Phytotaxa 124 (1): 1–12 (2013)
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.124.1.1

Morphology and taxonomy of *Psammodiscus* Round & Mann (Bacillariophyceae: Rhaphoneidales) with a description of the new species *Psammodiscus calceatus*

TSUYOSHI WATANABE[1*], TAMOTSU NAGUMO[2], ZHONGMIN SUN[3], KAZUKIYO HASEGAWA[3], TOMOFUMI MIYAGAWA[3], MISATO KUMADA[3] & JIRO TANAKA[3]

[1] *Tohoku National Fisheries Research Institute, Fisheries Research Agency, 3-7-25 Shinhamacho, Shiogama-shi Miyagi 985-0001 Japan (Email: tsuyoshiw@affrc.go.jp)*

[2] *Department of Biology, The Nippon Dental University, Chiyoda-ku, Tokyo 102-8159 Japan*

[3] *Department of Marine Science, Tokyo University of Marine Science and Technology, Minato-ku, Tokyo108-8477 Japan*

Abstract

Part of the definition of *Psammodiscus* is that there is always a small pore and sometimes a rimoportula present on the valve centre. A new species *Psammodiscus calceatus* Tsuy.Watanabe, Nagumo & J. Tanaka is described, which lacks a central small pore. And the valves of *P. nitidus* were found that have two marginal rimoportulae. Living cell of *P. nitidus* attached on sand grain solitary and it has many discoid plastids. The structures of rotae with fin-like projections in *Psammodiscus* differ from those of Rhaphoneidaceae genera. The epicingulum of *Psammodiscus* consists of three or four open bands with the valvocopula and second band opening at 180° to one another alternately at one apex.

Key words: cingulum, morphology, *Psammodiscus*, *Psammodiscus calceatus sp. nov.*, Rhaphoneidales

Introduction

Round established the order Rhaphoneidales to include two families, Rhaphoneidaceae Forti and Psammodiscaceae Round & D.G. Mann (Round *et al.* 1990: 662). The family Rhaponeidaceae includes 13 genera: *Adoneis* G.W. Andrews & P. Rivera (1987: 2); *Delphineis* G.W. Andrews (1977: 249); *Neodetonia* S. Blanco (= *Detonia* Frenguelli (1949: 119); *Dickensoniaforma* R.P. Scherer (1997: 85); *Diplomenora* K.L. Blazé (1984: 218); *Drewsandria* P.A. Sims & R. Ross (1996: 302); *Incisoria* Hajós in M. Hajós & H. Stradner (1975: 937); *Lancineis* G.W. Andrews (1990: 128); *Meloneis* Louvrou, Danielidis & Economou-Amilli (2012: e32198, 2); *Neodelphineis* Takano (1982: 45); *Perissonoë* G.W. Andrews & Stoelzel (1984: 226); *Rhaphoneis* Ehrenberg (1844: 74); *Sceptroneis* Ehrenberg (1844: 264). The family Psammodiscaceae consists of only one monotypic genus *Psammodiscus* Round & Mann (1980: 371), with *P. nitidus* (Gregory) Round & Mann (1980: 371) as its generitype. *P. nitidus* was originally described under the name of *Coscinodiscus nitidus* Gregory (1857: 499) as a radial centric diatom because of its circular valve and radiating striae. However, *C. nitidus* is epipsammic and has areolae occluded by rotae without slits and small sessile rimoportulae, which resembles of *Rhaphoneis* and related genera. Thus, *C. nitidus* was judged not to be a species of *Coscinodiscus* but related to *Rhaphoneis* and placed in the monotypic genus (Round & Mann 1980). Part of the definition of *Psammodiscus* is that there are always a small pore and sometime a rimoportula present on the valve centre. And it was known that *P. nitidus* has the rota with several spokes and the cingulum consisting open bands (Round & Mann 1980).

Cells of *Psammodiscus* were collected from marine coast in Japan and observed using light (LM) and scanning electron microscopy (SEM). The object of this study is to clarify the morphology of species in the genus *Psammodiscus*, as our examination of specimens from *Psammodiscus* revealed differences with previous studies and some new structures leading to the description of the new species, *Psammodiscus calceatus sp. nov.*, which lacks central small pore.

Accepted by David M. Williams: 2 July 2013; published: 15 August 2013

Materials & methods

Samples of sand grains were collected by T. Watanabe in a few meters water depth at two locations: 1) beach of Kume Island (26°20'10"N, 126°49'42"E, Okinawa Prefecture, Japan on 10 May 2006 and 14 September 2007, deposited in personal collection of T. Watanabe under the accession number TW156, TW159, TW166 and TW485); 2) shore of the Sea of Japan in Kutsu (35°45'24"N, 136°01'25"E, Tsuruga-shi, Fukui Prefecture, Honshū Island, Japan, on 16 July 2006, deposited in a private collection under the accession number TW229).

Diatom valves were cleaned following the method of Nagumo & Kobayashi (1990). Cleaned frustules were then mounted onto glass slides with Mountmedia (Wako, Osaka). An Optiphot light microscope (Nikon, Tokyo) with bright field (BF) was used to observe living cells and cleaned frustules. The confocal laser scanning microscope (CLSM) Leica TCSNT system (Leica Microsystems, Heidelberg) with differential interference contrast (DIC) was used to examine living cells and, with fluorescence, was used to detect autofluorescence of plastids and DNA stained by 4',6' diamino-2-phenylindole 2HCl (DAPI) (Watanabe & Nagumo 2006). For SEM, cleaned material was placed onto cover slips, air dried and coated with platinum (Pt) or osmium tetroxide (OsO_4) using E-1030 (Hitachi, Tokyo, Japan) or NEOC-AN (Meiwa fosis, Tokyo) coater, respectively. S-4000 and S-5000 scanning electron microscopes (Hitachi, Tokyo) were used for SEM observations at an accelerating voltage of 3–5 kV, and 10–15 mm working distance.

Valve dimensions (length) were determined from digital images using the image analysis software LIA for Windows 32 ver.0.376ß1 (http://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/index-e.html).

