

Taxonomy and phylogeny of the three marine diatom genera, *Crucidenticula*, *Denticulopsis* and *Neodenticula*

Yukio YANAGISAWA* and Fumio AKIBA**

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Abstract: Taxonomic refinements are made on some 30 taxa belonging to the marine diatom genera, *Crucidenticula*, *Denticulopsis* and *Neodenticula*, and their most probable evolutionary lineages are presented based on their morphology as well as their stratigraphic and geographic distributions. Fifteen new species and varieties are herein described, and two new combinations are established. They are, in alphabetical order, *Crucidenticula kanayae* var. *pacifica* n. var., *C. paranicobarica* var. *tropica* n. var., *C. sawamurae* n. sp., *Denticulopsis barronii* n. sp., *D. crassa* n. sp., *D. delicata* n. sp., *D. dimorpha* var. *areolata* n. var., *D. ichikawae* n. sp., *D. okunoi* n. sp., *D. ovata* (SCHRADER) n. comb., *D. praedimorpha* var. *minor* n. var., *D. praedimorpha* var. *robusta* n. var., *D. praedimorpha* var. *intermedia* n. var., *D. praekatayamae* n. sp., *D. simonsenii* n. sp., *D. tanimurae* n. sp. and *D. vulgaris* (OKUNO) n. comb.

I. Introduction

The late Cenozoic diatom genera *Crucidenticula*, *Denticulopsis* and *Neodenticula* include many short-ranging and widely distributed taxa, most of which are extremely valuable for the Neogene diatom biostratigraphy. The diatom taxa included in these three genera had long been recognized as "marine species of *Denticula* KÜTZING" (SIMONSEN and KANAYA, 1961), and were later placed in the genus *Denticulopsis* by SIMONSEN (1979), until AKIBA and YANAGISAWA (1986) recently clarified their generic distinctions.

The number of taxa of this species group has been greatly increased as their biostratigraphic utility has become clear (Fig. 1).

* Geology Department

** JAPEX Research Center (Japan Petroleum Exploration Co. Ltd.)

When SIMONSEN and KANAYA (1961) made taxonomic revision of this group, only five species were known. Over a decade later, SCHRADER (1973a, b) recognized 12 taxa, adding many new forms, and he first suggested a possible evolutionary lineage of this diatom group. However, his idea is basically contradictory to ours in that this diatom group is not monogenetic but clearly polygenetic. By the successive descriptions of new forms or refinements of previously described species (MCCOLLUM, 1975; SCHRADER, 1976; SCHRADER and FENNER, 1976; AKIBA, 1982, 1986; MARUYAMA, 1984a; AKIBA and YANAGISAWA, 1986; TANIMURA, 1989), some 20 taxa have been counted in our recent synthesis of the taxonomic and morphological details of this diatom group (AKIBA and YANAGISAWA, 1986).

The main purpose of our previous paper was to circumscribe the specific concepts of the group as clearly as possible in order to

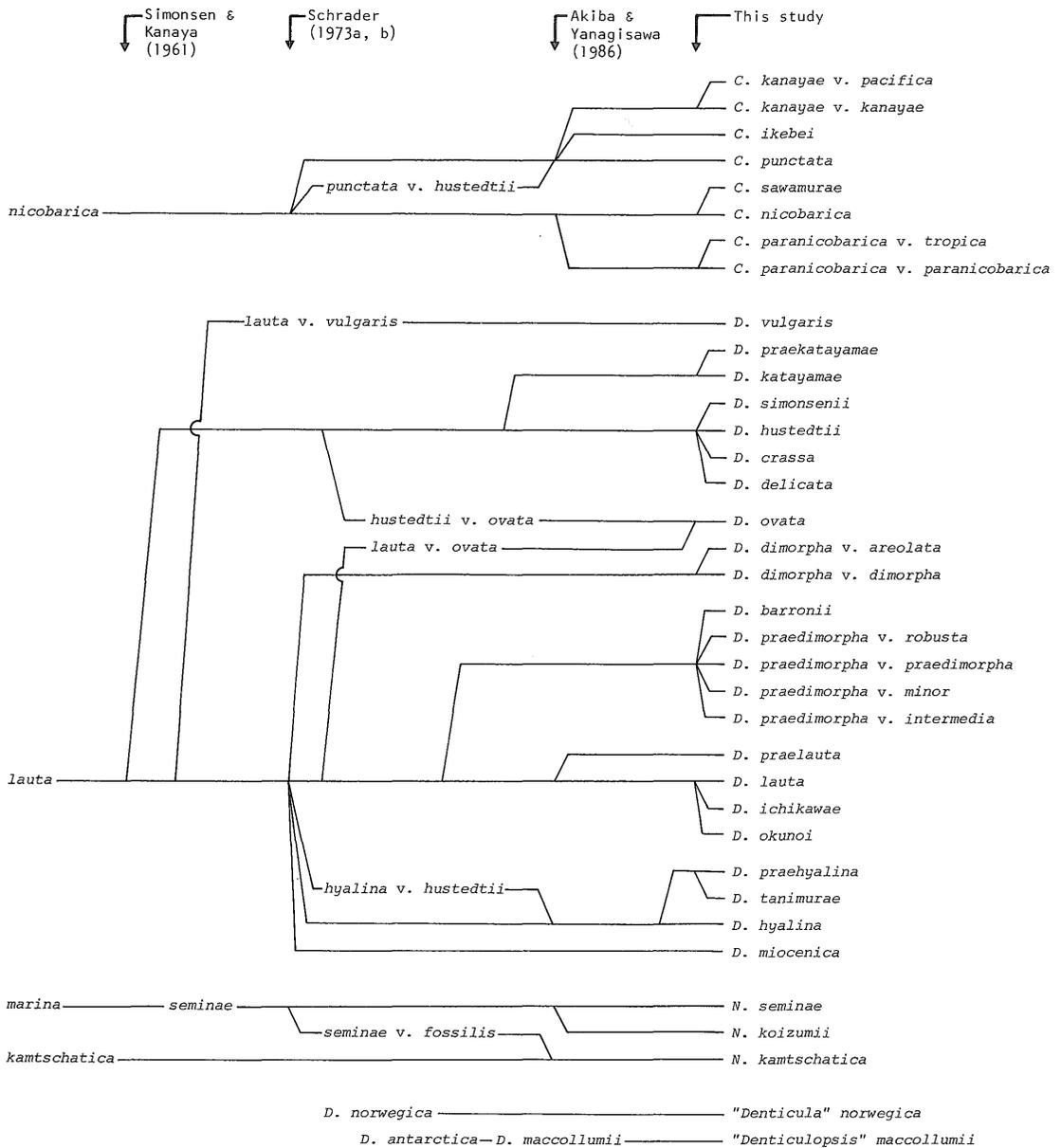


Fig. 1 Taxonomic history of taxa of the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula*.

better understand its stratigraphic significance. Another aim of our study was to trace the evolutionary lineage of these taxa. However, we could not complete this study because available evidence useful for the purpose was not extensive at that time.

Continued study during the last several years allows us to propose the most probable phylogenetic relationship of this species group based on the latest information available. This diatom group now includes more than 30 taxa, many of which are newly described here.

The taxonomic relationship, morphological diagnoses and time-and-space distribution of this group are described in detail as well.

II. Materials and methods

For biostratigraphic study, samples from the Lower Miocene through Pliocene sequences of DSDP Site 438 (Hole A, Cores 1-85; Hole B, Cores 6-16) and the Lower Miocene to Upper Miocene sections of DSDP Site 77 (Hole B, Cores 17-24) and Site 71 (Cores 19-29) were analyzed.

Holes 438A and 438B are located in the northwestern Pacific, off northeast Honshu of Japan (Fig. 2), containing the most complete reference sections for the Lower Miocene through Quaternary North Pacific diatom biostratigraphy (BARRON, 1980; AKIBA *et al.*, 1982; MARUYAMA, 1984b; KOIZUMI, 1985; ODA, 1986; AKIBA, 1986; ORESHKINA and RADIONOVA, 1987). In this study, the samples analyzed by AKIBA *et al.* (1982), MARUYAMA (1984b) and AKIBA (1986) and those deposited in DSDP Reference Center in the National

Science Museum (Tokyo) are re-examined with special attention to the three genera treated in this paper.

Holes 77B and 71 were drilled in the eastern equatorial Pacific (Fig. 2), and offer one of the most valuable Lower Miocene to Middle Miocene sections for the diatom biostratigraphy of this area (BARRON, 1981b, 1983, 1985a). We examined the slides of some selected samples studied by BARRON (1983, 1985a).

For taxonomic study, especially for SEM observation, several selected samples from on-land sequences of Japan and from deep-sea cores in the Southern Ocean were used as well as the DSDP samples mentioned above.

Preparation method for LM studies varied but mostly followed KOIZUMI and TANIMURA (1985), BARRON (1983) and MARUYAMA (1984a). For SEM observation, samples were prepared after AKIBA and YANAGISAWA (1986).

One hundred diatom valves were counted for each sample at 1000 \times magnification. After the counting, each slide was scanned to record other species missed during the count-

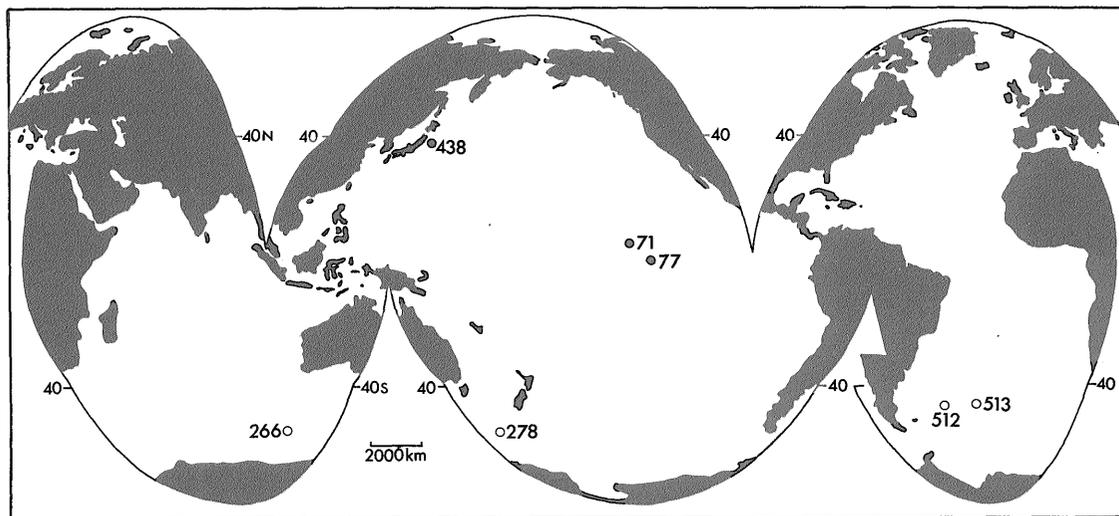


Fig. 2 Geographic locations of DSDP sites examined in this study (solid circles) and the Southern Ocean DSDP sites of which diatom stratigraphic records are used to summarize stratigraphic ranges of taxa treated in this paper (open circles).

ing. The copulae of *Denticulopsis praedimorpha*, *D. barronii*, *D. dimorpha*, *D. crassa* and *Neodenticula* species were counted separately during the routine counting of valves, because they serve to identify these species rather easily. Resting spores of *Chaetoceros* were also counted separately at the DSDP Site 438.

