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Taxonomy of the fossil marine diatom resting spore morpho-genera *Xanthioisthmus* Suto gen. nov. and *Quadrocistella* Suto gen. nov. in the North Pacific and Norwegian Sea

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ABSTRACT – The morphology and taxonomy of the fossil diatom resting spore morpho-genera *Xanthioisthmus* Suto gen. nov. and *Quadrocistella* Suto gen. nov. are described. The two new genera are probably fossil resting spores of the marine diatom genus *Chaetoceros*. They were studied by examining samples from DSDP Sites 436, 438 (northwest Pacific) and 338 (Norwegian Sea), and the Newport Beach Section (California). The genus *Xanthioisthmus* is characterized by an elongate valve composed of two flat circles joined together by a hyaline broad isthmus and includes five species: *X. biscoctiformis* (Forti) Suto comb. nov., *X. specticularis* (Hanna) Suto comb. nov., *X. panduraeformis* (Pantocsek) Suto comb. nov., *X. praemaculata* sp. nov. and *X. maculata* (Hanna) Suto comb. nov. The genus *Quadrocistella* differs from *Xanthioisthmus* by its elongate and rectangular valve and bears five new species: *Q. rectagonuma* sp. nov., *Q. tubera* sp. nov., *Q. paliesa* sp. nov., *Q. montana* sp. nov. and *Q. palmesa* sp. nov. *J. Micropalaeontol.* **25**(1): 3–22, April 2006.

KEYWORDS: *Xanthioisthmus, Quadrocistella, fossil diatom resting spore, ODP, taxonomy*

INTRODUCTION

The genus *Chaetoceros* Ehrenberg is one of the largest marine planktonic diatom genera (Van Landingham, 1968; Hasle & Syvertsen, 1996) and the most important marine planktonic diatoms, contributing 20–25% of the total marine primary production (Werner, 1977) in nearshore upwelling regions and other coastal areas. Most *Chaetoceros* species in the coastal area are known to form thick-walled resting spores when faced with nutrient depletion (e.g. Garrison, 1981; Hargraves & French, 1983; Stockwell & Hargraves, 1984; Kuwata & Takahashi, 1990; Kuwata *et al*., 1993) which are morphologically distinct from vegetative cells (Garrison, 1984). Because of their thick silicification, spores are preserved as fossils in sediments and a number of morpho-genera have been proposed for fossil resting spores such as *Dicladia*, *Syndendrium*, *Xanthiopyxis*, *Liradiscus*, *Monocladia* etc. (e.g. Ehrenberg, 1844, 1854; Greville, 1865; Suto, 2003a, b, 2004a–e, 2005). However, diatomists have realized that fossil resting spores are often difficult or impossible to classify correctly because their respective vegetative frustules are not preserved with the resting spores in general. Therefore, systematic and stratigraphic studies on fossil *Chaetoceros* resting spores have been rather limited (e.g. Gersonde, 1980; Lee, 1993) and the taxonomy of *Chaetoceros* resting spores has been poorly understood. Resting spores have been neglected and not included in previous biostratigraphic and palaeoenvironmental analyses of diatoms, with the exception of Akiba (1986) and Stockwell (1991). Due to the importance of *Chaetoceros* in marine primary production, however, it is crucial to include fossil resting spores in future studies for a better understanding of past productivity and palaeoenvironmental change in upwelling regions.

This study was prompted by the need to build a firmer taxonomic basis for fossil *Chaetoceros* resting spores for both biostratigraphic and palaeoceanographic research. For this purpose, resting spores were examined from Middle Eocene to Recent samples of the Deep Sea Drilling Project (DSDP) and from an onland section using LM and SEM observations. As a result, a number of resting spore species were recognized (Suto 2003a, b, 2004a–e, 2005). This paper describes the morphology and stratigraphic range of the new morpho-genera, *Xanthioisthmus* and *Quadrocistella*.

SAMPLES, METHODS AND TERMINOLOGY

In this study, samples from DSDP Sites 338 (67° 47.11′ N, 05° 23.26′ E; water depth 400.8 m; Cores 8–29), 436 (39° 55.96′ N, 145° 33.47′ E; water depth 5240 m; Cores 1–29), 438A and 438B (40° 37.79′ N, 143° 14.15′ E; water depth 1558 m; Site 438A, Cores 1–85; Site 438B, Cores 6–16) and from the Capistrand and Monterey Formations in Newport Beach, California were examined (Fig. 1).

Strewn slides preparation, counting and identification methods follow the procedures of Akiba (1986) and Suto (2003a).

The various forms of the genera *Xanthioisthmus* and *Quadrocistella* may be resting spores of *Chaetoceros*, but the

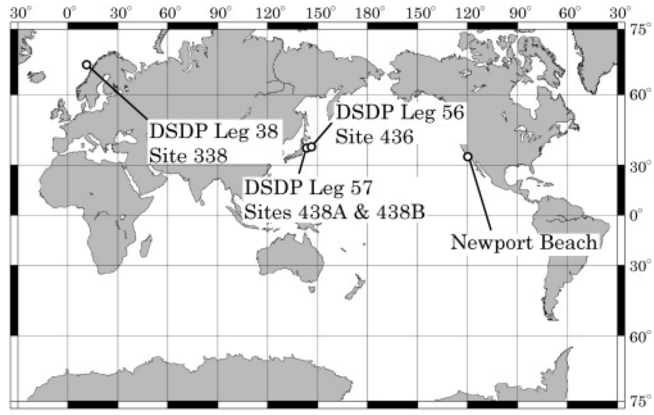


Fig. 1. Location of DSDP Sites 338, 436 and 438 and the Newport Beach Section.

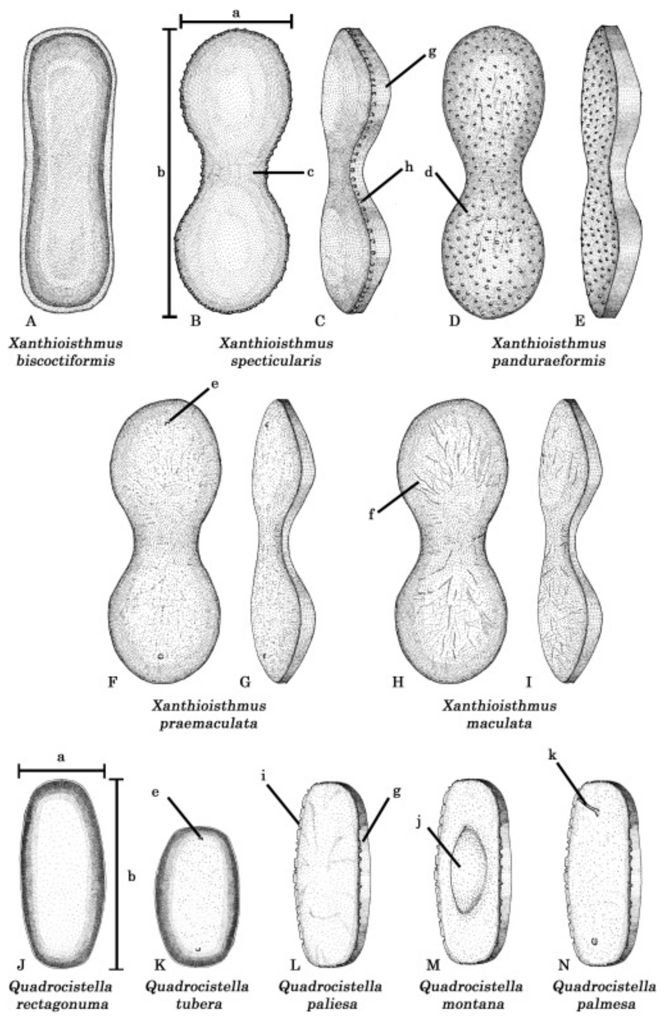


Fig. 2. Sketches of valve and oblique girdle view of species of *Xanthioisthmus* and *Quadrocistella*: (**A**) *Xanthioisthmus biscoctiformis*; (**B**–**C**) *X. specticularis*; (**D**–**E**) *X. panduraeformis*; (**F**–**G**) *X. praemaculata*; (**H**–**I**) *X. maculata*; (**J**) *Quadrocistella rectagonuma*; (**K**) *Q. tubera*; (**L**) *Q. paliesa*; (**M**) *Q. montana*; (**N**) *Q. palmesa*. A, B, D, F, H, J, K: valve view; C, E, G, I, L, M, N: oblique girdle view. Key to structures: a, apical axis; b, transapical axis; c, isthmus; d, puncta; e, puncta near apex; f, wrinkles; g, mantle; h, a single ring of puncta; i, a single ring of palisade ridges; j, central vaulted area; k, spine. All sketches were made using LM.

correspondence between vegetative cells and resting spores can never be determined in fossil material because vegetative cells are usually dissolved. Resting spores are the only remains typically preserved in sediments (Suto, 2003a). Therefore, it is best to use morpho-genera or morpho-species for fossil resting spores according to Articles 3.3 and 3.4 of the *International Code of Botanical Nomenclature* (Greuter *et al*., 2000), as in the case of fossil cysts of dinoflagellates (Edwards, 1991).

Some of the characteristic structures common to *Xanthioisthmus* and *Quadrocistella* are shown in Figure 2 and defined below. General morphological terms follow Anonymous (1975) and Ross *et al*. (1979).

- Epivalve: the first-formed valve of a resting spore. It differs morphologically from the hypovalve as the frustule is heterovalvate.
- Hypovalve: the second-formed valve of a resting spore. In *Chaetoceros* spores observed by Hargraves (1979), hypovalves possess a sub-marginal flange, which fits into the epivalve. The hypovalve possesses a single ring of puncta at the base of mantle. This single row of puncta is a characteristic feature that distinguishes the hypovalve from the epivalve which lacks such a ring (Suto, 2003a).
- Mantle: the marginal part of the valve differentiated by slope, and sometimes also with such structures as spines, perpendicular to the valve face (Fig. 2g).
- Ring of puncta: row of perforations at the base of the hypovalve mantle (Fig. 2h).
- Isthmus: a narrow strip of valve centre connecting two larger valve areas (Fig. 2c).
- Palisade ridges: a row of low walls along the valve margin (Fig. 2i).

RESULTS

Tables 1–4 show the numbers of *Xanthioisthmus* and *Quadrocistella* species encountered during counting 100 resting spore valves in LM, while Figures 3–6 show their stratigraphical distributions. This study follows the diatom zonation of Akiba (1986) and Yanagisawa & Akiba (1998) for the Miocene, Pliocene and Pleistocene, and the diatom zonation of Schrader & Fenner (1976) for the Eocene and Oligocene.

SYSTEMATIC PALAEONTOLOGY

Class **Bacillariophyceae** Schütt, 1896
Order **Centrales** Schütt, 1896
Suborder **Biddulphineae** Schütt, 1896
Family **Chaetoceraceae** Schütt, 1896
Genus *Xanthioisthmus* Suto gen. nov.

Type species. *Xanthioisthmus panduraeformis* (Pantocsek) Suto comb. nov.

Derivation of name. The Latin *Xanthioisthmus* means ‘cocklebur with strait’.

Description. In valve view, valve constricted and composed of two flat circles joined together by a hyaline broad isthmus, with distinct mantle. Surface of circles marked with numerous wrinkles or puncta. Mantle of valve hyaline.

Stratigraphic occurrence. This genus may appear before the Middle Eocene as the core examined in this study did not penetrate older sediments, and becomes extinct in the late Middle Miocene (Fig. 3).