Type slides have been deposited in BM and Museum of Tokyo University of Marine Science and Technology, Tokyo, Japan (MTUF).

Morphological terminology follows Anonymous (1975), Cox & Ross (1981), Kobayasi *et al.* (2006), Ross *et al.* (1979) and Round *et al.* (1990).

Taxonomic results

Psammodiscus nitidus (Gregory) Round & D.G. Mann (1980: 371) (Figs 1–18)
Basionym: *Coscinodiscus nitidus* Gregory (1857: 499, pl. 10, fig. 45)
TYPE:—UK: Scotland, Lamlash Bay (BM 1343, Hendey 1964: 76, syntype).

Size and shape: Cells solitary, attached to sand grains (Figs 1a, b). Valves circular to slightly elliptic in valve view (Figs 2–4). Valve diameter 13.5–28.5 µm, 8–9 striae in 10 µm, 8 areolae in 10 µm (Table 1).

Plastids and nucleus: Discoid plastids located along valve surface, number ca. 90 (Fig. 5). Nucleus lies at cell centre (Fig.5).

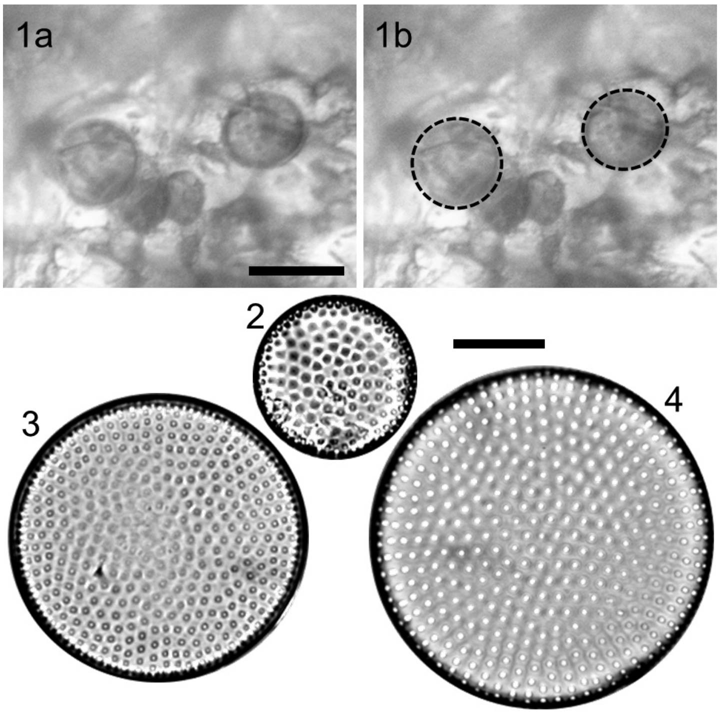
Fine structures of valve: Valve face flat (Fig. 6), striae radiate, reaching mantle (Fig. 6). Areola on valve face (Figs 7, 8) and mantle (Fig. 8) occluded by rotae with 2–3 spokes. Internal views of small valves not observed. Larger valves (Figs 9 and 12) originate from same frustule. Striae and areolae of large valves morphologically similar to those in smaller valves (Figs 9–11); occasionally areola abnormalities visible (Fig. 10). Spokes in areolae not observed from internal view (Fig. 14).

Rimoportula: Number of rimoportulae 0–2 (Figs 6, 12, 15) per valve. Rimoportula external opening located near valve centre (Figs 6, 7). Some valves lack central rimoportula (Fig. 15). In larger valves, external opening of rimoportula observed near valve margin (Fig. 10). In internal view, two rimoportulae located at opposite sides near valve margin (Figs 12–14). Rimoportula sessile with simple slit surrounded by ridge (Figs 13, 14).

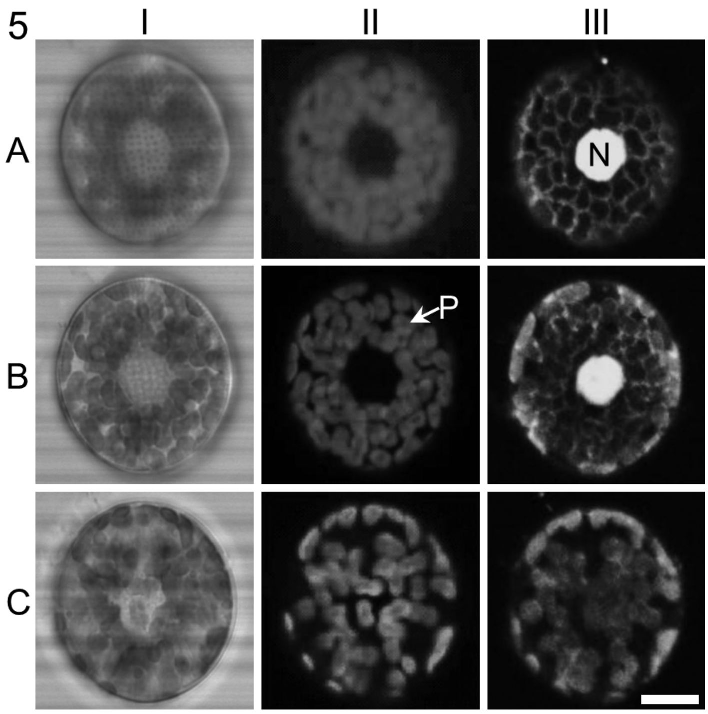
Central small pore: Central small pore located near valve centre (Figs 6, 7).

Additional small pore: In larger valve, external opening of small pore observed near valve margin (Fig. 10). Additional small pore situated close to rimoportula near margin (Fig. 14).

