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New epizoic diatom (Bacillariophyta) species from sea turtles in the Eastern Caribbean and South Pacific

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Obligately epizoic diatoms (Bacillariophyta) on vertebrates were first described from cetaceans, but turtles, both freshwater and marine, also host very specific floras. Several scrapings of juvenile *Chelonia mydas* have allowed the description of two new diatom taxa whose valves are asymmetrical about the transapical axis, *Tripterion societatis* sp. nov. and *Chelonicola caribeana* sp. nov. These taxa are very small and show some morphological plasticity. Such plasticity might suggest their inclusion in genera with slightly different characteristics from *Tripterion* and *Chelonicola* as originally delimited. Based on our observations, an emended diagnosis is proposed for *Chelonicola*.

Keywords: *Chelonia mydas*, *Chelonicola*, new species, Lesser Antilles, Society Archipelago, *Tripterion*

Introduction

Epizoic or epibiontic diatom assemblages are known from various hosts and diverse localities, including freshwater and marine invertebrates (Round et al. 1961, Gibson 1979, Gaiser & Bachmann 1993, Wuchter et al. 2003, Totti et al. 2011, Riaux-Gobin & Witkowski 2012, Riaux-Gobin et al. 2013, Romagnoli et al. 2014, Sar & Sunesen 2014), with some species such as *Falcula hyalina* Takano and *Pseudohimantidium pacificum* Hustedt & Krasske in Krasske (Prasad et al. 1989, Fernandes & Calixto-Feres 2012, Gao et al. 2012) shown to be obligately epizoic. Among the vertebrate hosts, whales and cetaceans are the most studied, and several epizoic monoraphid genera, *Bennettella* R.W. Holmes and *Epipellis* R.W. Holmes (Holmes 1985, Holmes & Nagasawa 1995, Denys & Van Bonn 2001, Denys & De Smet 2010) have been described. The biraphid genera *Epiphallina* R.W. Holmes, Nagasawa & Takano, *Plumosigma* T. Nemoto, *Tursiocola* R.W. Holmes, Nagasawa & Takano, *Tripterion* R.W. Holmes, Nagasawa & Takano (Nemoto 1956, Holmes et al. 1993a, 1993b, Denys 1997), have also been described from these vertebrate hosts. Recently, a manatee from Florida Bay was investigated, resulting in the description of three new

Tursiocola species (Frankovich et al. 2015a). Marine and freshwater turtles have also been studied, resulting in the description of two new species of *Tursiocola* (Wetzel et al. 2012, Frankovich et al. 2015b), one species of *Luticola* (Wetzel et al. 2010), one species of *Mastogloia* Thwaites (Pavlov et al. 2016) and three new genera, *Chelonicola* Majewska, De Stefano & Van de Vijver, *Poulinea* Majewska, De Stefano & Van de Vijver (Majewska et al. 2015, Robinson et al. 2016) and *Medlinella* Frankovich, Ashworth & M.J. Sullivan (Frankovich et al. 2016). The cetaceous diatom taxa, as well as the chelonian and manatee species, seem to be obligately epizoic. When these diatoms are reported from abiotic or other biotic substrata, their occurrence is shown to be accidental or related to the behaviour of their host (Holmes et al. 1993a, Denys 1997), for example, epizoic diatoms found on the sediments at whaling stations (Nagasawa et al. 1989, Nagasawa 1993), in the stomach of *Euphausia superba* Dana (Nemoto 1956), or the possible transfer from dolphin to turtle (Wetzel et al. 2012). While Holmes et al. (1993a) commented on 'the apparent specificity of these few diatom taxa to the skin of cetaceans', they (Holmes et al. 1993b) also stated that 'diatoms which are consistently observed on cetacean

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skin do not appear to be host specific'. Frankovich *et al.* (2015b) suggested the degree of host specificity of these diatoms is largely unknown.

Among the genera and species described as epizoic on vertebrates, several *Stauroneis* Ehrenberg species (Hustedt 1952, Nemoto 1956) were transferred to *Epiphialaina* and *Tursiocola* (Holmes *et al.* 1993a), while *Tripterion* was created by Holmes *et al.* (1993a), with several other species in Holmes *et al.* (1993b) and Fernandes & Sar (2009). *Chelonicola* and *Poulinea* were established by Majewska *et al.* (2015) to accommodate two small epizoic taxa that are asymmetrical to the transapical axis (i.e., heteropolar), while *Medlinella* is described as isopolar, with a dorsiventral valve face and areolae partially occluded by volae (Frankovich *et al.* 2016). Like *Chelonicola* and *Poulinea*, *Tripterion* is heteropolar and wedge-shaped in girdle view, and *Epiphialaina* and *Tursiocola* also share these features, although to different degrees (see Denys 1997: 16). Therefore, these five genera may be described as 'gomphonemoid' taxa, and with the lack of stigmata and often a typical apical pore field, show some similarities to several marine gomphonemoid genera, that is, *Gomphonemopsis* Medlin, *Gomphoseptatum* Medlin, *Cuneolus* Giffen, *Gomphosphenia* Lange-Bertalot and *Pseudogomphonema* Medlin (Table 1). Denys (1997) suggested a relationship between *Epiphialaina* and *Tursiocola* and the Rhoicospheniaceae, but also with *Stauroneis s.l.*, adding that 'heteropolarity is well-known to have evolved independently in a number of sessile genera from quite different lineages'. Majewska *et al.* (2015) showed that at least three lineages of naviculoid diatoms have become asymmetrical about the transapical axis, so that the concept of 'marine gomphonemoid diatoms' may be artificial.

Numerous scrapings of juveniles *Chelonia mydas* Linnaeus (green turtle) from the Lesser Antilles (Eastern Caribbean) were obtained during ANTIDOT surveys, and one from the South Pacific. These allowed us to describe two dominant diatom species, and to discuss their taxonomic and systematic affinities with other diatoms, including other epibionts. Wild juvenile chelonians are known to remain at their birth areas, reducing the intermingling of florae. An emended diagnosis is proposed for the genus *Chelonicola* and new *Chelonicola* and *Tripterion* species are described.

Materials and methods

Materials used in this study were derived from two sources:

(1) A scraping (12 November 2014) of the carapace of a green turtle *C. mydas*, named 'Moon', originating (April 2014) from Tetiaroa atoll (17 01'30''S, 149 33'29''W, Society Archipelago) where it was found caught on the bottom of its nest (26 g, 5.5 cm long). Moon was immediately transferred to Papetoai, at the 'Sea turtle clinic – "Te mana o te moana" association' (17 28' 59.999'' S, 149 52' 0.001'' W, Papetoai, Moorea Island, French Polynesia). During its

stay at Papetoai, Moon was in contact with several other turtles from different places, Tahiti and Tetiaroa (Society Archipelago) and Rangiroa (Tuamotu Archipelago).

(2) Scraping of the carapace of 14 wild juvenile *C. mydas* from Martinique Island (Grande Anse d'Arlet 14 30'10.95''N, 61 05'13.00''E and Anse du Bourg 14 29'13.43''N, 61 04'58.88''E, 12–13 October 2015). These samplings were carried out by D.C. during surveys (ANTI-DOT program, CNRS-IPHC) with the aim of understanding the migratory behaviour of different species of marine turtles. The samples are housed at CRIOBE–USR 3278 CNRS, Perpignan, France.

For light microscopical (LM) examination, samples were washed with distilled water to remove salts, treated with 30% H₂O₂ for 2 h at 70°C to remove organic matter, rinsed several times in distilled water, alcohol-desiccated and mounted on glass slides using Naphrax[®]. Diatom slides were examined with a Zeiss Axiophot 200, with differential interference contrast (DIC) optics and photographed with a Canon PowerShot G6 digital camera (CRIOBE–USR 3278, Perpignan, France). For SEM examination, the samples were filtered through 1 µm Nuclepore[®] filters and rinsed twice with deionized (milliQ) water to remove salts. Filters were air-dried and mounted onto aluminium stubs before coating with gold-palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi S-4500 SEM operated at 5 kV, calibrated with a Silicon grating TGX01 (C2M, Perpignan, France).

Valve length and width are expressed as minimum–maximum (in µm), means (µm) ± standard deviation (SD = σ , quantifying the dispersion) and number of examined specimens (n). The length/width ratio (L/W ± σ) quantifies the degree of elongation of the valve. 'Foot pole' (F) and 'head pole' (H) designate 'the length between the apex of the valve (foot or head) and the middle of the central area of the valve'. The ratio (F/H ± σ) permits a rough estimate of the degree of heteropolarity of the cell. Stria density in 10 µm is expressed as minimum–maximum and mean (± σ). The term 'copula closed pole' refers to the closed apex of the open cingular bands.

Terminology and abbreviations: For the description of the frustule and its parts, terminology follows Anonymous (1975), Ross *et al.* (1979) and Round *et al.* (1990).

