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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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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. pliocenus* (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

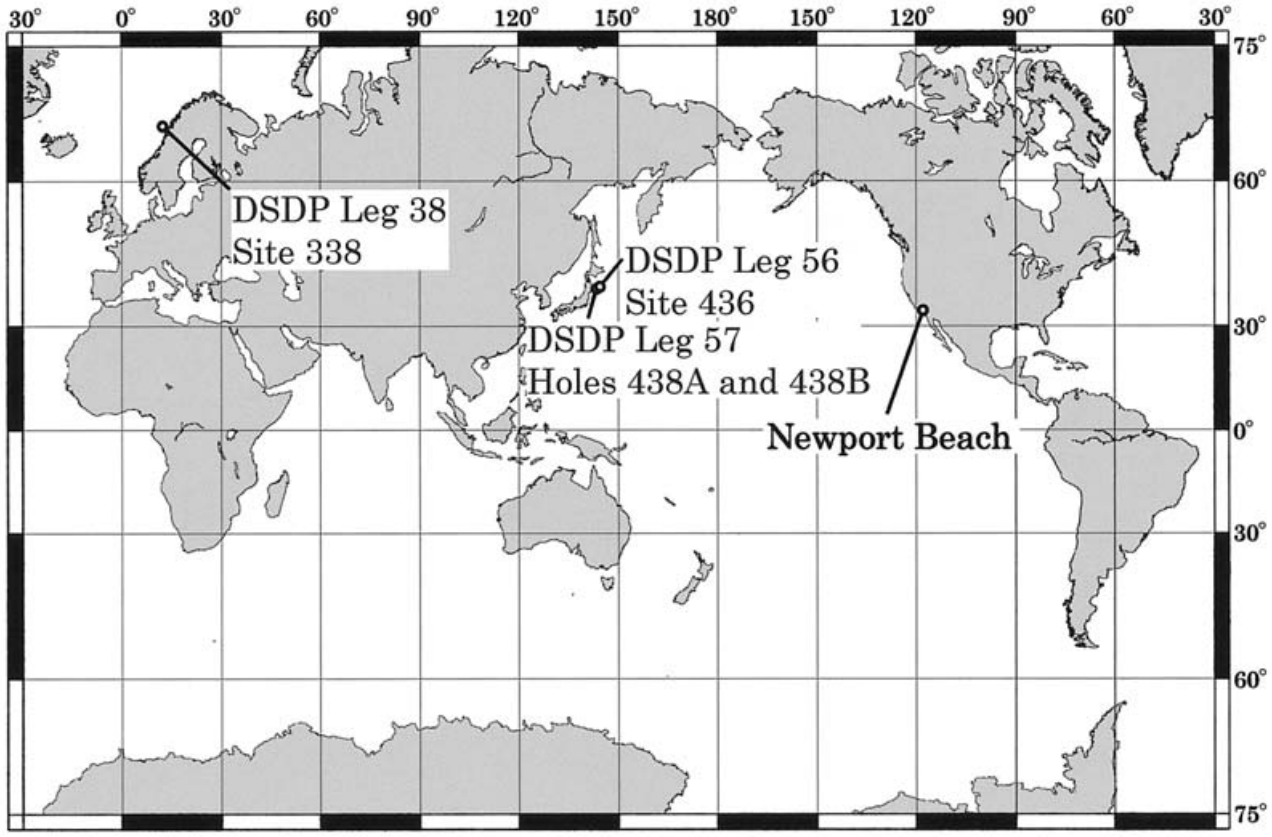


Figure 1. Location of DSDP Sites 338, 436 and 438 and the Newport Beach Section.

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. pliocenus* (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. pliocenus*
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

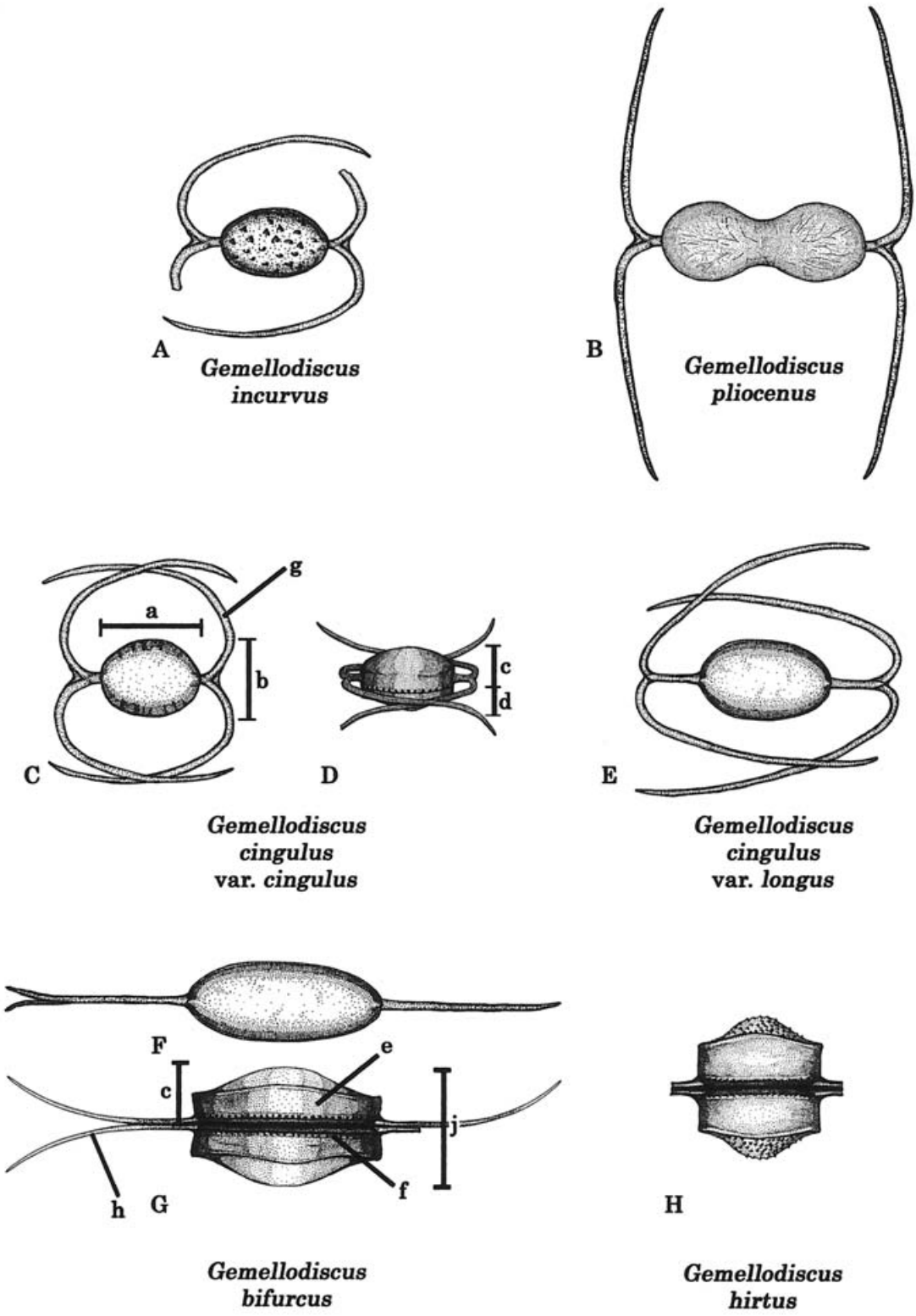


Figure 2. Sketches of *Gemellodiscus* species; **A:** *G. incurvus*, **B:** *G. pliocenus*, **C, D:** *G. cingulus* var. *cingulus*, **E:** *G. cingulus* var. *longus*, **F, G:** *G. bifurcus*, **H:** *G. hirtus*.

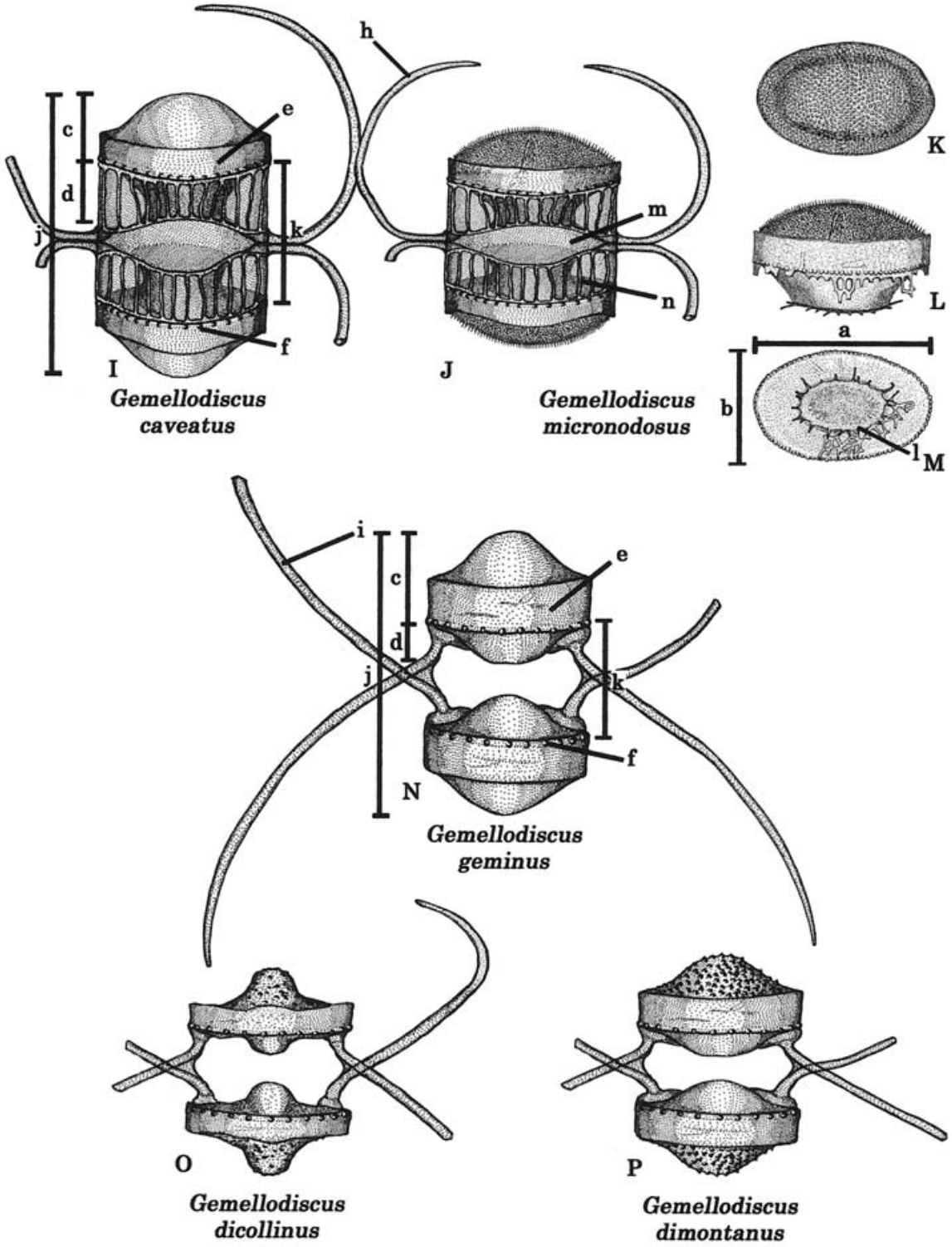


Figure 2. (Continued) **I:** *G. caveatus*, **J–M:** *G. micronodosus*, **N:** *G. geminus*, **O:** *G. dicollinus*, **P:** *G. dimontanus*, (**A, B, C, E, F, K:** valve view of epivalve, **D, L:** girdle view of frustule, **G, H, I, J, N, O, P:** girdle view of paired valve, **M:** valve view of hypovalve). 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.

