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Observations on Late Cretaceous *Micrampulla* (Corethrales, Bacillariophyceae) from the Campbell Plateau (Zealandia), southwest Pacific Ocean

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Abstract

Late Cretaceous (late Campanian) diatom assemblages from the Campbell Plateau (Zealandia), southwest Pacific Ocean, obtained from Deep Sea Drilling Project (DSDP) Leg 29 Site 275, contain well-preserved specimens of two enigmatic diatom species currently assigned to the genus *Ktenodiscus*; *Micrampulla parvula* originally described from the Maastrichtian-age Moreno Shale, California, and *Pterotheca cretacea* from DSDP Site 275. In general, the two species share a number of common features with modern *Corethron* (domed valves, probable heterovalvate frustules,

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T-shaped serrated articulated spines, marginal sockets), but differ in the location of the sockets (i.e. vertically at the base of the valve dome and not on the rim), the design of the spines and sockets, and the hollow structure extending from the valve center. Although hooked spines are absent, equivalent 1-spine and 2-spine valves can be recognized in these two species. The recently described genus *Praecorethron* from the same late Campanian sediments shares many features with *Micrampulla*, but lacks the inflated central valve structure. As a result of our studies, the relevant subclass, order and family definitions are emended, as well as those of *Micrampulla*, *M. parvula* and *M. cretacea* comb. nov., and a new family, Micrampullaceae fam. nov., is erected to distinguish the ancient genera (*Micrampulla* and *Praecorethron*) from modern *Corethron*.

Keywords: *Campanian*, *Corethron*, *Ktenodiscus*, *morphology*, *Praecorethron*, *taxonomy*

Introduction

The diatom genus *Pterotheca* Grunow ex Forti has been in use for over 130 years, but as Fourtanier & Kociolek (1999) pointed out, it was invalidly published (i.e. no formal description), assigned a *nomen nudum* as a lectotype, and is a later homonym of the spermatophyte *Pterotheca* Cassini. To alleviate this problem, the original species of *Pterotheca* (*P. aculeifera* Grunow, *P. kittoniana* Grunow and *P. subulata* Grunow), as well as *Stephanogonia* (*Pterotheca*?) *danica* Grunow, were transferred to *Ktenodiscus* Pantocsek and *Furthecca* Blanco & Wetzel, respectively (Blanco & Wetzel 2016). In an attempt to organize this group of resting spores, the enigmatic genus *Micrampulla* Hanna was also synonymized with *Ktenodiscus*, despite a lack of morphological evidence supporting the transfer, and consequently *Pterotheca parvula* (Hanna) Hajos & Stradner, the type species of *Micrampulla*, was transferred to *Ktenodiscus* (Blanco & Wetzel 2016).

Herein, we present light and scanning electron microscope (SEM) observations on two species of *Micrampulla*, a poorly understood genus from Late Cretaceous sediments from the southeast margin of Campbell Plateau, South Pacific, which clarify its taxonomic position, and leads us to emend the descriptions of *Micrampulla parvula* Hanna and establish one new combination, *Micrampulla cretacea* (Hajos & Stradner) comb. nov. Given the strong morphological similarity, in possessing a ring of marginal sockets and serrated T-shaped spines, we infer a close connection between *Micrampulla*, *Corethron*

Castracane sensu stricto and *Praecorethron* Abe et al. As a consequence, the descriptions of the Corethrophycidae, Corethrales and Corethraceae are emended herein, and *Micrampulla* and *Praecorethron* are placed in the Micrampullaceae fam. nov.

Materials and methods

Samples and microscopy

Four samples from Deep Sea Drilling Project (DSDP) Leg 29, Site 275 were observed in this study; three from Core 1-1 (118–119 cm, 129–130 cm and 130–131 cm) and one from Core 1-2 (75–77 cm). It should be noted that, when requesting the sample 1-1, 118–119 cm the repository corrected the sample interval to 1-1, 22–23 cm, because the upper 96 cm of the core-liner was void. However, no such corrections were made when requesting the other two samples many years later. A sample from the Hustedt Diatom Collection labelled ‘Moreno Shale, Water Canon, Californien P33’ (AM 1457) was also investigated and found to contain *M. parvula*. Subsamples were prepared as permanent mounts using Mountmedia (Wako Pure Chemical Industries, Ltd.; refractive index = 1.50) following standard laboratory methods. Light microscope (LM) observations were carried out on an Olympus BX40 LM at $\times 400$ and $\times 1000$ magnifications, and digital images were taken with an EOS KISS Xgi camera. For SEM observations, subsamples were filtered, then pieces of the nitrocellulose HA-type Millipore membrane filter were cut out and attached to an aluminum stub and coated with gold in a JEOL JFC-1500 ion sputter coater or with osmium in a POC-3 coater (Meiwafosis, Sendai, Japan). Observations were carried out on a JEOL JSM-6510 LV SEM, with images taken using the built-in digital camera.

Results

Based on light and SEM observations, two species of *Ktenodiscus* investigated and documented herein are bona fide members of the Corethrales, and thus *Ktenodiscus cretaceus* (Hajos & Stradner) Blanco

& Wetzel should be transferred to *Micrampulla*, and the original descriptions of the latter genus and its generitype, *M. parvula*, should be emended. Given the taxonomic affinities of *Micrampulla*, there is also a need to emend the definitions of the higher taxa.

Corethrophycidae F. E. Round & R. M. Crawford emend.

Original description: *Peripheria unius valvae frustuli processibus unguiformibus munita* (Round et al. 1990, p. 651) – The periphery of one frustule valve armed with claws.

Emended description: Vegetative valves bearing articulated spines in sockets.

Note: With the inclusion of *Micrampulla* and *Praecorethron*, which lack hooked spines, there is a need to redefine the subclass based on a common character.

Corethrales F. E. Round & R. M. Crawford emend.

Original description: *Cellulae solitariae heterovalvares. Valvae tholiformes annulum peripheralem spinorum serratorum munitae, una valva processibus unguiformibus etiam praedita, poris simplicibus dispersis. Portulae nullae. Plantae marinae planctonicae* (Round et al. 1990, p. 653) – Solitary cells heterovalvate. Dome-shaped valve armed with a ring of serrated spines around the periphery, one valve process clawed as previously discussed, covered by simple pores. No portulae. Marine planktonic plants.

Typus: *Corethron* Castracane

Emended description: Frustules heterovalvate, with domed valves. Type 1 (1-spine) valves with one type of spine, generally few in number. Type 2 (2-spine) valves with one or two spine types, generally greater in number (often twice as many as Type 1 valves). No portulae. Marine, planktonic.

Note: For a number of reasons, we wish to retain one order for the three genera. Whilst the *Corethron* frustule is known to be heterovalvate, heterovalvy in the other two genera (*Praecorethron* and *Micrampulla*) is only presumed following the discovery of two valve (and spine) types. A second order would only be warranted if, in the future, these two genera are shown to be non-heterovalvate, or a new non-heterovalvate genus is discovered.

Corethraceae Lebour emend.

Original description: Cells cylindrical with rounded valves, solitary. Valves with long spines radiating outwards at an angle from the margin. Scale-like intercalary bands, very inconspicuous. (originally designated as the Corethronaceae – Lebour 1930, p. 79).

Emended description: Cells cylindrical, generally solitary. Type 2 valves with two types of articulated spines. Scale-like intercalary bands, very inconspicuous.

Typus: *Corethron* Castracane

Note: This seems the best rank to separate *Corethron* from *Praecorethron* and *Micrampulla*. On a nomenclatural note, we are not sure who orthographically emended the original family name Corethronaceae to Corethraceae, but the latter is used in Silva (1980, p. 21).

Micrampullaceae fam. nov.

Type 2 valves sporting one type of articulated spine.

Typus: *Micrampulla* Hanna

***Micrampulla* Hanna emend.**

Complete frustule unknown, presumed to be heterovalvate. Frustule fragment tubular, with rectangular (in girdle view), perforated girdle region, and reticulate domed valve with hollow ‘shaft’ extending into flared or globular distal structure. Domes of both valves associated with thickened reticulate poroid walls, and with vertically-positioned sockets at base of dome. Sockets associated with T-shaped, serrated articulated spines held in place by supporting structures on either side of socket. Type 1 valve with fewer sockets than type 2 valve, and possessing different supporting structures. Mid-portion of ‘shaft’ with low costae but without reticulate network. Distal structure heavily silicified and reticulate.

Etymology: *micro* (L.) *ampulla* (L.) meaning small globular flask; inferring that Hanna only saw fragments of the distal portion, not the basal portion.

Type species: *Micrampulla parvula* Hanna emend.

***Micrampulla parvula* Hanna emend. (Figs 1–55)**

Basionym: *Micrampulla parvula* Hanna (1927), p. 26, pl. 3, fig. 15.

Synonyms:

Archaeomonas elegante Rampi (1940), p. 67, fig. 6.

