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Source: Paleontological Research, 8(4) : 255-282

Published By: The Palaeontological Society of Japan

URL: <https://doi.org/10.2517/prpsj.8.255>

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Fossil marine diatom resting spore morpho-genus *Gemellodiscus* gen. nov. in the North Pacific and Norwegian Sea

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Received May 28, 2004; Revised manuscript accepted October 4, 2004

Abstract. A new fossil marine diatom resting spore morpho-genus *Gemellodiscus* Suto gen. nov. is described using samples from DSDP Site 338 in the Norwegian Sea, Sites 436 and 438 in the northwest Pacific and the onland Newport Beach Section, California. *Gemellodiscus* is characterized by possessing a valve with setae of several types: bifurcated seta, fused seta and crossed seta. Eleven taxa are described and their stratigraphic ranges are presented: *G. incurvus* (Bailey) Suto comb. nov., *G. pliocen* (Brun) Suto comb. nov., *G. cingulus* Suto var. *cingulus* sp. nov., *G. cingulus* var. *longus* Suto var. nov., *G. bifurcus* Suto sp. nov., *G. hirtus* Suto sp. nov., *G. caveatus* Suto sp. nov., *G. micronodosus* Suto sp. nov., *G. dicollinus* Suto sp. nov., *G. geminus* Suto sp. nov. and *G. dimontanus* Suto sp. nov.

Key words: *Gemellodiscus*, fossil resting spore, diatom, ODP, taxonomy

Introduction

Chaetoceros Ehrenberg is one of the largest and most diverse of all marine planktonic diatom genera (VanLandingham, 1968; Rines and Hargraves, 1988; Hasle and Syvertsen, 1996). It plays an important role in marine primary production, especially in nearshore upwelling regions. Most species of the section *Hyalochaete* are known to form resting spores under various unfavorable conditions, such as nutrient depletion, darkness, and low temperature (e.g., Durbin, 1978; Garrison, 1981; Hargraves and French, 1983; Kuwata and Takahashi, 1990; Kuwata *et al.*, 1993; Oku and Kamatani, 1995, 1997, 1999; McQuoid and Hobson, 1996). The resting spores of *Chaetoceros* are differentiated from the vegetative frustules by possessing more heavily silicified valves, and occur frequently in nearshore sediments with other fossil diatom valves. However, taxonomic and biostratigraphic studies on these fossil resting spores have been limited, except for some studies such as Gersonde (1980), Lee (1993) and Suto (2003a, b, 2004a).

In this study, a new morpho-genus *Gemellodiscus*, including eleven taxa, is described from the middle Eocene through Recent sediments at DSDP Sites 338

(Norwegian Sea), 438 and 436 (Northwest Pacific) and an onland section at Newport Beach, California (Figure 1) to clarify the systematics of this genus.

Terminology

Some of the characteristic structures common to the new resting spore genus *Gemellodiscus* are shown in Figure 2. General morphological terms are after Anonymous (1975) and Ross *et al.* (1979). New terms used to describe *Gemellodiscus* are defined below.

Epivalve: the first-formed valve of a resting spore. It differs morphologically from the hypovalve, i.e., the frustule is heterovalvate (Figure 2c).

Hypovalve: the second-formed valve of a resting spore. In *Chaetoceros* spores observed by Hargraves (1979), hypovalves possess a submarginal flange, which fits into the epivalve. The hypovalve possesses a single ring of puncta at the base of the mantle, a characteristic feature that clearly distinguishes the hypovalve from the epivalve, which lacks such structures (Suto, 2003a) (Figure 2d).

Heterovalvate: the two valves of a frustule being dissimilar.

Mantle: the marginal part of the valve differentiated

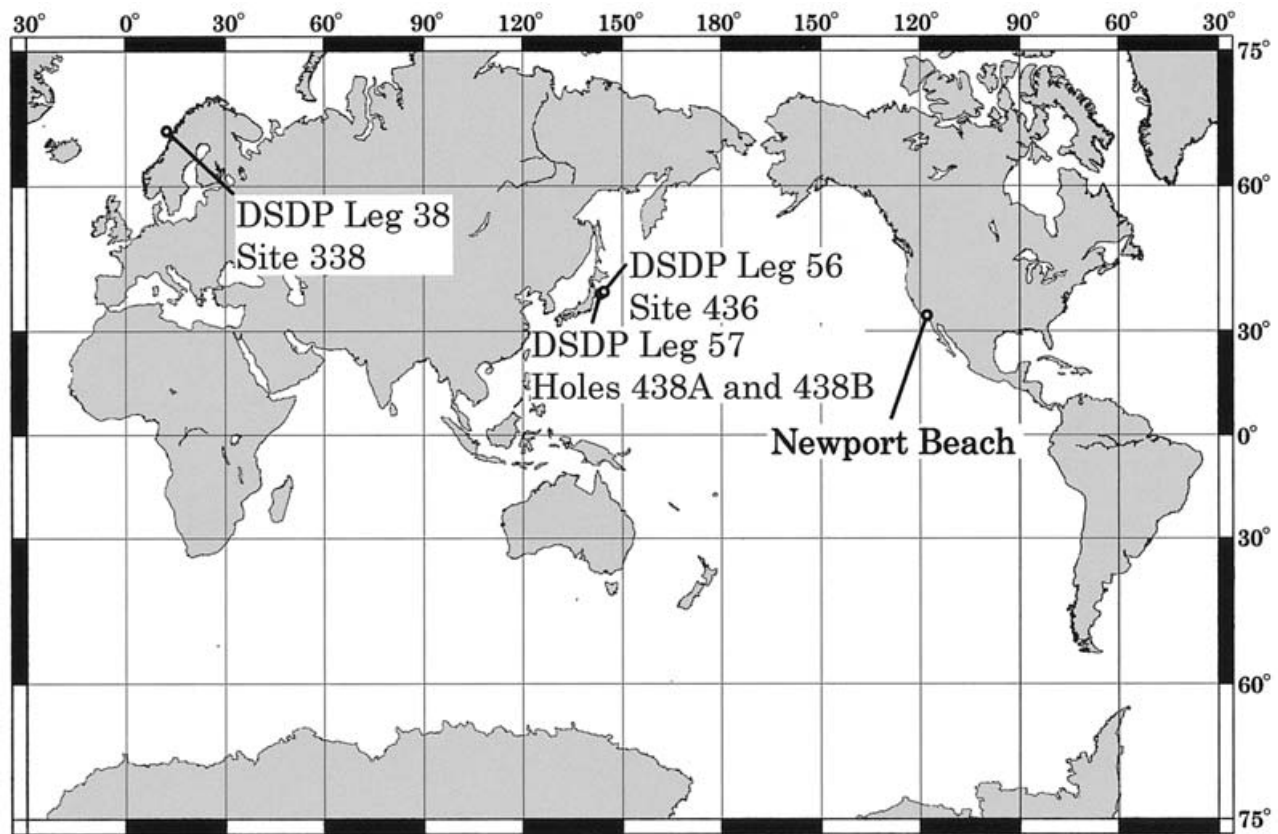


Figure 1. Location of DSDP Sites 338, 436 and 438 and the Newport Beach Section.

by slope, and sometimes also with structures such as spines, perpendicular to the valve face (Figure 2e).

Ring of puncta: a row of perforations at the base of the hypovalve mantle. The ring of puncta can be seen when the frustule is observed under LM, but using SEM the puncta cannot be observed because the epivalve mantle covers the hypovalve mantle (Figure 2f).

Seta: a tubular outgrowth of the valve projecting outside the valve margin, with a structure different from that of the valve. **Bifurcated seta:** a seta bifurcated at or near its base (Figure 2g). **Fused seta:** a nearly straight or strongly curved seta connected to other setae at the base of a paired valve, and then separated for a rather long distance (Figure 2h). **Crossed seta:** a seta crossed and fused with other setae of a paired valve (Figure 2i).

Sheath: a sleeve-like siliceous membrane attached to the resting spore mantle, hyaline or with a series of perforate slots (Figures 2m, n).

Paired valve: two spores connected by the setae which originate on their hypovalves, formed with basal plate of each entirely connected or joined by setae with basal plate of each disconnected (Figure 2k).

Results

Samples and methods in this study are described in Suto (2004b). The results of counting and the stratigraphic distribution of each species are shown in Figures 3–7 and Tables 1–4. All values listed in Tables 1–4 indicate numbers of valves. The stratigraphic ranges and ages are described according to the NPD (Neogene North Pacific Diatom Zone) code of Akiba (1986) and Yanagisawa and Akiba (1998) for the Miocene, Pliocene and Pleistocene, and to the diatom zones for the Eocene and Oligocene after Schrader and Fenner (1976).

Gemellodiscus species are similar to the resting spores of extant *Chaetoceros* species, but the taxonomic relationship between fossil species of *Gemellodiscus* and resting spores of extant species of *Chaetoceros* cannot be determined because the vegetative valves of *Gemellodiscus* species were not preserved as fossils. Accordingly, it is appropriate to use the genus name *Gemellodiscus* as a morpho-genus for the fossil resting spores according to Articles 3.2 and 3.3 of the ICBN (Greuter *et al.*, 2000), as in the case of fossil

resting spores of dinoflagellates (Edwards, 1991). The synonym lists in this paper include only fossil spores.

Systematic paleontology

Division Bacillariophyta
 Subdivision Bacillariophytina
 Class Mediophyceae
 Order Chaetocerotales
 Suborder Biddulphineae
 Family Chaetocerotaceae
 Genus *Gemellodiscus* Suto gen. nov.

Type species.—*Gemellodiscus cingulus* sp. nov.

Description.—Frustule heterovalvate and formed in pairs. Valve oval to elliptical in valve view. In girdle view, epivalve face vaulted, hyaline or covered with numerous knobs or spines, with high mantle. Mantle of epivalve hyaline. Hypovalve face hyaline, vaulted, with two tapered setae, and a mantle. The tapered setae are strong, smooth, and paired. Some bifurcated and fused at the base, but curve back to encircle the girdle (bifurcated seta). Some nearly straight or strongly curved and fused at the base for a rather long distance before bifurcating at an acute angle (fused seta). Some crossed and joined for a rather long distance, polygonal in cross-section (crossed seta). In the case of completely paired spores, two frustules are connected by these setae. Paired valve formed with the entirely connected basal plates of two hypovalves or joined by two setae with a disconnected basal plate. Mantle of hypovalve hyaline, with a single ring of puncta at its base.

Stratigraphic occurrence.—This genus occurs from pre-middle Eocene to the Recent (Figure 3).

Remarks.—This genus includes eleven taxa: *G. incurvus* (Bailey) Suto comb. nov., *G. pliocenensis* (Brun) Suto comb. nov., *G. cingulus* Suto var. *cingulus* sp. nov., *G. cingulus* var. *longus* Suto var. nov., *G. bifurcus* Suto sp. nov., *G. hirtus* Suto sp. nov., *G. caveatus* Suto sp. nov., *G. micronodosus* Suto sp. nov., *G. dicollinus* Suto sp. nov., *G. geminus* Suto sp. nov. and *G. dimontanus* Suto sp. nov. (Figure 2).

In general, *Chaetoceros* spores differ morphologically from vegetative cells by lacking setae. In *Gemellodiscus* species (and some modern *Chaetoceros* spores), however, the valves are held in tandem by fusion of the setae. Although similar in surface structure to a vegetative seta, the seta of a resting spore is more robust and there are only two per spore. In some species, the paired valve may also fuse or coalesce (i.e., *G. cingulus* and *G. bifurcus*). The formation of a paired valve characterizes the fossil morpho-genus

Gemellodiscus of *Chaetoceros* resting spores.

Etymology.—From Latin *gemellus*, “twin” and *discus*, “disc”.

Key to species

- 1a. Two tapered setae on the hypovalve are bifurcated 2
- 1b. Two tapered setae on the hypovalve are fused 5
- 1c. Two tapered setae on the hypovalve are crossed 8
- 2a. Valve face hyaline..... 3
- 2b. Valve face with numerous spines and knobs *Gemellodiscus incurvus*
- 3a. Valve circular in valve view 4
- 3b. Valve composed of two flat circles joined together by isthmus..... *G. pliocenensis*
- 4a. Bifurcated seta are fused for a short distance *G. cingulus* var. *cingulus*
- 4b. Bifurcated seta are fused for a long distance *G. cingulus* var. *longus*
- 5a. Basal plate connected to hypovalve of the paired valve 6
- 5b. Basal plate and hypovalve of the paired valve are unconnected 7
- 6a. Valve face hyaline..... *G. bifurcus*
- 6b. Valve face with numerous spines and knobs *G. hirtus*
- 7a. Valve face hyaline..... *G. caveatus*
- 7b. Valve face with numerous small spines and knobs *G. micronodosus*
- 8a. Epivalve domed 3
- 8b. Epivalve center vaulted with numerous knobs *G. dicollinus*
- 9a. Valve face hyaline..... *G. geminus*
- 9b. Valve face with numerous knobs *G. dimontanus*

Gemellodiscus incurvus (Bailey) Suto comb. nov.