Observations

***Tripterion societatis* Riaux-Gobin, Witkowski & Ector sp. nov.** (Figs 1–7 LM, Figs 8–28 SEM)

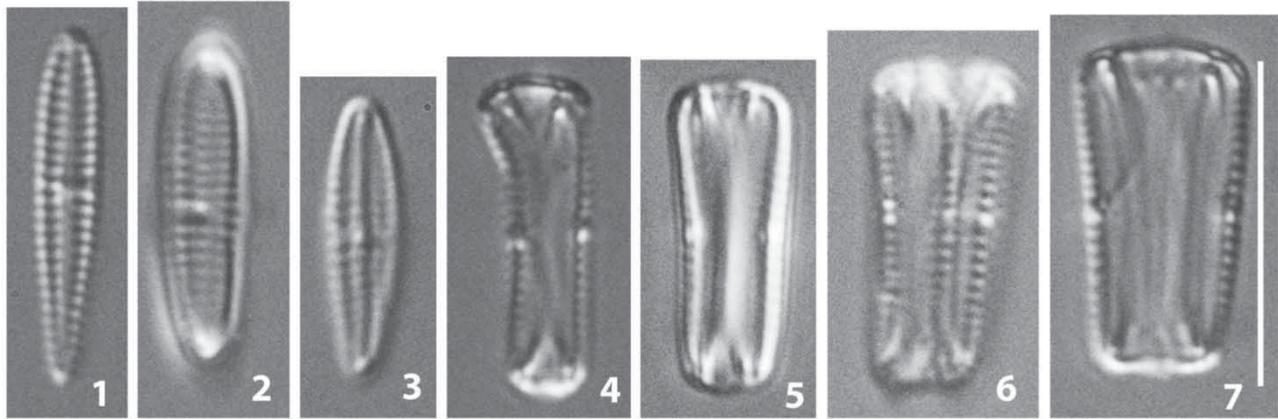
Description

Valves small, narrow-elliptical to slightly clavate, heteropolar (Figs 1, 3, 8, 10, 11), with round apices. Frustule lightly silicified, biraphid, isovalvar, wedge-shaped in girdle view (head pole larger than foot pole, Figs 5, 7, 11, 15).

Table 1. Features of *Epiphialaina*, *Tursiocola*, *Chelonicola*, *Poulinea* and *Tripterion* from their original descriptions and more recent investigations.

	<i>Epiphialaina</i> R.W. Holmes, Nagasawa & Takano	<i>Tursiocola</i> R.W. Holmes, Nagasawa & Takano	<i>Chelonicola</i> Majewska, De Stefano & Van de Vijver	<i>Poulinea</i> Majewska, De Stefano & Van de Vijver	<i>Tripterion</i> R.W. Holmes, Nagasawa & Takano
Frustule outline	Lanceolate	Narrowly to broadly lanceolate	Clavate	Clavate	Cuneate, (head pole longer than foot pole), raphe branches mostly equal in size**
Frustule in girdle view	Parallel sides	Rectangular***	Wedge-shaped	Wedge-shaped to rectangular	Wedge-shaped
Heteropolarity	–, slightly heteropolar valves*,	–, slightly heteropolar valves*, isopolar***, isopolar to slightly heteropolar°	+	+	+
Central area	Thickened, without puncta	Small, diamond shaped	Fascia never present (but one stria shorter on both sides)	Wide fascia, occasionally shortened striae	Without puncta, except 1–2 isolated puncta near the valve edge
Girdle bands	Closed, probably not always the case*, with a single row of circular to somewhat elongate puncta	2, closed, with a double row of puncta, three open bands with one row of pores***, closed valvocopulae in part biseriate and multiple open copulae uniseriate°	Open, up to 12, one row of poroids	> 10, open, occasionally 2 irregular rows of poroids	Closed, four open bands with a single row of poroids**
Septa	–	–	Small	Conspicuous	Short, second copula with a more developed septum**
Internal raphe fissure	Raphe slit expanded in the central area	–, slightly eccentric°	Asymmetrically positioned	–	Lateral, raphe opens slightly laterally**
Pseudosepta	Well developed on both ends of the valve	Well developed	Absent	Absent	Absent
Striae toward the foot pole	–	–	–	Striae somewhat denser near the poles	Striae more closely spaced toward the foot pole
Terminal endings	Fissures strongly hooked and recurved	Recurved	Elongated, weakly deflected	Elongated, deflected, covered by a large flap	Terminated before reaching the apices, strongly hooked, almost T-shaped in the foot pole**, terminal area thickened**
Pore field	Absent	Absent	Absent	Absent, but presence of several small areolae surrounding the foot pole	A few irregularly scattered elongate puncta at foot pole, discrete pore field**
Unique structures	Small amorphous sphere on the internal raphe slit	1–2 small humps on each side of the internal raphe slit	Internal proximal raphe endings covered by a silica flap	Internal proximal raphe endings covered by a silica flap	–
Original description	Holmes et al. (1993a)	Holmes et al. (1993a)	Majewska et al. (2015)	Majewska et al. (2015)	Holmes et al. (1993a)

Notes: (*Denys 1997; **Fernandes & Sar 2009; ***Wetzel et al. 2012; °Frankovich et al. 2015a, 2015b). + = present; – = not specified; () = as observed from the original illustration.



Figures 1–7. (LM). *Tripterion societatis* sp. nov. Note the clavate shape in valve face view (Figs 1, 3) and the wedge-shape and apical septa in cingulum views (Figs 5–7). Scale bars = 10 µm.

Valve length 7.3–10.6 µm, $9.0 \mu\text{m} \pm 0.8$; valve width 1.0–2.7 µm, $1.6 \mu\text{m} \pm 0.5$; L/W 6.4 ± 1.3 ; F/H 1.06 ± 0.05 ; $n = 26$ (SEM). The head pole is more bluntly rounded than the foot pole. Striae slightly radiate in mid-valve to parallel at apices (24–39 in 10 µm, 30.5 in $10 \mu\text{m} \pm 3.6$; $n = 26$), composed of two rows (exceptionally three areolae per stria, Fig. 13, arrow) of oblong to subquadrangular transapical areolae, with the areolae on the mantle being often the longer. Striae slightly denser near both poles (Figs 8, 10–13), particularly near the foot pole (Figs 11–12 arrows). Areolae with internally domed hymenate pore occlusions (Figs 20, 22). Fascia present, sometimes with a marginal short areola on one or both sides (Figs 8, 10–13). 15–17 minute, round or irregular, more or less regularly scattered areolae at the foot pole, on both sides of the terminal raphe ending (Fig. 9), also closed internally by domed hymenes (Fig. 24 arrow). Stigma and pseudosepta absent. Raphe straight, not filiform (Figs 8, 10). Raphe branch slightly shorter towards the head pole. In external view the proximal raphe endings are quite widely separated and spatulate, straight or very slightly curved opposite to the raphe terminal endings (Figs 8, 10). Terminal raphe endings are strongly hooked towards the same side, with an oblique reinforcement and no real flap (Figs 9–10, 17 arrowhead) similar on both poles. Internally, the raphe is lateral on a ridge (Fig. 20) and the proximal raphe endings terminate at the narrow central nodule which is slightly expanded on one side but with no real flap (Fig. 20 arrowhead). Helictoglossae very slightly deflected (Fig. 24). The cingulum consists of several narrow open bands (< 10) (Figs 10–11, 13–17). A short septum is present on the valvocopula at the head pole (Figs 11, 23), and at the closed pole of the 2nd copula (Figs 22 arrow, 25–28). The pars interior of the valvocopula has an irregular edge, without fimbriae (Figs 21–22 arrowheads), but with thickenings between each poroid (Fig. 21 right arrowhead). Poroids on the copulae are round to quadrangular (Figs 21, 27) denser than the valve striae (Fig. 21), appearing apically

elongated when the copulae are still in place, partly hiding the poroids (Figs 18–19). The copulae each possess one row of poroids, but the 2nd and 4th copulae also show a short supplementary row of poroids towards the closed pole of the copula (frustule foot pole, Figs 16–17 arrows). Furthermore, a double row of loosely arranged poroids is present at the closed pole of the 3rd copula (frustule head pole, Fig. 11 framed arrow; Figs 18–19 arrows). Near the head pole of the frustule, several copulae also show a double row of poroids, that is, a row of supplementary small and round poroids on the enlarged edge of the 4th–6th copulae (Figs 15, 19 arrowheads).

Holotype

Specimen on SEM stub, BM001231515 (Natural History Museum, London, UK), ‘2’ Moon 5 CM 28/11/2014, illustrated in Fig. 11.