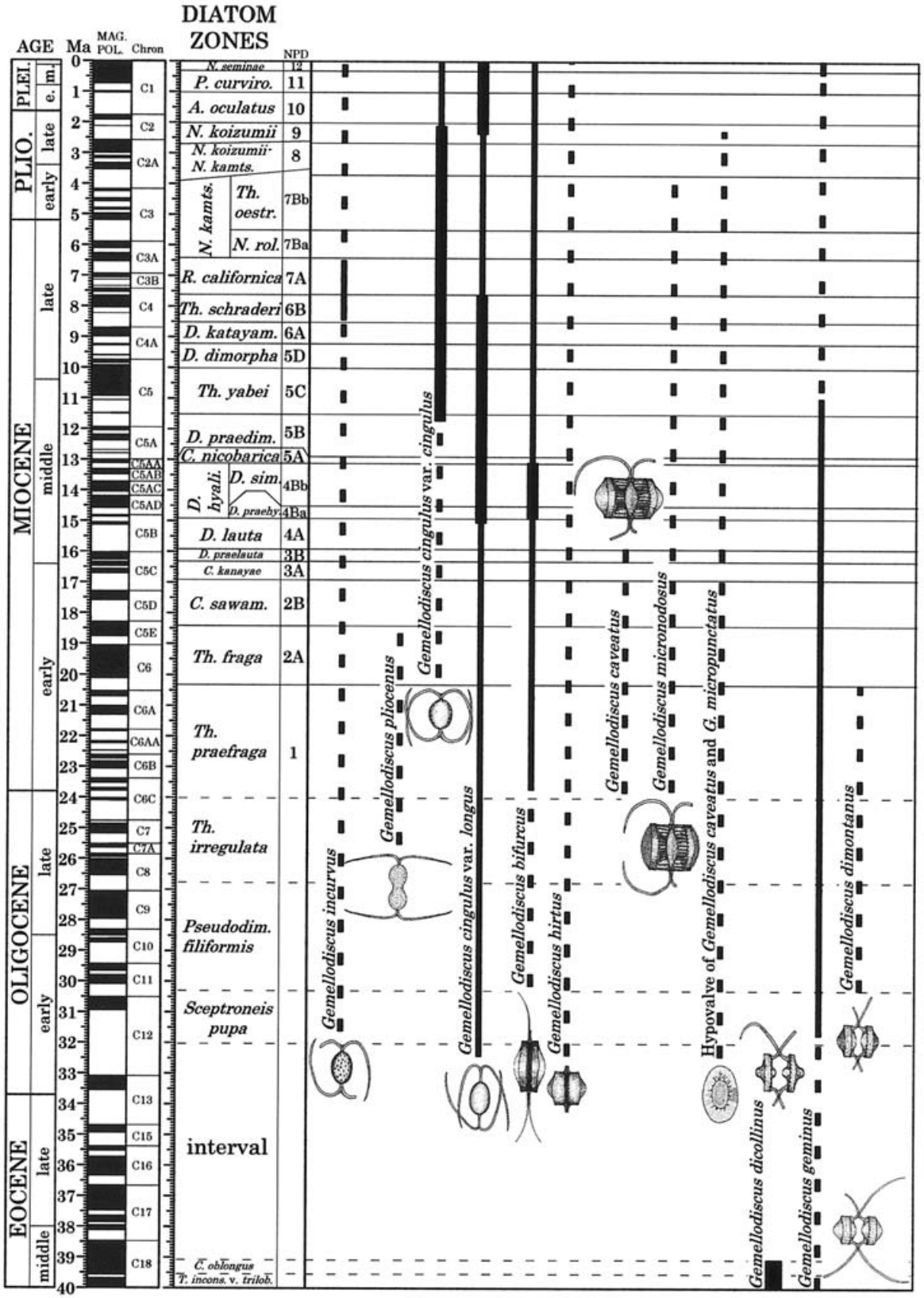


Figure 3. Stratigraphic ranges of *Gemellodiscus* species in the North Pacific and the Norwegian Sea. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998) for the Miocene, Pliocene and Pleistocene, and after Schrader and Fenner (1976) for the Eocene and Oligocene.

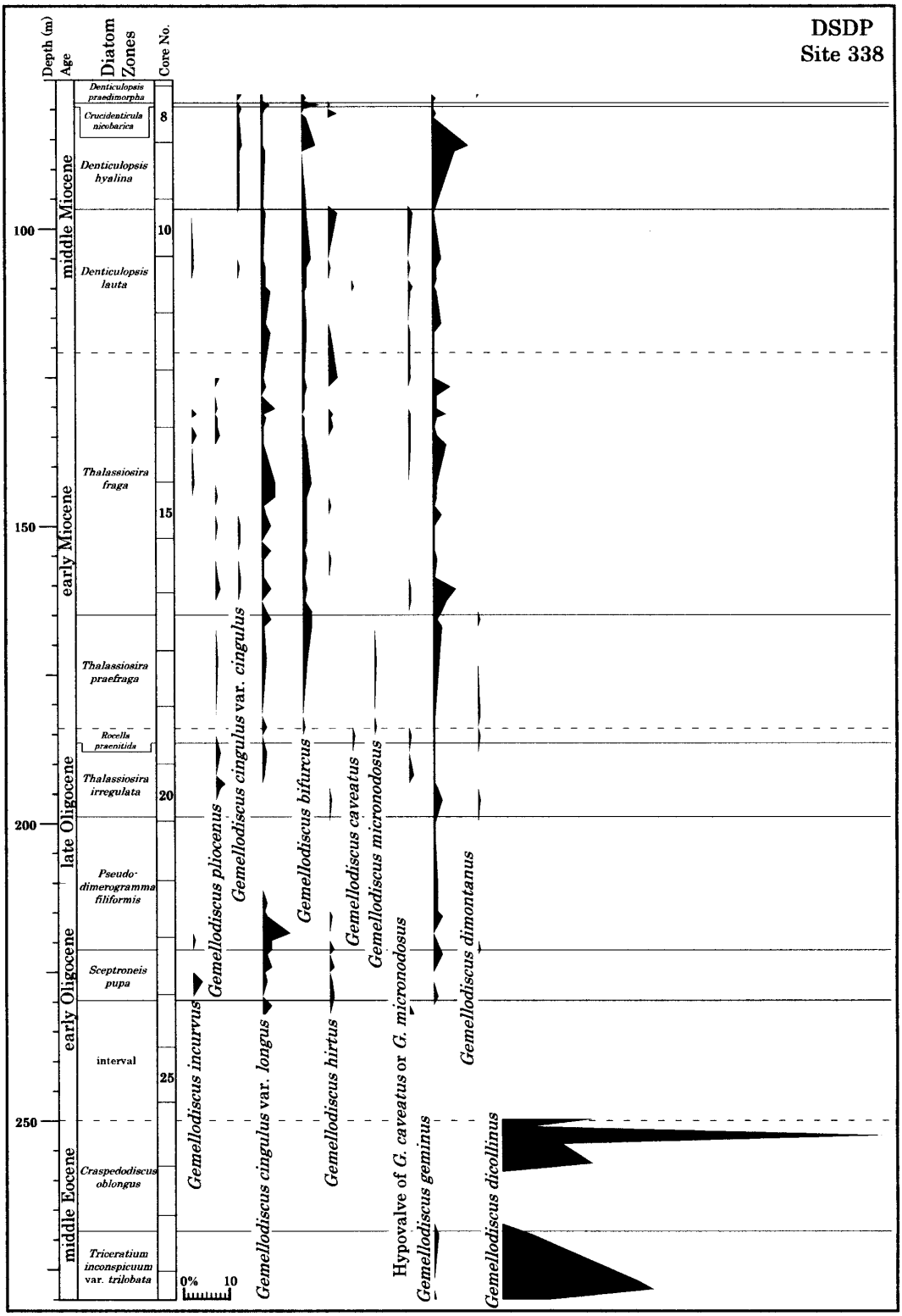
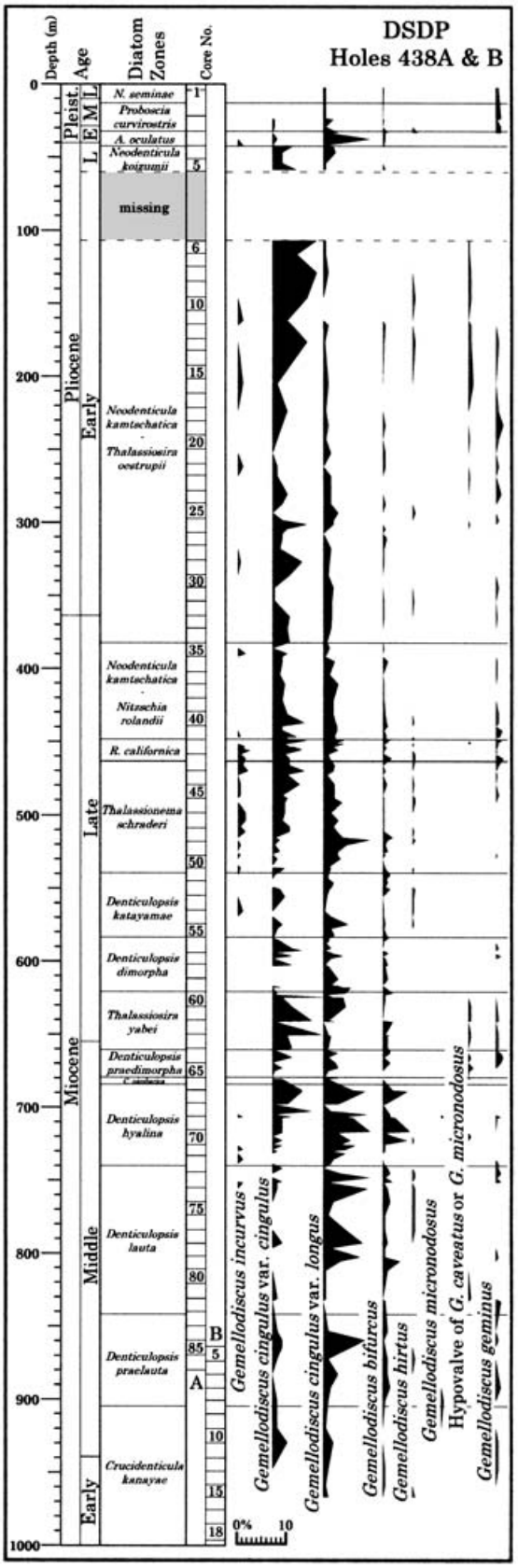


Figure 4. Stratigraphic occurrences of *Gemellodiscus* species at DSDP Site 338. Diatom zones are after Schrader and Fenner (1976).



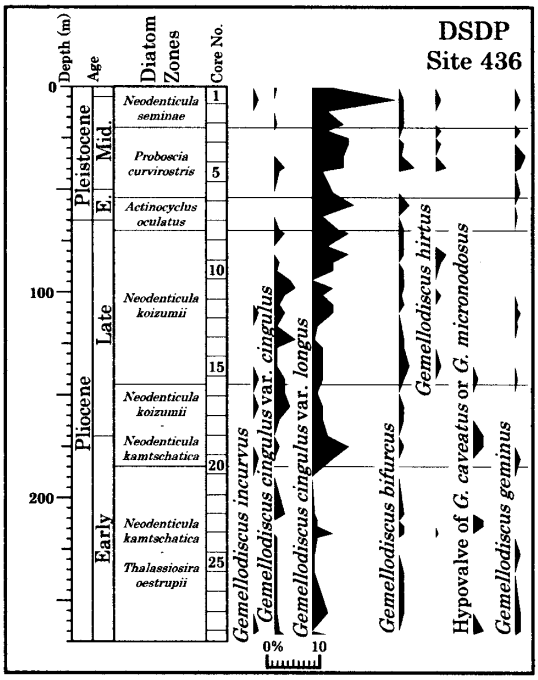


Figure 6. Stratigraphic occurrences of *Gemellodiscus* species at DSDP Site 436. Diatom zones are after Yanagisawa and Akiba (1998).

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 Chincha 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).

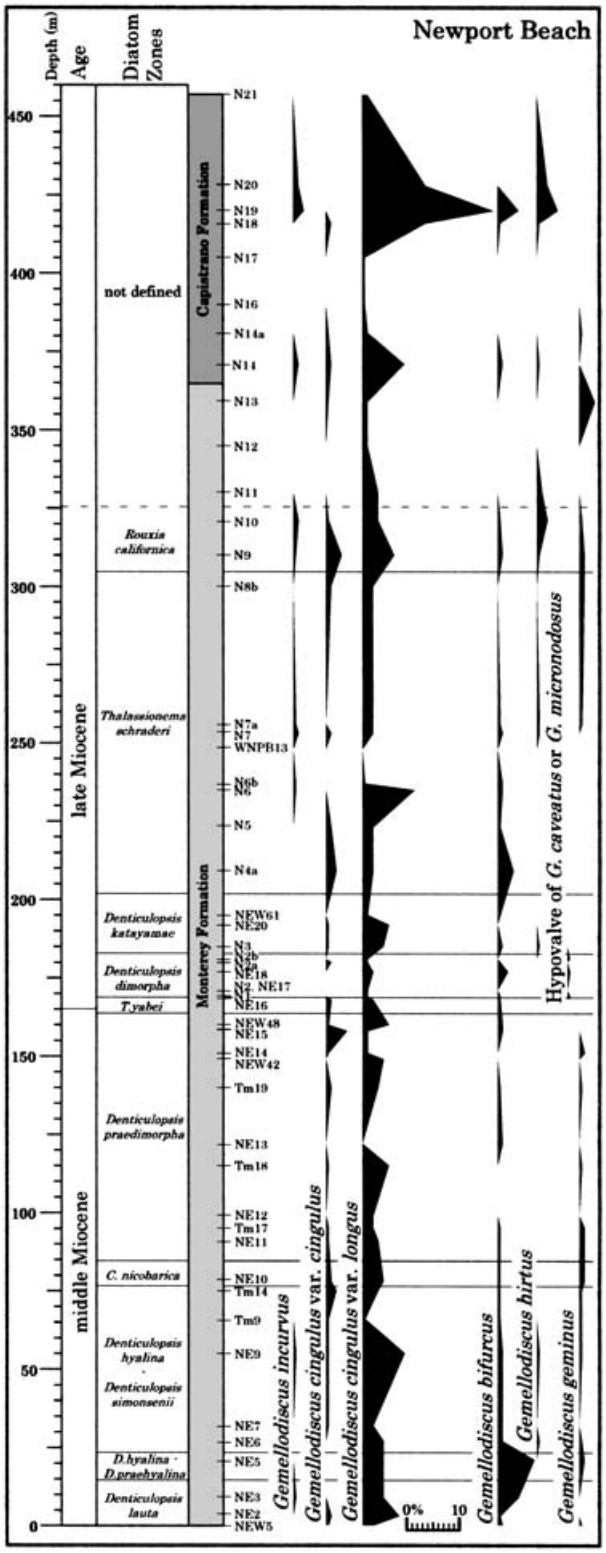


Figure 7. Stratigraphic occurrences of *Gemellodiscus* species in the Newport Beach Section. Diatom zones are after Yanagisawa and Akiba (1998).