Archaeomonas Chiarugii Rampi (1940), p. 64, fig. 8; (?) Hajos & Stradner (1975), p. 937, pl. 14, figs 14–16; pl. 39, fig. 2.

Pterotheca (Micrampulla) parvula (Hanna) Hajos & Stradner (1975), p. 934, pl. 12, figs 12–15, pl. 37, figs 1–4.

Pterotheca parvula (Hanna) Hajos & Stradner (1975), p. 735, figs 13.13–13.14.

Micrampulla doldingi Chambers (1996), p. 262, pl. 14, fig. 7. (invalid)

Ktenodiscus parvulus (Hanna) S. Blanco & Wetzel (2016), p. 199.

References: *Micrampulla parvula* Hanna – Hanna (1934), p. 355, pl. 48, fig. 6; Deflandre (1952), p. 565, fig. 433, O; Cornell (1972), p. 46, pl. I, figs 1–3; Perch-Nielsen (1975), p. 883, pl. 13, figs 1–4, 10–14, 16–27; Chambers (1996), p. 263, pl. 14, figs 5–8; Nikolaev et al. (2001), p. 26, pl. 39, fig. 10.

Holotype: CAS 2025 (see Nikolaev et al. 2001, pl. 39, fig. 10).

Type locality: Moreno Gulch, Dosados Canyon, Marca Canyon, California.

Repository: California Academy of Sciences (CAS).

Emended descriptions

Moreno Shale specimens (**Figs 1–17**)

LM observations: Only fragments of the globular, inflated central structure and ‘shaft’ have been observed in this study. The straight to slightly curved tubular ‘shaft’ flares at both ends to support the proximal ‘dome’ and distal inflation (Fig. 4b), and bears longitudinal low costae along part of its length (Figs 4b, 6). The distal end is associated with an inflated globular structure, with a surface covered by a reticulate network. The top of the globular structure may be somewhat flattened (Figs 2a, 8).

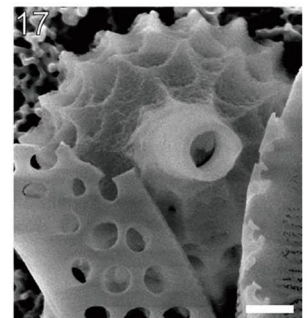
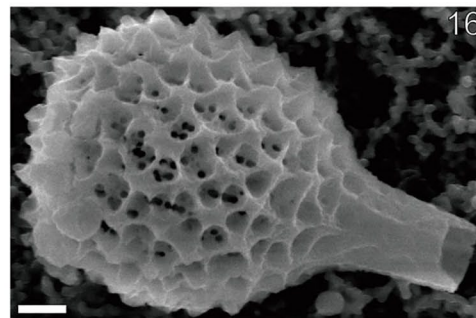
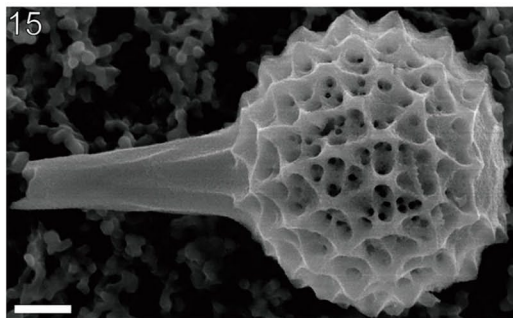
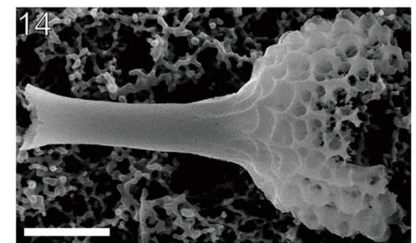
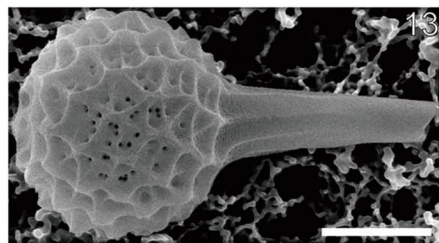
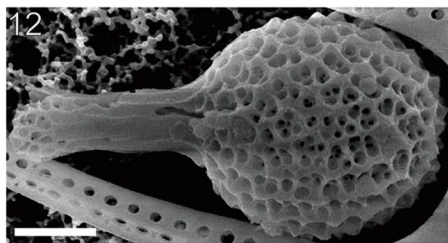
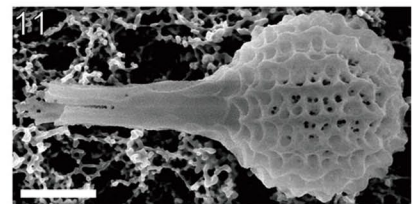
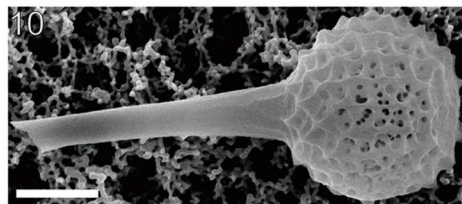
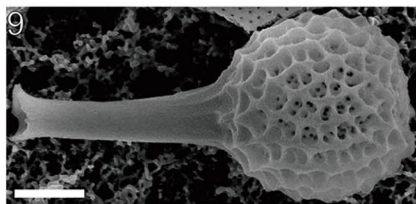
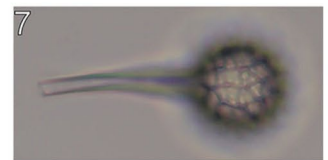
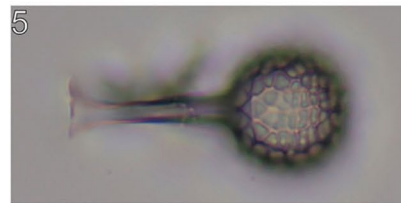
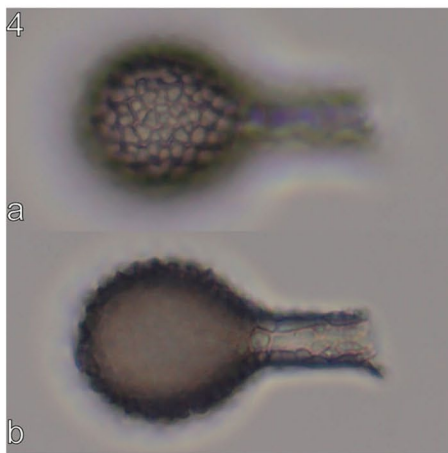
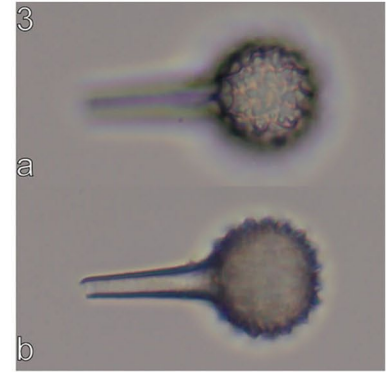
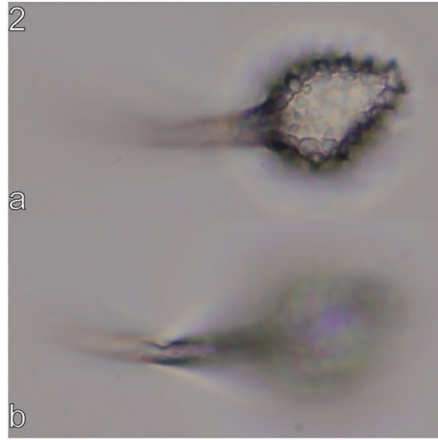
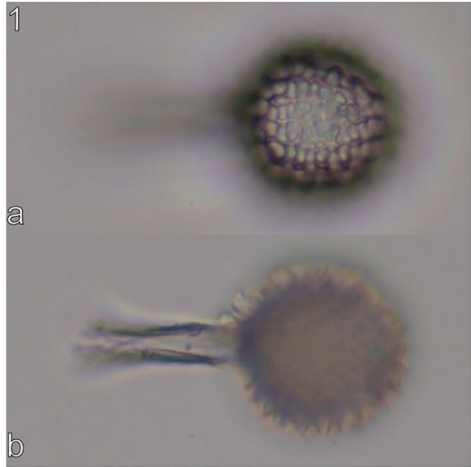
SEM observations: The tubular ‘shaft’ (1.7–3.4 μm wide, at least 9.8–16.3 μm long) is hollow and circular in cross-section (Fig. 17),

bearing low costae largely at the distal end, with the rest of the 'shaft' being smooth (Fig. 14). The globular structure (7.8–14.1 μm wide, 8.9–15.4 μm long) is covered by a densely reticulate network of thickened silica, with round pores at the bottom of the 'pits' (Figs 15, 16). The top of the globular structure is sometimes slightly flattened (Figs 10, 15).

DSDP Site 275 specimens (**Figs 18–55**).