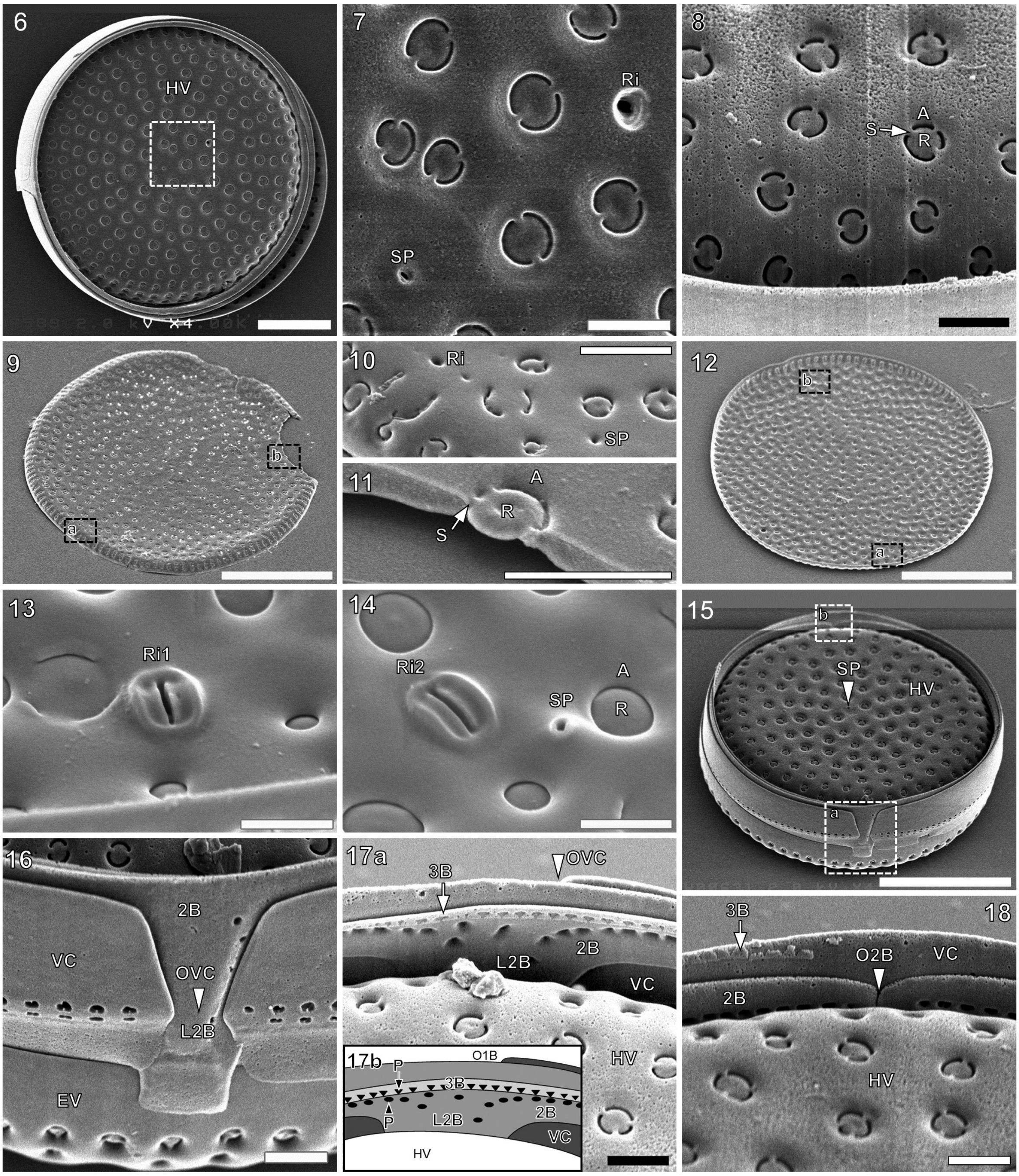
Cingulum: epicingulum consisting of three open bands: valvocopula (VC), second (2B) and third (3B) bands (Figs 17a, b). Valvocopula and second girdle bands open at 180° to each other (Figs 15, 16, 18). VC with two rows of pores (Fig. 16), its opening covered by ligula of 2B (Figs 16, 17a, 17b). 2B with single row of pores (Fig. 17a, b). 3B narrow with single row of triangular non-occluded pores (Figs 17a, b).



FIGURES 1–4. *Psammodiscus nitidus* (LM).
Figs 1a, b: Solitary cells attached to sand grains, living cells from TW153 (BF), solitary attached cells (two circles in fig. 1b) to a sand grain (figs 2a and b are the same image at different focal depths). Figs 2–4. Valves (BF): Fig. 2 from TW166, figs 3 and 4 from TW159. Scale bars = 50 µm (Fig. 2), 10 µm (Figs 3–5).



FIGURES 5. *Psammodiscus nitidus* (CLSM).
Each row (A, B, C) taken at valve surface, shallow and deep focuses, respectively. Note numerous discoid plastids. Column I, DIC; Column II, autofluorescence of plastids; Column III, DAPI stained nucleic acid. P = plastid; N = nucleus. Scale bar = 10 µm.



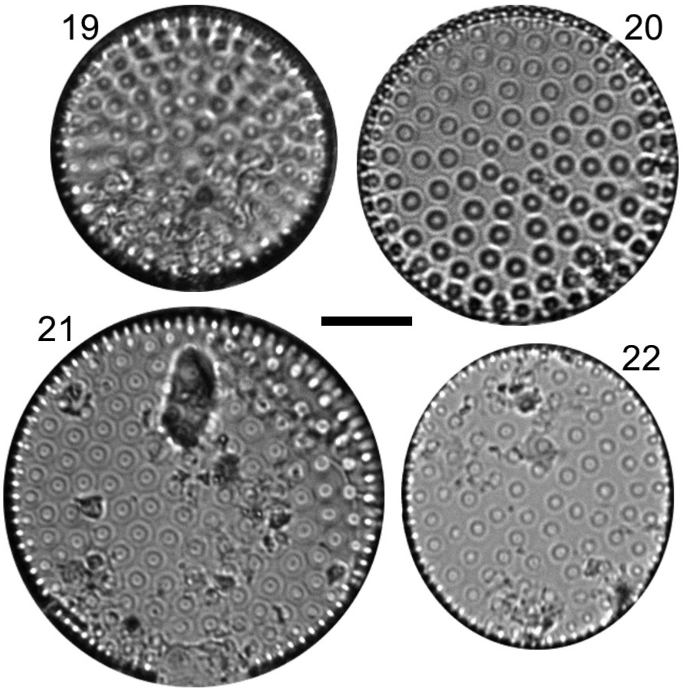
FIGURES 6–18. *Psammodiscus nitidus* (SEM).