Table 1. Occurrences of *Gemellodiscus* species at DSDP Site 338. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes in the Miocene are after Yanagisawa and Akiba (1998), and diatom zones in the Oligocene and Eocene after Schrader and Fenner (1976).

	Diatom zones	NPD	Core-Section, Interval (cm) Leg 38 Site 338	Depth (m)	Preservation	Abundance	*Gemellodiscus incurvus*	*G. pliocenus*	*G. cingulus* var. *cingulus*	*G.cingulus* var. *longus*	*G. bifurcus*	*G. hirtus*	*G. caveatus*	*G. micronodosus*	Hypovalve of *G. caveatus* or *G. micronodosus*	*G. decollinus*	*G. geminus*	*G. dimontenus*	Total number of resting spore valves counted
middle Miocene	*Denticulopsis praedimorpha*	5B	8-1, 140-141	77.40	G	A			1	+	+							+	100
			8-2, 48-49	77.98	G	A			+	+	1						1		100
			8-2, 99-100	78.49	G	A				+	+						+		100
	C. nicobarica	5A	8-3, 10-11	79.10	G	A			+	2	4	+					+		100
	Denticulopsis hyalina	4B	8-3, 80-81	79.80	G	A			1	1	+						+		100
			8-4, 10-11	80.60	G	A			+	+		2					1		100
			8-4, 80-81	81.30	G	A			+	+	1						+		100
			9-1, 50-51	86.00	G	A			1	+	3						8		100
			9-1, 148-149	86.98	G	A			+	1							5		100
			10-1, 106-107	96.06	G	A			+	+	1						1		100
	Denticulopsis lauta	4A	10-2, 80-81	97.30	G	A				1	1	2			1		+		100
			11-1, 50-51	105.00	G	A	+			+	2						2		100
			11-2, 50-51	106.50	G	C	+		+	1	1	+			+		1		100
			11-3, 98-99	108.48	G	A				1	1						1		100
			11-4, 70-71	109.70	G	A				1	1		+		1		+		100
			11-4, 148-149	110.48	G	A				2	+				+		1		100
			12-2, 40-41	115.90	G	A				1	1						2		100
			12-3, 38-39	117.38	G	A				2	1	+			+		+		100
early Miocene	*Thalassiosira fraga*	2A	13-1, 148-149	124.98	G	A		1		+	+	2			+		+		100
			13-2, 148-149	126.48	G	A				1	1						4		100
			13-3, 148-149	127.98	G	A					+						1		100
			13-5, 70-71	130.20	G	A		+		3	+						1		100
			13-6, 10-11	131.10	G	A	1			+		1			+		3		100
			13-6, 70-71	131.70	G	A		+		1	+	+			+		1		100
			14-1, 20-21	133.20	G	A		+		+	+	1			+		+		100
			14-2, 20-21	134.70	G	A	1	1		+	+				+		1		100
			14-3, 20-21	136.20	G	A				+	1				+		3		100
			15-1, 30-31	142.80	G	A	+			3	2						1		100
			15-2, 100-101	145.00	G	A		+		3	1						1		100
			15-3, 100-101	146.50	G	A				+	1	+					+		100
			15-4, 100-101	148.00	G	A				1	1						2		100
			15-5, 138-139	149.88	G	A		+	+	2	1						+		100
			16-1, 10-11	152.55	G	A			+		1						+		100
			16-2, 10-11	154.05	G	A				2	+						+		100
			16-3, 10-11	155.55	G	A				+	1	+					1		100
			16-5, 10-11	158.55	G	A		+	+	+	+						+		100
			16-6, 50-51	160.45	G	A		1	+	2	1				+		5		100
			17-1, 100-101	162.50	G	A					+				+		3		100
			17-2, 119-120	164.19	G	A				1	2						2		100
	Thalassiosira praefraga	1	17-3, 110-111	165.60	G	A				2	2						1	+	100
			17-4, 79-80	166.79	G	A				+	2						2		100
			18-1, 148-149	172.48	G	A		+		1	1			+			+		100
			19-1, 130-131	181.80	G	A											+	+	100
			19-3, 20-21	183.70	G	A				1	+			+			+		100
late Oligocene	*R. praenitida*		19-4, 10-11	185.10	G	A							+		+		1	+	100
	Thalassiosira irregulata		19-5, 148-149	187.98	G	A		1		1							+		100
			20-2, 30-31	191.80	G	A				+					1		+		100
			20-3, 20-21	193.20	G	C		2									+		100
			20-3, 90-91	193.90	G	C		1									1		100
			20-4, 148-149	195.98	G	A						+					2	+	100
early Oligocene	*Pseudodimerogramma filiformis*		21-1, 32-33	199.82	G	A											+		100
			21-2, 148-149	202.48	G	A											+		100
			22-2, 10-11	211.00	G	R											1		100
			22-3, 80-81	213.20	G	C				1							+		100
			22-4, 79-80	214.69	G	R				+							1		100
			22-5, 10-11	215.50	G	C				1		+					2		100
			22-6, 148-149	218.38	G	C				6									100
			23-1, 80-81	219.60	G	C	+			2							+		100
			23-2, 80-81	221.10	G	A				2		1					+	+	100
	Sceptroneis pupa		23-3, 10-11	221.90	G	C				1							2		100
			23-4, 80-81	224.10	G	C				2		1					+		100
			23-5, 10-11	224.90	G	C				+									100
			23-6, 10-11	226.40	G	A	2			1		+							100
			24-1, 100-101	229.00	G	R						1					1		100
	interval		24-2, 100-101	230.50	G	C				2		+							100
			24-3, 100-101	232.00	G	R				+					1				100
			barren until:																
middle Eocene	*Craspedodiscus oblongus*		26-2, 110-111	249.60	G	R										6			30
			26-3, 80-81	250.80	G	R										2			30
			26-4, 80-81	252.30	G	R										84			100
			26-5, 80-81	253.80	G	R										4			30
			27-1, 58-59	257.08	G	R										6			30
			27-2, 50-51	258.50	G	R													30
			27-3, 40-41	259.90	G	R													30
			27-4, 30-31	261.30	G	R													30
			27-5, 19-20	262.69	barren														0
			28-1, 120-121	267.20	G	R													30
	Triceratium inconspicuum var. *trilobata*		28-2, 148-149	268.98	G	R										2	1		30
			29-1, 130-131	276.80	G	R										9			30
			29-2, 120-121	278.20	G	R										11			30
			29-3, 148-149	279.98	G	R										1	+		10

and the correspondence between vegetative cells and resting spores can never be determined in fossil material.

The *Chaetoceros* spores (cf. *radicans*) of Whiting and Schrader (1985) from the upper Miocene to lower

Table 2. Occurrences of *Gemellodiscus* 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).

	Diatom Zones (NPD)	Core-Section, Interval (cm) Leg 57 Site 438	Depth (m)	Preservation	Abundance	*Gemellodiscus incurvus*	*G. cingulus* var. *cingulus*	*G. cingulus* var. *longus*	*G. biturus*	*G. hirtus*	*G. micronodosus*	Hypovalve of *G. caveatus* or *G. micronodosus*	*G. geminus*	Total number of resting spore valves counted
DSDP Hole 438A	*N. seminae* (NPD12)	1-2, 80-82	2.31	G	A			1	+				1	100
	Proboscia curvirostris (NPD 11)	2-1, 10-14	23.12	G	A			1					2	100
		2-1, 96-98	23.97	G	A		+	4	+				+	100
		2-5, 5-9	29.07	G	A		+	1					2	100
	Actinocyclus oculatus (NPD 10)	3-1, 31-33	32.82	G	A			6	2	2			2	100
		3-3, 140-142	32.91	G	A			2	1					100
		3-4, 10-14	37.12	G	A		1	19	1					100
		3cc	41.65	G	A	1		1	+					100
	Neodenticula koizumii (NPD 9)	4-1, 40-74	42.72	G	A		4	4						100
		4-4, 8-12	46.6	G	A		2	5						100
		5-2, 96-100	53.98	G	A		2	1						100
		5cc	58.5	G	A		5	1	1					100
	Neodenticula kamtschatica (NPD 7B-8)	6-1, 18-22	106.7	G	A		9	1				+		100
		7-1, 19-22	116.2	G	A		5	1				+		100
		8-3, 30-34	128.8	G	A		9	2				1		100
		10-2, 15-18	146.2	G	A		7			1		1		100
		11-6, 20-24	161.7	G	A	1	3							100
		12-1, 138-140	164.9	G	A		4	2	1			1		100
		13-3, 19-23	176.2	G	A		7	+	+	1		1	1	100
		16-3, 36-39	204.9	G	A	1	1	2				2		100
		18-3, 10-14	223.6	G	A		3	1					1	100
		19-3, 10-14	233.1	G	A		2	2	1				3	100
		20-3, 26-30	242.8	G	A		1	1				+	1	100
		21-3, 20-24	252.2	G	A			3	1					100
		22-3, 20-24	261.7	G	A	1	1		1				1	100
		23-1, 10-14	268.1	G	A		1	3				+		100
		24-3, 10-12	280.6	G	A		3	3					2	100
		25-1, 35-39	287.4	G	A		2	3	1					100
		25-5, 16-20	293.2	G	A			6		1				100
		26-2, 29-33	298.3	G	A		2	4					2	100
		26-4, 10-14	301.1	G	A		7	4				+		100
		26-6, 15-19	304.2	G	A		3	2	1					100
		27-2, 20-24	307.7	G	A		2							100
		27-4, 20-24	310.7	G	A		4	2	3				1	200
		28-2, 20-24	317.7	G	A		3	6	1					200
		29-2, 20-24	326.7	G	A	1	12	5	1					200
		30-2, 20-24	336.2	G	A		7	4						200
		31-1, 20-24	344.2	G	A		1	8					2	200
		32-1, 24-28	353.8	G	A		1	7	1	1				200
		33-1, 120-124	364.2	G	A		7	7	1				1	200
		34-1, 22-24	372.7	G	A		6	6						200
		35-1, 24-28	382.3	G	A		7	3						200
		35-3, 24-28	385.9	G	A			5	1					200
		35-6, 24-28	389.8	G	A	3	6	3						200
		36-1, 32-36	391.8	G	A		4	1						200
		36-3, 32-36	394.8	G	A		4	9	4				1	200
		37-3, 10-14	404.1	G	A		3	5					1	200
		38-1, 11-15	410.6	G	A		5	12	1					200
		39-2, 11-15	421.6	G	A		4	8	1					200
		40-2, 20-24	431.2	G	A		6	8	2				2	200
		40-6, 10-14	437.1	G	A		13	10	3	1			2	200
		41-1, 45-49	439.5	G	A		4	11	4					200
		41-3, 30-34	442.3	G	A		4	11	1				5	200
		41-6, 10-14	446.6	G	A	1	10	9	3				3	200
		41cc	447.1	G	A		6	10		1				200
	Rouxia californica (NPD 7A)	42-1, 14-18	448.7	G	A		6	10	6	1			1	200
		42-1, 90-91	449.4	G	A		14	17	5				5	200
		42-2, 95-96	451	G	A		8	9	3			2	1	200
		42-3, 15-16	451.7	G	A		5	17	1	1			2	200
		42-4, 50-54	453.5	G	A	3	7	8	2				1	200
		42-4, 73-74	453.7	G	A	2	9	8	3				1	200
		42-5, 100-101	455.5	G	A	3	12	11	2					200
		42-6, 16-20	456.2	G	A	5	11	12	1				1	200
		43-1, 59-63	458.6	G	A	1	5	4	1	2				200
		43-3, 30-34	461.3	G	A	3	7	5	7	2			6	200
	Thalassionema schraderi (NPD 6B)	43-6, 82-86	466.3	G	A	2	7	9		1			2	200
		44-1, 60-64	470.1	G	A	4	13	8	2					200
		44-3, 10-14	472.6	G	A		6	3					1	200
		45-1, 54-58	479.6	G	A	1	11	9	3	1				200
		45-6, 30-34	486.8	G	A	1	4	9					2	200
		46-1, 18-20	488.7	G	A		6	9	1	2			1	200
		46-3, 18-22	491.7	G	A		5	15	1	2				200
		47-1, 10-14	498.1	G	A	3	5	6	1					200
		47-4, 110-114	503.6	G	A	3	4	12	1					200
		48-1, 14-18	507.7	G	A	1	7	8	1					200
		48-3, 46-50	511	G	A	3	7	11	1	1				200
		48-6, 26-30	515.3	G	A		1	16	8					200
		48-7, 30-31	516.8	G	A		3	38	4	2				200
		49-3, 10-14	520.1	G	A	1	1	19	2					200
		49-6, 10-14	524.6	G	A		3	12	4					200
		49-7, 10-11	526.1	G	A		1	12						200
		50-1, 20-24	526.7	G	A	1		11	2				1	200
		50-3, 20-24	529.7	G	A		2	14						200
		50-6, 20-24	534.2	G	A			6	1					200
		50-7, 10-11	535.6	G	A	1		5	2					200
		51-1, 16-20	536.2	G	A	1	5	6	2	1				200
	Denticulopsis katayamae (NPD 6A)	51-4, 16-20	540.7	G	A		1	4	6					200
		51-6, 16-20	543.7	G	A			4	3					200
		52-1, 36-38	545.9	G	A			8	4					200
		52-3, 36-38	548.9	G	A			7	2					200
		52-4, 36-38	550.4	G	A		3	5	6	2				200
DSDP Hole 438A	*Denticulopsis katayamae* (NPD 6A)	53-1, 77-81	555.8	G	A		5	3		1				200
		54-1, 110-114	565.6	G	A	2		1	1	1				200
		54-4, 125-127	569.3	G	A			6	1					200
		55-1, 70-74	574.7	G	A		4	20	2	1				200
		55-3, 70-74	577.7	G	A		2	6	1					200
		55-6, 76-78	582.3	G	A		1	9	3					200
		56-1, 20-24	583.7	G	A			5	5					200
	Denticulopsis dimorpha (NPD 5D)	56-3, 20-24	586.7	G	A		2	2						100
		56-3, 60-62	587.1	G	A		2	1	+					100
		56-6, 20-24	591.2	G	A		4	3					1	100
		56cc	592.6	G	A		6	+						100
		57-1, 115-117	594.2	G	A			3	2					100
		57-2, 31-35	594.8	G	A		2	4	2					100
		57-3, 31-35	596.3	G	A		4	8					2	100
		57-4, 59-61	598.1	G	A			3	1					100
		58-1, 16-20	602.7	G	A		4	+	2					100
		58-1, 101-103	603.5	G	A			2	1					100
		59-1, 17-21	612.2	G	A			6	2					100
		59-3, 135-137	616.4	G	A			3						100
		59-4, 17-21	616.7	G	A			6						100
		59-5, 5-6	618.1	G	A		2	8	1					100
		59-5, 17-21	618.2	G	A			11	1					100
	Thalassiosira yabei (NPD 5C)	60-1, 34-38	621.9	G	A		1	9	4					100
		60-1, 134-136	622.9	G	A		+	1	1					100
		60-3, 26-27	624.8	G	A		12	4	1					100
		60-3, 27-29	624.8	G	A		2	8	1					100
		61cc	631.1	G	A		4	9	+			)	+	100
		62-1, 20-24	640.7	G	A		8	2				1	1	100
		62-1, 80-81	641.3	G	A		2	5	3				+	100
		62-1, 110-112	641.6	G	A		+		4					100
		63-1, 16-20	650.2	G	A		10	2	1			1	1	100
		63-1, 88-89	650.9	G	A		+	2	3					100
		63-1, 110-112	651.1	G	A		3	3	2			1	1	100
		64-1, 10-14	659.6	G	A		4	2	2				1	100
		64-1, 121-128	660.8	G	A			+	3					100
	Denticulopsis praedimorpha (NPD 5B)	64-3, 10-14	662.6	G	A		2	6	3				2	100
		64-5, 30-32	665.8	G	A		4	2	+			1	3	100
		65-1, 54-56	669.6	G	A			5	3				2	100
		65-3, 100-103	673	G	A		2	6	1			2		100
		65-5, 18-21	675.2	G	A		+	2				+		100
		66-1, 118-122	679.7	G	A			+						100
		66-2, 25-27	680.3	G	A			6						100
		66-2, 34-36	680.4	G	A		+	2				1		100
	C. nicobarica (5A)	66-2, 82-84	680.8	G	A		2	2						100
	Denticulopsis hyalina (NPD 4B)	67-1, 27-32	688.3	G	A		6	12	4					100
		67-1, 112-113	689.1	G	A		6	17	10					100
		68-1, 30-34	697.8	G	A		3	6	1					100
		68-1, 101-103	698	G	A									100
		68-4, 68-72	702.7	G	A		8	3	2					100
		68-6, 105-108	705.1	G	A			18	3					100
		68-7, 24-26	706.8	G	A	1	4	8	3		1		2	100
		69cc	707.1	G	A		2	12	5				+	100
		70-1, 16-20	716.7	G	A		2	19	11					100
		70-1, 78-81	717.3	G	A		2	6	1					100
		70-3, 49-53	720	G	A			8	4			1		100
		70-5, 23-27	722.8	G	A		2	11	10	+				100
		70-7, 5-7	725.6	G	A			7	+					100
		71-1, 12-16	726.1	G	A		2	13	1					100
		71-3, 7-11	729.1	G	A	1		9	1					100
		71-3, 114-116	730.2	G	A		1	3	1					100
		71-5, 8-12	731.6	G	A			9						100
		72-1, 14-18	735.7	G	A	1		4						100
		72-3, 15-17	738.7	G	A			3	+				1	100
	Denticulopsis lauta (NPD 4A)	72-5, 11-13	741.6	G	A		2		2				1	100
		73-1, 27-31	745.3	G	A			7	3	1			2	100
		73-3, 27-31	748.3	G	A			19	1	1			+	100
		73-5, 9-11	751.1	G	A		2	4	4				2	100
		73-5, 46-48	751.5	G	A	1	1	2	+					100
		74-1, 124-126	755.8	G	A		1	18	2	1				100
		75-1, 70-71	764.7	G	A			4	3	1				100
		76-1, 32-34	773.8	G	A			2	1	1				100
		77-1, 81-83	783.8	G	A			9	1	1				100
		78-1, 54-56	793.1	G	A		2	16	2					100
		78-3, 92-94	796.4	G	A			3	1					100
		79-1, 51-54	802.5	G	A			15	1				1	100
		79-3, 55-57	805.6	G	A			7	7					100
		80-1, 20-22	811.7	G	A			1	2					100
		82-1, 73-75	831.2	G	A		1	1				1		100
		82-2, 73-75	832.7	G	A				1				2	100
DSDP Hole 438B	*Denticulopsis praelauta* (NPD 3B)	84-3, 63-65	853.1	G	A		1	2	2					100
		85-1, 48-50	859.5	G	A		2	17	+				1	100
		85-4, 25-27	863.8	G	A		2	12	1					100
		6-1, 16-19	872.3	G	A		1	2	2	1				100
		7-1, 128-130	882.8	G	A			6	2				1	100
		8-1, 90-92	891.8	G	A		+	3	3				2	100
		9-1, 85-87	901.2	G	A		1	2	1		1			100
	Crucidenticula kanayae (NPD 3A)	11-1, 60-62	919.8	G	A		1	1						100
		12-1, 81-82	929.5	G	A		3	4					1	100
		14cc	947.6	G	A			2	1				1	100
		15-2, 61-62	959	G	A			1	1					100
		16-1, 82-84	967.1	G	A			2		1				100