Isotypes (here designated)

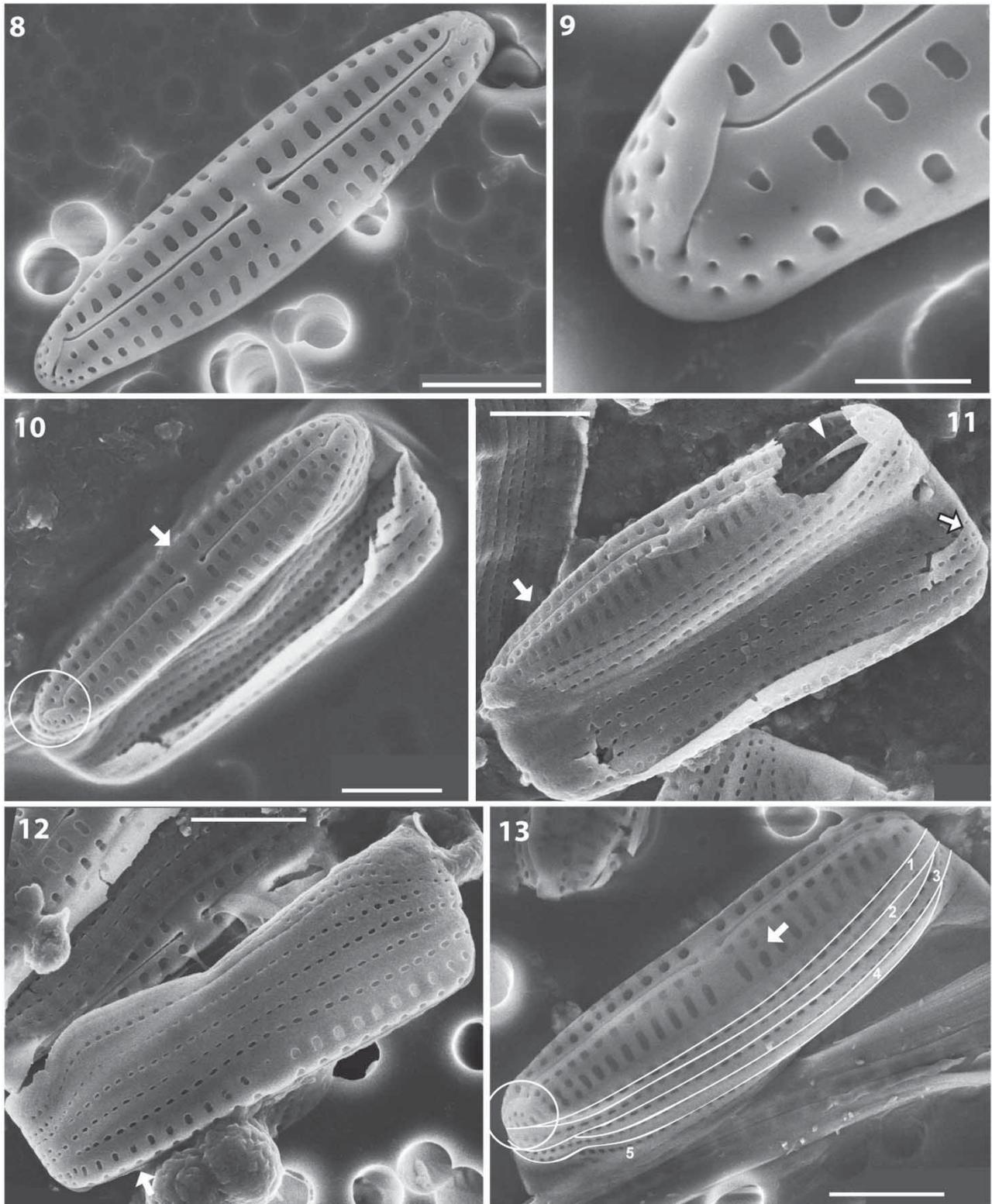
BM 101845 (Natural History Museum, London, UK), MOOR 3 in collection C. Riaux-Gobin (CRIOBE, Perpignan, France), SZCZ 23532 in collection A. Witkowski (The Faculty of Geosciences, Szczecin, Poland).

Type locality

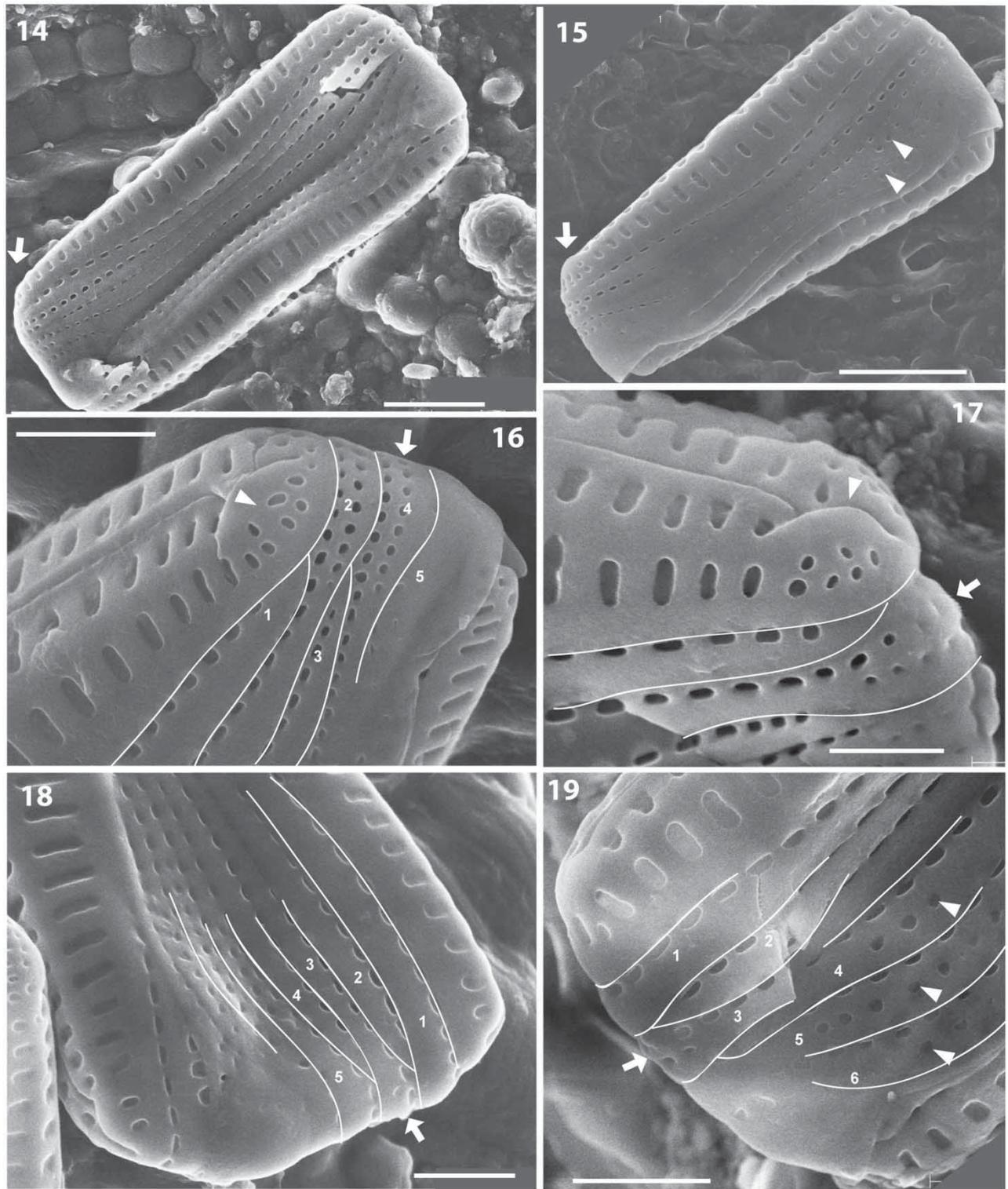
Juvenile *C. mydas* named ‘Moon’, from Papetoai (Sea turtle clinic, ‘Te mana o te moana’), Opunohu Bay, Moorea Island ($17^{\circ} 28' 59.999''$ S, $149^{\circ} 52' 0.001''$ W). Sampling date: 12 November 2014. Collector: Magali Soria.