Remarks. This genus has been identified as the fossil *Chaetoceros* resting spore morpho-genus *Xanthiopyxis* (e.g. Forti, 1913; Hanna, 1927; Proschkina-Lavrenko & Sheshukova-Poretzkaya, 1949; Harwood & Bohaty, 2000; Suto, 2004e), but *Xanthioisthmus* differs from *Xanthiopyxis* by its constricted valve. This genus is characterized by an elongate valve composed of two flat circles joined together by a hyaline broad isthmus and bears five extinct species: *X. biscoctiformis*, *X. specticularis*, *X. maculata*, *X. praemaculata* and *X. panduraeformis* (Fig. 2).

	Diatom zones	NPD	Core-Section, Interval (cm) Leg 38 Site 338	Depth (m)	Preservation	Abundance	*Xanthioisthmus biscoctiformis*	*X. specticularis*	*X. panduraeformis*	*X. praemaculata*	*X. maculata*	*Quadrocistella rectagonuma*	*Q. tubera*	*Q. paliesa*	*Q. montana*	*Q. palmesa*	Total number of resting spore valves counted
middle Miocene	*Denticulopsis praedimorpha*	5B	8-1, 140-141	77.40	G	A						4		6	2		100
			8-2, 48-49	77.98	G	A						1		12	1		100
			8-2, 99-100	78.49	G	A						5	+	12			100
	C. nicobarica	5A	8-3, 10-11	79.10	G	A						1		6	1		100
	Denticulopsis hyalina	4B	8-3, 80-81	79.80	G	A						6		7	+		100
			8-4, 10-11	80.60	G	A						9		7	1		100
			8-4, 80-81	81.30	G	A						2	+	7	+		100
			9-1, 50-51	86.00	G	A						+		3	+		100
			9-1, 148-149	86.98	G	A						2	+	2	+		100
			10-1, 106-107	96.06	G	A						1	1	6			100
	Denticulopsis lauta	4A	10-2, 80-81	97.30	G	A					+	1		3	1		100
			11-1, 50-51	105.00	G	A					+	+	1	1	1		100
			11-2, 50-51	106.50	G	C					+		1	9	+		100
			11-3, 98-99	108.48	G	A		+	+		+	+	1	2	+		100
			11-4, 70-71	109.70	G	A					+	2	+	3	+		100
			11-4, 148-149	110.48	G	A					+	1		1	1		100
			12-2, 40-41	115.90	G	A					+	3		1	1		100
			12-3, 38-39	117.38	G	A					+	1		4	1		100
early Miocene	*Thalassiosira fraga*	2A	13-1, 148-149	124.98	G	A		1	+		1	3	+	3	1		100
			13-2, 148-149	126.48	G	A	2	+			+	2		1	+		100
			13-3, 148-149	127.98	G	A	+		1		1	3		2	+		100
			13-5, 70-71	130.20	G	A	+		+		+	2		+			100
			13-6, 10-11	131.10	G	A			+		+	1		1	+		100
			13-6, 70-71	131.70	G	A			+		+	5		4	+		100
			14-1, 20-21	133.20	G	A			+		+	3		4			100
			14-2, 20-21	134.70	G	A					+		+	4			100
			14-3, 20-21	136.20	G	A	+	+	+		+	1		4	+		100
			15-1, 30-31	142.80	G	A		1	+			+	+	3	+		100
			15-2, 100-101	145.00	G	A	+		+			1		+	+		100
			15-3, 100-101	146.50	G	A			+		+	2		2	+		100
			15-4, 100-101	148.00	G	A					1	+	+	1			100
			15-5, 138-139	149.88	G	A			+			+		+	+		100
			16-1, 10-11	152.55	G	A			1		+	+		+			100
			16-2, 10-11	154.05	G	A					+	1		2			100
			16-3, 10-11	155.55	G	A			1		+	+		+	+		100
			16-5, 10-11	158.55	G	A			+			1		2	+		100
			16-6, 50-51	160.45	G	A			1		+	1		+	1		100
			17-1, 100-101	162.50	G	A								1			100
			17-2, 119-120	164.19	G	A		+	+		+	+	+	2	+		100
	Thalassiosira praefraga	1	17-3, 110-111	165.60	G	A		+			+	1		+	1		100
			17-4, 79-80	166.79	G	A					+	1		2			100
			18-1, 148-149	172.48	G	A	+	+			+	+		2	2		100
			19-1, 130-131	181.80	G	A					+		+	+			100
			19-3, 20-21	183.70	G	A		+			+	2		3	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				+	1			+			100
			20-3, 90-91	193.90	G	C				+	+			1			100
			20-4, 148-149	195.98	G	A				+				1		+	100
	Pseudo-dimerogramma filiformis		21-1, 32-33	199.82	G	A								+		+	100
			21-2, 148-149	202.48	G	A				+	+			2		+	100
			22-2, 10-11	211.00	G	R								1		+	100
			22-3, 80-81	213.20	G	C										2	100
early Oligocene			22-4, 79-80	214.69	G	R				+				+		1	100
			22-5, 10-11	215.50	G	C								1		1	100
			22-6, 148-149	218.38	G	C										2	100
			23-1, 80-81	219.60	G	C										1	100
			23-2, 80-81	221.10	G	A										+	100
	Sceptroneis pupa		23-3, 10-11	221.90	G	C								+		+	100
			23-4, 80-81	224.10	G	C										1	100
			23-5, 10-11	224.90	G	C								1		1	100
			23-6, 10-11	226.40	G	A								+		+	100
			24-1, 100-101	229.00	G	R											100
	interval		24-2, 100-101	230.50	G	C										1	100
			24-3, 100-101	232.00	G	R								1		1	100
			barren until:														
middle Eocene			26-2, 110-111	249.60	G	R											30
	Craspedodiscus oblongus		26-3, 80-81	250.80	G	R											30
			26-4, 80-81	252.30	G	R											100
			26-5, 80-81	253.80	G	R											30
			27-1, 58-59	257.08	G	R											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												
			28-1, 120-121	267.20	G	R											30
	Triceratium inconspicuum var. *trilobata*		28-2, 148-149	268.98	G	R	1										30
			29-1, 130-131	276.80	G	R	2										30
			29-2, 120-121	278.20	G	R	2										30
			29-3, 148-149	279.98	G	R											10

Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa; G indicates good preservation; A denotes abundant, C denotes common and R, rare. Diatom zones and NPD codes in the Miocene are after Yanagisawa & Akiba (1998) and diatom zones in the Oligocene and Eocene after Schrader & Fenner (1976).

Table 1. Occurrences of *Xanthioisthmus* and *Quadrocistella* species at DSDP Site 338.