Figures 2.A; 8.16, 8.17

Basionym.—*Chaetoceros incurvus* Bailey, 1854, p. 9, pl. 1, figs. 30?, 31, 32.

Reference.—*Chaetoceros incurvus* Bailey, Mereschkowsky, 1889, p. 484, pl. 16, figs. 1, 2.

Synonymy.—*Chaetoceros* spores (cf. *radicans*) of Whiting and Schrader, 1985, pl. 5, fig. 3 *nec* fig. 2.

Description.—Valve oval to elliptical in valve view, apical axis 12.0–17.0 μm, transapical axis 9.0–10.0 μm. In girdle view, epivalve face vaulted, covered with numerous knobs and spines. Valve with two tapered bifurcated setae, and a mantle. Bifurcated setae hyaline, smooth, emerging from valve apices, fused for

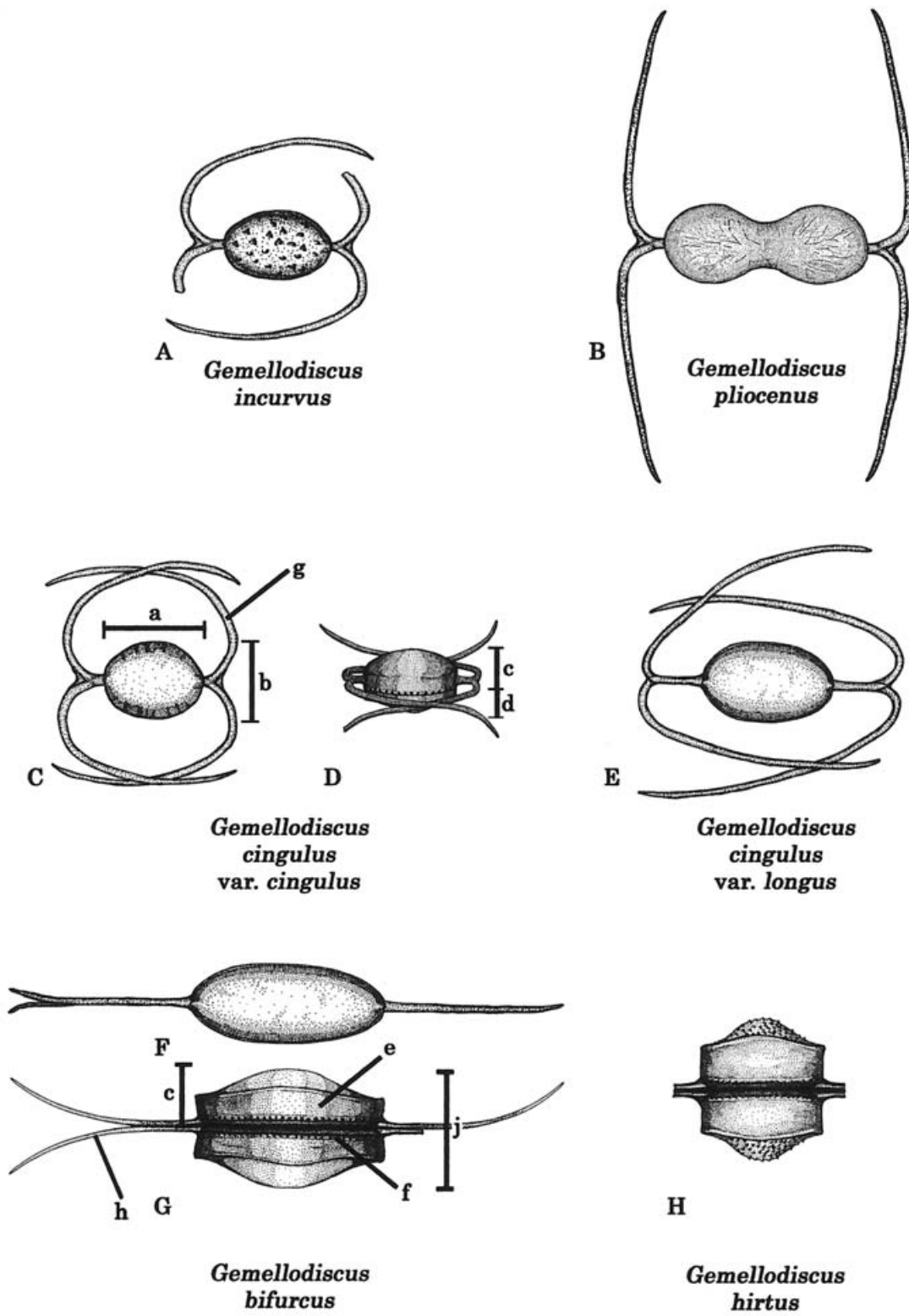


Figure 2. Sketches of *Gemellodiscus* species; **A:** *G. incurvus*, **B:** *G. pliocenus*, **C, D:** *G. cingulus* var. *cingulus*, **E:** *G. cingulus* var. *longus*, **F, G:** *G. bifurcus*, **H:** *G. hirtus*.

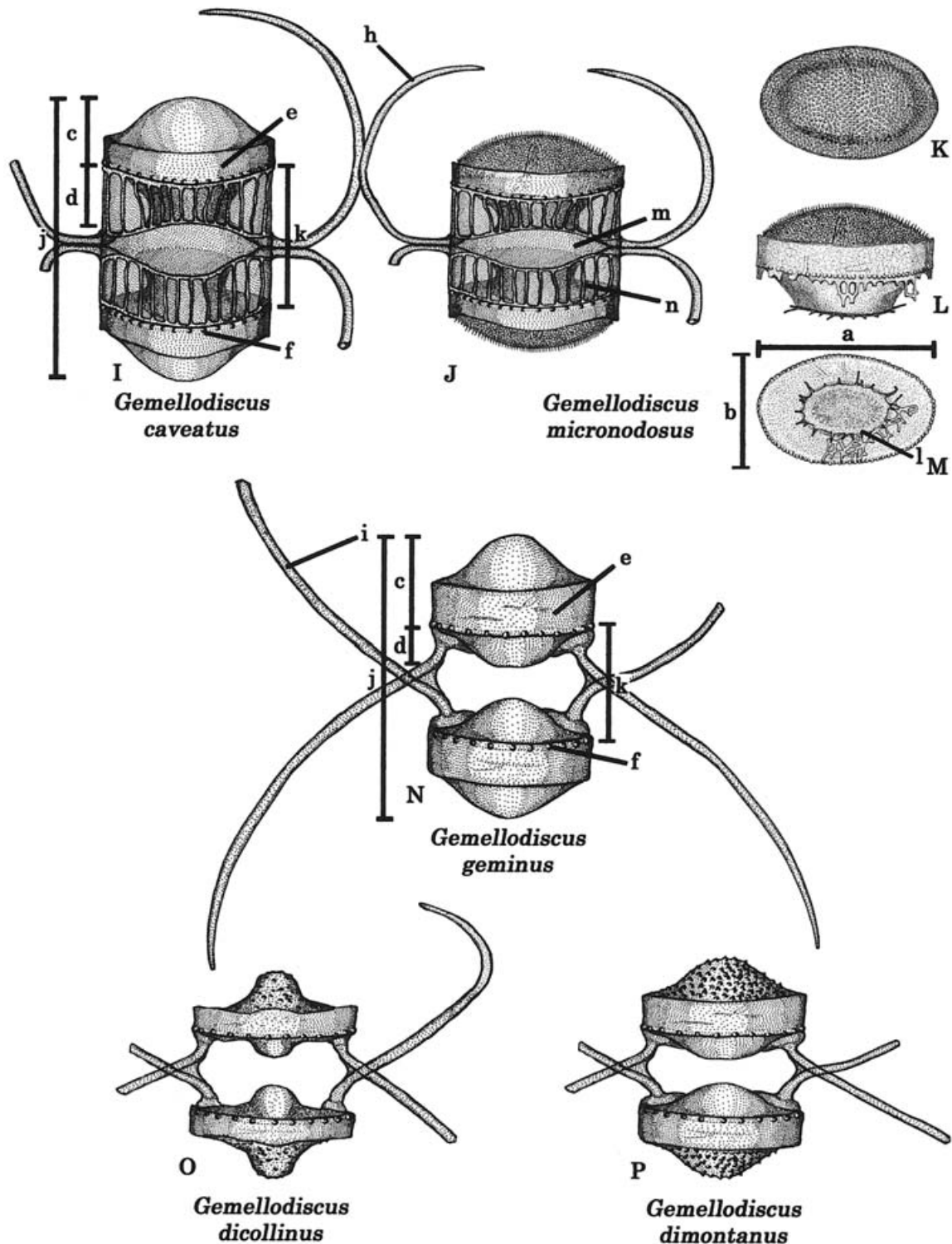


Figure 2. (Continued) **I:** *G. caveatus*, **J–M:** *G. micronodosus*, **N:** *G. geminus*, **O:** *G. dicollinus*, **P:** *G. dimontanus*, (**A, B, C, E, F, K:** valve view of epivalve, **D, L:** girdle view of frustule, **G, H, I, J, N, O, P:** girdle view of paired valve, **M:** valve view of hypovalve). Key to structures: **a:** apical axis, **b:** transapical axis, **c:** pervalvar axis of epivalve, **d:** pervalvar axis of hypovalve, **e:** mantle, **f:** a single ring of puncta, **g:** bifurcated seta, **h:** fused seta, **i:** crossed seta, **j:** paired valve, **k:** unconnected hypovalves, **l:** truncated elevation with a basal flat plate, **m:** hyaline sheath, **n:** cage-like sheath. All sketches were made using LM.

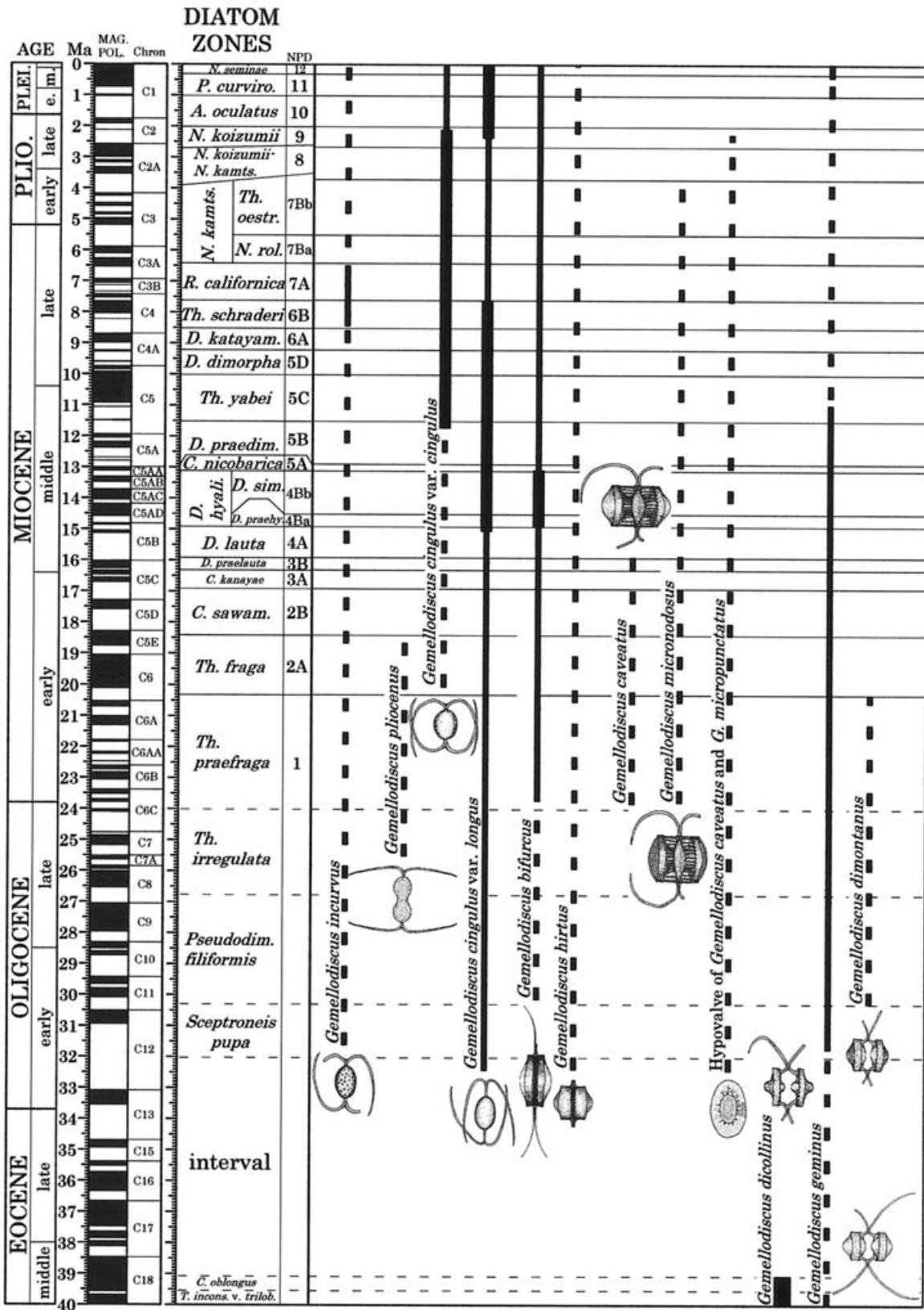


Figure 3. Stratigraphic ranges of *Gemellodiscus* species in the North Pacific and the Norwegian Sea. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998) for the Miocene, Pliocene and Pleistocene, and after Schrader and Fenner (1976) for the Eocene and Oligocene.