Fig. 6. Complete frustule, view of hypovalve (HV), square is enlarged view in fig. 7. **Fig. 7.** Valve face, external openings of rimoportula (Ri) and small pore (SP), note small pore located near valve centre. **Fig. 8.** Mantle, areolae (A) occluded by plated rotae (R) with 2–3 spokes (S). **Fig. 9.** External view of large valve, note valves in figs 9 and 12 generated from the same cell; rectangle (a) is enlarged view in fig. 10; rectangle (b) is enlarged view in fig. 11. **Fig. 10.** External openings of small pore (SP) and rimoportula (Ri). **Fig. 11.** External view of fractured valve; areolae (A) occluded by plated rotae (R) with 3 spokes (S). **Fig. 12.** Internal view of large valve, rectangle (a) is enlarged view in fig. 13; rectangle (b) is enlarged view in fig. 14. **Fig. 13.** First rimoportula (Ri1), note rimoportula located near margin. **Fig. 14.** Second rimoportula (Ri2) and small pore (SP), note both rimoportula and small pore are located near the margin. **Fig. 15.** Complete frustule, note small pore (SP) located near centre of hypovalve (HV); no rimoportula; square (a) is enlarged view in fig 16; square (b) is enlarged view in fig 18. **Fig. 16.** Valvocopula (VC) opening (OVC) occluded by ligula (L2B) of second band (2B); epivalve (EV). **Fig. 17a.** Opposite view from fig. 16; hypovalve (HV), valvocopula (VC) opening (OVC), ligula (L2B) of second band (2B), third band (3B). **Fig.17b.** Schematic drawing of fig. 17a; Pores (P), note pores of second band are circular holes, pores of third band are triangle. **Fig. 18.** Second band (2B) opening (O2B); valvocopula (VC) and third band (3B). Note third band either in formation or is eroded. Scale bars = 10 µm (Figs 9, 12, 15), 5 µm (Fig. 6), 1 µm (Figs 7, 8, 10, 11, 16–18), 0.5 µm (Figs 13, 14).

Psammodiscus calceatus Tsuy.Watanabe, Nagumo & Ji. Tanaka, *sp. nov.* (Figs 19–52)

TYPE:—JAPAN: Honshū Island, Fukui Prefecture, Tsuruga-shi, Kutsu, sandy beach 35°45'24"N, 136°01'25"E, epipsammic (BM 101648!, illustrated in Fig. 20, holotype designated here as marked specimen on slide; MTUF-AL-43009, marked specimen, isotype).

Size and shape: Cells discoid. Valves circular to elliptic, 25.5–28.5 μm in diameter, striae ca. 8 in 10 μm, areolae 4–5 in 10 μm (Figs 19–22). Single small rimoportula occasionally present, situated near valve centre. Apical pore fields and central pores absent.



FIGURES 19–22. *Psammodicus calceatus sp. nov.* (LM. BF); **Fig. 20 =** holotype. Scale bar = 10 μm.

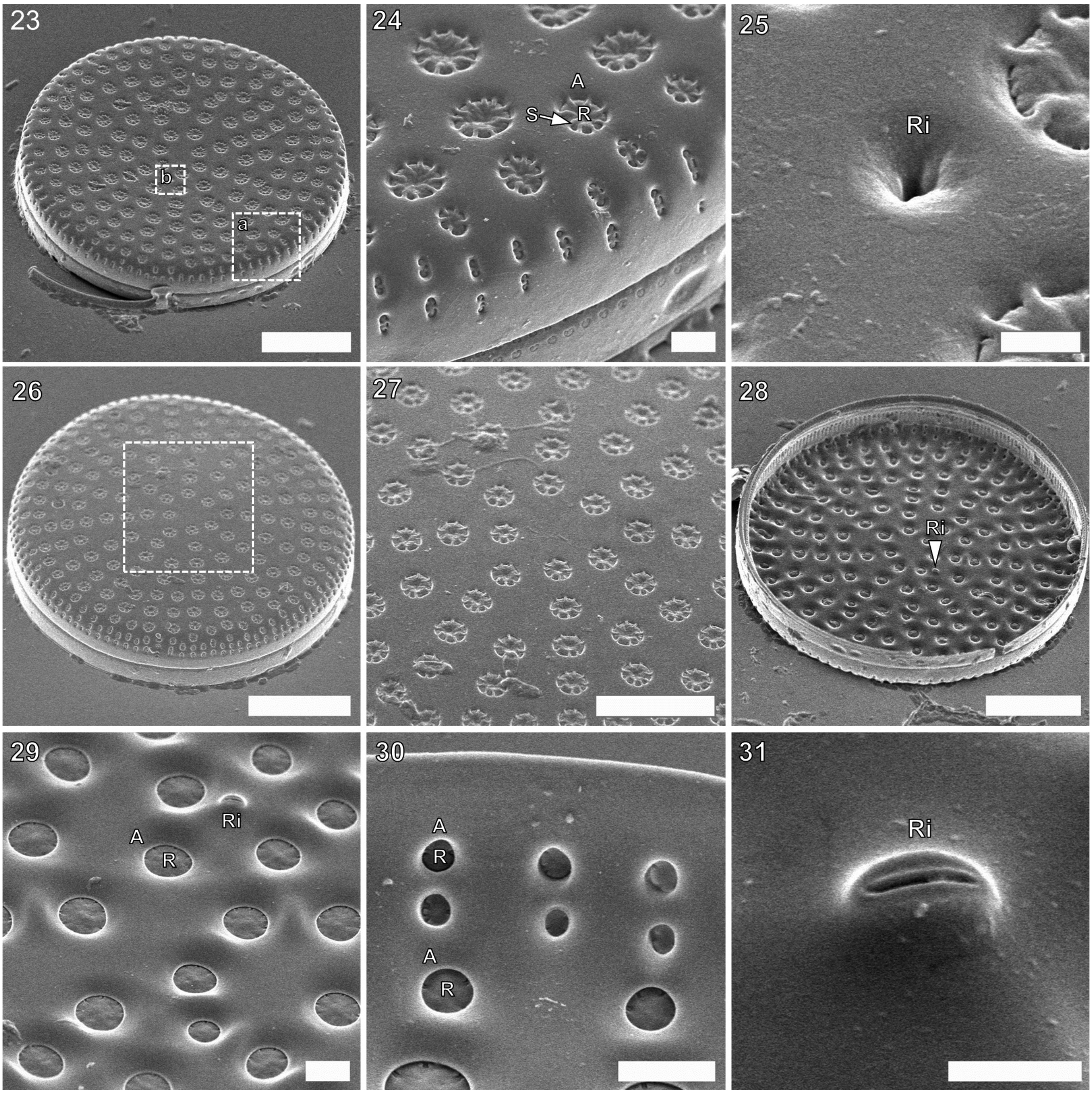
Fine structure of valve: Striae radiating from centre to mantle (Fig. 23). Areolae much smaller in mantle than valve face (Fig. 24). Areolae circular to elliptical, occluded by plated rotae with 5–9 spokes (Fig. 24). Spokes connect rotae to external valve surface (Fig. 32), connecting part of rota, concave at margin (Fig. 33). Ring structure surrounding inside bases of areolae (Fig. 34). Spokes of areolae not evident internally (Fig. 35). Rotae with seven to eight pairs of fin-like projections (Figs 35, 36). Spokes connecting to rotae between fin-like projections (Fig. 36). Spoke located behind ring structure and fin-like projections (Figs 35, 36).