Several biometrical parameters (e. g. valve length and width) were measured for some taxa to obtain objective diagnostic criteria, using a micrometer scale in LM.

III. Morphology and terminology

Some of the common characteristic structures to the three genera are discussed, since there has been serious confusion or misinterpretation concerning the valve structures of this diatom group. They are clarified here

with illustrations of frustules of the genus *Denticulopsis* (Figs. 3-5). General morphological terms are after ANONYMOUS (1975) and ROSS *et al.* (1979) and special terms for this diatom group are used after SIMONSEN and KANAYA (1961), AKIBA (1979), MARUYAMA (1984a, 1988) and AKIBA and YANAGISAWA (1986) with some modifications. Basic characteristics of the three genera are summarized in Table 1.

Primary pseudoseptum: The primary pseudoseptum, a basic valve structure common to the three genera, penetrates very deeply and forms complete chambers of the valve interior. At the basal part, it accompanies a capitate end, which was called a "crossbar" of septum by SIMONSEN and KANAYA (1961). The "crossbar" is, however, not a element of septum (=copula) but

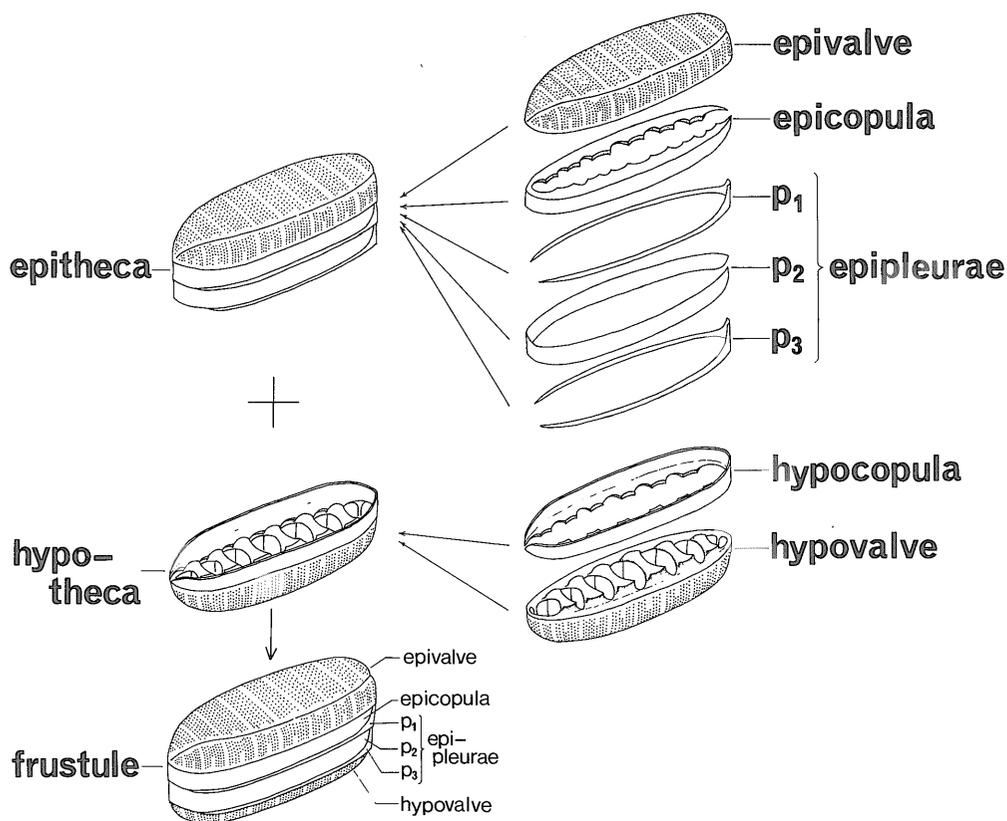


Fig. 3 Composition of frustule of *Denticulopsis lauta* (BAILEY) SIMONSEN.

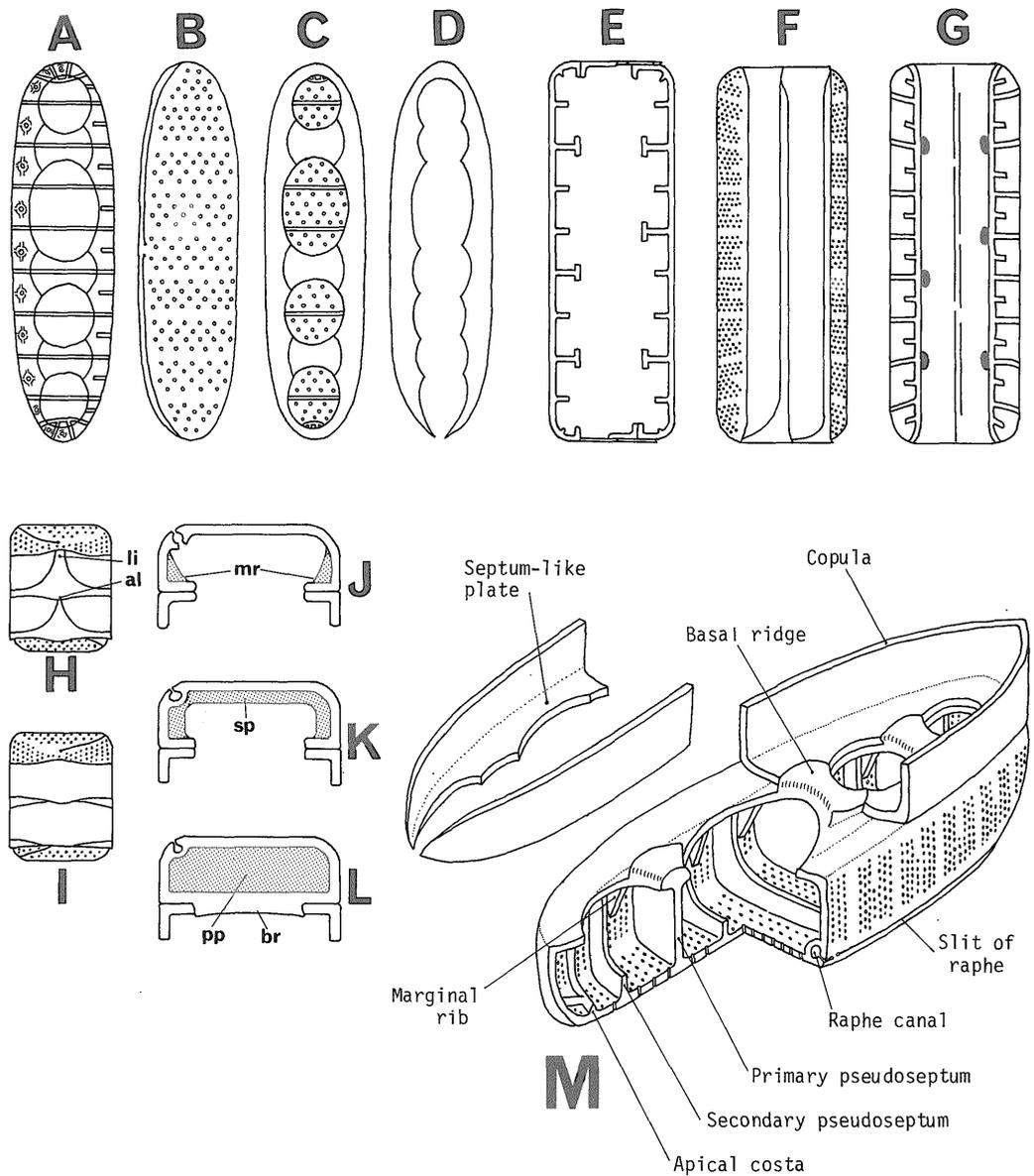


Fig. 4 Frustule of *Denticulopsis simonsenii* n. sp. A : inner valve view by LM ; B : outer valve view by SEM ; C : inner valve view by SEM ; D : valve view of copula ; E : broad girdle view of frustule in cross section ; F : broad girdle view of frustule by SEM ; G : broad girdle view of frustule by LM ; H, I : narrow girdle view of frustule by SEM, showing a lingula (li) and an antilingula (al) of the first pleura ; J : cross-sectional view at marginal rib(mr) ; K : cross-sectional view at secondary pseudoseptum (sp) ; L : cross-sectional view at primary pseudoseptum (pp) and basal ridge (br) ; M : inner valve structure.

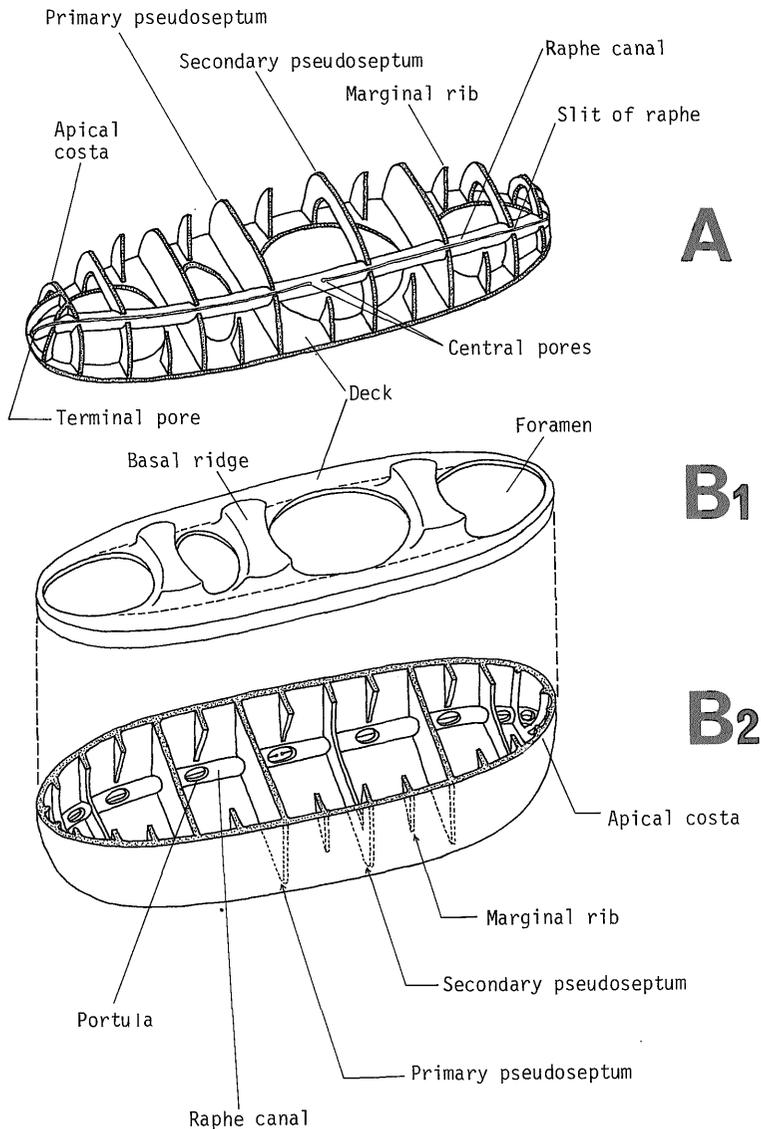


Fig. 5 Valve structure of *Denticulopsis simonsenii* n. sp. A: valve without valve face and mantle; B₁: deck of valve; B₂: valve without deck.

belongs to the valve as SIMONSEN (1979) pointed out. This term is, therefore, inadequate in usage according to ROSS *et al.* (1979). Instead of this term, MARUYAMA (1984a) introduced a name, "tuzumi" after a Japanese traditional hand drum, whose outline is very similar to this structure. However, this term seems also to be inadequate because it is

exotic among other morphological terms which are named in Latin or European languages. In this paper, this capitate structure is termed a **basal ridge**.

