaceae, cited -or originally described- from other tropical or subtropical parts of the world are available in the bibliography (i.e. Indian Ocean, Riaux-Gobin et al. 2011c; South Korea, Joh 2021; Gulf of California, Siqueiros Beltrones et al. 2023), bearing in mind that a lot of small taxa only documented using the LM, were unidentified, misidentified or wrongly classified, such as *Cocconeis disculoides* Hustedt (1955, 17) (figs q,e in Siqueiros Beltrones et al. 2023) currently regarded as *Amphicocconeis disculoides* (Hustedt) De Stefano & Marino (2003, 362). Furthermore, some taxa such as *Cocconeis scutellum* Ehrenberg (1838, 194), are now considered to be part of large complexes, composed of numerous entities (including the Loculatae, Riaux-Gobin et al. 2021) only fully identifiable via the SEM [with *C. santandrea* Riaux-Gobin, Witkowski & Bemiasa (2021, 152) present in Mangareva].

During our stay in Mangareva (4–7 Dec. 2021), 15 marine intertidal samples were taken from Gatavake Bay, Rikitea shore line and the Totegegie lagoon shore (Table 1). Furthermore, 5 scrapings of one- and two-year old *Pinctada margaritifera* (Linnaeus 1758), from a pearl oyster farm in Gatavake Bay, along with macroalgae growing on plastic ropes used for the immersion of the grafted oysters, permitted a survey of some benthic subtidal substrates (>15 m deep).

Concurrently, a short technical stop-over on 7 Dec. 2021 in Hao (South Tuamotu, Fig. 1), a 720 km^2 atoll in the mid-south of the Tuamotu alignment (830 km west of Mangareva), permitted enough time to sample the lagoon shore. Hao is a very old structure, taking its origin from the Trail hot spot, with a plate age of 46.3–41.3 Ma (https://earthref.org/SC/SMNT-182S-1409W/). Hao has a unique pass (Kaki pass) connecting the lagoon to the open ocean. Three intertidal samples permitted some remarks on the benthic microflora linked to a true and ancient atoll, compared to that of the younger almost-atoll Gambier. The latter assemblages were also compared to those off Napuka ('Île de la Désolation', north Tuamotu, Fig. 1), an insulated and small atoll (with some hoa, but no navigable pass), that was studied some years ago, using the same methodologies (Riaux-Gobin et al. 2015).

The main goal of this study was to characterize the diatom communities concerning Achnanthales and *Olifantiella* from Mangareva and Hao, mentioning the numerous formae that may characterize a potential endemism. A Non-Metric Multidimensional Scaling (NMDS) applied to our data permitted groups of locations and biotopes to be delineated, and their significance was tested via a PERMANOVA analysis. Finally, the variable degree of potential endemism, with respect to the Gambier island complex position in the SEC and its geographical remoteness from other Polynesian islands is briefly discussed although quantitative data could provide more reliability to these remarks.

Materials and Methods

Several marine locations were sampled off Mangareva (4–7 Dec. 2021: Gatavake Bay, Rikitea near-shore, Totegegie lagoon-shore, Table 1), from diverse intertidal and subtidal habitats [coral sands, macroalgae, short turfs and scrapings of invertebrates (*Holothuria atra* (Jaeger 1833) ('black sea cucumber'), *Rochia nilotica* (Linnaeus 1767) ('commercial top shell' or 'common turban shell'), *Pinctada margaritifera* ('black-lipped pearl oyster')]. Empty tubes of *Teredo* (Linnaeus 1758) ('naval shipworm') on a driftwood in Gatavake Bay, were also scraped. Three intertidal samples were collected from Hao lagoon (7 Dec. 2021, i.e. dead corals and turfs). Raw material (RM) was preserved with 90% ethanol. The SEM was systematically used (ML illustrations of several taxa are available in association with the original descriptions). Every SEM stub was prepared with 2 drops of RM filtered onto a Whatman® Nuclepore filter (1 µm pore size, 13 mm in diameter) and rinsed twice with deionized water (Milli-Q®) to remove salts. Filters were air-dried, mounted onto aluminum stubs, before coating with gold-palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi FEG S4500 model I SEM (cold-tip field-effect source), operated at 5 kV, calibrated with a Silicon grating TGX01 (C2M, Perpignan, France). Diatoms, most often small-sized (10–20 µm in length), were determined in the SEM at high magnification. Due to their overall scarcity in Mangareva, diatoms were not ranked in terms of abundance (supplementary material).

Table 1. Date, GPS, substrate, sample name, location.

Date	Latitude S	Longitude W	Substrate-biotope	Sample Name	Location
04 12 2021	23° 07.053	134° 58.626	green filamentous algae on hard substrate	RIK1	Gatavake Bay
"	23° 07.046	134° 58.618	dark embedding with ?*Rissoa* sp.	RIK2	"
"	23° 07.086	134° 58.636	red calcareous short algae	RIK3	"
05 12 2021	23° 07.039	134° 58.617	short brown algae	RIK4	"
"	"	"	scraping of calcareous tubes of *Teredo* sp. on wood	RIK6	"
05 12 2021	23° 07.068	134° 58.618	scraping of *Holothuria atra,*	RIK5	"
"	"	"	*Halimeda* sp. and sandy substrate	RIK7	"
"	23° 07.234	134° 58.126	*Padina* sp. on hard substrate	RIK8	Rikitea, close cathedral
"	"	"	scraping of *Rochia nilotica*.	RIK9	Rikitea, gendarmerie wharf
"	23° 07.365	134° 58.026	intertidal sandy beach small arborescent macroalgae,	RIK10	Rikitea, shallow pool
06 12 2021	23° 07.038	134° 58.718	short brown and red algae on hard substrate	RIK11	Gatavake Bay
06 12 2021	23° 06.767	134° 59.356	scraping of *Pinctada margaritifera*	RIK12	Pearl oyster farm, Gatavake Bay
"	"	"	"	RIK13	"
"	"	"	"	RIK14 RIK14bis	One year oyster
"	"	"	macroalgae on plastic rope collectors	RIK15	"
"	23° 07.365	134° 58.026	scraping of *Holothuria atra*, near King fish Reserve	RIK16	Rikitea shallow pool
"					
07 12 2021	23° 05.065	134° 53.240	*Colpomenia* sp.	Mang1	Totegegie lagoon shore
"	"	"	*Turbinaria* sp.	Mang2	"
"	"	"	filamentous macroalgae on plastic rope	Mang3	"
07 12 2021	18° 03.800	140° 57.400	Short macroalgal turf on dead coral	Hao1	Hao lagoon shore
"	"	"	dark embedding on dead coral	Hao2	"
"	"	"	dead coral with algal embedding	Hao3	"

In order to visualize the level of similarity among samples or groups of samples as a function of their diatom assemblages, an NMDS was performed using the package 'vegan' in R (Oksanen et al. 2018), by first estimating the Jaccard dissimilarity indices among samples from the abundance matrix described in the previous section. We then performed an NMDS by means of the metaMDS algorithm which tries to find a stable solution from several random starts. Using this approach, we performed the analysis forcing it to 2 dimensions (k = 2) and 1 to 500 random starts. We then performed a PERMANOVA analysis to test for the effect of both biotope and location on the differences in community composition. For this, we used the function adonis2 of the R package "vegan". We used the Jaccard dissimilarity matrix estimated previously, and ran a PERMANOVA. 1000 permutations were used to assess statistical significance.

Note that no quantitative data have been implemented in this study, but our numerous cruises in Polynesia and Melanesia, mainly focused on taxonomy (conducted on diverse archipelagos from 2010 to 2023), were always conducted with the same above-cited methodologies (Riaux-Gobin et al. 2022, Riaux-Gobin et al. 2023). This gave us some basis for comparing the more or less dense diatom assemblages on the sampled substrata. Of course, quantitative data would refine our findings, if they were available.

Typography of authorities for each taxon is intentionally simplified in eluding the first names (full typography available in the original descriptions). As with our previous papers the following acronyms are used in the text, SV (sternum valve), RV (raphe valve), SVVC (sternum valve valvocopula) and RVVC (raphe valve valvocopula).

Results

GENERAL TRENDS

Among the marine benthic microalgae present in Mangareva and Hao lagoon near-shore, some Dinophyceae were present but rare, while coccolithophorids were relatively abundant and diverse (Riaux-Gobin pers. obs.). If compared to assemblages from high Polynesian islands (i.e. Society Archipelago, studied with the same methodology as in the present study), a very low diatom colonization was observed at the two latter islands (Riaux-Gobin pers. obs., no quantitative data). Only qualitative data are reported here. The Achnanthales showed a relatively high species richness (Table 2). The most species-rich samples were from Mangareva (see supplementary material): Rik7 [*Halimeda* (Lamouroux 1812), sp., 13 taxa], Rik10 (undetermined macroalgae, 36 taxa) and Rik16 [epizoic taxa on *Holothuria atra* (Jaeger 1833), 28 taxa]. In contrast, Rik2, a shallow bedrock embedded with blackish cyanobacteria-like organisms, intensively colonized by small gastropods 'minute sea snail' similar to Rissoa (Desmarest 1814). Mang1,2, and 3 from motu Totegegie (north of the reef, Fig. 2 insert), were very poor in diatoms, both qualitatively and quantitatively. A few epiphytic taxa were encountered on Hao1 and Hao3, whereas Hao2 (detrital coral with green embedding, Table 1) was almost diatom-free. From our Hao sampling sites (shallow and more or less detrital coral environments subjected to high insolation and intermittent desiccation), neither holothurians nor large mollusks were present to study epizoic taxa.

The benthic diatom assemblages pertaining to the order Achnanthales (Table 2) were dominated by the genera *Cocconeis* Ehrenberg 1837 (29 taxa), *Planothidium* Round & Bukhtiyarova 1996 (5 taxa) and *Amphicocconeis* De Stefano & Marino 2003 (5 taxa). Several other monoraphid genera were present, but rare.

Amphicocconeis rodriguensis Riaux-Gobin & Al-Handal (*in* Riaux-Gobin et al. 2011a, 181), (Figs 3–6), was recurrently present in a great number of the samples (except in Hao, Totegegie and the subtidal epizoic samples), while absent at previously studied Polynesian sites. Among the genus *Cocconeis*, small taxa bearing similarities with *C. mascarenica* Riaux-Gobin & Compère (2008, 140) were dominant, with several morphs or formae (Figs 7–12, and remarks below). *Cocconeis* sp., a linear-elliptic taxon, probably pertains to the *C. mascarenica* complex (see description below and

Figs 13–18). Several taxa pertaining to the *C. molesta* Kützing (1844, 71) complex, including a relatively large taxon provisionally related to *C. diaphana* Smith (1853, 22), were common in several samples (Figs 19–30; see remarks below).