Table 3. Occurrences of *Gemellodiscus* species at DSDP Site 436. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

	Diatom zones & NPD	Core-Section, Interval (cm) Leg 56 Site 436	Depth (m)	Preservation	Abundance	*Gemellodiscus incurvus*	*G. cingulus* var. *cingulus*	*G. cingulus* var. *longus*	*G. bifurcus*	*G. hirtus*	Hypovalve of *G. caveatus* or *G. micronodosus*	*G. geminus*	Total number of resting spore valves counted
l. Pleisto.	*Neodenticula seminae* 12	1-1, 49-50	0.49	G	R		+	4					100
		1-5, 50-52	6.40	G	C	1		16	1	1		1	100
		2-3, 100-102	12.00	G	R			3	1				100
		3-1, 102-104	18.52	G	R		+	6	1				100
mid. Pleistocene	*Proboscia curvirostris* 11	3-3, 100-102	21.50	G	C			3	+	1		1	100
		3-6, 10-12	25.10	G	R			7					100
		4-1, 50-52	27.50	G	R			7	1	1			100
		4-5, 50-52	33.50	G	C			6	+			2	100
		5-2, 148-150	39.48	G	A		2	6	3	2		1	100
		5-4, 22-24	41.12	G	R		1	2					100
		6-4, 100-102	51.50	G	C			4				1	100
e. Plei.	*Actinocyclus oculatus* 10	7-2, 54-56	57.54	G	R			8	2				100
		7-6, 50-52	63.00	G	C			2				+	100
		8-3, 148,-150	69.48	G	A		1	5	1				100
late Pliocene	*Neodenticula koizumii* 9	8-5, 18-20	71.18	G	C		2	7	1				100
		9-2, 148-150	77.48	G	A			3	1				100
		9-5, 95-97	81.35	G	R			7	1	2			100
		10-1, 148-150	85.48	G	A		1	4		1			100
		10-4, 98-100	89.48	G	R		+	4	1	+			100
		11-1, 50-52	94.00	G	R		3		1				100
		11-3, 148-150	97.88	G	A		4	4	1				100
		11-6, 100-102	101.40	G	C		2	2	+	1			100
		12-2, 148-150	105.98	G	C		1	4	1			+	100
		12-5, 98-100	109.98	G	C	1	2	4				1	100
		13-3, 100-102	116.50	G	C		+	1	+			+	100
		14-1, 100-102	123.00	G	C		4	+	1				100
		14-4, 48-50	126.98	G	C		+	2	1				100
		15-3, 141-143	135.91	G	C		+	2	2	1			100
		16-1, 130-132	142.30	G	C	1	2	2	1		+	+	100
	Neodenticula koizumii - *Neodenticula kamtschatica* 8	16-6, 47-49	148.87	G	R		2	1					100
		17-4, 50-52	155.50	G	C	1	3	2	1				100
		18-2, 45-47	161.95	G	A		1	2	1				100
		19-1, 50-52	170.00	G	C			3			1		100
		19-4, 148-150	174.98	G	C		1	7	1		1		100
		20-2, 38-40	180.88	G	C	1		4				1	100
early Pliocene	*Neodenticula kamtschatica* - *Thalassiosira oestrupii* 7Bb	21-1, 110-112	189.60	G	C								100
		23-1, 48-50	207.98	G	A		2	+	1				100
		23-3, 48-50	210.98	G	A			1			1		100
		23-5, 50-52	214.00	G	C			1	1		1		100
		24-1, 50-52	217.50	G	R			4	1	+			100
		24-2, 110-112	219.30	G	R		+	1					100
		25-1, 70-72	227.20	G	R		+	+				1	100
		26-1, 60-62	236.47	G	C		+	+	1				100
		28-1, 102-104	256.02	G	R		+	3	1			1	100
		29-1, 48-50	264.98	G	R	1	1				1	1	100
		29-2, 70-72	266.70	G	R		2	3					100

Table 4. Occurrences of *Gemellodiscus* species in the Newport Beach Section. Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa. Diatom zones and NPD codes are after Yanagisawa and Akiba (1998).

	Diatom zones & NPD	Sampled section (W: western; E: eastern)		Sample number	Depth (m)	Preservation	Abundance	*Gemellodiscus incurvus*	*G. cingulus* var. *cingulus*	*G. cingulus* var. *longus*	*G. bifurcus*	*G. hirtus*	Hypovalve of *G. caveatus* or *G. micronodosus*	*G. geminus*	Total number of resting spore valves counted
not defined		W	Capistrano Fm.	N21	457	M	R			1					100
		W		N20	428	M	R	1		12		2			100
		W		N19	420	G	C	2		25	4	4			100
		W		N18	416	G	A		1	12	+	+			100
		W		N17	405	G	C			+					100
		W		N16	390	G	A			+					100
		W		N14a	381	G	C		+	1				+	100
		W		N14	371	G	C	1	1	8	1	1			100
		W		N13	359	G	A		+	1				3	100
		W		N12	345	G	R			1					100
		W		N11	330	G	A			3		1			100
late Miocene	*R. californica* 7A	W	Monterey Formation	N10	321	G	A	1	+	3	+	2		+	100
		W		N9	310	G	A	+	3	6	1	+		1	100
	Thalassiosira schraderi 6B	W		N8b	300	G	C		1	2				1	100
		W		N7a	256	G	C	+		2	+	+		+	100
		W		N7	253	G	R	1	1	2	1	+			100
		W		WNPB13	248	G	A								100
		W		N6b	237	G	A	+		+	1				100
		W		N6	235	G	C	+		10	1				100
		W		N5	223	G	R		1	2	+				100
		W		N4a	209	M	R		2	2	3				100
	Denticulopsis katayamae 6A	E		NEW61	195	G	C			1	+				100
		E		NE20	192	G	R		+	5					100
		W		N3	185	G	R		+	4	1	+			100
	Denticulopsis dimorpha 5D	W		N2b	181	M	R			1			+		100
		W		N2a	180	G	R		1	1	+				100
		E		NE18	177	G	A			2	2		+		100
		E		NE17	171	M	R			1					100
		W		N1	169	G	C			1	+		+		100
	5C	E		NE16	168	M	R		1	2	+				100
middle Miocene	*Denticulopsis praedimorpha* 5B	E		NEW48	160	G	R		+	5	1				100
		E		NE15	158	G	C		4	1	1				100
		E		NE14	151	G	C		+	1				1	100
		E		NEW42	149	G	C			4					100
		E		Tm19	140	G	C		1	3	+			+	100
		E		NE13	122	G	R				1				100
		E		Tm18	115	G	C		+	5				+	100
		E		NE12	99	G	C			2					100
		E		Tm17	95	G	A		+	2	+			1	100
		E		NE11	91	G	A		+	3	+			1	100
	5A	E		NE10	78	G	C		1	4	+			1	100
	Denticulopsis hyalina 4Bb	E		Tm14	75	G	A		2	3	+			+	100
		E		Tm9	66	G	A		+	+	+			+	100
		E		NE9	55	G	A	+	+	8	1	+		+	100
		E		NE7	32	G	A		+	2	1			+	100
		E		NE6	27	G	A			4	1	+		+	100
	4Ba	E		NE5	21	G	A			4	7			1	100
	Denticulopsis lauta 4A	E		NE3	9	G	A	+		4	4				100
		E		NE2	3	G	A		1	7	+				100
		E		NEW5	0	G	A		+	2	1			+	100

Pliocene marine sediments of the Oregon coast and continental shelf are identified as *G. incurvus*, because the valve face is covered with numerous spines.

Etymology.—Latin *incurvus*, meaning ''curved inside''.

