PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Volume 55, No. 14, pp. 300–337, 11 pls. September 30, 2004

A SEM Study of the Diatom Genus *Porodiscus* Greville; Morphology of the Species and Comparison with Related Genera

N.I. Strelnikova[1], E. Fourtanier[2], J.P. Kociolek[2], and J.A. Barron[3]

[1] *Department of Botany, Biological Faculty, St. Petersburg State University, Universitetskaya Emb. 7/9, St. Petersburg 199034, Russia; Email: diatomspb@mail.ru.* [2] *Diatom Collection, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, USA; Email: efourtanier@calacademy.org, pkociolek@calacademy.org.* [3] *United States Geological Survey, MS910, 345 Middlefield Rd, Menlo Park, California 94025, USA; Email: jbarron@usgs.gov.*

We carried out SEM studies on the poorly known middle Eocene marine diatom genus *Porodiscus* Greville. Species examined include, *Porodiscus splendidus* Greville, *P. nitidus* Greville, *P. conicus* Greville, *P. oblongus* Greville. Selected species in the related genera *Coscinodiscus* Ehrenberg, *Craspedodiscus* Ehrenberg and *Annellus* Tempère are also considered. Two new combinations, *Porodiscus splendidus* var. *excentricus* (Olshtinskaya) Olshtinskaya n. comb. and *Porodiscus splendidus* var. *corniger* (Brun) Fourtanier n. comb. are proposed, and we designate *Porodiscus nitidus* Greville as the lectotype of *Porodiscus* Greville. *Porodiscus* resembles both *Coscinodiscus* and *Craspedodiscus* in the presence of locular areolae, which possess external cribra and internal foramina, and the presence of marginal rimoportulae. *Porodiscus* has unique characters, however, such as spines occurring in some taxa, which are not present in *Coscinodiscus* or *Craspedodiscus*. *Porodiscus* possesses a distinctive central cavity (or "sack"), similar to that of *Craspedodiscus*; however, in *Porodiscus*, the central cavity is very steep (tube-like) and well defined, being bordered by a hyaline rim. *Craspedodiscus* species usually do not have such hyaline rim (except for some tropical Miocene forms of *Craspedodiscus coscinodiscus*) and lack a well-defined central depression.

Porodiscus Greville 1863 is a small, poorly known genus of fossil centric marine diatoms closely allied to *Coscinodiscus* Ehrenberg from which it differs by the presence of a deep concavity at the center of the valve. The genus has received little attention by taxonomists, and the only SEM observations to date are those of Sims (1989) on a species identified as *Porodiscus nitidus* var. *armatus* Rattray from Joe's River, Barbados. Sims' specimens were not sufficiently well preserved to observe the shape of the rimoportulae and the nature of the cribrum. Her observations, however, confirm the affinity of *Porodiscus* with *Coscinodiscus,* which was first noted by Greville (1863). We present here new information on the morphology of this intriguing genus based on detailed SEM observations and reexamination of Greville's original slides.

Our interest in the genus first arose after the observation under SEM of *Porodiscus splendidus* (?) from a sample taken from DSDP Site 206, Core 16, Section 5 (Tasman Sea), a specimen with spines. A review of the literature indicated that *P. splendidus* Greville was the most cited and the most widely distributed species of *Porodiscus.* Illustrations of the reported specimens, however, showed both specimens with spines (Gombos 1983) and specimens without spines (Fenner 1985). This prompted us to reexamine the type material of Greville for that species and to consider the other species in the genus.

Historical Perspective

Greville (1863:63) described the genus *Porodiscus* from samples prepared by Johnson from the sediments of the Cambridge Estate in Barbados (middle-late Eocene according to the stratigraphic scheme of Mitchell-Thome 1979). He originally included five species: *P. nitidus, P. elegans, P. major, P. conicus* and *P. oblongus (P. ovalis* in plate caption), but did not designate a generitype. Subsequently, Greville (1865:46) described *Porodiscus splendidus* from the sediments of the Springfield Estate, Barbados, whose precise stratigraphic position is not known. Greville (1865) noted that *P. splendidus* was not found in the Cambridge Estate sediments.

Greville (1863) described the genus in these words: "Frustules free, disciform, composed of two discs, united by an intermediate, ring-like zone; discs very convex, minutely radiato-cellulate or punctate, with a conspicuous central pseudo-opening." Greville continued: "This genus is evidently closely allied to *Coscinodiscus,* differing chiefly in the remarkable pore-like pseudo-opening, which is not a mere blank circular space produced by the absence of cellulation at the apex, but a well-defined, concave, apparent orifice, provided with a thickened margin." Greville added that "all the species described from Barbados had very convex valves, and puncta [areolae] arranged in radial rows. In nearly all the species certain of the radial rows start from the margin and continue to the valve apex, dividing the valve into perceptible sections [fascicles]. Surface is either plane or armed with variously arranged minute spines." The types of Greville's *Porodiscus* are illustrated by Williams (1988:44–45, pl. 52, figs. 1–9, pl. 53, fig. 5).

Castracane (1886) described *P. stolterfothii,* which he considered an extant species, from the tropical area of the Pacific Ocean. Grove and Sturt (1887) described two other species of *Porodiscus: P. hirsutus* and *P. interruptus,* from Oamaru (New Zealand, upper Eocene). Rattray (1890) described *Porodiscus spiniferus, P. splendidus* var. *marginata, P. major* var. *densa,* and *P. nitidus* var. *armata* from Barbados. *Porodiscus corniger* Brun (1896) was also described from Barbados from the Chimborazo sediments (unknown age) and Mount Hillaby (late Eocene). *Porodiscus calyciflos* Tempère and Brun *in* Brun and Tempère, 1889, is known from a Neogene limestone of Yedo, Yedo Bay, Japan, and is also known as living in the Sandwich Islands (Brun and Tempère 1889). Prema and Desikachary (1989) described *Porodiscus minor* and *Porodiscus venkataraminii* from the Oligocene of the Indian Ocean.

The generic placement of these species has been questioned. Mann (1907:237), noted that *P. calyciflos, P. interruptus, P. hirsutus* (which he placed in synonymy) have nothing in common with Greville's genus. Jousé in Proschkina-Lavrenko (1949:33) created the illegitimate name *Pseudopodosira pileiformis* as a synonym of *P. calyciflos.* Various authors (e.g., Gombos 1982; Prema and Desikachary 1989) have also recognized the similarity of *Porodiscus* with *Craspedodiscus* Ehrenberg, a closely related genus with a central depression. Grunow 1881 *in* Schmidt (pl. 66, figs. 7–9) transferred *Porodiscus oblongus* Grev. to *Craspedodiscus oblongus.* Gombos (1982:232) transferred *Porodiscus splendidus* Grev. to *Craspedodiscus splendidus.*

Based on our observations of original illustrations and descriptions, we recognize that the genus *Porodiscus* in Greville's original sense currently contains the species of Greville *(P. conicus, P. elegans, P. oblongus, P. nitidus, P. major, P. spendidus),* Rattray's taxa *(P. major* var. *densa, P. nitidus* var. *armata, P. splendidus* var. *marginata), P. corniger* Brun, and *P. stolterfothii* Castracane. As Grunow suggested (Grunow in Schmidt 1881, pl. 66, fig. 6), we believe that *Craspedodiscus ovalis* Grunow belongs to *Porodiscus splendidus* Greville. The specimen illustrated by Grunow is slightly oval and has a well defined depressed central area bordered by a rim. All these species are the focus of this paper.

We agree with Mann (1907:237) that *P. calyciflos, P. interruptus*, and *P. hirsutus* do not belong

in *Porodiscus*. We also doubt that *Porodiscus minor* and *Porodiscus venkataraminii* Prema and Desikachary (1989) belong to *Porodiscus*, as these species are only slightly depressed at the center with the central area that is not surrounded by a hyaline rim. As argued by Mann (1907), *Porodiscus coronarius* (Mann) Mills 1934 (based on *Melosira coronaria* Mann) does not belong in *Porodiscus*. Specimens identified by Jousé (1954:128, pl. 3, fig. 1–2) as *Porodiscus pliocenicus* (an invalid name) do not belong in *Porodiscus* and were later placed in the genus *Cosmiodiscus* by Jousé (1961).

Materials and Methods

The following slides were examined:

British Museum slides

BM 10602. Coll. Deby. L.H. no. 714. Barbados, Diatomaceae selected. *Porodiscus splendidus*.
BM 10603. Coll. Deby. Named by Greville no. 10. "L.H. no. 715. Barbados Diatomaceae selected. *Asterolampra affinis*."
BM 10604. Coll. Deby. Named by Greville no. 19. "L.H. no. 716. Barbados. Diatomaceae selected. *Porodiscus splendidus*."
BM 10605. Coll. Deby. Named by Greville no. 17. "L.H. no. 714. Barbados. Diatomaceae selected. *Porodiscus splendidus*."
BM 10399. Coll. Deby. "L.H. no. 505. Springfield Estate. Barbados. Diatomaceae selected. *Porodiscus splendidus*".
BM 2045. Coll. Greville. "Barbados Earth. *Porodiscus ovalis*".
BM 2745. Coll. Greville. "Bridgewater. Barbados. Johnson. *Porodiscus conicus*."
BM 2744. Coll. Greville. "Cambridge. Barbados. Johnson. 1863. *Porodiscus nitidus*."
BM 2751. Coll. Greville. "Bridgewater. Barbados. Johnson. *Porodiscus nitidus* — Holotype."
BM 2812. Coll. Greville. "Cambridge. Barbados. Johnson.1862. *Porodiscus conicus*."
BM 2844. Coll. Greville. "Cambridge. Barbados. Johnson.1863. *Porodiscus major* — type."

CAS Collection, Barbados

CAS 611174. Joe's River. St. John District. 13°13′N, 59°32′W.
CAS 611205, CAS 611235. Cambridge Estate, Adams Hill, St. James District.
CAS 611193. Springfield. St. Peter District.
CAS 611223, CAS 611226. Chimborazo village.

Collection N. Strelnikova

Sample CAS 624819, DSDP Leg 21, 206–16–5, 111–113 cm, Tasman Sea (Middle Eocene).

Collection A.P. Olstinskaya

Sample 74163, Ukraine, Settlement Staroverovka, Kievskaya Formation, middle-upper Eocene.

Coll. L.H. Robinson (slides)

At CAS, received from the New York Botanical Garden.

Notes on Collections

The history of collections from Barbados of the British Museum and the Diatom Collection of CAS is very interesting and is described by J.H. Robinson (1934, 1936, 1941). She indicates the absence of good information about the exact locality and the geological position of the samples that Dr. Davy collected in 1846 and sent to R.K. Greville under the name "Barbadoes Earth": "more than two hundred and fifty of these are from Barbados fossil deposit and more than two-thirds of these are cited as "Cambridge Estate" in slides communicated by C. Johnson Esq. From one sample of earth received by Mr. Johnson, the majority of the new species were obtained. Although it was never definitely ascertained where this good sample came from, Dr. Greville seems to have

been under the impression that it was picked up on the Cambridge Estate" (Robinson 1934:3).

The samples from Barbados at CAS were received from J.H. Robinson. She provided information about the localities Joe's River Estate (Robinson 1941, V, p. 1), Springfield (Robinson, 1941, VI, p. 84), and Cambridge Estate (Robinson 1941, VII, p. 181) and gave a list of the species she observed in these localities.

Microscopy

Specimens were photographed and examined under light microscopy (Leica DMRB) and by scanning electron microscopy (SEM) (Leo 1450VP).

Systematic Account

***Porodiscus splendidus* Greville, 1865: 46, pl. V, fig. 5.**
(Figs. 1–7, 9–10, 24–33)

Synonyms (taxonomic):
Craspedodiscus ovalis Grunow in Schmidt, 1881, Atlas Diat., Taf. 66, fig. 6.
Porodiscus splendidus var. *marginatus* Rattray, 1890:672.

This species was described by R.K. Greville from the Springfield Estate, Barbados. Picked valves of this species are arranged among the selected valves of different species on the type slide from the British Museum. Williams (1988:45) indicates that the lectotype is on slide BM 10602 (L.H. no. 714). Greville wrote on the slide the words "Diatomaceae selected. *Porodiscus splendidus.*" This species was also selected and marked by Greville on slides: BM 10604 (L.H. no 716, named by Greville no. 19) and BM 10605 (L.H. no. 717, named by Greville no. 17). All slides mentioned above are from Deby's collection and have no locality information. Slide BM 10399 (L.H. no. 505), however, also from Deby's collection bears the notes: "Springfield Estate. Barbadoes. Diatomaceae selected. *Porodiscus splendidus.*"

Occurrence.— In the material from Barbados at CAS, *Porodiscus splendidus* was found at all localities in Barbados (Springfield, Joe's River, Cambridge and Chimborazo) but more often in the Joe's River material. *Porodiscus splendidus* is the *Porodiscus* species that is the most often cited in contemporary literature (Glezer et al. 1965; Glezer 1969, 1974; Glezer and Jousé 1974; Olshtynskaya 1976; Jousé et al. 1977; Gombos 1983; Fenner 1985; Strelnikova 1992). The distribution of *P. splendidus* (based on the literature) indicates that it is confined to middle Eocene sediments. However, the accuracy of this distribution is in question as the species occurrence may be poorly documented and identification inaccurate.

Our SEM and light microscope (LM) observations add more detail on the valve morphology of this species.

Description.— We measured all the valves (a total of 6 specimens) of *Porodiscus splendidus* in Greville's slides (BM 10602, BM 10399, BM 10604, BM 10605, BM 2844), and a total of 50 valves from Barbados sediments in the CAS collection, mostly from Joes's river (CAS 611174 [1345], slides 581128–581131), but also from Springfield (CAS 611193 [3368], slide 581122), Cambridge (CAS 611205 [3142, 3143, 3144], slides 581107, 581108, 581109; CAS 611235 [3375, 3376], slides 581111–581113) and Chimborazo (CAS 611226 [3088, 3089, 3090], slides 58116–58118; CAS 611223 [3570], slide 581101).