Cocconeis coronatoides Riaux-Gobin & Romero (in Riaux-Gobin et al. 2011b, 88) was present in almost all samples, with several morphs, among which was a sub-circular and large forma, commonly observed in the South Pacific, along with smaller formae, one of which corresponds to the type (Riaux-Gobin et al. 2010a, figs 1–13 under *Cocconeis coronata*, taxon afterwards renamed as *C. coronatoides* Riaux-Gobin & Romero *nomen novum*, Riaux-Gobin et al. 2011b). This observed high morphological plasticity is possibly linked to the reproductive cycle of the taxon, but it remains to be demonstrated. This taxon differs from *Cocconeis scutellum* Ehrenberg 1838 by several features (Riaux-Gobin et al. 2010a), particularly the robust RVVC with 'irregularly located pegged fimbriae (with an expanded terminal lobe)' (ref. cit.). This taxon was possibly illustrated in Montgomery (1978, pl. 60 E, F, and G) as *Cocconeis* sp. 4.

Some cosmopolitan taxa, commonly encountered in Polynesia, such as *Cocconeis scutellum*, were here restricted to a few localities, while *C. santandrea* Riaux-Gobin, Witkowski & Bemiasa (in Riaux-Gobin et al. 2021, 152), pertaining to the same *C. scutellum* complex and originally described from Marquesas (ref. cit.), was sporadically observed in Mangareva. Several taxa first observed from the Mascarenes (Indian Ocean) were also present in Mangareva, as rare, i.e. *C. borbonica* Riaux-Gobin & Compère (2008, 138), *C. angularipunctata* Riaux-Gobin, Romero, Compère & Al-Handal (2011c, 20), *C. cupulifera* Riaux-Gobin, Romero, Compère & Al-Handal (2011c, 24), *C. sigillata* Riaux-Gobin & Al-Handal (Riaux-Gobin et al. 2011d), and *Achnanthidium glyphos* Riaux-Gobin, Witkowski & Compère (2010b, 161) [with a morph very close to the type, and a second one with a double SV marginal row of oblong areolae in place of only one row in the original description (Riaux-Gobin et al. 2010b, figs 31–33)]. Among the observed taxa (Table 2), some were rare, including a taxon close to *Majewskaea istriaca* Van de Vijver, Robert, Witkowski & Bosak (in Van de Vijver et al. 2020, 114), also close to the genus *Scalariella* Riaux-Gobin (i.e. *S. oblongella* Riaux-Gobin & Witkowski and *S. pseudofallacia* (Witkowski, Metzeltin & Lange-Bertalot) Riaux-Gobin & Witkowski *in* Riaux-Gobin et al. 2012b). More observations, i.e. on the RV of the latter taxon, will permit a better classification.

Among these assemblages (Table 2), some taxa have an intricate history which requires taxonomic remarks:

COCCONEIS MASCARENICA COMPLEX AND *COCCONEIS* SP.

A small-sized taxon with strong similarities to *Cocconeis mascarenica* Riaux-Gobin & Compère (2008, figs 33–40, 48–51), here listed as *C.* cf. *mascarenica* (Table 2), showed several morphs, i.e. with SV apical rows of areolae (Fig. 12), one apical and marginal row of longer SV areolae (Fig. 10 arrow), and dense (up to 6) and dash-like SV areolae with no particular arrangement (Figs 7, 9, 11). The above mentioned morphs have their valvocopulae devoid of true fimbriae (RVVC, Fig. 8 arrowhead; SVVC, Fig. 11 arrowhead). Note the presence of an RV marginal hyaline rim (Fig. 8 arrow). All these morphs have a largely elliptic valve shape and biometrics similar to what was originally observed (Table 3).

From a pearl oyster farm in Gatavake Bay (owner Michel Teakarotu), *Cocconeis* sp. (Table 3, Figs 13–15) was found as subtidal, epizoic on *Pinctada margaritifera*, also present on ropes lying at the same depth (i.e. 15 m, Rik15). This taxon had small dimensions, an oblong-elliptic to linear valve shape (Figs 13–14), blunt apices, measurements close to that in the *C. mascarenica* type (Table 3). *Cocconeis* sp. had short and dense dash-like SV areolae (up to 6 per stria, with no axial alignment), SV hymenes with marginal short slits (Fig. 15), and elliptic SV sternum. Valves measured 8.0–9.4 µm in length and 3.5–4.3 µm in width, with 32–36 SV striae in 10 µm, regularly spaced (no areolae on SV apex), and 39–45 RV striae in 10 µm, regularly spaced, with a marginal hyaline area and low

Table 2. Marine Achnanthales and *Olifantiella* taxa, from Mangareva and Hao (2021). See full data, with presence-absence, biotopes and location, presented as 'supplementary material'.

Taxon	**acronym**
Achnanthales	
Achnanthes cf. *brevipes* Agardh	acbre
Achnanthidium glyphos Riaux-Gobin, Compère & Witkowski	acgly
Achnanthidium glyphos morph	acgly2
Achnanthidium pseudodelicatissimum Riaux-Gobin, Witkowski & Compère	acpse
Achnanthidium sp. aff. *Achnanthes fogedii* Håkansson	acfog
Amphicocconeis clypeus Riaux-Gobin & Witkowski	amcly
Amphicocconeis cf. *mascarenica* Riaux-Gobin & Compère	ammas
Amphicocconeis rodriguensis Riaux-Gobin & Al-Handal	amrod
Amphicocconeis ruatara Riaux-Gobin	amrua
Amphicocconeis sp.	amsp
Astartiella sp.	assp
Cocconeis angularipunctata Riaux-Gobin, Romero, Compère & Al-Handal	coang
Cocconeis cf. *borbonica* Riaux-Gobin & Compère	cobor
Cocconeis carinata Riaux-Gobin, Ector & Witkowski	cocar
Cocconeis coralliensis Riaux-Gobin & Compère	cocor
Cocconeis coronatoides Riaux-Gobin & Romero 'type'	cocid
Cocconeis coronatoides discoid morph	cocid2
Cocconeis cupulifera Riaux-Gobin, Romero & Al-Handal	cocup
Cocconeis cf. *delapunctata* Hohn	codel
Cocconeis cf. *diaphana* W.Smith	codia
Cocconeis distans Gregory	codis
Cocconeis guttata Hustedt & Aleem	cogut
Cocconeis cf. *geometrica* Riaux-Gobin, Romero, Compère & Al-Handal	cogeo
Cocconeis heteroidea Hantzsch	cohet
Cocconeis margaritata Riaux-Gobin & Al-Handal	comar

Taxon	**acronym**
Cocconeis mascarenica Riaux-Gobin & Compère	comas
Cocconeis mascarenica forma	conew
Cocconeis cf. *molesta* Kützing	comol
Cocconeis paucistriata Riaux-Gobin, Romero, Compère & Al-Handal	copau
Cocconeis peltoides Hustedt	copel
Cocconeis peltoides var. *archaeana* Riaux-Gobin & Compère	coarc
Cocconeis placentula Ehrenberg complex	copla
Cocconeis pseudodiruptoides Foged	copsd
Cocconeis pseudograta Hustedt	copsg
Cocconeis pseudomarginata Gregory	copsm
Cocconeis santandrea Riaux-Gobin, Witkowski & Bemiasa	cosan
Coccconeis scutellum Ehrenberg	coscu
Cocconeis sigillata Riaux-Gobin & Al-Handal	cosig
Cocconeis suzukii Riaux-Gobin, Compère, Coste, Straub & Taxböck	cosuz
Cocconeis sp. 5 (= sp. 4 *in* Riaux-Gobin et al. 2015c)	cosp5
Madinithidium flexuistriatum (Riaux-Gobin, Compère & Witkowski)	mafle
Madinithidium scalariforme (Riaux-Gobin, Compère & Witkowski)	masca
?Majewskaea Van de Vijver, Robert, Witkowski & Bosak	maj
Planothidium cf. *delicatulum* (Kützing) Round & Bukhtiyarova	pldel
Planothidium mathurinense Riaux-Gobin & Al-Handal	plmat
Planothidium rodriguense Riaux-Gobin & Compère	plrod
Planothidium sp1 oblong without fascia	plsp1
Planothidium sp2 elliptic sternum	pls2
Schizostauron citronella (Mann) Górecka, Riaux-Gobin & Witkowski	sccit
Olifantiella	
Olifantiella cf. *rodriguensis* Riaux-Gobin	olrod
Olifantiella pilosella Riaux-Gobin	olpil
Olifantiella muscatinei (Reimer & Lee) Van de Vijver, Ector & Wetzel	olmus

helictoglossae. Figs 17–18 are possibly illustrating the RV of C. sp., with no RV central area, RVVC with undulated edge and no fimbria (Fig. 17 insert, twin arrowheads), but with the SVVC not observed. *Cocconeis* sp. was rare and observations on several characteristics are still lacking to finalize its exact taxonomic position. This taxon may pertain to the *C. mascarenica* complex, but with a subtidal ethology. One SV found in Hao (Fig. 16, intertidal locality) had some similarities with the SV of C. sp., but the adjoining RV was not found. There are some similarities between *C.* sp. and *C. neothumensis* var. *marina* De Stefano, Marino & Mazella (De Stefano et al. 2000, Sar et al. 2003), but the latter is less linear, with more acute apices, and RV striae (26 to 32 in 10 µm, ref. cit.) denser than the SV striae (20 to 26 in 10 µm, ref. cit.). Also there are some similarities with the SV of *C. coralliensis* Riaux-Gobin & Compère 2008, with lower stria density (36–40 in *C. coralliensis* versus 32–36 in *C*. sp.), round SV endings (versus sharp in *C. coralliensis*), a lower number of areolae per stria, no areolae on apices versus areolae perpendicular to the margin on apices in *C. coralliensis*, and a SV sternum slightly elliptical in *C*. sp., versus narrow and straight in *C. coralliensis*. Note that the RV of *C. coralliensis* has no marginal hyaline area (ref. cit.).

Remarks: *Cocconeis mascarenica* (Riaux-Gobin & Compère 2008) was originally compared to *C. neodiminuta* Krammer & Lange-Bertalot 1991 and to *C. neothumensis* Krammer 1990, but the RV of *C. neothumensis* (Krammer 1990, fig. 34) was also attributed to *C. neodiminuta* (Krammer & Lange-Bertalot 1991, pl. 55, fig. 3). Furthermore, the shape of the SV areolae in *C. mascarenica* differs from that of *C. neodiminuta* (ref. cit., pl. 55, fig. 1) in being much shorter, and the SV sternum in *C. mascarenica* being narrow-straight in place of largely elliptical ones. Note that a picture illustrating *C. neothumensis* in Krammer (1990, fig. 39) was also used to illustrate *C. neodiminuta* by Krammer & Lange-Bertalot (1991, pl. 55, fig. 1), causing taxonomic confusion between *C. mascarenica* and the two latter taxa. Furthermore, the freshwater taxa *C. neodiminut*a and *C. neothumensis* have dissimilar RV and SV stria densities, while *C. mascarenica* has the same stria density on both valves (see discussion in Riaux-Gobin et al. 2018). Also, there are some similarities with the later described *C. neothumensis* var. *marina* (De Stefano et al. 2000, figs 53–65), but with differences (see above remarks). In the original description of *C. mascarenica* off Mascarenes, the taxon demonstrated an obvious phenotypic plasticity, with two morphs described from Rodrigues (morphs 1 and 2 in Riaux-Gobin et al. 2011c). The *Cocconeis mascarenica* complex probably includes several species that can only be separated via genetics.