Although it has sometimes been called merely a "pseudoseptum", the term "primary pseudoseptum" is used in this paper to avoid confusion with secondary and apical pseudo-

Table 1 Characteristics of the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula*.

	<i>Crucidentricula</i>	<i>Denticulopsis</i>	<i>Neodenticula</i>
Morphology			
Punctuation	Coarse (0.4-0.55 μm in diameter)	Fine (less than 0.1 μm in diameter)	Very fine (indiscernible in LM)
Location of Marginal ribs	Between each two transapical striae on both sides	Between each two pseudosepta on both sides	Formed by branching of pseudosepta, only on raphe side
Location of portulae of raphe	About two between each two pseudosepta	One between each two pseudosepta	One between each two marginal ribs
Raphe slit	Divided	Divided	Continuous
Stratigraphic range	17.8-10.6 Ma	16.4-7.9 Ma	7.2-0 Ma
Ancestor	<i>Nitzschia</i> <i>maleinterpretaria</i>	<i>a Nitzschia</i> species resembling <i>N. challengerii</i>	<i>Nitzschia rolandii</i>
Geographic distribution	Originally and mainly in the low-latitude, later expanded to the middle- to high-latitude	Originally and mainly in the middle- to high- latitude, later expanded to the low-latitude	Endemic in the high- latitude in the Northern Hemisphere

septa.

Secondary pseudoseptum: This pseudoseptum is differentiated from the primary pseudoseptum in that it does not penetrate very deeply and that it lacks a basal ridge. It is present only in some limited species.

Apical pseudoseptum: This term was proposed by MARUYAMA (1988) for a shallow pseudoseptum which is recognized near the apex in some valves of *Denticulopsis lauta* and its related species. It is very similar to the secondary pseudoseptum in lacking a basal ridge, but differs from the latter in that it is located only near apex and not located between primary pseudosepta and that it is not present all valves of *D. lauta*. This pseudoseptum is also recognized in *D. praedimorpha*, *N. kamtschatica* and their related taxa.

Apical costa: This structure is a shallow costa situated near each apex, consisting of a transapical costa and two or three longitudinal costae running to the apex. MARUYAMA (1984a, 1988) called these longitudinal costae "apical branchings".

Marginal rib: This is a short thickening which protrudes inward from the valve mantle between pseudosepta. Though this structure was originally named a "marginal rib-like wall thickening" by SIMONSEN and KANAYA (1961), it is here termed merely a marginal rib for simplicity. The distribution pattern of marginal ribs is one of the most diagnostic features that distinguish the three genera (Table 1; AKIBA and YANAGISAWA, 1986).

Deck: This is a plate, which would correspond to the deck of ship if the valve of *Denticulopsis* were a ship. The deck is sometimes isolated (Pl. 8, Fig. 16).

Chamber: This is a space or interval formed between each two primary pseudosepta (MARUYAMA, 1988).

Raphe: The raphe of normal vegetative valve is situated along the valve edge, but that of the initial valve is located along the valve center (Pl. 2, Figs. 38, 44, 45; Pl. 3, Fig. 29; Pl. 5, Figs. 20, 42; Pl. 9, Figs. 10, 11; Pl. 10, Figs. 3-9). The raphe canal is a round tube with inner portulae. The raphe of *Crucidentricula*

or *Denticulopsis* is interrupted at the middle, divided into two branches of raphe, whereas that of *Neodenticula* is continuous. Indistinct central and terminal pores of raphe are observed by SEM. The distribution pattern of portulae is unique to each of the three genera (Table 1; AKIBA and YANAGISAWA, 1986).

Punctuation: The valve face and valve mantle are perforated by puncta which form transapical striae. The puncta are arranged in clear quincunx so that oblique rows are formed in *Denticulopsis*, *Neodenticula* and the younger group of *Crucidentricula*, whereas those of the older group of *Crucidentricula* are in non-quincunx arrangement. The size of puncta is one of the most important features that distinguish the three genera (Table 1). The puncta of *Crucidentricula* are large enough to recognize their shape in ordinary LM observation, with each punctum occluded by a cross-shaped rota. The puncta of *Denticulopsis* are fine, but they are easily discernible in LM with high magnification. *Denticulopsis* has two types of punctuation; single- and double-layered types. The former (S-type) is a single perforated wall (Pl. 12, Fig. 4), whereas the later (D-type) is composed of outer fine perforation and inner coarse punctuation (Pl. 9, Fig. 7; Pl. 12, Figs. 15, 16). The puncta of *Neodenticula* are too fine to recognize in ordinary LM observation. They can be seen only by oblique illumination in LM (Pl. 7, Figs. 30, 37).

The distribution patterns of puncta on the valve face can be classified into the following three basic types; full punctuation, reduced punctuation and hyaline (the absence of puncta) (Fig. 6).

Cingulum: The cingulum of the three genera is basically composed of a **copula** (intercalary band) and three **pleurae** (connecting bands) (Fig. 3). Since this diatom group was previously believed to possess only a single band in its theca (SIMONSEN, 1979), the copula has been erroneously called a connecting band (AKIBA, 1979, 1982; MARUYAMA, 1984a).

The copulae of the three genera are classi-

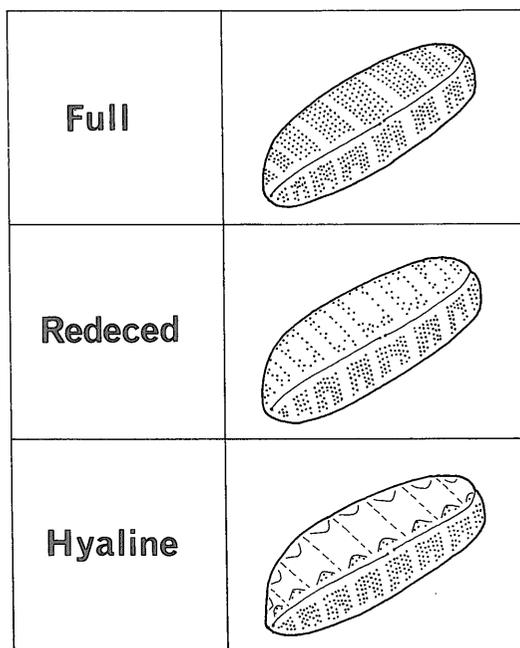


Fig. 6 Distribution patterns of puncta on valve face.

fied into four types as follows (Fig. 7):

- open band with non-punctated sides (Con)
- open band with punctated sides (Cop)
- closed band with a serrate edge (Ccr)
- closed band with a smooth edge (Ccm)

The copula has a **septum-like plate** (GOTOH, 1984), a plate projecting in valvar plane from the edge of copula into the valve interior (Fig. 4, M). This plate has **pairs of inner extensions** (KANAYA, 1959), which correspond to the basal ridges of valve and combine the valve and copula (Fig. 7, Con). In *Denticulopsis dimorpha* and *D. ovata*, these extensions extrude from both sides to form a **cross rod** (Fig. 7, Ccm). The cross rods are also developed partially in *D. praedimorpha* var. *robusta* and var. *intermedia*. The closed copula of the advanced varieties of *Denticulopsis praedimorpha* have a silicified inner **apical thickening** at each apex (Fig. 7, Ccr).

The pleurae are all non-punctated open

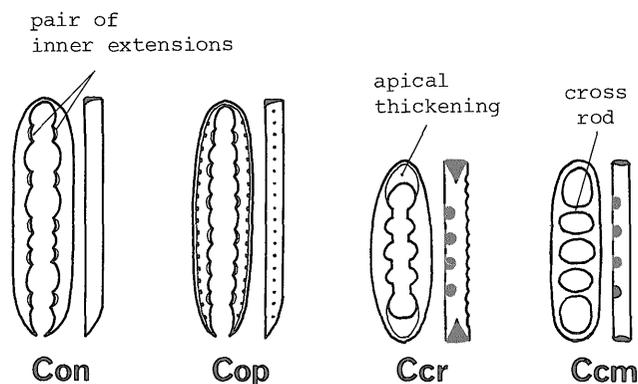


Fig. 7 Types of copula in the genera *Crucidentricula*, *Denticulopsis*, *Neodenticula* and their related species. Con: open band with non-punctated sides (*Denticulopsis simonsenii*); Cop: open band with punctated sides (*Crucidentricula sawamurae*); Ccr: closed band with a serrate edge (*Denticulopsis praedimorpha* var. *praedimorpha*); Ccm: closed copula with a smooth edge (*Denticulopsis dimorpha* var. *dimorpha*).

bands. The first and third ones (P_1 and P_3) are narrow and the second one (P_2) is broad (Fig. 3).

Each of copula and pleurae has a lingula and an antilingula at the closed apex (Fig. 4, H). The lingulae of the first and third pleurae are high and distinct, while those of copula and the second pleura are low and indistinct.

Polymorphism: Some species of *Denticulopsis* show clear polymorphism. *Denticulopsis praelauta* and probably the primitive form of *Denticulopsis lauta* have three types of frustules formed by combinations of two types of copulae (Cop, Con). Polymorphism of *Denticulopsis praedimorpha*, *D. barronii* and *D. dimorpha* is more complicated due to the

combinations of three types of copulae (Cop, Ccr and Ccm). In addition, these species have two types of valves; Types V_0 and V_c (Table 2). The V_0 valve combines with open copula, whereas the V_c valve corresponds to closed copula. These V_0 and V_c valves are called shallower and deeper valves, respectively by AKIBA (1979, 1982) and MARUYAMA (1984a). However, their terminology is inadequate because the two types of valves are not much different in depth.

The three types of copulae might theoretically form nine (3×3) combinations in frustule (Table 3). However, not all of them have been recognized so far.

Table 2 Valve types in *Denticulopsis praedimorpha*, *D. barronii*, *D. dimorpha* and *D. ovata* with their corresponding copulae.

Type of valve	Corresponding copula	AKIBA (1979, 1982) MARUYAMA (1984 a)
V_0	Cop	shallower valve
V_c	Ccr, Ccm	deeper valve

Table 3 Frustule types formed by combination of three types of copulae in *Denticulopsis praedimorpha*. Numbers indicate plate-figure numbers in this paper.

Hypocopula	Epicopula		
	Cop	Ccr	Ccm
Cop	Pl. 4-5	—	—
Ccr	Pl. 4-17	Pl. 4-35	+
Ccm	Pl. 5-10	Pl. 5-11	Pl. 5-12

+ : recognized,

— : not recognized at present

IV. Stratigraphic ranges

Tables 4-6 present the stratigraphic occurrence charts of the taxa of *Denticulopsis*, *Crucidenticula* and *Neodenticula* with some related and marker species at DSDP Holes 438A, 438B, 77B and 71, respectively. For Holes 438A and 438B, the North Pacific diatom zones of AKIBA (1986) are utilized with slight modification of age controls of the Middle to Late Miocene after ODA (1986). The low-latitude diatom zones of BURCKLE (1972) and BARRON (1983, 1985a, b) are applicable for DSDP Holes 71 and 77B.