LM observations: Valves, always seen in girdle view, comprising a domed basal part connected by a tubular 'shaft' to a club-shaped, often elongate distal portion. Dome covered by reticulate network, with a marginal series of large holes (sockets), from which articulated spines often protrude (Figs 29, 33). Diameter of inflated distal region is slightly smaller than diameter of basal dome and girdle band. Two types of valves have been observed; in general, Type 1 valve with few sockets, steep dome, long 'shaft' and an elongate club with few large holes (Figs 18–27), whereas Type 2 valve has twice as many sockets, broader dome, shorter 'shaft' and more globular club with higher density of large holes (Figs 28–34). Occasionally, cylindrical girdle bands attached to valves of both types (Figs 18, 29).

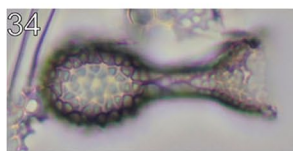
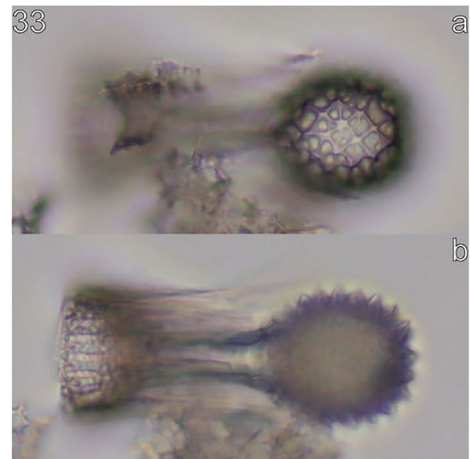
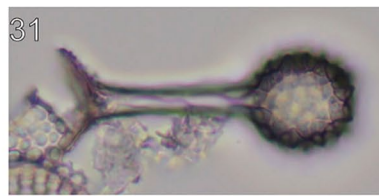
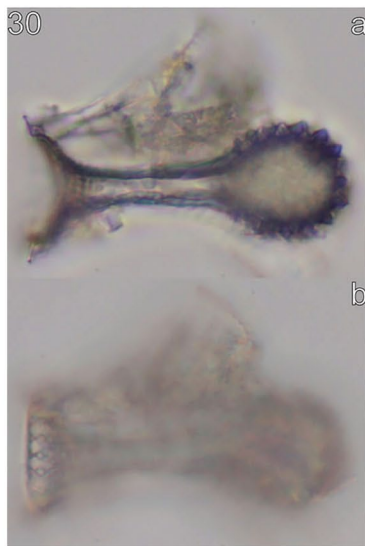
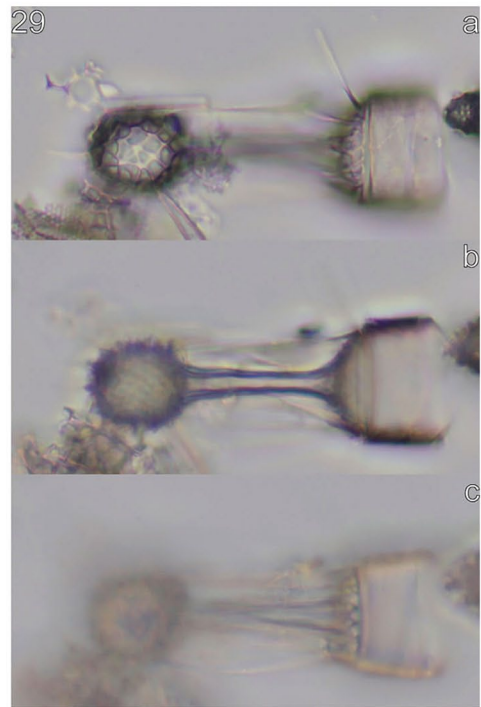
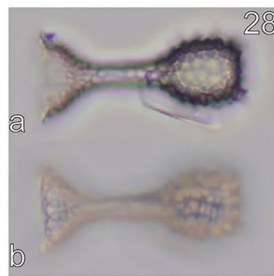
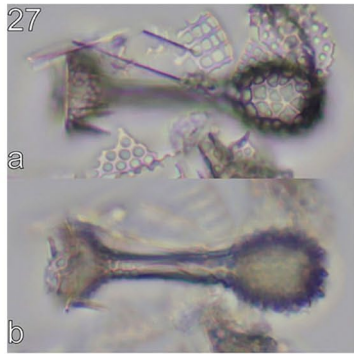
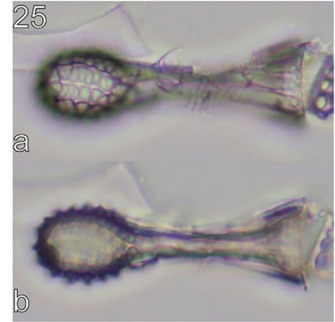
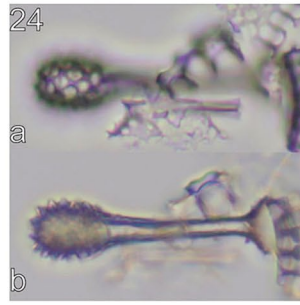
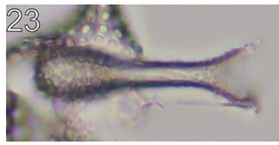
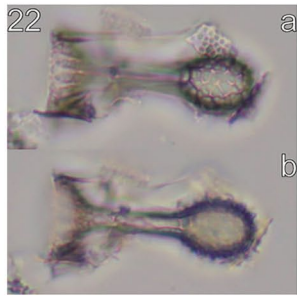
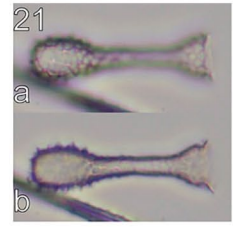
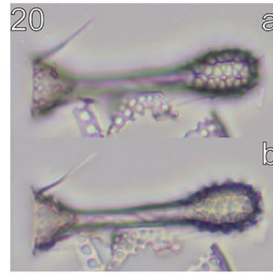
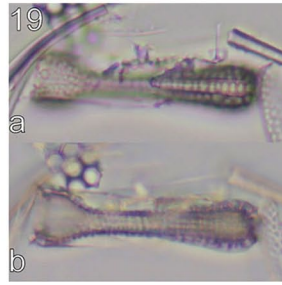
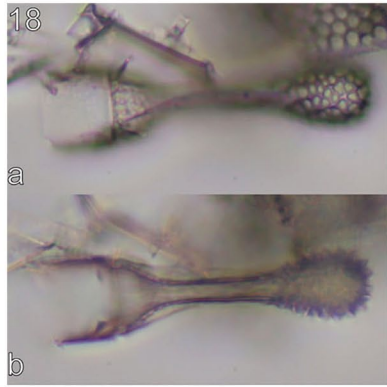
SEM observations: Frustule shape unknown, but assumed to be cylindrical, heterovalvate (with Type 1 and Type 2 valves). Type 1 valves circular in valve view (Figs 46–47), 7.4–14.1 μm in diameter in girdle view. Valve base characterized by about ten to 15 sockets alternating with an equal number of H-shaped supporting structures (Figs 40, 44). Each socket associated with articulated spine, flattened and hyaline at the base, opening distally into characteristic *Corethron*-like form, with serrations and T-shaped cross-section (Fig. 44), with top of the T oriented toward the center of the valve (Fig. 47). H-shaped structures on either side of articulated spine with notches on inner wall that accommodates wider basal part of spine (Figs 42, 44). Marginal area narrow, but with prominent rim (Fig. 44). Dome, 3.7– 7.6 μm high, arising from valve center, with wide, central tubular process ('shaft') extending distally to support club-shaped structure. Total valve height, 21.7–38.3 μm , from valve base to top of club-head. Club 'shaft', 1.8–4.2 μm wide, 6.6–17.8 μm long, hyaline with pronounced low costae.



Figs 1–17. *Micrampulla parvula*. Moreno Shale (AM1457).