In addition, *Cocconeis mascarenica* and *C*. cf. *mascarenica* and all the above-mentioned morphs present in Mangareva (Tables 2–3, Figs 7–18) have some similarities with *C. placentula sensu lato* (as referred to by Potapova & Spaulding 2013), but with overall smaller valve dimensions, higher stria densities on both valves, and valvocopulae without conspicuous fimbriae [*C. placentula sensu lato* (see ref. cit. above) has 20–24 striae in 10 µm on RV, and 15–25 on SV]. Note that the bibliography of the *C. placentula sensu lato* complex is complicated, with several new taxa that can only be distinguished through SEM, such as the recently described *C. fetscheriana* Stancheva (2022, 128). The morphological plasticity in such taxa can also be *pro parte* imputed to the reproductive stages of the taxon (see Jahn et al. 2020), rendering cultures and genetics essential in definitively splitting taxa.

COCCONEIS MOLESTA KÜTZING COMPLEX AND *COCCONEIS* CF. *DIAPHANA* W.SMITH

A rare and small epiphytic taxon, with a round-elliptic shape and a reduced RV fascia (Figs 21–22 twin arrowheads), is closely related to *C. dirupta* Gregory (see Kobayasi & Nagumo 1985, fig. 19; Riaux-Gobin et al. 2016, figs 35–38), while lacking the characteristic bi-lanceolate large SV sternum, more delicate SV areolae, and denser SV and RV stria (Table 3). Note the strongly sigmoid RV in *C. dirupta* (refs cit.), while our taxon (Figs 19–22) has helictoglossae only slightly bent in the opposite direction, such as observed in the *C. molesta* type (Riaux-Gobin et al. 2016). The latter taxon from Mangareva (Figs 19–22) is here provisionally assigned to *C. molesta* Kützing.

An oblong-elliptic and relatively large taxon (Figs 23–30, Table 3), was common in the subtidal samples Rik13, Rik15 and Rik16, and characterized by its SV short areolae arranged in a regular decussate pattern, with apical rows arranged along a 135° grid-pattern (Fig. 27, white lines). The open SVVC (Fig. 29, ellipse) has a smooth edge (Fig. 30, arrowhead). The SV sternum is narrow, irregular, concave, with a reduced to absent central area (Fig. 27 arrowhead). SV striae are more or less parallel in median valve and abruptly radiate near the apices (Fig. 28 arrowhead). At the apices, a marginal row of SV areolae are perpendicular to the margin. The RVVC was not observed. The RV fascia is narrow and straight, reaching the margins, and central raphe endings are close to each other (Fig. 24). Helictoglossae slightly curved (Fig. 26). RV areolae present at the apices (Figs 23, 25–26). This taxon is provisionally assigned to *C.* cf. *diaphana* Smith 1853 (see Remarks).

Remarks: The latter taxon (Figs 23–30) has affinities with *Cocconeis diaphana* Smith var. *diaphana*, except for a RV fascia reaching both margins, and striae on both valves much denser than in the *C. diaphana* var. *diaphana* type (BM 23161, *in* Riaux-Gobin et al. 2016). We can also compare our images with those illustrating the iso-lectotype of *C. diaphana* Smith var. *diaphana* (mica labelled as *Cocconeis diaphana* n. sp., Jersey, Aug. 14 1852, deposited in the Van Heurck collection in Meise, in Riaux-Gobin et al. 2016, figs 21–26). In the latter taxon, the RV and SV stria densities are also dissimilar, being less dense than in the Mangareva taxon (Table 3). Furthermore, the SV and RV striae (in the iso-lectotype) are often marginally dichotomous while uniseriate until the margin in the Mangareva taxon. The latter also has some affinities with *Cocconeis molesta*, except for its larger dimensions, oblong shape, and RV fascia expanding up to both margins. Also, there are some affinities with *C. molesta* var. *crucifera* Grunow *in* Van Heurck (1880, pl. 30), as illustrated by Kobayasi & Nagumo (1985, figs 1–12), and by De Stefano et al. (2000, figs 33–36), but in the latter taxon, the RV fascia is much shorter, and the valve shape is less oblong than in the Mangareva taxon. Note that *C. molesta* var. *crucifera* was proposed as a synonym of *C. molesta* (Riaux-Gobin et al. 2016).

PLANOTHIDIUM ROUND & BUKHTIYAROVA

Planothidium was the second most species-rich genus in the Achnanthales off Mangareva (Table 2), with two small taxa closely related to species first described from the Indian Ocean: *P. mathurinense* Riaux-Gobin & Al-Handal (in Riaux-Gobin et al. 2012a) (Figs 31–34) and *P. rodriguense* Riaux-Gobin & Compère (ref. cit.) (Figs 35–40). *Planothidium delicatulum* (Kützing) Round & Bukhtiyarova 1996 (see also e.g. Witkowski et al. 2000, Bahls et al. 2018, Van de Vijver et al. 2018b) was rare in several samples. Several rare and small-sized taxa, also pertaining to *Planothidium*, were insufficiently documented to be definitively classified (Table 2).

OLIFANTIELLA RIAUX-GOBIN & COMPÈRE

Olifantiella cf. *rodriguensis* Riaux-Gobin (*in* Riaux-Gobin & Al-Handal 2012, Riaux-Gobin 2015) was present in Rik16 (east Mangareva), epizoic on *Holothuria atra*. The latter taxon was also present in Rik10 (same site, intertidal sand and macroalgae). *Olifantiella* cf. *rodriguensis* was rare, with no internal SEM view available to check for its buciniportula. A mucus thread was observed through the external opening of the buciniportula, confirming previous remarks on a possible physiological role for this process, in the relationships between the cell and the external environment (Riaux-Gobin & Al-Handal 2012). A second taxon, *O. pilosella* Riaux-Gobin (*in* Riaux-Gobin & Al-Handal 2012), with all original morphological characters, was found as epizoic in Rik16. A third taxon, *Olifantiella muscatinei* (Reimer & Lee) Van de Vijver, Ector & Wetzel (2018a, 1), was observed as an epiphyte in Rik4. Note that no *Olifantiella* specimens were observed in the holothurian scraping Rik5 (west Mangareva).

Table 3. Morphometrics of some discussed taxa
* From Mangareva (SEM), **,*** type [**Riaux-Gobin et al. 2016, ***Riaux-Gobin et al. 2008)]
Stria densities and axial rows in 10 µm, length & width in µm.

Taxon	Length	Width	L/l	RV str.	SV str.	SV axial rows	RV fascia
**Cocconeis* cf. *mascarenica* (n=27)	7.2	4.1	1.76	37.8	40.6	not always	no
****Cocconeis mascarenica* (n=31)	6.7	3.8	ca.1.7	38	25-35	not always	no
**Cocconeis* sp. (n=8)	7.8	3.8	2.08	38.8	37.2	no	no
**Cocconeis* cf. *diaphana* (n=12)	14.4	6.6	2.20	39.8	52.8	decussate pattern	up margins
**Cocconeis* cf. *molesta* (n=5)	9.1	6.6	1.38	46.9	52.8	no	half valve
***Cocconeis molesta* Kütz. BM 18381 (n=4)	LM	16.4	9.7	1.96	ca. 30 >30	in zig-zag 22-23	<half valve
***Cocconeis diaphana* W.Sm. var. *diaphana* BM 23161 (n=11) LM	33-42	21-26	1.65	25	26	in zig-zag ca. 23	short, elliptic
***Cocconeis diaphana* W.Sm. Isolectotype SEM	ca. 38	ca. 23	1.65	22	35	unclear	short, elliptic
***Cocconeis dirupta* W.Greg. BM 1420 (n=16) LM	18-37	17-31	1.12	18.9	16.6	ca. zig-zag	<half valve

EPIZOIC DIATOM ASSEMBLAGES

Rik5 and Rik16 were both cumulative scrapings of several individuals pertaining to a well circumscribed population of *Holothuria atra* collected in small areas (ca 3 m2), 1) from Gatavake Bay (west Mangareva, Rik5), 2) from Rikitea nearshore (east Mangareva, Rik16). The two epizoic assemblages were highly dissimilar (Table 2), with a higher number of taxa in Rik16 (Table 2). Note that the assemblage in Rik7 (sediments close to the location of the holothurian scraping Rik5) and in Rik10 (sediments close to the holothurian scraping Rik16), are also highly different from what was found in each holothurian's population. Some taxa present on the holothurians were absent from the nearby environment and *vice versa*, but the species richness is similar among epizoic and non-epizoic assemblages, being higher for Rik16–Rik10 (Rikitea environment) than for Rik5–Rik7 (Gatavake Bay). There were no diatom taxa unique to a particular epizoic population, or particularly dominant with regards to its abundance in the nearby substrates.

From a shallow and well-oxygenated zone (exposed intertidal zone), Rik9, a scraping of several living specimens of *Rochia nilotica* (Syn.: *Trochus niloticus* Linnaeus 1767), (ca. 5 cm in length, colonized by diminutive filamentous algae and encrusting red algae, probably pertaining to Corallinaceae, Maggy Nugges comm. pers.), was quantitatively diatom-poor, but with the presence of large diatoms such as *Achnanthes* cf. *brevipes* Agardh 1824 and *Cocconeis pseudodiruptoides* Foged (1975, 18). Note that the latter taxon was only observed in Rik9 (see supplementary material), possibly linked to the ethology of this mollusk migrating from intertidal to subtidal substrates, whereas the other studied samples (except for the pearl oyster farm samples) were strictly intertidal (<50 cm deep).

The scraping of empty green-colored tubes of *Teredo* sp. (probably colonized by unicellular chlorophytes) was almost void of benthic diatoms. This driftwood was subjected to drastic conditions such as high light exposure and intermittent desiccation.