Rimoportula: Number of rimoportula 0–1 (Figs 23, 26) per valve. When present, rimoportula always central and always one per valve. External opening of rimoportula either present (Fig. 25) or absent (Figs 26, 27). From internal view, valve surface flat (Fig. 28) and spokes of rotae not evident (Figs 29, 30). Small sessile rimoportula present near valve centre, with simple slit (Figs 28, 31). Rimoportula not located in internal view.

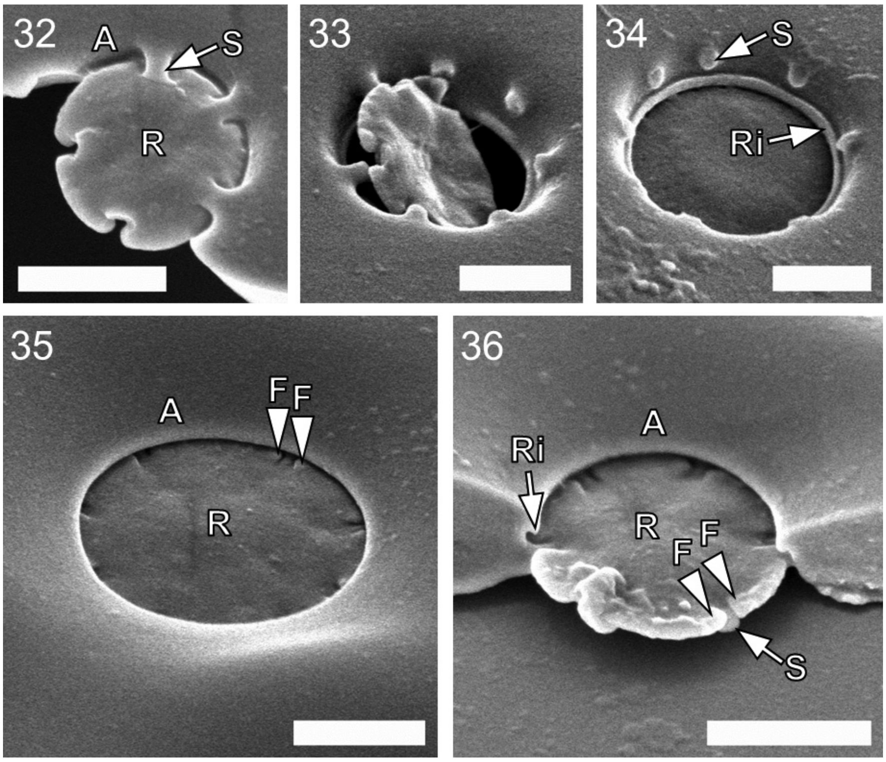
Small pore: Central and additional small pores always absent (Figs 23–30).

Cingulum: Epicingulum consists of four open bands: the valvocopula (VC), second (2B), third (3B) and fourth (4B) band (Figs 37, 38, 39). VC and 3B open on same side of frustule whereas (Figs 42, 43); 2B and 4B open on opposite sides (Figs 38, 39). Position of band openings shift slightly, offsetting each other (Figs 38, 39). Ends of VC have rounded corners (Fig. 40). Pars interior of VC almost equal in size to pars exterior (Fig. 40). VC with two rows of small pores (Fig. 41) occluded by rotae with 1 or 2 spokes (Fig. 42). VC highly visible, other bands less so (Fig. 41). Internally, bands form a line in sequence from 4B to VC (Fig. 43). Pars interior of VC slightly undulate to fit valve (Fig. 43). Single row of elongated grooves advalvar to pores in VC (Figs 43, 44, marked G). Tongue-like ligula of second band occludes opening of VC (Fig. 45). Opening of 2B evident in external view (Fig. 38). Single row of pores present on pars interior of second band (Fig. 46); pores occluded by rotae with either 1 or 2 spokes (Fig. 47). 3B with small trapezoid ligula (Fig. 48). Single row of pores lacking rotae present on pars interior (Figs 48, 49). 4B with very small trapezoid ligula (Fig. 50). 4B opens as narrow slit (Fig. 51). Pars interior with single row of triangular areolae lacking rota (Figs 50, 51; Fig. 52 = schematic drawing of epitheca).

Etymology:—The type locality 'Kutsu' means shoes in Japanese; *calceatus* is Latin for shoe and shod.