Site	Diatom Zones (NPD)	Core-Section, Interval (cm) Site 438A	Depth (m)	Preservation	Abundance	*Xanthioisthmus maculata*	*Quadrocistella rectagonuma*	*Q. tubera*	*Q. paliesa*	*Q. montana*	Total number of resting spore valves counted
DSDP438A	*N. seminae* (NPD12)	1-2, 80-82	2.31	G	A						100
	Proboscia curvirostris (NPD 11)	2-1, 10-14	23.12	G	A						100
		2-1, 96-98	23.97	G	A						100
		2-5, 5-9	29.07	G	A						100
	Actinocyclus oculatus (NPD 10)	3-1, 31-33	32.82	G	A						100
		3-3, 140-142	32.91	G	A		1				100
		3-4, 10-14	37.12	G	A						100
		3cc	41.65	G	A						100
	Neodenticula koizumii (NPD 9)	4-1, 40-74	42.72	G	A						100
		4-4, 8-12	46.6	G	A		1		1		100
		5-2, 96-100	53.98	G	A						100
		5cc	58.5	G	A						100
	Neodenticula kamtschatica (NPD 7B-8)	6-1, 18-22	106.7	G	A		4		1		100
		7-1, 19-22	116.21	G	A		1		3		100
		8-3, 30-34	128.82	G	A		1		4	1	100
		10-2, 15-18	146.17	G	A		1	1	1		100
		11-6, 20-24	161.72	G	A		2	1	4	1	100
		12-1, 138-140	164.89	G	A		1				100
		13-3, 19-23	176.21	G	A		2	1	1	1	100
		16-3, 36-39	204.88	G	A		1	1			100
		18-3, 10-14	223.62	G	A		2	1	+	+	100
		19-3, 10-14	233.12	G	A		3		3		100
		20-3, 26-30	242.78	G	A		4	1	3	1	100
		21-3, 20-24	252.22	G	A			+	2		100
		22-3, 20-24	261.72	G	A		1	1	1	1	100
		23-1, 10-14	268.12	G	A		+	+	+		100
		24-3, 10-12	280.61	G	A		2		1	1	100
		25-1, 35-39	287.37	G	A		4		1	1	100
		25-5, 16-20	293.18	G	A		2	+	2	2	100
		26-2, 29-33	298.31	G	A		7	1	2		100
		26-4, 10-14	301.12	G	A		3		1	1	100
		26-6, 15-19	304.17	G	A		4		1		100
		27-2, 20-24	307.72	G	A		1		1		100
		27-4, 20-24	310.72	G	A			1	7	3	200
		28-2, 20-24	317.72	G	A			1	2	2	200
		29-2, 20-24	326.72	G	A				2	2	200
		30-2, 20-24	336.22	G	A		2	1	6	2	200
		31-1, 20-24	344.22	G	A		2		3	3	200
		32-1, 24-28	353.76	G	A		1		5	4	200
		33-1, 120-124	364.22	G	A		2		4	2	200
		34-1, 22-24	372.73	G	A			1	2		200
		35-1, 24-28	382.26	G	A		3		11		200
		35-3, 24-28	385.86	G	A				4	3	200
		35-6, 24-28	389.76	G	A		2	2	3		200
		36-1, 32-36	391.84	G	A		3	1			200
		36-3, 32-36	394.84	G	A		2	2	2		200
		37-3, 10-14	404.12	G	A		2	1	3		200
		38-1, 11-15	410.63	G	A		1	1			200
		39-2, 11-15	421.63	G	A		4			1	200
		40-2, 20-24	431.22	G	A		2		1		200
		40-6, 10-14	437.12	G	A			1			200
		41-1, 45-49	439.47	G	A			1	2	1	200
		41-3, 30-34	442.32	G	A		1		1		200
		41-6, 10-14	446.62	G	A		1		2	1	200
		41cc	447.13	G	A				4	1	200
	Rouxia californica (NPD 7A)	42-1, 14-18	448.66	G	A		5		7		200
		42-1, 90-91	449.41	G	A		3	1	1	1	200
		42-2, 95-96	450.96	G	A		5		7	1	200
		42-3, 15-16	451.66	G	A		8		4		200
		42-4, 50-54	453.52	G	A		1		5	2	200
		42-4, 73-74	453.74	G	A		2		4	1	200
		42-5, 100-101	455.51	G	A		8	1	4		200
		42-6, 16-20	456.18	G	A		1	1	2	1	200
		43-1, 59-63	458.61	G	A				7	3	200
		43-3, 30-34	461.32	G	A		1		14	1	200
	Thalassionema schraderi (NPD 6B)	43-6, 82-86	466.34	G	A		3	1	13	1	200
		44-1, 60-64	470.12	G	A		1		5		200
		44-3, 10-14	472.62	G	A				2	1	200
		45-1, 54-58	479.56	G	A		2		7		200
		45-6, 30-34	486.82	G	A		1	1	2		200
		46-1, 18-20	488.7	G	A				1		200
		46-3, 18-22	491.7	G	A				5	1	200
		47-1, 10-14	498.12	G	A		2		8	1	200
		47-4, 110-114	503.62	G	A		1	1	10	3	200
		48-1, 14-18	507.66	G	A		4		16		200
		48-3, 46-50	510.98	G	A		3		5		200
		48-6, 26-30	515.28	G	A		9		10	2	200
		48-7, 30-31	516.81	G	A		3		6	1	200
		49-3, 10-14	520.12	G	A		2		5		200
		49-6, 10-14	524.62	G	A		6		8	2	200
		49-7, 10-11	526.11	G	A		4		3	4	200
		50-1, 20-24	526.72	G	A		2	3	10		200
		50-3, 20-24	529.72	G	A		9	1	12		200
		50-6, 20-24	534.22	G	A		7		8	1	200
		50-7, 10-11	535.61	G	A		3		22	6	200
		51-1, 16-20	536.18	G	A		4		27	1	200
	Denticulopsis katayamae (NPD 6A)	51-4, 16-20	540.68	G	A				14	4	200
		51-6, 16-20	543.68	G	A		3		16	6	200
		52-1, 36-38	545.87	G	A		4		14	4	200
		52-3, 36-38	548.87	G	A		3	1	18	6	200
		52-4, 36-38	550.37	G	A		4		16	2	200
		53-1, 77-81	555.79	G	A		3		12	5	200
		54-1, 110-114	565.62	G	A		2	3	16	2	200
		54-4, 125-127	569.26	G	A		5	1	19	1	200
		55-1, 70-74	574.72	G	A		9		21	2	200
		55-3, 70-74	577.72	G	A		4		24	4	200
		55-6, 76-78	582.27	G	A		2	1	31	2	200
		56-1, 20-24	583.72	G	A		6		26	2	200
	Denticulopsis dimorpha (NPD 5D)	56-3, 20-24	586.72	G	A		11		4	2	100
		56-3, 60-62	587.11	G	A		8		1	1	100
		56-6, 20-24	591.22	G	A		9	2	6	1	100
		56cc	592.63	G	A		12		9		100
		57-1, 115-117	594.16	G	A		3		1		100
		57-2, 31-35	594.83	G	A		4	1	3	+	100
		57-3, 31-35	596.33	G	A		4	1			100
		57-4, 59-61	598.1	G	A		3	1	6	+	100
		58-1, 16-20	602.68	G	A		10	1	7		100
		58-1, 101-103	603.52	G	A		3		1		100
		59-1, 17-21	612.19	G	A		6		4	1	100
		59-3, 135-137	616.36	G	A		4		7	1	100
		59-4, 17-21	616.69	G	A		14		6		100
		59-5, 5-6	618.06	G	A		7		3	1	100
		59-5, 17-21	618.19	G	A		10		7		100
	Thalassiosira yabei (NPD 5C)	60-1, 34-38	621.86	G	A		13	2	3		100
		60-1, 134-136	622.85	G	A		2		+		100
		60-3, 26-27	624.77	G	A		15		2		100
		60-3, 27-29	624.78	G	A		18	2	2		100
		61cc	631.08	G	A		14		2		100
		62-1, 20-24	640.72	G	A		25	4	4	2	100
		62-1, 80-81	641.31	G	A		19		7		100
		62-1, 110-112	641.61	G	A		4		3	2	100
		63-1, 16-20	650.18	G	A		11		6		100
		63-1, 88-89	650.89	G	A		10		4		100
		63-1, 110-112	651.11	G	A		2		1		100
		64-1, 10-14	659.62	G	A		7		8		100
		64-1, 121-128	660.75	G	A		4	1	1		100
	Denticulopsis praedimorpha (NPD 5B)	64-3, 10-14	662.62	G	A		1		2		100
		64-5, 30-32	665.81	G	A	+	7	1	1		100
		65-1, 54-56	669.55	G	A		5		4		100
		65-3, 100-103	673.02	G	A		10	2	1	1	100
		65-5, 18-21	675.2	G	A		9		2		100
		66-1, 118-122	679.7	G	A	1	12		2		100
		66-2, 25-27	680.26	G	A		1		+		100
		66-2, 34-36	680.35	G	A		8				100
	C. nicobarica (5A)	66-2, 82-84	680.83	G	A		9		1		100
	Denticulopsis hyalina (NPD 4B)	67-1, 27-32	688.3	G	A		5	1			100
		67-1, 112-113	689.13	G	A		5				100
		68-1, 30-34	697.82	G	A		10	1	1		100
		68-1, 101-103	698.02	G	A		3		1		100
		68-4, 68-72	702.7	G	A	1	6				100
		68-6, 105-108	705.07	G	A		8	+			100
		68-7, 24-26	706.75	G	A		9	1	1		100
		69cc	707.13	G	A		2				100
		70-1, 16-20	716.68	G	A	1	7		1		100
		70-1, 78-81	717.3	G	A		6		3	1	100
		70-3, 49-53	720.01	G	A		7		2		100
		70-5, 23-27	722.75	G	A		6		1		100
		70-7, 5-7	725.56	G	A		7				100
		71-1, 12-16	726.14	G	A		8		1		100
		71-3, 7-11	729.09	G	A		5	1	1		100
		71-3, 114-116	730.15	G	A		5		2		100
		71-5, 8-12	731.6	G	A		4		+		100
		72-1, 14-18	735.66	G	A		9		3		100
		72-3, 15-17	738.66	G	A	2	8		6	1	100
	Denticulopsis lauta (NPD 4A)	72-5, 11-13	741.62	G	A		8		2		100
		73-1, 27-31	745.29	G	A		5	1	3		100
		73-3, 27-31	748.29	G	A		5		2		100
		73-5, 9-11	751.1	G	A		9		1		100
		73-5, 46-48	751.47	G	A		7	1	2		100
		74-1, 124-126	755.75	G	A		2		1		100
		75-1, 70-71	764.71	G	A		5		2		100
		76-1, 32-34	773.83	G	A		4		2		100
		77-1, 81-83	783.82	G	A	1	9		2		100
		78-1, 54-56	793.05	G	A		10	1	4		100
		78-3, 92-94	796.43	G	A		13		2		100
		79-1, 51-54	802.53	G	A	+	10	1	4		100
		79-3, 55-57	805.56	G	A	1	4		6		100
		80-1, 20-22	811.71	G	A		12		3		100
		82-1, 73-75	831.24	G	A		4		5		100
		82-2, 73-75	832.74	G	A		6		4	1	100
	Denticulopsis praelauta (NPD 3B)	84-3, 63-65	853.14	G	A		4		3	1	100
		85-1, 48-50	859.49	G	A		1				100
		85-4, 25-27	863.76	G	A	3	3				100
DSDP438B		6-1, 16-19	872.28	G	A		+		3		100
		7-1, 128-130	882.79	G	A		3		1		100
		8-1, 90-92	891.81	G	A	2	4		1		100
		9-1, 85-87	901.16	G	A		3		2		100
	Crucidenticula kanayae (NPD 3A)	11-1, 60-62	919.81	G	A		1			1	100
		12-1, 81-82	929.52	G	A		1				100
		14cc	947.6	G	A		4		1		100
		15-2, 61-62	959.02	G	A		2	1			100
		16-1, 82-84	967.13	G	A		2	1	+		100

Values are for counts of 100 or 200 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa; G indicates good preservation; A denotes abundant. Diatom zones and NPD codes are after Yanagisawa & Akiba (1998).

Table 2. Occurrences of *Xanthioisthmus maculata* and *Quadrocistella* species at DSDP Sites 438A and 438B.

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

Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa; G indicates good preservation; A denotes abundant, C denotes common and R, rare. Diatom zones and NPD codes are after Yanagisawa & Akiba (1998).

Table 3. Occurrences of *Xanthioisthmus maculata* and *Quadrocistella* species at DSDP Site 436.

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

Numbers indicate individuals encountered during counts of 100 resting spore valves; + indicates valves encountered after the count; blank indicates absence of any taxa; G indicates good preservation; A denotes abundant, C denotes common and R, rare. Diatom zones and NPD codes are after Yanagisawa & Akiba (1998).

Table 4. Occurrences of *Xanthioisthmus maculata* and *Quadrocistella* species in the Newport Beach Section.

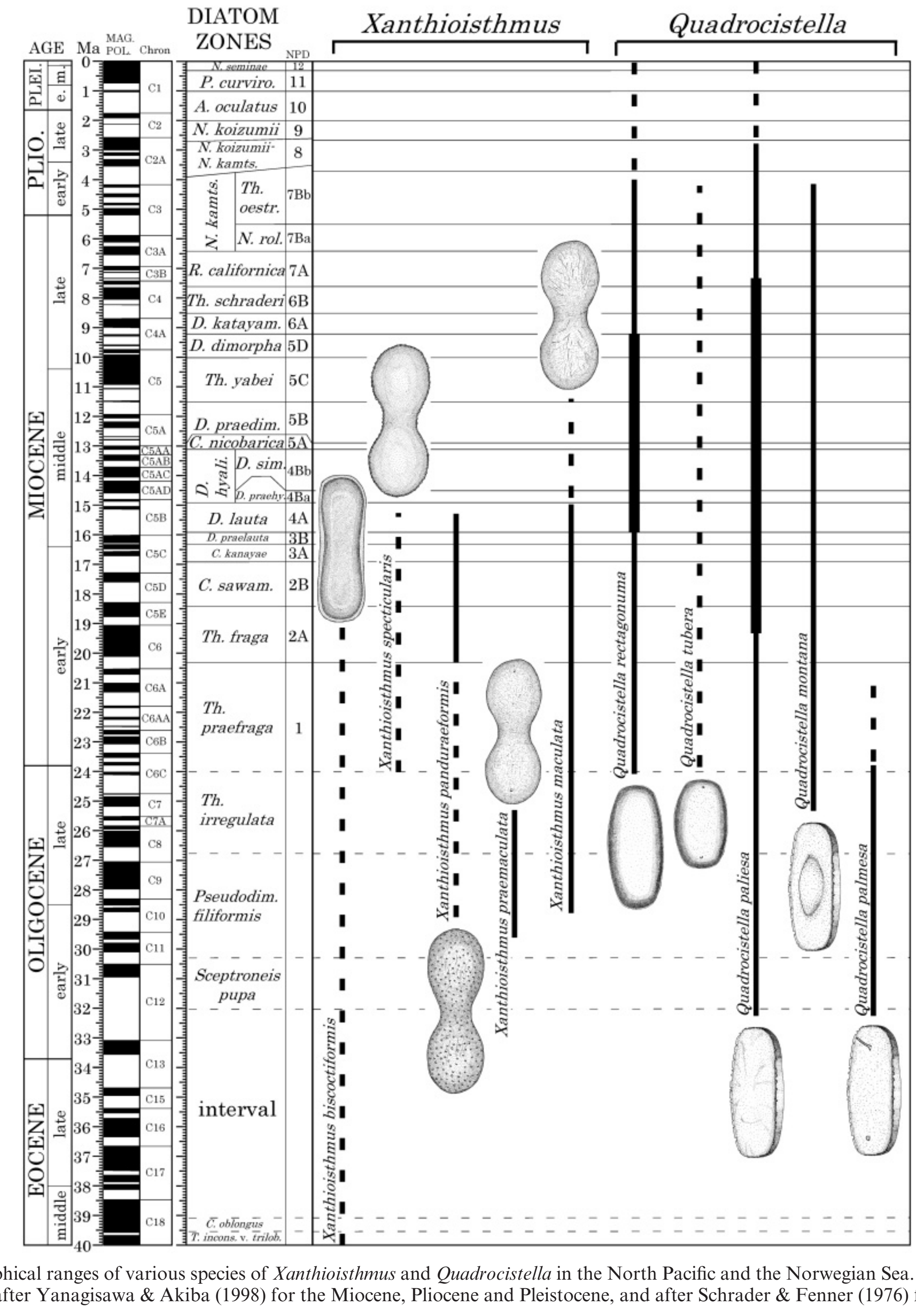


Fig. 3. Stratigraphical ranges of various species of *Xanthioisthmus* and *Quadrocistella* in the North Pacific and the Norwegian Sea. Diatom zones and NPD codes are after Yanagisawa & Akiba (1998) for the Miocene, Pliocene and Pleistocene, and after Schrader & Fenner (1976) for the Eocene and Oligocene.