The scrapings of living two-year old *Pinctada margaritifera* ('Black-lipped Pearl Oyster'), before grafting (before nucleus transplant) (Rik12–14, Table 2), as well as a one-year old individual (Rik14bis), were surprisingly diatom poor, quantitatively and qualitatively, whereas the macroalgae living on mooring ropes at the same depth (Rik15) were colonized by a diverse array of diatoms, apparently absent from the oyster's fouling. This low diatom colonization may be related to the fact that the oysters were cleaned every 3 months (via a passage to kärcher, followed by scraping with a knife), which drastically lowers the biofouling potentially detrimental to the oyster growth. This biofouling was composed of macroalgae and small fauna (i.e. bryozoans, ascidians, sponges, see also Lacoste et al. 2021) potentially colonized by diatoms. Note that the subtidal assemblages from the pearl oyster farm (epizoic as well as epiphytic, Table 2) seem to be characterized by the presence of taxa absent in intertidal samples from the same bay, such as *Schizostauron citronella* (Mann) Górecka, Riaux-Gobin & Witkowski (*in* Górecka et al. 2021, 1480), *Cocconeis pseudomarginata* Gregory (1857, 492) and *Cocconeis peltoides* var. *archaeana* Riaux-Gobin & Compère (*in* Riaux-Gobin et al. 2011d, 330).

NMDS ANALYSES

In order to visualize the level of similarity among samples or groups of samples as a function of their diatom assemblages, an NMDS analysis was carried out. The full data are given as supplementary material. Note that the NMDS is testing the grouping of samples in relation to their assemblage compositions, and not whether a certain taxon is a reflection of a particular biotope or ethology. The analysis illustrated the relationships between samples (Fig. 41).

The epizoic assemblages (blue points in Fig. 41, upper diagram) slightly group (but not significantly, see PERMANOVA results below), while the other assemblages (epiphytic and epipsammic taxa) have no particular grouping (Fig. 11, upper diagram). Concurrently, the different locations and bathymetries appear to have a significant influence on the assemblages (see PERMANOVA results below) (Fig. 41, bottom diagram), with Hao atoll and Togegegie motu grouping together negatively, possibly due to the low species richness and particular calcic environment. The subtidal samples group positively on the left of the analysis (violet points, Fig. 41 bottom diagram) with a particular colonization in terms of species, as noted above in, for example *Schizostauron citronella* (Mann) Górecka, Riaux-Gobin & Witkowski and also *Cocconeis coronatoides* Riaux-Gobin & Romero 'discoid morph' (acronym cocid2, see supplementary material). The subtidal epizoic assemblage was slightly different from that growing as non-epizoic at the same depth (see supplementary material and violet point), but still grouping with the other subtidal samples. The samples from Gatavake Bay (red points, bottom diagram) group slightly differently from the samples from the Rikitea shore line (blue points).

The PERMANOVA results provide a statistical basis for the above remarks, and indicate that the biotope (upper diagram) did not have a significant effect on the community dissimilarity (Permanova R2 = 0.10, F = 1.14, 2df, p-value = 0.262). In contrast, the effect of the location (bottom diagram) was statistically significant (Permanova R2 = 0.42, F = 3.083, 2df, p-value = 0.001). Furthermore, results from an ad-hoc pairwise comparison among locations (excluding location H - Hao atoll- because of its small sample size), indicated that site S (subtidal samples, pearl oysters) was statistically significant from the rest (p-values < 0.01), site R (Rikitea) was statistically different from sites G (Gatavake Bay) and M (Totegegie motu) (p-value <0.01), and sites G and R were also statistically different (p-value <0.01).

Discussion

INDO-PACIFIC DISTRIBUTION OF MOST ACHNANTHALES AND *OLIFANTIELLA* SPECIES FOUND IN GAMBIER

The Achnanthales and *Olifantiella* found off Mangareva, Totegegie and Hao were dominated by Indo-Pacific to probably pantropical taxa, confirming the tropical ubiquity of a great number of these small-sized benthic diatoms. These observations also confirm the overall scarcity of several of them, among which *Olifantiella* was only revealed by careful SEM examination.

SPECIFICITIES OF GAMBIER, WITH RARE TAXA ABSENT ELSEWHERE IN THE SOUTH PACIFIC AND ABSENCE OF SOME OTHERS, ONLY PRESENT IN NORTH TUAMOTU

Several taxa from Gambier were previously rarely encountered in the South Pacific during our last 12-year survey (Riaux-Gobin et al. 2022, Riaux-Gobin et al. 2023): i.e. *Amphicocconeis rodriguensis* was frequent in Mangareva whereas rare in Melanesia (i.e. only reported from New Caledonia, Riaux-Gobin et al. 2022) and absent from French Polynesia (ref. cit.). *Planothidium mathurinense* Riaux-Gobin & Al-Handal and *P. rodriguense* Riaux-Gobin & Compère were also found to be relatively numerous in Gambier while rarely observed during our Polynesian survey. *Cocconeis santandrea* Riaux-Gobin, Witkowski & Bemiasa was present in Mangareva while previously only listed from Rapa (Austral) and Nuku Hiva (Marquesas, from where it was first described). Several morphs, along with *Achnanthidium glyphos*, a morph with double marginal SV areolation, and two taxa here provisionally listed under *Cocconeis* sp. and *C.* cf. *diaphana* were unique to the East Pacific sector. On the other hand, several taxa found in Napuka (insulated small atoll of North Tuamotu, Fig. 1, with restricted hoa and a probable low renewal of the lagoon water masses) are absent from Gambier [i.e. *Cocconeis tuamotuana* Riaux-Gobin, Compère & Jordan (2015, 191) and *C. napukensis* Riaux-Gobin, Compère, Coste, Straub & Taxböck (2014, 2014)].

POSSIBLE INFLUENCE OF THE GEOLOGIC HISTORY ON THE DIATOM DISTRIBUTION IN ATOLLS AND ALMOST-ATOLLS

The diatom assemblages found in Hao were quantitatively (to be confirmed) and qualitatively very poor, but our samplings are too scarce to make definitive conclusions. Nevertheless, our investigation on the lagoon of Napuka (a small North Tuamotu atoll, with no navigable pass and a probable low oceanic influence), also shows a very low benthic diatom colonization, with proportionally a high number of newly described taxa (see above remarks). On atolls, the benthic primary production may be driven by microphytes other than diatoms, such as Dinophyceae, coccolithophorids (found abundantly in Hao samples) or green unicellular chlorophytes. During a survey on Takapoto (Tuamotu), Sournia (1976) found a high benthic primary production attributed to the symbiotic flora of sand foraminifera (see taxonomic position of these diverse symbiotic algae *in* Hallock 1999).

The Gambier island complex benefits from protected hydrological conditions due to a barrier reef around more than 50% of the system, and concurrently of volcanic silicic geochemical influences, along with a typically calcic influence from the reef. Note that the Gambier island complex is largely open to the ocean in its southern part, probably giving it a particular hydrology and water renewal (Serge Planes pers. comm.).

Nevertheless, even if the lagoon benefits from the influence of the remaining high islands and from a high water renewal, the benthic diatoms were found to be quantitatively quite poor in Mangareva, as was also the case on true atolls such as Napuka, Takaroa and Takatopo (Tuamotu Archipelago) (Riaux-Gobin pers. obs.).

EPIZOIC DIATOMS ON *HOLOTHURIA ATRA*, COMMENSALISM OR OPPORTUNISM?

As already documented, the teguments of sea cucumbers such as *Holothuria atra* are colonized by benthic diatoms (i.e., Riaux-Gobin & Witkowski 2012). The holothurian teguments may act as a protected area, with low predator pressure, benefiting from favorable conditions (good water renewal and optimal light exposure). *Olifantiella* taxa were observed in one of these epizoic assemblages, and concurrently in the surrounding environment, so is possibly linked to the locality more than to the fact that the biotope was epizoic or epiphytic. No taxa were unique to each epizoic population, or particularly dominant if one considers its abundance in the nearby substrates (contrarily to what was found in Juan de Nova, where the genus *Cocconeiopsis* seemed only present as epizoic on *Holothuria*, see Riaux-Gobin & Witkowski 2012). It can only be referred to as a protected area, with no dominance of a particular taxon. The latter taxa may take advantage of low predation, a relatively protected surface, good oxygenation, along with shelter and a good nutrient supply due to the discontinuous displacement of their host. These epizoic assemblages may only be opportunistic and probably not really commensal.

Conclusion

The benthic diatom assemblages off Mangareva and Totegegie had a relatively low species richness and lack several species present at other islands from French Polynesia. Nevertheless, these assemblages were more species-rich than those reported from Marquesas (Riaux-Gobin pers. obs.), where there is no active coral reef but a 90 m-deep flooded fossil reef, with diatoms found as relatively rare, possibly due to a complex food web, where benthic diatoms are a less important trophic link in the food chain.

The colonization by diatoms, in terms of biomass, seems relatively low off Mangareva, whatever the substrate (Riaux-Gobin pers. obs.), while largely open to the ocean, with a good renewal of nutrients, and volcanic islets that may be a source of silica. Quantitative data would help to confirm these subjective findings.

Following our first results on Hao, this atoll seems diatom poor as was previously noted on Napuka lagoon, a small Tuamotu atoll with only intermittent access to the open ocean. On the other hand, the presence of rare and new diatom taxa may possibly be higher on true atolls (Riaux-Gobin pers. obs.), due to factors that still need to be clarified.

The Gambier island complex is located south of the Tuamotu alignment, in the southern sector of the SEC, a subtropical current characterized by a north-western flow. Thus, Gambier may experience low influence from other islands, except from the close-by Pitcairn and Temoe Islands, from where no data on diatoms are available. In this context, the poorly-known marine benthic diatom assemblages of Easter Island, located 2000 km to the east, should warrant more dedicated investigations (results obtained after our 2023 Easter Island samplings will possibly give some indications).

There is actually little evidence (without solid proof) of endemism in marine benthic diatoms even at a large scale, while numerous papers discuss the biogeography of freshwater diatoms, particularly Austral and Antarctic taxa at high latitudes (i.e., Vyverman et al. 2010). The notion of endemism in diatoms is also hypothesized for some isolated islands such as New Caledonia (Moser et al. 1998), Madagascar (Metzeltin & Lange-Bertalot 2002), or in larger sectors such as the Australasia province (Australia, New Zealand *in* Sabbe et al. 2001). Diatoms are also cited as good paleoceanographic indicators (Cremer et al. 2005), proving that diatom assemblages are a function of the environment, that can act as proxy recorders of the interglacial/glacial cycles. Furthermore, the studies on cryptic taxa are currently booming, with spectacular advances in genetics (see Pinseel et al. 2019), which will be able, when fully applied to marine environments, to alter the approach we have to endemism in benthic marine eukaryotes.

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Supplementary Table. Full data concerning marine Achnanthales and *Olifantiella* taxa from Mangareva and Hao (sampling 2021, see Table 1), with Presence (P) versus absence. Biotope: epizoic (Z), epiphytic (E), Diverse (epiphytic & epipsammic, D). Location: Hao lagoon intertidal (H); west Gatavake bay, Mangareva intertidal (G); east Gatavake bay, Rikitea intertidal (R); Totegegie motu lagoon intertidal (M); west Gatavake bay oyster farm, subtidal (S). See full names in Table 2.