FIGURES 23–31. *Psammodicus calceatus sp. nov.* (SEM).
Fig. 23. External view of theca; square (a) enlarged view in fig. 24; square (b) enlarged view in fig. 25. **Fig. 24.** Valve face and mantle, areolae (A) occluded by plated rotae (R) with 3–10 spokes (S). Note areolae elongate with small number of spokes at the mantle. **Fig. 25.** External opening of rimoportula (Ri). **Fig. 26.** External view of theca, square enlarged view in fig. 27. **Fig. 27.** Valve lacking small pore and rimoportulae. **Fig. 28.** Internal valve view, arrowhead indicating rimoportula (Ri). **Fig. 29.** Internal opening of rimoportula (Ri), areolae (A) occluded by plated rotae (R), spokes not seen in internal views. **Fig. 30.** Areolae (A) occluded by plated rotae (R) on valve face and mantle. **Fig. 31.** Lips of rimoportula (Ri). Scale bars = 10 µm (Figs 23, 26, 28), 1 µm (Figs 24, 27, 30), 0.5 µm (Figs 25, 31).

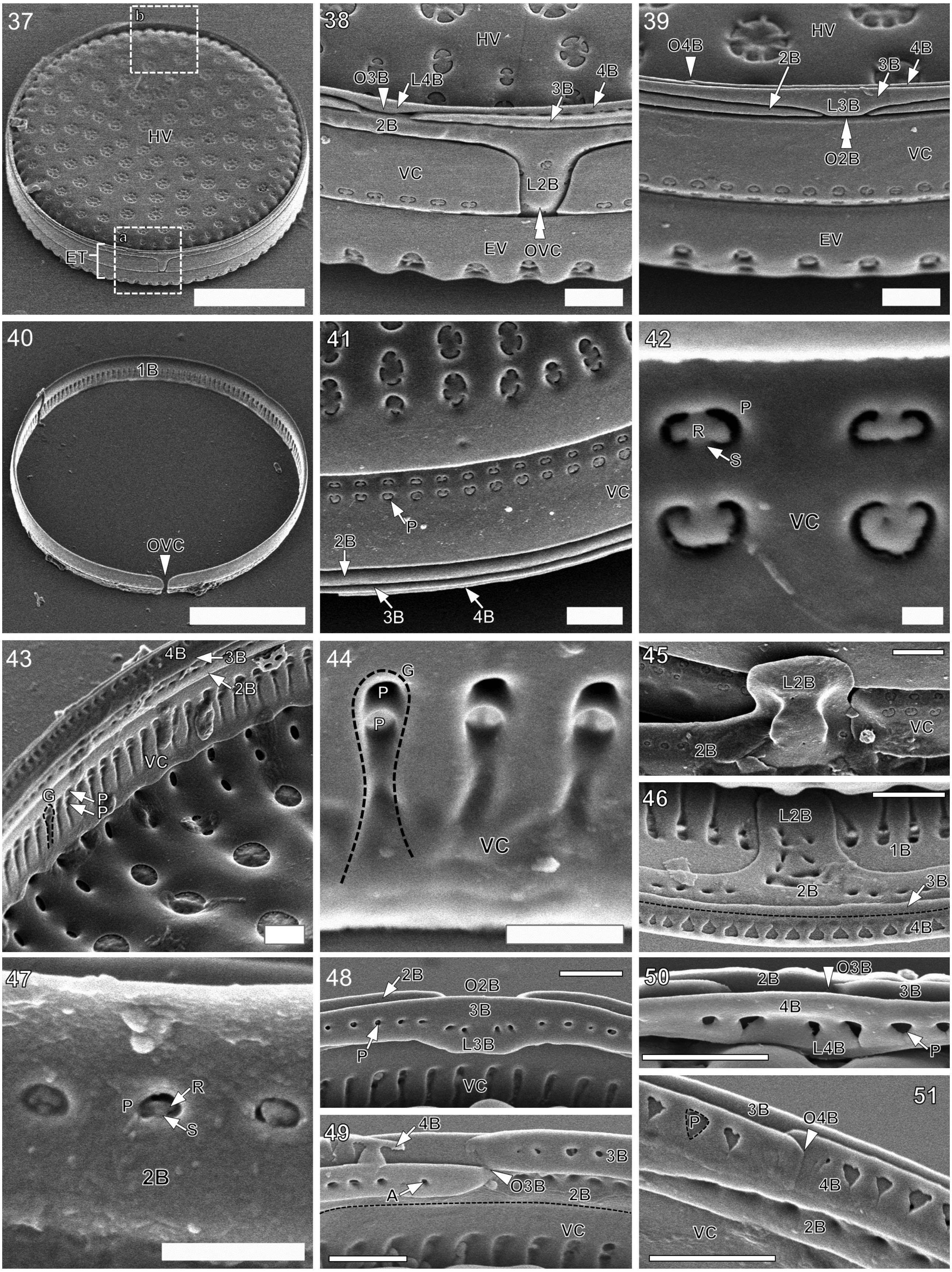


FIGURES 32–36. *Psammodicus calceatus sp. nov.*, areolae structure.
Figs 32–34. External views. **Fig. 32.** Areola (A), rotae (R) with two broken spokes (S) total = 5. **Fig. 33.** Rotae broken (spokes appear to = 7). **Fig. 34.** Areola without rota, showing ring structure (Ri). Note knob-like projections are traces of spokes (S, as a 'tree stump'). **Fig. 35.** Internal view of areola (A) and rota (R), with fin-like projections (F; rather than spokes). **Fig. 36.** Internal view of areola fracture (A), spoke (S) connecting to rota between fin-like projections (F). Note spokes located behind ring structure (Ri) and fin-like projections. Scale bars = 0.5 μm.