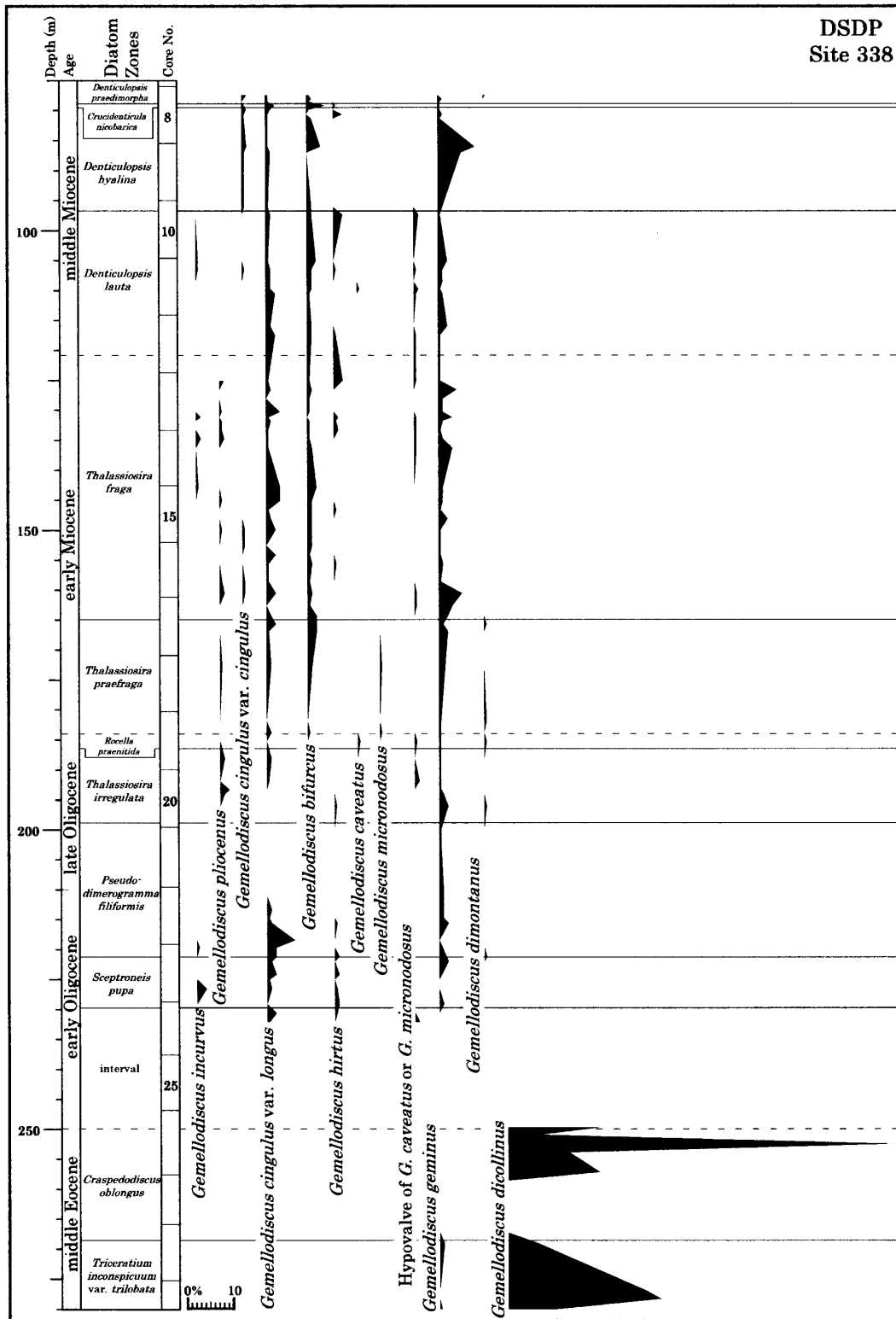


Figure 4. Stratigraphic occurrences of *Gemellodiscus* species at DSDP Site 338. Diatom zones are after Schrader and Fenner (1976).

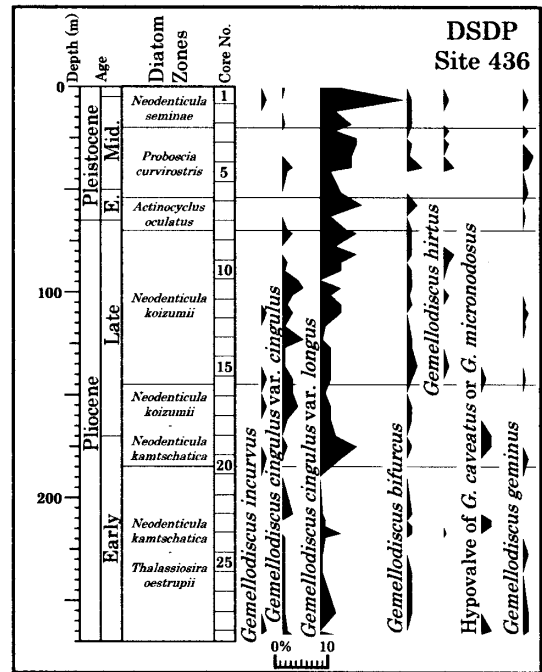
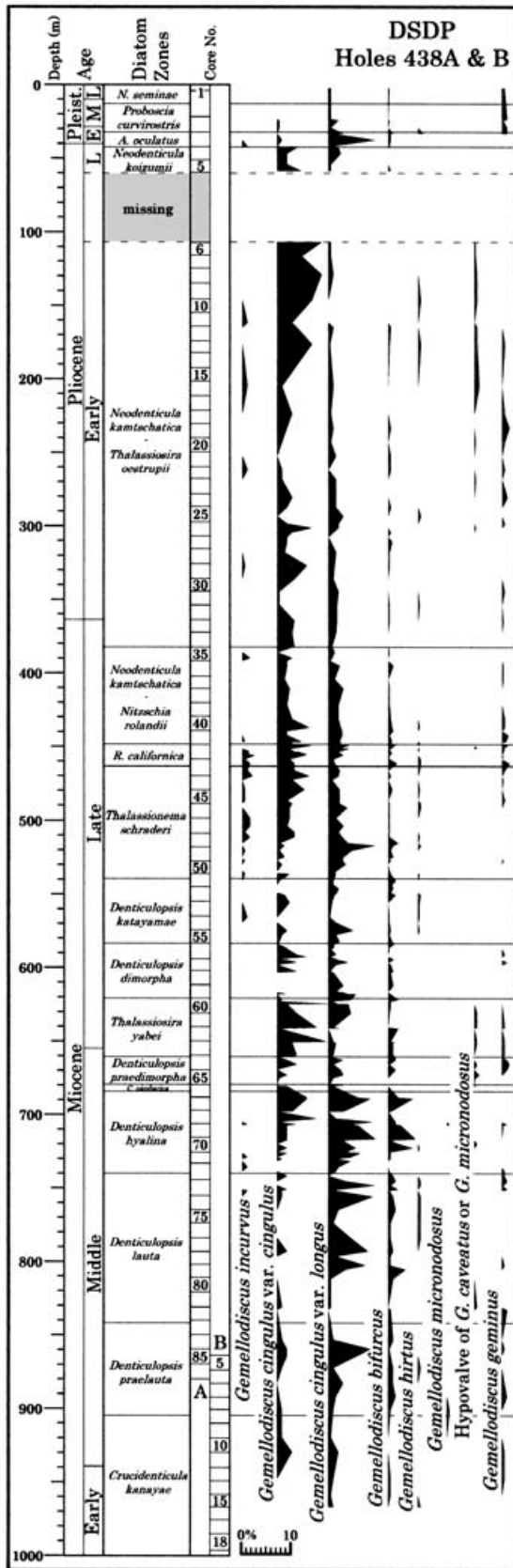


Figure 6. Stratigraphic occurrences of *Gemellodiscus* species at DSDP Site 436. Diatom zones are after Yanagisawa and Akiba (1998).

a short distance, then curved back around the valve away from the apical axis to encircle the girdle. Mantle hyaline. Frustule not observed, hypovalve unknown.

Type locality.—Not given (probably middle Miocene, Hawthorn Formation).

Similar taxa.—This species is very similar to *G. cingulus* var. *cingulus* and *G. cingulus* var. *longus*, but is distinguished by its epivalve covered with numerous knobs and spines. This species differs from *G. pliocenus* by its oval to elliptical valve shape.

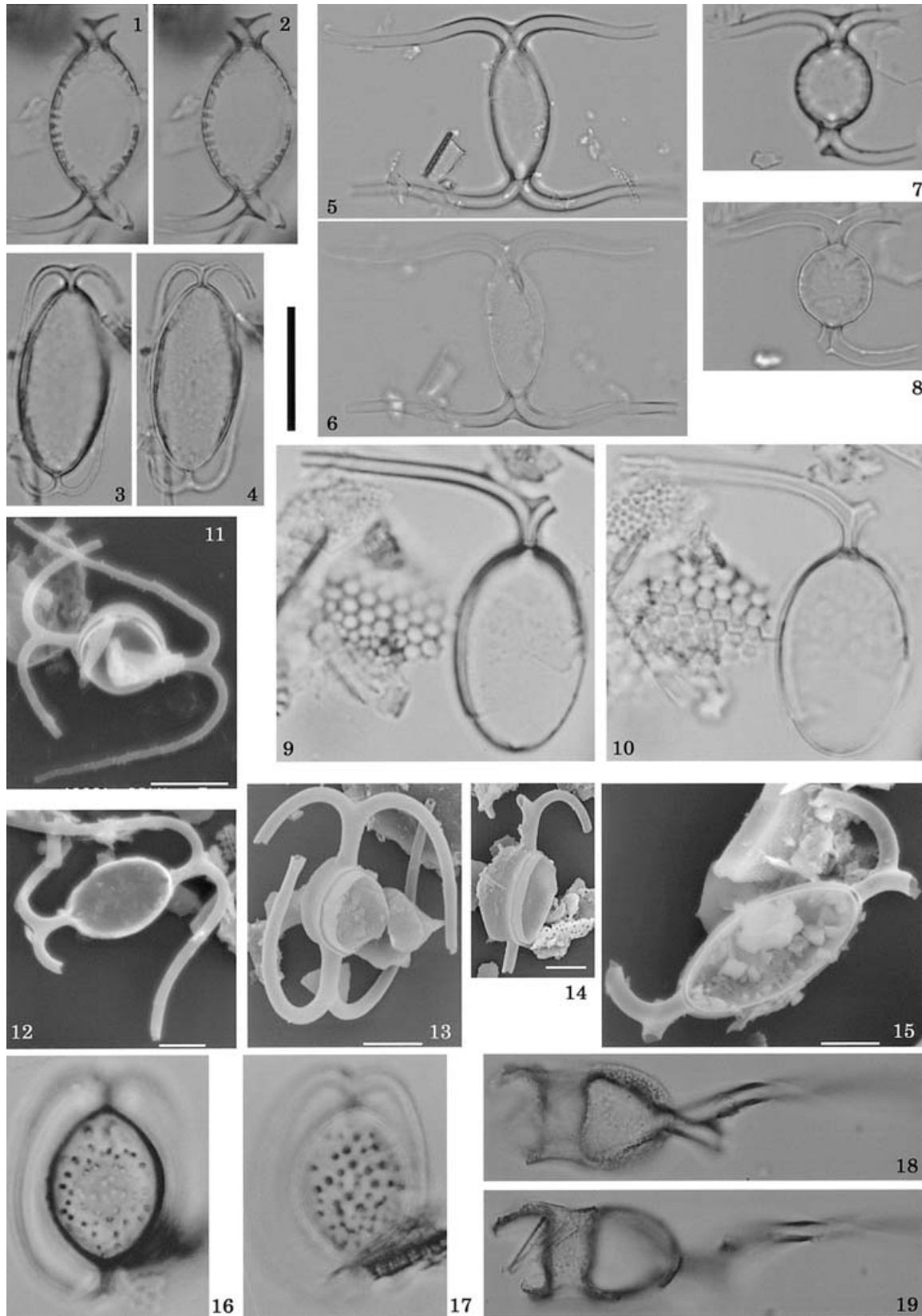
Stratigraphic occurrence.—This species occurs rarely and sporadically from the lower Oligocene to the Recent (Figure 3)

Remarks.—Specimens illustrated by Bailey (1854) probably from the middle Miocene Hawthorn Formation and that of Mereschkowsky (1889) from the Chinchu guano in Peru were described as *Chaetoceros incurvus*, but these specimens are fossil spores. Therefore, the morpho-genus *Gemellodiscus* is proposed for the fossil resting spores in this paper, because the respective vegetative cells were dissolved

Figure 5. Stratigraphic occurrences of *Gemellodiscus* species at DSDP Holes 438A and B. Diatom zones are after Yanagisawa and Akiba (1998).