Key to species

1a Valve slightly concave at isthmus area ....*Xanthioisthmus biscoctiformis*

1b Valve strongly concave at isthmus area 2

2a A single ring of puncta at valve mantle ......*X. specticularis*

2b A single ring of puncta not at valve mantle......................3

3a Valve surface with numerous puncta .....*X. panduraeformis*

3b Valve surface with no or rare puncta................................4

4a Two puncta near each apex of valve.........*X. praemaculata*

4b Valve face only with faint wrinkles..................*X. maculata*

Xanthioisthmus biscoctiformis (Forti) Suto comb. nov.
(Pl. 1, figs 1–8; Fig. 2A)

Basyonym. 1913 *Xanthiopyxis biscoctiformis* Forti: 1553, pl. 2, figs 6, 10, 21.

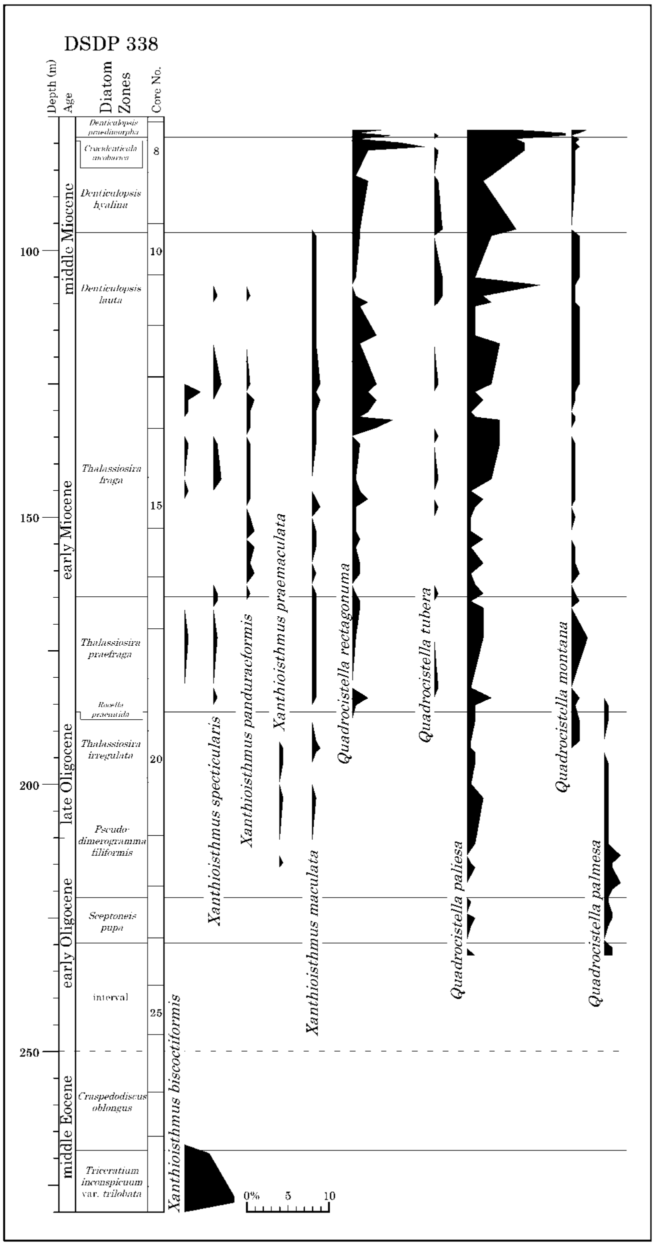


Fig. 4. Stratigraphical occurrences of various species of *Xanthioisthmus* and *Quadrocistella* at DSDP Site 338. Diatom zones are from Yanagisawa & Akiba (1998) for the Miocene and after Schrader & Fenner (1976) for the Eocene and Oligocene.

1949 *Xanthiopyxis biscoctiformis* Forti; Proschkina-Lavrenko & Sheshukova-Poretzkaya: 87, pl. 84, figs 11a–c.

Derivation of name. The Latin *biscoctiformis* means 'two separated shape'.

Type locality. Marmorito, Italy. Miocene deposits.

Description. Epivalve slender in valve view, apical axis 30.5–39.5 μm, transapical axis 9.4–11.7 μm, width of isthmus 8.4–10.0 μm. Valve composed of two flat elliptical circles joined together by a broad hyaline isthmus. Valve slightly constricted at isthmus area on each side, with numerous wrinkles, surrounded with thin and narrow hyaline process on the edge, with distinct mantle. Mantle of epivalve hyaline. Vegetative frustules not observed and hypovalve unknown.

Stratigraphic occurrence. This species occurred rarely and sporadically in the Lower Miocene at DSDP Site 338 (Fig. 4).

Remarks. *Xanthiopyxis biscoctiformis* of Dzinoridze *et al.* (1978, pl. 17, fig. 9) collected in the Middle Miocene of the DSDP Site 338-10cc is obviously identical with *X. panduraeformis* because it possesses numerous puncta on the valve face.

This species is characterized by the slightly constricted valve shape at the isthmus area on each side with thin and narrow hyaline process. This species is similar to *Quadrocistella* species in the elongate valve, but is identified from them by its slightly concave valve shape.

Xanthioisthmus specticularis (Hanna) Suto comb. nov.
(Pl. 1, figs 9–14; Figs 2B, 2C)

Basyonym. 1927 *Xanthiopyxis specticularis* Hanna: 124, pl. 17, fig. 10.

1949 *Xanthiopyxis specticularis* Hanna; Proschkina-Lavrenko & Sheshukova-Poretzkaya: 87, pl. 84, fig. 10.

1977 *Xanthiopyxis* aff. *specticularis* Hanna *sensu* Shirshov: pl. 30, fig. 54.

1986 *Xanthiopyxis specticularis* Hanna; Hajós: pl. 4, fig. 18.

Derivation of name. The Latin *specticularis* means 'conspectus'.

Type locality. Phoenix Canyon, 7 miles north of Coalinga, Fresno County, California. Lower Miocene.

Description. In valve view, hypovalve slender, apical axis 40.5–54.0 μm, transapical axis 15.5–17.2 μm, width of isthmus 7.8–10.0 μm. Hypovalve composed of two ovals joined together by a broad hyaline isthmus. Hypovalve strongly constricted at isthmus area on each side, with numerous wrinkles extending roughly in fan shape from the junction of isthmus and circle, with distinct mantle. Mantle of hypovalve hyaline, with a single ring of puncta at its base. Vegetative frustules not observed and epivalve unknown.

Stratigraphic occurrence. Rare and sporadic occurrences of this species are recognized from the lowest Miocene through the lower Middle Miocene at DSDP Site 338 (Fig. 4).

Remarks. This species may be hypovalves of *X. panduraeformis*, *X. praemaculata* and *X. maculata*, because the valve shapes of these species are very similar to each other. However, the correspondence between these taxa cannot be clarified because these species have not been observed as frustules, therefore the morpho-species *X. specticularis* is used in this study.

Xanthioisthmus specticularis is very similar to *X. praemaculata* and *X. maculata* in the valve shape marked with numerous wrinkles, but is differentiated from them by the single ring of puncta of the valve mantle. This species also resembles *X.*

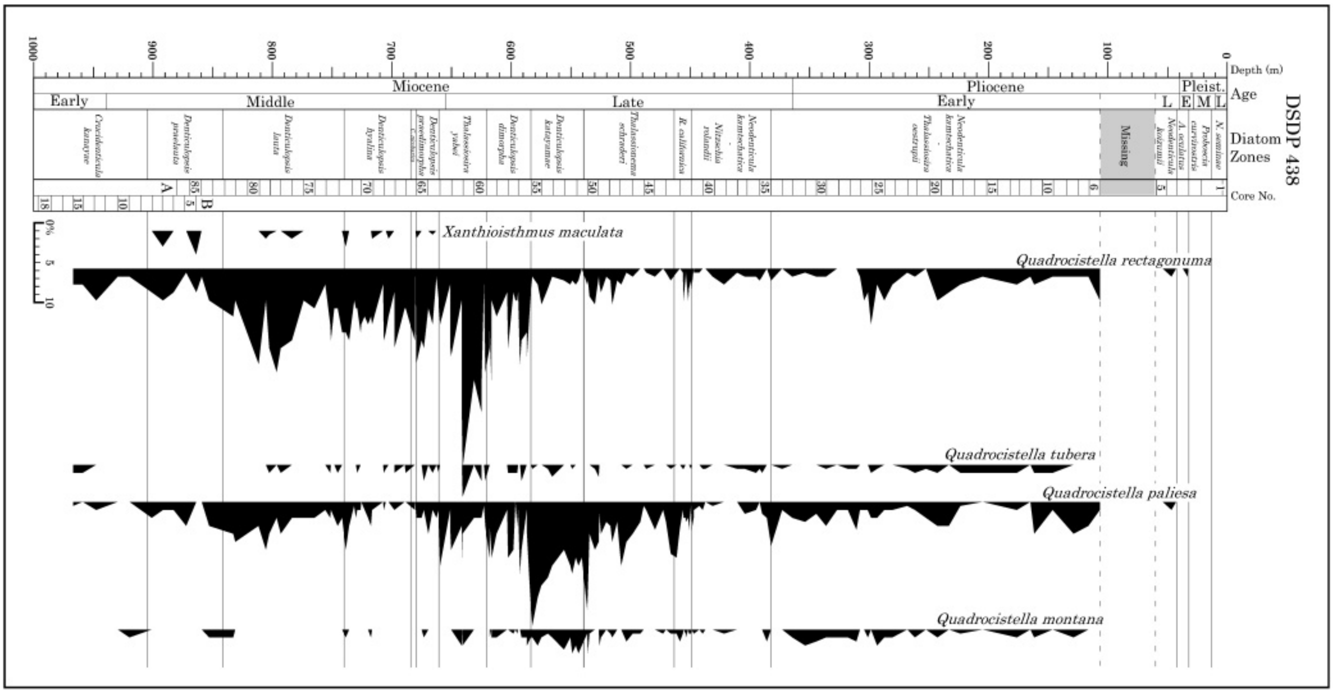


Fig. 5. Stratigraphical occurrences of various species of *Xanthioisthmus* and *Quadrocistella* at DSDP Sites 438A and B. Diatom zones are after Yanagisawa & Akiba (1998).