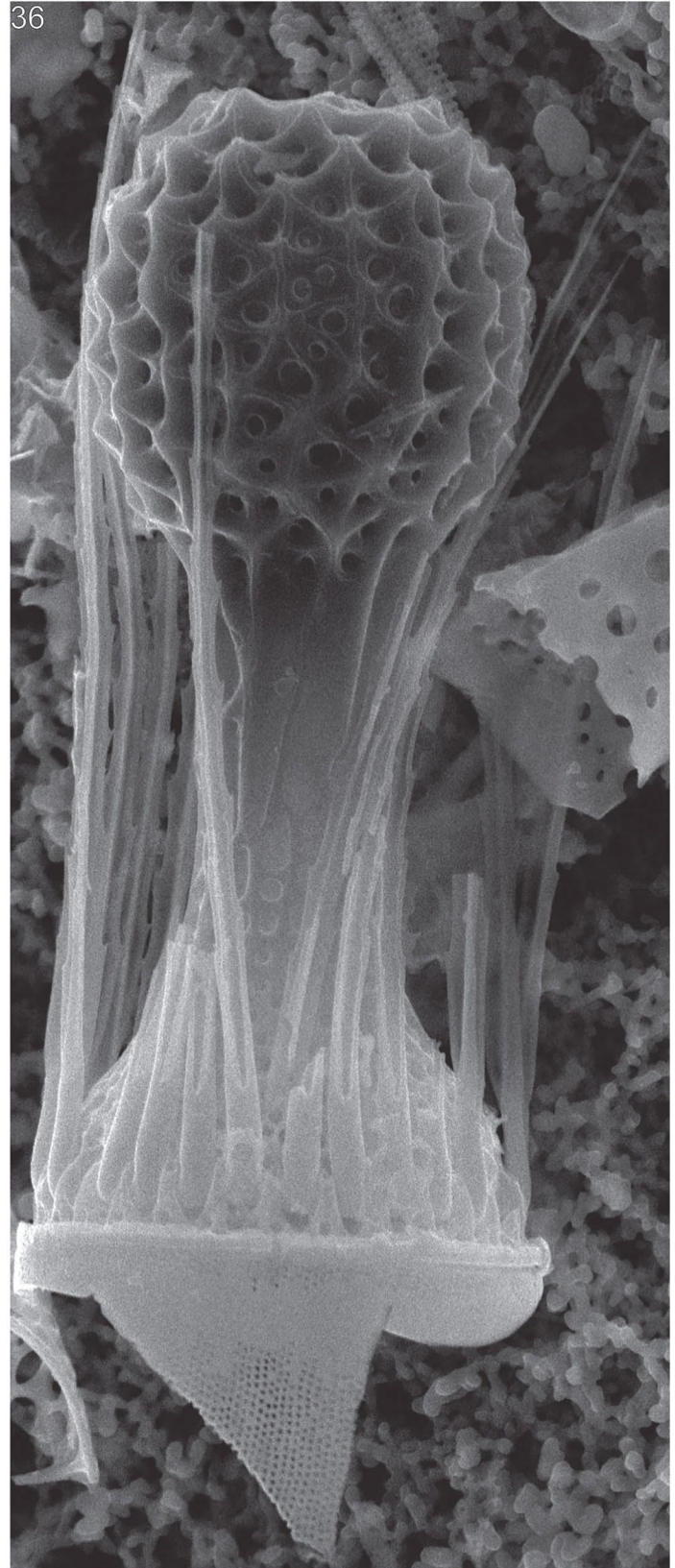
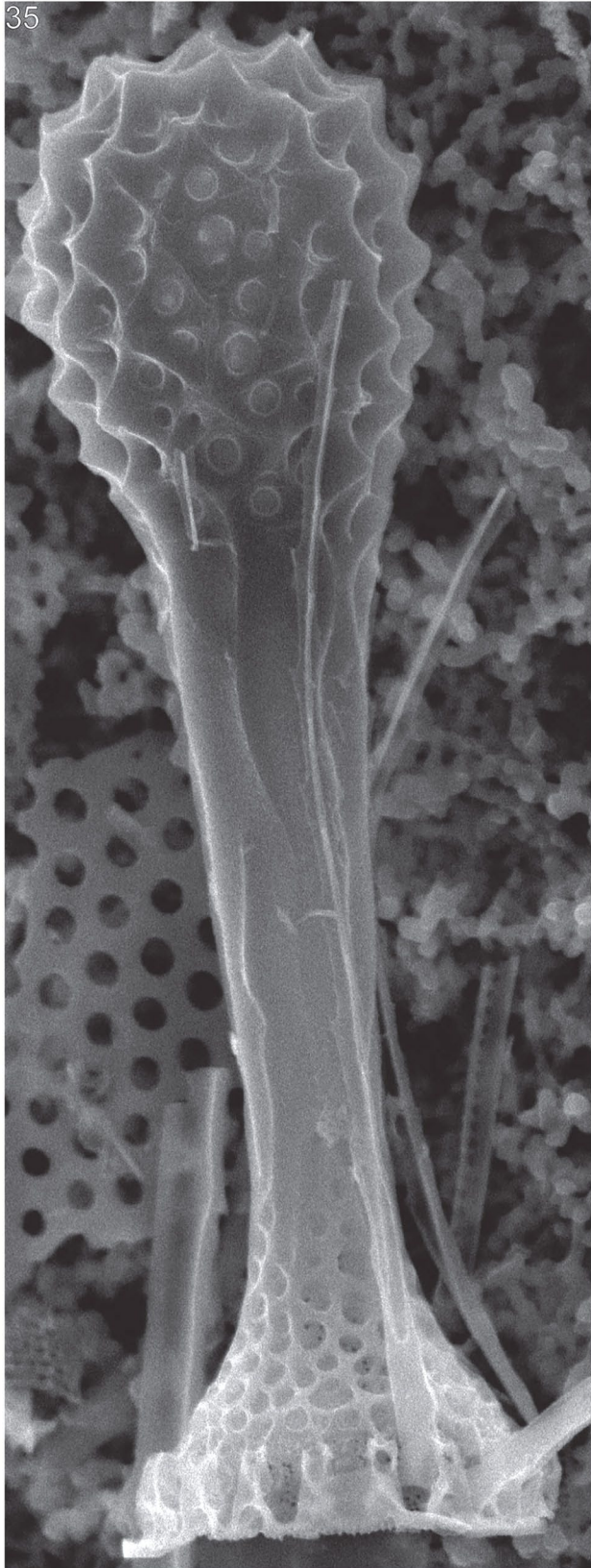
Figs 1–8 . LM. Fragments of globular central structures in side view, including four specimens shown in two different focuses (labelled as ‘a’ and ‘b’). Scale bar = 10 μm .

Figs 9–17 . SEM. Fragments of globular central structures in side view, apart from Fig. 17 , which is in proximal view. Note, smooth ‘shaft’ and pores at bottom of each ‘pit’ of the reticulate network. Scale bars = 2 μm (Figs 15–17) or 5 μm (Figs 9–14).



Figs 18–34. *Micrampulla parvula*. LM. DSDP 29-275-1-2, 75–77 cm. Fragments of central structures in side view, including 14 specimens shown in two or three different focuses (labelled as ‘a’, ‘b’ and in one case ‘c’).

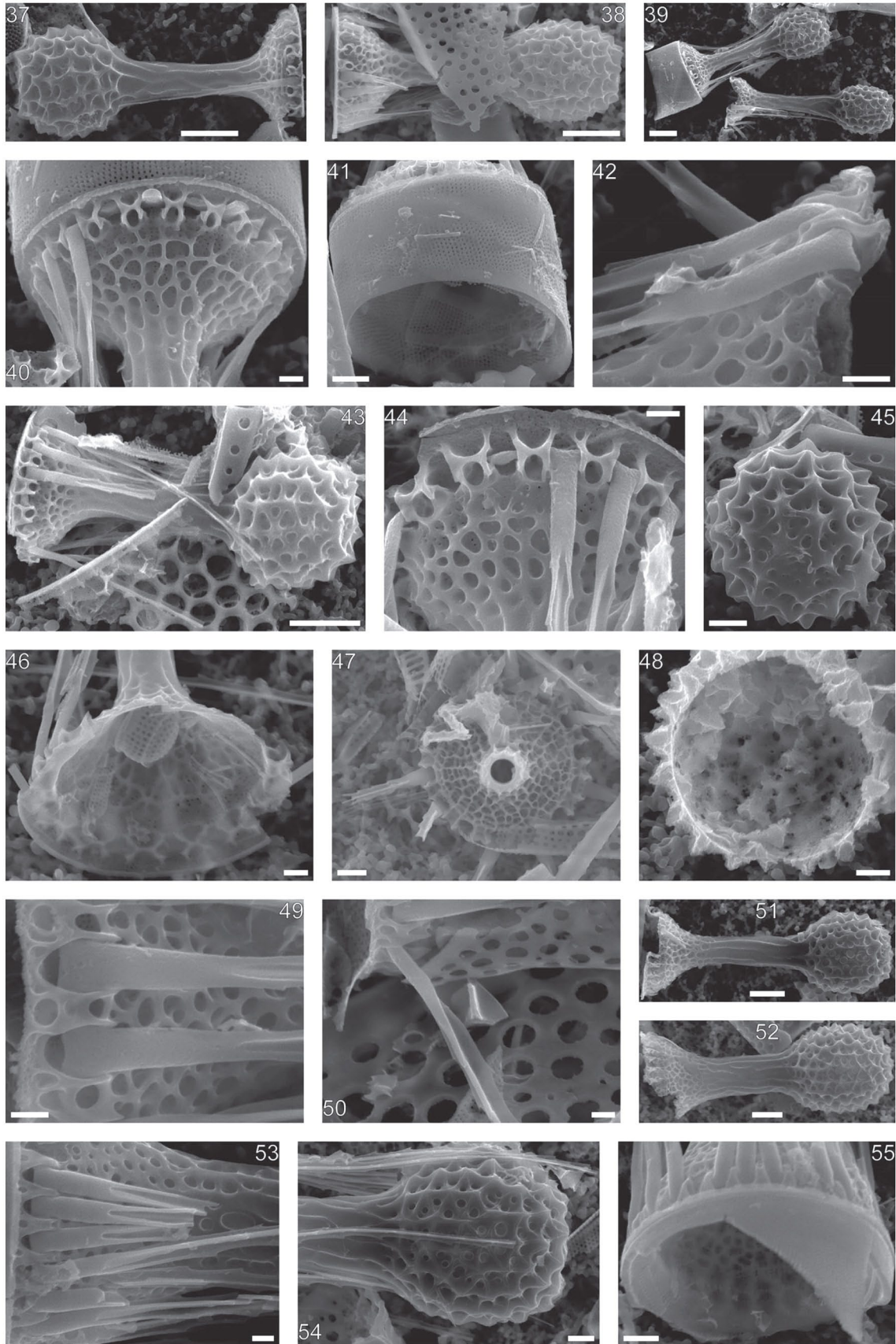
Figs 18–27 . Type 1 valve, with elongate central structure (‘cotton-bud’-like in shape). Figs 28–34 . Type 2 valve, with more globular central structure. Scale bar = 10 μm .