Discussion

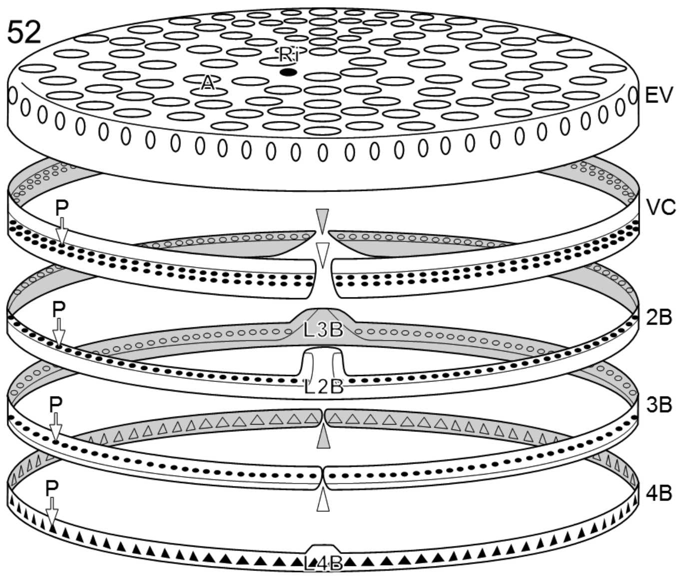
Cells of *P. nitidus* were observed growing on the surface of sand grains, the first observation of the growth habit of species in the genus *Psammodiscus*. Species of other members of the Rhaphoneidaceae – *Rhaphoneis*, *Perissonoë*, *Delphineis* – are epipsammic (Table 1, Drebes 1974, Sato *et al.* 2011, Watanabe unpublished data). The cells of species from *Rhaphoneis*, *Perissonoë* and *Delphineis* have several to many discoid plastids (Table 1, Drebes 1974, Sato *et al.* 2011, Watanabe unpublished data); the numbers of discoid plastids in *P. nitidus* is similar to those in species of both *Rhaphoneis* and *Perissonoë*. The epipsammic habitat and multiple discoid plastids can be considered characters common to members of Rhaphoneidales.

SEM observations revealed the structures of areola in valves of *Psammodiscus*, showing pairs of fin-like projections on rota, a structure not known in *Psammodiscus*. Round and Mann (1980) observed the fine structure of rota, which has several spokes per areola and no slits. In all Rhaphoneidaceae genera, rotae always have two spokes per areola and no fin-like projections with or without slit (Andrews & Rivera 1987, Blazé 1984, Louvrou *et al.* 2012, Round *et al.* 1990, Sar *et al.* 2007, Takano 1982). Thus, it is suggested that the number of spokes and the pairs of fin-like projections are taxonomically important characters for separating the family Psammodiscaceae from Rhaphoneidaceae.



FIGURES 37–51. *Psammodicus calceatus sp. nov.*, epicingulum.

Fig. 37. Complete frustule, epitheca (ET) and hypovalve (HV). Square (a) indicates enlarged view in fig. 38; square (b) indicates enlarged view in fig. 39. **Fig. 38.** Openings (OVC, O3B) of valvocopula (VC) and third band (3B) occluded by ligulae (L2B, L4B) of second (2B) and forth (4B) bands, respectively. Note positions of openings slightly offset with respect to each other. Epivalve (EV) and hypovalve (HV). **Fig. 39.** Openings (O2B, O4B) of second band (2B) and fourth band (4B). Note positions of openings slightly offset with respect to one another, the former occluded by the ligula (L3B) of third band (3B); valvocopula (VC), epivalve (EV) and hypovalve (HV). **Fig. 40.**Valvocopula (VC) and its opening (OVC). **Fig. 41.** Cingulum. Note valvocopula (VC) with two rows of pores (P); second (2B), third (2B) and fourth (4B) bands. **Fig. 42.** Pores (P) occluded by rotae (R) with one or two spokes (S) of valvocopula (VC). **Fig. 43.** Internal view of cingulum, note groove structure (G, dotted line) along advalve edge from uppermost pore (P) row of valvocopula (VC); second (2B), third (2B) and fourth (4B) bands. **Fig. 44.** Groove structure (G, dotted line) along advalve edge to pores (P) of valvocopula (VC) in internal view. **Fig. 45.** External view of ligula (L2B) of second band (2B); valvocopula (VC). **Fig. 46.** Internal view of ligula (L2B) of second band (2B); valvocopula (VC), third (3B) and fourth (4B) bands. Note dotted line showing border of third and fourth bands. **Fig. 47.** Pores (P) occluded by rotae (R) with one or two spokes (S) of second band (2B). **Fig. 48.** Third band (3B) with a single row of pores (P) lacking rotae. Opening (O2B) of second band (2B) occluded by ligula of third band (L3B). **Fig. 49.** Opening (O3B) of third band (3B); valvocopula (VC), second (2B) bands and broken fourth (4B). Note dotted line showing the border of valvocopula and second bands. **Fig. 50.** Fourth band (4B) with a single row of triangular pores (P); opening (O3B) of third band (3B) occluded by ligula of fourth band (L4B); second band (2B). **Fig. 51.** Opening (O4B) of fourth band (4B) with a single row of triangular pores (P, dotted line); valvocopula (VC), second (2B) and third (3B) bands. Scale bars = 10 µm (Figs 37, 40), 1 µm (Figs 38, 39, 41, 43, 45, 46, 48–51). 0.5 µm (Figs 44, 47), 0.1 µm (Fig. 42).



FIGURES 52. Schematic drawing of epitheca of *Psammodiscus calceatus*. A, areola; EV, epivalve; Ri, rimoportula; 2B, second band; 3B, third band; 4B, fourth band; L2B, ligula of 2B; L3B, ligula of 3B; L4B, ligula of 4B; Pores, P; VC, valvocopula; arrowheads, openings of bands.

Furthermore, the epicingulum structure in species *Psammodiscus*, based on SEM observations, was recorded for the first time. The following structural components of the epicingulum, present in both species of *Psammodiscus*, characterize the genus: an absence of granules; all bands have a single opening and at least one row of pores; the pores are occluded by rotae without slits having one or two spokes; the outermost band has a single row of triangular pores. The cingulum of *Psammodiscus* has previously been reported that the valvocopula (VC) is open with two rows of areolae, the gap in the open end of the band being closed by the ligula of the second band, which is much narrower than the VC and nonporous (Round & Mann 1980). The epicingulum of *Rhaphoneis* and *Perissonoë* consist of three bands covered by granules and have pores occluded by rotae with slits (Watanabe *et al.* 2007, Watanabe unpublished data). The outermost band is closed and, in *Perissonoë,* is ornamented, its edge has a fine sharp structure resembling a finely toothed edge (Watanabe *et al.* 2007, Watanabe unpublished data). The epicingulum of *Delphineis* consists of four to five bands without granules and pores (Watanabe *et al*. in press); the outermost and second outermost bands are short. Thus, in the case of *Psammodiscus*, the epicingulum structure can help define a genus and variations within it can distinguish species, at least in orders such as the Rhaphoneidales.