Table 2. Occurrences of Gemmelodiscus species at DSDP Holes 438A and 438B. Values are for counts of 100 or 200 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any new taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

Table with 12 columns: Diatom Zones (NPD), Core-Section Interval (cm) Leg 57 Site 438, Depth (m), Preservation, Abundance, Gemmelodiscus incurvus, G. cingulus var. cingulus, G. cingulus var. longus, G. hirtus, G. microonodous, Hypovalve of G. carvatus or G. microonodous, G. geminus, Total number of resting spore valves counted. The table is split into two main sections for DSDP Hole 438A and DSDP Hole 438B, each containing multiple rows of species occurrence data.



the valve away from the apical axis to encircle the girdle. Mantle hyaline. Frustule not observed and hypovalve unknown in this study.

Type locality.—Unknown (probably marine pelagic sediment in the *Rouxia californica* Zone at Sendai (Brun, 1891)).

Similar taxa.—This species is characterized by having a valve joined by a broad hyaline isthmus.

Stratigraphic occurrence.—This species occurs rarely but continuously in restricted intervals from the upper Oligocene to the lower Miocene at DSDP Site 338 (Figure 4).

Etymology.—Latin from Greek, *pliocenus*, i.e., “Pliocene”.

Gemellodiscus cingulus Suto var. *cingulus* sp. nov.

Figures 2.C, D; 8.1–8.10, 8.15

Synonymy.—*Chaetoceros cinctus* Gran *sensu* Sheshukova-Poretzkaya, 1967, p. 206, pl. 33, fig. 9; Gleser *et al.*, 1974, pl. 54, figs. 1a, b, pl. 80, fig. 6 *nec* pl. 48, fig. 7; *Chaetoceros incurvus* Bailey *sensu* Sheshukova-Poretzkaya, 1967, p. 207, pl. 8, fig. 8, pl. 33, fig. 10; *Chaetoceros didymus* Ehrenberg *sensu* Hanna, 1970, p. 182, figs. 62, 98 *nec* fig. 97.

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 6.5–17.0 μm , transapical axis 4.5–11.0 μm . In girdle view, epivalve face vaulted, hyaline, with two tapered bifurcated setae, and a mantle. Bifurcated setae hyaline, smooth, emerging from valve apices, fused at the base, then curved back around the valve away from the apical axis to encircle the girdle. Mantle of epivalve hyaline. Hypovalve vaulted, hyaline with mantle. Mantle of hypovalve hyaline with a single ring of puncta at its base.

Holotype.—Slide MPC-02583 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder E38-1N, illustrated in Figures 8.5, 8.6).

Type locality.—DSDP Site 436-11-3, 148–150 cm, northwestern Pacific Ocean.

Similar taxa.—The nominate variety is distinguished from *G. cingulus* var. *longus* by its bifurcated

seta fused at the base. This species differs from *G. incurvus* by its hyaline valve face.

Stratigraphic occurrence.—Lower Miocene to Recent (Figure 3).

Remarks.—The abundance of the nominate variety and *G. cingulus* var. *longus* differs through time. In the northwestern Pacific Ocean, the nominate variety occurs less than *G. cingulus* var. *longus* in the Pleistocene, but to an equal or greater extent in the Pliocene. The difference in abundance between the two varieties may be due to paleoceanographic changes.

The nominate variety and *G. cingulus* var. *longus* are very similar to the resting spore of the extant species *Chaetoceros cinctus* Gran and *C. radicans* Schütt. *Chaetoceros cinctus* differs from *C. radicans* by its smaller valve size, thinner setae and lack of characteristic spines covering the setae (Stockwell and Hargraves, 1984). The bifurcated setae of *G. cingulus* lack spines, and therefore *G. cingulus* may be a fossil resting spore of *C. cinctus* or more likely the *C. cinctus* lineage.

Etymology.—From Latin *cingulus*, meaning “belt”.

Gemellodiscus cingulus var. *longus* Suto var. nov.

Figures 2.E; 8.11–8.14; 9.1–9.15

Synonymy.—*Chaetoceros cinctus* Gran *sensu* Hajós, 1968, p. 129, pl. 33, figs. 18, 19, pl. 34, fig. 1; Schrader, 1973, pl. 17, figs. 14, 15; Gleser *et al.*, 1974, pl. 48, fig. 7, pl. 80, fig. 6 *nec* pl. 54, figs. 1a, b; Hasegawa, 1977, p. 81, pl. 23, fig. 16; Shirshov, 1977, pl. 24, fig. 15; Lee, 1993, p. 32, pl. 1, fig. 13; *Chaetoceros* spores (cf. *radicans*) of Whiting and Schrader, 1985, pl. 5, fig. 2 *nec* fig. 3; *Chaetoceros* sp. B of Lee, 1993, p. 37, pl. 1, fig. 10.

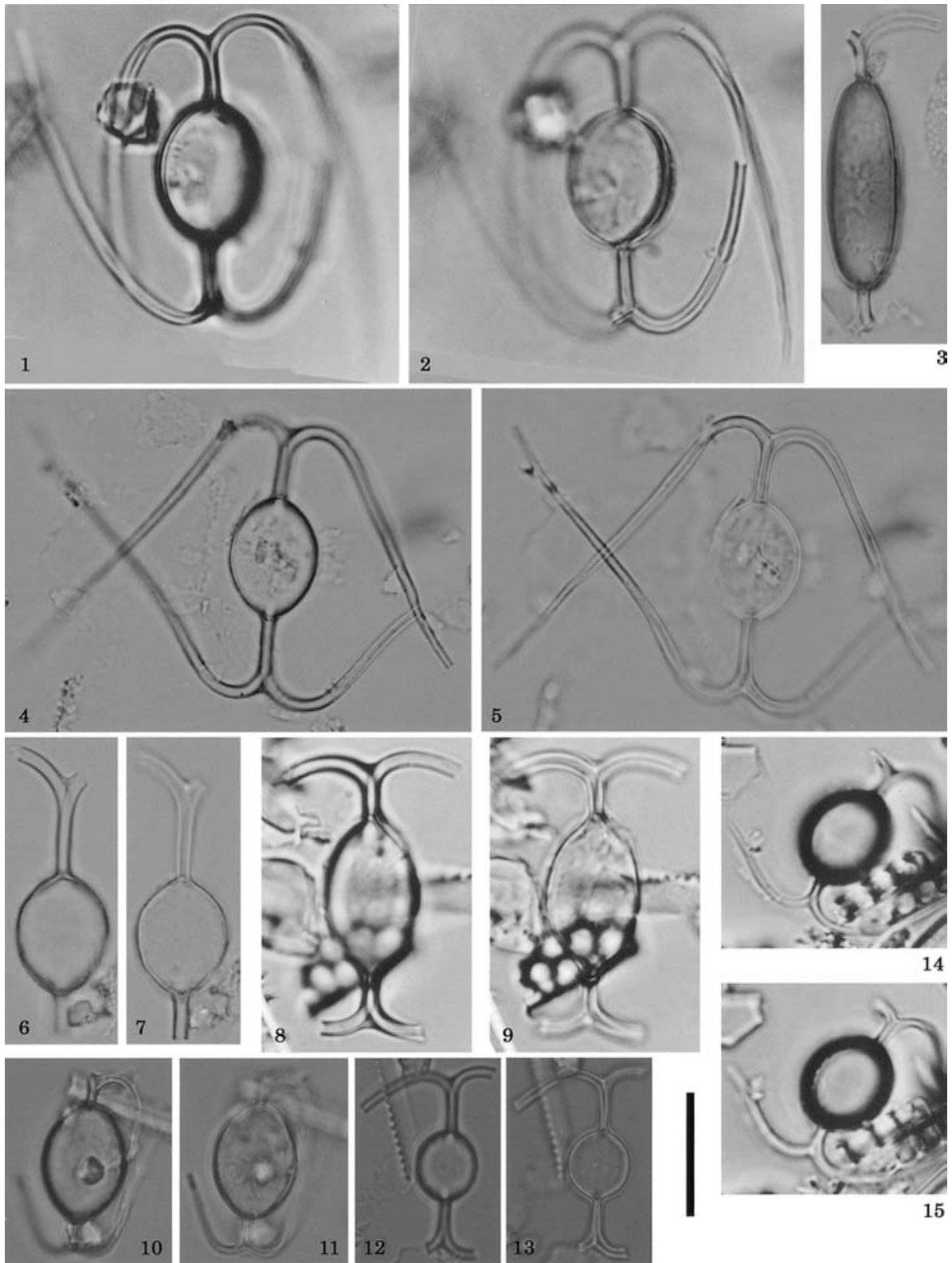
Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 5.0–17.5 μm , transapical axis 5.0–9.0 μm . In girdle view, epivalve vaulted, hyaline, with two bifurcated setae, and a mantle. Bifurcated setae hyaline, smooth, emerge from valve apices, fused for a short distance, then curved back around the valve away from the apical axis to encircle the girdle. Mantle of epivalve hyaline. Hypovalve vaulted, hyaline with mantle. Mantle of hypo-

◆ **Figure 8. 1–10, 15.** *Gemellodiscus cingulus* var. *cingulus* Suto sp. nov., LM scale bar = 10 μm for figures 1–10; SEM. Scale bar = 5 μm . **1, 2.** Valve view of epivalve, DSDP Site 436-11-1, 50–52 cm. **3, 4.** Valve view of epivalve, Newport Beach Section, N2b. **5, 6.** Holotype. Valve view of epivalve, DSDP Site 436-11-3, 148–150 cm. **7, 8.** Valve view of epivalve, DSDP Site 436-14-1, 100–102 cm. **9, 10.** Valve view of epivalve, DSDP Hole 438A-11-6, 20–24 cm. **15.** Inner valve view of epivalve, DSDP Hole 438A-44-3, 10–14 cm.

11–14. *Gemellodiscus cingulus* var. *longus* Suto var. nov., SEM. Scale bar = 5 μm for each figure. **11.** Inner valve view of epivalve, DSDP Hole 438A-32-1, 24–28 cm. **12.** Inner valve view of epivalve, DSDP 438A-37-3, 10–14 cm. **13.** Oblique girdle view of epivalve, DSDP Hole 438A-67-1, 112–113 cm. **14.** Oblique girdle view of epivalve, DSDP Hole 438A-67-1, 112–113 cm.

16, 17. *Gemellodiscus incurvus* (Bailey) Suto comb. nov., LM. Scale bar = 10 μm for each figure. **16, 17.** Valve view of frustule, DSDP Hole 438A-42-4, 50–54 cm.

18, 19. *Gemellodiscus pliocenus* (Brun) Suto comb. nov., LM. Scale bar = 10 μm for each figure. **18, 19.** Valve view of epivalve, DSDP Site 338-13-1, 148–149 cm.



valve hyaline with a single ring of puncta at its base.

Holotype.—Slide MPC-02582 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder Q27-1S, illustrated in Figures 9.4, 9.5).

Type locality.—Newport Beach section, sample no. NEW 48 of Barron (1976), California.

Similar taxa.—This variety differs from *G. cingulus* var. *cingulus* by having bifurcated setae fused for a short distance.

Stratigraphic occurrence.—Lower Oligocene to Recent (Figures 3–7).

Etymology.—Latin *longus*, “distant”.

Gemellodiscus bifurcus Suto sp. nov.

Figures 2.F, G; 10.1–10.25

Synonymy.—*Chaetoceros furcellatus* Bailey *sensu* Sheshukova-Poretzkaya, 1967, p. 205, pl. 33, fig. 8; Hajós, 1968, p. 129, pl. 34, fig. 2; Gleser *et al.*, 1974, pl. 58, fig. 3, pl. 88, fig. 4; Shirshov, 1977, pl. 2, fig. 17; Sancetta, 1982, pl. 2, figs. 7, 9; Lee, 1993, p. 33, pl. 1, fig. 11; *Chaetoceros* sp. IV of Hajós, 1968, p. 130, pl. 34, fig. 10; *Chaetoceros septentrionalis* Oestrup *sensu* Sancetta, 1982, pl. 2, fig. 8; *Chaetoceros didymus* Ehrenberg *sensu* Whiting and Schrader, 1985, pl. 5, fig. 4.

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 5.0–18.0 μm , pervalvar axis 3.0–7.0 μm . In girdle view, epivalve vaulted, hyaline. Mantle of epivalve hyaline. Hypo- valve slightly vaulted, hyaline with two fused setae, and a mantle. Fused setae hyaline, smooth, nearly straight, emerging from apices, curved tubular outgrowth of the valve projecting outside the valve margin, connected to setae of paired valve, separated for a rather long distance, parallel to apical plane. Mantle of hypo- valve hyaline with a single ring of puncta at its base. Paired valve formed by completely connected basal plates of two hypo- valves.