Figs 35–36. *Micrampulla parvula*. SEM. DSDP 29-275-1-2, 75–77 cm. Showing the two valve types side by side.

Fig. 35 . Type 1 valve, with elongate central structure ('cotton-bud'-like shape), small number of sockets and H-shaped socket supports at valve base.

Fig. 36. Type 2 valve, with more globular central structure, larger number of sockets and triangular socket supports at valve base. Scale bars = 5 μm .



Figs 37-55. *Micrampulla parvula*. SEM. DSDP 29-275-1-2, 75-77 cm (Figs 37-47 , 49-55), DSDP 29-275-1-1, 118-119 (Fig. 48).

Figs 37-50 . Type 1 valve, with H-shaped socket support. Note: Figs 40-41 represent higher magnifications and different orientations of the upper valve in Fig. 39, while Fig. 42 represents a higher magnification and different orientation of the lower valve in Fig. 39. Also, Figs 43-45 are different orientations of the same specimen, while Figs 49-50 are from the same specimen.

Figs 51-55. Type 2 valve, with triangular socket support. Note: Figs 53-55 are higher magnifications and different orientations of the specimen in Fig. 36. Scale bars = 1 μm (Figs 40, 42, 44, 46, 49, 50, 53), 2 μm (Figs 41, 45, 47, 48, 54, 55) or 5 μm (Figs 37-39, 43, 51, 52).

Club-head, 6.2–12.1 μm wide, 8.7–14.3 μm long, heavily silicified and hollow, sometimes elongate, ‘cottonbud’-like in shape (Fig. 35) or somewhat flattened at the apex (Fig. 38). Dome and club-head structure with round pores at bottom of reticulate openings (‘pits’). Reticulate network smooth and relatively flat on the dome (Figs 40, 44), but pointed at the corners on the club-head (Fig. 45). Girdle sometimes preserved, perforated by vertical rows of small round pores, except near the valve base (Figs 40–41). Rimoportula seemingly absent.

Type 2 valves circular in valve view, 12.8–14.2 μm in diameter in girdle view. Valve base characterized by about 25–30 sockets alternating with an equal number of triangular, basal supporting structures (Figs 36, 53, 55). Each socket associated with articulated spine, flattened and hyaline at the base, opening distally into the characteristic T-shape (Fig. 53), with all spines opening a uniform distance from spine base. Triangular basal support structures on either side of spine with notches on inner wall that accommodate wider basal part of spine (Fig. 49). Marginal area narrow, but with prominent rim (Fig. 51). Central dome taller than Type 1 valve, 8.5–9.8 μm high. Total valve height, 33.7–41.7 μm , from valve base to top of club-head. Club ‘shaft’, 3.4–6.5 μm wide, 10.7–18.6 μm long, supporting heavily silicified, club-shaped, hollow globular structure, 11.5–19.1 μm wide, 12.6–20.8 μm long. Club-head structure with more depressions between reticulations than those of Type 1 valve (Fig. 52). Girdle sometimes preserved, perforated by vertical rows of small round pores, except near rim (Figs 36, 55). Rimoportula seemingly absent.

Etymology: *parvula* (L.) could be interpreted as tiny or insignificant – if the former, then *micro* and *parvula* seem to be doubling up on the same meaning, if the latter, then what may have seemed insignificant at the time, is now an amazing piece in the jigsaw puzzle of Cretaceous diatom evolution.

Distribution: Originally described and illustrated from Maastrichtian sediments of the Moreno Shale, California (Hanna 1927) and found there by subsequent workers (Rampi 1940, Deflandre 1952, Cornell 1972, Chambers 1996, Nikolaev et al. 2001). It has also been recorded in DSDP Leg 22 Site 216 (Fenner 1985) and DSDP Leg 29 Site 275 sediments (Perch-Nielsen 1975, Hajos & Stradner 1975),

of Maastrichtian to Campanian age (Zones I to VIII (1) of Hajos & Stradner 1975). Chambers (1996) found this taxon in samples 216-30R-3W, 20–22 cm and 275-2-1, 64–65 cm, but also described two new species, *Micrampulla butleri* Chambers and *M. doldingi*, both of which are considered herein to be invalid, and synonymized with *M. cretacea* and *M. parvula*, respectively. We have investigated three well-preserved samples from Site 216 in the eastern Indian Ocean (216-30R-1W, 70–71 cm; 216-31R-1W, 90–91 cm; 216-32R-4W, 1–2 cm), but there does not appear to be any morphological differences with those specimens found in the Moreno Shale and at Site 275 (data not shown here).

Comments: Its affinity has long been debated, with various authors suggesting it is either a diatom (Hanna 1927; Nikolaev et al. 2001), chrysophyte (Farr et al. 1979) or another group of organisms (Nikolaev et al. 2001). Perch-Nielsen (1975) noted that in late Campanian Site 275 sediments the forms are more elliptical (elongate) rather than round in the Maastrichtian Moreno Shale (type material). Our data suggest that the elongate and globular forms may be Type 1 and Type 2 valves of heterovalvate frustules, respectively, and that our globular valves from Moreno Shale represent only Type 2 valves. Chambers (1996) described and illustrated a new species, *M. doldingi*, from DSDP Leg 29 Hole 275 (sample 275-1-2, 122–123 cm). However, he did not designate a holotype and therefore it must be deemed invalid. Besides, his description matches perfectly with that of *M. parvula*, which has priority over *M. doldingi*.

***Micrampulla cretacea* (Hajós and Stradner) comb. nov. & emend.
(Figs 56–91)**

Basionym: *Pterotheca cretacea* Hajos and Stradner (1975), p. 934, pl. 12, fig. 16–18, 21; pl. 26, fig. 1.

Synonyms:

Micrampulla? sp. – Perch-Nielsen (1975), p. 883, pl. 13, figs 5–8, 15.

Pterotheca cretacea Hajos & Stradner (1975) – Chambers (1996), pl. 15, figs 11–13.

Micrampulla butleri Chambers (1996), p. 261, pl. 14, figs 2–4. (invalid)

Ktenodiscus cretaceus (Hanna) S. Blanco & Wetzel (2016), p. 199.

Holotype: Prep. 2799/1 HGS; pl. 12, figs 17–18 of Hajos and Stradner (1975).

Type locality: DSDP 29, Site 275 (50°26.34′S, 176°18.99′E).

Type sample and sample repository: Sample 275-1-1, 118–120 cm; IODP East Coast Repository.