Gemellodiscus pliocenus (Brun) Suto comb. nov.

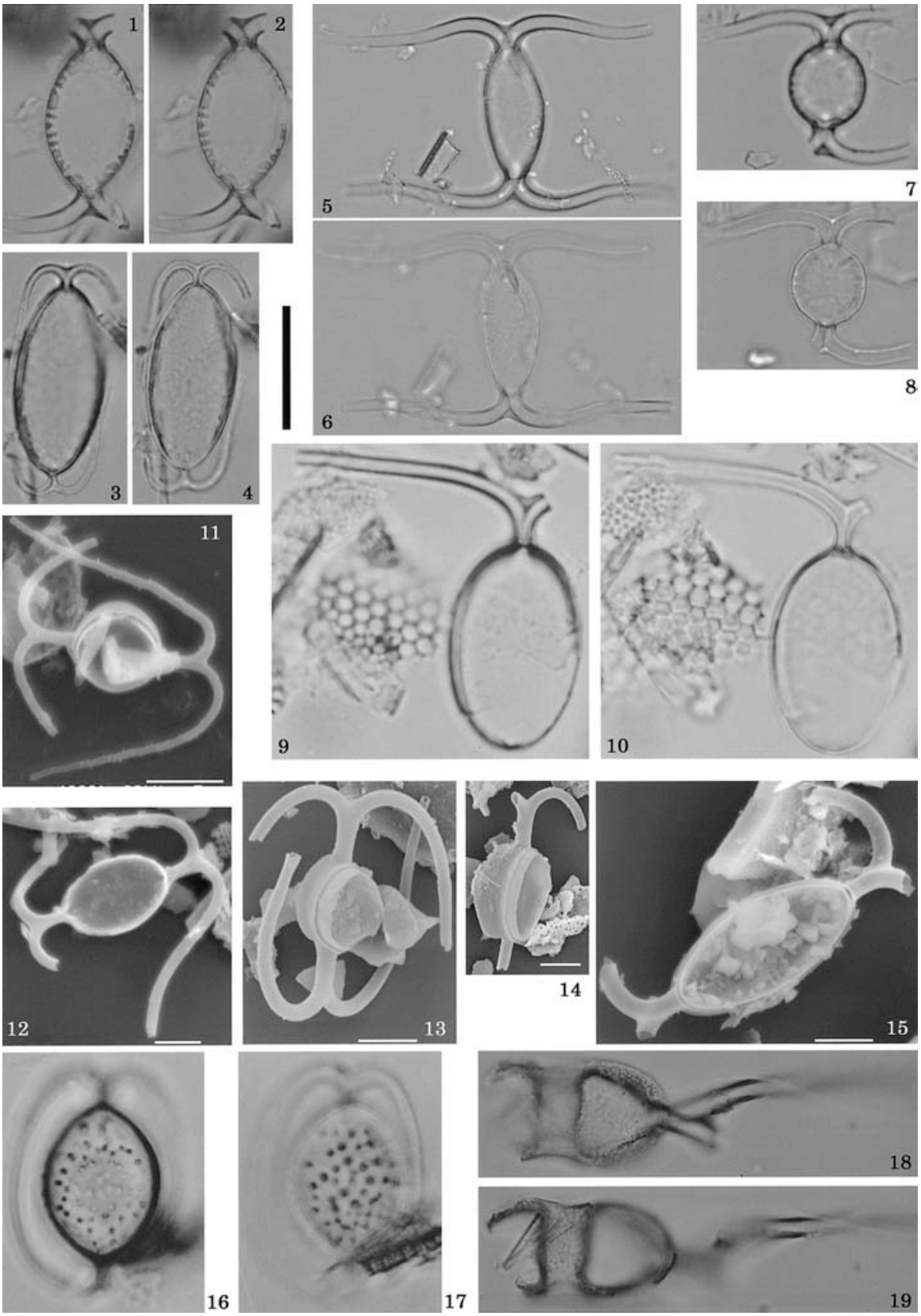
Figures 2.B; 8.18, 8.19

Basionym.—*Chaetoceros pliocenus* Brun, 1891, p. 15, pl. 19, figs. 1a–c

References.—*Chaetoceros pliocenus* Brun, Sheshukova-Poretzkaya, 1967, p. 207, pl. 24, figs. 10a, b; Dzinoridze *et al.*, 1979, p. 49, fig. 182.

Synonymy.—*Chaetoceros* sp. A of Gombos, 1976, p. 592, pl. 24, figs. 1–6; *Chaetoceros panduraeformis sensu* Barron and Mahood, 1993, p. 38, pl. 5, fig. 14, pl. 6, figs. 6, 7.

Description.—In valve view, epivalve slender, apical axis 12.5–50.0 μm, transapical axis 5.5–20.0 μm, width of isthmus 3.5–14.0 μm. Valve panduriform with broad hyaline isthmus. Valve strongly concave in the isthmus area on each side, with numerous wrinkles extending roughly in fan shape from the junction of the isthmus, with two bifurcated setae, and a mantle. Bifurcated setae hyaline, smooth, emerging from valve apices, fused for a short distance, then curved back around



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.

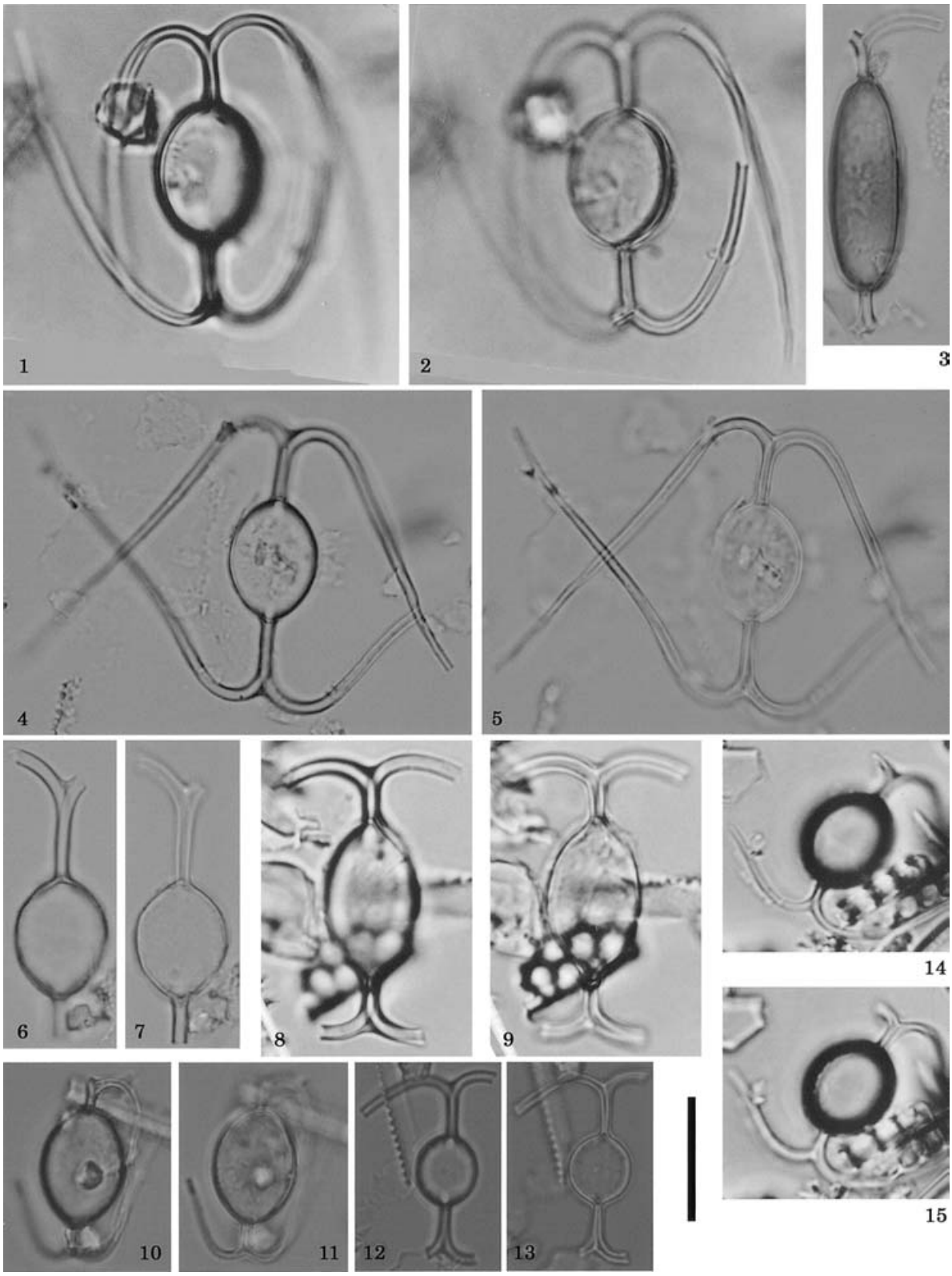
Description.—Frustule heterovalvate. Valve oval to elliptical in valve view, apical axis 5.0–17.5 μm, transapical axis 5.0–9.0 μm. In girdle view, epivalve vaulted, hyaline, with two bifurcated setae, and a mantle. Bifurcated setae hyaline, smooth, emerge from valve apices, fused for a short distance, 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. Hypovalve 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 hypovalve hyaline with a single ring of puncta at its base. Paired valve formed by completely connected basal plates of two hypovalves.

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 furcillatus*, 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. Hypovalve 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 hypovalve hyaline with a single ring of puncta at its base. Paired valve formed completely by the connected basal plates of two hypovalves.

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).

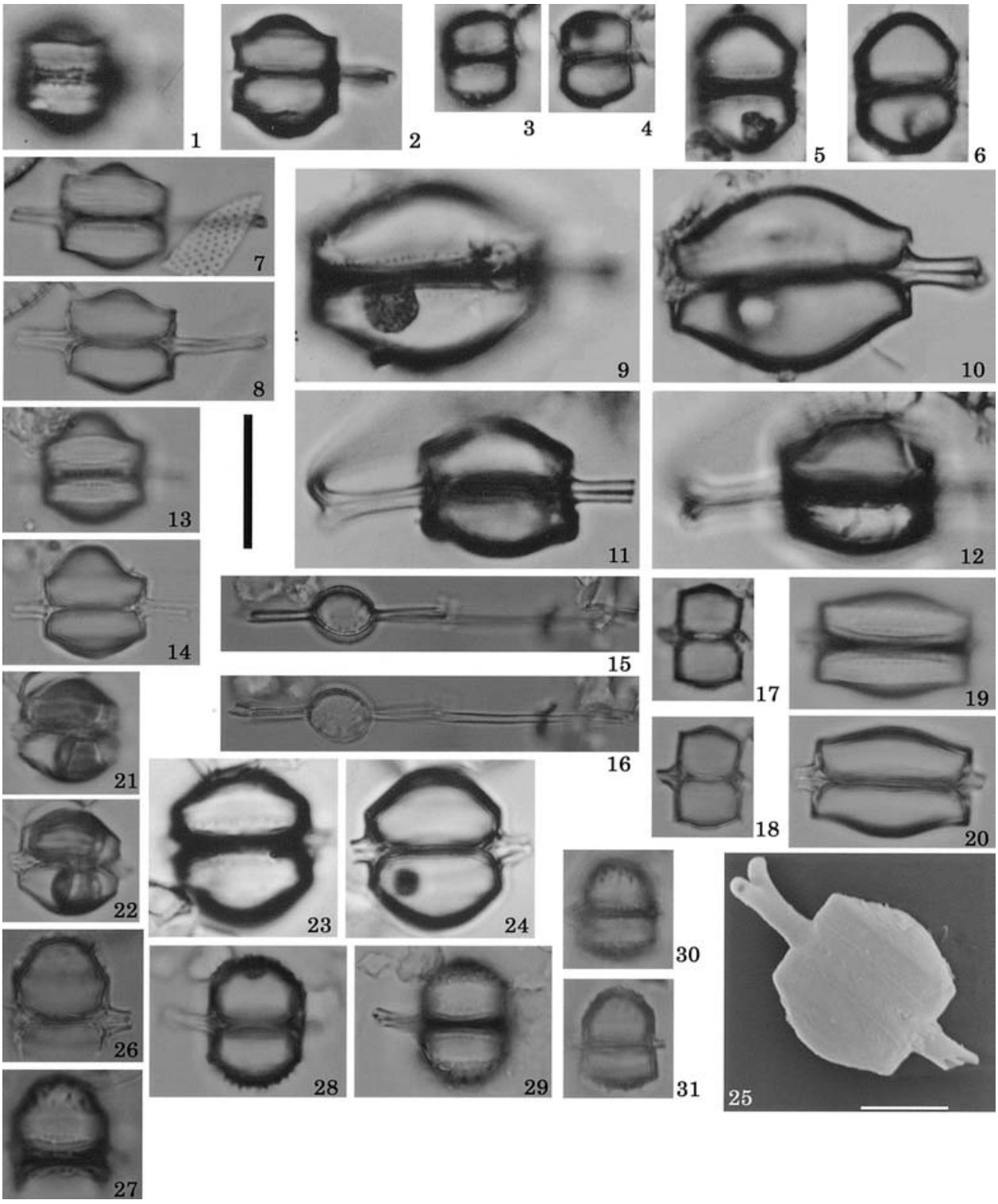
Etymology.—Latin *hirtus*, meaning ''shaggy.''