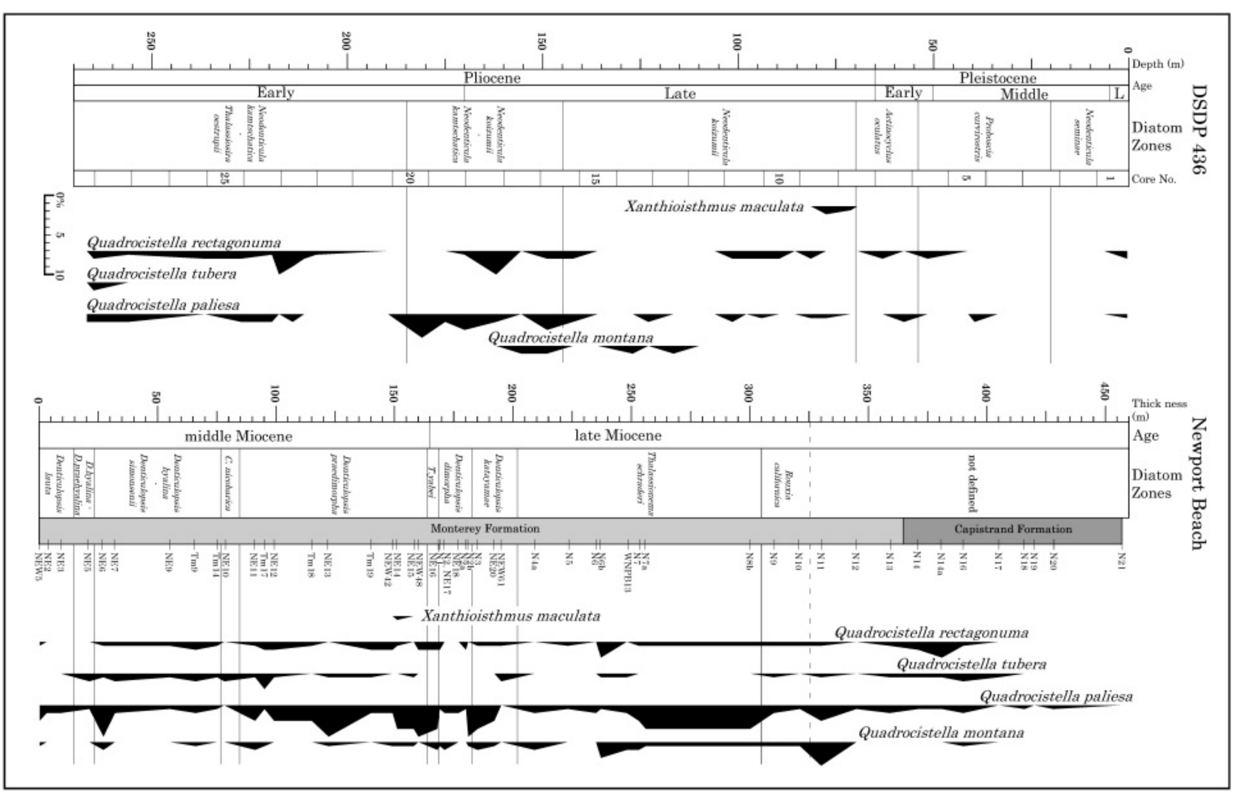
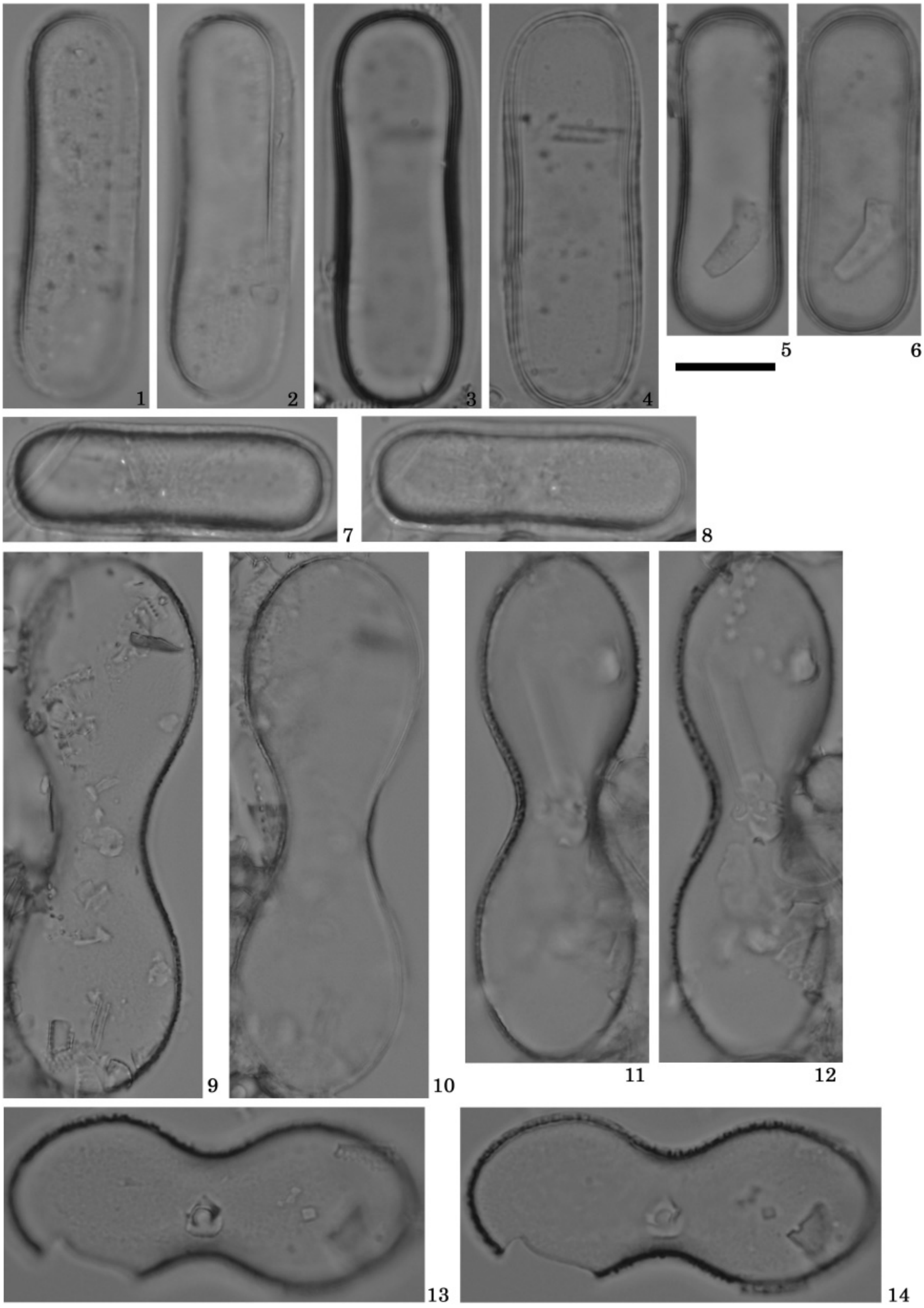


Fig. 6. Stratigraphical occurrences of various species of *Xanthioisthmus* and *Quadrocistella* at DSDP Site 436 and in the Newport Beach Section. Diatom zones are after Yanagisawa & Akiba (1998).



Explanation of Plate 1.

figs 1–8. *Xanthioisthmus biscoctiformis* (Forti) Suto comb. nov., LM. Scale bar 10 μm: **1, 2.** valve view of epivalve, DSDP Site 338-13-2, 148-149 cm; **3, 4.** valve view of epivalve, DSDP Site 338-18-1, 148–149 cm; **5, 6.** valve view of epivalve, DSDP Site 338-13-3, 148–149 cm; **7, 8.** valve view of epivalve, DSDP Site 338-13-2, 148–149 cm. **9–14.** *Xanthioisthmus specticularis* (Hanna) Suto comb. nov., LM. Scale bar 10 μm: **9, 10.** valve view of hypovalve, DSDP Site 338-17-2, 119–120 cm; **11, 12.** valve view of hypovalve, DSDP Site 338-13-1, 148–149 cm; **13, 14.** valve view of hypovalve, DSDP Site 338-13-1, 148–149 cm.

biscoctiformis but is identified by the strongly constricted valve composed of two ovals. This species differs from *X. panduraeformis* by the valve surface lacking spines or knobs.

Xanthioisthmus panduraeformis (Pantocsek) Suto comb. nov.
(Pl. 2, figs 1–14; Figs 2D, 2E)

Basyonym. 1886 *Xanthiopyxis panduraeformis* Pantocsek: 45, pl. 29, fig. 297.
1913 *Xanthiopyxis panduraeformis* Pantocsek; Forti: 1551, pl. 2, figs 20, 25.
1949 *Xanthiopyxis panduraeformis* Pantocsek; Proschkina-Lavrenko & Sheshukova-Poretzkaya: 87, pl. 84, figs 8a, b.
1976 *Xanthiopyxis panduraeformis* Pantocsek; Hajós: 826, pl. 11, fig. 5; pl. 17, fig. 9 (?).
1977 *Xanthiopyxis panduraeformis* Pantocsek; Shirshov: pl. 31, fig. 18; pl. 33, fig. 12.
1979 *Xanthiopyxis panduraeformis* Pantocsek; Dzinoridze *et al.*: 63, fig. 83.
2000 *Xanthiopyxis panduraeformis* Pantocsek; Harwood & Bohaty: 94, pl. 9, fig. 10.

Synonymy. 1913 *Xanthiopyxis panduraeformis* Pantocsek var. *soleiformis* Forti: 1552, pl. 2, figs 2, 4.
1949 *Xanthiopyxis panduraeformis* Pantocsek var. *soleiformis* Forti; Proschkina-Lavrenko & Sheshukova-Poretzkaya: 87, pl. 84, fig. 9.
1976 *Chaetoceros* sp. A *sensu* Gombos: 592, pl. 24, fig. 6 *nec* figs 1–5.
1977 *Xanthiopyxis maculata* Hanna *sensu* Hasegawa: 90, pl. 23, fig. 14.
1978 *Xanthiopyxis biscoctiformis* Forti *sensu* Dzinoridze *et al.*: pl. 17, fig. 9.
1978 *Chaetoceros panduraeformis* (Pantocsek) Gombos *sensu* Fenner: 513, pl. 36, figs 7, 8, 12.
1986 *Chaetoceros panduraeformis* Pantocsek *sensu* Harwood: pl. 1, fig. 15.
2000 *Chaetoceros panduraeformis* (Pantocsek) Gombos *sensu* Fenner; Scherer *et al.*: 431, pl. 5, fig. 11.

Derivation of name. The Latin *panduraeformis* means 'form of violin'.

Type locality. Szakal, Hungary. Miocene.

Description. Epivalve slender in valve view, apical axis 34.4–58.8 μm, transapical axis 13.3–17.8 μm, width of isthmus 7.2–8.9 μm. Valve composed of two flat ovals joined together by a broad hyaline isthmus. Valve strongly constricted at isthmus area on each side, covered by scattered numerous puncta and short spines over the whole valve face, with distinct mantle. Mantle of epivalve hyaline. Vegetative frustules not observed and hypovalve unknown.

Stratigraphic occurrence. This species occurs rarely and continuously from the middle Lower Miocene through the lower Middle Miocene at DSDP Site 338 (Fig. 4).

Remarks. This species was found in the Miocene sediments from Szakal in Hungary (Pantocsek, 1886), Miocene deposits in Italy (Forti, 1913), Upper Oligocene sediments in the South Atlantic (Gombos, 1976), the Upper Miocene Nakayama Formation in Sado Island in Japan (Hasegawa, 1977), Middle Miocene sediments in the Atlantic Ocean (Shirshov, 1977), Middle Eocene sediments at DSDP Site 356 (Fenner, 1978), Upper Oligocene sediments in Ross Sea (Harwood, 1986), Middle to lower Upper Eocene formation in McMurdo Sound of Antarctica (Harwood & Bohaty, 2000) and uppermost Oligocene sediments in Victoria Land Basin of Antarctica (Scherer *et al.*, 2000). As a result of these studies, it can be safely said that *X. panduraeformis* occurs from the Upper Eocene through the Upper Miocene. *Xanthiopyxis panduraeformis sensu* Schrader & Fenner (1976, p. 1003, pl. 45, fig. 7) is identified as *Xanthioisthmus maculata* by its valve face lacking puncta.

This species is separated from other species by its epivalve covered by scattered numerous puncta and short spines covered over the whole valve face.

Xanthioisthmus praemaculata Suto sp. nov.
(Pl. 3, figs 1–12; Figs 2F, 2G)

Derivation of name. The Latin *praemaculata* means 'pre-dirt'.

Holotype. Slide MPC-02609 (Micropalaeontology Collection, National Science Museum, Tokyo, England Finder P27-2W; illustrated in Pl. 3, figs 3, 4).

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

Description. In valve view, epivalve slender, apical axis 26.1–39.4 μm, transapical axis 10.0–14.4 μm, width of isthmus 6.1–10.6 μm. Valve composed of two ovals joined together by a broad hyaline isthmus. Valve strongly constricted at isthmus area on each side, with numerous wrinkles extending roughly in fan shape from the junction of isthmus and circle, with a puncta near each apex of valve, with distinct mantle. Mantle of epivalve hyaline. Vegetative frustules not observed and hypovalve unknown.