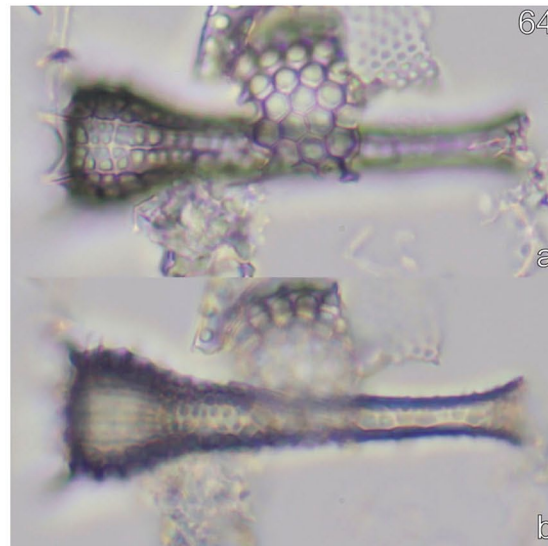
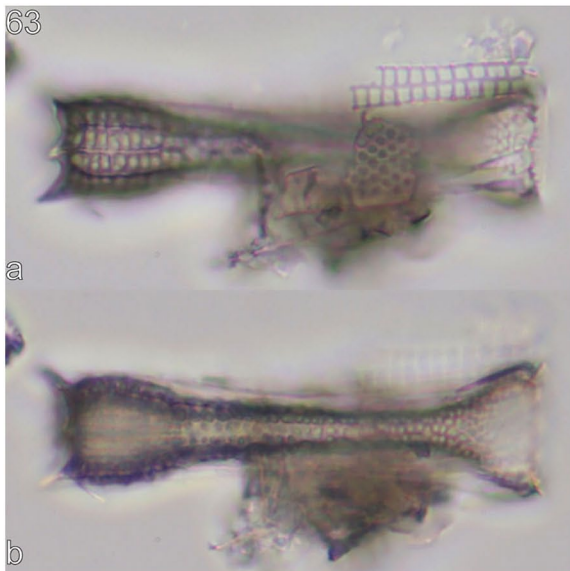
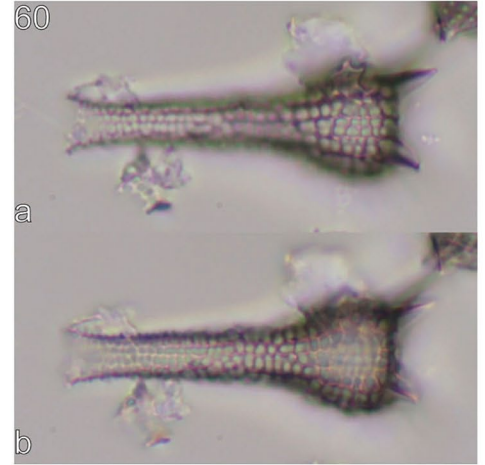
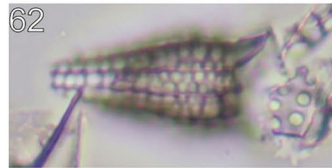
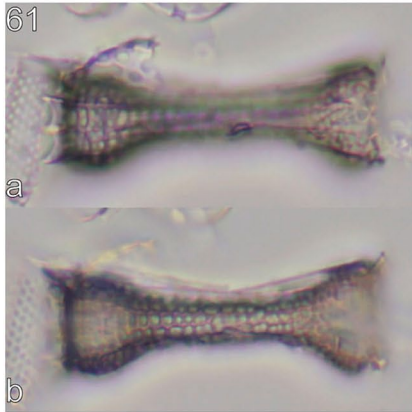
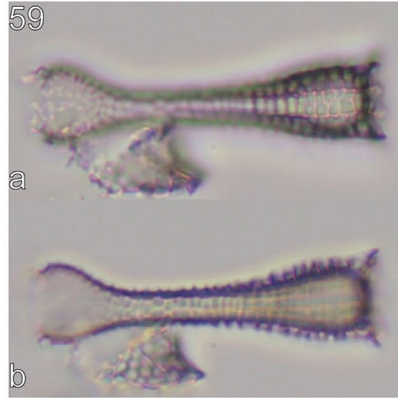
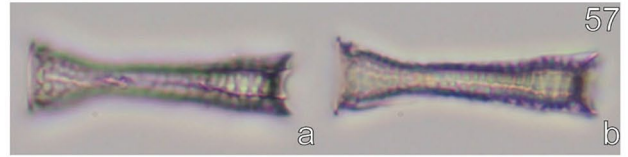
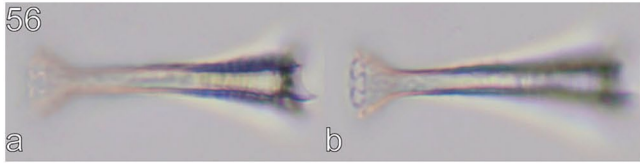
Emended description

LM observations: Two valve types known, presumed to represent opposing ends of one frustule. Type 1 valves flared at both ends. Domed valve base somewhat triangular, with a few large holes (sockets) near the base, margin with prominent rim (Fig. 57b). Occasionally, articulated spines seen still attached to valve base (Fig. 57b). Domed valve with long, narrow ‘shaft’ extending into flared tower-like distal end. ‘Shaft’ with weak longitudinal costae. Top of distal portion characterized by small number of large finger-like projections (Fig. 57a). Both domed base and flared distal portion with reticulate network. Type 2 valves somewhat dumbbell-shaped (Fig. 61b). Valve base more robust than that of Type 1 valve, with steeper dome, and denser reticulation. Holes (sockets) near valve base (Fig. 61a). Occasionally, articulated spines seen still attached to valve base (Fig. 63). Domed valve with thick, somewhat shorter ‘shaft’ extending into a more bulbous distal portion (Fig. 60a). Distal portion with strong longitudinal costae, which terminate in small finger-like projections (Figs 61a, 63a, 64a).

SEM observations: Frustule shape unknown, but assumed to be cylindrical, heterovalvate (with Type 1 and Type 2 valves). Type 1 valves circular in valve view, 3.8–12.0 µm in diameter in girdle view. Valve base characterized by about eight sockets alternating with an equal number of cup-shaped supporting structures (Fig. 65). Each socket associated with one articulated spine, flattened and hyaline at the base, opening distally into characteristic *Corethron*-like form, with serrations and T-shaped cross-section (Figs 65, 69), with the top of the ‘T’ directed to the valve center. Cup-shaped structures on

either side of spine with notches on inner wall that accommodates wider basal part of spine (Fig. 69). Marginal area wide and perforate, with prominent rim (Fig. 69). Dome, 4.0–6.8 μm high, arising from valve center, with long, narrow, central tubular process ('shaft') extending distally to support distally-flaring tower-shaped structure. Total valve height, 19.5–41.8 μm , from valve base to distal point of finger-like projections of tower. Valve 'shaft', 1.9–4.2 μm wide, 5.3–20.0 μm long (Fig. 65). Flared part (tower), 4.9–12.6 μm wide, 7.4–18.5 μm long (or 4.0–11.1 μm wide, 6.1–13.8 μm long without finger-like projections, respectively), heavily silicified and hollow. Both dome and distally-flaring portion with round pores at bottom of depressions in reticulate framework, but narrow mid-portion is hyaline with about six ridges (costae), that become stronger distally, with each ridge terminating in a large finger-like projection (Figs 65, 67, 75). Girdle bands not observed. Rimoportula seemingly absent.

Type 2 valves circular in valve view, 7.7–15.1 μm in diameter in girdle view. Valve base characterized by about 16 sockets alternating with an equal number of weakly H-shaped supporting structures (Fig. 66). Remnants of spines observed in two specimens (Figs 66, 91), but details of spine morphology and spine-socket mechanism are currently unknown. Marginal area and rim not intact in the specimens seen in this study. Dome, 7.1–12.6 μm high (broader than Type 1 valve, with short, near-vertical walls, extending higher than in Type 1 valves), arising from valve center, with long, narrow, central tubular process ('shaft') extending distally to support distally-flaring bulbous structure. Total valve height, 29.6–52.9 μm , from valve base to distal point of finger-like projections of bulbous structure. Valve 'shaft', 3.4–6.6 μm wide, 12.4–at least 27.3 μm long. Flared part (bulbous structure), 8.5–17.6 μm wide, 10.0–18.8 μm long, heavily silicified and hollow (Figs 66, 87, 89). Distal portion with about 16 strong ridges (costae), each terminating in a short finger-like projection (Figs 66, 90). Top of distal structure flattened (Fig. 90). Both dome and distal structure with reticulate openings, those on dome with round pores at the bottom. Girdle bands not observed. Rimoportula seemingly absent.