The valves are convex, sometimes almost hemispherical, round or slightly oval 30–91 μm in diameter. A deeply concave cavity (4–18 μm in diameter), which is sometimes a little eccentric in outline, is positioned in the center of the valve. The central concave part or "apparent orifice" (or 'sack') juts into the frustule to different depths (6–16 μm). The ratio diameter of valve/diameter of

center ranges between 3 and 12. There is no apparent correlation between the diameter of the center and the depth of the "sack." Usually, the center is surrounded by a hyaline ring crest, but this ring is sometimes absent (Fig. 26). Areolae are arranged in radial rows 4–5 (sometimes 6) in 10 µm. Rattray (1890:672) noted that areolae are a little larger at semi-radius, however, this is not confirmed by our observations. Areolae loculate, locula pear-shaped, diameter of foramen about 1 µm. Velum not observed. Rimoportulae arranged on the margin of the valve at distances of 1 to 3–4 areolae from the margin (Figs. 28–29), with 3–4 areolae between rimoportulae. Rimoportulae open externally as small round holes (Fig. 26). Internally, they appear as simple small round holes, but it is not clear from our observations whether they are broken. Valves have no spines, only some protuberances around the areolae (Figs. 24–25). Girdle band is high (12–18 µm) with a group of vertical lines separated by narrow hyaline lines, 14–18 pores in 10 µm in a line (Figs. 31–33). These observations are consistent with Greville's original description, and Rattray's subsequent description (Rattray 1890:672).

Comments.— *Craspedodiscus ovalis* Grunow (= *Porodiscus splendidus* var.?) (Schmidt, 1881, Atlas Diat., Taf. 66, Fig. 6) from Springfield is a slightly oval specimen identical in shape and structure with *P. splendidus* Greville. Rattray (1890:672) treated *Craspedodiscus ovalis* Grunow as a variety of *Porodiscus splendidus* and named it *Porodiscus splendidus* var. *marginata*. Based on our observations of round and slightly oval valves of *P. splendidus* in BM and CAS materials, and Greville's original description of *P. splendidus* ("disc circular, occasionally broadly oval") we treat here *Craspedodiscus ovalis* Grunow (= *Porodiscus splendidus* var. *marginata* Rattray) as a synonym of *Porodiscus splendidus* Greville.

***Porodiscus splendidus* var. *corniger* (Brun) Fourtanier, new comb.**
(Figs. 37–40)

Basionym: *Porodiscus corniger* Brun, 1896:242, pl. XIX, fig. 15.

Porodiscus corniger Brun (1896:242, pl. XIX, fig. 15) (Figs. 37–40) was described from Chimborazo, Mount Hillaby, as a very rare form. Brun noted its similarity with *P. splendidus,* the two taxa differing only by the presence of spines in *P. corniger.* The valves of *Porodiscus* in the Chimborazo material are very rare. Only one frustule of *P. corniger* was observed in the Chimborazo material (CAS 611226); it was mixed with several forms without spines. As the two types are identical in structure and dimensions and differ only by the presence of spines, we believe that *P. corniger* should be treated as a variety of *P. splendidus*. Since we did not observe a continuum of morphological expressions between specimens with spines and specimens without spines, we are recognizing *P. splendidus* var. *corniger* and *P. splendidus* var. *splendidus* as two separate taxonomic entities.

***Porodiscus splendidus* var. *excentricus* (Olshtinskaya) Olshtinskaya, new comb.**
(Figs. 8, 11–12, 34–36)

Basionym: *Porodiscus nitidus* var. *excentricus* Olshtinskaya, 2001:452, pl. I, figs. 1–3.

Olshtinskaya (2001) described a new diatom taxon from the upper Eocene sediments of the Pristen village, Ukraine, as a variety of *Porodiscus nitidus (Porodiscus nitidus* var. *excentricus).*

We studied specimens from Staroverovka (coll. A.P. Olshtinskaya) near the type locality of her taxon and in the same geological interval (Kievskaya Formation, middle to upper Eocene). Olshtinskaya's taxon differs from *Porodiscus splendidus* only by the eccentric position of the "sack." In the material from Barbados, there are a few forms with an eccentric "sack." In the

Ukrainian material, however, the eccentric type is dominant, and the external surface of Ukrainian forms are smooth, without small bumps.

***Porodiscus nitidus* Greville, 1863, p. 65, pl. IV, fig. 4.**
(Figs. 13–16, 41–56)

Synonyms:
Porodiscus nitidus var. *armatus* Rattray, 1890:672-673, pl. III, fig. 17.
Porodiscus spiniferus Rattray, 1890:674, pl. III, fig. 19.

Greville described *P. nitidus* from the Cambridge Estate. Two slides in the Greville collection (slides BM 2751 and BM 2744) bear the indication *"Porodiscus nitidus."* Slide BM 2751 is a smear slide and, according to Williams (1988), is the probable holotype slide for *P. nitidus*. The slide bears no locality information besides "Barbadoes. Johnson Coll. Greville." *P. nitidus* is also present in slide BM 2812.

Greville (1863:65) stated in his original description of *P. nitidus,* "Disc convex, unarmed, the longest lines of puncta single (not in pairs), alternating with two or three series of shorter ones; puncta distinct, all of them becoming much more minute towards the margin. Diameter .0026. Barbadoes deposit, from Cambridge Estate; C. Johnson Esq. . . . It is a scarce species."

Porodiscus nitidus var. *armatus* Rattray (1890:672–673) was also described from the Cambridge Estate. Rattray noted the presence of spines ("spines acicular, about .01 mm., long, sometimes shorter, inserted about ¾ of radius from center"). It appears from Rattray's description and illustration that the main difference between *P. nitidus* var. *armatus* and the nominal variety is the presence of spines. The two varieties are otherwise identical in valve structure and dimensions. *Porodiscus spiniferus* Rattray (1890:674) was also described from the Cambridge deposit. It appears from Rattray's description that *P. spiniferus* is similar to *P. nitidus* var. *armatus,* but it has more robust spines, more evident fascicles, and possibly more dome-shaped valves.

Although Greville 1863 was clear in his original description of *Porodiscus nitidus* that spines were not present ("unarmed"), the slides in his collection (BM 2751, BM 2744) feature both specimens with spines and without spines. Our observations indicate that there is a continuum between specimens lacking spines, specimens with minute spines, and specimens with robust spines. There is also a great variability in the appearance of the fascicules, from very faint to evident. Despite three taxa having being described for this material, our observations suggest a continuum of morphological expressions within a single taxon, and support the synonymy between *Porodiscus nitidus* var. *nitidus*, *P. nitidus* var. *armatus* and *P. spiniferus*.

Our description of *P. nitidus* is supported by the observation of 12 specimens (on 11 slides) from Barbados from slides at the British Museum (BM 2744, BM 2751, BM 2745, BM 2812) and at CAS (CAS 61174[1345], Joe's River, slide 581129; CAS 611235[3376], Cambridge, slide 581112; CAS 611226[3089], Chimborazo, slide 581117). We found the best preserved specimens of *P. nitidus* in DSDP Leg 21, Sample 206-16-5, 111–113 cm, Tasman Sea (CAS 624819), from which we studied 25 valves in LM and SEM.

Description.— Valves circular, convex, 40–118 µm in diameter, with a deeply concave central part, round or very slightly oval, 5–7 µm in diameter that is either surrounded by a hyaline ring or lacks a ring. Ratio valve diameter/diameter of center 8–20. Areolae loculate with external cribrum and internal foramen, 5–8 in 10 µm. Loculae cylindrical. Areolae arranged in radial rows, 5–8 in 10 µm in a row, organized in fascicles, separated by hyaline lines. Fascicles are usually faint, sometimes more distinct. The hyaline lines and fascicles may be more distinct internally. Valve surface smooth or with spines. There is great variability in the size of the spines from barely notice-

able to very long. Spines are situated on the hyaline lines at mid-radius or closer to the margin (¾ of radius from center according to Rattray's original description) (Figs. 41–42). Rimoportulae are positioned in the hyaline lines at the distance of 1 areola from the valve margin (Fig. 56). They consist of small round holes externally, and small round or oval holes internally. It is possible, however, that they are eroded. Cribrum consists of several pores. In well preserved cribra there are 5–7 marginal pores surrounding a single (but sometimes 2–3) central pore (Figs. 52–55). Rattray (1890:672) noted that the areolae were more dense near the margin; however, this is not confirmed by our observations.

Comments.— Sims (1989:366, figs. 48–52) published SEM photos on specimens identified as *P. nitidus* var. *armatus* Rattray from Joe's River, Barbados (material from CAS collection: A.L. Brigger's samples, presented to British Museum by R.W. Holmes). Her specimens have spines, but unlike the specimens we observed, there are several spines on one hyaline ray. Spines nearest to the center (ca ¼ radius) are long and thick, spines closer to the margin are of moderate size. The presence of more than one concentric row of spines in *P. nitidus* was not observed by us and not mentioned by Rattray in the description of *P. nitidus* var. *armatus* or *P. spiniferus*. This suggests that the specimens illustrated by Sims may belong to a different taxon. Further study of her population is needed to determine if it represents a separate taxonomic entity.

The main differences between *P. nitidus* and *P. splendidus* are:

1) The ratio of valve diameter to diameter of the concave center, which is smaller for *P. splendidus* (3–9) and larger for *P. nitidus* (9–18). The diameter of the center is therefore larger in *P. splendidus* (5–18 µm) than in *P. nitidus* (4–6 µm);

2) Areolae are larger in *P. splendidus* (4–6, commonly 5 in 10 µm) than in *P. nitidus* (5–8, commonly 6–8 in 10 µm);

3) Areolae are arranged in radial lines in both species, but *P. nitidus* has slightly more evident fasciculae, which are separated by hyaline lines that are more distinct internally;

4) Spines are absent in *P. splendidus*, they are often (but not always) present in *P. nitidus*.

***Porodiscus conicus* Greville, 1863: 65, pl. IV, fig. 3.**
(Figs 17, 18, 64?)

Synonym:
Porodiscus elegans Greville, 1863:64, pl. IV, fig. 1.

This species was described by Greville from Cambridge Estate, Barbados. We studied it only from the type slides of the British Museum as we did not find any specimen in the CAS Collection material from Cambridge, Barbados. This species has not been reported since Greville's work. A complete frustule is present in slide BM 2812, the holotype according to Williams (1988). We also found this species on slides BM 2744 and BM 2745. We did not find definite specimens of this species in the CAS Collection.

Description.— Greville's description is short: "Small; disc conical, unarmed, with an obtusely truncate apex; radiating lines of puncta extremely minute. Diameter .0014″ [36 µm]." In the comments to this description Greville writes — "The smallest of the species hitherto discovered, and occurring not infrequently in perfect frustules. The length of the connecting zone is considerable, and that of the entire frustule, when both valves are symmetrical, about .0040″ [98 µm]. The valve is decidedly conical, but obtusely truncate at the top when seen in profile. It hardly ever happens that the valves are equal in the same specimen. Indeed, I do not think that I have seen a single example perfectly symmetrical, one valve being almost always considerably shorter than the other. The length of the connecting zone gives the frustule a cylindrical appearance."

The diameter of the specimen illustrated by Greville is 45 µm. Rattray (1890) restudied Greville's and Johnson's material and added to Greville's description: "Diameter .025 to .0525 mm. Major axis of frustule from .0625 to .0875 mm. Surface a more or less elongate regular cone, transversely truncate at the extremities, the opposite valves of a frustule of unequal height. Central space? Markings obtusely angular or subareolate, 6 in .01 mm, subequal; rows radial, straight, non-fasciculate; secondary oblique decussating rows evident, from the truncated ends of the cone a few short tapering clear lines, distinct. Girdle cylindrical, from .025 to .0325 mm, broad; a narrow band at each extremity, hyaline, the intervening portion clouded with diffuse parallel lines."

In Greville's slides, we found the valve diameter of *Porodiscus conicus* to range between 40–43 µm, the height of conical valves to be 30–35 µm, the height of the second valve to be 16 µm, and the girdle band to be 27–32 µm in width. Areolae on the valves are arranged in radial rows, 7–8 in 10 µm in a row, 8 rows in 10 µm. On the shorter valve 5–6 rows of areolae alternate with thin hyaline lines.

Comments.— Greville (1863:64) described *Porodiscus elegans* from Cambridge and other localities. "Disc very convex, unarmed, divided into compartments by pairs of the radiating lines of very minute puncta, extending from the margin to the centre. Diameter .0020″ [51 µm] to .0033″ [84 µm]." The specimen illustrated by Greville has a diameter of 77 µm. Greville (1863:64) commented: "This species is distinguished by the disc being divided into numerous compartments, by pairs of radiating lines of puncta, very distinctly seen under a moderately magnifying power, and at the same time being quite destitute of spines. It is the most frequent species, three or four valves sometimes occurring in a single slide. The connecting zone is rarely seen *in situ*." Rattray (1890:673) added: "Circular. Diameter .0625 to .095 mm. Surface rounded and dome-shaped. Central space circular, 0075 mm. broad, sharply defined, hyaline. Markings obtusely angular or subareolate, decreasing gradually from the central space outwards, around the central space 6, near the border 10 to 12, in .01 mm; rows radial, straight; fasciculi distinct; interspaces minute, largest around the central space. Girdle cylindrical, .03 mm, broad, in a frustule, .06 mm in diameter; a narrow hyaline band at each extremity; the interval minutely punctate; at subregular intervals narrow hyaline straight lines at right angles to the edges of the valve. The fasciculi are bounded by two adjacent radial rows, somewhat more conspicuous than the intervening rows. In one of the valves in Greville's collection it is possible to trace downwards from the central space a cylindrical siliceous tube which is of sufficient length to have passed to a plane corresponding in position to the edges of the valve." Our measurements of the specimen from slide BM 2745, the holotype of *Porodiscus elegans* according to Williams (1988) are: diameter of valve 45 µm, diameter of center 8 µm, areolae in a row 7 in 10 µm.