Distribution

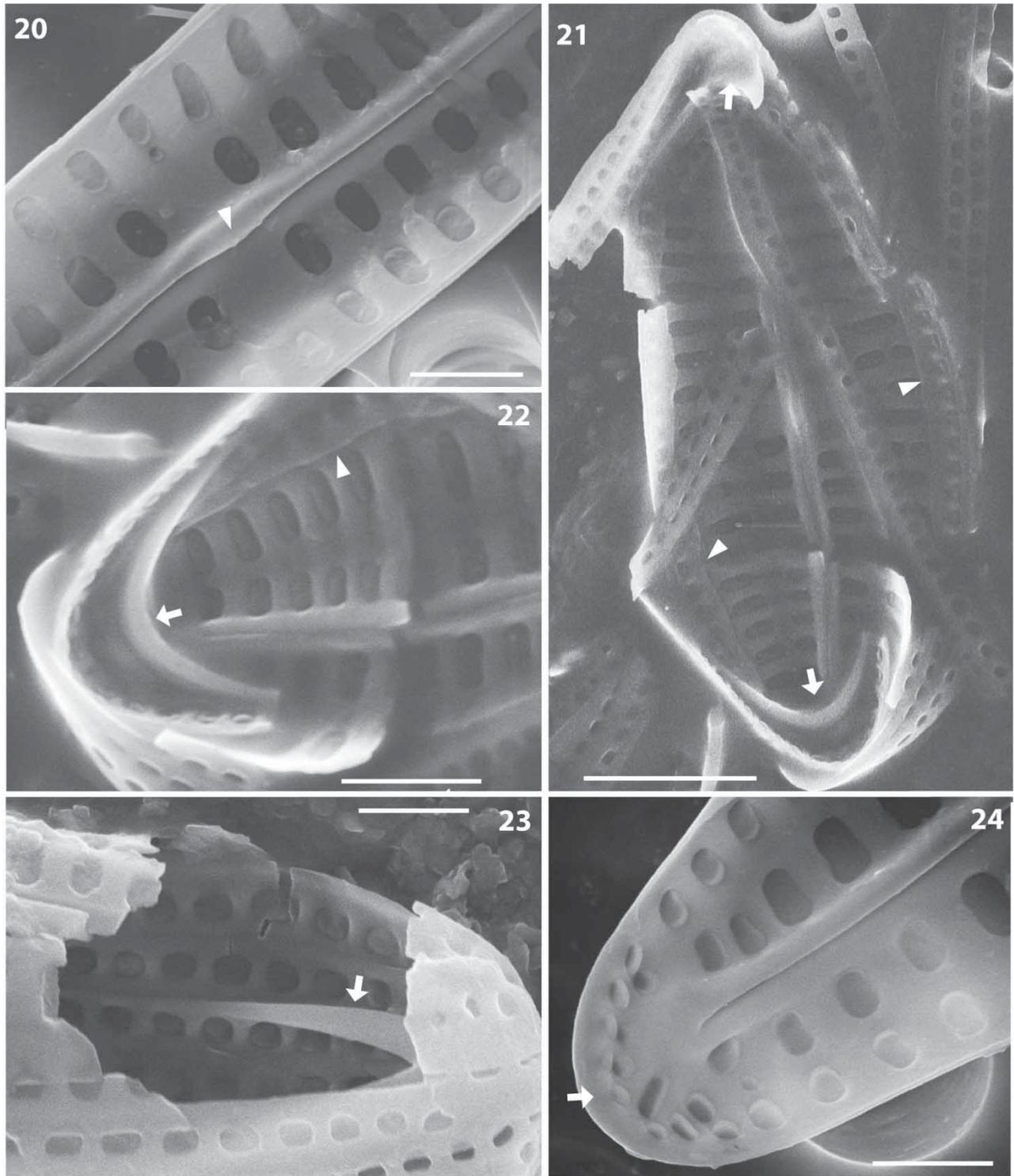
Tripterion societatis sp. nov. is present on Moorea Island (Society Archipelago) as epizoic on a juvenile *C. mydas*.



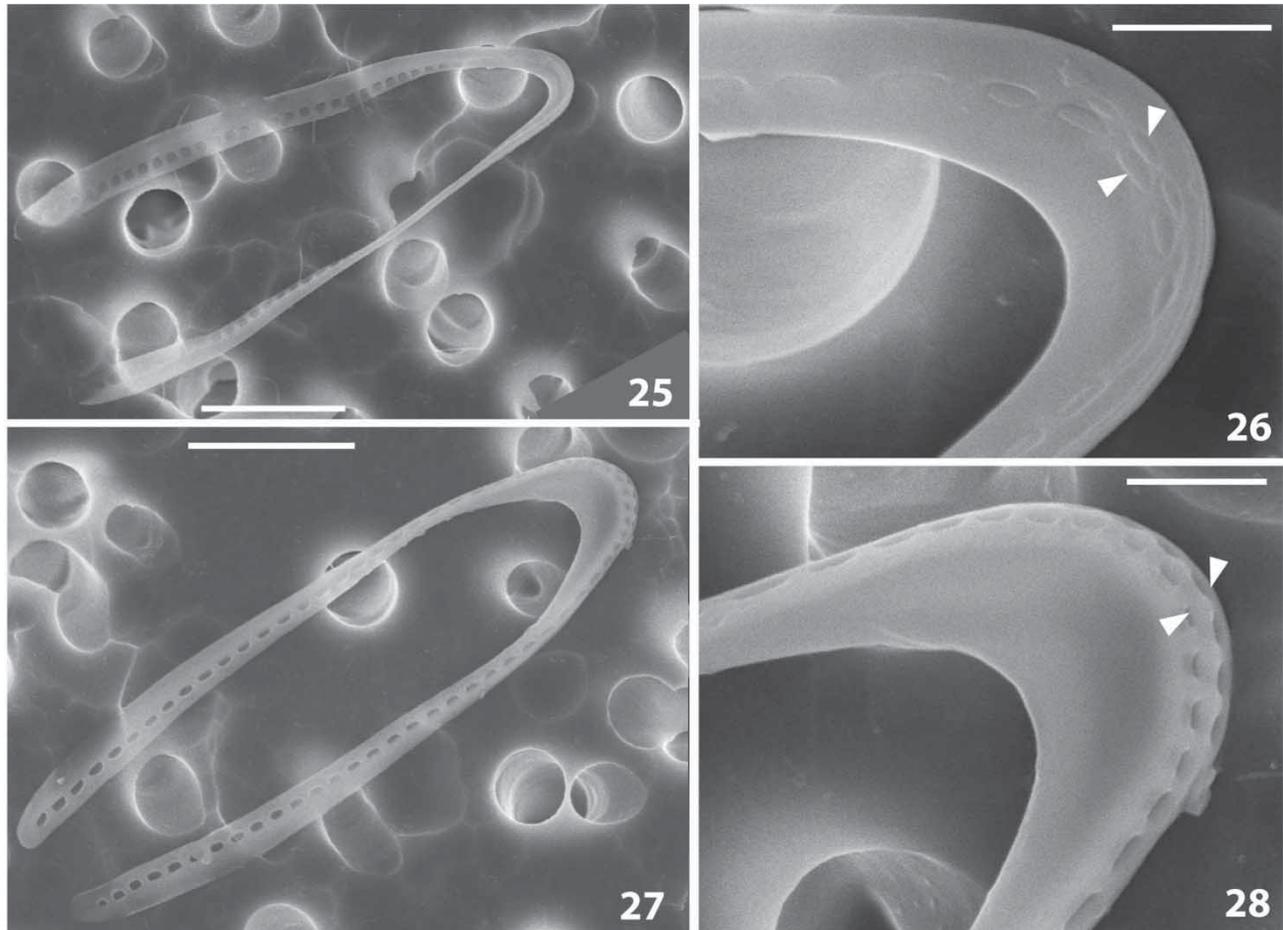
Figures 8–13. (SEM external views). *Tripterion societatis* sp. nov. The circles highlight the foot pole area with minute areolae. Striae composed of two rows of oblong areolae, presence of a fascia (Fig. 10 arrow). Striae rarely composed of three areolae (Fig. 13, arrow), often slightly denser at both poles and particularly at the foot pole (Figs 11–12 arrow). Holotype specimen illustrated in Fig. 11. Broken frustule showing the septate valvocopula (Fig. 11 arrowhead). Open copulae with one row of pores (Fig. 13), some with two rows of pores at their foot pole. Scale bars = 2 μ m (Figs 8, 10–13); 500 nm (Fig. 9).



Figures 14–19. (SEM, external views). *Tripterion societatis* sp. nov. Two specimens clearly wedge-shaped in girdle view (Figs 14–15), with a foot pole (arrow) narrower than the head pole and showing small apical areolae and copulae with a supplementary row of pores (Fig. 15 twin arrowheads). Detail of the frustule foot pole (Figs 16–17) with an area with scattered pores (Fig. 16 arrowhead), 2nd and 4th copulae with two rows of pores at their closed pole (Fig. 16 arrows), and reinforced terminal raphe fissures (Fig. 17 arrowhead). Details of the frustule head pole (Figs 18–19), 3rd copula with two rows of pores at their closed pole (arrows) and 4th to 6th copulae with two rows of small and round pores near the head pole of the valve (Fig. 19 arrowheads). Scale bars = 2 μm (Figs 14–15); 1 μm (Figs 16, 18–19); 700 nm (Fig. 17).



Figures 20–24. (SEM, internal views). *Tripterion societatis* sp. nov. The areolae are internally closed by domed hymenes (Figs 20, 22, 24). Note the raphe lateral on the top of the raphe ridge and the proximal raphe endings hidden by a reinforcement of the central nodule (Fig. 20 arrowhead). Valvocopula with small thickenings between each poroid and irregular edge, but no fimbriae (Figs 21–22 arrowheads). Septate copulae (Figs 21–23 arrows). Foot pole area with scattered small areolae with domed hymenes (Fig. 24 arrow). Scale bars = 700 nm (Fig. 20); 2 μ m (Fig. 21); 1 μ m (Fig. 22); 600 nm (Fig. 23); 500 nm (Fig. 24).



Figures 25–28. (SEM). *Tripterion societatis* sp. nov. Advalvar view of the internal side of the septate 2nd copula (Figs 25–26), detail of the copula closed pole with dense pores (denser than on the rest of the copula) closed by domed hymenes (Fig. 26 twin arrowheads). Abvalvar view of the external side of the septate 2nd copula (Figs 27–28), with the double row of pores at its closed pole (Fig. 28 twin arrowheads). Scale bars = 2 μ m (Figs 25, 27); 400 nm (Fig. 26); 500 nm (Fig. 28).

Etymology

The epithet *societatis* refers to the Society Archipelago whence the species is described.