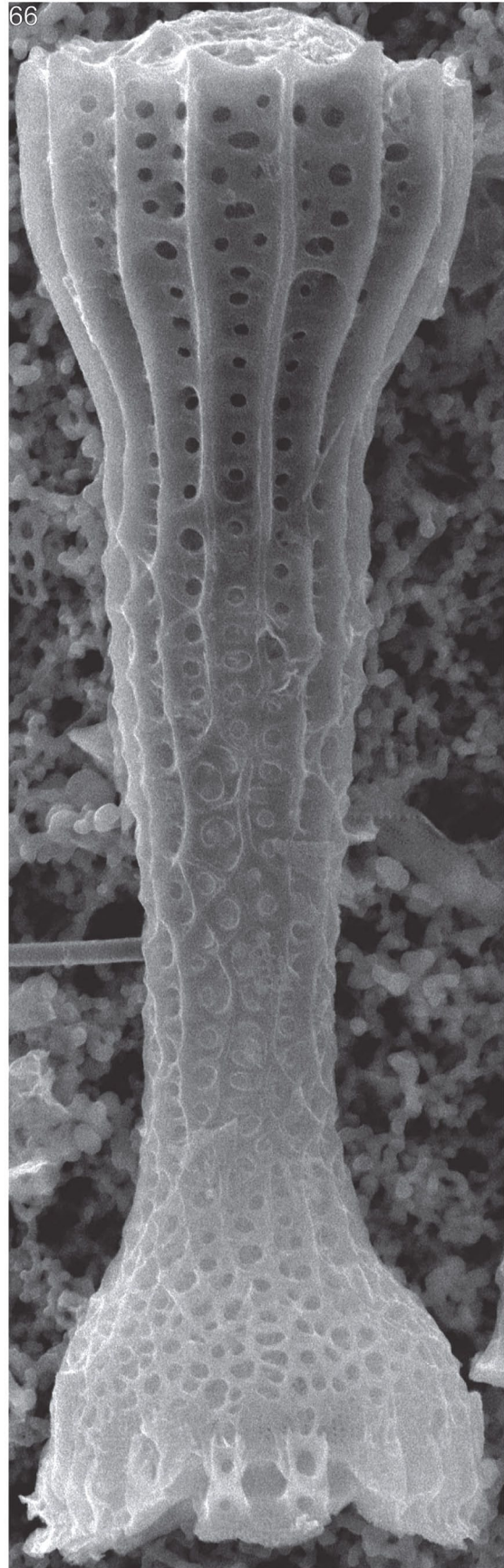
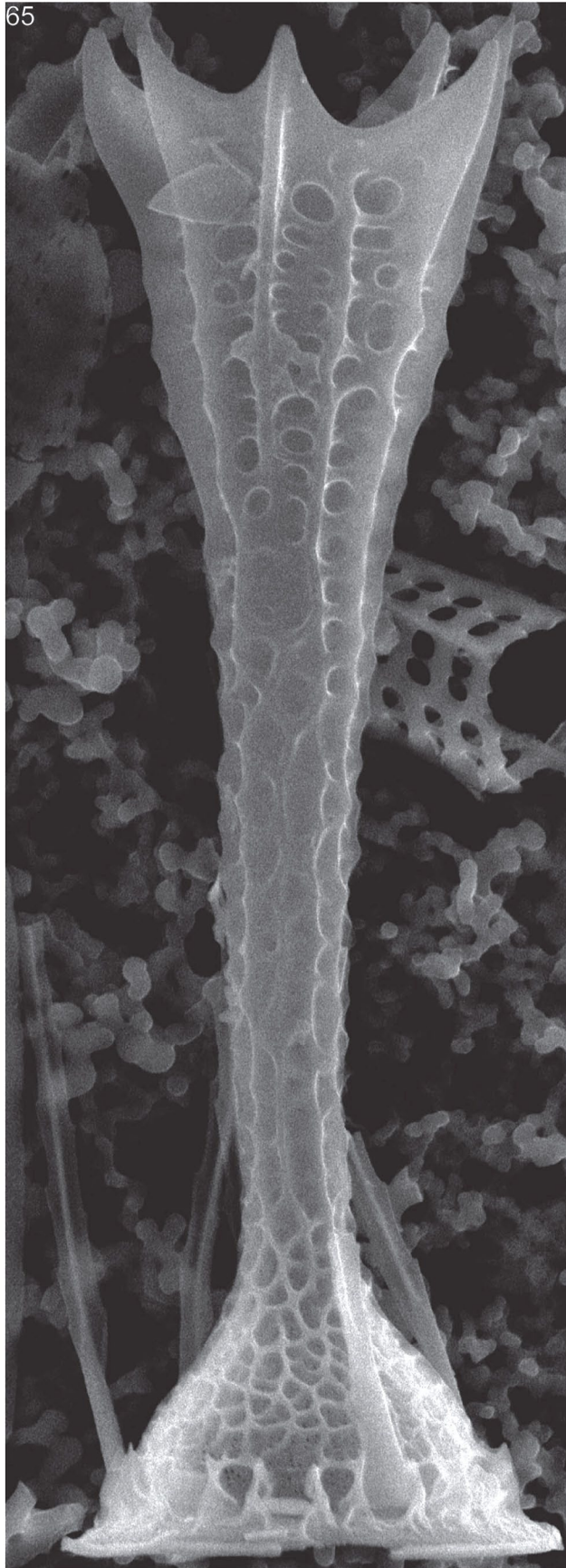


Figs 56–64. *Micrampulla cretacea*. LM. DSDP 29-275-1-2, 75–77 cm.

Valves in side view, including seven specimens shown in two different foci (labelled as ‘a’ and ‘b’).

Figs 55–59 . Type 1 valve.

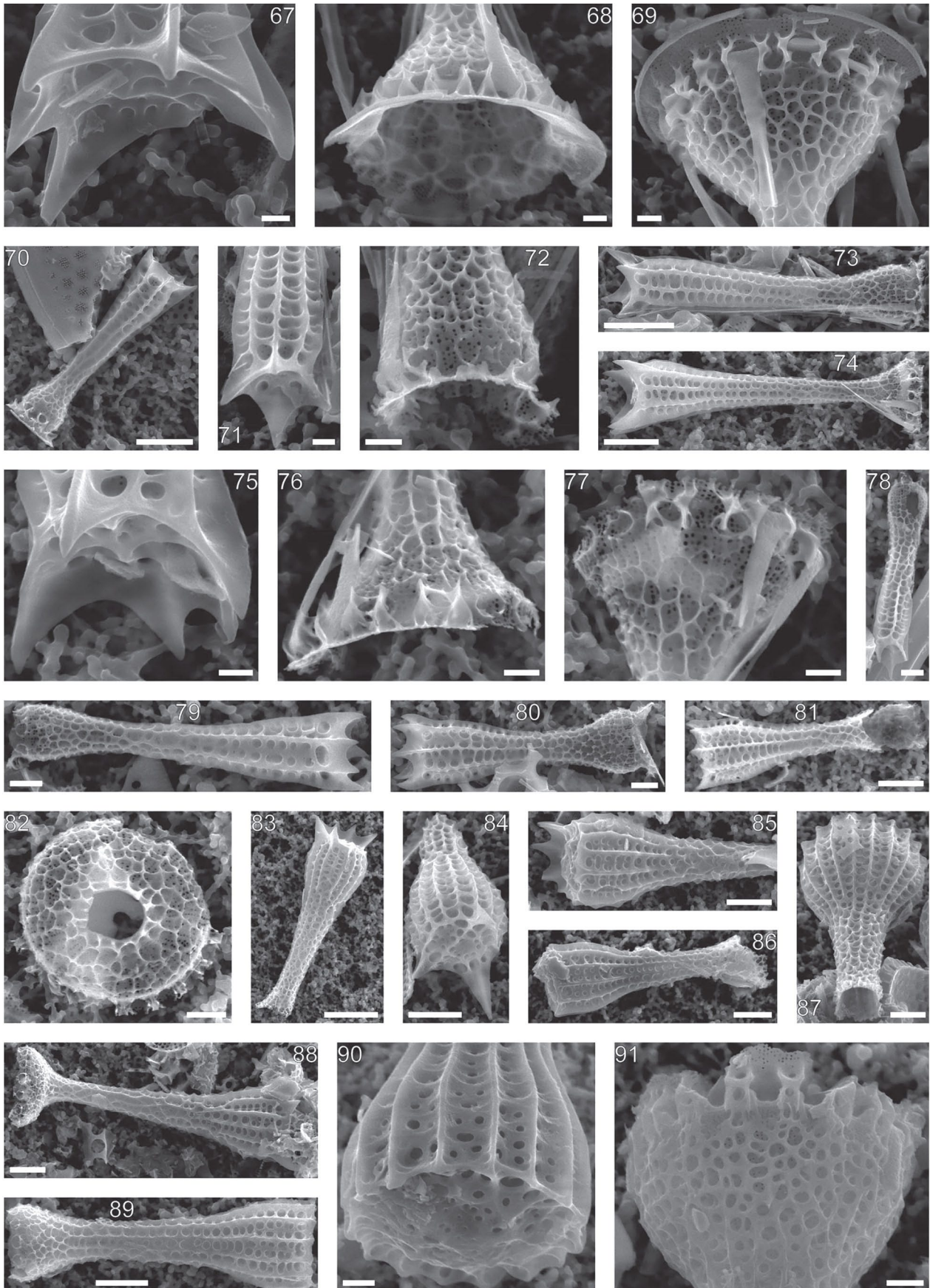
Figs 60–63 . Type 2 valve. Scale bar = 10 μm .



Figs 65–66. *Micrampulla cretacea*. SEM. DSDP 29-275-1-2, 75–77 cm.
Showing the two valve types side by side.

Fig. 65 . Type 1 valve, with a few articulated spines still attached in their sockets, supported by cup-shaped structures. Domed valve with narrow ‘shaft’ extending into a flared distal portion, with longitudinal ridges, each terminating in a robust finger-like projection.

Fig. 66 . Type 2 valve, with slightly more sockets and H-shaped supporting structures. Domed valve with thicker ‘shaft’ extending into a bulbous distal portion, with a larger number of longitudinal ridges, each terminating in a small finger-like projection. Scale bars = 5 μm .



Figs 67–91. *Micrampulla cretacea*. SEM. DSDP 29-275-1-2, 75–77 cm (Figs 67–73 , 78–81 , 84 , 85 , 89–91), DSDP 29-275-1-1, 118–119 cm (Fig. 87), DSDP 29-275-1-1, 129–130 cm (Fig. 86), DSDP 29-275-1-1, 130–131 cm (Figs 74–77 , 82 , 83 , 88).