Holotype.—Slide MPC-02587 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder L31-1W, illustrated in Figures 10.13, 10.14).

Type locality.—DSDP Site 436-3-3, 100–102 cm, northwestern Pacific Ocean.

Similar taxa.—This species is very similar to *G. hirtus*, but is distinguished from the latter by its hyaline valve face.

Stratigraphic occurrence.—Lower Oligocene to Recent (Figure 3).

Remarks.—This species may be an ancestor of the extant species *Chaetoceros furcellatus*, often misspelled as *C. furcellatus* (e.g., Stockwell and Hargraves, 1984), but the relationship between them cannot be determined because the vegetative valves were not preserved as fossils.

Etymology.—Latin *bifurcus*, meaning “two-pronged”.

Gemellodiscus hirtus Suto sp. nov.

Figures 2.H; 10.26–10.31

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 5.0–8.0 μm , pervalvar axis 4.0–6.0 μm . In girdle view, epivalve vaulted, with numerous knobs and spines. Mantle of epivalve hyaline. Hypo- valve hyaline, slightly vaulted, with two fused setae, and a mantle. Fused setae hyaline, smooth, nearly straight, emerging from valve apices as curved tubular outgrowths of the valve projecting outside the valve margin, connected to setae of paired valve, separated for a rather long distance, parallel to apical plane. Mantle of hypo- valve hyaline with a single ring of puncta at its base. Paired valve formed completely by the connected basal plates of two hypo- valves.

Holotype.—Slide MPC-02588 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder S37-3N, illustrated in Figures 10.28, 10.29).

Type locality.—Newport Beach section, sample no. N20 of Barron (1976), California.

Similar taxa.—This species is very similar to *G. bifurcus*, but differs by possessing a valve face covered with numerous knobs and spines. This species resembles *G. incurvus* in valve view, but differs by having fused setae.

Stratigraphic occurrence.—Lower Oligocene to Recent (Figure 3).

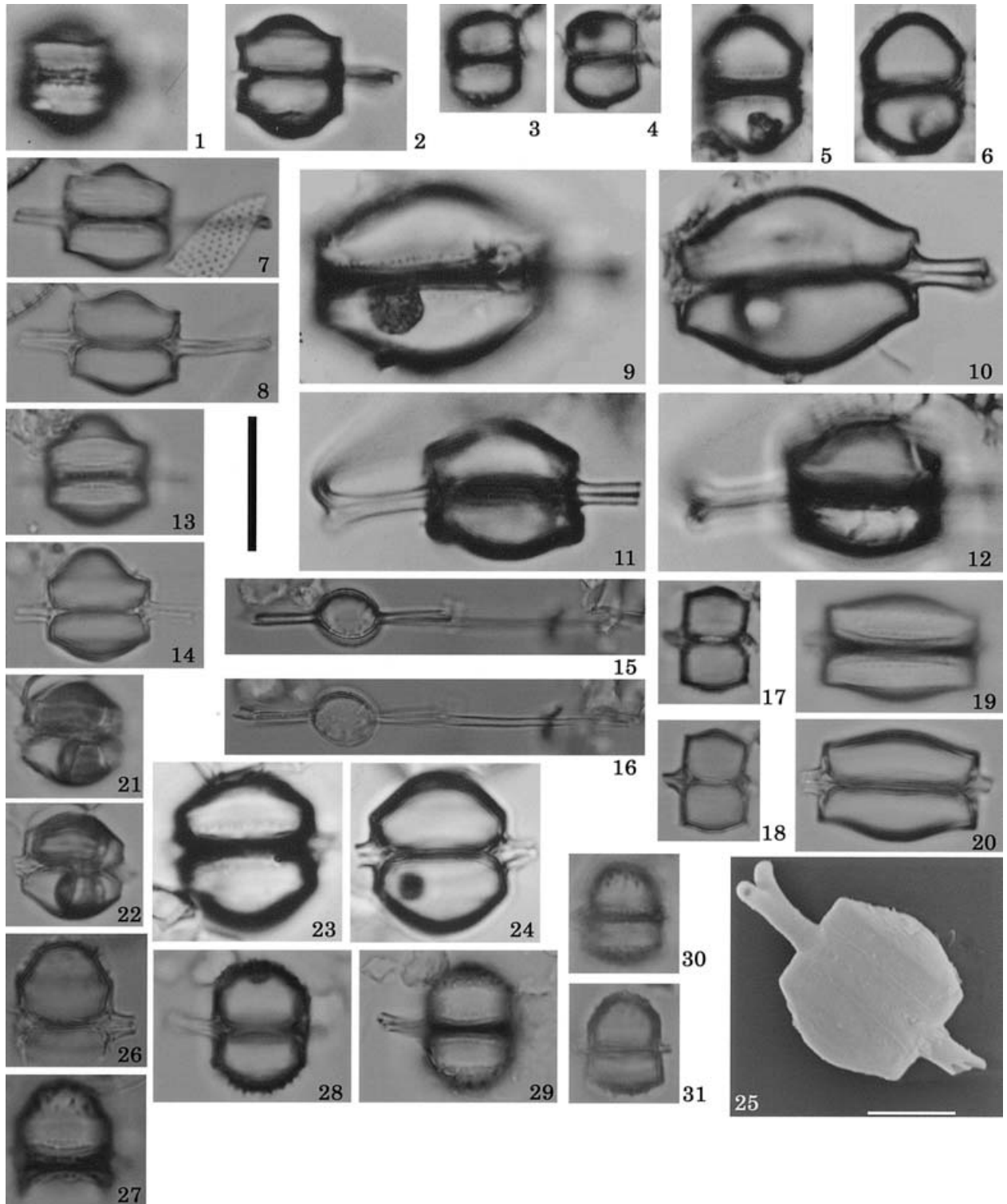
Etymology.—Latin *hirtus*, meaning “shaggy.”

Gemellodiscus caveatus Suto sp. nov.

Figures 2.I; 11.1–11.4

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 12.0–34.0 μm , pervalvar axis 6.5–15.0 μm . In girdle view, epivalve

← **Figure 9.** 1–15. *Gemellodiscus cingulus* var. *longus* Suto var. nov., LM. Scale bar = 10 μm for each figure. **1, 2.** Valve view, DSDP Hole 438A-25-5, 16–20 cm. **3.** Valve view, DSDP Site 338-15-2, 100–101 cm. **4, 5.** Holotype. Valve view, Newport Beach Section NEW48. **6, 7.** Valve view, DSDP Site 338-8-1, 140–141 cm. **8, 9.** Valve view, DSDP Hole 438A-26-4, 10–14 cm. **10, 11.** Valve view, DSDP Site 436-3-6, 11–12 cm. **12, 13.** Valve view, DSDP Site 436-6-4, 100–102 cm. **14, 15.** Valve view, DSDP Hole 438A-26-6, 15–19 cm.



vaulted, hyaline. Mantle of epivalve hyaline. Hypo- valve slightly vaulted, with a truncated elevation in the center with a flat plate, marginal zone, two fused setae, outer cage-like sheath and mantle. Flat plate of hypo- valve oval to elliptical, slightly concave, with marginal net-like spines connected to the outer cage-like sheath. Fused setae hyaline, smooth, emerging from valve apices of basal plate as curved tubular outgrowths of the valve projecting outside the valve margin, connected to the setae of paired valve. Mantle of hypo- valve hyaline with a single ring of puncta at its base. Paired valve formed by two fused setae and hyaline sheath with disconnected basal plate.

Holotype.—Slide MPC-02581 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder O40-1S, illustrated in Figures 11.3, 11.4).

Type locality.—DSDP Site 338-12-2, 40–41 cm, Norwegian Sea.

Similar taxa.—This species resembles *G. micronodosus*, but is distinguished by its hyaline epivalve face.

Stratigraphic occurrence.—This species occurs very rarely and sporadically in the uppermost Oligocene *Rocella praenitida* Zone and in the middle Miocene *Denticulopsis lauta* Zone (NPD 4A) at DSDP Site 338 (Figure 4).

Remarks.—It is very difficult to identify the hypo- valve of this species vis a vis that of *G. micronodosus* (Figures 13.1–13.14; 14.4), and therefore, this type of hypo- valve was counted as “hypo- valve of *G. caveatus* and *G. micronodosus*” when only hypo- valves occurred.

Etymology.—From Latin *caveatus*, “caged”.

Gemellodiscus micronodosus Suto sp. nov.

Figures 2.J–2.M; 12.1–12.14; 14.1

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 12.0–25.5 μm , pervalvar axis 7.0–10.0 μm . In girdle view, epivalve vaulted, with numerous small spines. Mantle of epivalve hyaline. Hypo- valve slightly vaulted, with a trun-

cated elevation in the center with a flat plate, marginal zone, two fused setae, outer cage-like sheath and mantle. Flat plate of hypo- valve oval to elliptical, slightly concave, with marginal net-like spines connected to the outer cage-like sheath. Fused setae hyaline, smooth, emerging from valve apices of basal plate as curved tubular outgrowths of the valve projecting outside the valve margin, connected to the setae of paired valve. Mantle of hypo- valve hyaline with a single ring of puncta at its base. Paired valve formed by two fused setae and hyaline sheath with disconnected basal plate.

Holotype.—Slide MPC-02589 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder O30-2S, illustrated in Figures 12.9, 12.10).

Type locality.—DSDP Site 338-19-3, 20–21 cm, Norwegian Sea.

Similar taxa.—This species differs from *G. caveatus* by having an epivalve face with numerous small spines.

Stratigraphic occurrence.—The frustule of this species occurs very rarely and sporadically in the lowest Miocene *Denticulopsis praefraga* Zone (NPD 1) at DSDP Site 338 (Figure 4).

Remarks.—The epivalve of this species is very difficult to distinguish from that of *Xanthiopyxis hirsuta* (Suto, 2004b). Thus, this type of valve was counted as “valve of *X. hirsuta* and epivalve of *G. micronodosus*” when an isolated epivalve was encountered. The hypo- valves of *G. caveatus* and *G. micronodosus* (Figures 13.1–13.14; 14.4) are very similar and therefore, they were counted as “hypo- valve of *G. caveatus* and *G. micronodosus*”.

Etymology.—From the Greek and Latin *micronodosus*, “with minute knobs”.

Hypo- valves of *Gemellodiscus caveatus* and *G. micronodosus*

Figures 2.M; 13.1–13.14; 14.4

Same type hypo- valve.—*Xanthiopyxis* sp. A of Lee, 1993, p. 46, pl. 2, fig. 14.

◆ **Figure 10.** 1–25. *Gemellodiscus bifurcus* Suto sp. nov., LM scale bar = 10 μm for figures 1–24; SEM scale bar = 5 μm for figure 25. **1, 2.** Girdle view of frustule, DSDP Hole 438A-62-1, 20–24 cm. **3, 4.** Girdle view of frustule, DSDP Hole 438A-70-1, 16–20 cm. **5, 6.** Girdle view of frustule, DSDP Hole 438A-70-1, 16–20 cm. **7, 8.** Girdle view of frustule, DSDP Site 338-12-2, 40–41 cm. **9, 10.** Girdle view of frustule, DSDP Hole 438A-70-1, 16–20 cm. **11, 12.** Girdle view of frustule, DSDP Hole 438A-49-3, 10–14 cm. **13, 14.** Holotype. Girdle view of frustule, DSDP Site 436-3-3, 100–102 cm. **15, 16.** Valve view of frustule, DSDP Site 436-5-2, 148–150 cm. **17, 18.** Girdle view of frustule, DSDP Site 338-8-1, 140–141 cm. **19, 20.** Girdle view of frustule, DSDP Site 338-11-1, 50–51 cm. **21, 22.** Girdle view of frustule, Newport Beach Section N9. **23, 24.** Girdle view of frustule, DSDP Hole 438A-42-1, 14–18 cm. **25.** Girdle view of frustule, DSDP Hole 438A-67-1, 112–113 cm.

26–31. *Gemellodiscus hirtus* Suto sp. nov., LM. Scale bar = 10 μm for each figure. **26, 27.** Girdle view of epivalve with paired valve, DSDP Site 436-1-5, 50–52 cm. **28, 29.** Holotype. Girdle view of frustule, Newport Beach Section N20. **30, 31.** Girdle view of frustule, Newport Beach Section N7.