Location	**H**	**H**	**H**	**G**	**G**	**G**	**G**	**G**	**G**	**G**	**R**	**R**	**R**	**G**	**S**	**S**	**S**	**S**	**S**	**R**	**M**	**M**	**M**
	Hao	**Hao**	**Hao**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik**	**Rik1**	**Rik1**	**Rik1**	**Rik1**	**Rik1**	**Rik14bi**	**Rik1**	**Rik1**	**Mang**	**Mang**	**Mang**
Sample	**1**	**2**	**3**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**s**	**5**	**6**	**1**	**2**	**3**
Biotope																							
Acronym	**E**	**D**	**D**	**E**	**D**	**E**	**E**	**Z**	**D**	**E**	**E**	**Z**	**E**	**E**	**Z**	**Z**	**Z**	**Z**	**E**	**Z**	**E**	**E**	**E**
acbre						P	P			P		P	P	P									
acgly								P					P							P			
acgly2													P							P			
acpse													P			P							
acfog													P			P							
amcly													P							P			
ammas	P		P					P														P	
amrod				P		P		P		P	P		P	P					P	P			
amrua													P										
amsp									P					P						P			
assp										P			P		P				P				
coang							P							P						P			
coarc														P									
cobor										P			P										
cocar												P			P					P			
cocor									P				P						P	P			
cocid										P			P		P								
cocid2										P					P	P	P		P	P			
cocup																				P			
codel										P									P	P			
codia										P	P		X		P	P			P	P			
codis	P																						
cogut								P					P										
cogeo							P																
cohet											P	P	P							P			
comar													P	P									P
comas			P	P			P	P				P	P							P	P		
conew			P									P	P	P	P				P	P			
comol													P						P				
copau										P			P							P			
copel													P							P			
copla	P									P			P		P				P	P			
copsd												P											
copsg													P							P			
copsm																			P				
cosan											P		P										
coscu					P	P		P		P		P		P					P	P			
cosig				P	P	P	P		P				P	P						P			
cosuz							P						P	P						P		P	
cosp5													P							P			
mafle													P										
masca													P			P							
maj													P						P	P			

Supplementary Table (Cont'd).

Location	**H**	**H**	**H**	**G**	**G**	**G**	**G**	**G**	**G**	**G**	**R**	**R**	**R**	**G**	**S**	**S**	**S**	**S**	**S**	**R**	**M**	**M**	**M**
Sample	**Hao1**	**Hao2**	**Hao3**	**Rik1**	**Rik2**	**Rik3**	**Rik4**	**Rik5**	**Rik6**	**Rik7**	**Rik8**	**Rik9**	**Rik10**	**Rik11**	**Rik12**	**Rik13**	**Rik14**	**Rik14bis**	**Rik15**	**Rik16**	**Mang1**	**Mang2**	**Mang3**
Biotope																							
Acronym	**E**	**D**	**D**	**E**	**D**	**E**	**E**	**Z**	**D**	**E**	**E**	**Z**	**E**	**E**	**Z**	**Z**	**Z**	**Z**	**E**	**Z**	**E**	**E**	**E**
pldel						P	P	P	P	P			P										
plmat				P		P			P	P			P	P						P			
plrod													P	P						P			
plsp1													P										
pls2													P										
sccit															P		P	P	P				
olrod													P							P			
olpil																				P			
olmus							P																

Figures (1-41)

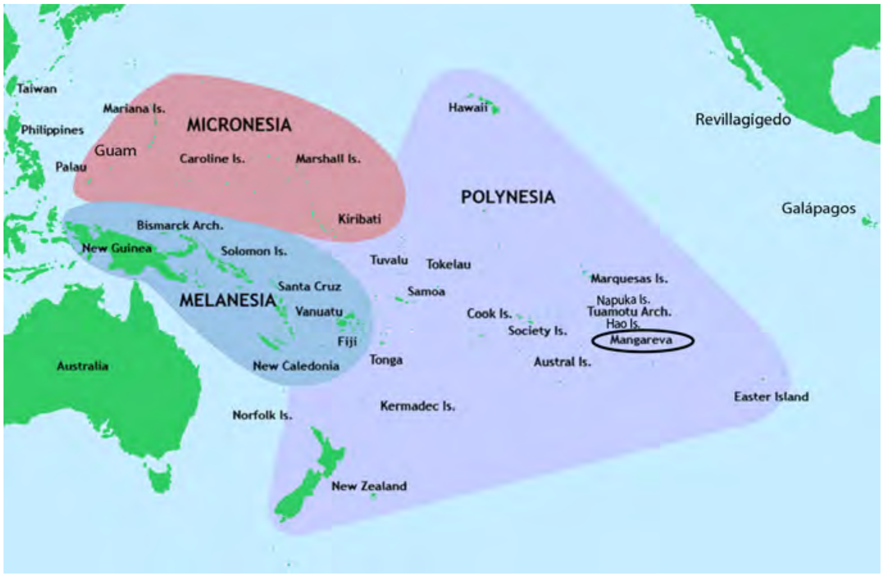

Fig. 1. Position of Mangareva (ellipse) in the South Pacific, small volcanic island pertaining to the Gambier island complex (almost-atoll, Polynesia area). Modified from ‘Pacific Ocean culture areas’: https://upload.wikimedia.org/wikipedia/commons/thumb/a/aa/Pacific_Culture_Areas.png/800px-Pacific_Culture_Areas.png, no copyrights

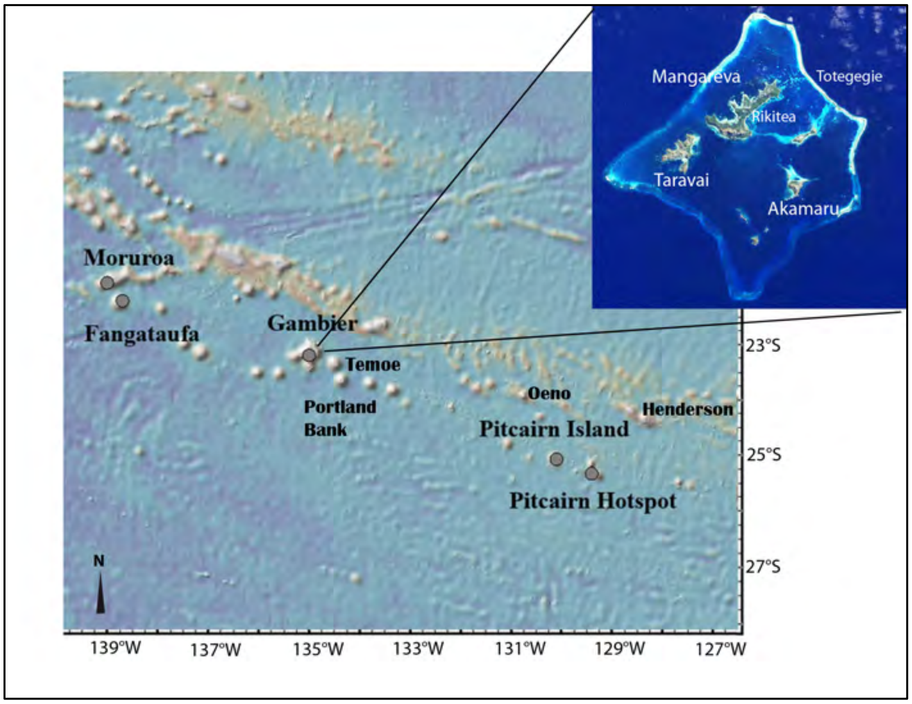

Fig. 2. Gambier and surrounding island alignments (modified from a photo available under CC-BY-SA-4.0 license. Credit: Ryan W.B.F., S.M. Carbotte, J.O. Coplan, S. O'Hara, A. Melkonian, R. Arko, R.A. Weissel, V. Ferrini, A. Goodwillie, F. Nitsche, J. Bonczkowski & R. Zemsky). In insert, Gambier almost-atoll with name of the largest islets, and motu Totegegie (modified from a NASA photo, public domain, http://earthobservatory.nasa.gov/Study/Coral/Images/gambier.jpg).

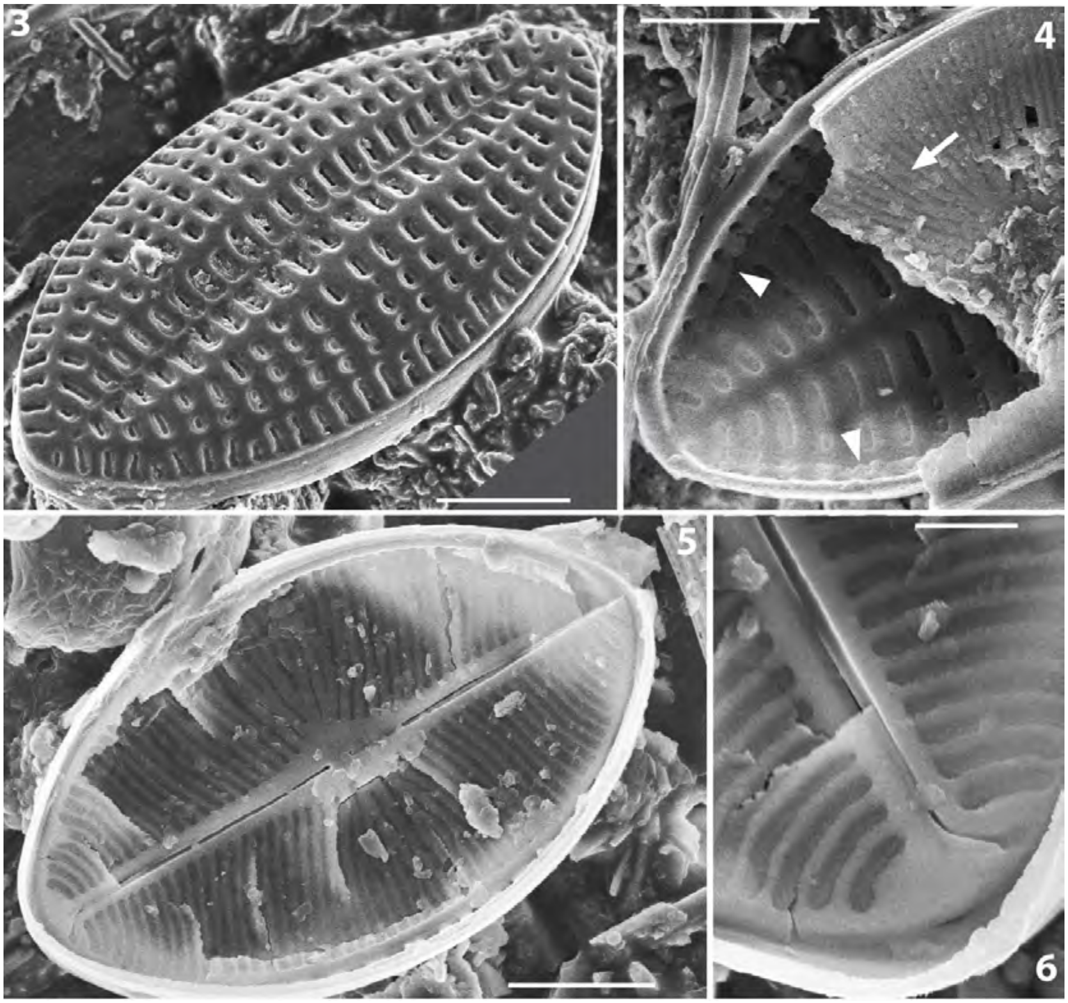

Fig. 3–6. *Amphicocconeis rodriguensis* Riaux-Gobin & Al-Handal. SV external side (3), both valves with detail of the narrow RVVC (4 arrow heads) and RV narrow macro-areolae (4 arrow), RV external side (5), detail of the external RV apex with the curved raphe ending. Scale bars: 3 µm (3, 4), 2 µm (5), 500 nm (6).