Taxonomic notes

Tripterion societatis sp. nov. has several features permitting it to be assigned to this genus, particularly the foot pole area with scattered minute areolae (that may be vestigial areolae, see pseudocellus description in Louvrou *et al.* 2012), the slightly higher stria density near the poles, particularly the foot pole, the septate valvocopulae and second copula, and the fascia often delineated by a short marginal areola.

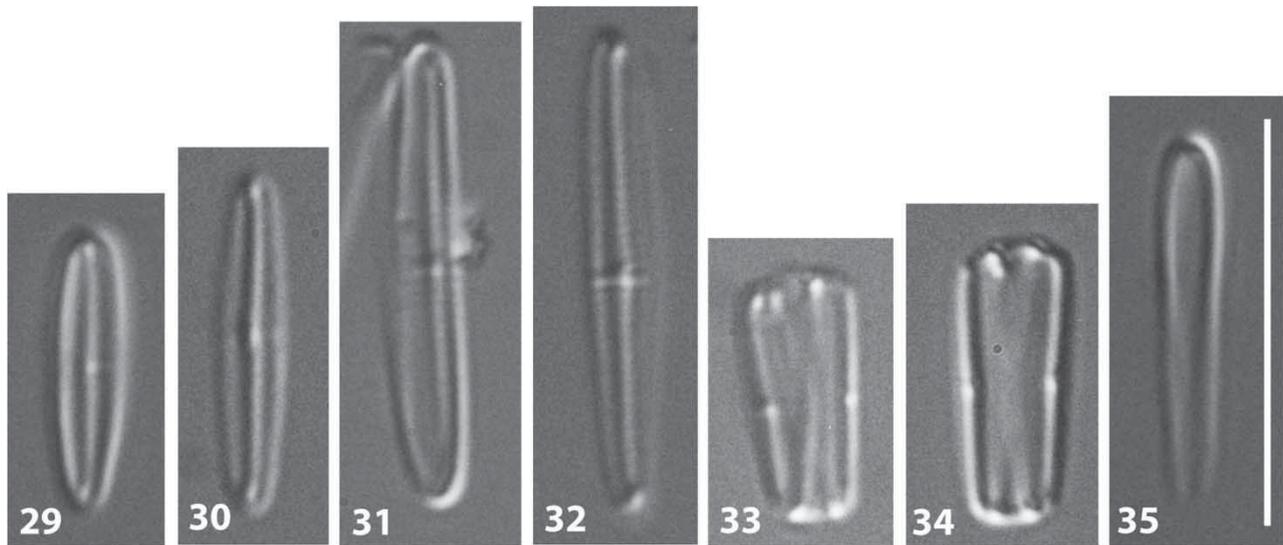
Table 2 details the morphology of the published species of *Tripterion*, *Tripterion kalamensis* R.W. Holmes, Nagasawa & Takano, *Tripterion margaritae* (Frenguelli & Orlando ex Fernandes & Sar) Fernandes & Sar, *Tripterion philoderma* R.W. Holmes, Nagasawa & Takano, *T. societatis* Riaux-Gobin, Witkowski & Ector and of *Poulinea*

lepidochelicola Majewska, De Stefano & Van de Vijver. Within *Tripterion*, *T. margaritae* is significantly different, with small round areolae over the whole valve, a very large fascia, and an apical foot field composed of numerous closer small areolae. *Tripterion kalamensis* and *T. philoderma* both have a less-developed fascia than *T. margaritae*, one row of elongate areolae near the raphe and a few irregularly scattered elongate areolae at the foot pole. Following Holmes *et al.* (1993b, 131), the areolae close the raphe in *T. philoderma* ‘are narrower and more elongate’ and ‘do not become as tightly packed’ near the foot pole as in *T. kalamensis*. *Tripterion societatis*, particularly its small individuals, shows some similarities with *T. philoderma*, but their striae are generally composed of only two areolae, of which the one near the raphe is never longer than that on the mantle. Furthermore, the foot pole area in *T. philoderma* is composed of closer, oblong areolae, rather than the minute, scattered round areolae in *T. societatis*. The raphe branch lengths are also dissimilar between these two taxa (Table 2).

Table 2. Structure and morphometrics of *T. margaritae* (Frenguelli & Orlando ex Fernandes & Sar) Fernandes & Sar (Fernandes & Sar 2009), *T. kalamensis* R.W. Holmes, Nagasawa & Takano (Holmes et al. 1993a), *T. philoderma* R.W. Holmes, Nagasawa & Takano (Holmes et al. 1993b), *T. societatis* sp. nov. (present paper) and *P. lepidochelicola* Majewska, De Stefano & Van de Vijver.

	<i>T. margaritae</i> (Frenguelli & Orlando ex Fernandes & Sar) Fernandes & Sar	<i>T. kalamensis</i> R.W. Holmes, Nagasawa & Takano	<i>T. philoderma</i> R.W. Holmes, Nagasawa & Takano	<i>T. societatis</i> sp. nov.	<i>P. lepidochelicola</i> Majewska, De Stefano & Van de Vijver
Areola occlusion	Hymenes	Hymenes	Hymenes	Hymenes, internally domed	Hymenes
Valve face	(foot pole narrower than head pole), transapically heteropolar, raphe branches mostly equal in size	Cuneate, heteropolar, head pole raphe branch longer than foot pole branch	(foot pole narrower than head pole), gomphonemoid, valve face flat, curving sharply downward near the second puncta, head pole raphe branch 4–15% longer than foot pole branch	Head pole raphe branch slightly shorter than foot pole branch	Clavate, more acutely rounded foot pole, head pole raphe branch shorter than foot pole branch
Frustule in girdle view	Cuneate	Wedge-shaped	Wedge-shaped	Wedge-shaped	Wedge-shaped
Areola shape	Circular in external view, transapically elongate in internal view	Striae punctate, a single row of large puncta on either side of the raphe, oval on foot pole, circular on head pole, mantle areolae smaller	Puncta adjacent to the raphe narrow and elongate	Stria composed of two (up to 3) oblong to subquadrangular areolae, the one on the mantle being often longer	Stria composed of two transapically elongate areolae
Central area	Wide transverse fascia	With 1–2 isolated puncta, otherwise apunctate	(Fascia with 1–2 isolated puncta, otherwise apunctate)	Fascia with occasionally a marginal areola	Rectangular fascia, widening towards the margins, with occasionally a short stria
Girdle bands	Four open bands, with a single row of poroids	One robust closed band, sometimes two, with short septa at each pole, with a single row of puncta	Four bands, valvocopulae open at one end, with a single row of elongate puncta	< 10 narrow open copulae with round to quadrangular poroids denser than the valve striae, several copulae in part with two row of puncta within a specific scheme	Up to 12 open copulae, with one row of slit-like poroids, near the foot pole a double row of poroids
Septa	Valvocopula with septum at head pole, second band with a septum at the valve foot pole	See above	nd	Valvocopula with septum at head pole, second band with a septum at the valve foot pole	Valvocopula with septum at head pole, second band with a septum at the valve foot pole
Internal raphe fissure	Opens slightly laterally	Lateral	nd	Slightly lateral	(Slightly lateral)
Striae towards the foot pole	Closer than elsewhere, convergent	Closely spaced	(Closely spaced)	Closely spaced on both poles, particularly on foot pole	Closely spaced on both poles
Stria number in 10 µm	24–28 at centre, 32–34 near foot pole	16–24 puncta near central area and on longer half-valve, 25–38 near the foot pole	21–30 at centre, 26–36 near foot pole (not as tightly packed as in <i>T. kalamensis</i>)	24–39, slightly denser on apices	25–36, slightly denser on apices
Terminal raphe endings	Abruptly bent to same side, not reaching the mantle, sometimes T-shaped	Terminating before reaching the apices, strongly hooked, deflected to same side	Elongate slit frequently observed	Strongly hooked towards the same side, oblique reinforcement on both poles	Unilaterally bent, terminating near the pole, presence of a silica flap
Proximal raphe endings	Pore-like or opening into spathulate groove	Expanded, depressed and pore-like	nd	Spathulate, unilaterally weakly deflected	Spathulate, unilaterally weakly deflected
Pore field	Foot pole apical discrete field composed of closer small areolae, the foot pole bears striae extending to the mantle	A few elongate puncta at foot pole, more abundant circular pores at the head pole	One (or 2) sets of elongate puncta at foot pole, sometimes also present at head pole	Foot pole area with up to 15–17 minute areolae along 1–3 rows	One (to 2) row of small areolae surrounding the foot pole
Reference	Fernandes & Sar (2009)	Holmes et al. (1993a)	Holmes et al. (1993b)	Present study	Majewska et al. (2015)

Note: nd = no data. () = as observed from the original illustration.



Figures 29–35. (LM). *Chelonicola caribeana* sp. nov. Note the barely visible valve striation (Fig. 32), wedge-shape in cingular view (Figs 33–34) and a detached open copula (Fig. 35). Scale bars = 10 µm.