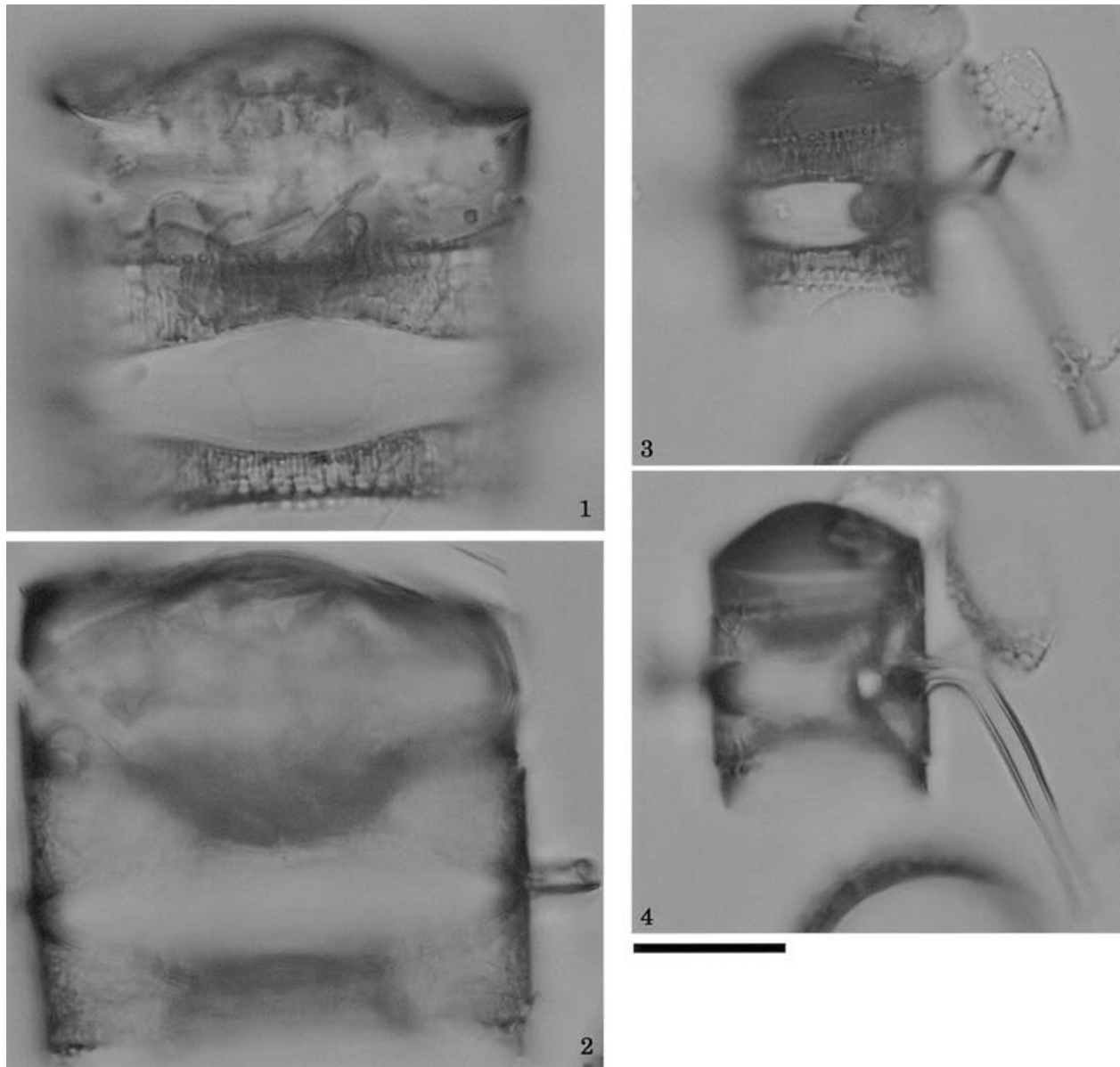
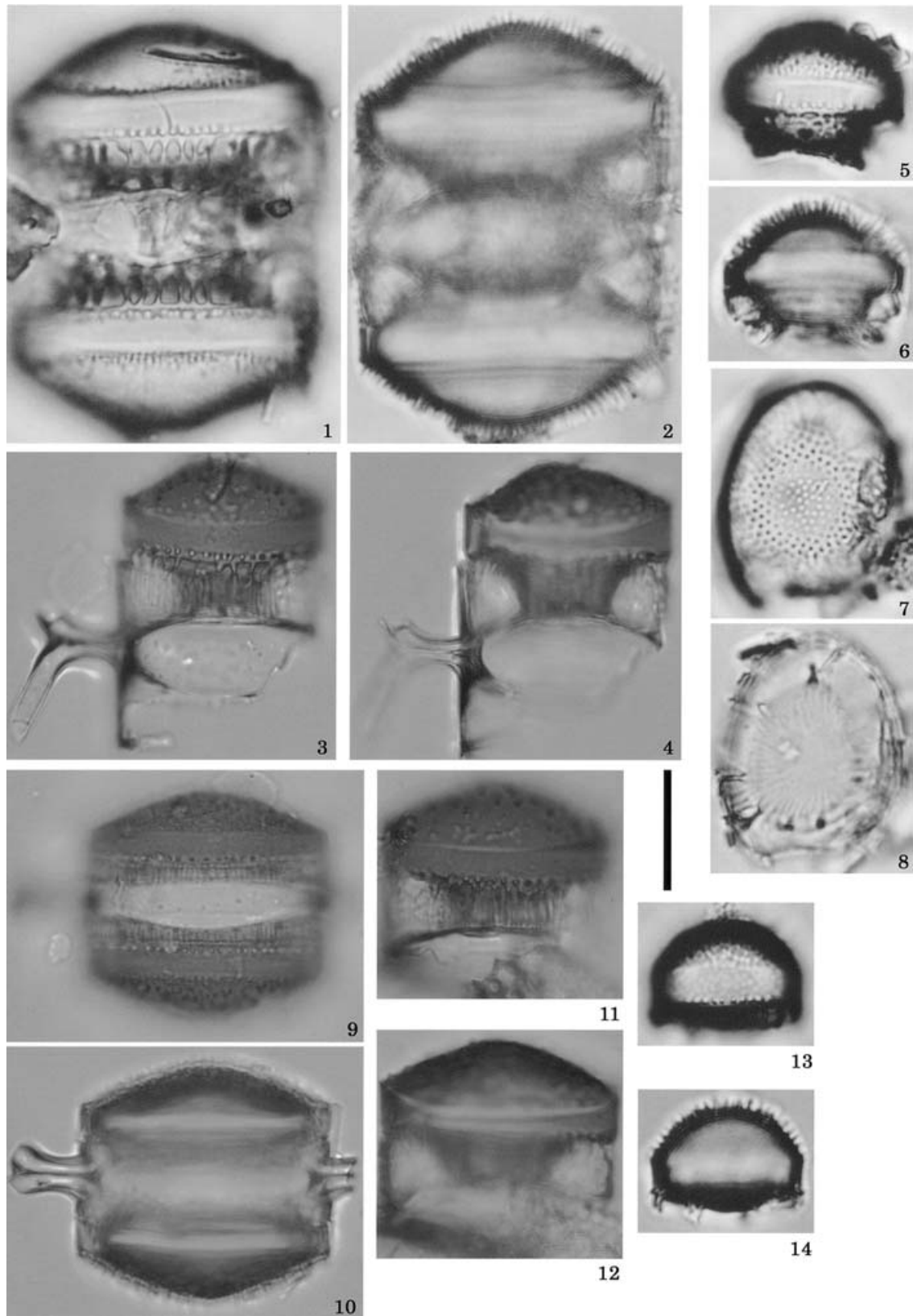
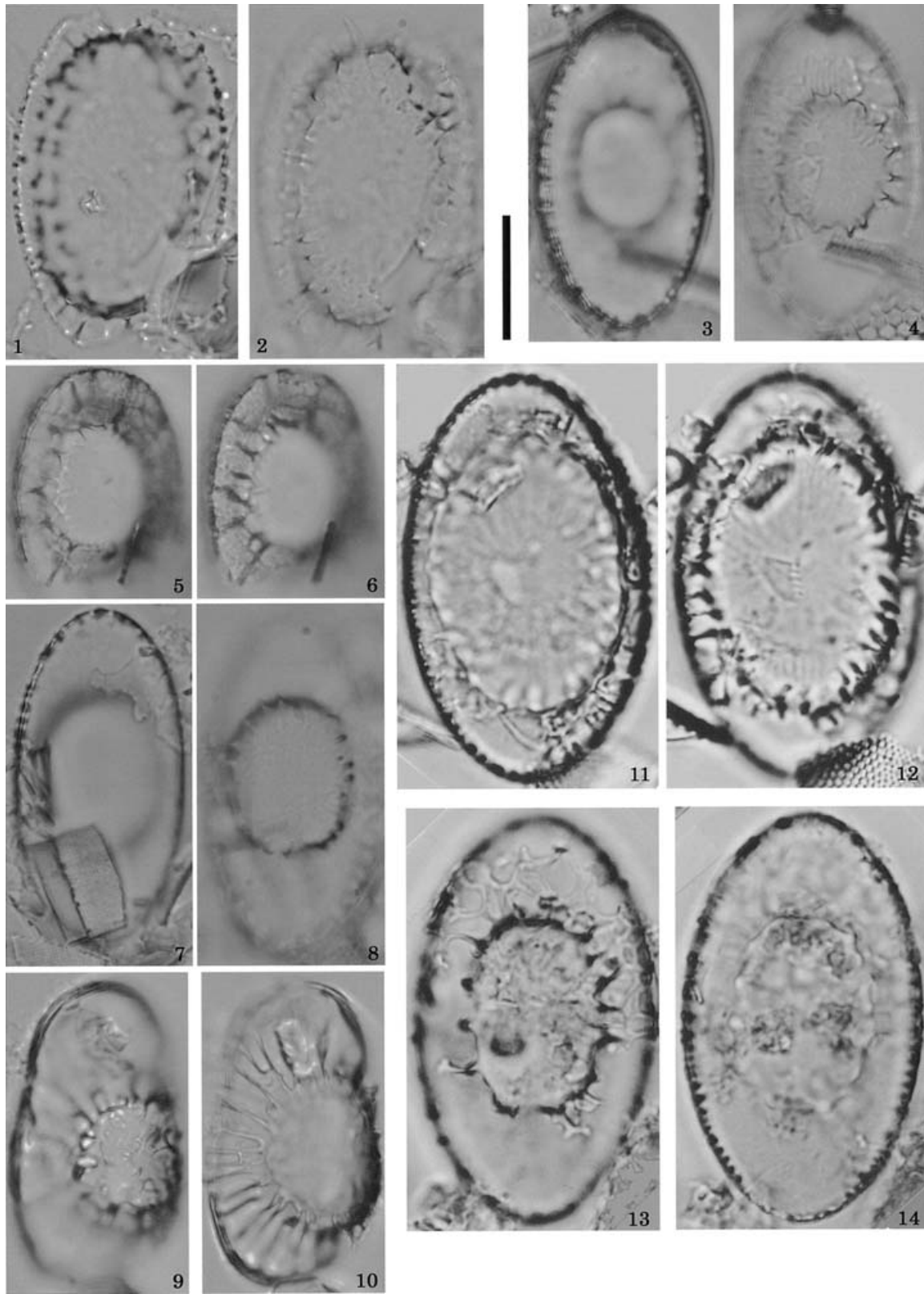


Figure 11. 1–4. *Gemelodiscus caveatus* Suto sp. nov., LM. Scale bar = 10 μ m for each figure. 1, 2. Girdle view of one frustule with one hypovalve, DSDP Site 338-11-4, 70–71 cm. 3, 4. Holotype. Girdle view of one frustule with one hypovalve, DSDP Site 338-12-2, 40–41 cm.

➔ **Figure 12.** 1–14. *Gemelodiscus micronodosus* Suto sp. nov., LM. Scale bar = 10 μ m for each figure. 1, 2. Girdle view of paired frustule, DSDP Hole 438A-64-1, 10–14 cm. 3, 4. Girdle view of frustule, DSDP Site 338-18-1, 148–149 cm. 5, 6. Girdle view of frustule, DSDP Hole 438A-62-1, 20–24 cm. 7, 8. Valve view of frustule, DSDP Hole 438A-63-1, 16–20 cm. 9, 10. Holotype. Girdle view of paired frustule, DSDP Site 338-19-3, 20–21 cm. 11, 12. Girdle view of frustule, DSDP Site 338-18-1, 148–149 cm. 13, 14. Girdle view of frustule, DSDP Hole 438A-66-1, 119–122 cm.