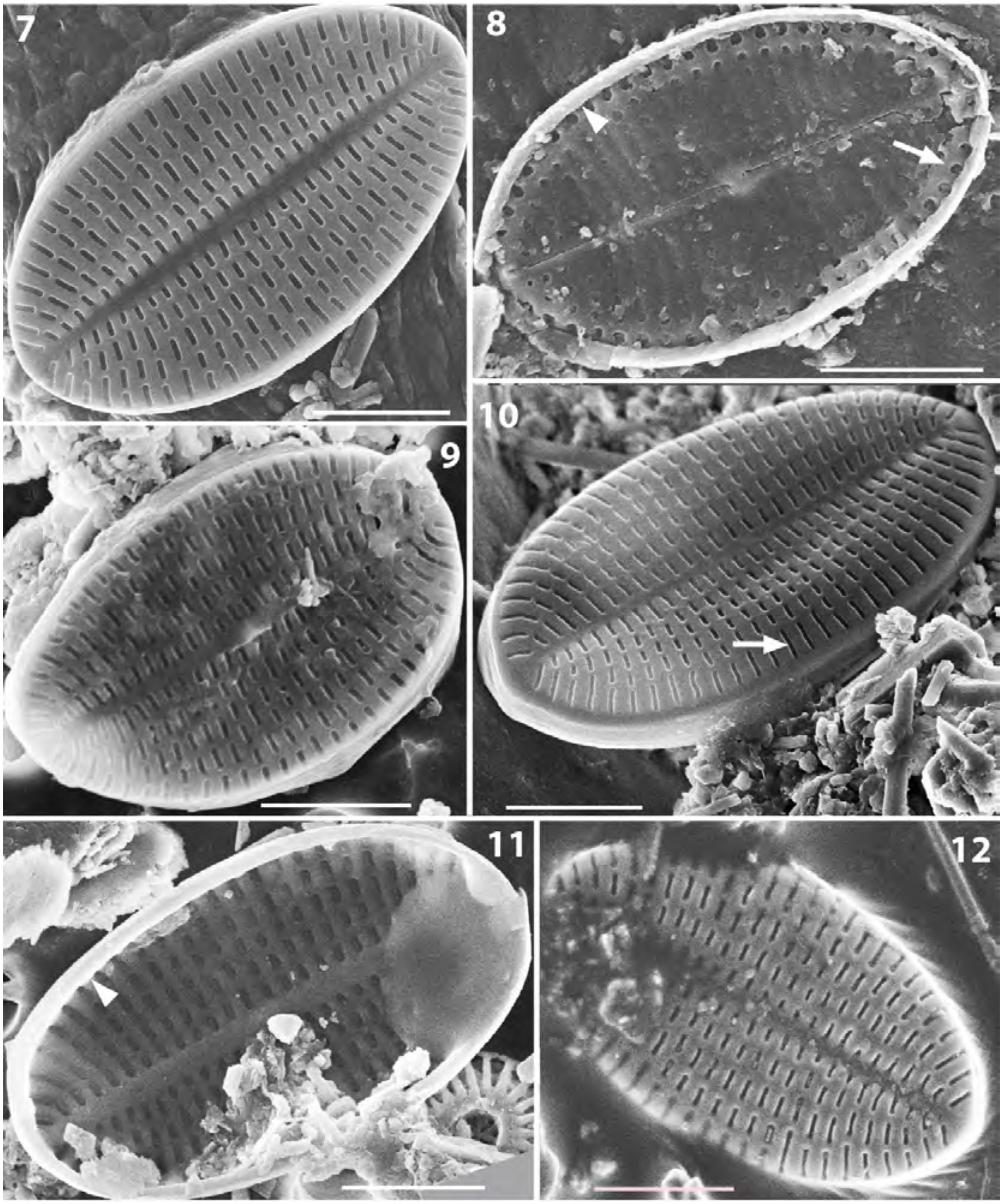

Fig. 7–12. *Cocconeis* cf. *mascarenica* Riaux-Gobin & Compère. SV areolae with no axial rows (7, 9), SV areolae with one marginal row of larger areolae (10 arrow), SV areolae with axial rows (12), SV internal view with undulated SVVC edge (11 arrowhead), RV in internal view with very slightly undulated to straight edge (8 arrowhead) and marginal rim (8 arrow). Scale bars: 2 µm (7–12).

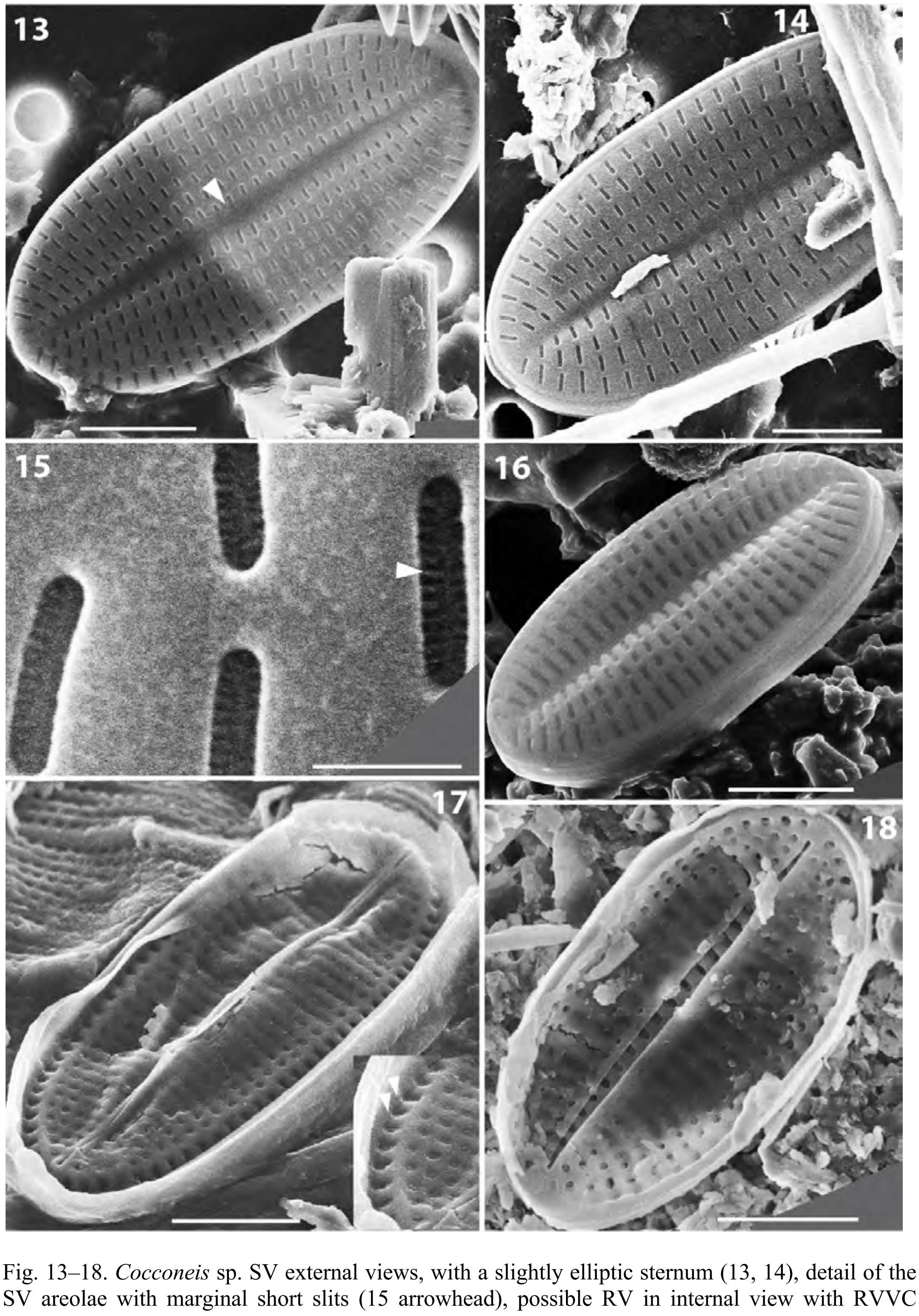

Fig. 13–18. *Cocconeis* sp. SV external views, with a slightly elliptic sternum (13, 14), detail of the SV areolae with marginal short slits (15 arrowhead), possible RV in internal view with RVVC undulated edge (17 arrowheads in insert), RV in external view (18), SV of an individual from Hao (16). Scale bars: 2 µm (13–14, 16–18), 200 nm (15).