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. Hypovalve 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 hypovalve 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 hypovalve 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 hypovalve of this species vis a vis that of *G. micronodosus* (Figures 13.1–13.14; 14.4), and therefore, this type of hypovalve was counted as ''hypovalve of *G. caveatus* and *G. micronodosus*'' when only hypovalves 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. Hypovalve 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 hypovalve 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 hypovalve 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 hypovalves of *G. caveatus* and *G. micronodosus* (Figures 13.1–13.14; 14.4) are very similar and therefore, they were counted as ''hypovalve of *G. caveatus* and *G. micronodosus*''.

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

Hypovalves of ***Gemellodiscus caveatus*** and ***G. micronodosus***

Figures 2.M; 13.1–13.14; 14.4

Same type hypovalve.—*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.

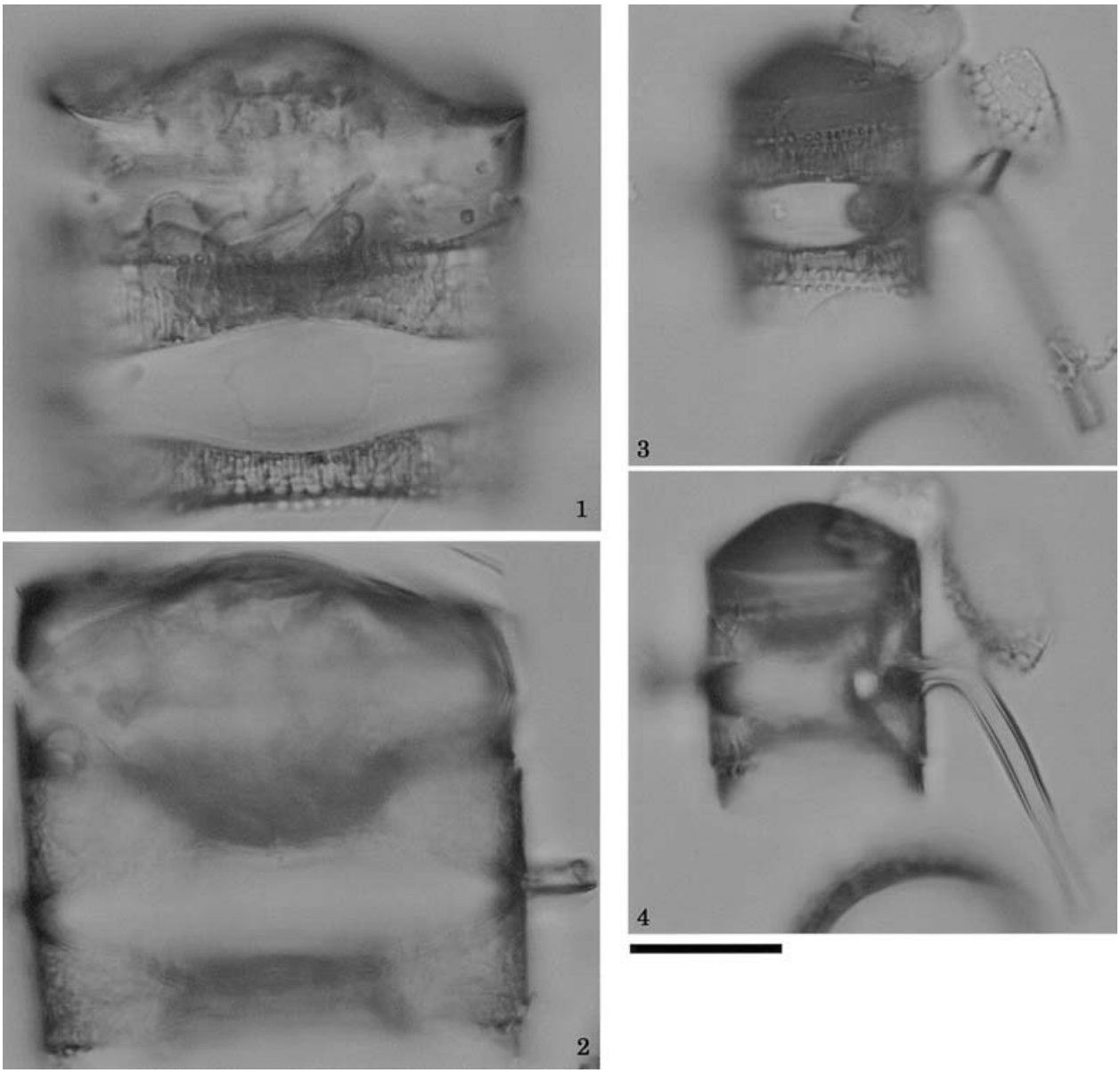
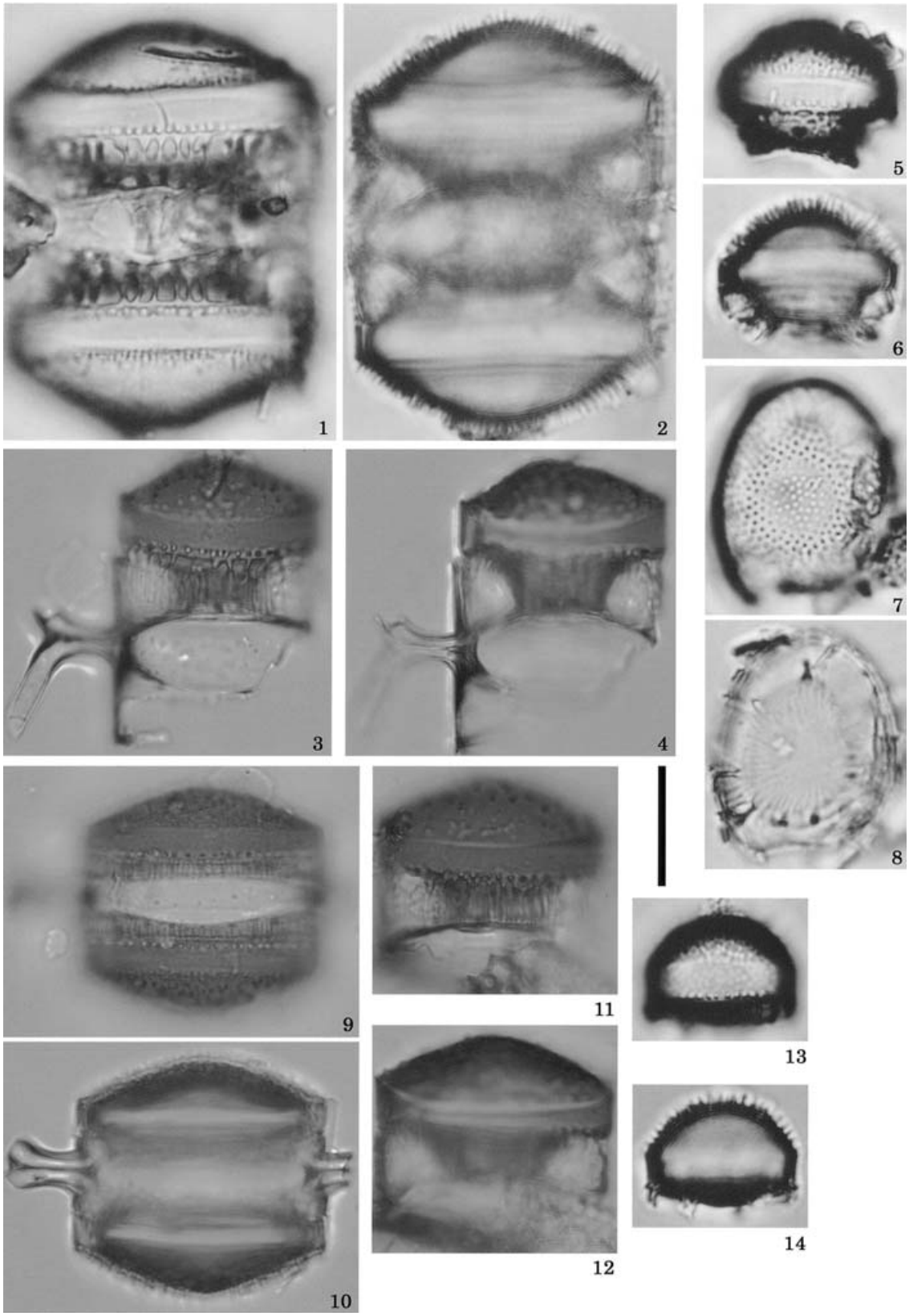
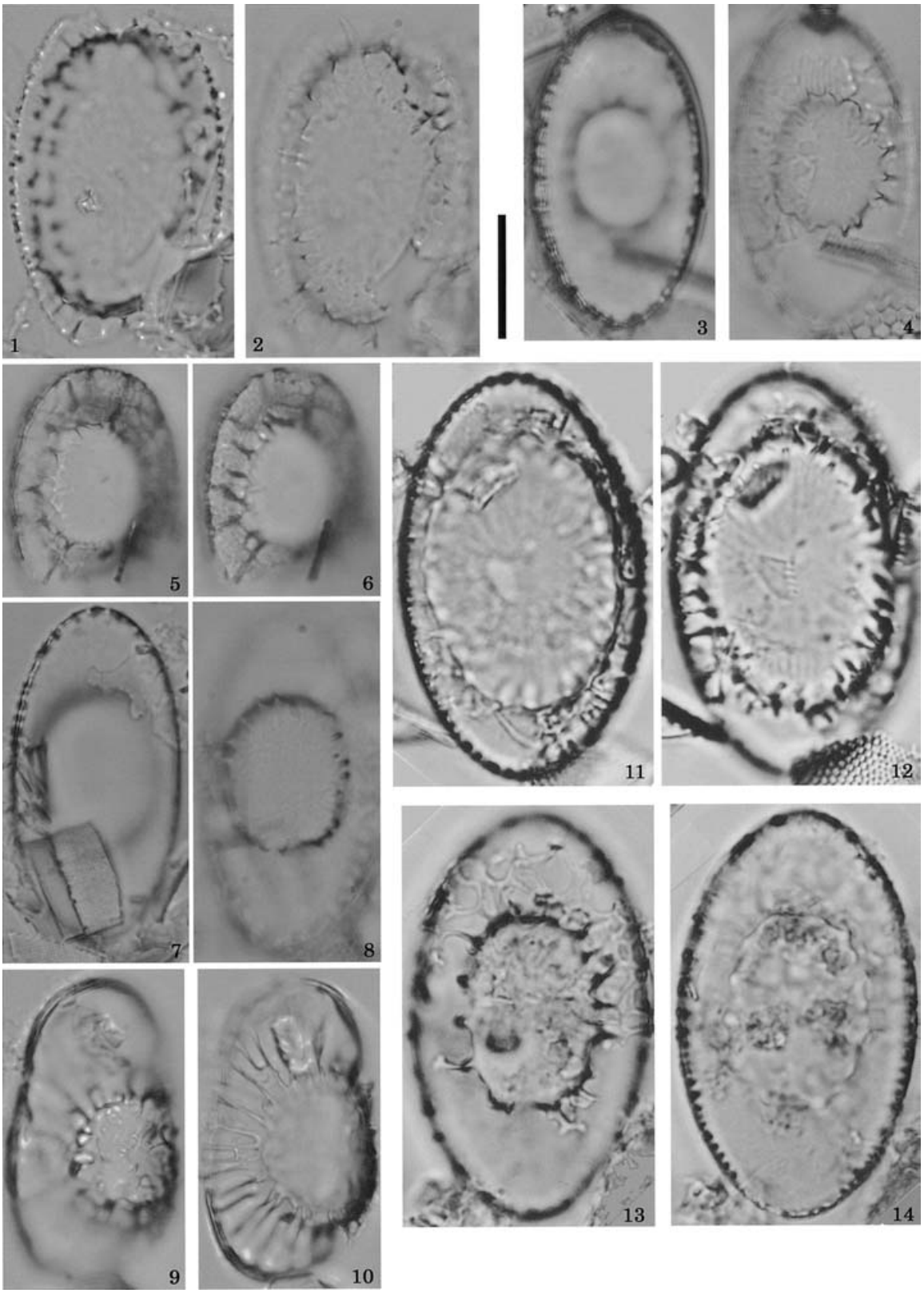


Figure 11. **1–4.** *Gemellodiscus caveatus* Suto sp. nov., LM. Scale bar = 10 μm for each figure. **1, 2.** Girdle view of one frustule with one hypovalve, DSDP Site 338-11-4, 70–71 cm. **3, 4.** Holotype. Girdle view of one frustule with one hypovalve, DSDP Site 338-12-2, 40–41 cm.

➡ **Figure 12.** **1–14.** *Gemellodiscus micronodosus* Suto sp. nov., LM. Scale bar = 10 μm 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.