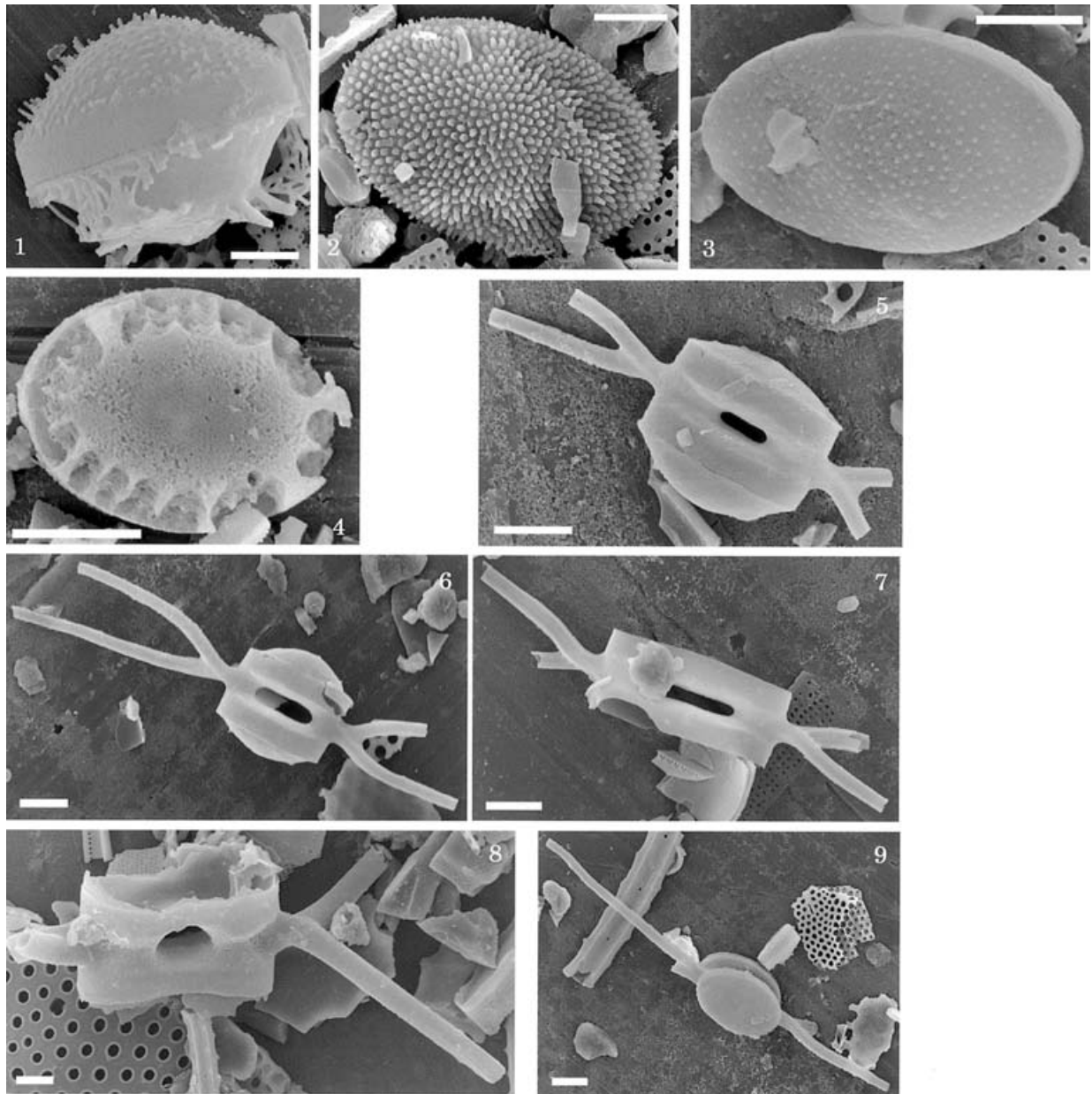


Figure 14. **1.** *Gemmelodiscus micronodosus* Suto sp. nov., SEM. Scale bar = 5 μ m. **1.** Girdle view of frustule, DSDP Site 338-18-1, 148–149 cm.

2–3. Valve of *Xanthiopyxis hirsuta* and epivalve of *G. micronodosus*, SEM. Scale bar = 5 μ m for each figure. **2.** Valve view, DSDP Site 338-18-1, 148–149 cm. **3.** Valve view, DSDP Site 338-18-1, 148–149 cm.

4. Hypovalve of *G. caveatus* or *G. micronodosus* **4.** Valve view of hypovalve, DSDP Site 338-11-4, 148–149 cm.

5–9. *Gemmelodiscus geminus* Suto sp. nov., SEM. Scale bar = 5 μ m for each figure. **5.** Girdle view of frustule, DSDP Site 338-17-1, 100–101 cm. **6.** Girdle view of frustule, DSDP Site 338-17-1, 100–101 cm. **7.** Girdle view of paired valve, DSDP Site 338-15-2, 100–101 cm. **8.** Oblique valve view of paired valve, DSDP Site 338-20-3, 90–91 cm. **9.** Oblique valve view of frustule, DSDP Site 338-15-2, 100–101 cm.

◆ **Figure 13.** **1–14.** Hypovalve of *Gemmelodiscus caveatus* and *G. micronodosus*, LM. Scale bar = 10 μ m for each figure. **1, 2.** Valve view of hypovalve, Newport Beach Section N2b. **3, 4.** Valve view of hypovalve, DSDP Site 338-15-4, 100–101 cm. **5, 6.** Valve view of hypovalve, DSDP Site 338-12-3, 38–39 cm. **7, 8.** Valve view of hypovalve, DSDP Site 338-17-1, 100–101 cm. **9, 10.** Oblique valve view of hypovalve, Newport Beach section NEW42. **11, 12.** Valve view of hypovalve, DSDP Hole 438A-26-4, 10–14 cm. **13, 14.** Valve view of hypovalve, DSDP Hole 438A-42-2, 95–96 cm.

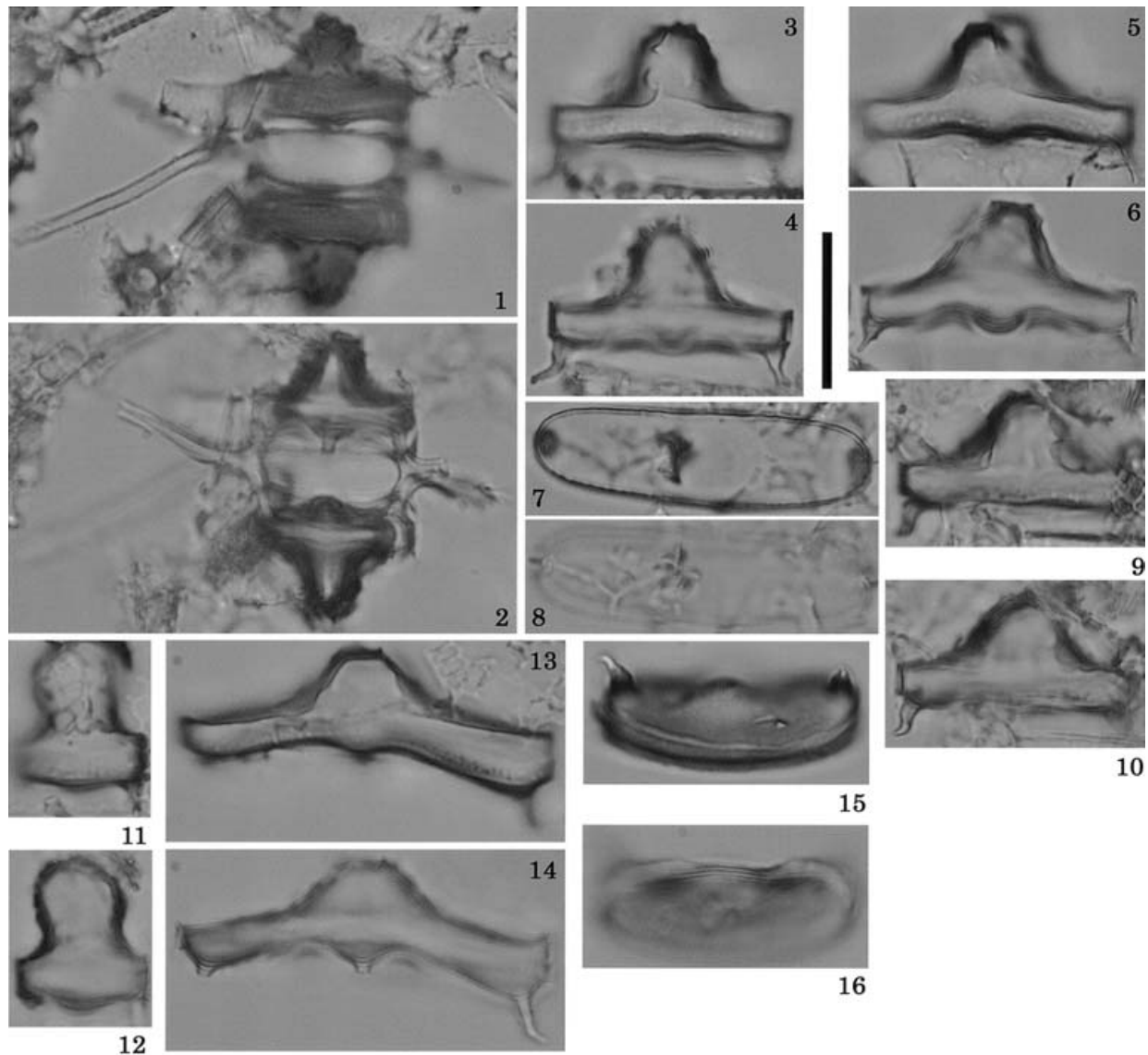
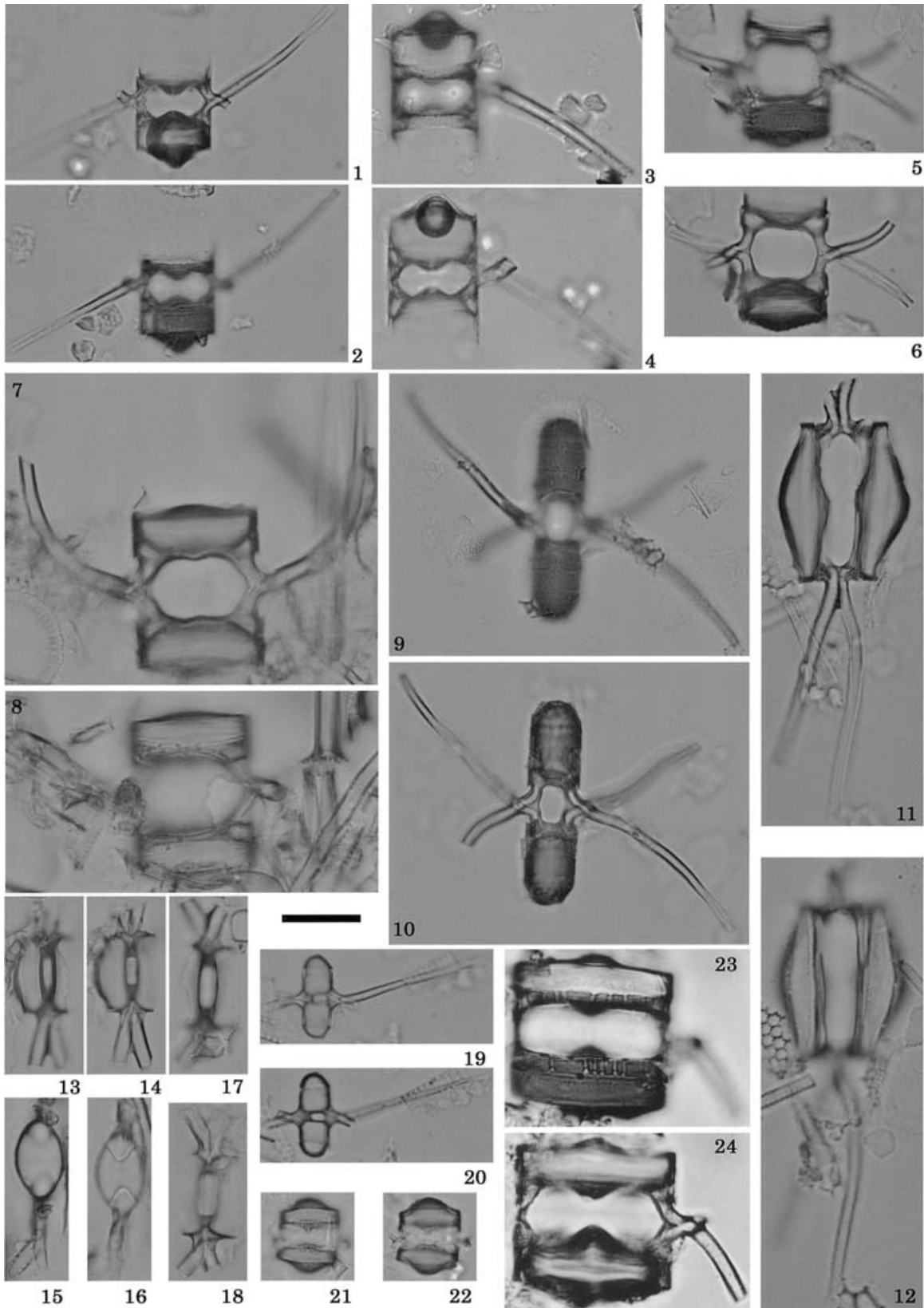


Figure 15. 1–24. *Gemellodiscus dicollinus* Suto sp. nov., LM. Scale bar = 10 μ m for each figure. 1, 2. Holotype. Girdle view of paired frustule, DSDP Site 338-26-4, 80–81 cm. 3, 4. Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. 5, 6. Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. 7, 8. Valve view of frustule, DSDP Site 338-26-4, 80–81 cm. 9, 10. Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. 11, 12. Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. 13, 14. Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. 15, 16. Oblique valve view of frustule, DSDP Site 338-38-2, 148–149 cm.