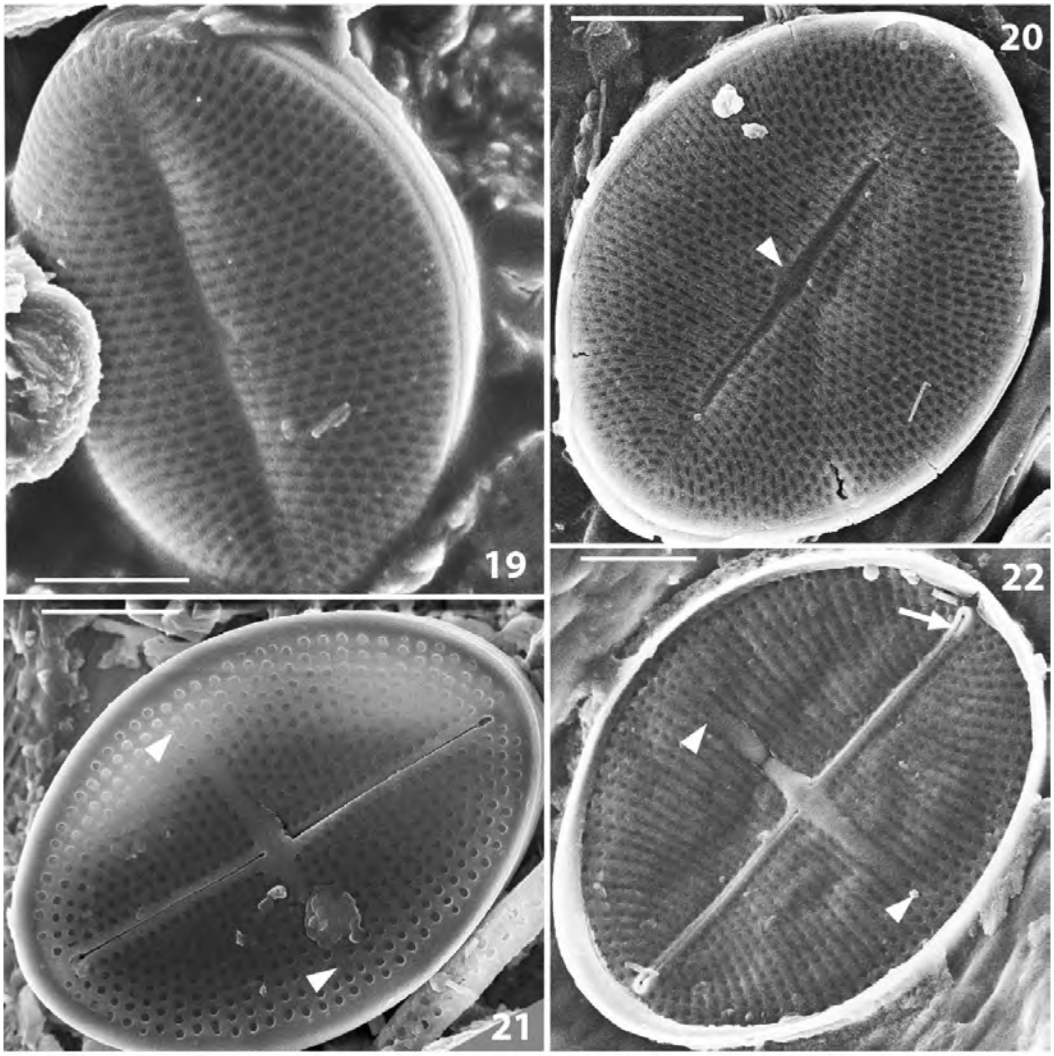

Fig. 19–22. *Cocconeis* cf. *molesta Kützing*. SV external views with a narrow straight sternum (19–20) and a small central area (20 arrowhead), RV external view with a 2/3 valve wide fascia (21 arrowheads), in internal view, with the fascia (22 arrowheads) and slightly bent helictoglossae (22 arrow). Scale bars: 3 µm (20), 2 µm (19, 21–22).

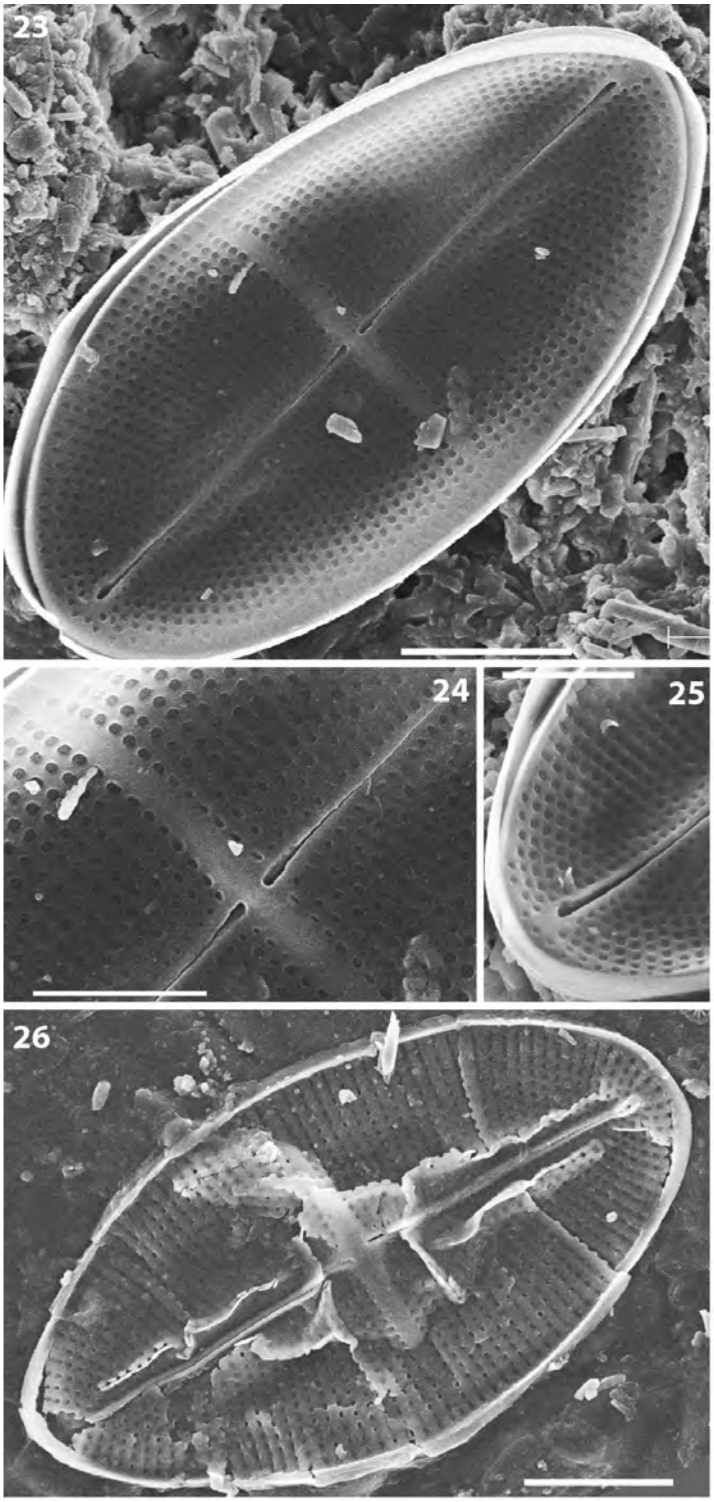

Fig. 23–26. *Cocconeis* cf. *diaphana* W.Smith. RV external views (23–25) with a fascia reaching both margins (23), RV apex in external view with areolae present (25), RV internal view (26). Scale bars: 3 µm (23, 26), 2 µm (24–25).

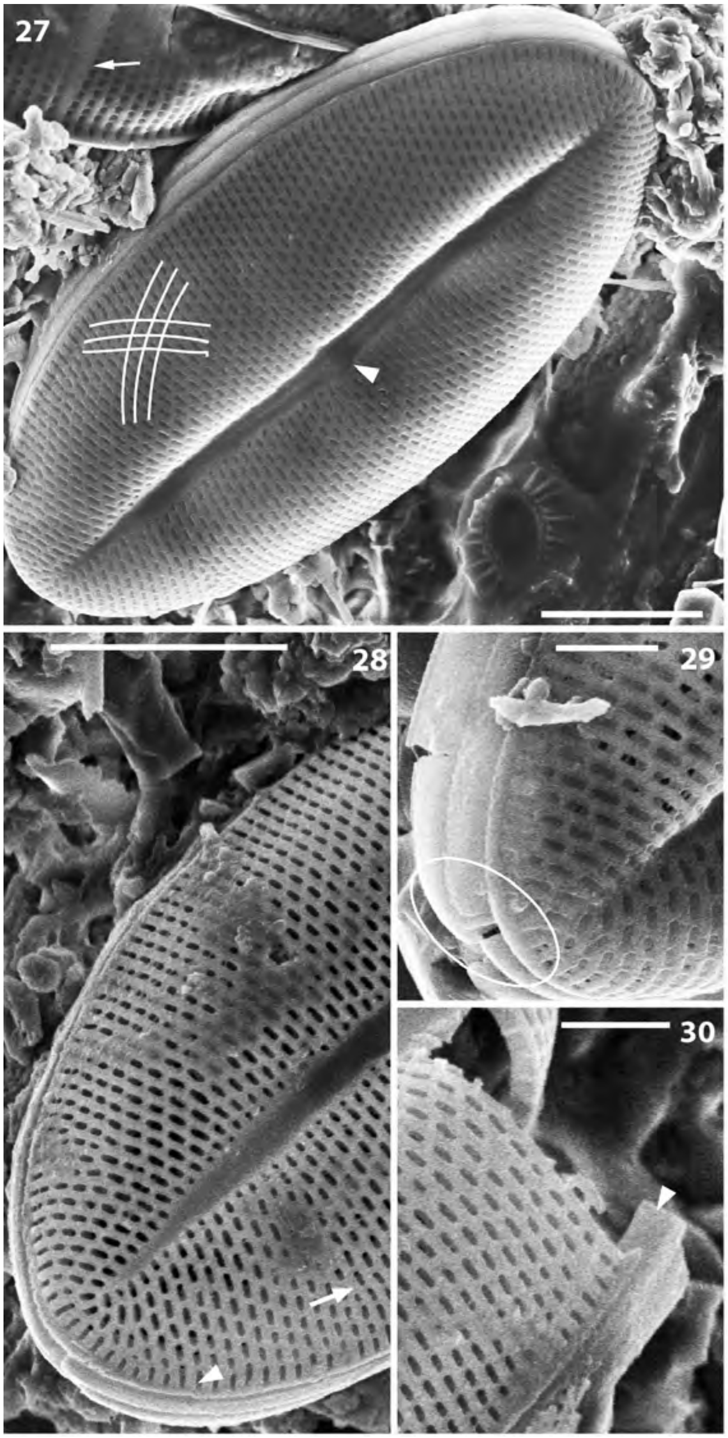

Fig. 27–30. *Cocconeis* cf. *diaphana* W.Smith. SV external view with a 135° diagonal pattern (27 white lines), and very small central area (27 arrowhead), SV supplementary striae (28 arrow) and a marginal continuous row of areolae perpendicular to the SV margin (28 arrowhead). Apex with open SVVC (29 ellipse), SVVC with straight edge (30 arrowhead). Scale bars: 3 µm (27–28), 1 µm (29–30).