Figs 67–81 . Type 1 valve. Note: Figs 67–69 represent different magnifications and orientations of the same specimen, in Fig. 65, while Figs 71–73 and Figs 74–77 represent two specimens at different magnifications and orientations, respectively.

Figs 82–91. Type 2 valve. Note: Figs 90–91 represent different magnifications and orientations of the same specimen shown in Fig. 66. Scale bars = 1 μm (Figs 67–69, 71, 72, 75–77), 2 μm (Figs 78–80, 82, 90, 91), 5 μm (Figs 70, 73, 74, 81, 84–89) or 10 μm (Fig. 83).

Distribution: Originally described and illustrated from late Campanian sediments cored at DSDP Leg 29 Site 275, in samples from Core 1-1, 118–120 cm (holotype) and Core 2-1, 130–132 cm (Hajos & Stradner 1975), and subsequently recorded from Core 2-1, 41–43 cm and Core 2-1, 63–64 cm (Chambers 1996). Sample location not indicated by Perch-Nielsen (1975). In the present study, this taxon was noted in four samples from Site 275; Core 1-1, 118–119 cm (the holotype sample, in part); Core 1-1, 129–130; Core 1-1, 130–131 cm; Core 1-2, 75–77 cm.

Comments: Chambers (1996) described and illustrated a new species, *M. butleri*, from DSDP Leg 29 Hole 275 (samples 275-1-2, 122–123 cm and 275-2-1, 64–65 cm). However, he did not designate a holotype and therefore it must be deemed invalid. Besides, his description matches perfectly with the type 2 valve of *M. cretacea*, which has priority over *M. butleri*. He recognized that the ‘head’ and ‘base’ were of the same diameter, the ‘head’ had distinctive longitudinal ridges, and that the ‘base’ had a ring of 6–9 long thin spines, each with a thickened ridge in its center.

Discussion

The diatom genus *Corethron* is assumed to be from an ancient lineage, because it has no close living relatives and is often shown in phylogenetic trees as a sister taxon to the rest of the diatoms, or in a clade with *Leptocylindrus* and sister to the rest of the diatoms (Theriot et al. 2010, Nakov et al. 2018). Thus, studies on its evolutionary history are clearly needed. However, modern *Corethron* spp. have delicate structures, thinly silicified valves and do not produce resting stages. So, there are only a few reports of fossil *Corethron* from well-preserved siliceous oozes, of mostly Pleistocene age (Jordan et al. 1991; Leventer et al. 1993; Alley et al. 2018). Recently, two breakthroughs have occurred. Firstly, two specimens of a *Corethron*-like diatom were discovered in amber of Cenomanian–Santonian age in northwest France (Saint Martin et al. 2015). One of these was a cylindrical frustule, 50 μm in diameter, possessing girdle bands, and exhibiting heterovalvy, with 11 articulated T-shaped barbed spines at one end and five at the other end (Saint Martin et al. 2015). Secondly, well-preserved valves of

a new species, *Praecorethron crawfordii* Abe et al., were reported from Campanian-Maastrichtian sediments from the South Pacific (Abe et al. 2021). These valves possessed fragments of articulated spines still locked inside their sockets and were of two types suggesting that, *in vivo*, they were once part of a heterovalvate frustule (Abe et al. 2021). So, the confirmation herein of another Late Cretaceous diatom genus (*Micrampulla*) with articulated spines and sockets will, we hope, shed more light on the evolution of this unique lineage, and encourage diatomists to search for more *Corethron*-like ancestors.

From the data presented herein, we now know that at least three genera of the Corethrales share a set of key characters; heterovalvy, domed valves, sockets, articulated T-shaped spines, and also lack rimoportulae. In addition, the location of the sockets and the association of only one spine type with each valve, strongly supports the erection of a new family, the Micrampullaceae, for *Micrampulla* and *Praecorethron*. This also means that *Micrampulla* should no longer be considered a synonym of *Ktenodiscus* (Blanco & Wetzel 2016).

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References

- Abe K., Lam D.W., Ashworth M.P., Harwood D.M. & Jordan R.W. 2021. Observations on *Praecorethron crawfordii* gen. et sp. nov. (Corethrales, Bacillariophyceae) from Upper Cretaceous marine sediments, southwest Pacific. *Nova Hedwigia, Beiheft* 151: 273–314.
- Alley K., Patacca K., Pike J., Dunbar R. & Leventer A. 2018. Iceberg Alley, East Antarctic Margin: continuously laminated diatomaceous sediments from the late Holocene. *Marine Micropaleontology* 140: 56–68.
- Blanco S. & Wetzel C.E. 2016. Replacement names for botanical taxa involving algal genera. *Phytotaxa* 266: 195–205.
- Chambers P.M. 1996. *Late Cretaceous and Palaeocene marine diatom floras*. PhD thesis, University College London, U.K., 521 pp.

- Cornell W.C. 1972. Late Cretaceous chrysomonad cysts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 12: 33–47.
- Deflandre G. 1952. Chrysomonadines fossiles. In: *Traité de Zoologie* (Ed. by P. Grasse), Vol. 1. Masson et Cie, Paris. pp. 560–570.
- Farr E.R., Leussink J.A. & Stafleu F.A. 1979. Index Nominum Genericorum (Plantarum), supplement. In: *Regnum Vegetabile* (Ed. by Bohn, Scheltema & Holkema, Utrecht), Vol. 100, 101, 102. dr. W. Junk b.v. Publishers, The Hague, 1, 2, 3. pp. 1896.
- Fenner J. 1985. Late Cretaceous to Oligocene planktic diatoms. In: *Plankton stratigraphy* (Ed. by H.M. Bolli, J.B. Saunders, K. Perch-Nielsen), Vol. 2. Cambridge University Press, Cambridge. pp. 713–762.
- Fourtanier E. & Kociolek J.P. 1999. Catalogue of the diatom genera. *Diatom Research* 14: 1–190.
- Hajós M. & Stradner H. 1975. Late Cretaceous Archaeomonadaceae, Diatomaceae and Silicoflagellatae from the South Pacific Ocean. Deep Sea Drilling Project, Leg 29, Site 275. *Initial Reports of the Deep Sea Drilling Project* 29: 913–1009.
- Hanna G D. 1927. Cretaceous Diatoms from California. *Occasional Papers of the California Academy of Sciences* 12: 5–49, 5 pls.
- Hanna G D. 1934. Additional notes on diatoms from the Cretaceous of California. *Journal of Paleontology* 8: 352–355.
- Jordan R.W., Priddle J., Pudsey C.J., Barker P.F. & Whitehouse M.J. 1991. Unusual diatom layers in Upper Pleistocene sediments from the northern Weddell Sea. *Deep-Sea Research* 38: 829–843.
- Lebour M.V. 1930. *The Plankton Diatoms of Northern Seas*. Ray Society, London. [Reprinted 1978 by Otto Koeltz Science Publishers]
- Leventer A., Dunbar R.B. & DeMaster D.J. 1993. Diatom evidence for late Holocene climatic events in Granite Harbour, Antarctica. *Paleoceanography* 8: 373–386.
- Nakov T., Beaulieu J.M. & Alverson A.J. 2018. Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). *New Phytologist* <https://doi.org/10.1111/nph.15137>.
- Nikolaev V.A., Kociolek J.P., Fourtanier E., Barron J.A. & Harwood D.M. 2001. Late Cretaceous diatoms (Bacillariophyceae) from the Marca Shale member of the Moreno Formation, California. *Occasional Papers of the California Academy of Sciences* 152: 1–39, 39 pls.
- Perch-Nielsen K. 1975. Late Cretaceous to Pleistocene archaeomonads, ebridians, endoskeletal dinoflagellates, and other siliceous microfossils from the subantarctic southwest Pacific, DSDP, Leg 29. Deep Sea Drilling Project, Leg 29, Site 275. *Initial Reports of the Deep Sea Drilling Project* 29: 873–907.
- Rampi L. 1940. Archaeomonadaceae del cretaceo americano. *Atti Della Società Italiana di Scienze Naturali* 79: 60–68.
- Round F.E., Crawford R.M. & Mann D.G. 1990. *The diatoms. biology & morphology of the genera*. Cambridge University Press, Cambridge, U.K. 747 pp.

- Saint Martin S., Saint Martin J.-P., Schmidt A.R., Girard V., Neraudeau D. & Perrichot V. 2015. The intriguing marine diatom genus *Corethron* in Late Cretaceous amber from Vendee (France). *Cretaceous Research* 52 (Part A): 64-72.
- Silva P.C. 1980. Names of classes and families of living algae. *Regnum Vegetabile* 103: 1-156.
- Theriot E.C., Ashworth M., Ruck E., Nakov T. & Jansen R.K. 2010. A preliminary multigene phylogeny of the diatoms (Bacillariophyta): challenges for future research. *Plant Ecology and Evolution* 143: 278-296.