Stratigraphic occurrence. This species occurs rarely from the uppermost Lower Oligocene through the uppermost Oligocene at DSDP Site 338 (Fig. 4).

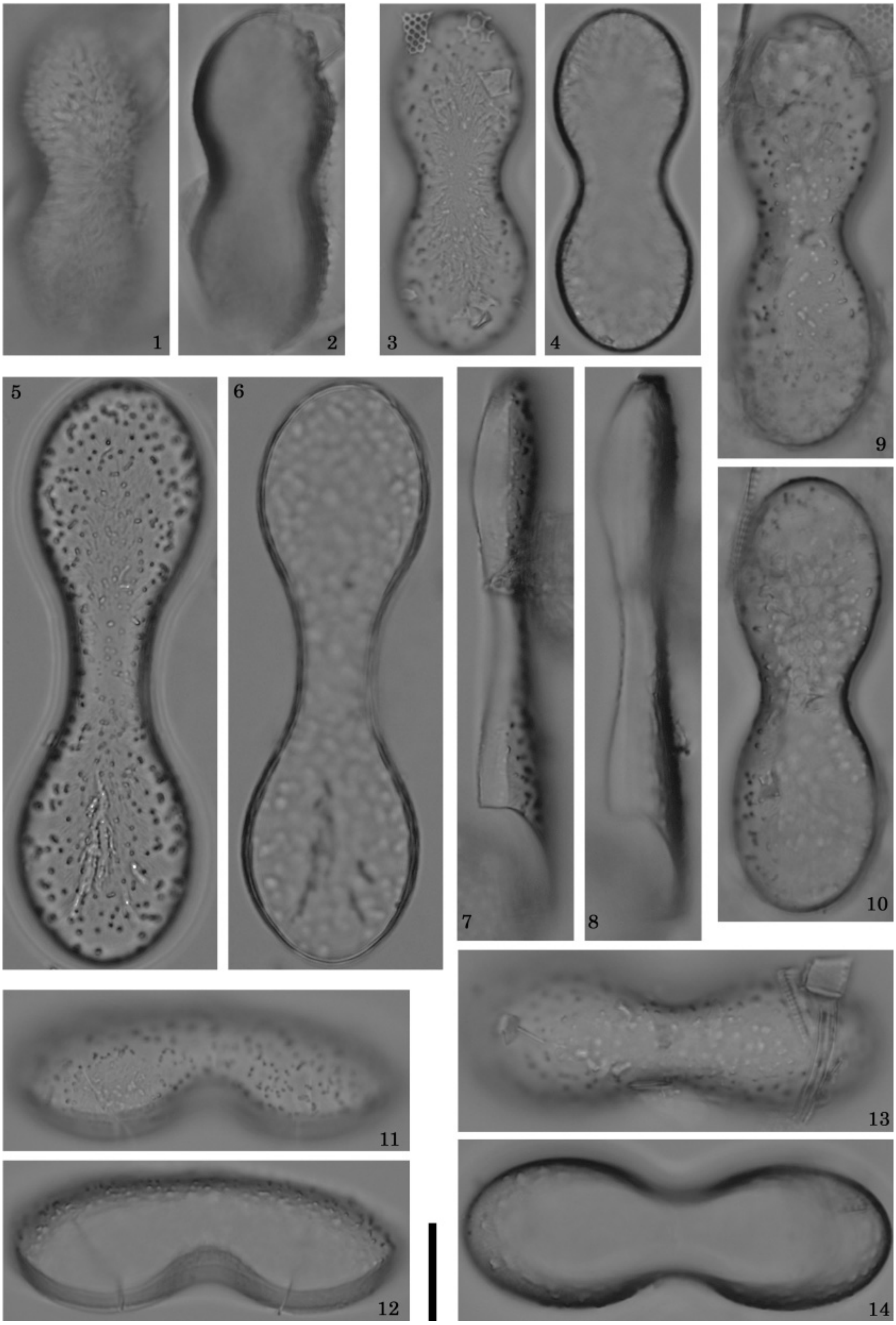
Remarks. *X. praemaculata* is separated from *X. maculata* by the puncta near each apex of valve. This species is similar to *X. specticularis*, but is distinguished by lacking a single ring of puncta. This species is close to *X. panduraeformis*, but lacks the bold heavy knobs on the valve face.

Xanthioisthmus maculata (Hanna) Suto comb. nov.
(Pl. 4, figs 1–11; Figs 2H, 2I)

Basyonym. 1932 *Xanthiopyxis maculata* Hanna: 225, pl. 18, fig. 4.

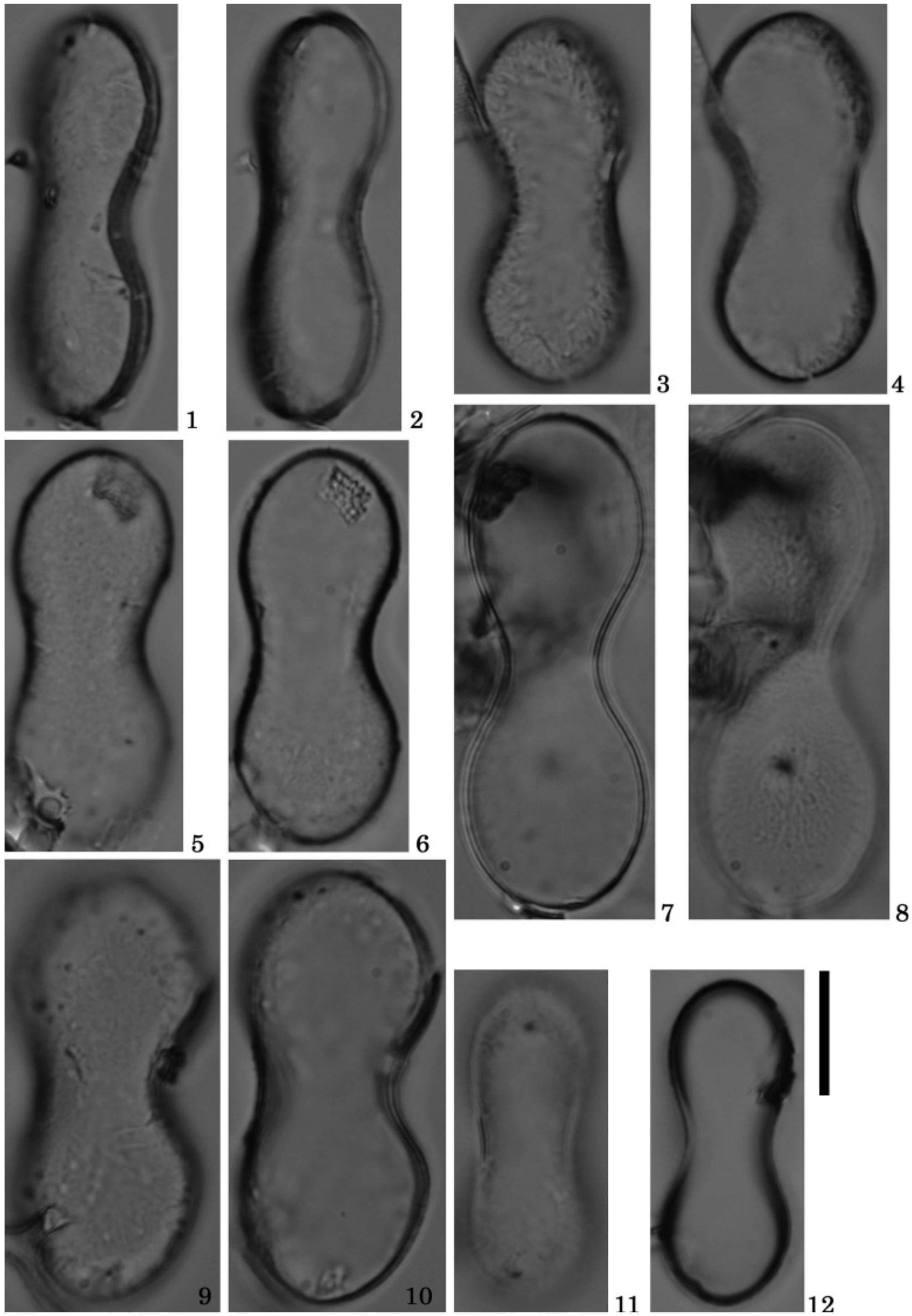
Synonym. 1976 *Xanthiopyxis panduraeformis* Pantocsek *sensu* Schrader & Fenner: 1003, pl. 45, fig. 7.

Derivation of name. The Latin *maculata* means 'dirt'.



Explanation of Plate 2.

figs 1–14. *Xanthioisthmus panduraeformis* (Pantocsek) Suto comb. nov., LM. Scale bar 10 μm: **1, 2.** valve view of epivalve, DSDP Site 338-10-2, 80–81 cm; **3, 4.** valve view of epivalve, DSDP Site 338-13-1, 148–149 cm; **5, 6.** valve view of epivalve, DSDP Site 338-13-3, 148–149 cm; **7, 8.** girdle view of epivalve, DSDP Site 338-13-3, 148–149 cm; **9, 10.** valve view of epivalve, DSDP Site 338-13-1, 148–149 cm; **11, 12.** oblique girdle view of epivalve, DSDP Site 338-17-2, 119–120 cm; **13, 14.** valve view of epivalve, DSDP Site 338-16-3, 10–11 cm.

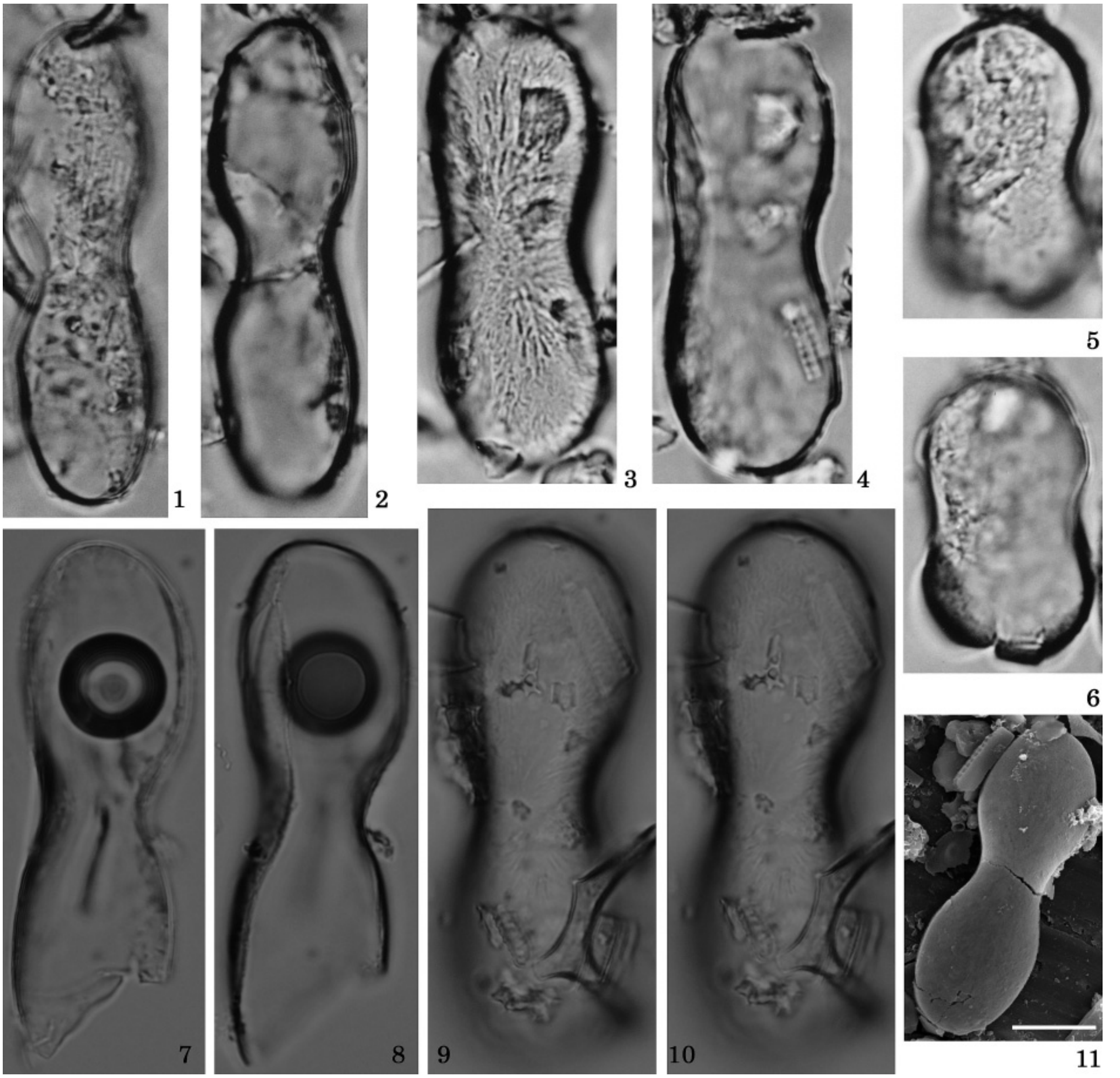


Explanation of Plate 3.