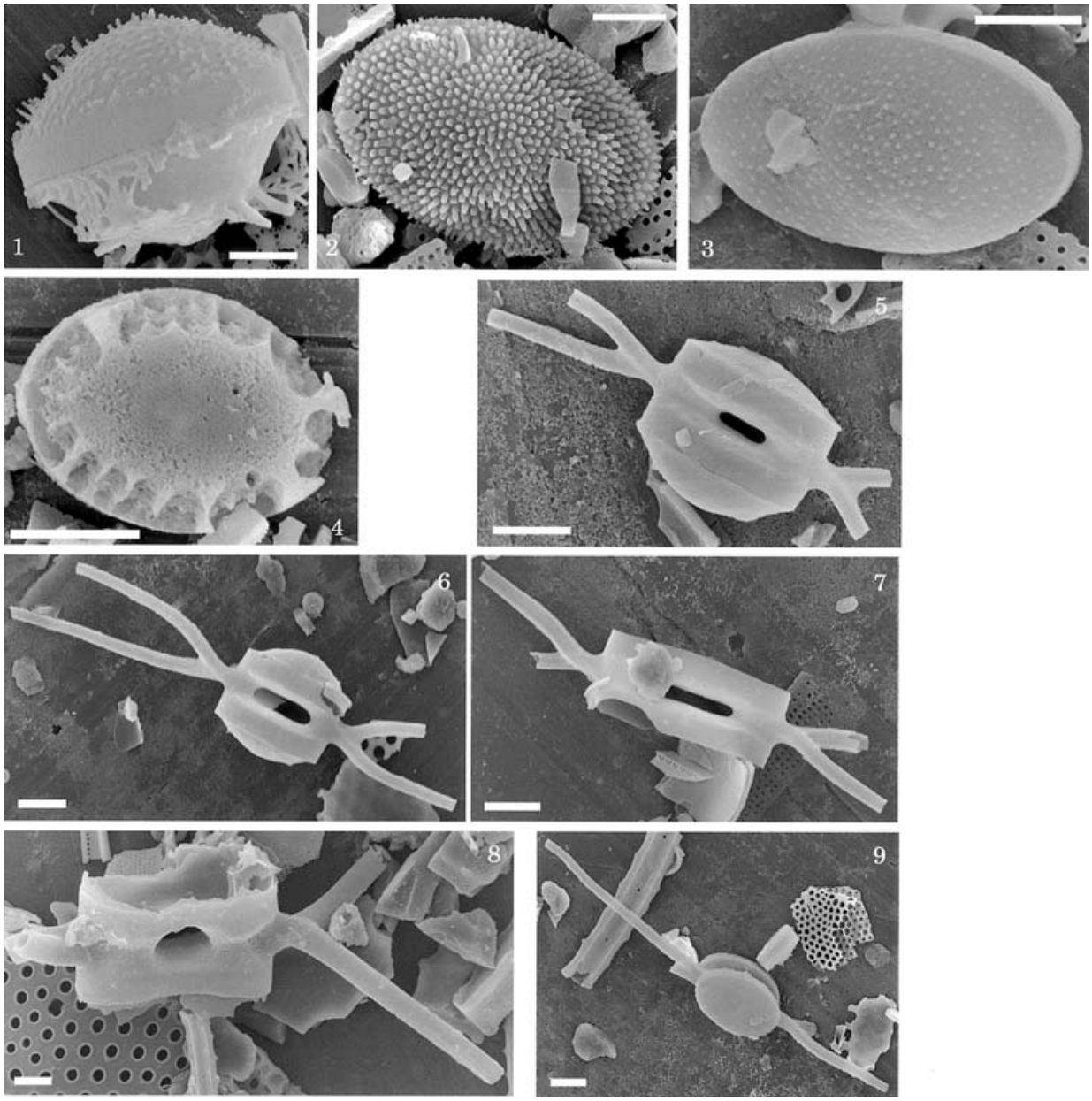


Figure 14. **1.** *Gemellodiscus micronodosus* Suto sp. nov., SEM. Scale bar = 5 μm. **1.** Girdle view of frustule, DSDP Site 338-18-1, 148–149 cm.

2–3. Valve of *Xanthiopyxis hirsuta* and epivalve of *G. micronodosus*, SEM. Scale bar = 5 μm 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. *Gemellodiscus geminus* Suto sp. nov., SEM. Scale bar = 5 μm 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 *Gemellodiscus caveatus* and *G. micronodosus*, LM. Scale bar = 10 μm 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.

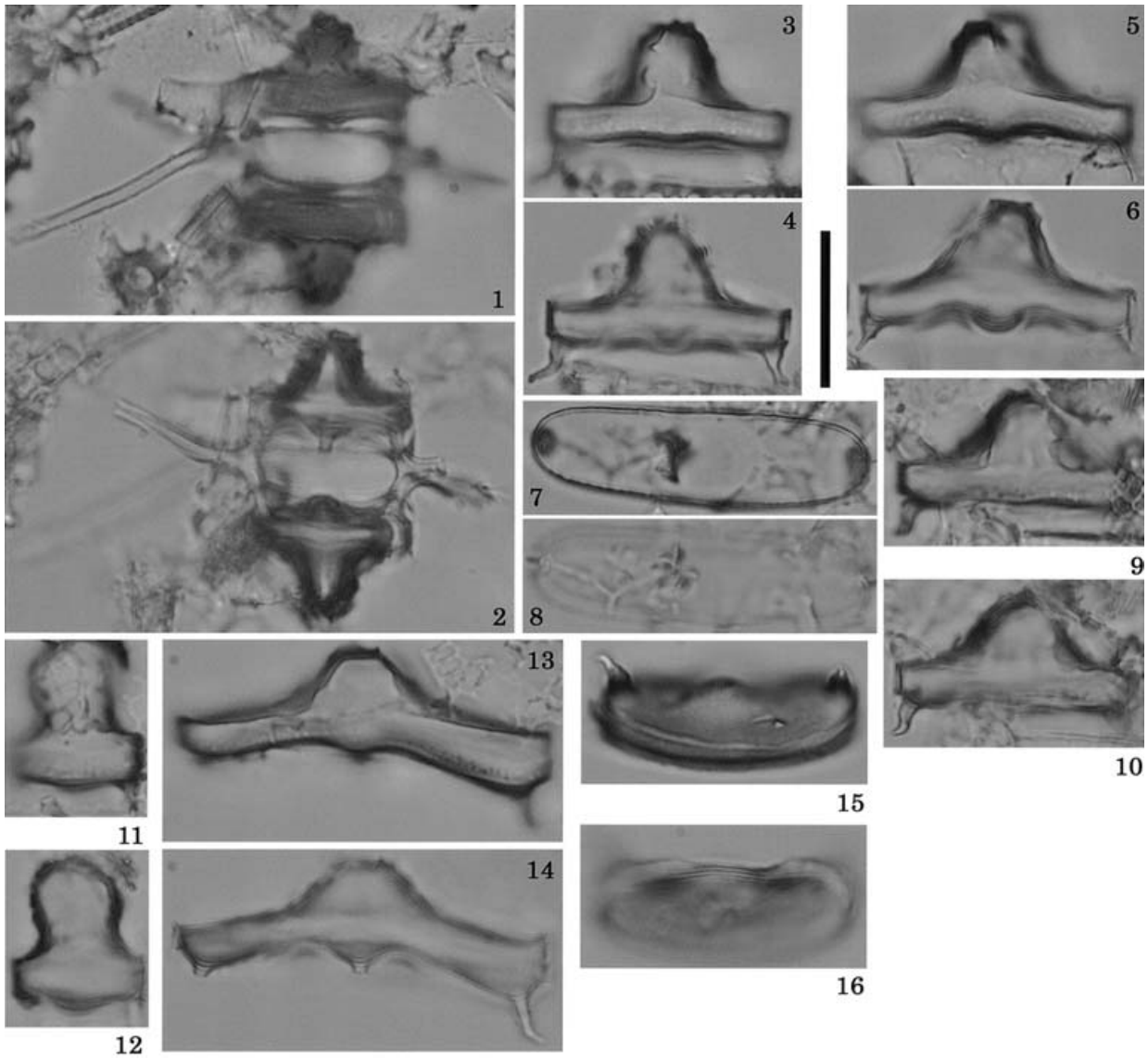
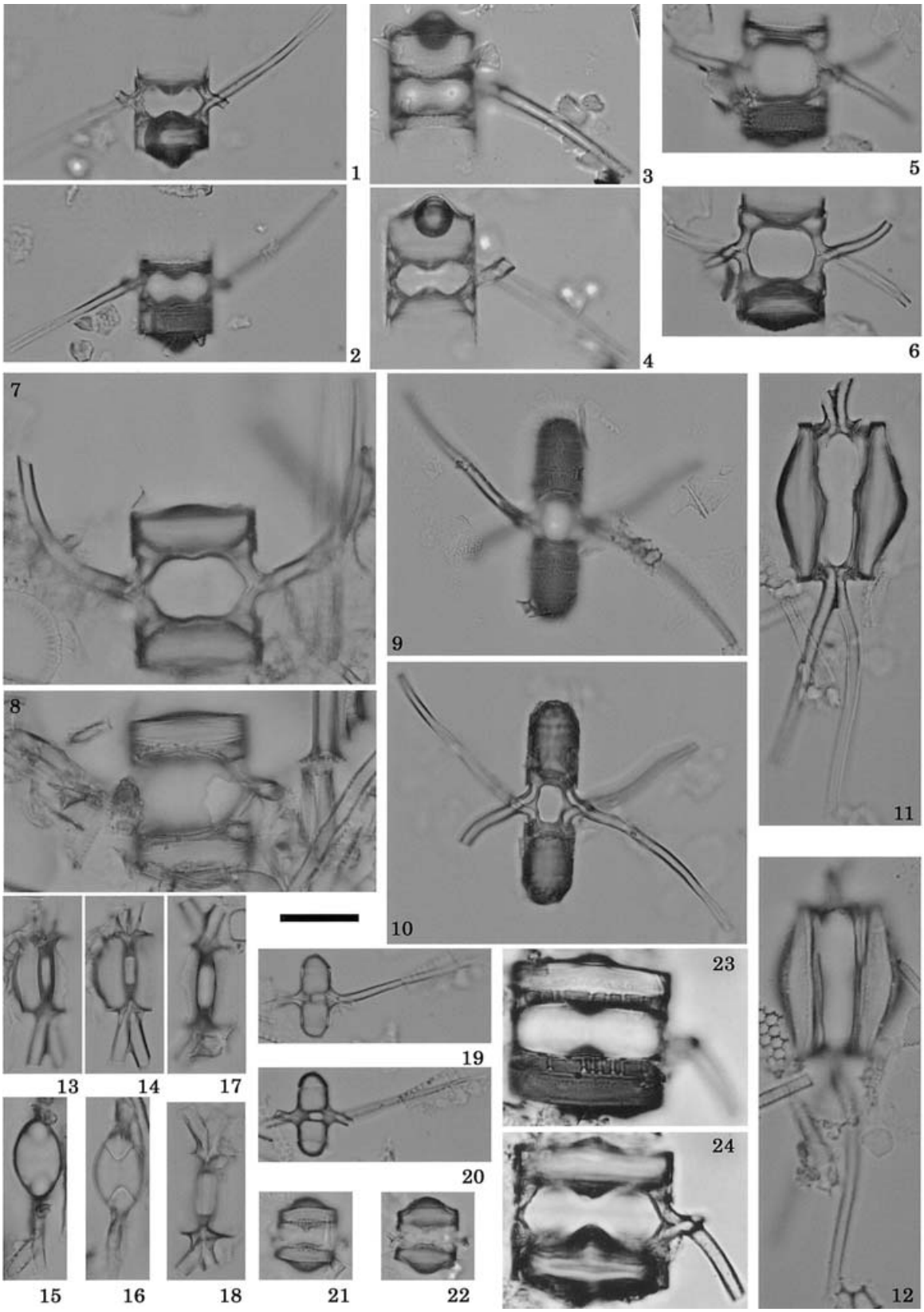


Figure 15. **1–24.** *Gemellodiscus dicollinus* Suto sp. nov., LM. Scale bar = 10 μm for each figure. **1, 2.** Holotype. Girdle view of paired frustule, DSDP Site 338-26-4, 80–81 cm. **3, 4.** Girdle view of frustule, DSDP Site 338-26-4, 80–81 cm. **5, 6.** Girdle view of frustule, DSDP Site 338-26-4, 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 μm 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 inflated 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.