As stated by BARRON (1985b), late Cenozoic diatom stratigraphic studies have developed different zonations for three main areas of the oceans: the middle- to high-latitude North Pacific, the low-latitude areas (eastern equatorial Pacific and tropical Indian Ocean) and the Southern Ocean (Antarctic and sub-Antarctic), because each area contains largely an endemic diatom assemblage. In this paper, therefore, the stratigraphic range of the taxa of the genera *Crucidenticula*, *Denticulopsis*, *Neodenticula* and their related species are shown separately for these three areas, using different biostratigraphic zonations.

Figure 8 shows summarized stratigraphic ranges of taxa treated in this paper in the middle- to high-latitude North Pacific. This figure is based on this study at DSDP Holes 438A and 438B and several previous studies (AKIBA and ICHINOSEKI, 1983; BARRON, 1985b, AKIBA, 1985, 1986, KOIZUMI and TANIMURA, 1985). The Miocene North Pacific diatom assemblage is represented by the abundant occurrence of highly diversified *Denticulopsis* species. The genus *Crucidenticula* is lower in abundance and less diversified than in the low-latitude area. From the Pliocene through the Quaternary, the abundant occurrence of the genus *Neodenticula* characterizes the diatom assemblage in this region.

Figure 9 presents stratigraphic ranges of the taxa of *Denticulopsis*, *Crucidenticula* and their

related species in the low-latitude area. This is mainly based on this study at DSDP Holes 71 and 77B, as well as those of BARRON (1983, 1985a, b). In the low-latitude areas, a number of *Crucidenticula* species occur abundantly in the Lower to Middle Miocene sequences, whereas *Denticulopsis* is apparently lower both in diversity and abundance than in the middle- to high-latitude North Pacific. No *Neodenticula* species occurs in this region.

As we have not yet thoroughly examined the Southern Ocean diatom assemblage, stratigraphic ranges of the taxa treated in this study are compiled for the Southern Ocean (Fig. 10) from previous biostratigraphic studies at DSDP Site 278 (SCHRADER, 1976), Site 266 (MCCOLLUM, 1975; WEAVER and GOMBOS, 1981) and Sites 512, 513 (CIESIELSKI, 1983), utilizing the Southern Ocean diatom zonation of WEAVER and GOMBOS (1981). Since the Miocene diatom assemblage in the Southern Ocean has very similar composition to that in the North Pacific except for several endemic species, the North Pacific diatom zonation may be employed to the Miocene intervals of the Southern Ocean (BARRON, 1985b). The stratigraphic distributions of *Denticulopsis* and *Crucidenticula* in the Southern Ocean are essentially equal to those in the middle- to high-latitude North Pacific. However, the Pliocene and Quaternary diatom assemblages are fundamentally different between the two areas; *Neodenticula* species, the most important constituents in the North Pacific diatom assemblage, are absent in the Southern Ocean.

V. Geographic distribution

The Recent planktonic diatom assemblage exhibits distinct latitudinal provincialism in the oceans (KANAYA and KOIZUMI, 1966). During the Miocene, however, the provincialism was not so severe as at present (SANCETTA, 1978); for example, there are many common species between the North Pacific and the Southern Ocean diatom assemblages

Table 4 Occurrences of taxa of the genera *Denticulopsis*, *Crucidentricula*, *Neodenticula* and their related species in DSDP Hole 438A. *Denticulopsis lauta* group includes *D. lauta*, *D. ichikawae* and *D. okunoi*. *Denticulopsis hyalina* group includes *D. tanimurae*, *D. praehyalina*, *D. hyalina* and *D. miocenica*. *Denticulopsis simonsenii* group includes *D. simonsenii*, *D. vulgaris*, *D. praekatayamae*, *D. katayamae*, *D. hustedtii* and *D. ovata*.

Diatom zones	Core-Section, Interval (cm)	Hole 438A														
		<i>Neodenticula kamtschatica</i>	<i>N. koizumii</i>	<i>N. sp. A</i>	<i>N. seminae</i>	(Open copula of <i>Neodenticula</i>)	(Closed copula of <i>Neodenticula</i>)	<i>Thalassiosira antiqua</i>	<i>Actinocyclus oculatus</i>	<i>Rhizosolenia curvirostris</i>	<i>Nitzschia reinholdii</i>	<i>N. marina</i>	<i>N. fossilis</i>	<i>Pseudoemotia doliolus</i>	<i>Thalassiosira oestrupii</i>	Resting spore of <i>Chaetoceros</i>
<i>N. seminae</i>	1-2, 80-82	-	-	-	8	-	44	-	-	-	-	-	-	-	3	124
<i>Rhizosolenia curvirostris</i>	2-1, 10-14	-	-	-	8	-	17	-	-	1	1	1	-	-	2	125
	2-1, 96-98	-	-	-	2	-	13	-	-	1	-	-	-	2	2	157
<i>Actinocyclus oculatus</i>	2-5, 5-9	1	1	-	3	-	8	-	-	3	2	+	-	1	1	61
	3-1, 31-33	-	-	-	3	-	7	-	+	-	-	+	-	2	4	84
	3-3, 140-142	1	-	3	22	-	75	-	-	17	-	-	-	1	1	42
	3-4, 10-14	-	-	3	24	-	99	-	3	10	+	+	-	-	1	43
3cc	-	-	4	17	-	48	-	15	1	2	-	-	-	5	386	
<i>Neodenticula koizumii</i>	4-1, 40-74	-	1	16	28	8	98	1	11	-	+	+	-	-	3	234
	4-4, 8-12	2	2	6	13	3	22	1	1	-	-	+	2	-	+	140
	5-2, 96-100	-	37	49	-	59	-	+	+	-	+	-	-	-	2	48
	5cc	-	23	61	-	53	-	+	1	-	+	-	-	-	-	18

Note: This table also includes occurrences of some zonal marker species, but those of other species recognized in this hole are omitted for simplicity. Numbers represent valve numbers during routine 100 count. However, numbers of resting spores of *Chaetoceros* and copulae of some *Denticulopsis* and *Neodenticula* species indicate individuals encountered during 100 count of valves; + indicates valves encountered after the count; - indicates absence.

of the Miocene. However, the detailed Miocene diatom biogeography of the oceans is poorly understood at present due to the lack of thorough studies concerning this theme.

In order to understand the geographic distribution of each taxon treated in this paper, three major provinces are roughly classified according to the regions used in the biostratigraphic part (Table 7): the middle- to high-latitude Northern Hemisphere, the low-latitude area and the Southern Ocean.

The middle- to high-latitude Northern Hemisphere includes the middle- to high-latitude circum-North Pacific (Northwest Pacific, high-latitude North Pacific and Northeast Pacific), the middle- to high-latitude North Atlantic (Norwegian Sea, Atlantic coast of the United States), and the Mediterranean and Paratethys. The low-latitude region contains the eastern equatorial Pacific and the tropical Indian Oceans. The Southern Ocean is composed of the Indian, Pacific and

	32-1, 24-28	- - - - -	+ - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - 2 41 2	- - - 6 + + 15
	33-1, 120-124	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 2 12 37 2	- - - 2 1 2 - 8
	34-1, 22-24	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 3 13 34 2	- - - 1 1 2 - 12
	35-1, 24-28	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 1 6 50 2	- - - 1 2 + 14
	35-3, 24-28	- - - + -	- - - - -	+ - - - -	- - - - -	- - - - -	- - - - -	- + 8 40 2	- + + 2 8 - 47
	35-6, 24-28	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 5 35 +	- - - 2 2 - + 76
	36-1, 32-36	- - - - -	- - - - -	- - - - -	- - - 1 -	- - - - -	- - - - -	- 18 20 +	- - - + - 1 - 22
	36-3, 32-36	- - - 1 -	- - - - -	1 - - - -	- - - - -	1 - - - -	- - - - -	- 6 11 +	- + - - 2 + 14
	37-3, 10-14	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 2 26 3 +	- 4 - - 5 + 23
	38-1, 11-15	- - - - -	- - - - -	- - - - -	- - - - 2	- - - - +	- - - - -	- 9 3 +	- + - - 11 - 31
	39-2, 11-15	- - - - -	- - - + -	- - - - -	- - - - -	- - - - -	- - - - -	- 8 10 +	- 3 - - 3 - 25
	40-2, 20-24	- - - - -	- - - + 1	+ - - - -	- - - - -	- 1 + - -	- - - - -	- 3 3 2 1	- + - - 1 + 24
	40-6, 10-14	- - - + -	- - - + -	+ - - - +	- - - - -	- - - - -	- - - - -	- 5 15 17 2	- + - - + + 19
	41-1, 45-49	- - - + -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 8 6 10 1	- - - - 3 + 14
	41-3, 30-34	- - + - -	- - + - -	- - - + -	- - - - -	+ + - - -	- - - - -	- 2 2 6 +	- + - - + 1 13
	41-6, 10-14	- - - - -	- - - + -	+ - - - +	- - - - -	- - - - -	- - - - -	- 13 7 2 +	- + - - 4 - 26
	41cc	- - - - + - + -	+ - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- 2 5 4 +	- 1 - - + + 55
<i>Rouxia californica</i>	42-1, 14-18	- - - - -	- - - + -	2 + - + + +	- - - + -	- - - + -	- - - - -	+ 2 + + -	- 4 - - + + 95
	42-1, 90-91	- - - - -	- - - 1 -	+ + + + +	- - - + +	- - - + +	- - - - -	- 1 + + +	- 5 - - 1 + 39
	42-2, 95-96	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -	- + + + -	- 9 - - 6 + 33
	42-3, 15-16	- - - + -	- - - + -	+ - - - -	- - - - -	- - - - -	+ - - - -	- 2 + + +	- 5 - - 1 + 52
	42-4, 50-54	- - - - -	- - - + +	+ - - - -	- - - - -	- - - - -	- - - - -	- + 1 + +	- 7 - - + - 52
	42-4, 73-74	- - - - -	- - - + -	+ - - - -	- - - - -	- - - - -	- - - - -	- 2 2 + -	- 2 - - + - 78
	42-5, 100-101	- - + - -	- - - + -	1 - - - -	- - - - -	- - - + -	- - - - -	- 2 + + -	+ 5 - - - 68
	42-6, 16-20	- - - - -	- - - + -	+ + - - -	- - - - -	- - - - -	- - - - -	- 3 3 + -	- 5 - - 2 - 100
43-1, 59-63	- - - + -	- - - + -	+ - - - +	- - - - -	- - - + -	- - - - -	- 2 + + -	+ 5 - - 1 - 120	
43-3, 30-34	- - - + -	- - - - -	- - - + -	- - - - -	- - - + -	- - - - -	- 5 + + -	- + - - + - 97	
<i>Thalassionema schraderi</i>	43-6, 82-86	- - - 1 -	- - - 1 +	+ + - - -	- - - - -	- - - - -	- - - - -	- 2 + - -	25 1 - - - 138
	44-1, 60-64	- - - + -	- - - 1 -	1 - - - + -	+ + - - +	- - - + -	- - - - -	- 10 3 - -	29 3 - - - 174
	44-3, 10-14	- - - + -	- - - + -	1 + - - -	- - - +	1 - - - -	- - - - -	- + + - -	12 3 - - - 134
	45-1, 54-58	- - - 1 -	- - - 2 -	+ + + - -	- - - + -	- - - + -	- - - + -	+ 2 + - -	36 2 - - - 170
	45-6, 30-34	- - - + -	- - - + -	1 + - - -	+ + - - +	- - - - -	- - - 1 -	- 7 - - -	26 2 - - - 237
	46-1, 18-20	- - - + -	- - - - -	+ - - - 1 -	+ + - - -	- - - - -	- - - - -	- 8 - - -	16 7 - - - 280
	46-3, 18-20	+ - - + -	- - - + -	1 - - - + -	- - - - -	- - - - -	- - - - -	- 6 - - -	19 10 - - - 225
	47-1, 10-14	- - - + -	- - - + -	1 + - - -	- - - - -	2 + + - -	- - - - -	- 2 - - -	39 5 - - - 172
	47-4, 110-114	- - - - -	- - - 1 -	+ - - - -	- - - - -	- - - 1 -	- - - - -	- 1 - - -	41 4 - - - 90
	48-1, 14-18	- - - 1 +	1 - 1 1	1 - - - 1 -	+ - - - -	- - - 1 -	- - - 2 -	- 6 - - -	15 4 - - - 203
	48-3, 46-50	- - - + -	- - - + -	2 1 1 + -	- - - - -	+ - - - +	- - - - -	- 3 - - -	18 7 - - - 266
	48-6, 26-30	- - - + -	- - - 1 -	+ + - 1 -	- - - - -	- - - - -	- - - 2 +	+ - - - -	17 1 - - - 154
	48-7, 30-31	- - - 1 -	- - - 1 -	- - - - -	- - - - -	- - - - -	- - - + -	- - - - -	16 2 - - - 220
	49-3, 10-14	- - - - -	- - - + -	1 - - - -	- - - - -	- - - - -	- - - - -	+ - - - -	9 8 - - - 162
	49-6, 10-14	- - - - -	- - - 3 -	6 2 + - -	- - - + -	- - - - -	- - - - -	- - - - -	5 5 - - - 189
49-7, 10-11	- - - + -	- - - 1 -	2 - - - -	- - - - -	- - - + -	- - - - -	- - - - -	5 5 - - - 146	
50-1, 20-24	- - - - -	- - - 3 -	3 + + 1 -	+ + - - -	- - - - -	- - - - -	- - - - -	+ + - - - 235	