Porodiscus conicus and *P. elegans* are found on the same slides (BM 2812 and BM 2745). The non-conical valve of *P. conicus* seems identical to valves attributed to *P. elegans.* They both have a fasciculate arrangement of areolae and the same areolae density. Given that the two morphologies occur together as part of a single frustule, we believe that *P. conicus* and *P. elegans* are conspecific. We treat the two names as synonyms and retain *P. conicus* for the name of the species, since it was originally applied to a complete frustule.

***Porodiscus major* Greville, 1863: 64, pl. 4, fig. 2.**

Porodiscus major was described from Cambridge Estate, Barbados, from a slide communicated by C. Johnson (Greville 1863:64). The description was later amended by Greville (1865:46–47). We did not study this species as we did not find any additional specimens besides the valve on slide BM 2844 (holotype?) that was illustrated by Williams (1988, pl. 52, figs 5–6). Based on our observations of slide BM 2844, we believe that this species belongs in *Porodiscus*.

***Porodiscus oblongus* Greville, 1863: 65, pl. 4, fig. 5.**
(Figs. 22–23, 57–61)

Nomenclatural synonyms:
Porodiscus ovalis Greville, 1863, explan. pl. 4, fig. 5 (alternate name).
Craspedodiscus oblongus (Greville) Grunow in Schmidt, 1881, explan. pl. 66, Figs. 7–9.

Greville (1863:65) described *Porodiscus oblongus* from "Barbadoes deposit" and illustrated it as *P. ovalis* (Greville 1863, explan. pl. 4, fig. 5). Slide BM 2045 bears the note "Coll. Greville. Barbadoes earth" and the name *"Porodiscus ovalis."* Williams (1986) cites this slide as possibly the holotype. This species is not rare in the British Museum slides. On slides BM 10602 and BM 10399, valves of *P. oblongus* were selected (picked) by Greville.

Greville's original description is short (Greville 1863:65): "Disc elliptical-oblong; pseudo-opening large. Long diameter about .0028″ [71 µm]". He also added, "The pseudo-opening is very large, the radiating lines of granules are less crowded, and the granules themselves larger than in any of the preceding species". Greville (1865:46) adds to the description: "The diameter of the disc is .0030″ [77 µm]. Radiating cellules about 8 in .001." The specimen figured in Greville's original illustration (Greville 1863, fig. 5), has a diameter of 70-35 µm, and there are about 5 areolae in 10 µm on a row. Rattray (1890:674) added to this description: "Subacutely elliptical. Major axis .05 mm long, about 2.5 times minor. Surface sloping gradually downwards from edge of central space. Central space roundly elliptical, with major axis corresponding in direction to minor axis of valve. Markings angular, decreasing regularly and somewhat rapidly from central space to border; around the central space 4.5 at border 10 in .01 mm; rows radial, substraight. Border narrow, hyaline."

Description.— We measured five valves of *P. oblongus* from slides BM 2045, BM 1062, BM 1063, BM 10399, and five valves from sample CAS 611193[3368], Springfield (slide 581122).

Valves oval, length (54–78 µm) two times larger than width (26–37 µm), with round or slightly elliptical center (9–11 µm diameter). Areolae organized in rows radiating from the center, 5–6 areolae in 10 µm. Locula with velum better preserved on the elongated ends of the valves (Fig. 58), foramen about 1 µm in diameter (Fig. 60). Velum consisting of a central cribral pore surrounded by 4–6 marginal cribral pores (Figs. 57–58). The central depression ("sack") is not bordered by a real hyaline ring, but the areolae walls surrounding the depression form a little boundary around it that appears like a ring. Areolae in the depression are smaller than on the valve. Rimoportulae arranged along the margin of the valve, with more distance from the margin in the middle of valve (2–3 areolae from margin) and closer to the margin (1 areola from margin) at the ends of the valve. Rimoportulae opening externally as round small holes, internally also as holes, but may be broken (Fig. 60).

Comments.— Castracane (1886) described a similar species *P. stolterfothii* from the equatorial part of the Pacific Ocean as a living species; it differs from *P. oblongus* by a more rhombic shape. Also similar to *P. oblongus* is *Coscinodiscus oblongus* Greville (1866a:4, figs. 9–10) from Springfield Estate, Barbados. Both species (*P. oblongus* and *C. oblongus*) are present in British Museum slides BM 2045, BM 10605, BM 10604, BM 10603, BM 20602 and BM 10399. The main difference between the two taxa is a deeper (steeper) cavity in *Porodiscus oblongus*. *Porodiscus oblongus* Greville from Springfield is illustrated in Schmidt's Atlas (Schmidt 1881, Taf. 66, figs. 7–9) as *Craspedodiscus oblongus* (Grev.) Grunow [in Schmidt] (a valid new combination). Schmidt also illustrates from Springfield *Coscinodiscus oblongus* Greville (Taf. 66, figs. 10–11) for which he suggests a generic placement in *Craspedodiscus* ("unbedingt zu *Craspedodiscus* zu rechnen"). Schmidt, however, did not validly publish the new combination, which seems to have been first published by Hanna (1931:194).

Craspedodiscus oblongus (Greville) Hanna (= *Coscinodiscus oblongus* Greville) and *Craspedodiscus oblongus* (Greville) Grunow in Schmidt (= *Porodiscus oblongus* Greville) are similar species; however, *Craspedodiscus oblongus* (Greville) Grunow in Schmidt belongs to *Porodiscus*, whereas *Craspedodiscus oblongus* (Greville) Hanna belongs to *Craspedodiscus* and had been renamed *Craspedodiscus ellipticus* by Gombos (1982). Fenner (1985) refers to two species, *Craspedodiscus ellipticus* Gombos (= *Coscinodiscus oblongus* Greville) and *Craspedodiscus oblongus* (Greville) Grunow (= *Porodiscus oblongus* Greville). Many works (e.g., Barron et al. 1984; Strelnikova 1992) cite *Craspedodiscus oblongus* (Grev.) Grunow from Middle Eocene sediments, which corresponds to *Coscinodiscus oblongus* Greville (= *Craspedodiscus ellipticus* Gombos). This species has a wide distribution in the Middle Eocene in tropical and non-tropical regions. *Porodiscus oblongus* Grev. has a narrower distribution limited to the tropical region. We found it only in samples from Barbados.

***Craspedodiscus ellipticus* Gombos, 1982, p. 231, figs 13, 14.**
(Figs. 19, 21, 62, 63)

Nomenclatural synonyms:
Coscinodiscus oblongus Greville, 1866a:4, pl. 1, figs 9, 10.
Craspedodiscus oblongus (Greville) Hanna, 1931:194 (illegitimate name, later homonym).
Craspedodiscus oblongus (Greville) Grunow in Schmidt, 1881, caption Taf. 66, figs. 10–11 (invalid name).

Greville's original description is short "Disc more or less oblong, having the center depressed, and an umbilicus containing a number of subremote granules; surface filled up with radiating granules, which diminish in size next the umbilicus and towards the margin, where they resemble minute puncta. Length .0028″ to .0050″ [71 to 127 µm]." It was described from Springfield.

Description.— We measured several valves from slide BM 10603 and slide CAS 581122 (CAS 611193[3368]).

We found that the valves, characterized by their elongated shape, are 56–67 µm in length, nearly 30 µm in width, with areolae arranged in rows radiating from a concave center, 6 areolae in 10 µm on a row. The concave center is oval, with diameter 10–12 × 6–8 µm. Rimoportulae arranged along the margin, opening externally as a small round holes, and internally also as round holes (they may be broken, however).

Comments.— Williams (1988, pl. 28, figs 1–4) illustrated two specimens that he referred to *Coscinodiscus oblongus* Greville. Only the specimen illustrated in figures 3–4 belongs to *Craspedodiscus ellipticus* Combos (= *Coscinodiscus oblongus* Greville). The other specimen (figs. 1–2), which has a round center, belongs to *Porodiscus oblongus* Greville.

***Craspedodiscus umbonatus* Greville, 1866b:79, pl. 8, fig. 15.**
(Figs. 65–70, 74)

Craspedodiscus umbonatus Greville was described from "Cambridge Estate Barbados deposits in slides communicated by C. Johnson Esq." The original description is short: "Disc hexagonally cellulate, the border nearly equal to half the radius, the centre rather sharply umbonate." Greville further commented: "Distinguished at once by its umbonate centre. Cellules near the margin of the border 8 in .001″." Williams (1988, pl. 33, fig. 7) illustrated the holotype from slide BM 5469.

Description.— We did not study the holotype slide, but this species was common on slides from the CAS Collection, especially from material from Joe's River (CAS 611174[1345], slides 581129, 581130).

The valves are circular, diameter 42–74 µm, convex, sometimes hemispherical with deeply concave center, 7–10 µm diameter. The ration of the valve diameter to the diameter of the center is 6–8. Areolae are arranged in radial rows, 4–5 in 10 µm. External cribrum consists of one or several central pores surrounded by marginal pores. Areolae are a little smaller on the concave center. Rimoportulae are arranged around the margin, opening externally as small round holes, sometimes one of them situated in smaller cavities (Fig. 74) on the margin. They open internally as simple round holes; however, they may be broken. Valves have no spines.

Comments.— This species has been reported only from Barbados. *Craspedodiscus umbonatus* differs from *Porodiscus* only by the absence the hyaline ring around the cavities and the little depression for one rimoportula at the margin (Fig. 74).

Typification of the Genus *Porodiscus* with *Porodiscus nitidus* Grev.

In the original publication of *Porodiscus,* Greville included five species *(P. nitidus, P. elegans, P. major, P. conicus,* and *P. oblongus = P. ovalis* in the plate caption), but he did not designate a type. The most common species of *Porodiscus, P. splendidus* Grev. is not a candidate as generitype inasmuch as it was not one of the original species. We designate here *Porodiscus nitidus* Grev. as the lectotype of genus *Porodiscus* Greville. Although not as common as *P. splendidus, P. nitidus* has been reported in various fossil localities, and it is a better choice than any of the other four species that have never been observed other than on Greville's original slides. The holotype of *P. nitidus* is on slide BM 2751 (Bridgewater, Barbados).

Discussion

Coscinodiscus Ehrenberg, *Craspedodiscus* Ehrenberg, *Porodiscus* Greville, and *Annellus* Tempère are closely allied genera in the family Coscinodiscaceae; they differ only by the structure and shape of the cavity in the valve center. Based on the shapes and arrangements of the rimoportulae, *Craspedodiscus* and *Porodiscus* are similar. Stratigraphically, *Coscinodiscus* is the oldest of these genera (Cretaceous). *Craspedodiscus* apparently separated from *Coscinodiscus* during the early Paleocene. *Porodiscus* separated from *Coscinodiscus* or *Craspedodiscus* only during the Middle Eocene, whereas *Annellus* is restricted to the Miocene. The Cretaceous genus *Pomphodiscus* Barker and Meakin has locular areolae, and a central cavity that is reminiscent of some species of *Porodiscus* and *Craspedodiscus*. The central cavity in *Pomphodiscus* is a chamber that is formed by an inflation and separation of the basal siliceous layer into two layers. The shape and the central position of the rimoportulae, however, places this genus in the family Stellarimaceae (Nikolaev and Harwood 2000). Even more distant in the classification, but with a central chamber, is the Cretaceous genus *Benetorus* (family Stictodiscaceae). The uvular process of the Early Cretaceous genus *Archaegladiopsis* (family Archaegladiopsidaceae) is also reminiscent of the cavity of *Porodiscus*. The uvular process, centrally located is a funnel-shaped depression with a round opening in the valve exterior and a uvula-shaped intrusion on the inside, without visible openings (Nikolaev and Harwood 1997). We believe that the higher level classification of these fossil genera is still valid (i.e., we are not suggesting that these genera are closely related), and that their superficial similarities are due to parallel evolution.

The following section will concentrate on the morphological differences between *Porodiscus* and *Craspedodiscus* and between *Annellus* and *Craspedodiscus*, because it is presently difficult to separate them.

***Craspedodiscus* Ehrenberg**

We recognize three informal divisions among the diatoms that have been referred to *Craspedodiscus*. The classical concept of *Craspedodiscus* is represented by *C. coscinodiscus* (Figs. 81–86) and is characterized by a large internal depression that has a diameter that is at least one half of the entire valve. The central depression typically has a nearly flat bottom and has areolae that are reduced in size compared to those of the outer valve surface (Figs. 84–85). The transition from the outer valve surface to this internal depression is abrupt, often close to 90° (Figs. 82–85). Similar to *Porodiscus*, a hyaline rim occurs at this transition (Figs. 82–85) in most Miocene forms. The edge of the central depression is rough, as if a weakly silicified covering, now missing, was present over a chamber in that species. Such covering was never observed in *Craspedodiscus*.

The majority of diatoms that have been referred to *Craspedodiscus* comprise a second group, represented by *C. elegans*, the lectotype of *Craspedodiscus* (see Ross in Farr et al. 1979). Diatoms of this group have an internal depression that is less distinct, characterized by a more gradual transition from the valve's mantle and by areolae that are not distinctly different from those on the valve's margin. Some Oligocene diatoms that have traditionally been referred to *Craspedodiscus coscinodiscus*, but are better assigned to *Craspedodiscus barronii* Bukry (Figs. 76–77), have gently sloping central depressions and could be referred to this group. Other taxa, including *Craspedodiscus undulatus* Gombos, *C. elegans* Ehrenberg and *C. moelleri* A. Schmidt, have undulated valve surfaces, reminiscent of the undulated valve surfaces of certain species of *Actinocyclus* and *Cestodiscus*. Diatoms of this group appear to be closely related to *Coscinodiscus*, and it is not clear why they should be separated from it. Indeed, *Coscinodiscus excavatus* (Fig. 92) might be placed in this group, although no formal transfer to *Craspedodiscus* has been proposed. We do not, however, wish to discuss the taxonomic implications of transferring *Craspedodiscus elegans* and other diatoms of this group to *Coscinodiscus* in the present paper.