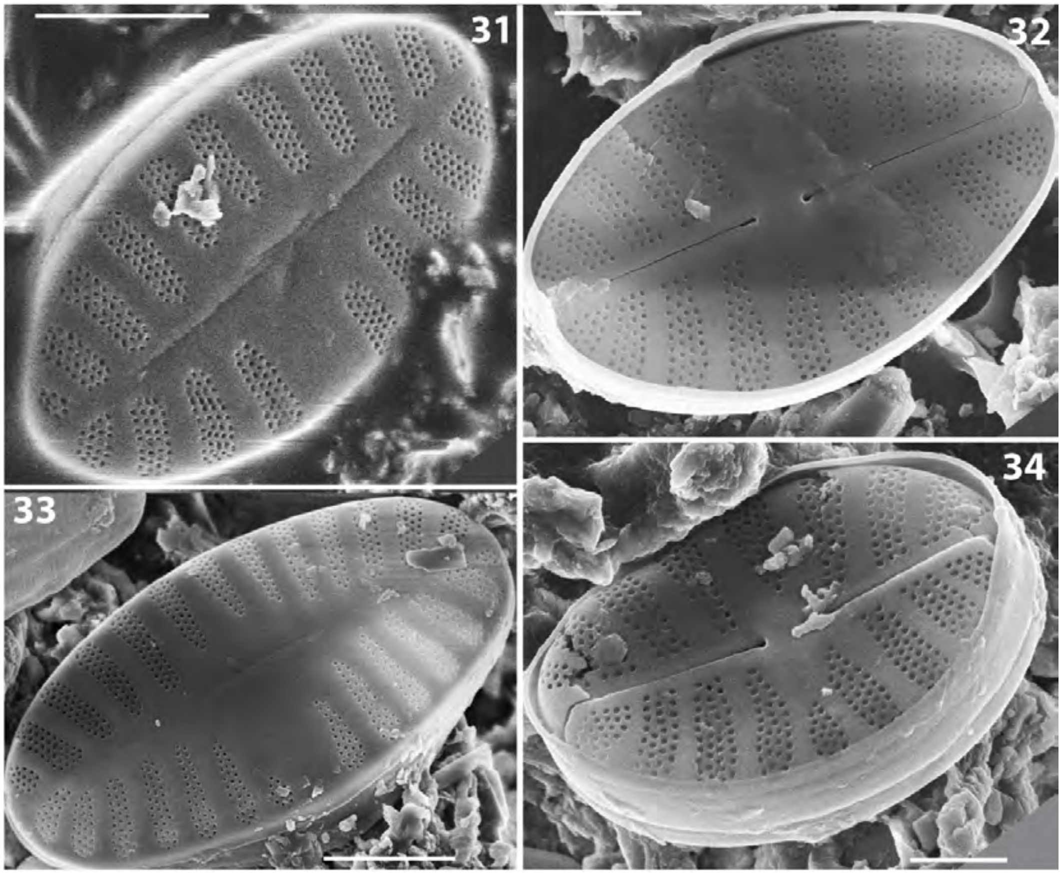

Fig. 31–34. *Planothidium mathurinense* Riaux-Gobin & Al-Handal. SV external views with quadriseriate striae, large fascia in one hemivalve, and largely elliptical sternum (31, 33). RV external views (32, 34). Scale bars: 2 µm (31, 33), 1 µm (32, 34).

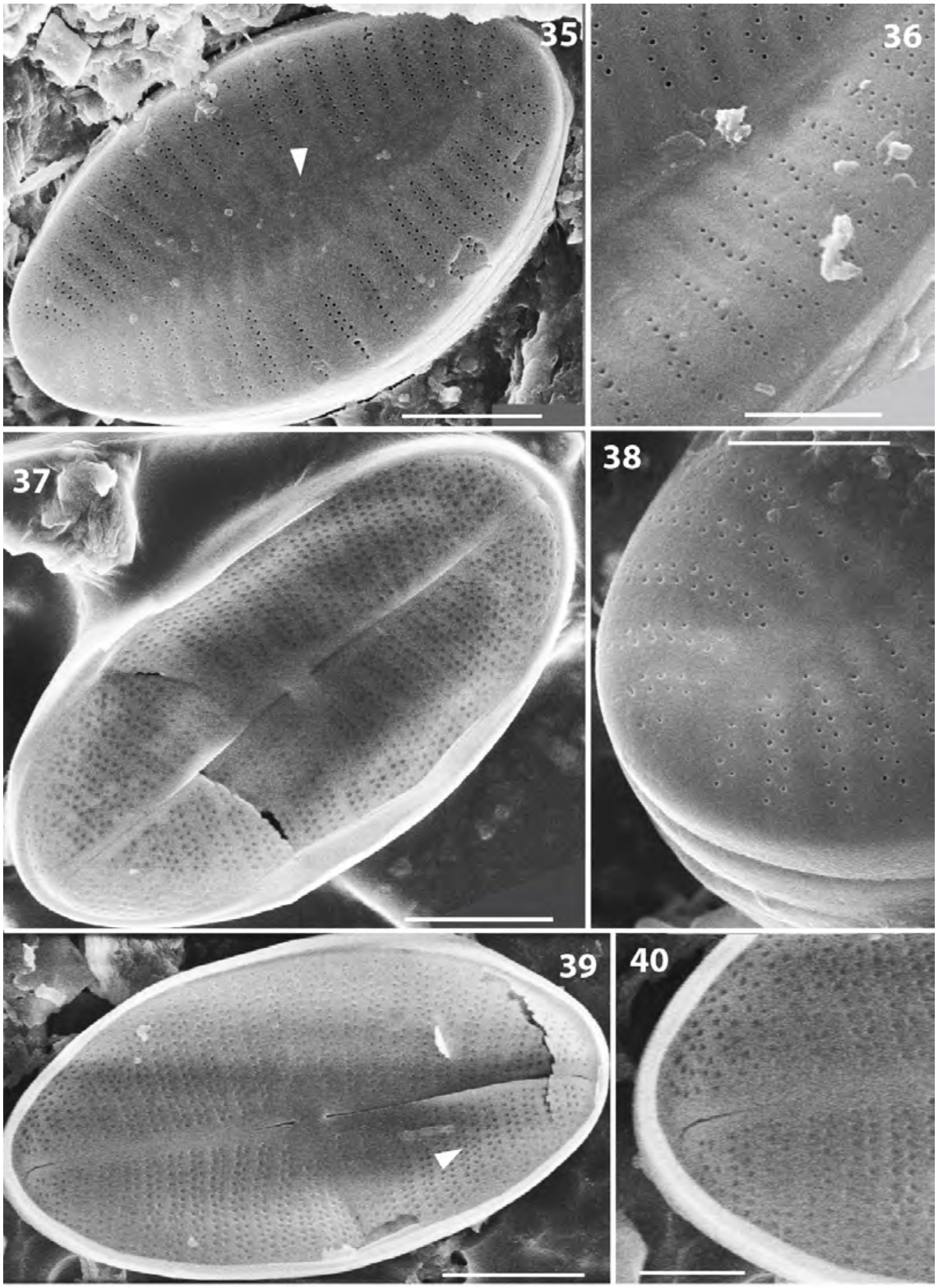

Fig. 35–40. *Planothidium rodriguense* Riaux-Gobin & Compère. SV in external view (35–36, 38) with a largely elliptical and concave sternum (35), delicate SV striae bi-seriated on margin. RV in external view (37, 39–40) with delicate and partly irregular biseriate striae (up to rarely triseriate on margin). Scale bars: 2 (35, 37, 39), 1 µm (36, 38, 40).

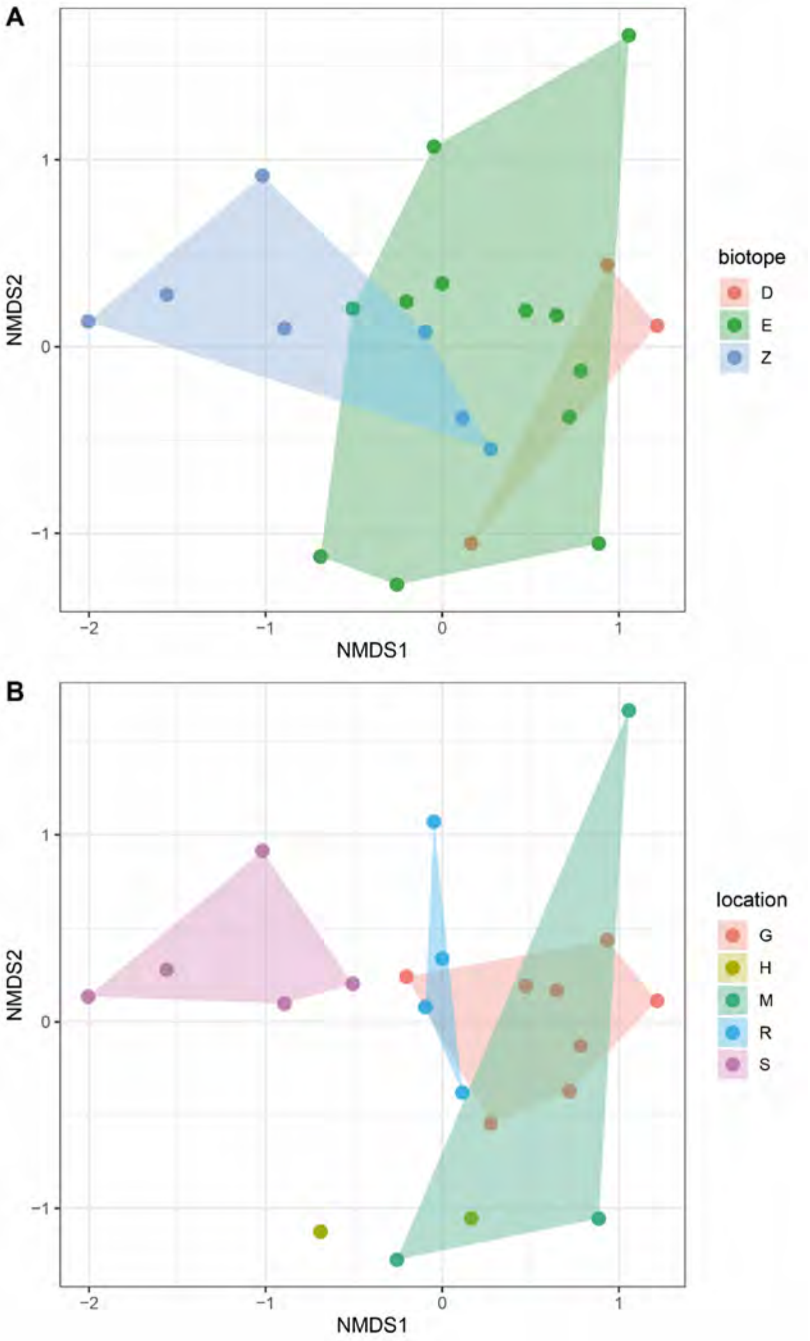

Fig. 41. Non-metric Multidimensional Scaling (NMDS) performed on the presence-absence of Achnanthales and *Olifantiella* diatom taxa observed in Mangareva and Hao islands (see supplementary material). Within different biotopes [upper diagram, green = epiphyte (E), red = diverse (D), blue = epizoic (Z)], along different localities [bottom diagram, red = Gatavake Bay (G), blue = Rikitea (R), kaki = Hao (H), green = Totegegie motu (M), violet = pearl oyster farm, subtidal samples (S)].