Table 4 (continued)

Diatom zone	Core-Section Interval (cm)	Hole 438A	<i>Nitzschia challengerii</i>	<i>Denticulopsis praelauta</i>	<i>D. lauta</i>	<i>D. ichikawae</i>	<i>D. okumoi</i>	Girdle view of <i>D. lauta</i> group	<i>D. tanimurae</i>	<i>D. prae-hyalina</i>	<i>D. hyalina</i>	<i>D. miocenica</i>	Girdle view of <i>D. hyalina</i> group	<i>D. simonsenii</i>	<i>D. vulgaris</i>	<i>D. praekataiyamae</i>	<i>D. katayamae</i>	<i>D. hustedtii</i>	<i>D. crassa</i>	(Closed copula)	D-type girdle view } <i>D. simonsenii</i>	S-type girdle view } group	<i>D. praedimorpha</i> var. <i>minor</i>	(Closed copula)	<i>D. praedimorpha</i> var. <i>praedimorpha</i>	(Closed copula)	<i>D. praedimorpha</i> var. <i>robusta</i>	(Closed copula)	<i>D. dimorpha</i> var. <i>dimorpha</i>	(Transitional form)	(Closed copula)	<i>D. dimorpha</i> var. <i>arsolata</i>	(Closed copula)	<i>Crucidenticula ikebei</i>	<i>C. kanayae</i> var. <i>kanayae</i>	<i>C. paranicobarica</i> v. <i>paranicobarica</i>	<i>C. nicobarica</i>	<i>C. punctata</i>	<i>Nitzschia rolandii</i> (primitive asymmetric)	<i>Thalassiosira yabei</i>	Resting spore of <i>Chaetoceros</i>			
<i>Thalassionema schraderi</i>	50-3, 20-24		-	-	+	-	-	-	+	-	1	-	-	1	1	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	186	
	50-6, 20-24		-	-	-	-	-	-	1	-	1	-	-	5	3	+	-	-	-	-	+	+	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	122	
	50-7, 10-11		-	-	-	-	-	-	-	-	3	-	-	+	4	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	227	
	51-1, 16-20		-	1	-	-	-	-	-	-	3	-	-	4	1	-	-	-	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	276	
	51-4, 16-20		-	-	-	-	-	-	-	-	1	-	-	+	-	-	-	-	-	-	-	+	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	92	
<i>Denticulopsis katayamae</i>	51-6, 16-20		-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76	
	52-1, 36-38		-	-	-	-	-	-	-	-	+	-	-	1	1	2	30	-	-	-	11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	71	
	52-3, 36-38		-	-	-	-	-	-	-	-	-	-	-	+	1	2	18	-	-	-	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	62	
	52-4, 36-38		-	-	-	-	-	-	-	-	-	-	-	+	1	2	35	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	73	
	53-1, 77-81		-	-	-	-	-	-	-	-	1	-	-	+	1	3	16	-	-	-	9	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	
	54-1, 110-114		-	-	-	-	-	-	-	-	+	-	-	1	-	5	30	-	-	-	10	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19	
	54-4, 125-127		-	-	-	-	-	-	-	-	+	-	-	1	-	6	26	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	
	55-1, 70-74		-	-	-	-	-	-	-	-	-	-	-	+	-	2	23	-	-	-	12	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	170	
	55-3, 70-74		-	-	-	-	-	-	-	-	-	+	-	-	4	2	48	-	-	-	13	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	
	55-6, 76-78		-	-	+	-	-	-	-	-	-	-	-	-	+	1	46	-	-	-	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	43	
	56-1, 20-24		-	-	-	-	-	-	-	-	-	+	-	-	+	+	42	-	-	-	15	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	
	<i>Denticulopsis dimorpha</i>	56-3, 20-24		-	-	-	-	-	-	-	-	-	-	-	3	1	2	38	-	-	16	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
56-3, 60-62			-	-	-	-	-	-	-	-	1	-	-	2	+	1	4	-	-	12	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	42
56-6, 20-24			-	-	-	-	-	-	-	-	-	-	-	2	+	4	12	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18	
56CC			-	-	-	-	-	-	-	-	-	-	-	1	15	8	1	-	-	-	+	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
57-1, 115-117			-	-	-	-	-	-	-	-	-	-	-	2	1	6	1	-	-	-	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18
57-2, 31-35			-	-	-	-	-	-	-	-	1	-	-	3	1	2	+	-	-	-	+	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	
57-3, 31-35			-	-	-	-	-	-	-	-	-	-	-	2	1	2	+	-	-	-	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	
57-4, 59-60			-	-	-	-	-	-	-	-	-	-	-	+	15	+	+	-	-	-	+	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
58-1, 16-20			-	-	-	-	-	-	-	-	+	-	-	4	10	+	+	-	-	-	+	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	
58-1, 101-103			-	-	-	-	-	-	-	-	-	+	-	1	9	3	-	-	-	-	2	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	
59-1, 17-21			-	-	-	-	-	-	-	-	+	-	-	13	4	-	-	-	-	-	+	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	
59-3, 135-137			-	-	-	-	-	-	-	-	-	1	-	16	11	-	-	-	-	-	1	3	27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19
59-4, 17-21			-	-	-	-	-	-	-	-	1	-	-	17	5	-	-	-	-	-	3	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22	
59-5, 5-6			-	-	-	-	-	-	-	-	1	-	-	20	6	-	-	-	-	-	3	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	
59-5, 17-21			-	-	-	-	-	-	-	-	1	-	-	30	5	-	-	-	-	-	+	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	
<i>Thalassiosira yabei</i>		60-1, 34-38		-	-	-	-	-	-	-	+	-	-	24	1	-	-	-	-	-	+	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21
		60-1, 134-136		-	-	-	-	-	-	-	1	-	-	38	3	-	-	-	-	-	1	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	60-3, 26-27		-	-	-	-	-	-	-	-	2	-	23	1	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	64	
	60-3, 27-29		-	-	-	-	-	-	-	-	+	-	20	1	-	-	-	-	-	-	10	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76
	61CC		-	-	-	-	-	-	-	-	-	-	34	+	-	-	-	-	-	-	5	+	+	2	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
	62-1, 20-24		-	-	-	-	-	-	-	-	1	-	-	21	1	-	-	-	-	-	2	18	+	1	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	41	
	62-1, 80-81		-	-	-	-	-	-	-	-	-	1	-	24	+	-	-	-	-	-	+	43	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	

Table 5 Occurrences of taxa of the genera *Denticulopsis*, *Crucidentricula*, their related species and several zonal marker species in DSDP Hole 438B. Note: See Table 4 for explanation of numbers and symbols.

Diatom zone	Core-Section, Interval (cm)										
	Hole 438B	<i>Nitzschia challengeri</i>	<i>Denticulopsis praelauta</i>	<i>Crucidentricula ikebei</i>	<i>C. kanayae</i> var. <i>kanayae</i>	<i>Kisseleviella carina</i>	<i>Actinocyclus ingens</i> f. <i>planus</i>	<i>A. ingens</i> f. <i>ingens</i>	Resting spore		
<i>Denticulopsis praelauta</i>	6-1, 16-19	5	18	-	-	4	6	5	94		
	7-1, 128-130	+	22	-	-	8	12	7	81		
	8-1, 90-92	1	27	-	-	9	3	6	113		
	9-1, 85-87	-	2	1	-	1	23	38	36		
<i>Crucidentricula kanayae</i>	10-1, 9-10	-	-	1	5	2	6	1	69		
	11-1, 60-62	-	-	+	-	4	28	1	54		
	12-1, 81-82	-	-	-	+	11	3	1	24		
	13-1, 68-70	-	-	-	5	+	9	1	35		
	14CC	-	-	+	18	3	9	1	80		
	15-2, 61-62	-	-	2	5	-	13	2	60		
	16-1, 82-84	-	-	3	8	2	10	+	56		

Atlantic sectors.

On the basis of many biostratigraphic studies listed in Table 8, the geographic distributions of all taxa studied in this paper are presented in Table 7.

VI. Phylogenetic developments

Temporal and spatial distributions of the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula* are shown in Figure 11. Phylogenetic relationship in generic level is presented in Figure 12.

As discussed in AKIBA and YANAGISAWA (1986), the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula* have no phylogenetic relationship to each other, although they are morphologically very similar to each other and were grouped in a single genus by SIMONSEN (1979). The three genera evolved individually from the genus *Nitzschia* in different

times (Fig. 12). The genus *Crucidentricula* evolved from the genus *Nitzschia* in the late Early Miocene and disappeared near the end of the Middle Miocene. The genus *Denticulopsis* was born in the latest Early Miocene and became extinct in the early Late Miocene. The genus *Neodenticula* gradually developed from the genus *Nitzschia* in the latest Miocene, following the extinction of the genus *Denticulopsis* and is extant in the high-latitude of the Northern Hemisphere. Thus, close morphologic similarity within the three genera can be explained by evolutionary convergence.