A third group of taxa that have been referred to *Craspedodiscus* are similar to *Porodiscus* in that they possess a distinct internal depression that is typically confined to only the centermost portion of the valve. This group is represented by *Craspedodiscus ellipticus* Gombos (= *Coscinodiscus oblongus* Greville) (Figs. 62–63) and *C. umbonatus* Greville (Figs. 65–70). As in *Porodiscus,* the central depression is deeply invaginated with a concave central valvar surface. The transition from the outer valve surface to the interior depression, however, is not as abrupt as in *Porodiscus,* and no hyaline ring is present. Valves of *Craspedodiscus ellipticus,* with their sloping central depression (Figs. 62–63), clearly differ from valves of *Porodiscus oblongus* (Figs. 57–61) with their central depression more circular and sloping more abruptly. On his Figure 17, however, Gombos (1982) illustrates a diatom, which he refers to *Craspedodiscus oblongus* (Greville) Schmidt, which has a circular internal depression like that of *P. oblongus,* but it also possesses a gradual or sloping transition from the outer valve surface, as in *C. ellipticus.* This specimen may be transitional between *P. oblongus* and *C. ellipticus.*

***Annellus* Tempère**

The genus *Annellus* is restricted to the late-early and early-middle Miocene, separated by at least 15 million years from the Eocene records of *Porodiscus.* At present, *Annellus* is monospecific, with *A. californicus* Tempère, as the only species. As discussed by Ryde (1962), *Annellus* is closely related to Miocene forms of *Craspedodiscus coscinodiscus.*

Ryde (1962) made a detailed morphologic study of *Annellus californicus* Tempère, noting that the valve was "formed of an outer cylinder inturned at one end (and) deeply invaginated to produce within the first, a co-axial cylinder closed at the lower end." He mentioned that the "inner cylinder

often tends to bulge somewhat and its length is equal to the depth of the valve mantle," appearing as a dome when viewed from the inside of the valve. Ryde (1962) stated that the diameter of the areolae on the valve surface of the inner cylinder is very much reduced in size compared to those of the valve mantle and the surface consists of rather fragile, diaphanous silica that is often not preserved. Ryde (1962) further commented on the rather abrupt transition from the inner valve mantle to the inner cylinder. Based on comparison with the internal valve surface of *Craspedodiscus coscinodiscus,* Ryde (1962) chose to transfer *Annellus californicus* Tempère to *Craspedodiscus californicus* (Tempère) Ryde. We feel, however, that the high mantle of *Annellus californicus,* which results in valves often being orientated in valve view on slides, is a unique feature to *Annellus,* distinguishing it from the *Craspedodiscus coscinodiscus* group. *Annellus* also lacks the hyaline rim, which is present in typical forms of *Craspedodiscus coscinodiscus* (Figs. 82–86). Barron (1983) argued that the shallower mantle of his new species, *Craspedodiscus rhydei,* warranted placing it into *Craspedodiscus* rather than *Annellus;* however, *C. rhydei* (Fig. 91) clearly lacks a hyaline ring and closely resembles valves of *Annellus californicus* (Figs. 87–88).

Concluding Remarks on *Porodiscus* Greville

Porodiscus resembles both *Coscinodiscus* and *Craspedodiscus* with the presence of locular areolae with external cribrum and internal foramina, and marginal rimoportulae. It has unique characters, however, such as spines (in some species), which are not present in *Coscinodiscus* nor in *Craspedodiscus*. The central cavity, which also characterizes *Craspedodiscus*, seems to be of a different nature in *Porodiscus*, where it is very steep (tube-like) and well defined, being bordered by a hyaline rim. *Craspedodiscus* species usually do not have such hyaline rims (except for some tropical Miocene forms of *Craspedodiscus coscinodiscus*) and lack a well-defined central depression. The hyaline rim in these forms may be the edge of a broken outer surface of a chamber. Miocene forms of *Craspedodiscus coscinodiscus* and *Annellus californicus*, which have a well defined central depression, typically have a central depression that covers at least half of the diameter of the valve. This character, and the separation in geologic time of more than 15 million years between the Eocene forms of *Porodiscus* and the Miocene forms of *Craspedodiscus coscinodiscus* and *Annellus*, are arguments in support of *Porodiscus* being retained as a valid taxonomic entity.

Acknowledgments

We thank Dr. David Williams of the British Museum who made possible the study of the type slides of R. Greville. The work was supported by Russian Fund for Fundamental Research (RFFI) Grant 00-04-49333 and the Diatom Collection of the California Academy of Sciences. We are also thankful to D. Ubick, Scott Serata, M. Potapova, and E. Ruck for assistance in the preparation of this article, Dr. David Harwood for his review of the manuscript and helpful suggestions, and Dr. Michele L. Aldrich, who read the near final version of the manuscript and saved us from memoralizing a number of grammatical and other baby blunders.

Literature Cited

Barron, J.A. 1981. Late Cenozoic diatom biostratigraphy and paleoceanography of the middle latitude eastern North Pacific, DSDP Leg 63. *Initial Reports, Deep Sea Drilling Project* 63:507–538.

Barron, J.A. 1983. Latest Oligocene through early middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology* 7:487–515.

Barron, J.A., D. Bukry, and R.Z. Poore. 1984. Correlation of the middle Eocene Kellogg Shale of northern California. *Micropaleontology* 30(2):138–170.

Brun, J. 1896. Diatomées Miocènes. *Le Diatomiste* 2(24):229–260, pl. 19–24.

Brun, J., and J. Tempère. 1889. Diatomées fossiles du Japon. Espèces marines et nouvelles des calcaires argileux de Sendaï et de Yedo. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* 30(9):3–75.

Castracane, F. 1886. *Report on the Diatomaceae collected by H.M.S. Challenger during the years 1873–1876.* Report on the scientific results of the voyage of *H.M.S.Challenger* during the years 1873–76. Botany, Vol. 2. 178 pp.

Farr, E.R., J.A. Leussonk, and Y. Stafleu. 1979. *Index Nominum Genericorum (Plantarium)* Supplement. Regnum Vegetabile 113. 126 pp.

Fenner, J. 1985. Late Cretaceous to Oligocene planktonic diatoms. Pages 713–762 *in* H.M. Bolli, J.B. Saunders, and K. Perch-Nielsen, eds., *Planktonic Stratigraphy.* Cambridge University Press, Cambridge.

Glezer, Z.I. 1969. Late Eocene complexes of diatoms, silicoflagellates and ebriidea of the south-western part of the Turgai depression. *Proceedings of the VSEGEI (All-Union Geological Institute),* new series, V. 130. Biostratigraphy (Biostratigraficheskii Sbornik), 4:67–84.

Glezer, Z.I. 1974. Diatoms of the Paleogene. Pages 109–146 *in* Glezer et al., eds., *The Diatoms of the USSR. Fossil and Recent.* Publishing House Nauka, Leningrad Branch, 1.

Glezer, Z.I., and A.P. Jousé. 1974. Diatoms and silicoflagellates of the Eocene of equatorial Atlantic. Pages 49–63 in *Micropaleontology of Seas and Oceans.* Nauka, Moscow, USSR.

Glezer, Z.I., V.Yu. Zosimovich, and M.N. Klyushnikov. 1965. Diatoms of the Paleogene sediments of the Severny Donez River basin, and their stratigraphic position. *Paleontologicheski sbornik* 2(2):73–84.

Gombos, A.M., Jr. 1982. Early and middle Eocene diatom evolutionary events. Bacillaria 5:225–242.

Gombos, A.M. 1983. Middle Eocene diatoms from the South Atlantic. Initial Reports of the Deep Sea Drilling Project 71:565–581.

Greville, R.K. 1863. Descriptions of new and rare diatoms. Series IX. *Transactions of the Microscopical Society of London,* new series 11(3): 63–76, pls IV–V.

Greville , R.K. 1865. Descriptions of new and rare diatoms. Series XVI. *Transactions of the Microscopical Society of London,* new series 13:43–57, pls V–VI.

Greville , R.K. 1866a. Description of new and rare diatoms. Series XVIII. *Transactions of the Miscroscopical Society of London, n.s.,* 14:1–9, pls. I–II.

Greville , R.K. 1866b. Description of new and rare diatoms. Series XIX. *Transactions of the Miscroscopical Society of London, n.s.,* 14:77–86, pls. VIII–IX.

Grove, E., and G. Sturt. 1887a. On a fossil marine diatomaceous deposit from Oamaru, Otago, New Zealand. Part III. *Journal of the Quekett Microscopical Club,* series 2, 1887, 3(18):63–78, pls 5–6.

Grove, E., and G. Sturt. 1887b. On a fossil marine diatomaceous deposit from Oamaru, Otago, New Zealand. Appendix. *Journal of the Quekett Microscopical Club,* series 2, 1887, 3(19):131–148, pls 10–14.

Hanna, G D. 1931. Diatoms and silicoflagellates of the Kreyenhagen shale. Mining in California. *California Division of Mines, Report of the State Mineralogist* 27(2):187–201.

Hanna, G D. 1932. The diatoms of Sharktooth Hill, Kern county, California. *Proceedings of the California Academy of Sciences,* ser. 4, 20(6):161–263.

Jousé , A.P. 1949. The genus *Pseudopodosira* Jousé. In: Proschkina-Lavrenko, ed., Diatomovy Analiz, Botanicheskii Institut im V.L. Komarova Akademii Nauk S.S.S.R. *Gosudarstvennoe Izdatelystvo Geologicheskoi Literatury, Moskva-Leningrad* 2(1):238 pp.

Jousé, A.P. 1954. On diatoms of Tertiary age in bottom sediments of the Far Eastern Seas. *Proceedings of the Institute of Oceanography, Academy of Sciences of the USSR* 9:119–135. [In Russian]

Jousé, A.P. 1961. Diatomeae marinae Mioceni et Plioceni ex oriente extremo. *Botanicheskie Materialy okdela Sporovykh Rastenii (Notulae Systematicae e Sectione Cryptogamica Instituti Botanici Nomine V.L. Komarovii Academiae Scientiarum URSS)* 14:59–70, 3 pls.

Jousé, A.P. editor-in-chief. 1977. Atlas of Microorganisms in Bottom Sediments of the Oceans (Diatoms,Radiolarians, Silicoflagellates, Coccoliths) M. "Nauka". 196 pp.

Mann, A. 1907. Report on the diatoms of the *Albatross* voyages in the Pacific Ocean, 1888–1904.

Contributions from the United States National Herbarium 10(5):221–443, 11 pls.

MITCHELL-THOME, R.C. 1979. Pre-Quaternary stratigraphy of the Atlantic island. *Geologische Rundschau* 68(2):495–522.

NIKOLAEV, V.A., AND D.M. HARWOOD. 2000. Morphology and taxonomic position of the Late Cretaceous diatom genus *Pomphodiscus* Barker & Meakin. *Micropaleontology* 46(2):167-177.

NIKOLAEV, V.A., AND D.M. HARWOOD, D.M. 1997. New process, genus and family of Lower Cretaceous diatoms from Australia. *Diatom Research*, 12(1):43-53.

OLSHTYNSKAYA, A.P. 1976. Diatom algae of the stratotypic section of the Tishkinskaya sediments. *Geologichesky Zhournal* 36(4):147–151.

PREMA, P., AND T.V. DESIKACHARY. 1989. New and interesting fossil diatoms from the Indian Ocean. *Phykos* 28(1–2):127–131.

RATTRAY, J. 1890. A revision of the genus *Coscinodiscus,* Ehrb., and of some allied genera. *Proceedings of the Royal Society of Edinburgh* 16:449–692, 3 pls.

ROBINSON, J.H. 1934. The study of the organic remains in the oceanic beds of Barbados with special reference to the diatoms. *Journal of the Barbados Museum and Historical Society* 1(2):[*5* pp.]

ROBINSON , J.H. 1936. The occurrence and distribution of the diatoms in theoceanic beds of Barbados. II. *Journal of the Barbados Museum and Historical Society* 4(1):[4 pp.].

ROBINSON , J.H. 1941. The occurrence and distribution of the diatoms in theoceanic beds of Barbados. III–IV. *Journal of the Barbados Museum and Historical Society* 4(4):[4 pp.].

RYDE, J.W. 1962. A study of *Annellus californicus* Tempère. *Journal of the Royal Microscopical Society* 80(3):243–246.

SIMS, P.A. 1989. Some Cretaceous and Paleogene species of *Coscinodiscus:* a micromorphological and systematic study. *Diatom Research* 4(2):351–371.

STRELNIKOVA, N.I. 1992. *Diatoms of the Paleogene.* St. Petersburg University, St. Petersburg. 312 pp.

WILLIAMS, D.M. 1988. An illustrated catalogue of the type specimens in the Greville diatom herbarium. *Bulletin of the British Museum (Natural History)* 18(1):1–148, 74 pls.

PLATES

PLATE 1

Light microscopy. **Figures 1–7, 9–10.** ***Porodiscus splendidus*** **Greville.** Figure 1. Lectotype (internal view), BM 10602. Figures 2, 3. BM10399. Figure 4. CAS 611235 (Cambridge). Figure 5. CAS 611174 (Joe's River). Figure 6. CAS 611174 (Joe's River). Figure 7. BM 2844. Figure 9. CAS 611235 (Cambridge). Figure 10. CAS 611193 (Springfield). **Figures 8, 11, 12.** ***Porodiscus splendidus*** **var.** ***excentricus*** **(Olsht.) Olshtinskaya new comb**. Figure 8. Olst. Collection, Ukraine, Staroverovka. Figure 11. CAS 611174 (Joe's River). Figure 12. CAS 611174 (Joe's River).

Scale bars = 10 μm.