***Chelonicola caribeana* Riaux-Gobin, Witkowski, Ector & D.Chevallier sp. nov.** (Figs 29–35 LM, Figs 36–53 SEM).

Description

Valves small, narrow-elliptical, with round apices (Figs 36–37, 39–40). Frustule biraphid, isovalvar, very slightly wedge-shaped in girdle view (Figs 42–43). Valve length 4.5–13.1 µm, 7.6 µm ± 1.8; valve width 0.7–1.8 µm, 1.3 µm ± 0.3; L/W 6.4 ± 1.7; F/H 1.02 ± 0.05; $n = 68$ (SEM). No appreciable differentiation between foot and head pole areolation on the valve face (Fig. 36), whereas, in cingular view, the valve head pole is identifiable by the presence of the valvocopula closed pole with very large and sub-quadrangular poroids (Fig. 39 copula annotated '1', Figs 42–43 arrows, Figs 44–45 framed arrowheads). Striae dense (38–55 in 10 µm; 43.5 in 10 µm ± 3.6; $n = 68$), hardly discernible in LM (Fig. 32), uniseriate, equidistant, slightly coarser and radiate in mid-valve becoming parallel to slightly convergent at the apices (Figs 36–37, 42), composed most often of two (up to three, Fig. 38 arrowhead) oblong transapical areolae (Figs 36–38), the areolae on the mantle being longer (Figs 37–38, 41–43). The areolae have hymenate pore occlusions (Figs 41, 52). One stria shorter in mid-valve, but no real fascia. Apical pore field lacking. Raphe straight (Figs 36–38). Raphe branch very slightly shorter on the head pole [hardly appreciable, see foot/head (F/H) length and standard deviation]. In external view the proximal raphe endings are distant, dilated, round, straight or very slightly curved in opposite direction to the raphe terminal endings (Fig. 36). Terminal raphe endings doubly hooked on the same side, with a lateral reinforcement but no real flap

(Figs 36, 39 arrowhead) similar at both poles. Internally the raphe branches occur on an elevated central ridge. The branches are lateral, to one side of the ridge (Figs 37, 40–41, 53 arrowheads). Helictoglossae subtle and slightly deflected (Fig. 40). Cingulum composed of several narrow open bands (< 8). Reinforcement present at the closed pole of the valvocopula (Figs 48–49, 51 right arrowheads), and at the closed pole of the 2nd copula (Fig. 51 left arrowheads). The poroids are quadrangular and large on the valvocopula, at a slightly lower density than the striae (Figs 44–45 framed arrowheads), round and denser on the 3rd to 5th copulae. The copulae have one row of poroids, except at the closed pole of the 2nd and 3rd copulae where there are two rows (Figs 44, 46 arrowheads). Loosely arranged small poroids are present on the advalvar edge of the 5th copula (Figs 44–45 arrows).

Holotype

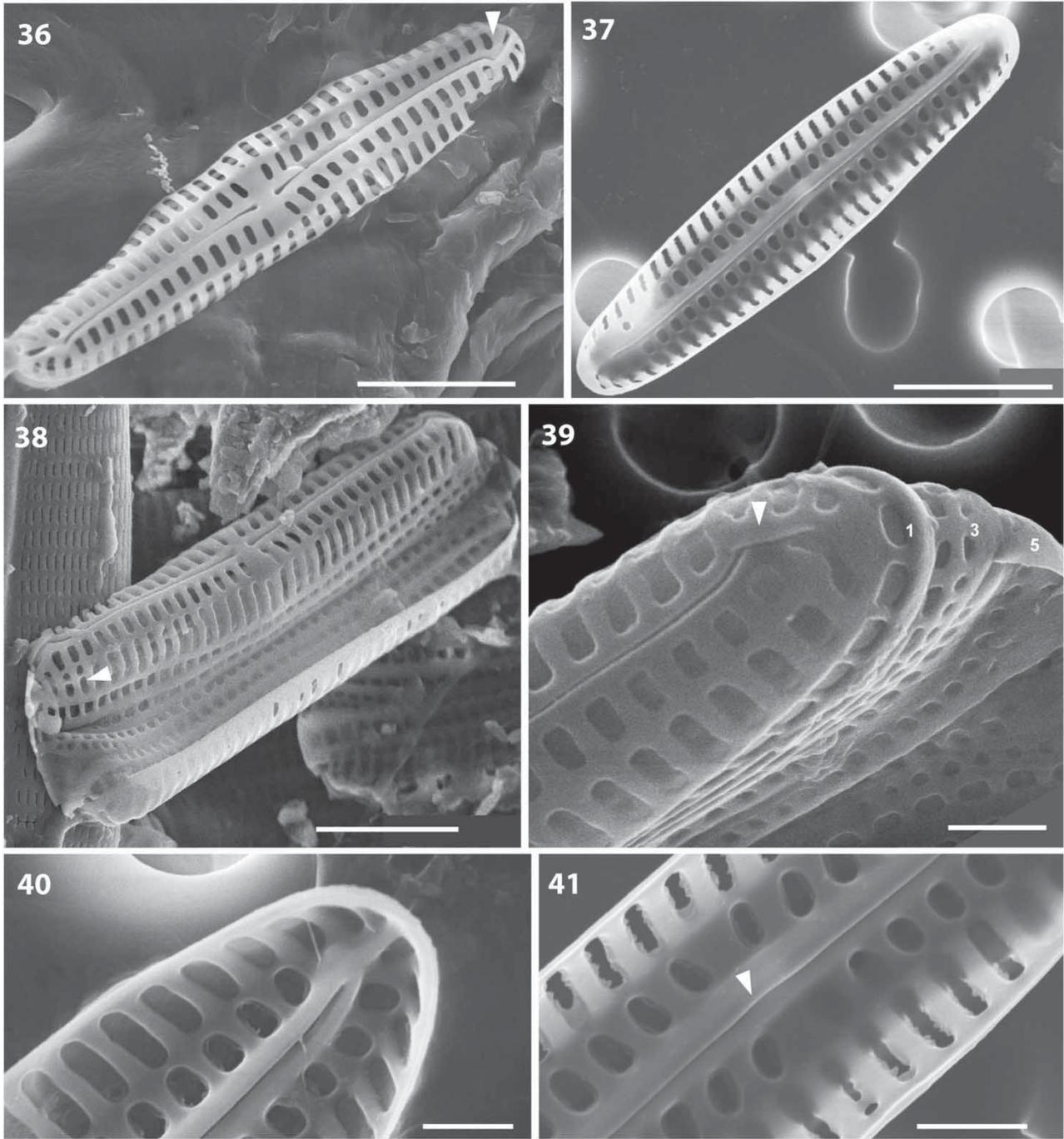
Specimen on SEM stub BM001231514 (Natural History Museum, London, UK), '2' 4 Ch 29/01/2016. Illustrated in Fig. 38.

Isotypes (here designated)

BM 101846, MART 1 in collection C. Riaux-Gobin (CRIOBE, Perpignan, France), SZCZ 23531 in collection A. Witkowski (The Faculty of Geosciences, Szczecin, Poland).

Type locality

Juvenile *C. mydas* from Martinique Island, Anse du Bourg (14 29' 13.43''N, 61 04' 58.88''E). Collector: Damien Chevallier.