Phylogenetic relationships in specific level are determined based on both morphologic similarity and time-and-space distribution (Fig. 13). In the following, phylogenetic developments of the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula* are briefly described. Evolutionary changes in morphology are illustrated in Figures 14-17.

Genus *Crucidentricula*

Crucidentricula is originally a low-latitude genus. It appeared in the low-latitude area in the late Early Miocene and later expanded to the high-latitudes (Fig. 11).

The origin of *Crucidentricula* can be traced to an Early Miocene diatom *Nitzschia maleinterpretaria* which possesses almost the same valve structure to that of *Crucidentricula*, except that it lacks pseudosepta. However, the ancestry of this species remains unknown at present. From *N. maleinterpretaria* evolved *Crucidentricula sawamurae*, the first species of *Crucidentricula*, by a gradual development of pseudosepta in the late Early Miocene. By the successive evolutionary changes including enlargement of valve structure, *C. sawamurae* gave rise to *C. ikebei* and *C. kanayae*. Moreover, *C. kanayae* split into two geographical varieties, var. *pacifica* and var. *kanayae*. This evolutionary lineage was geographically confined within the low-latitude at the early stage of evolution, but at its later stage it expanded its distribution to the high-latitudes, giving rise to the middle- to high-latitude

Table 6 Occurrences of taxa of the genera *Crucidentricula*, *Denticulopsis*, their related species and several zonal marker species in DSDP Holes 77B and 71. *Denticulopsis simonsenii* group includes *D. simonsenii*, *D. vulgaris* and *D. praekatayamae*. Note: See Table 4 for explanation of numbers and symbols.

Diatom Zone and Subzone	Core-Section, Interval (cm)	<i>Crucidentricula punctata</i>	<i>C. nicobarica</i>	<i>C. paranicobarica</i> var. <i>tropica</i>	<i>C. kanayae</i> var. <i>pacifica</i>	<i>C. sawamurae</i>	<i>Nitzschia maleinterpretaria</i>	<i>Denticulopsis simonsenii</i>	<i>D. vulgaris</i>	<i>D. praekatayamae</i>	Girdle view of <i>D. simonsenii</i> group	<i>Denticulopsis lauta</i>	<i>D. barronii</i> (Vc valve)	(Vo valve)	(Closed copula)	(Open copula)	<i>Actinocyclus moronensis</i>	<i>Amellus californicus</i>	<i>Cestodiscus peplum</i>	<i>Coscinodiscus lewisianus</i>	<i>Craspedodiscus coscinodiscus</i>	<i>C. elegans</i>	<i>Thalassiosira bukryi</i>	<i>T. brunii</i>	<i>T. grunowii</i>	<i>T. yabei</i>	<i>Triceratium pileus</i>	
<i>Coscinodiscus yabei</i> A	Hole 77B																											
	17-1, 18-20	-	-	-	-	-	-	1	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Actinocyclus moronensis</i>	17-6, 23-25	-	-	-	-	-	-	1	+	+	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	18-2, 23-25	-	-	-	-	-	-	1	6	+	1	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	
	18-6, 38-40	+	-	-	-	-	-	1	5	+	1	-	-	-	-	-	+	-	-	-	-	-	-	-	+	+	+	
	19-2, 38-40	-	-	-	-	-	-	16	-	-	2	-	-	-	-	-	+	-	-	-	-	-	-	-	2	+	+	
<i>Craspedodiscus coscinodiscus</i>	19-6, 38-40	-	-	-	-	-	-	1	-	+	-	-	-	-	-	-	3	-	-	-	-	-	-	-	4	2	+	+
	20-2, 38-40	1	-	-	-	-	-	2	-	-	+	-	-	-	-	-	2	-	-	-	-	-	-	-	+	+	1	
	20-4, 30-31	1	-	-	-	-	-	5	-	-	+	-	-	-	-	-	2	-	-	-	-	-	-	-	+	+	1	
<i>Coscinodiscus gigas</i> var. <i>diorama</i>	20-6, 38-40	1	-	-	-	-	-	18	-	-	-	3	3	97	2	+	+	-	-	-	-	-	-	-	-	-	-	
	21-2, 38-40	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	+	-	
	21-6, 35-37	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	+	-	
<i>Coscinodiscus lewisianus</i>	22-2, 35-37	+	6	-	-	-	-	13	-	+	-	-	-	-	-	-	1	-	-	5	-	-	-	-	+	-	-	
	22-6, 35-37	-	45	-	-	-	-	5	-	+	-	-	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	
	23-2, 35-37	-	21	-	-	-	-	+	-	-	+	-	-	-	-	-	1	-	1	2	-	-	-	-	-	-	-	
	23-6, 35-37	-	13	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	
<i>Cestodiscus peplum</i> A	24-6, 20-22	-	56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	+	-	-	-	-	-	-	-	
	Hole 71																											
	19-2, 108-110	-	1	17	-	-	-	-	-	-	-	-	-	-	-	-	-	+	1	1	1	-	-	-	-	-	-	
	19-4, 90-92	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	1	1	-	-	-	-	-	-	
	19-6, 86-88	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	1	+	-	-	-	-	-	-	
	20-2, 88-90	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	+	3	6	-	-	-	-	-	-	-	
	21-2, 89-91	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	
	21-4, 60-62	-	-	7	-	-	-	-	-	-	-	1	-	-	-	-	-	+	+	2	+	-	-	-	-	-	-	
	21-6, 91-93	-	-	26	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	2	+	-	-	-	-	-	-	
	22-2, 88-90	-	-	-	-	13	-	-	-	-	-	5	-	-	-	-	-	+	+	6	-	-	-	-	-	-	-	
	22-4, 29-31	-	-	-	-	5	-	-	-	-	-	3	-	-	-	-	-	+	1	3	+	-	-	-	-	-	-	
	22-6, 116-118	-	-	+	-	4	-	-	-	-	-	3	-	-	-	-	-	+	2	5	-	-	-	-	-	-	-	
	<i>Denticulopsis nicobarica</i> A	23-2, 117-119	-	-	6	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	1	+	-	-	-	-	-	-
23-4, 77-79		-	-	+	-	1	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	
24-2, 78-80		-	-	7	+	+	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	
24-6, 45-47		-	-	-	42	+	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1	-	-	-	-	-	
25-1, 128-130		-	-	-	44	2	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	
25-3, 96-98		-	-	-	74	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	
<i>Triceratium pileus</i>	25-5, 92-94	-	-	-	41	+	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
	26-2, 70-72	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	10	-	-	1	-	-	-	-	-	
	26-4, 70-72	-	-	-	60	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	+	-	-	-	-	2	
	26-6, 70-72	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	7	-	-	-	-	3	
<i>Craspedodiscus elegans</i>	27-1, 100-102	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	+	-	-	1	-	-	-	-	-		
	28-2, 70-72	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	5	-	+	4	-	-	-	-	2	
	28-4, 70-72	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	+	1	-	-	-	-		
	28-6, 70-72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-		
29-2, 70-72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	+	+	-	-	-	-	-		

taxa such as *C. ikebei* and *C. kanayae* var. *kanayae*. This geographic expansion coincides with a global climate optimum at the latest Early Miocene (Fig. 11). After the expansion, this lineage became extinct near the end of the Early Miocene. This extinction

is probably due to the beginning of cooling at this time.

After then, the second lineage started from *C. paranicobarica* var. *tropica* which arose from *C. sawamurae* by size reduction. This low-latitude variety gave rise to a middle-

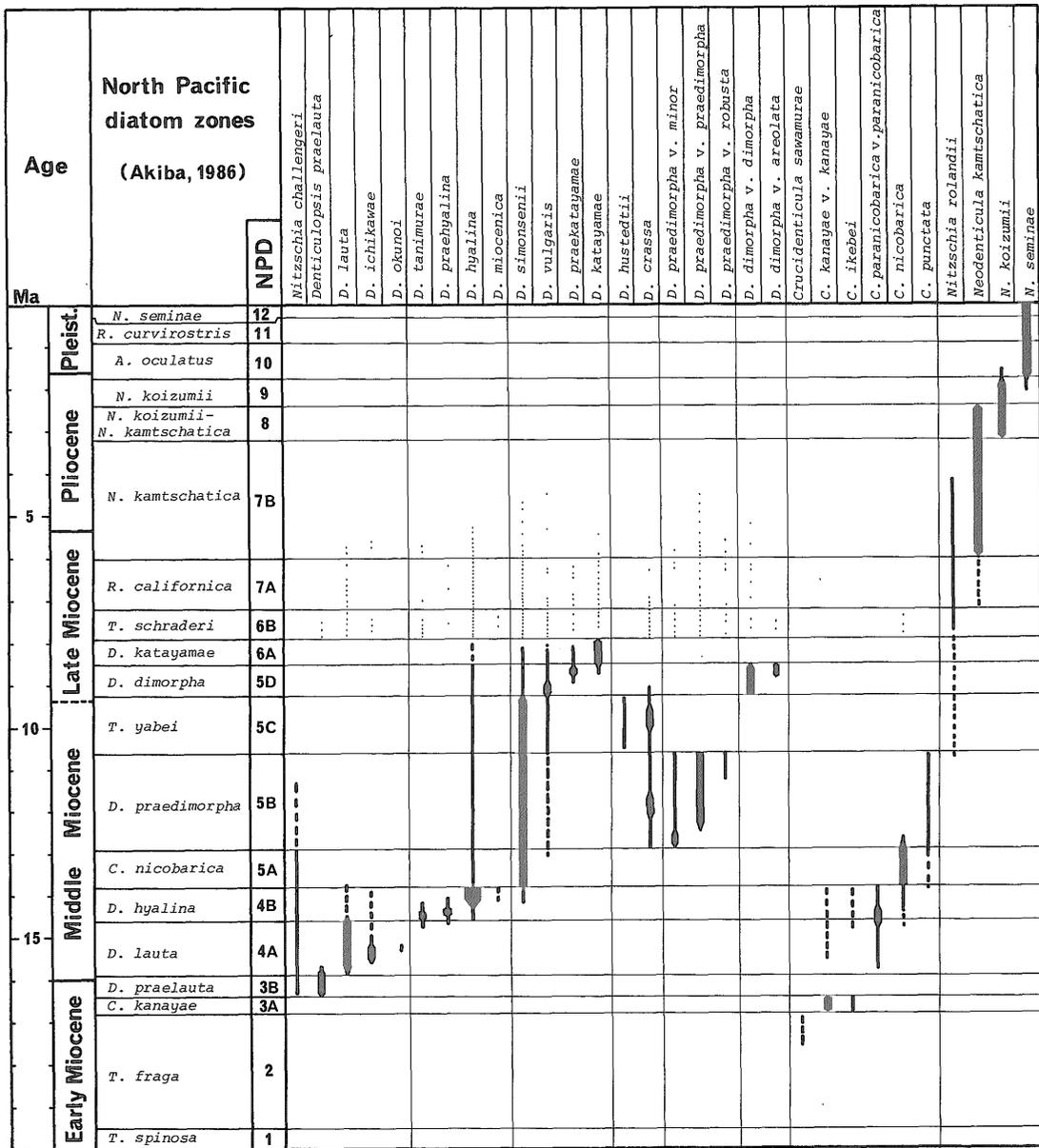


Fig. 8 Stratigraphic ranges of taxa of the genera *Denticulopsis*, *Crucidentricula*, *Neodenticula* and their related species in the middle- to high-latitude North Pacific. Width of solid line is roughly in proportion to abundance in occurrence of each taxon. Broken lines indicate sporadic occurrence. Narrow dotted lines show reworking observed in DSDP Hole 438A.