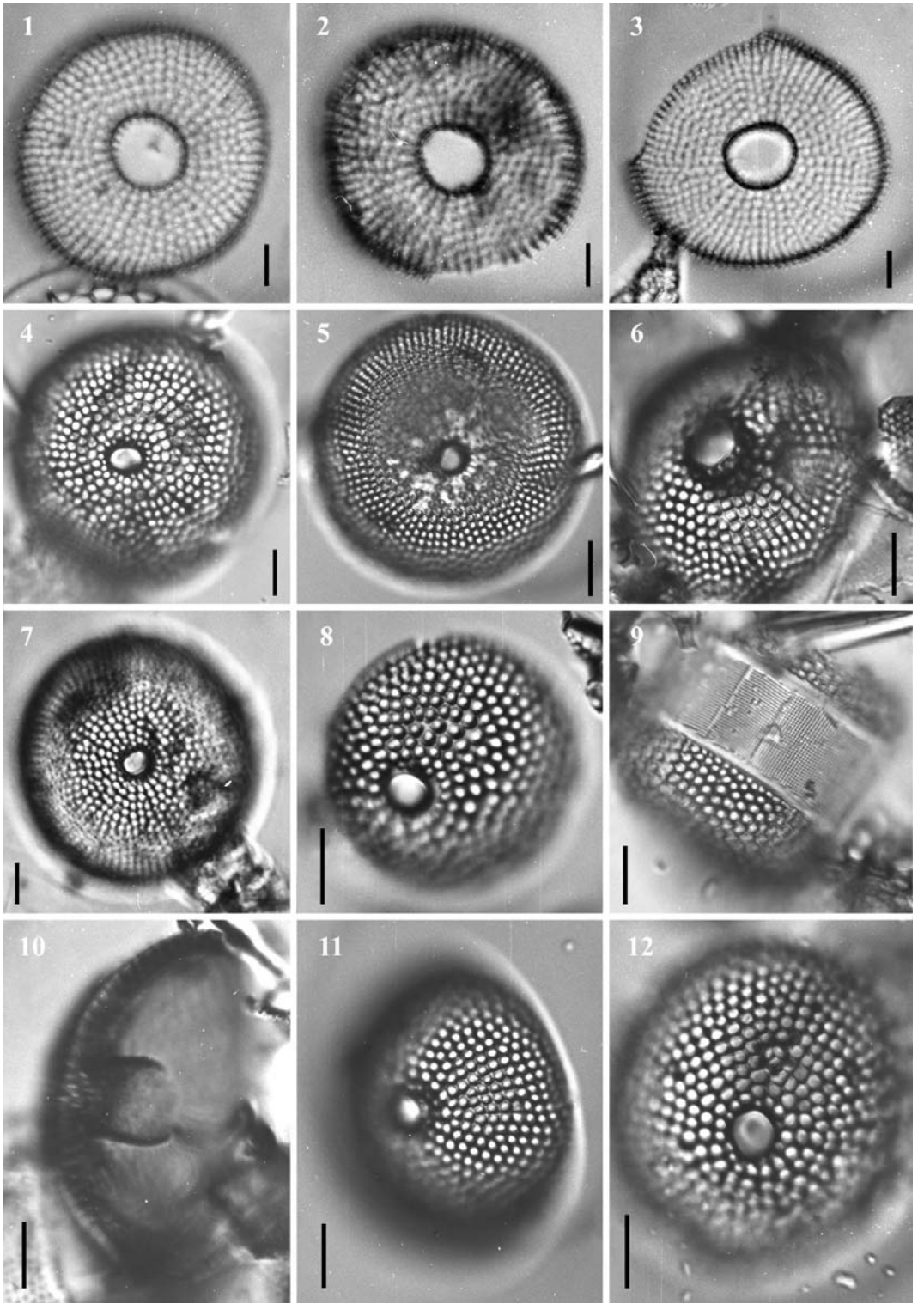

1
2
3
4
5
6
7
8
9
10
11
12

PLATE 2

Light microscopy. **Figures 13–16. *Porodiscus nitidus* Greville.** Figure 13. Valves with spines. BM 2751. Figure 14. Valves with no spines. BM 2751. Figure 15. Valves with spines. BM 2812. Figure 16. Valves with no spines. CAS 611174 (Joe's River). **Figure 17. *Porodiscus conicus* Greville.** (non-conical valve; Synonym: *Porodiscus elegans* Greville.) BM 2745. **Figure 18. *Porodiscus conicus* Greville.** BM 2812. Holotype. **Figures 19, 21. *Craspedodiscus ellipticus* Gombos.** Figure 19. BM 1063. Figure 21. CAS 611193 (Springfield). **Figure 20. *Coscinodiscus excavatus* Greville.** BM 2745. **Figures 22–23. *Porodiscus oblongus* Greville.** Figure 22. BM 2045. holotype? Fig 23. CAS 611193 (Springfield).

Scale bars = 10 μm.

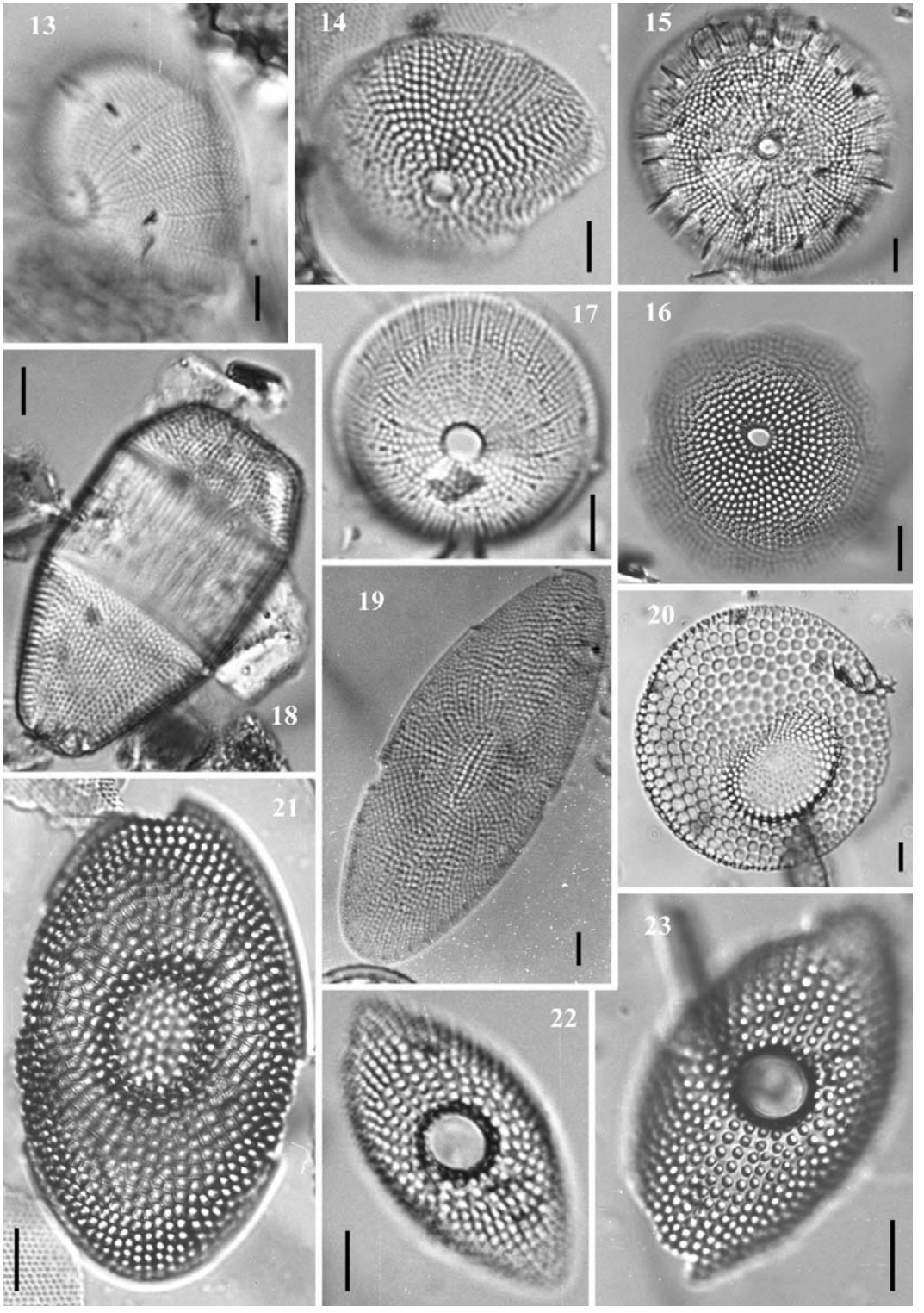
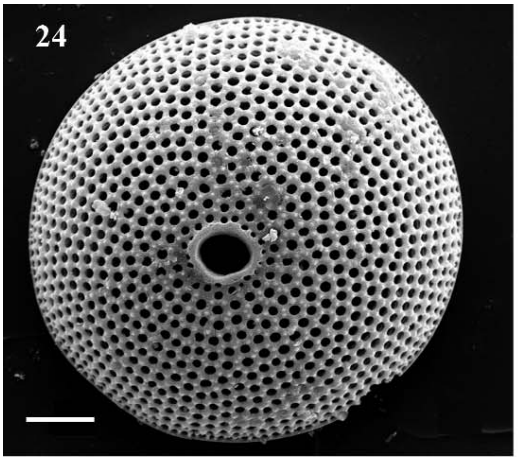
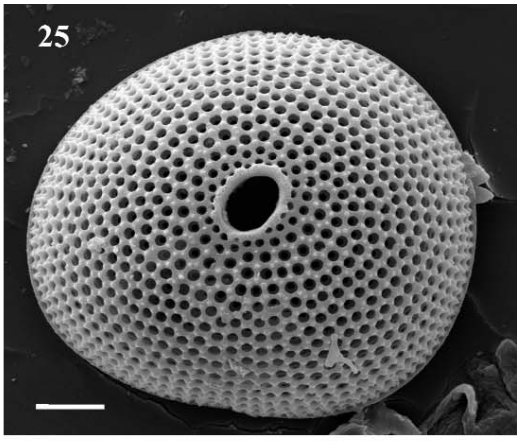

13
14
15
17
16
18
19
20
21
22
23

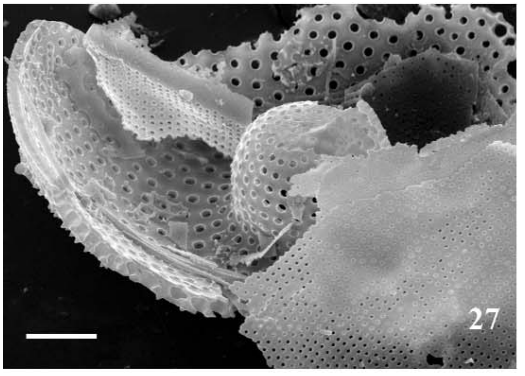
PLATE 3

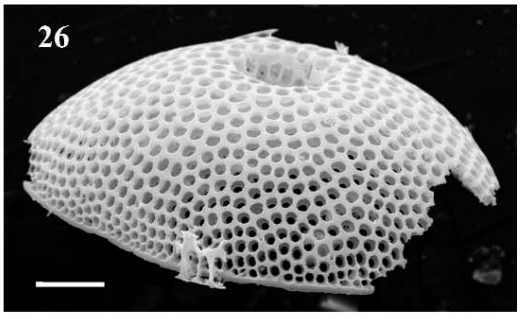
Scanning electron microscopy (SEM). **Figures 24–30.** ***Porodiscus splendidus* Greville.** Figures 24–26. External views. Figure 24. CAS 611226 (Chimborazo). Figure 25. CAS 711174 (Joe's River). Figure 26. CAS 611193 (Springfield). Figures 27–30. Internal views. Figures 27,28. Internal "sack". CAS (611193) Springfield. Figure 29. Broken "sack". Figure 30. Broken valve. Figures 29–30. CAS 611174 (Joe's River).

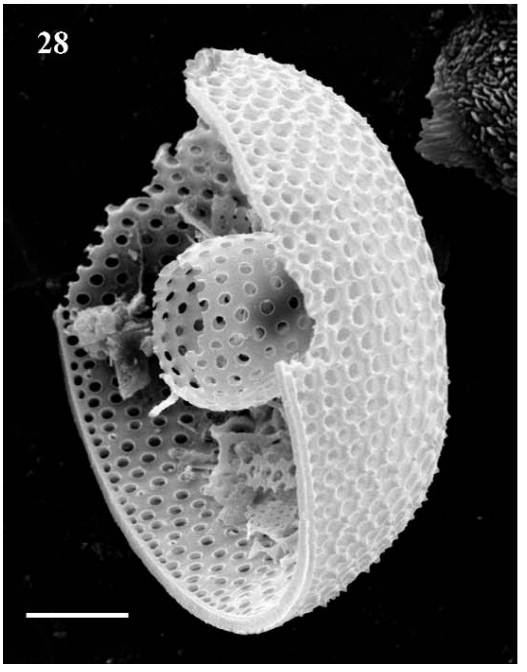
Scale bars = 10 μm.