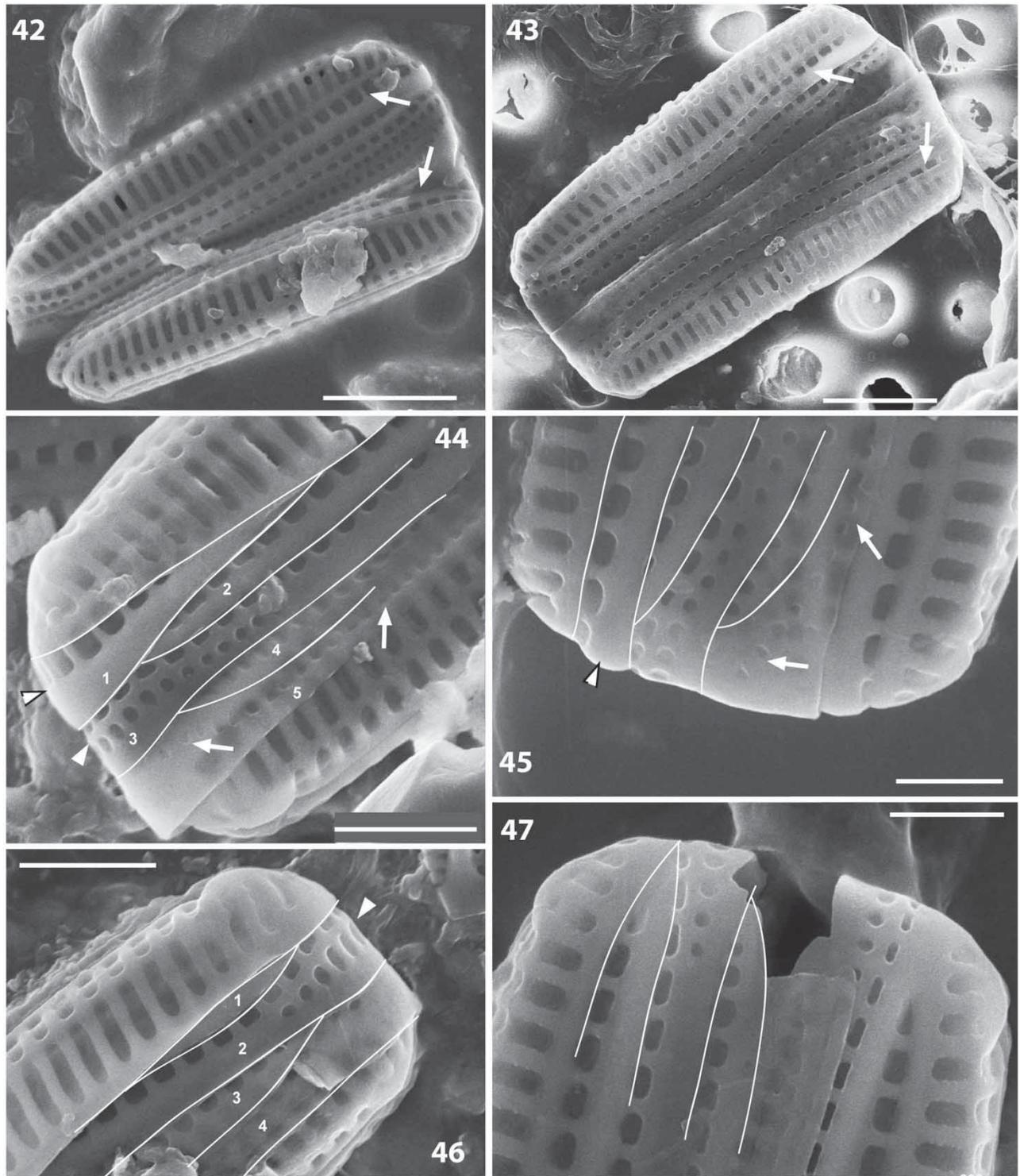


Figures 36–41. (SEM external views). *Chelonicola caribeana* sp. nov. Rod-like valve face, with equidistant striae composed of two elongate areolae (sometimes three, Fig. 38 arrowhead), distal raphe endings doubly hooked (Fig. 36 arrowhead). Holotype specimen illustrated in Fig. 38. External detail of a head pole with distal raphe ending and reinforcement (Fig. 39 arrowhead), robust valvocopula apex with large subquadrangular pores (Fig. 39 '1') and the 3rd copula with two rows of pores at its closed pole (Fig. 39 '3'). Internal views with a raphe system with lateral fissure (Fig. 37), proximal raphe endings terminating at the narrow central nodule (Fig. 41 arrowhead) and subtle helictoglossa slightly deflected towards one side (Fig. 40). Areolae on the mantle often longer than those on the valve face (Figs 38 arrowhead, 41). Scale bars = 2 μ m (Figs 36–38); 500 nm (Figs 39, 41); 1 μ m (Fig. 40).

Taxonomic notes

Chelonicola caribeana is difficult to classify since its heteropolarity is not always evident. Nevertheless the copulae are not pore free, as is usually the case in *Navicula*

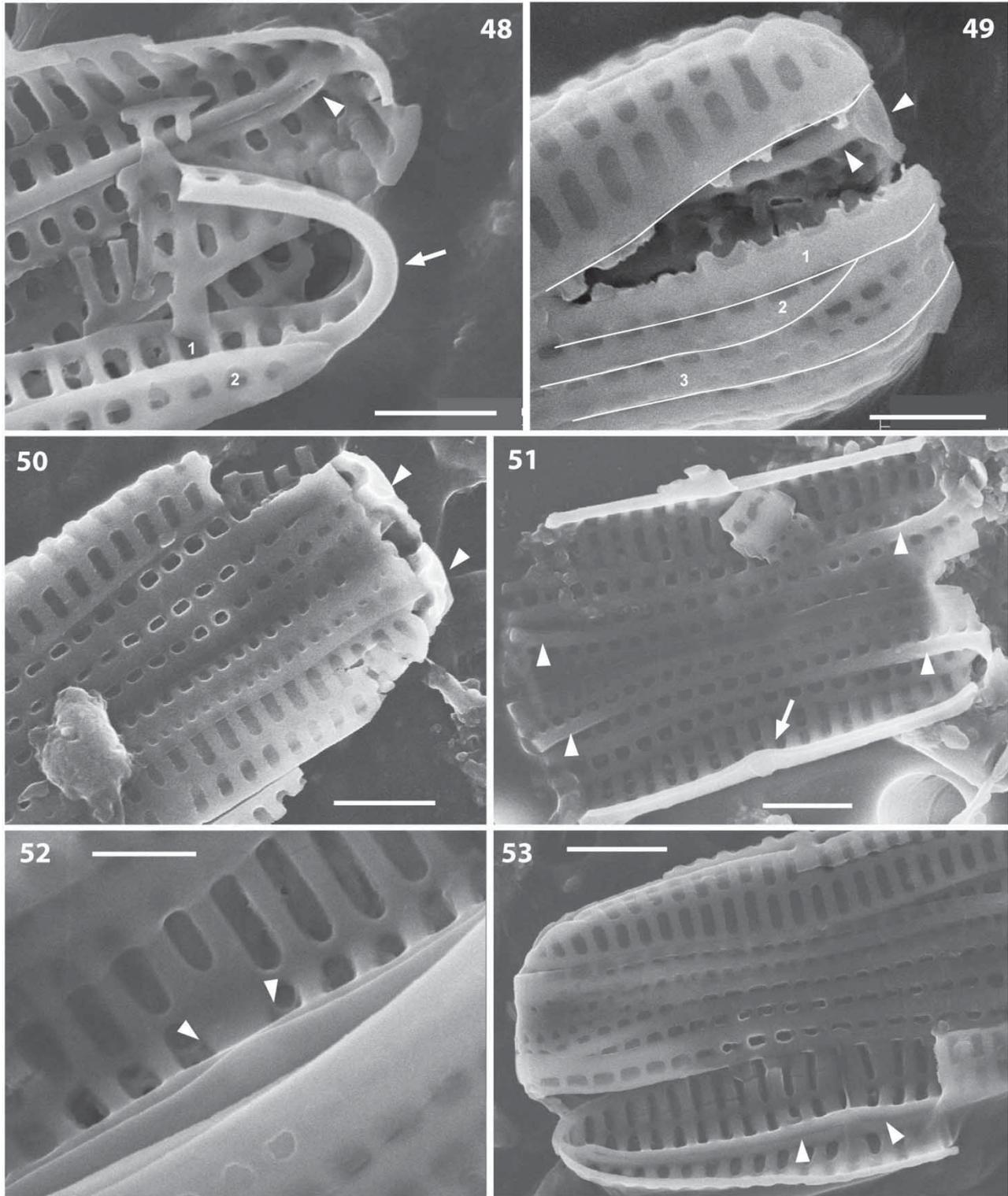
Bory (Round et al. 1990) and show characteristic reinforcements (reminiscent of pseudosepta). There is no real stauros as in *Stauroneis* or *Staurophora* Mereschkowsky. The complex cingulum of *C. caribeana* is similar to that



Figures 42–47. (SEM, external views). *Chelonicola caribeana* sp. nov. Two specimens, slightly wedge-shaped in girdle view with the valvocopula showing large pores (Figs 42–43 twin arrows). Details of the frustule head pole (Figs 44–45), valvocopula with quadrangular large pores (framed arrowheads), 3rd copula with two rows of pores at its closed pole (Fig. 44 arrowhead) and 5th copula with marginal small pores (arrows). Detail of the frustule foot pole (Figs 46–47), 2nd copula with two rows of pores at its closed pole (Fig. 46 arrowhead). Scale bars = 2 μm (Figs 42–43); 1 μm (Figs 44, 46); 600 nm (Figs 45, 47).

of *Gomphonemopsis* but differs by the presence of septa, while *Gomphoseptatum* has a more complex structure, with the presence of a well-developed pseudoseptum at the foot

pole, a valvocopula with a prominent septum at the head pole and ‘a cluster of densely packed round unoccluded (?) pores’ at the foot pole (Round *et al.* 1990). *Tripterion*



Figures 48–53. (SEM, internal views). *Chelonicola caribeana* sp. nov. Frustule head pole with the valvocopula with a reinforcement (short septa) on abvalvar side (Fig. 48 arrow). Slightly raised and deflected helictoglossa (Fig. 48 arrowhead). Septum section (Figs 49–50 arrowheads). Position of the septa at the head and foot pole of the frustule (Fig. 51 arrowheads) and domed central area (Fig. 51 arrow). Detail of the central area with proximal raphe endings (Fig. 52 arrowheads). Raphe branches laterally positioned on the raphe ridge (Fig. 53, arrowheads). Scale bars = 700 nm (Figs 48–49); 1 μ m (Figs 50–51, 53); 400 nm (Fig. 52).

is more clearly heteropolar with a rudimentary pore field. There are similarities with *Epiphallina* and *Tursiocola* in the absence of a pore field and slight heteropolarity, but these have well-developed pseudosepta (Holmes *et al.* 1993a, Denys 1997). Our new taxon is most similar to *Chelonicola* although the type of this genus, *C. costariensis* Majewska, De Stefano & Van de Vijver (Majewska *et al.* 2015), is described as having ‘wedge-shaped’ frustules in girdle view (versus very slightly wedge-shaped in *C. caribea* sp. nov.), striae ‘almost parallel throughout the entire valve’ (versus parallel becoming convergent at apices), proximal raphe endings internally ‘covered by a silica flap’, distal raphe endings ‘elongated’ (versus doubly hooked), ‘striae composed of several small round areolae’ (versus generally composed of only two oblong areolae, the one on the mantle being longer) and ‘up to 12 copulae’ (versus < 8 in *C. caribea*). Given these discrepancies, we propose an emended diagnosis for *Chelonicola* (see below).