figs 1–12. *Xanthioisthmus praemaculata* Suto sp. nov., LM. Scale bar 10 µm: **1, 2.** oblique valve view of epivalve, DSDP Site 338-20-3, 20–21 cm; **3, 4.** holotype, valve view of epivalve, DSDP Site 338-20-3, 20–21 cm; **5, 6.** valve view of epivalve, DSDP Site 338-20-3, 90–91 cm; **7, 8.** valve view of epivalve, DSDP Site 338-20-4, 148–149 cm; **9, 10.** valve view of epivalve, DSDP Site 338-21-1, 32–33 cm; **11, 12.** valve view of epivalve, DSDP Site 338-20-3, 20–21 cm.

Type locality. Diatomaceous shales on the southeast side of Sharktooth Hill, seven miles northeast of Bakersfield, Mt. Diablo Base and Meridian, Kern County, California. Middle Miocene, upper Temblor Formation.

Description. In valve view, epivalve slender, apical axis 23.8–43.3 µm, transapical axis 11.7–15.0 µm, width of isthmus 7.2–11.7 µm. Valve composed of two ovals joined together by a broad hyaline isthmus. Valve strongly constricted at isthmus



Explanation of Plate 4.

figs 1–11. *Xanthioisthmus maculata* (Hanna) Suto comb. nov., LM scale bar 10 μm for figs 1–10; SEM scale bar 10 μm for fig. 11. **1, 2.** Valve view of epivalve, DSDP Site 438A-60-3, 27–29 cm; **3, 4.** valve view of epivalve, DSDP Site 438A-66-1, 118–122 cm; **5, 6.** valve view of epivalve, DSDP Site 438A-85-4, 25–27 cm; **7, 8.** valve view of epivalve, Newport Beach Section, NE14. **9, 10.** valve view of epivalve, DSDP Site 338-12-3, 38–39 cm; **11.** valve view of epivalve, DSDP Site 338-19-3, 20–21 cm.

area on each side, with numerous wrinkles extending roughly in fan shape from the junction of isthmus and circle, with distinct mantle. Mantle of epivalve hyaline. Vegetative frustules not observed and hypovalve unknown.

Stratigraphic occurrence. Rare and sporadic occurrences of this species are recognized from the Lower Oligocene to the upper Middle Miocene in all sites observed in this study (Figs 3–6).

Remarks. This species is characterized by its hyaline valve composed of two flat circles joined together by a hyaline broad isthmus.

Genus *Quadrocistella* Suto gen. nov.

Type species. *Quadrocistella paliesa* Suto sp. nov.

Derivation of name. The Latin *quadrocistella* means 'quadrangular box'.

Description. Valve rectangular in valve view. Valve face slightly constricted, hyaline, with wrinkles, some with a single ring of palisade ridges at its edge, some with two puncta or spines near each apex of valve, with distinct mantle.

Stratigraphic occurrence. This genus occurs from the middle Lower Oligocene to the Recent (Fig. 3).

Remarks. This genus differs from *Xanthioisthmus* and other morpho-genera of *Chaetoceros* by its elongate and rectangular valve and bears five species: *Q. rectagonuma*, *Q. tubera*, *Q. paliesa*, *Q. montana* and *Q. palmesa* (Fig. 2).

Key to species

1a Valve lacking a single ring of palisade ridges at edge of the valve..2
1b Valve possessing a single ring of palisade ridges at edge of the valve..4
2a Valve surface hyaline ....*Quadrocistella rectagonuma*
2b Valve surface with two puncta or spines near each apex of valve...*Q. tubera*
3a Valve surface hyaline ....*Q. paliesa*
3b Valve vaulted in central part ....*Q. montana*
3c Valve surface with two puncta or spines near each apex of valve ....*Q. palmesa*

Quadrocistella rectagonuma Suto sp. nov.
(Pl. 5, figs 1–13; Fig. 2J)

Derivation of name. The Latin *rectagonuma* means 'rectangle'.

Holotype. Slide MPC-02598 (Micropalaeontology Collection, the National Science Museum, Tokyo, England Finder N37-2E, illustrated in Pl. 5, figs 1, 2).

Type locality. DSDP Site 436-6-4, 100–102 cm, northwestern Pacific Ocean.

Description. Valve rectangular in valve view, apical axis 11.4–33.6 µm, transapical axis 5.0–11.9 µm. Valve slightly concave, hyaline, with wrinkles, with distinct mantle. Mantle hyaline. Vegetative frustules not observed.

Stratigraphic occurrence. This species occurs continuously from the uppermost Oligocene to the top of the Lower Pleistocene in the North Pacific and Norwegian Sea (Figs 3–6).

Remarks. This species is differentiated from other *Quadrocistella* species by the rectangular valve lacking a single ring of palisade ridges at the edge of the valve and puncta or spines near each apex of valve.

Quadrocistella tubera Suto sp. nov.
(Pl. 5, figs 14–17; Fig. 2K)

Derivation of name. The Latin *tubera* means 'wen'.

Holotype. Slide MPC-02599 (Micropalaeontology Collection, the National Science Museum, Tokyo, England Finder Q31-1N, illustrated in Pl. 5, figs 14, 15).

Type locality. DSDP Site 438A-62-1, 80–81 cm, northwestern Pacific Ocean.

Description. Valve rectangular in valve view, apical axis 9.5–12.8 µm, transapical axis 7.2–9.0 µm. Valve slightly concave, hyaline, with wrinkles, with a puncta near each apex of valve, with distinct mantle. Mantle hyaline. Vegetative frustules not observed.

Stratigraphic occurrence. This species occurs rarely and sporadically from the uppermost Oligocene through to the Lower Pliocene at all DSDP Sites and in the Newport Beach Section (Figs 3–6).

Remarks. This species is characterized by its rectangular valve possessing a puncta near each apex of valve, and is differentiated from *Q. palmesa* by the valve lacking a single ring of palisade ridges at valve edge.

Quadrocistella paliesa Suto sp. nov.
(Pl. 6, figs 1–24; Fig. 2L)

1968 *Chaetoceros* ? sp. VI *sensu* Hajós: 131, pl. 34, figs 12, 13.

Derivation of name. The Latin *paliesa* means 'wall'.

Holotype. Slide MPC-02596 (Micropalaeontology Collection, the National Science Museum, Tokyo, England Finder N32-1E, illustrated in Pl. 6, figs 3, 4).

Type locality. DSDP Site 436-23-5, 50–52 cm, northwestern Pacific Ocean.

Description. Valve rectangular in valve view, apical axis 13.5–28.0 µm, transapical axis 6.4–12.0 µm. Valve slightly concave, hyaline, with wrinkles, with a single ring of palisade ridges at its edge, with distinct mantle. Mantle hyaline. Vegetative frustules not observed.

Stratigraphic occurrence. This species occurs continuously from the Lower Oligocene to the Recent in all sites and onland section observed in this study (Figs 3–6).

Remarks. *Chaetoceros* ? sp. VI *sensu* Hajós (1968), which was collected at the Miocene Szurdokpüspöki diatomite stop, is identified with *Q. paliesa* by a single ring of palisade ridges at its valve margin.

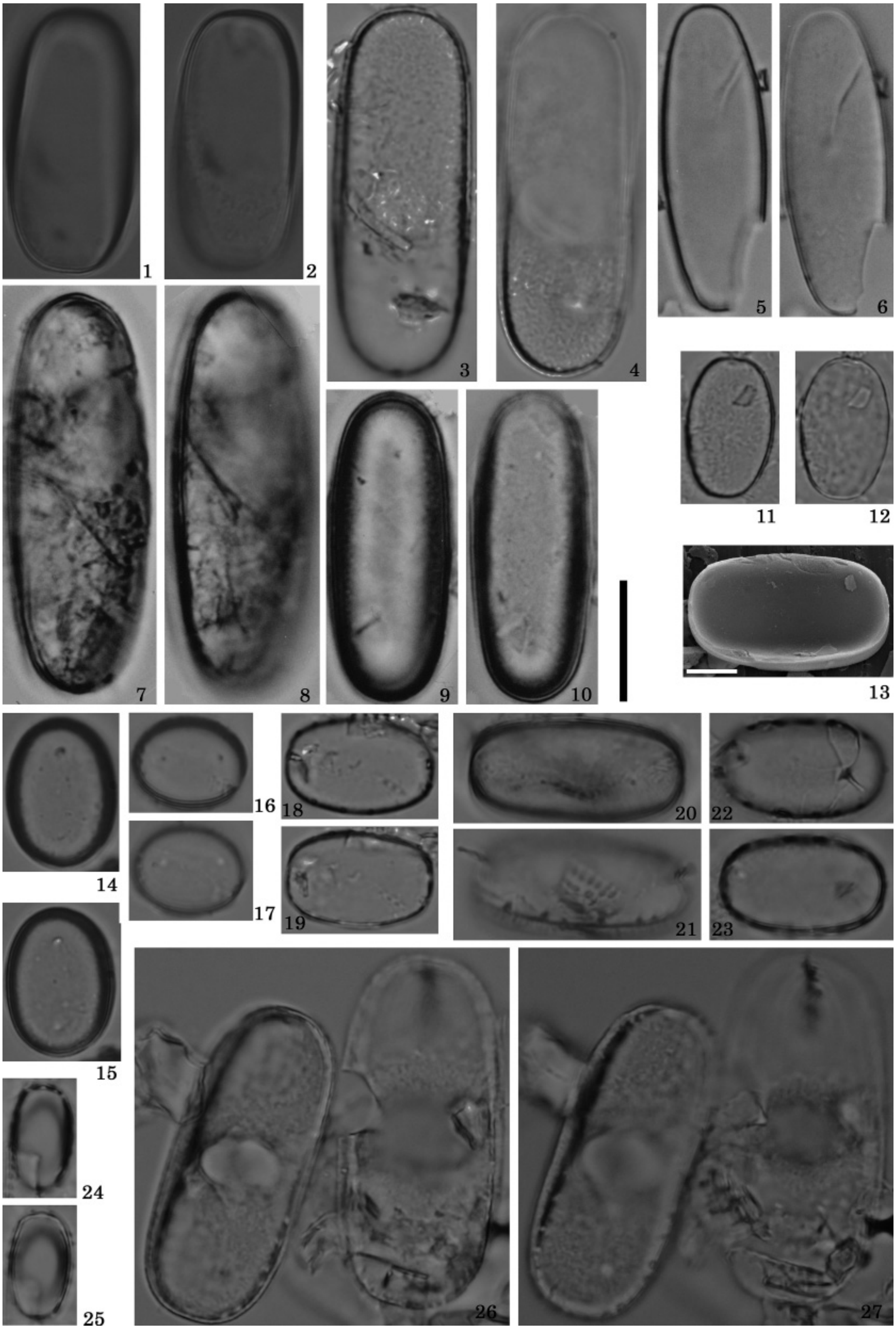
This species differs from other taxa by its valve possessing a single ring of palisade ridges at valve margin. This species is very similar to *Q. palmesa* in possessing a single ring of palisade ridges, but is identified by lacking two puncta near each apex of valve.