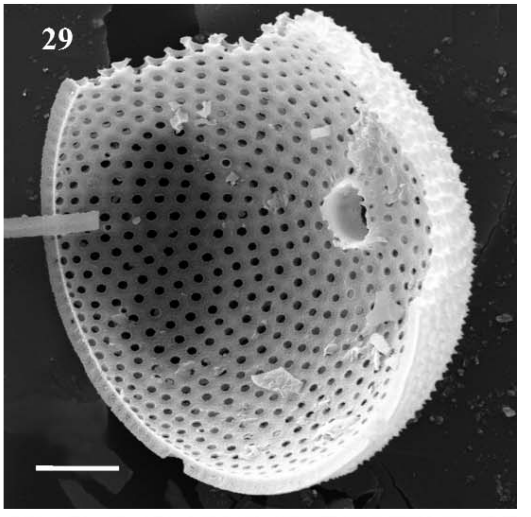

24


25


27


26


28


29

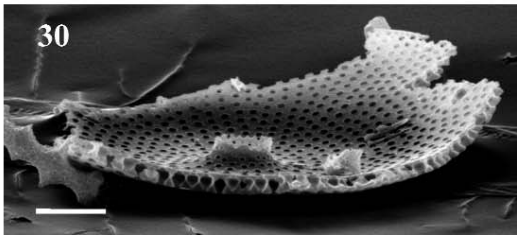
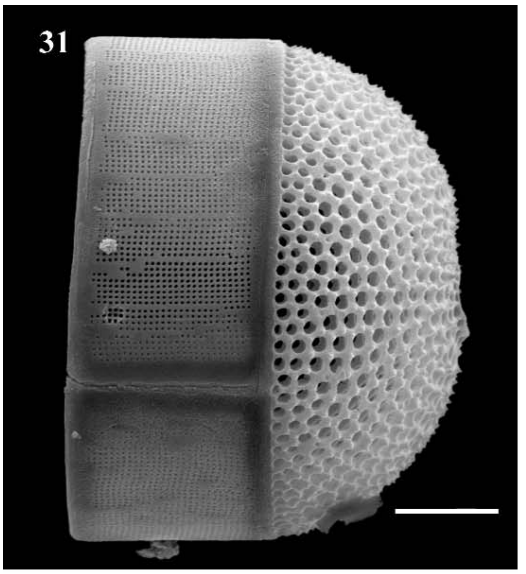
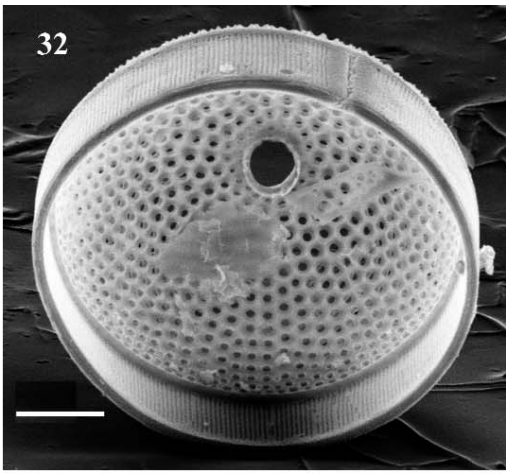

30

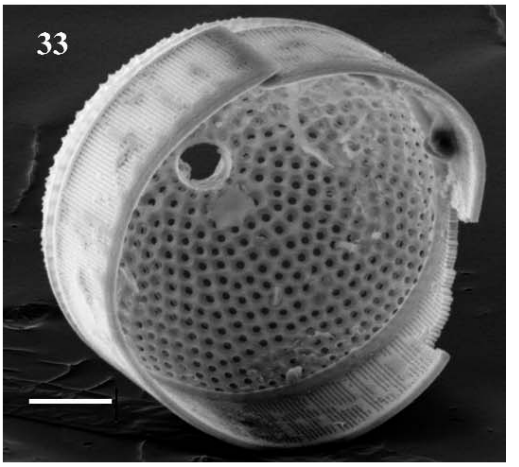
PLATE 4

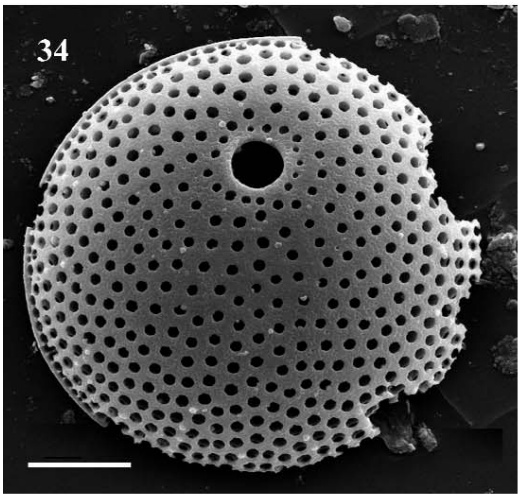
SEM. **Figures 31–33.** ***Porodiscus splendidus*** **Greville.** Valves with connection band. Figure 31. External view. Figures 32, 33. Internal view. CAS Joe's River 611174. **Figures 34–36.** ***Porodiscus splendidus*** **var.** ***excentricus*** **(Olsht.) Olshtinskaya new comb.** Figure 34. External view. Figures 35–36. Internal views. Figures 34, 36. Staroverovka. Figure 35. CAS 611174 (Joe's River).

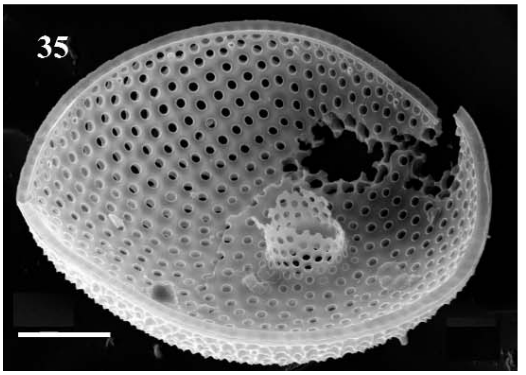
Scale bars = 10 μm.


31


32


33


34


35

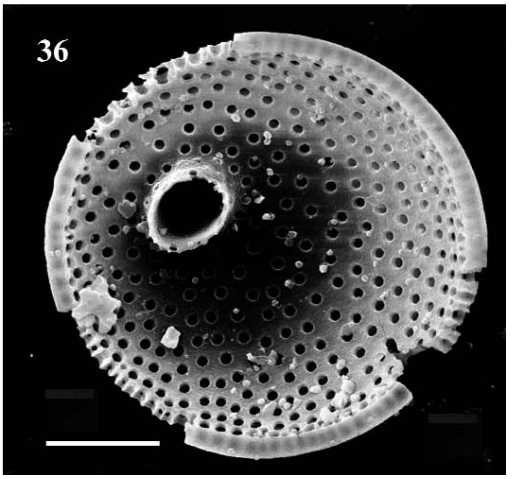
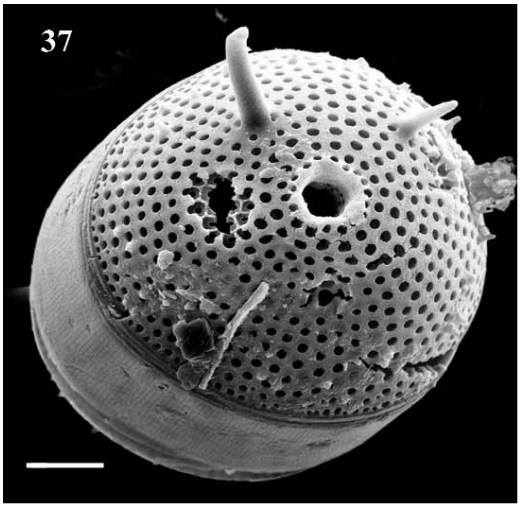
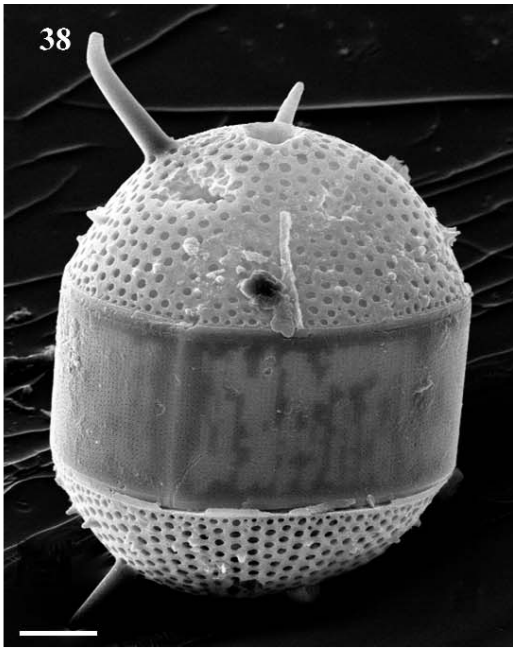

36

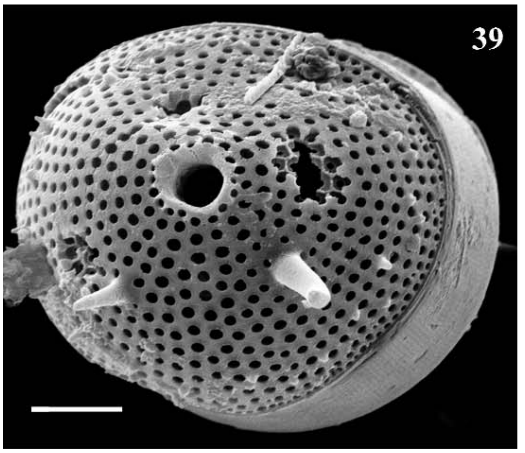
PLATE 5

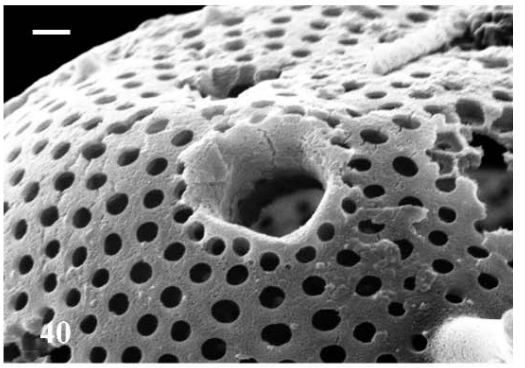
SEM. **Figures 37–40.** ***Porodiscus splendidus*** **var.** ***corniger*** **(Greville) Fourtanier n. comb.** Different positions of one frustule. Figure 40. "Sack" surrounded by hyaline ring. CAS 611226 (Chimborazo). **Figures 41–42.** ***Porodiscus nitidus*** **Greville.** External views; valves with spines. CAS 611174 (Joe's River).

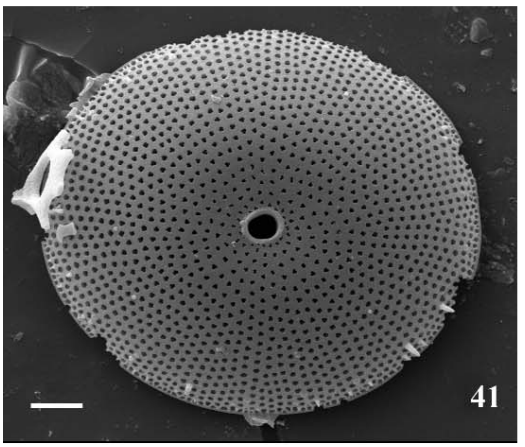
Scale bars = 2 μm (Figure 40), 10 μm (Figures 37–39, 41–42).


37


38


39


40


41

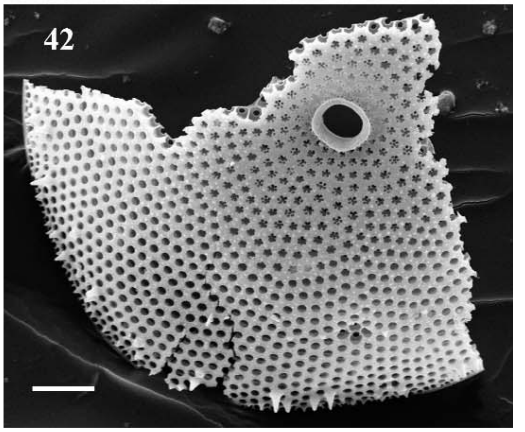
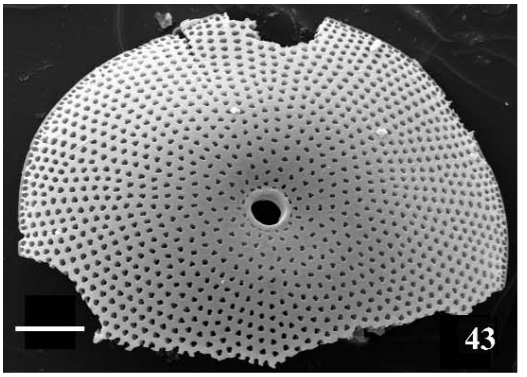
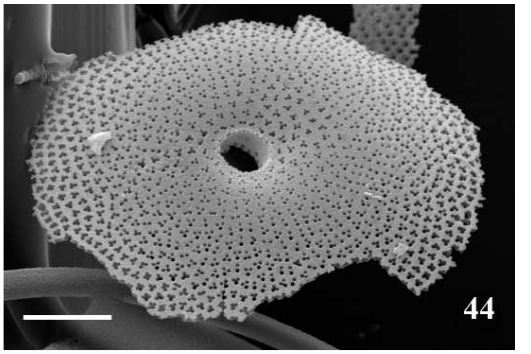

42

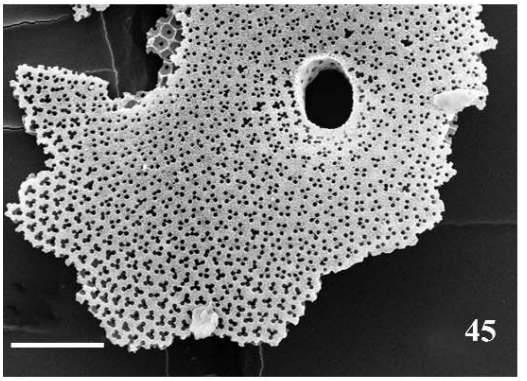
PLATE 6

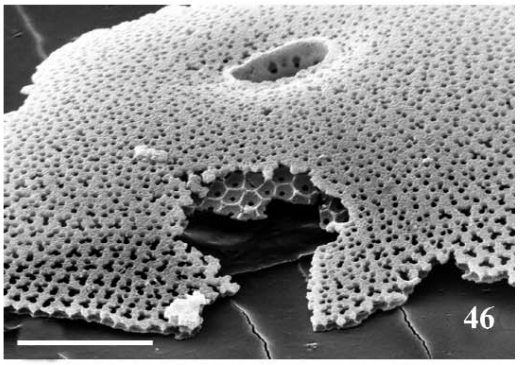
SEM. **Figures 43–50.** ***Porodiscus nitidus*** **Greville.** Figures 43–46. External views. Valves with velum. Figures 47–50. Internal views. Figures 43–44. Valves without spines. Figures 47, 49. Valves with spines. Figure 49. Rimoportulae at the ends of hyaline lines. Figures 44, 46. CAS 611226 (Chimborazo). Figures 45–50. CAS 611174 (Joe's River).