➔ **Figure 16.** 1–24. *Gemellodiscus geminus* Suto sp. nov., LM. Scale bar = 10 μ m for each figure. 1, 2. Girdle view of frustule and paired valve, DSDP Site 436-12-5, 98–100 cm. 3, 4. Girdle view of frustule and paired valve, DSDP Site 436-12-5, 98–100 cm. 5, 6. Girdle view of frustule and paired valve, DSDP Site 338-15-3, 100–101 cm. 7, 8. Holotype. Girdle view of paired frustule, DSDP Site 338-11-4, 70–71 cm. 9, 10. Girdle view of paired frustule, DSDP Site 338-19-1, 130–131 cm. 11, 12. Girdle view of paired frustule, DSDP Site 338-22-2, 10–11 cm. 13, 14. Girdle view of frustule and paired valve, DSDP Site 338-8-3, 80–81 cm. 15, 16. Valve view of frustule, DSDP Site 338-9-1, 50–51 cm. 17, 18. Girdle view of paired valve, DSDP Site 338-9-1, 50–51 cm. 19, 20. Girdle view of paired frustule, DSDP Site 338-9-1, 50–51 cm. 21, 22. Girdle view of paired frustule, DSDP Site 436-25-1, 70–71 cm. 23, 24. Girdle view of paired frustule, DSDP Hole 438A-27-4, 20–24 cm.



Description.—In valve view, hypovalve oval to broadly elliptical. In girdle view, hypovalve slightly vaulted, with a truncated elevation in the center, a flat plate and mantle. The flat plate of hypovalve oval to elliptical, slightly concave, with marginal net-like spines. Mantle of hypovalve hyaline with a single ring of puncta at its base.

Stratigraphic occurrence.—This type of hypovalve occurs from the lower Oligocene to the upper Pliocene (Figure 3).

Remarks.—*Xanthiopyxis* sp. A of Lee (1993) is assignable to this hypovalve, because the specimen possesses sharp spines surrounding the central hyaline zone.

***Gemellodiscus dicollinus* Suto sp. nov.**

Figures 2.O; 15.1–15.16

Synonymy.—Resting spore of Schrader and Fenner, 1976, pl. 45, fig. 16.

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 8.0–24.0 μm , pervalvar axis 6.0–10.0 μm . In girdle view, epivalve vaulted or inflated in the center, with numerous knobs. Mantle of epivalve hyaline. Hypovalve slightly vaulted in the center, with two crossed setae, and mantle. Crossed setae hyaline, smooth, emerging from valve apices of hypovalve as nearly straight or strongly curved tubular outgrowths of the valve projecting outside the valve margin, crossed and fused with the setae of paired valve for a rather long distance, polygonal in cross-section. Mantle of hypovalve hyaline with a single ring of puncta at its base. Paired valve formed by two crossed setae with disconnected basal plate.

Holotype.—Slide MPC-02584 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder N40-4N, illustrated in Figures 15.1, 15.2).

Type locality.—DSDP Site 338-26-4, 80–81 cm, Norwegian Sea.

Similar taxa.—This species is very similar to *G. dimontanus* and *G. geminus* but differs from them by having an epivalve vaulted in the center with numerous knobs.

Stratigraphic occurrence.—This species occurs very abundantly in the middle Eocene at DSDP Site 338 (Figure 4).

Remarks.—*Chaetoceros* sp. A of Harwood *et al.* (2000, fig. 7p) and *Chaetoceros* spp. of Iwai and Winter (2002, pl. 23, fig. 6), both of which were found in the Pliocene and Pleistocene sediments in the Antarctic, are very similar to *G. dicollinus* in the in-

flated epivalve with knobs. They may be related to this morpho-genus, but were not examined in this study.

Etymology.—From the Latin *dicollinus*, meaning “two-hilled”.

***Gemellodiscus geminus* Suto sp. nov.**

Figures 2N; 14.5–14.9; 16.1–16.24

Synonymy.—*Chaetoceros didymus* Ehrenberg *sensu* Makarova, 1962, p. 50, pl. 4, figs. 7–14; Hanna, 1970, p. 182, fig. 97 *nec* figs. 62, 98; Shirshov, 1977, pl. 24, figs. 10, 11; Harwood and Bohaty, 2000, p. 91, pl. 2, figs. j, k; *Chaetoceros* sp. V of Hajós, 1968, p. 131, pl. 34, fig. 14; *Chaetoceros debilis* Cleve *sensu* Schrader, 1973, pl. 17, figs. 12, 13; *Chaetoceros* sp. of Schrader and Fenner, 1976, p. 968, pl. 6, fig. 15, pl. 38, figs. 5, 7 *nec* fig. 6; Barron and Mahood, 1993, p. 38, pl. 6, figs. 3, 4.

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 3.5–21.0 μm , pervalvar axis 2.0–10.0 μm . In girdle view, epivalve hyaline, vaulted. Mantle of epivalve hyaline. Hypovalve vaulted, with two crossed setae, and mantle. Crossed setae hyaline, smooth, emerging from valve apices of hypovalve as nearly straight or strongly curved tubular outgrowths of the valve projecting outside the valve margin, crossed and fused with the setae of paired valve for a rather long distance, polygonal in cross-section, parallel to apical plane. Mantle of hypovalve hyaline with a single ring of puncta at its base. Paired valve formed by two crossed setae with disconnected basal plate.

Holotype.—Slide MPC-02585 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder H30-2C, illustrated in Figures 16.7, 16.8).

Type locality.—DSDP Site 338-11-4, 70–71 cm, Norwegian Sea.

Similar taxa.—This species differs from *G. dimontanus* and *G. dicollinus* by its hyaline epivalve.

Stratigraphic occurrence.—Middle Eocene to Recent (Figure 3).

Remarks.—This species may be an ancestor of the extant species *Chaetoceros didymus* Ehrenberg because of their similarity (e.g., Stockwell and Hargraves, 1984), but the relationship between them cannot be determined because the vegetative valves were not preserved as fossils. Therefore, the morpho-genus *Gemellodiscus* is used in this study.

Etymology.—From Latin *geminus*, meaning “twin”.

***Gemellodiscus dimontanus* Suto sp. nov.**

Figures 2P; 17.1–17.6

Synonym.—*Chaetoceros* sp. of Dzinoridze *et al.*, 1978, pl. 9, figs. 13–15.

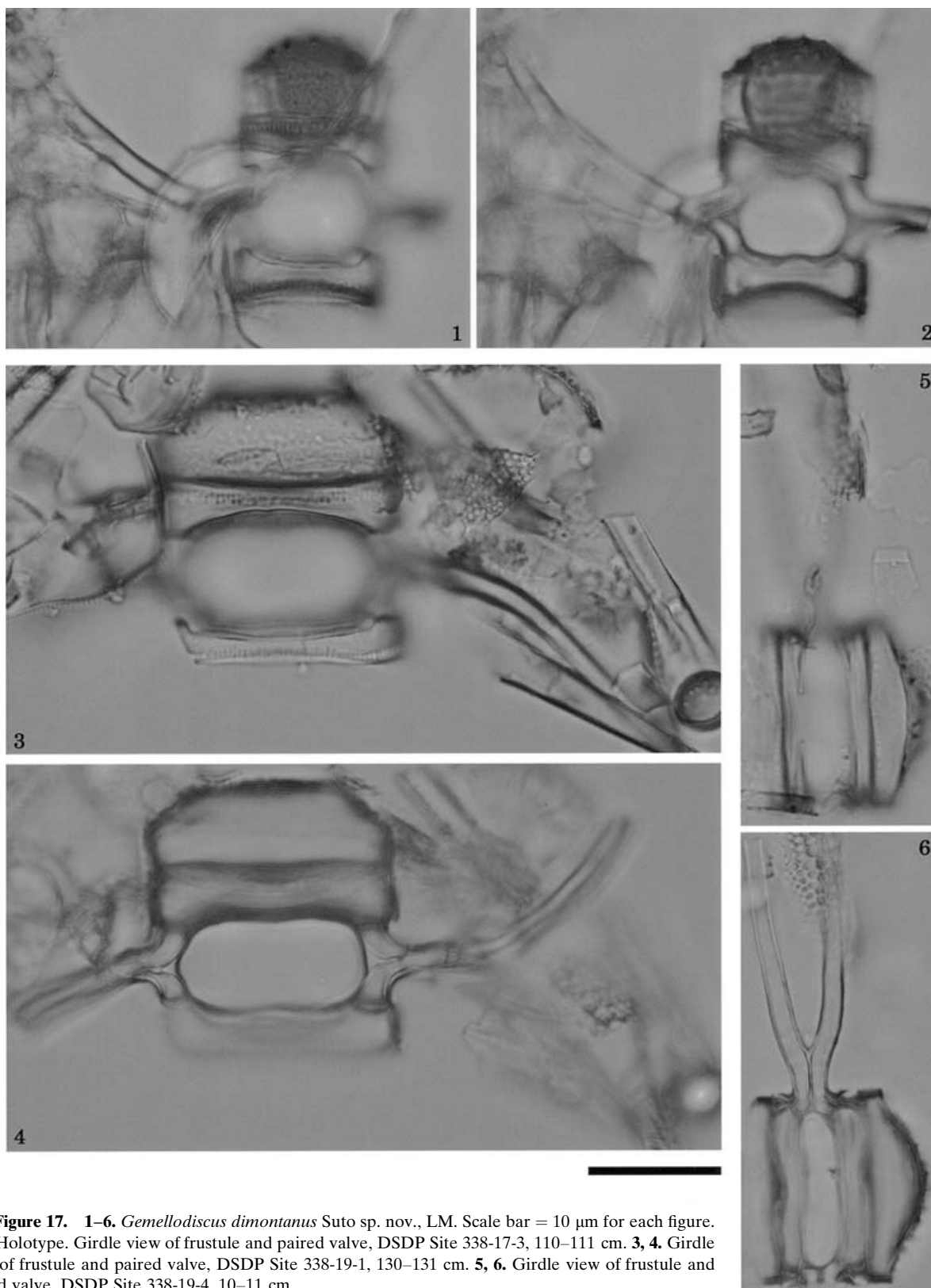


Figure 17. 1–6. *Gemellodiscus dimontanus* Suto sp. nov., LM. Scale bar = 10 μm for each figure. 1, 2. Holotype. Girdle view of frustule and paired valve, DSDP Site 338-17-3, 110–111 cm. 3, 4. Girdle view of frustule and paired valve, DSDP Site 338-19-1, 130–131 cm. 5, 6. Girdle view of frustule and paired valve, DSDP Site 338-19-4, 10–11 cm.

Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 11.0–19.0 μm , perivalvar axis 5.0–7.5 μm . In girdle view, epivalve vaulted, covered with numerous knobs. Mantle of epivalve hyaline. Hypovalve vaulted, with two crossed setae, and mantle. Crossed setae hyaline, smooth, emerging from valve apices of hypovalve as nearly straight or strongly curved tubular outgrowths of the valve projecting outside the valve margin, crossed and fused with the setae of paired valve for a rather long distance, polygonal in cross-section, parallel to apical plane. Mantle of hypovalve hyaline with a single ring of puncta at its base. Paired valve formed by two crossed setae with disconnected basal plate.

Holotype.—Slide MPC-02586 (Micropaleontology Collection, National Science Museum, Tokyo, England Finder L32-1W, illustrated in Figures 17.1, 17.2).

Type locality.—DSDP Site 338-17-3, 110–111 cm, Norwegian Sea.

Similar taxa.—This species is very similar to *G. geminus*, but differs by having an epivalve covered with numerous knobs. This species differs from *G. dicollinus* by having an inflated, rather vaulted epivalve.

Stratigraphic occurrence.—This species occurs rarely and sporadically in the interval from lower Oligocene to lower Miocene at DSDP Site 338 (Figure 4).

Etymology.—From Latin *dimontanus*, meaning “possessing two mountains”.

Acknowledgments

I am especially grateful to Yukio Yanagisawa (Geological Survey of Japan/AIST), who provided numerous helpful suggestions and reviewed the manuscript carefully. I wish to thank Fumio Akiba (Diatom Minilab Akiba Ltd.) for invaluable discussions and his careful review of the manuscript. I am grateful to John A. Barron (U.S. Geological Survey) for his permission to study the Newport Beach samples. I am very thankful to Yoshihiro Tanimura (National Science Museum, Tokyo), who kindly curated the holotype specimens described in this paper. I wish also to thank Kenshiro Ogasawara (University of Tsukuba) and my colleagues for their helpful advice and encouragement. This research used samples provided by the Ocean Drilling Program (ODP) which is sponsored by the U.S. National Science Foundation (NSF) and participating countries under the management of the Joint Oceanographic Institution (JOI), Inc.

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