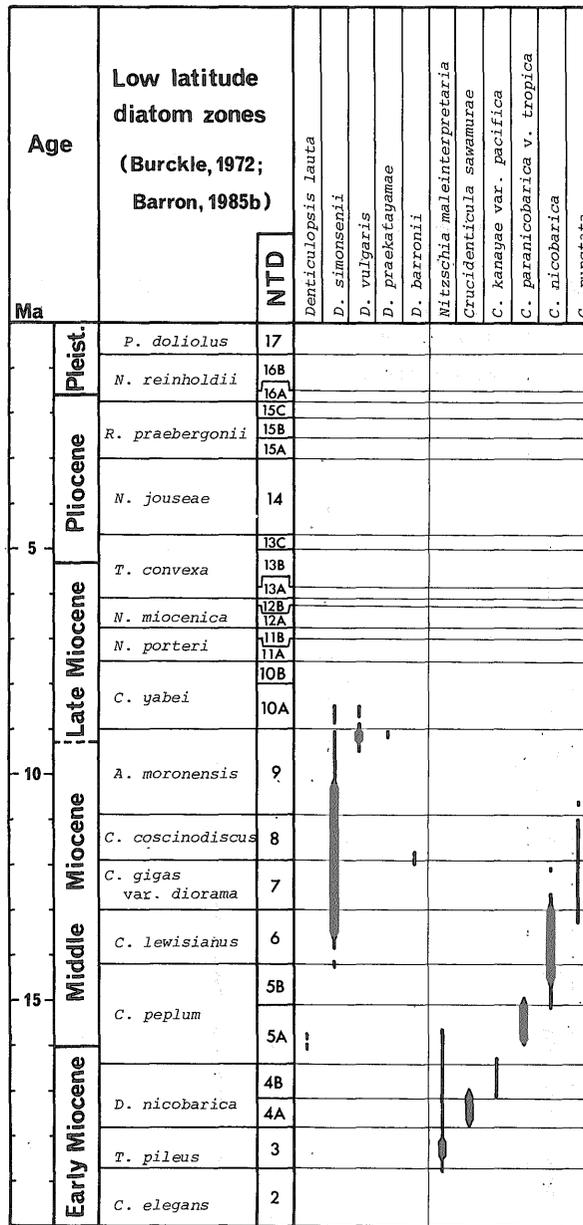


Fig. 9 Stratigraphic ranges of taxa of the genera *Denticulopsis*, *Crucidentacula* and their related species in the low-latitude Pacific. Ages of some middle Miocene diatom zones are modified after BARRON *et al.*, (1985). Width of solid line is roughly in proportion to abundance in occurrence of each taxon. Broken lines indicate sporadic occurrence.

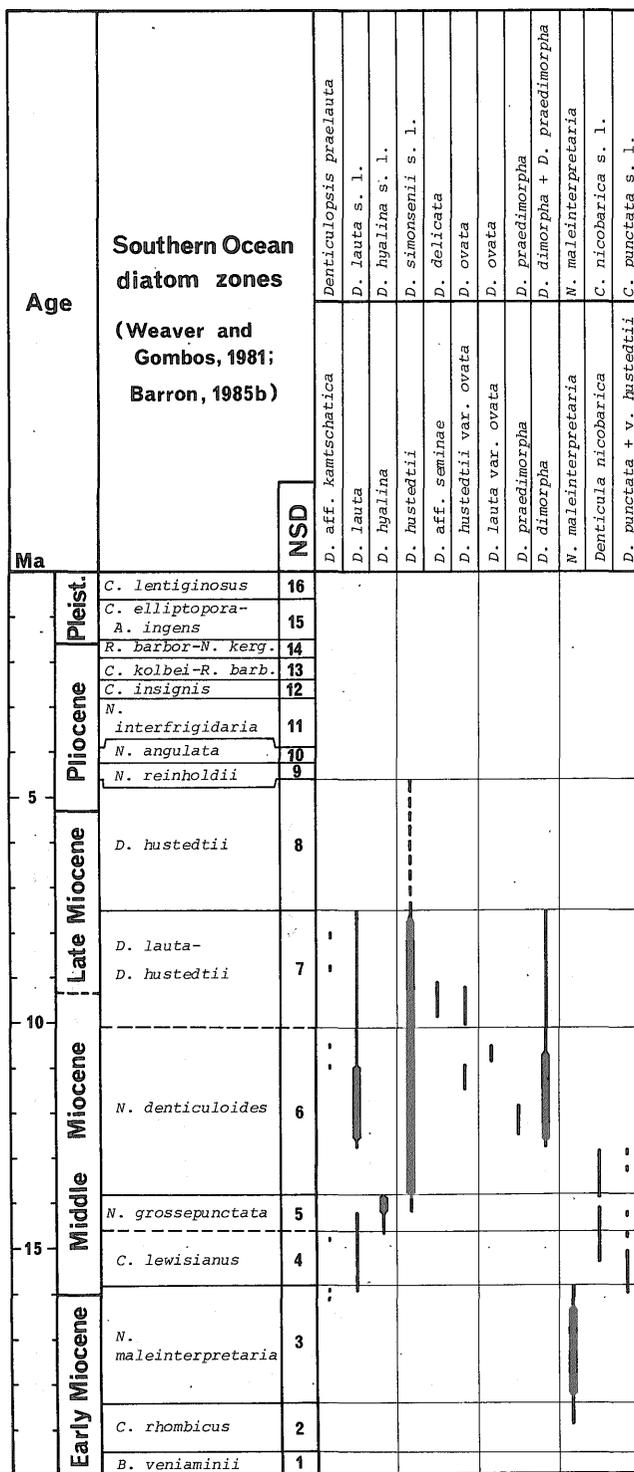


Fig. 10 Stratigraphic ranges of taxa of the genera *Denticulopsis*, *Crucidentacula* and their related species in the Southern Ocean. The figure is compiled from diatom stratigraphic records at DSDP Site 278 (SCHRADER, 1976), Site 266 (WEAVER and GOMBOS, 1981) and Sites 512 and 513 (CIESIELSKI, 1983). Lower specific names are original names used in these references, and upper ones are specific names used in this paper. Width of solid line is roughly in proportion to abundance in occurrence of each taxon. Broken lines indicate sporadic occurrence or reworking.

Diatom genera Crucidenticula, Denticulopsis and Neodenticula (Y. Yamagisawa and F. Akiba)

Table 7 Geographic distributions of taxa of the genera *Crucidenticula*, *Denticulopsis*, *Neodenticula* and their related species.

Species and varieties	Northern Hemisphere			Pacific Ocean					Indian Ocean					
	Middle- to high-latitude	Low-latitude area	Southern Ocean	Northwest Pacific	High-latitude North Pacific	Northeast Pacific	Norwegian Sea	Atlantic coast of U. S. A.	Mediterranean & Paratethys	Eastern equatorial Pacific	Tropical Indian Ocean	Indian sector	Pacific sector	Atlantic sector
<i>Nitzschia maleintrepretaria</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Crucidenticula sauwannae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. ikebei</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. kangyae</i> var. <i>pacifica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. kangyae</i> var. <i>kangyae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. paramnicobarica</i> var. <i>tropica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. paramnicobarica</i> var. <i>paramnicobarica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. nicobarica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>C. punctata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia challengeri</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Denticulopsis praelanata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. lauta</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. ichikawai</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. ohnoui</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. tamimurae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praehyalina</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. hyalina</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. miocenica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. simonsenii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. vulgarts</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praekalyaninae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. kalyaninae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. delicata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. hastadatii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. crassa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praedimorpha</i> var. <i>minor</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praedimorpha</i> var. <i>praedimorpha</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praedimorpha</i> var. <i>robusta</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. praedimorpha</i> var. <i>intermedia</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. barronii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. dimorpha</i> var. <i>dimorpha</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. dimorpha</i> var. <i>areolata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>D. ovata</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia rolandii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Neodenticula kantschatica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>N. koizumi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>N. seminiae</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
" <i>Denticulopsis</i> " <i>norvegica</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+
" <i>Denticulopsis</i> " <i>maccollumii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+

○ : abundant ; + : rare ; - : absent ; blank : no information
Note : See Table 8 for references.

Table 8 References for Table 7.

Middle- to high-latitude of the Northern Hemisphere	
Northwest Pacific	This paper ; BARRON, 1980 ; AKIBA <i>et al.</i> , 1982 ; AKIBA, 1985, 1986 ; MARUYAMA, 1984a, b ; ORESHKINA and RADIONOVA, 1987
High-latitude North Pacific	This paper ; KOIZUMI, 1973 ; ORESHKINA, 1985 ; AKIBA, 1986
Northeast Pacific	SIMONSEN and KANAYA, 1961 ; SCHRADER, 1973a, b, 1974b ; BARRON, 1975, 1976, 1981a ; BARRON and KELLER, 1983
Norwegian Sea	SCHRADER and FENNER, 1976 ; DZINORIDZE, <i>et al.</i> , 1978 ; BALDAUF, 1987 ; MONJANEL, 1987
Atlantic coast of U.S.A.	ANDREWS, 1978 ; ABBOTT, 1980, 1984 ; ABBOTT and ANDREWS, 1979 ; ABBOTT and ERNISSEE, 1983 ; POWERS, 1988
Mediterranean & Paratethys	HAJÓS, 1968, 1973, 1986 ; MONJANEL, 1987
Low-latitude area	
Eastern equatorial Pacific	This paper ; GOMBOS, 1975 ; BARRON, 1981b, 1983, 1985a
Tropical Indian Ocean	SCHRADER, 1974a
Southern Ocean	
Indian sector	This paper ; MCCOLLUM, 1975 ; WEAVER and GOMBOS, 1981 ; BARRON (personal comm.)
Pacific sector	SCHRADER, 1976 ; This paper ; AKIBA, 1982
Atlantic sector	GOMBOS, 1976 ; FENNER, 1978 ; CIESIELSKI, 1983

high-latitude variety *paranicobarica* by the reduction of puncta on valve face.

In the early Middle Miocene the third lineage started from *C. nicobarica* which itself developed from *C. paranicobarica* var. *tropica* by making clear quincunx arrangement of puncta on valve face. This evolutionary line went on evolving to *C. punctata* with enlargement of valve as a whole and terminated there

without leaving any descendants in the late Middle Miocene. This extinction of *Crucidentricula*, which is basically a warm water genus, was probably due to progressive cooling during the Middle Miocene (Fig. 11).