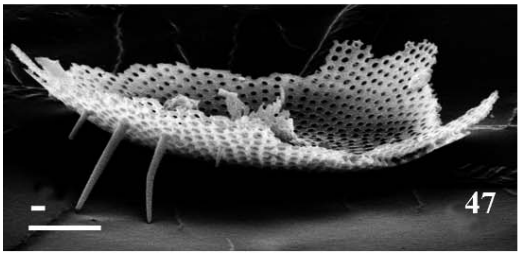
Scale bars = 10 μm.

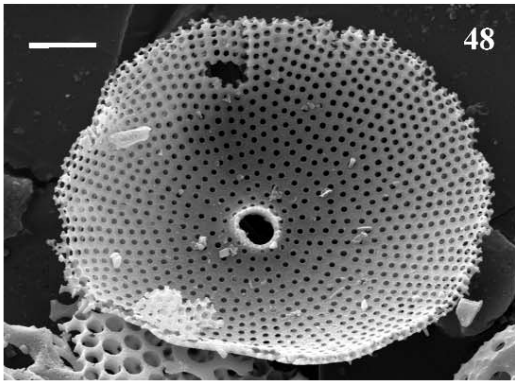

43

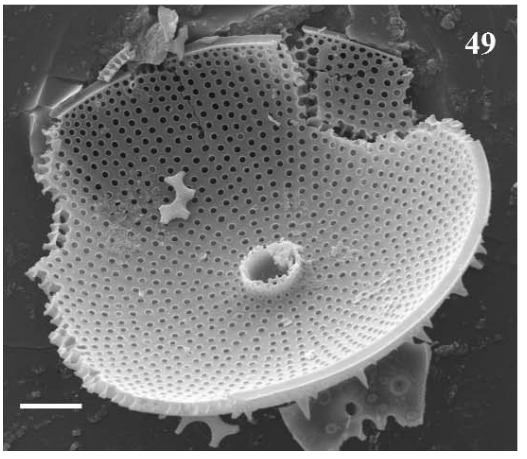

44


45


46


47


48


49

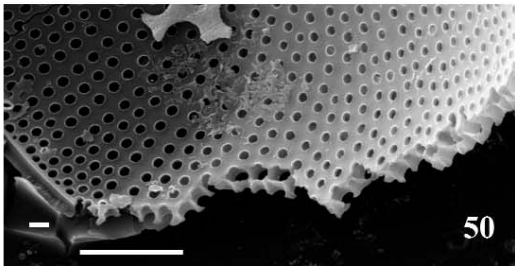
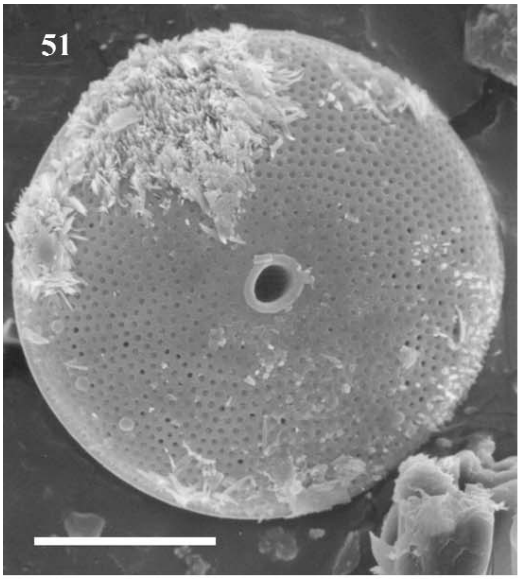
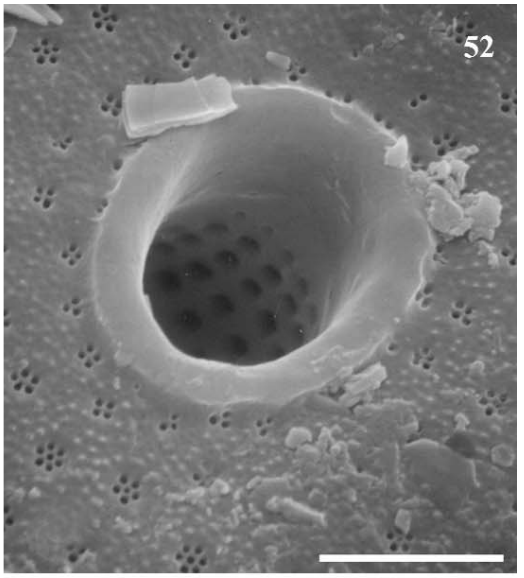

50

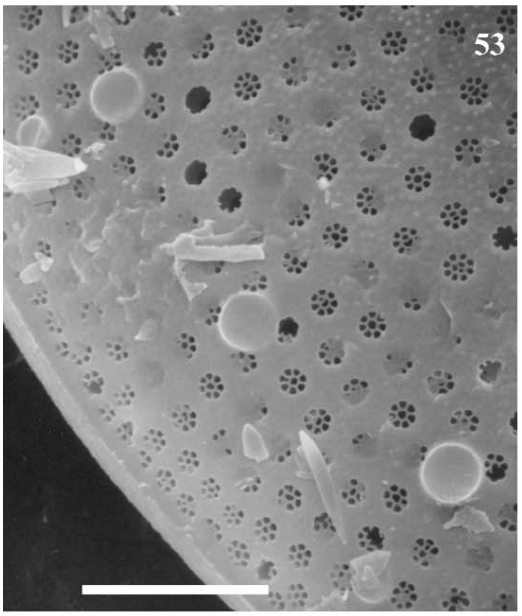
PLATE 7

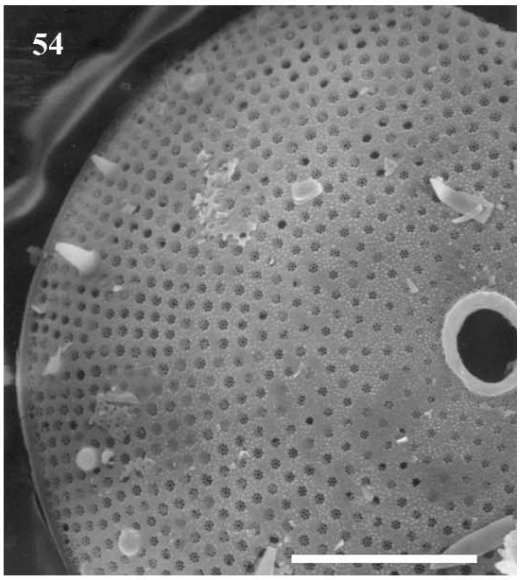
SEM. **Figures 51–56. *Porodiscus nitidus* Greville.** CAS 624819, Tasman Sea, DSDP Sample 206-16-5, 111–113 cm. Figures 51–55. External views. Figures 51, 54. Valves with spines. Figure 52. "Sack" surrounded by hyaline ring. Figure 53. The bases of broken spines, rimoportulae on the margin of valve on hyaline line under the spines. Figure 55. Velum. Figure 56. Internal view, rimoportulae.

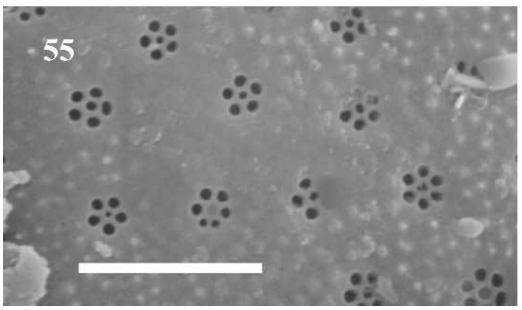
Scale bars = 25 μm (Figure 51), 15 μm (Figure 54), 6 μm (Figure 53), 4 μm (Figure 52), 3 μm (Figures 55–56).


51


52


53


54


55

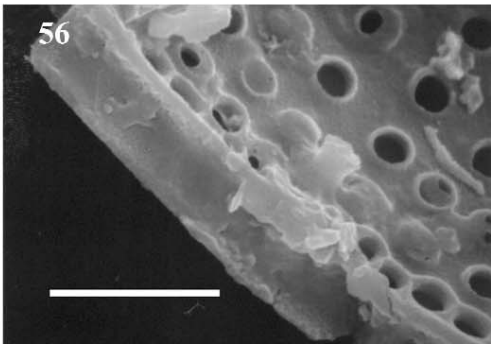
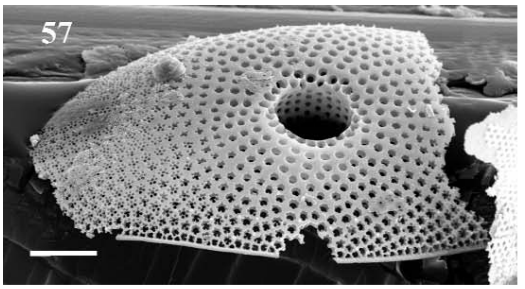
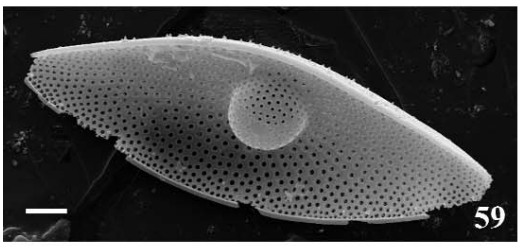

56

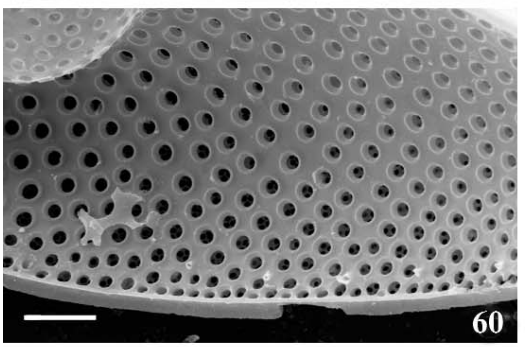
PLATE 8

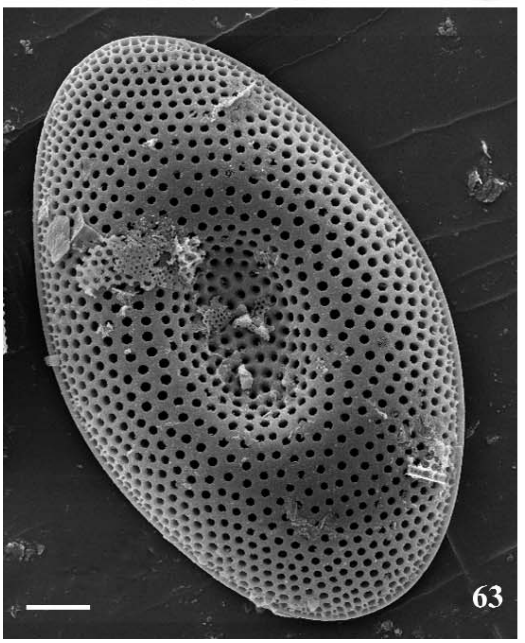
SEM. **Figures 57–61.** ***Porodiscus oblongus*** **Greville.** CAS 611193 (Springfield). Figures 57–58. External views. Velum and "sack" surrounded by hyaline ring. Figures 59–61. Internal views. Figures 59, 61. "Sack" and broken "sack." Figure 60. Rimoportulae on the margin of valve. **Figures 62–63.** ***Craspedodiscus ellipticus*** **Gombos.** CAS 611193 (Springfield). Figure 62. Internal view. Rimoportulae on the margin of the valve. Figure 63. External view. Rimoportulae on the margin. **Figure 64.** ***Porodiscus conicus*** **Greville ?** (non-conical valve; Synonym: *Porodiscus elegans* Greville.) CAS 611235 (Chimborazo).