Psammodiscus calceatus is the second species in the genus *Psammodiscus* to be described. It differs from *P. nitidus* in the following morphological features (Table 1): *P. calceatus* lacks the central small pore, which is always present in *P. nitidus*; *P. nitidus* usually has one or two rimoportulae, whereas they are often absent in *P. calceatus*; the density of areolae of *P. calceatus* is lower than that of *P. nitidus*; the number of spokes per rota in *P. calceatus* is greater than in *P. nitidus*; the epicingulum of *P. calceatus* consists of four bands, while there are only three in *P. nitidus*.

TABLE 1: Morphological comparison of *Psammodiscus nitidus*, *P. calceatus* sp. nov., *Rhaphoneis amphiceros*, *Perissonoë crucifera* and *Delphineis surirella* (* see Watanabe *et al.* 2007) n.d. = no data; +, present; -, absent.

family		Psammodiscaceae		Rhaphoneidaceae		
genus		*Psammodiscus*		*Rhaphoneis*	*Perissonoë*	*Delphineis*
species		*P. nitidus*	*P. calceatus* sp. nov.	*R. amphiceros*	*P. crucifera*	*D. surirella*
life form		epipsammic	epipsammic	epipsammic	epipsammic	epipsammic or plankton
habit		solitary	solitary	chain	solitary	chain
plastid shape		discoid	n.d.	discoid	discoid	discoid
number of plastids		ca. 90	n.d.	numerous	ca. 80	several
valve form		circular	circular to elliptic	elliptic to rhomboid	tetragon	broadly elliptic to lancelate
length (diameter) of valve		13.5–28.5	25.5–28.5	16.0–96.6	23.2–31.1	15.8–46.3
width of valve		-	-	13.6–24.4	22.7–29.7	11.7–19.7
width of sternum		-	-	1.0–1.5	1.0–1.5	1.0–1.5
striae in 10 μm		8-9	ca. 8	5.6–7.9	9.2–11.9	6.3–7.4
areolae in 10 μm		ca. 8	4–5	6.6–8.9	9.8–11.2	7.5–9.0
the ratio of length and width		-	-	1.12–3.11	0.96–1.05	1.4–2.4
the ratio of sternum and width		-	-	0.06–0.07	0.04–0.05	0.07–0.15
granules		-	-	+	+	-
spine or spine-like projections		-	-	-	+	+/-
number of sternum		-	-	1	3–4	1
striae		uniseriate	uniseriate	uniseriate	uniseriate	uniseriate
areolae		circular	circular	circular	circular	circular
slits of rota		-	-	concentric	perforated	-
spokes per rota		2–3	5–9	2	2	2
fin-like projections on rota		+	+	-	-	-
number of apical pore fields per valve		0	0	2	2-4	0
number of small pores per valve		1	0	0	0	4
position of small pores		centre (rarely margin)	-	-	-	pole
number of rimoportulae per valve		0–2	0–1	2	3–4	2
position of rimoportulae		centre (rarely margin)	centre	pole	pole	pole
epicingulum	granules	-	-	+	+	-
	number of bands	3	4	3	3	5
valvocopula	number of opens	1	1	1	4	1
	areolae	circular	circular	circular	circular	circular
	slits of rota	-	-	concentric	perforated	-
2nd band	number of opens	1	1	1	4	1
	ligulae	+	+	+	-	+
	areolae	circular	circular	circular	circular	circular
	slits of rota	-	-	concentric	perforated	-
second outermost band	number of opens	1	-	-	-	1
	ligulae	+	-	-	-	+
	areolae	circular	-	-	-	-
outermost band	number of opens	1	1	0	0	1
	ligulae	1	1	1	4	-
	areolae	+	+	-	-	-
	fine sharp structure*	-	-	-	+	-
References		This study	This study	Sato *et al*. 2011, Watanabe unpubl.	Watanabe *et al*. 2007, Watanabe unpubl.	Hasle & Syvertsen 1996, Sar *et al*. 2007, Watanabe *et al*. in press

Round & Mann (1980) defined the genus *Psammodiscus* having always a small central pore and sometimes a single small rimoportula near the valve centre. The change of the generic definition seems to be necessary for specimens lacking small central pore and having two rimoportulae near the valve margin. The morphology of the cingulum is similar in both species of *Psammodiscus* except for the number of bands. The third (outermost) band of *P. nitidus* corresponds morphologically to the fourth (outermost) band of *P.*

calceatus, *i.e*. both bands have an opening and a single row of triangular pores. The common morphologies of the cingulum, shared between both species, is a useful character for generic definition of *Psammodiscus* in Rhaphoneidales.

We found that valves of *P. nitidus* with two rimoportulae had them located at 180° from each other near the valve margin. Mann (1984) hypothesized that the ancestral elongate 'araphid' diatom was derived from the circular valve of *Psammodiscus* by a gradual reduction of the sternum – thus proposing the 'pseudocentric' pattern centre hypothesis (Mann 1984, p. 123, Fig. 3b, c). In the family Rhaphoneidaceae, valves of various species have two (or several) rimoportulae at each pole (Round *et al.* 1990). In *P. nitidus*, the two rimoportulae at opposite sides to each other near the valve margin may be the vestiges of bipolar valves. Thus, our observations support the hypothesis of a 'pseudocentric' pattern centre as primary evidence that *Psammodiscus* is not a radial 'centric' diatom.

Acknowledgements

We thank David M. Williams for valuable comments and correcting some of the English; Masanori Nasu for help using the CLSM; Fusako Mitsuhashi and Takanori Matsuoka for help using the SEM.

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