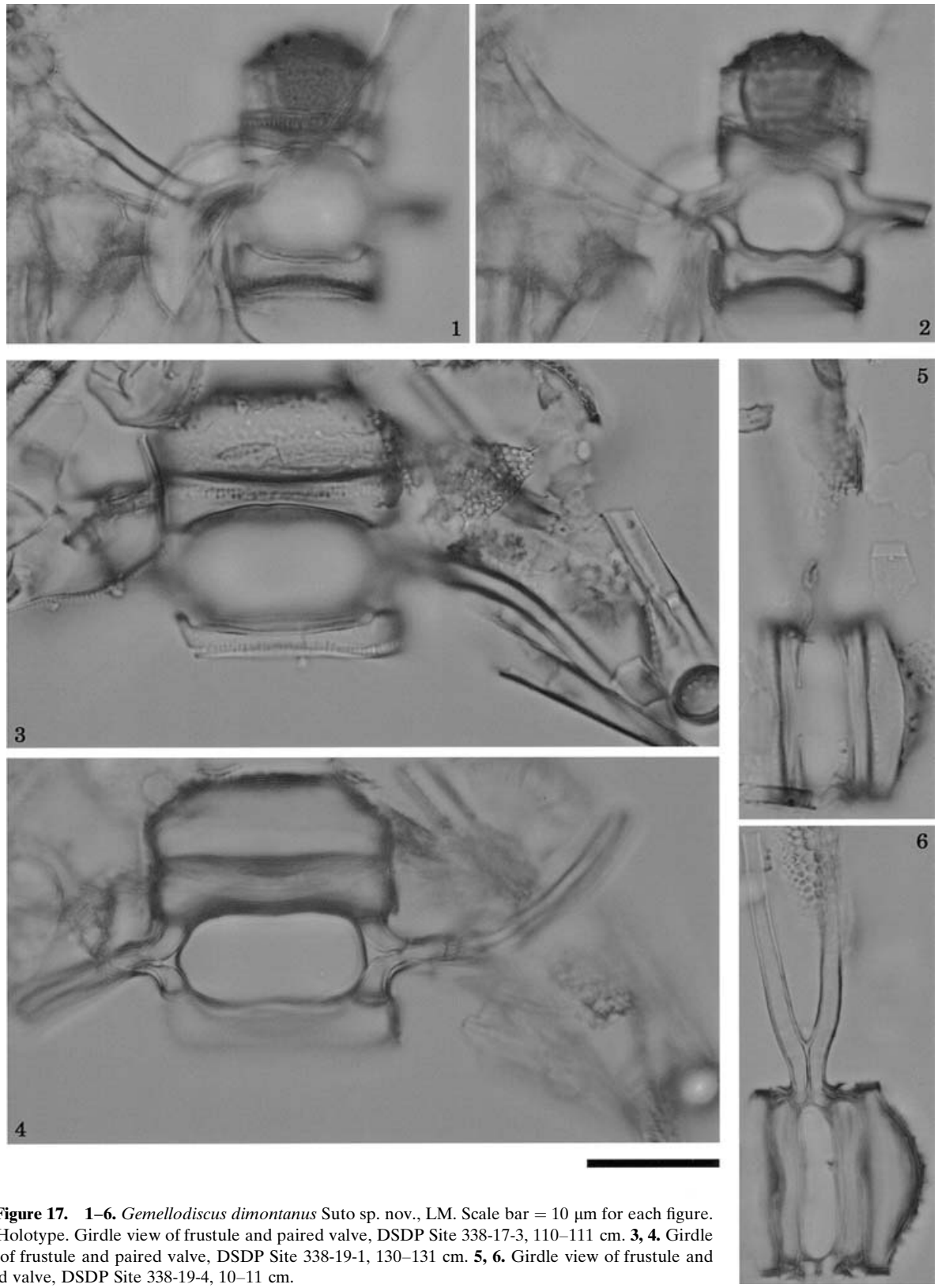


Figure 17. **1–6.** *Gemellodiscus dimontanus* Suto sp. nov., LM. Scale bar = 10 μm for each figure. **1, 2.** Holotype. Girdle view of frustule and paired valve, DSDP Site 338-17-3, 110–111 cm. **3, 4.** Girdle view of frustule and paired valve, DSDP Site 338-19-1, 130–131 cm. **5, 6.** Girdle view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

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References

Akiba, F., 1986: Middle Miocene to Quaternary diatom biostratigraphy in the Nankai Trough and Japan Trench, and modified Lower Miocene through Quaternary diatom zones for middle-to-high latitudes of the North Pacific. *In*, Kagami, H. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 87, p. 393–481. U. S. Govt. Printing Office, Washington, D.C.

Anonymous, 1975: Proposals for a standardization of diatom terminology and diagnoses. *Nova Hedwigia, Beiheft*, vol. 53, p. 323–354.

Bailey, J. W., 1854: Notes on new species and localities of microscopical organisms, article 3. *Smithsonian Contributions to Knowledge*, vol. 7, 16p.

Barron, J. A., 1976: Revised Miocene and Pliocene diatom biostratigraphy of upper Newport Bay, Newport Beach, California. *Marine Micropaleontology*, vol. 1, p. 27–63.

Barron, J. A. and Mahood, A. D., 1993: Exceptionally well-preserved early Oligocene diatoms from glacial sediments of Prydz Bay, East Antarctica. *Micropaleontology*, vol. 39, p. 29–45.

Brun, J., 1891: Diatomées Espèces nouvelles marines, fossiles ou pélagiques. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, vol. 31, p. 1–47.

Durbin, E. G., 1978: Aspects of the biology of resting spores of *Thalassiosira nordenskioeldii* and *Detonula confervacea*. *Marine Biology*, vol. 45, p. 31–37.

Dzinoridze, R. N., Jousé, A. P., Koroleva-Golikova, G. S., Kozlova, G. E., Nagaeva, G. S., Petrushevskaya, M. G. and Strelnikova, N. I., 1978: Diatom and radiolarian Cenozoic stratigraphy, Norwegian Basin; DSDP Leg 38. *In*, Supko, P. R. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, supplement to volume 38, p. 289–385. U. S. Govt. Printing Office, Washington, D.C.

Dzinoridze, R. N., Jousé, A. P. and Strelnikova, N. I., 1979: Description of diatoms. *In*, Jousé, A. P. *ed.*, *The History of the Microplankton of the Norwegian Sea (Based on DSDP Material)*, vol. 23, p. 32–70. (*in Russian*)

Edwards, L. E., 1991: Dinoflagellates. *In*, Lipps, J. H. *ed.*, *Fossil Prokaryotes and Protists*, p. 105–130. Blackwell Scientific Publications, Oxford.

Garrison, D. L., 1981: Monterey Bay phytoplankton. II. Resting spore cycles in coastal diatom populations. *Journal of Plankton Research*, vol. 3, p. 137–156.

Gersonde, R., 1980: *Paläoökologische und biostratigraphische Auswertung von Diatomeenassoziationen aus dem Messinium des Caltanissettabeckens (Sizilien) und einiger Vergleichs-profile in SO-Spanien. NW-Algerien und auf Kreta*, 393 p. Christian-Albrechts-Universität, Kiel.

Gleser, S. I., Jousé, A. P., Makarova, I. V., Proschkina-Lavrenko, A. I. and Sheshukova-Poretzkaya, V. S. (eds.), 1974: *The Diatoms of the USSR, Fossil and Recent*, vol. 1, p. 1–400. Nauka, Leningrad. (*in Russian*)

Gombos, A. M. Jr., 1976: Paleogene and Neogene diatoms from the Falkland Plateau and Malvinas Outer Basin: Leg 36, Deep Sea Drilling Project. *In*, Barker, P. F. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 36, p. 575–687. U. S. Govt. Printing Office, Washington, D.C.

Greuter, W., McNeill, J., Barrie, R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J. E., Trehane, P., Turland, N. J. and Hawksworth, D. L.,

2000: *International Code of Botanical Nomenclature (Saint Louis Code) adopted by the Sixteenth International Botanical Congress, St. Louis, Missouri*. *Regnum Vegetabile*, vol. 138, p. 1–474.

Hajós, M., 1968: Die Diatomeen der miozänen Ablagerungen des Matravorlandes. *Geologica Hungarica*, vol. 37, p. 1–401.

Hanna, G. D., 1970: Fossil diatoms from the Pribilof Islands, Bering Sea, Alaska. *Proceedings of the California Academy of Sciences*, vol. 37, p. 167–234.

Hargraves, P. E., 1979: Studies on marine plankton diatoms IV. Morphology of *Chaetoceros* resting spores. *Nova Hedwigia, Beiheft*, vol. 64, p. 99–120.

Hargraves, P. E. and French, F. W., 1983: Diatom resting spores: significance and strategies. *In*, Fryxell, G. A. *ed.*, *Survival Strategies of the Algae*, p. 49–68. Cambridge University Press, New York.

Harwood, D. M. and Bohaty, S. M., 2000: Marine diatom assemblages from Eocene and younger erratics, McMurdo Sound, Antarctica. *In*, Stilwell, J. D. *eds.*, *Paleobiology and Paleoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica*, Antarctic Research Series, vol. 76, p. 73–98.

Harwood, D. M., McMinn, A. and Quilty, P. G., 2000: Diatom biostratigraphy and age of the Pliocene Sørsdal Formation, Vestfold Hills, East Antarctica. *Antarctic Science*, vol. 12, p. 443–462.

Hasegawa, Y., 1977: Late Miocene diatoms from the Nakayama Formation in the Sado Island, Niigata Prefecture, Japan. *Publications from the Sado Museum*, vol. 7, p. 77–101. (*in Japanese*)

Hasle, G. R. and Syvertsen, E. E., 1996: Marine diatoms. *In*, Tomas, C. R., *ed.*, *Identifying Marine Diatoms and Dinoflagellates*, p. 5–385. Academic Press, San Diego.

Iwai, M. and Winter, D., 2002: Data report: Taxonomic notes of Neogene diatoms from the western Antarctic Peninsula: Ocean Drilling Program Leg 178. *In*, Barker, P. F. *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 178, p. 1–57. College Station, TX (Ocean Drilling Program).

Kuwata, A. and Takahashi, M., 1990: Life-form population responses of a marine planktonic diatom, *Chaetoceros pseudocurvisetus*, to oligotrophication in regionally upwelled water. *Marine Biology*, vol. 107, p. 503–512.

Kuwata, A., Hama, T. and Takahashi, M., 1993: Ecophysiological characterization of two life forms, resting spores and resting cells, of a marine planktonic diatom, *Chaetoceros pseudocurvisetus*, formed under nutrient depletion. *Marine Ecology Progress Series*, vol. 102, p. 245–255.

Lee, Y. G., 1993: The marine diatom genus *Chaetoceros* Ehrenberg flora and some resting spores of the Neogene Yeonil Group in the Pohang Basin, Korea. *Journal of the Paleontological Society of Korea*, vol. 9, p. 24–52.

Makarova, I. V., 1962: Ad cognitionem sporarum fossilium specierum generis *Chaetoceros* Ehr. *Notulae Systemticae e Sectione Cryptogamica Instituti Botanici Nomine V. l. Komarovii Academiae Scientiarium USSR*, vol. 15, p. 41–57. (*in Russian*)

McQuoid, M. R. and Hobson, L. A., 1996: Diatom resting stages. *Journal of Phycology*, vol. 32, p. 889–902.

Mereschkowsky, C., 1889: Note on diatoms from Chincha Guano. *Annals and Magazine of Natural History*, vol. 6, p. 481–489.

Oku, O. and Kamatani, A., 1995: Resting spore formation and phosphorus composition of the marine diatom *Chaetoceros pseudocurvisetus* under various nutrient conditions. *Marine Biology*, vol. 123, p. 393–399.

Oku, O. and Kamatani, A., 1997: Resting spore formation of the marine planktonic diatom *Chaetoceros anastomosans* induced by high salinity and nitrogen depletion. *Marine Biology*, vol. 127, p. 515–520.

Oku, O. and Kamatani, A., 1999: Resting spore formation and biochemical composition of the marine planktonic diatom *Chaetoceros pseudocurvisetus* in culture: ecological significance of decreased nucleotide content and activation of the xanthophyll cycle by resting spore formation. *Marine Biology*, vol. 135, p. 425–436.

Rines, J. E. B. and Hargraves, P. E., 1988: The *Chaetoceros* Ehrenberg (Bacillariophyceae) flora of Narragansett Bay, Rhode Island, U.S.A. *Bibliotheca Phycologica*, vol. 79, p. 1–196.

Ross, R., Cox, E. J., Karayeva, N. I., Mann, D. G., Paddock, T. B. B., Simonsen, R. and Sims, P. A., 1979: An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia, Beiheft*, vol. 64, p. 513–533.

Sancetta, C., 1982: Distribution of diatom species in surface sediments of the Bering and Okhotsk Seas. *Micropaleontology*, vol. 28, p. 221–257.

Schrader, H. J., 1973: Cenozoic diatoms from the Northeast Pacific, Leg 18. *In*, Kulm, L. P. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 18, p. 673–797. U. S. Govt. Printing Office, Washington, D.C.

Schrader, H. J. and Fenner, J., 1976: Norwegian Sea Cenozoic diatom biostratigraphy and taxonomy. *In*, Talwani, M. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 38, p. 921–1099. U. S. Govt. Printing Office, Washington, D.C.

Sheshukova-Poretzkaya, V. S., 1967: *Neogene Marine Diatoms of Sakhalin and Kamtschatka*. 482 p. Nauka, Leningrad. (*in Russian*)

Shirshov, P. P., 1977: *Atlas of Microorganisms in Bottom Sediments of the Oceans.* 32 p. Nauka, Moscow. (*in Russian*)

Stockwell, D. A. and Hargraves, P. E., 1984: Morphological variability within resting spores of the marine diatom genus *Chaetoceros* Ehrenberg. *In*, Ricard, M. *ed.*, *Proceedings of 8th Diatom Symposium*, p. 81–95. Koenigstein, Koeltz.

Suto, I., 2003a: Taxonomy of the marine diatom resting spore genera *Dicladia* Ehrenberg, *Monocladia* gen. nov. and *Syndendrium* Ehrenberg and their stratigraphic significance in Miocene strata. *Diatom Research*, vol. 18, p. 331–356.

Suto, I., 2003b: *Periptera tetracornusa* sp. nov., a new middle Miocene diatom resting spore species from the North Pacific. *Diatom*, vol. 19, p. 1–7.

Suto, I., 2004a: Taxonomy of the diatom resting spore form genus *Liradiscis* Greville and its stratigraphic significance. *Micropaleontology*, vol. 50, p. 59–79.

Suto, I., 2004b: Fossil marine diatom resting spore morphogenus *Xanthiopyxis* Ehrenberg in the North Pacific and Norwegian Sea. *Paleontological Research*, vol. 8, p. 283–310.

VanLandingham, S. M., 1968: *Catalogue of the Fossil and Recent Genera and Species of Diatoms and their Synonyms. Part II. Bacteriastrum* through *Coscinodiscus*, p. 494–1086. Verlag von J. Cramer, Lehre.

Whiting, M. C. and Schrader, H., 1985: Late Miocene to early Pliocene marine diatom and silicoflagellate floras from the

Oregon coast and continental shelf. *Micropaleontology*, vol. 31, p. 249–270.

Yanagisawa, Y. and Akiba, F., 1998: Refined Neogene diatom biostratigraphy for the northwest Pacific around Japan, with an introduction of code numbers for selected diatom biohorizons. *Journal of the Geological Society of Japan*, vol. 104, p. 395–414.