Quadrocistella montana Suto sp. nov.
(Pl. 5, figs 24–27; Fig. 2M)

1978 *Dicladia* sp. 2 Kanaya (1957) *sensu* Fenner: 519, pl. 34; figs 20, 21 *nec* pl. 35, fig. 1.

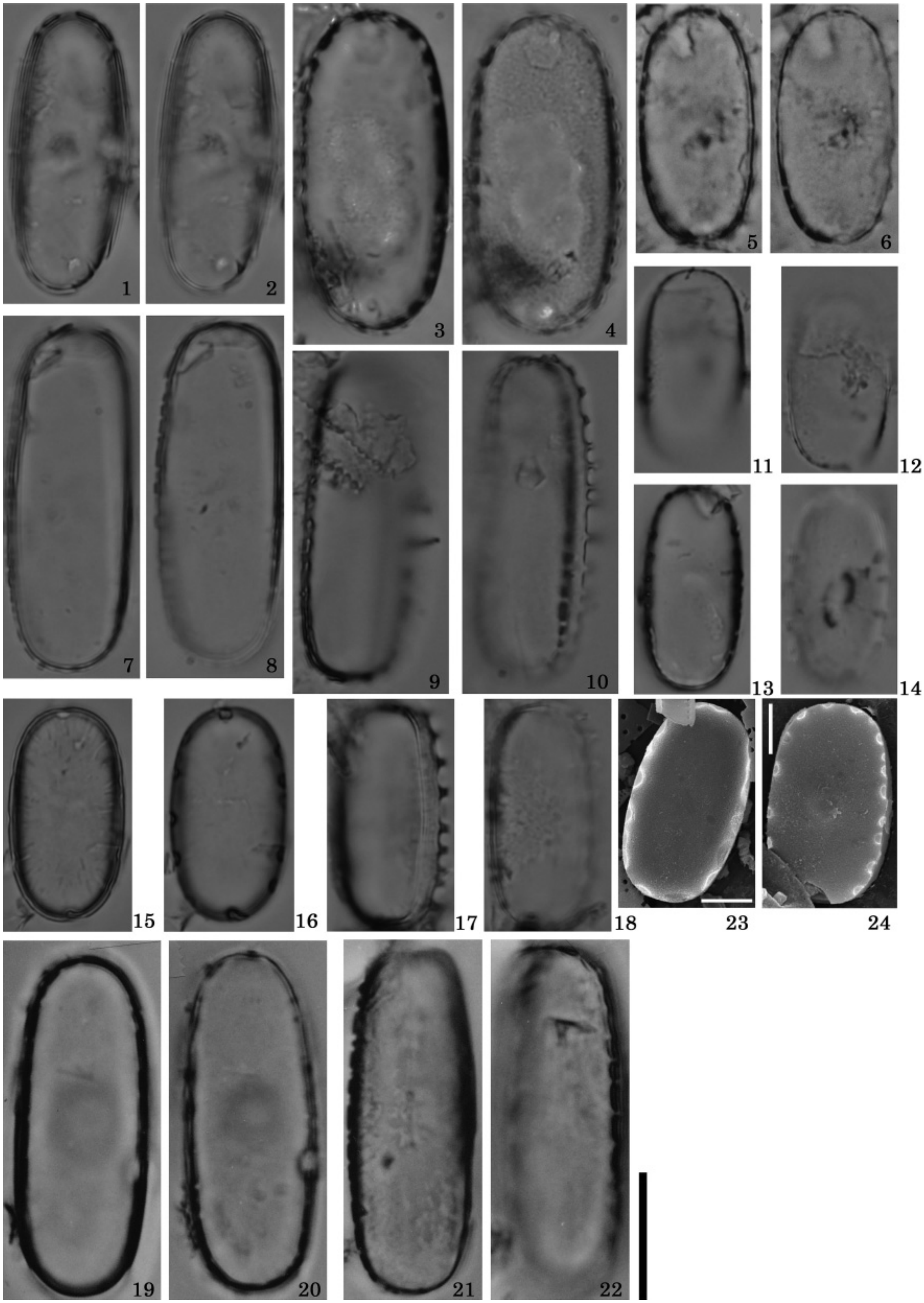
Derivation of name. The Latin *montana* means 'mountainous country'.

Holotype. Slide MPC-02595 (Micropalaeontology Collection, the National Science Museum, Tokyo, England Finder H33-2N, illustrated in Pl. 5, figs 24, 25).



Explanation of Plate 5.

figs 1–13. *Quadrocistella rectagonuma* Suto sp. nov., LM scale bar 10 µm for figs 1–12; SEM scale bar 5 µm for fig. 13: **1, 2.** holotype, valve view, DSDP Site 436-6-4, 100–102 cm; **3, 4.** valve view, DSDP Site 436-23-1, 48–50 cm; **5, 6.** valve view, DSDP Site 438A-46-3, 18–22 cm; **7, 8.** valve view, DSDP Site 438A-66-2, 82–84 cm; **9, 10.** valve view, DSDP Site 438A-65-5, 18–21 cm; **11, 12.** valve view, Newport Beach Section, N1; **13.** oblique valve view, DSDP 338-11-4, 148–149 cm. **14–17.** *Quadrocistella tubera* Suto sp. nov., LM. Scale bar 10 µm: **14, 15.** holotype, valve view, DSDP Site 438A-62-1, 80–81 cm; **16, 17.** valve view, DSDP Site 438A-62-1, 20–24 cm. **18–23.** *Quadrocistella palmesa* Suto sp. nov., LM. Scale bar 10 µm: **18, 19.** holotype, valve view, Newport Beach Section, NE13; **20, 21.** valve view, Newport Beach Section, NE12; **22, 23.** valve view, DSDP Site 338-19-4, 10–11 cm. **24–27.** *Quadrocistella montana* Suto sp. nov., LM. Scale bar 10 µm: **24, 25.** holotype. Newport Beach Section, N1; **26, 27.** valve view, DSDP Site 338-8-1, 140–141 cm.



Explanation of Plate 6.

figs 1–24. *Quadrocistella paliesa* Suto sp. nov., LM scale bar 10 µm for figs 1–22; SEM scale bar 5 µm for figs 23, 24. **1, 2.** Valve view, DSDP Site 436-11-6, 100–102 cm; **3, 4.** holotype, valve view, DSDP Site 436-23-5, 50–52 cm; **5, 6.** valve view, DSDP Site 438A-57-3, 31–35 cm; **7, 8.** valve view, Newport Beach Section, N7a; **9, 10.** oblique valve view, Newport Beach Section NE1; **11, 12.** valve view, Newport Beach Section, NE14; **13, 14.** valve view, Newport Beach Section, NE17; **15, 16.** valve view, DSDP Site 338-19-5, 148–149 cm; **17, 18.** oblique valve view, DSDP Site 338-8-1, 140–141 cm; **19, 20.** valve view, DSDP Site 438A-65-5, 18–21 cm; **21, 22.** valve view, DSDP Site 438A-25-5, 16–20 cm; **23.** valve view, DSDP Site 338-11-4, 148–149 cm; **24.** valve view, DSDP Site 338-17-1, 100–101 cm.

Type locality. The Newport Beach Section, sample no. N1 of Barron (1976), California.

Description. Valve rectangular in valve view, apical axis 8.6–29.6 µm, transapical axis 5.0–13.2 µm. Valve slightly concave, hyaline, with wrinkles, vaulted in the central area, with a single ring of palisade ridges at its edge, with distinct mantle. Mantle hyaline. Vegetative frustules not observed.

Stratigraphic occurrence. This species occurs rarely from the Upper Oligocene to the Lower Pliocene (Figs 3–6).

Remarks. Two specimens of *Dicladia* sp. 2 Kanaya (1957) *sensu* Fenner (1978) were collected from the Middle Eocene sediments of DSDP Site 356 at Sao Paulo Plateau.

This species is characterized by its central vaulted rectangular valve.

Quadrocistella palmesa Suto sp. nov.
(Pl. 5, figs 18–23; Fig. 2N)

Derivation of name. The Latin *palmesa* means 'twig'.

Holotype. Slide MPC-02597 (Micropalaeontology Collection, the National Science Museum, Tokyo, England Finder H33-1N, illustrated in Pl. 5, figs 18, 19).

Type locality. The Newport Beach Section, sample no. NE13 of Barron (1976), California.

Description. Valve rectangular in valve view, apical axis 11.3–18.2 µm, transapical axis 7.7–8.7 µm. Valve slightly concave, hyaline, with wrinkles, with two puncta or spines near each apex of valve, with a single ring of palisade ridges at its edge, with distinct mantle. Mantle hyaline. Vegetative frustules not observed.

Stratigraphic occurrence. A short interval of occurrence of this species is recognized from the Lower to the uppermost Oligocene at DSDP Site 338 (Figs 3, 4).

Remarks. This species differs from other taxa by its valve possessing two puncta or a spine near each apex of valve and a single ring of palisade ridges at valve margin.

DISCUSSION

The morphology, taxonomy and biostratigraphy of the fossil diatom resting spore morpho-genera *Xanthioisthmus* Suto gen. nov. and *Quadrocistella* Suto gen. nov. are described. The genus *Xanthioisthmus* is characterized by an elongate valve composed of two flat circles joined together by a hyaline broad isthmus and includes five species: *X. biscoctiformis* (Forti) Suto comb. nov., *X. specticularis* (Hanna) Suto comb. nov., *X. panduraeformis* (Pantocsek) Suto comb. nov., *X. praemaculata* sp. nov. and *X. maculata* (Hanna) Suto comb. nov. The genus *Quadrocistella* differs from *Xanthioisthmus* by its elongate and rectangular valve and bears five new species: *Q. rectagonuma* sp. nov., *Q. tubera* sp. nov., *Q. paliesa* sp. nov., *Q. montana* sp. nov.and *Q. palmesa* sp. nov.

Of these species, *X. praemaculata* and *Q. palmesa* are potentially useful for diatom biostratigraphy in the Norwegian Sea, because they are relatively short-ranging with specific characteristics that allow for easy identification in practical stratigraphical analysis. All other species occur continuously or very rarely in the interval examined in this study and, therefore, these species are not useful biostratigraphical markers.

The two new genera are probably fossil resting spores of the marine diatom genus *Chaetoceros*. Many descriptions of extant *Chaetoceros* vegetative cells are described in detail in the literature (e.g. Cupp, 1943; Rines & Hargraves, 1988; Hasle & Syvertsen, 1996). In contrast, the descriptions of their resting spores are scant and knowledge of the morphologies of extant *Chaetoceros* resting spores are little known because one cannot observe in detail a valve view in the case of resting spores in the frustule of vegetative cells. Moreover, many, but not all, diatomists have realized that fossil resting spores are often difficult to classify with certainty due to the fact that their respective vegetative cells are rarely preserved as fossils in association with resting spores. Therefore, more detailed studies on the morphology of extant and fossil resting spores are needed, especially in the Peruvian Ocean and Antarctic Sea, where *Chaetoceros* vegetative cells and resting spores occur abundantly both in the fossil record and Recent deposits. Once the morphology of resting spores and vegetative cells is clarified, it will be possible to identify the same species of resting spores and vegetative cells and understand past productivity and palaeoenvironmental change in upwelling regions.

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