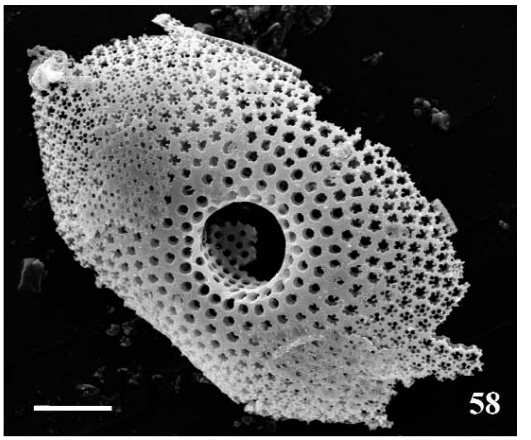
Scale bars = 5 μm (Figure 60), 10 μm (Figures 58–59, 61–63)

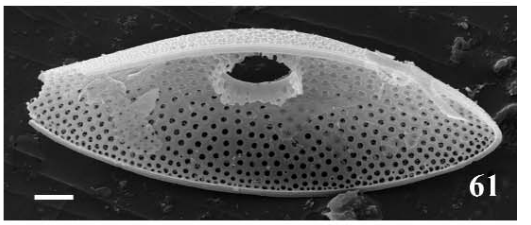

57

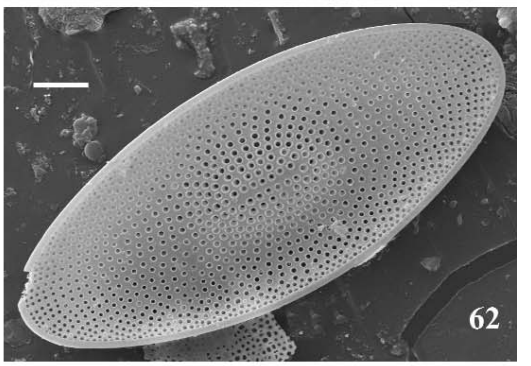

59


60


63


58


61


62

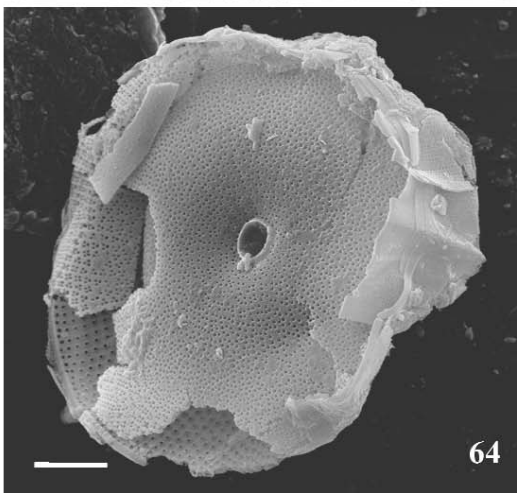
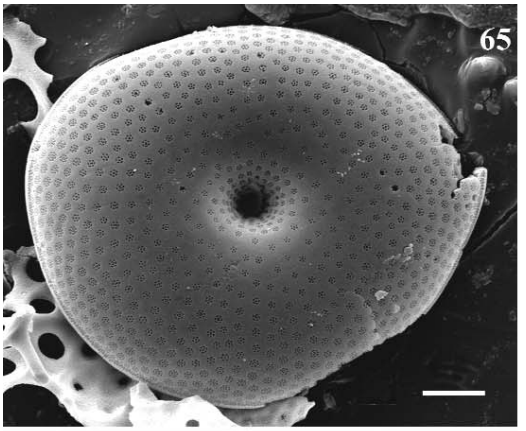
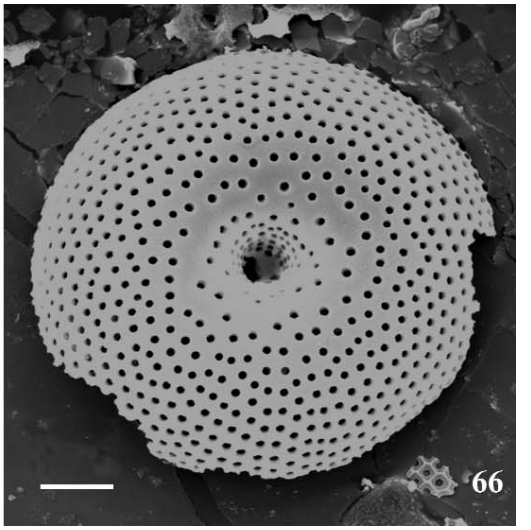

64

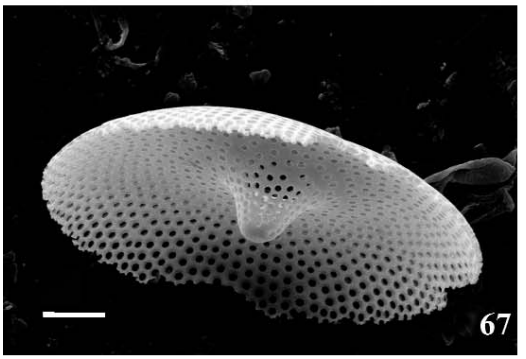
PLATE 9

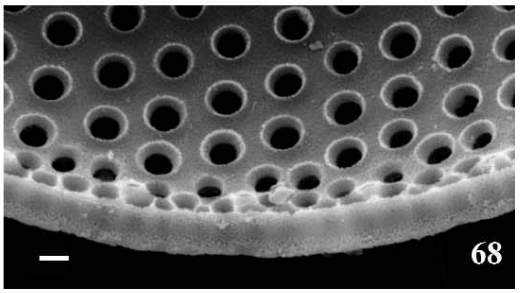
SEM. **Figures 65–70.** ***Craspedodiscus umbonatus*** **Greville.** Figures 65–66. External views. Figure 65. Velum. Figures 67–70. Internal views. Figures 67, 69. "Sack". Figures 68, 70. Rimoportulae on the valve margin. **Figures 71–72.** ***Coscinodiscus sp.*** Figure 71. External view. Figure 72. Internal view. Rimoportulae on the valve margin. Figures 65–72. CAS 611174 (Joe's River).

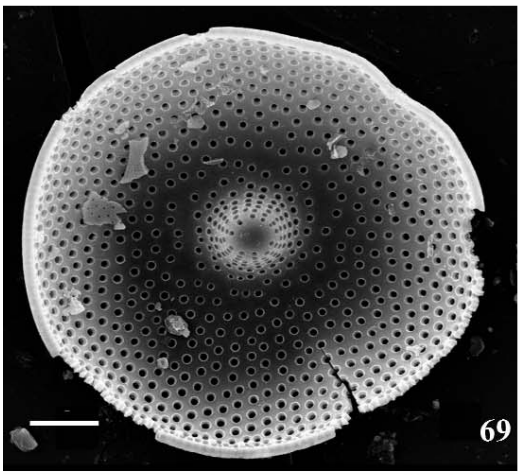
Scale bars = 1 μm (Figures 68, 70), 10 μm (Figures 65–67, 69, 71–72)

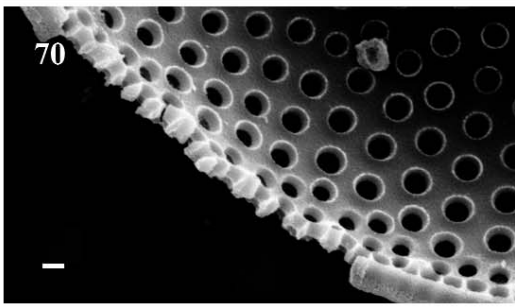

65

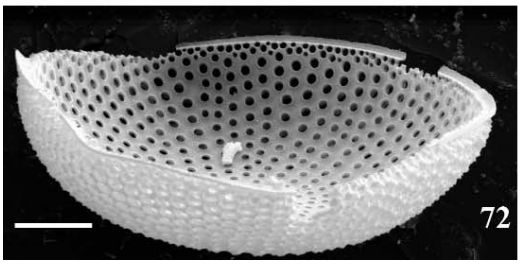

66


67


68


69


70


72

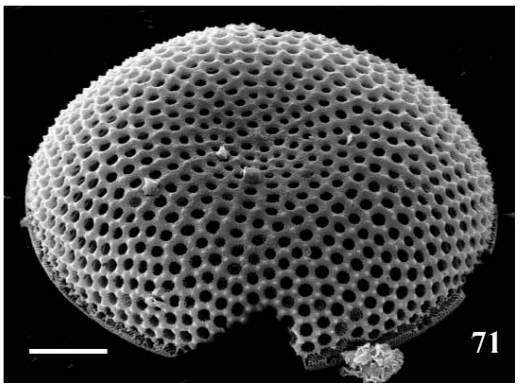
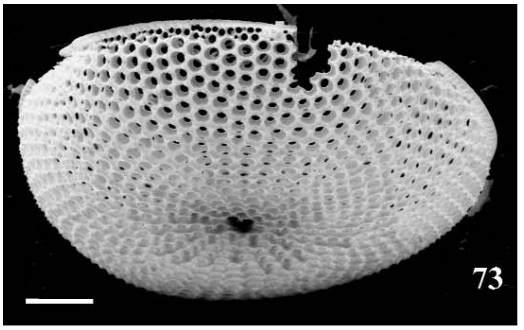
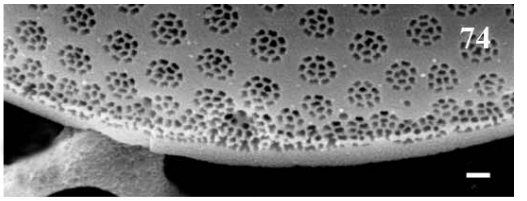

71

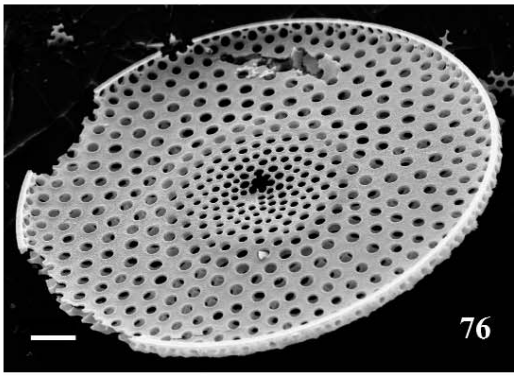
PLATE 10

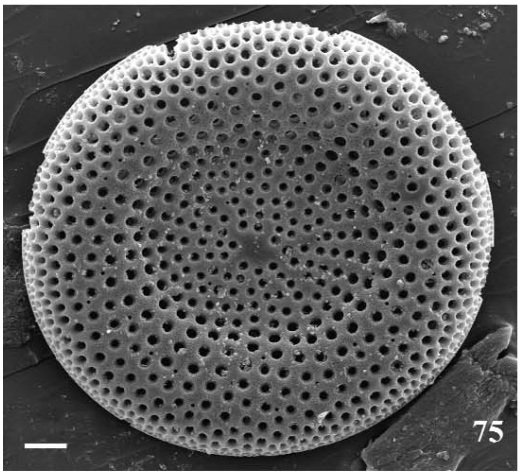
SEM. **Figure 73.** ***Coscinodiscus sp.*** External view. **Figure 74.** ***Craspedodiscus umbonatus*** **Greville**. Rimoportulae on the margin. Figures 73–74. CAS 611174 (Joe's River). **Figure 75.** ***Coscinodiscus radiatus*** **Ehrenberg** with slightly depressed center and rimoportulae on the valve face. Staroverivka (CAS 624820). **Figures 76–77.** ***Craspedodiscus barronii*** **Bukry.** Figure 76. Internal view. Rimoportulae on the margin. Figure 77. External view. Depressed center. CAS 611226 (Chimborazo). **Figures 78–80.** ***Coscinodiscus excavatus*** **Greville.** Figures 78–79. External view. Figure 79. Separate rimoportulae on the valve. Figure 80. Internal view. CAS 618793. Barbados, lower Oligocene.

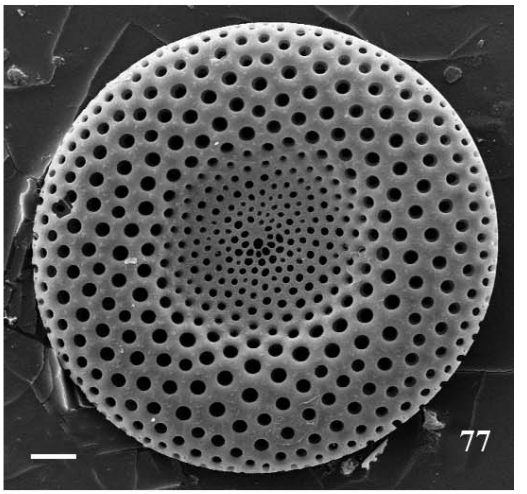
Scale bars = 1 μm (Figure 74), 10 μm (Figures 73, 75–77), 7 μm (Figure 79), 60 μm (Figures 78, 80)

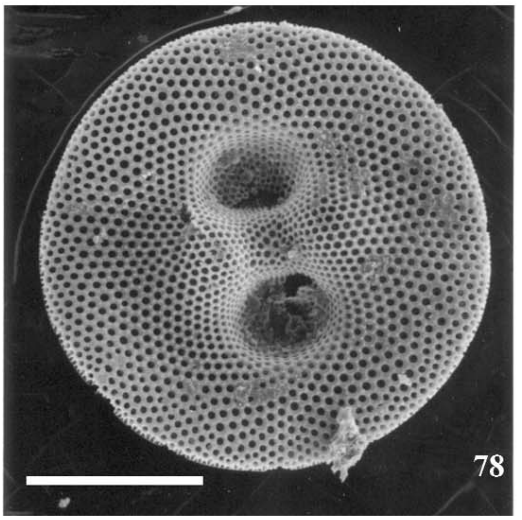

73

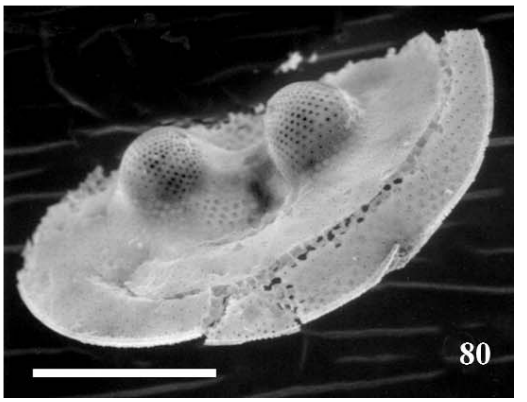

74


76


75


77


78


80

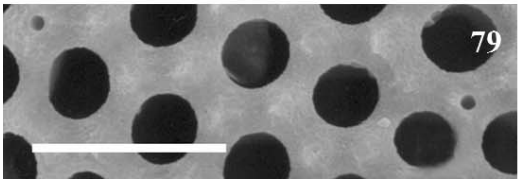

79

PLATE 11

Figures 81–86. ***Craspedodiscus coscinodiscus*** **Ehrenberg.** (CAS 621025, Trinidad). Figure 81. Internal view. Figures 82–85. External view. Figures 81–85. SEM. Figure 86. LM. **Figure 87.** ***Annellus californicus*** **var.** ***hannai*** **Barron**. Holotype USNM 304194, sample Mf5208, southern California Continental Borderland. SEM. **Figures 88–90.** ***Annellus californicus*** **var.** ***californicus*** **Tempère.** Figures 88–89. Valve view. Figure 90. Mantle view. Sample Mf 5192, southern California Continental Borderland. Figure 88. SEM. Fig 89. 90. LM. **Figure 91.** ***Craspedodiscus rhydei*** **Barron.** DSDP 77B-28-2, 28–30 cm. SEM. **Figure 92.** ***Coscinodiscus excavatus*** **Greville.** Inside view. SEM (CAS 621025, Trinidad).

Scale bars = 20 μm (Figures 81–82, 84), 10 μm (Figures 83, 85–91), 100 μm (Figure 92)