Distribution

Chelonicola caribea sp. nov. is dominant and relatively abundant on all scrapings from Martinique turtles (14 juveniles of *C. mydas*) but at different concentrations (< 100 cells per mL, up to 400–600 cells per mL). It should be noted that a rare, rod-like, densely striated taxon, without a foot pole area with small areolae, and not distinctly wedge-shaped in girdle view, was also found (ca. 10.9 µm in length, 1.7 µm in width, ca. 42.6 ± 3.3 striae in 10 µm; *n* = 7, SEM) in the scrapings from the turtle ‘Moon’ (Moorea Island, Society Archipelago). This rare taxon is morphologically very similar to *C. caribea* sp. nov.

Etymology

The epithet *caribea* was given in reference to the Eastern Caribbean where the species was found.

Chelonicola Majewska, De Stefano & Van de Vijver emend. Riaux-Gobin *et al.*

Frustules isovalvar, wedge-shaped to rectangular in girdle view. Cingulum composed of multiple open narrow copulae (from 8 to > 10), mostly uniseriate, with the 2nd and 3rd copulae biseriate at their closed pole (Majewska *et al.* 2015, fig. 7). Valvocopula with a short septum at the head pole and the 2nd copula with a short septum at the foot pole. Valves heteropolar with a broadly rounded head pole and an acutely rounded foot pole, or without appreciable difference in shape between both poles. Central area more or less discrete, not expanded to a fascia or stauros. Pseudosepta and apical pore field absent. Raphe straight to very weakly curving. Proximal raphe endings unilaterally weakly deflected towards the primary side. Distal raphe

fissures elongated to strongly hooked, deflected to the secondary side, continuing a short distance onto the mantle at both poles. Internal proximal raphe endings covered by a silica flap or with slight reinforcement, and distal raphe endings straight, terminating on weakly developed helictoglossae. Striae uniseriate, composed of a reduced number of small, round to elongate areolae. Areolae internally occluded by hymenes.

Discussion

The description of *T. societatis* sp. nov. and *C. caribea* sp. nov. adds to our knowledge of epizoic taxa found on sea turtles. As in other surveys (Wetzel *et al.* 2012; Frankovich *et al.* 2015b, 2016; Majewska *et al.* 2015), epizoic taxa are very small, often < 10 µm in length, requiring EM examination for a full description. In describing *T. societatis* sp. nov. it was clear that there were some similarities with the newly established genus *Poulinea*. The relationship between these genera was explored in Majewska *et al.*'s (2015) cladistic analysis. The affiliation of *Tripterion* with other gomphonemoid genera also needs evaluating.

Tripterion versus *Poulinea*

In order to differentiate their new genera, *Poulinea* and *Chelonicola*, from *Tripterion*, Majewska *et al.* (2015) used a cladistic analysis based on morphological characters (Majewska *et al.* 2015, tables 1 and 2). However, there are problems with this analysis due to some incorrect character coding by Majewska *et al.* (2015).

According to Holmes *et al.* (1993a: 8) *Tripterion* possesses hymenate pore occlusions, not pores ‘without hymenes’ (Majewska *et al.* 2015, table 2), areola openings that are parallel to the stria direction versus ‘0’, which is not defined by Majewska *et al.* (2015, table 1), internal raphe system with lateral fissure versus ‘central’ (Majewska *et al.* 2015, table 2), spatulate external proximal raphe endings almost straight (in opposite position), not deflected to the primary side (Majewska *et al.* 2015, table 2), and neither *Poulinea* nor *Chelonicola* have pseudosepta, contrary to Majewska *et al.*'s (2015, table 2) character coding. There are also other differences between Majewska *et al.* (2015) and Holmes *et al.* (1993a) in the interpretation of morphological characters. Majewska *et al.*'s (2015, table 2) coding of external areola openings in *Tripterion* as ‘0’ equates to ‘more or less circular’, whereas Holmes *et al.* (1993a: 8, figs 4, 6–7) show the areolae adjacent to the raphe to be typically ‘narrowly elliptical’. The description ‘more or less circular’ is also open to interpretation and may lead to confusion. Similarly, Majewska *et al.* (2015, table 2) code apical pore fields in *Tripterion* as ‘2’ (‘at one pole’), but *Tripterion* lacks a true apical pore field, having only ‘a few irregularly scattered elongate puncta at foot pole’ (Holmes *et al.* 1993a), later described as an ‘indistinct

or discrete pore field' by Fernandes & Sar (2009). Furthermore, Majewska et al. (2015) code this character as '0' ('absent') for *Poulinea*, although this genus has 1–2 rows of small areolae at its foot pole. There is a gradient of complexity in foot pole structure from *Tripterion* to *Poulinea* without any obvious discontinuities between the taxa. Morphological characters are being interpreted differently, with the coding used by Majewska et al. (2015) maximizing the perceived differences. If all these points were considered, the morphological proximity of *Poulinea* and *Tripterion* would probably be closer than suggested by the cladogram of Majewska et al. (2015). Because of this close similarity we prefer to describe the taxon from Moorea Island as a *Tripterion*.

Concerning the morphological variability observed within *Tripterion* (Fernandes & Sar 2009) it should be noted that small specimens of *T. philoderma* R.W. Holmes, Nagasawa & Takano (Holmes et al. 1993b, pl. 2, figs 2, 3, 7) have a similarly developed raphe system on both halves of the valve. Furthermore, the 'sets of elongate puncta at the foot pole' are discrete and only arranged in one row on the smaller specimens (Holmes et al. 1993b, pl. 2, figs 2, 3, 7), very similar to the structure observed in *T. societatis*.

Affiliation to other gomphonemoid genera

When describing *Tripterion*, *Epiphalaina* and *Tursiocola*, Holmes et al. (1993a) produced a table, modified from Medlin & Round (1986), comparing eight morphological characters among *Gomphonema* Ehrenberg, *Gomphoseptatum*, *Gomphonemopsis*, *Cuneolus*, *Pseudogomphonema* and *Tripterion*, and concluded that the erection of *Tripterion* was justified. Unfortunately, Holmes et al. (1993a, table 1) did not include *Epiphalaina* and *Tursiocola* in their comparative table. When Fernandes & Sar (2009) established the new combination, *T. margaritae*, they presented a comparative table and clarified several structural features of *Tripterion*, concluding that 'this genus is easily distinguished from the heterovalvar member of the Family, *Rhoicosphenia* and *Campylopyxis*, and less readily distinguished from the isovalvar, heteropolar members of the Family, *Gomphonemopsis*, *Gomphoseptatum* and *Cuneolus*'.

Tripterion, *Epiphalaina*, *Tursiocola*, *Chelonicola* and *Poulinea* all lack a stigma and most have no pore field (Table 2). *Tripterion* has a 'discrete or indistinct pore field' (Fernandes & Sar 2009), *T. societatis* sp. nov. has a foot pole area with scattered minute areolae and *Poulinea* has a few small, isolated areolae at the pole (Majewska et al. 2015). Thus their affiliation to other gomphonemoid genera is low. Grouping these genera as 'gomphonemoid taxa' reflects only their asymmetry about the transapical axis and the presence, in some, of a specific foot pole area. It is therefore an artificial grouping.

There is great variability in several morphological characters among *Epiphalaina*, *Tursiocola*, *Chelonicola*, *Poulinea* and *Tripterion* (Table 1): more or less dissimilar raphe branch length, valve heteropolarity, cingulum complexity (open or closed copulae, with one, or partially two, rows of poroids for each band), position of the raphe on a ridge, and density of the striae near the valve poles. *Tripterion* seems to possess particularly marked heteropolarity, with a well-developed apical pole field at the foot pole with small areolae. It remains to be determined if *Poulinea* represents *Tripterion* taxa that have lost some characteristics, since it seems to fall within a gradient of complexity among *Tripterion* species, from the most complex (*T. margaritae*) to the simplest (*T. philoderma*, *T. societatis*). *Poulinea* may be the simplest link in the chain.

The epizoic diatoms described here are small, not always notably heteropolar, and have a complex cingulum. SEM is therefore required for detailed morphological examination and their identification. It should be noted that a second, rare taxon, close to *Epiphalaina*, was also found in the epizoic assemblage observed on the Martinique *C. mydas* juveniles. It was not observed in LM but only in SEM and no internal view was obtained. The presence of pseudosepta, as well as other characteristics, needs to be confirmed before this taxon can be classified as either *Epiphalaina* or *Tursiocola*.

The present study, with samples from two different oceans (South Pacific Ocean and Caribbean Sea), seems to show differences in turtle colonization. Future investigations will focus on nesting adults of different species from French Guiana to establish whether diatom colonization is linked to the breeding area or to the turtle species themselves.

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