Genus *Denticulopsis*

Although the genus *Denticulopsis* was born in the high-latitudes, it later expanded to the

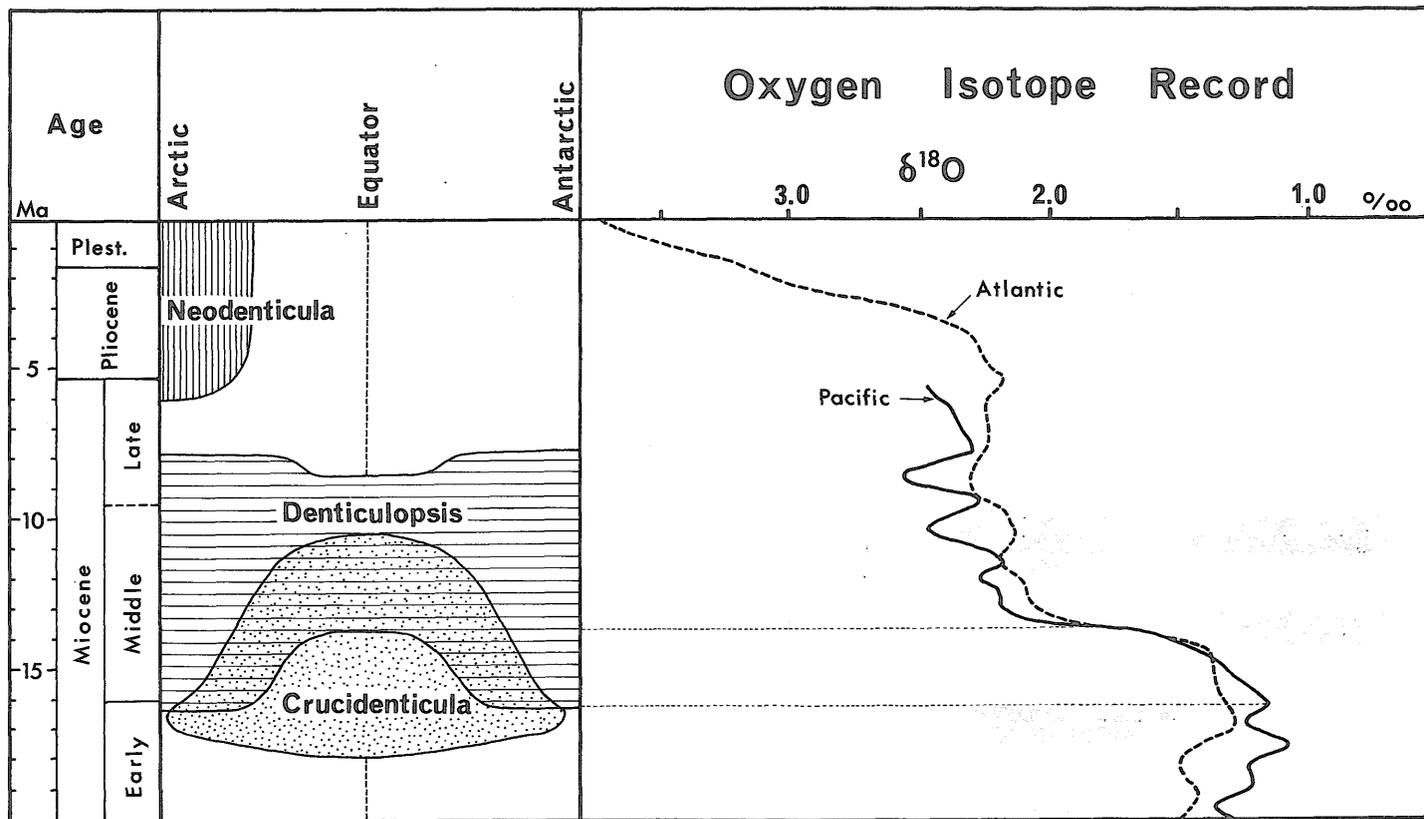


Fig. 11 Temporal and spatial distributions of *Crucidenticula*, *Denticulopsis* and *Neodenticula* with composite benthic foraminiferal oxygen isotope records for Pacific and Atlantic DSDP sites (MILLER *et al.*, 1987).

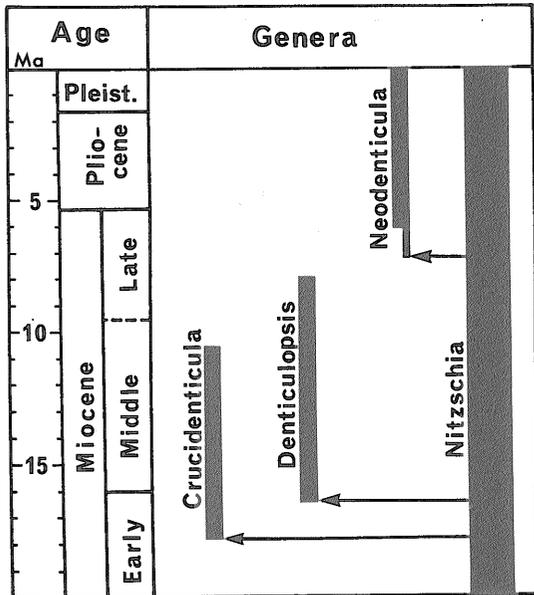


Fig. 12 Evolution and stratigraphic distribution of the genera *Crucidentacula*, *Denticulopsis* and *Neodenticula*.

low-latitudes and became a cosmopolitan diatom genus (Fig. 11).

Near the beginning of the Middle Miocene, *Denticulopsis praelauta*, the oldest species of *Denticulopsis*, arose abruptly in the stratigraphic records of the middle- to high-latitude areas of both Northern and Southern Hemispheres. This sudden appearance of *Denticulopsis* just coincides with the initiation of Middle Miocene cooling following the latest Early Miocene climate optimum (Fig. 11). Although the ancestor of *D. praelauta* remains unknown at present, it is likely that the ancestry of this species may be a small *Nitzschia* species resembling *N. challengeri*, because of close morphologic affinities between the two species. *D. praelauta* evolved from the unknown ancestor by acquiring primary pseudosepta with basal ridges, and it started the first evolutionary lineage reaching to *D. okunoi* through *D. lauta* and *D. ichikawae*. This lineage evolved rapidly by the development of marginal rib (*D. praelauta* to *D. lauta*),

the reduction of puncta on valve face (*D. lauta* to *D. ichikawae*) and a change in valve outline to oval form (*D. ichikawae* to *D. okunoi*), and then stopped there.

All species of this lineage are distributed mainly in the middle- to high-latitudes, except for a transient invasion of *D. lauta* into the low-latitude.

During the early Middle Miocene after the termination of the first *Denticulopsis* lineage at *D. okunoi*, three major evolutionary lineages radiated successively from *D. lauta* in various morphologic directions.

The first lineage led from *D. tanimurae* to *D. miocenica* through *D. praehyalina* and *D. hyalina*. This lineage originated from *D. lauta* through strong silicification associated with development of double-layered punctation on valve mantle. It shows tendencies to reduce the punctation on valve face (*D. tanimurae* to *D. praehyalina* to *D. hyalina*) and to change valve outline to oval form (*D. hyalina* to *D. miocenica*). The constituents of this lineage are all middle- to high-latitude species. Although this lineage terminated at *D. miocenica*, *D. hyalina* persisted up to the Late Miocene with very rare abundance. However, this persisted occurrence of *D. hyalina* is possibly due to reworking.

The second is a lineage that started from *D. simonsenii*, which itself evolved from *D. lauta* by creation of secondary pseudosepta. This lineage is composed of one principal lineage and two subordinate short lineages. The principal lineage led from *D. simonsenii* to *D. katayamae* via *D. vulgaris* and *D. praekatayamae* through successive reduction of puncta on valve face and gradual silicification associated with development of double-layered punctation on valve mantle. This lineage was born in the middle- to high-latitudes at ca. 14.5 Ma. After a brief incursion into the tropics just after 14.5 Ma, it was introduced into the low-latitude area from the middle- to high-latitudes at ca. 14 Ma, probably in response to severe polar cooling in the early Middle Miocene (Fig. 11; BARRON, 1986), and

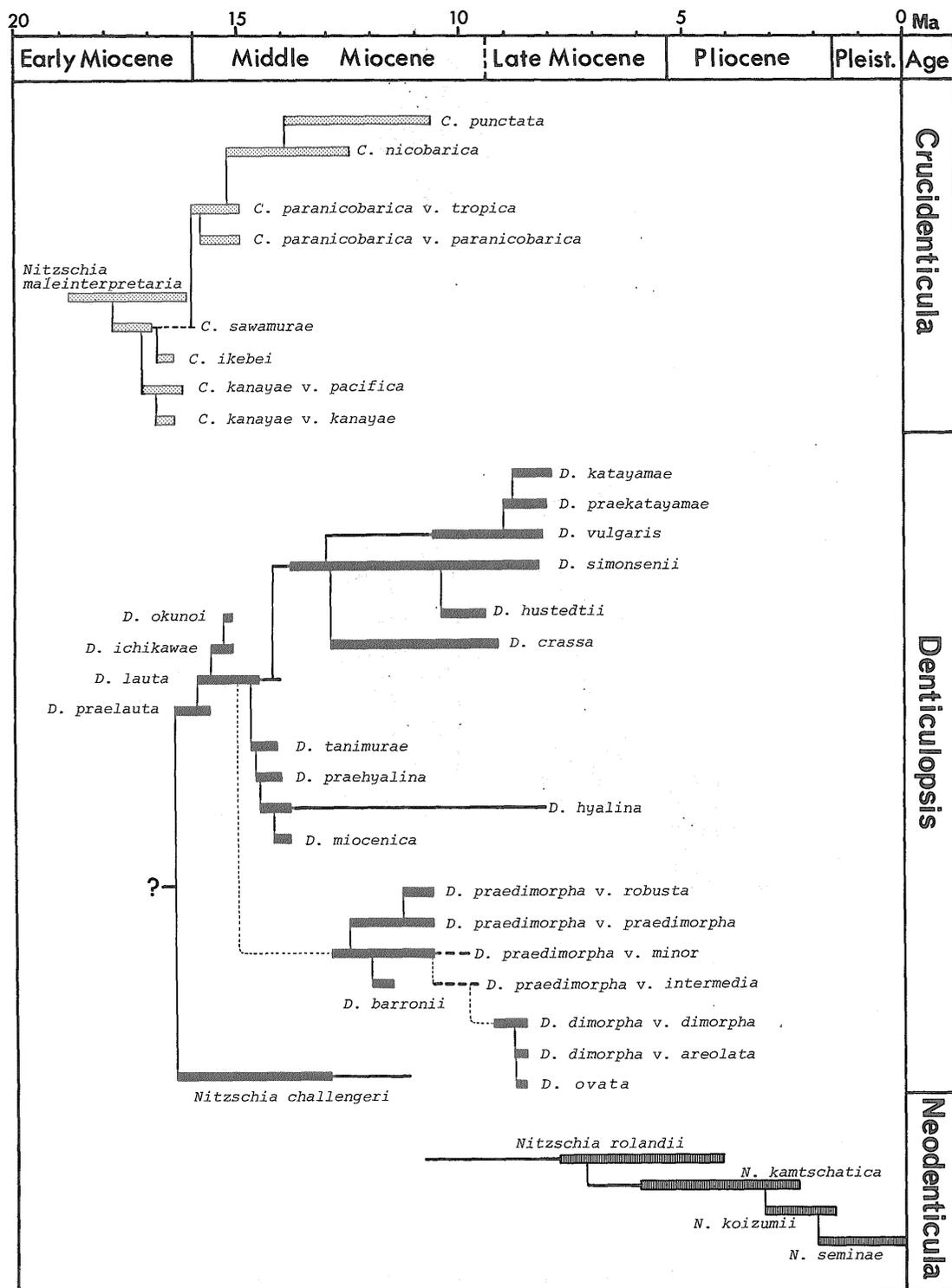


Fig. 13 Evolutionary lineages of the genera *Crucidentricula*, *Denticulopsis* and *Neodenticula*.

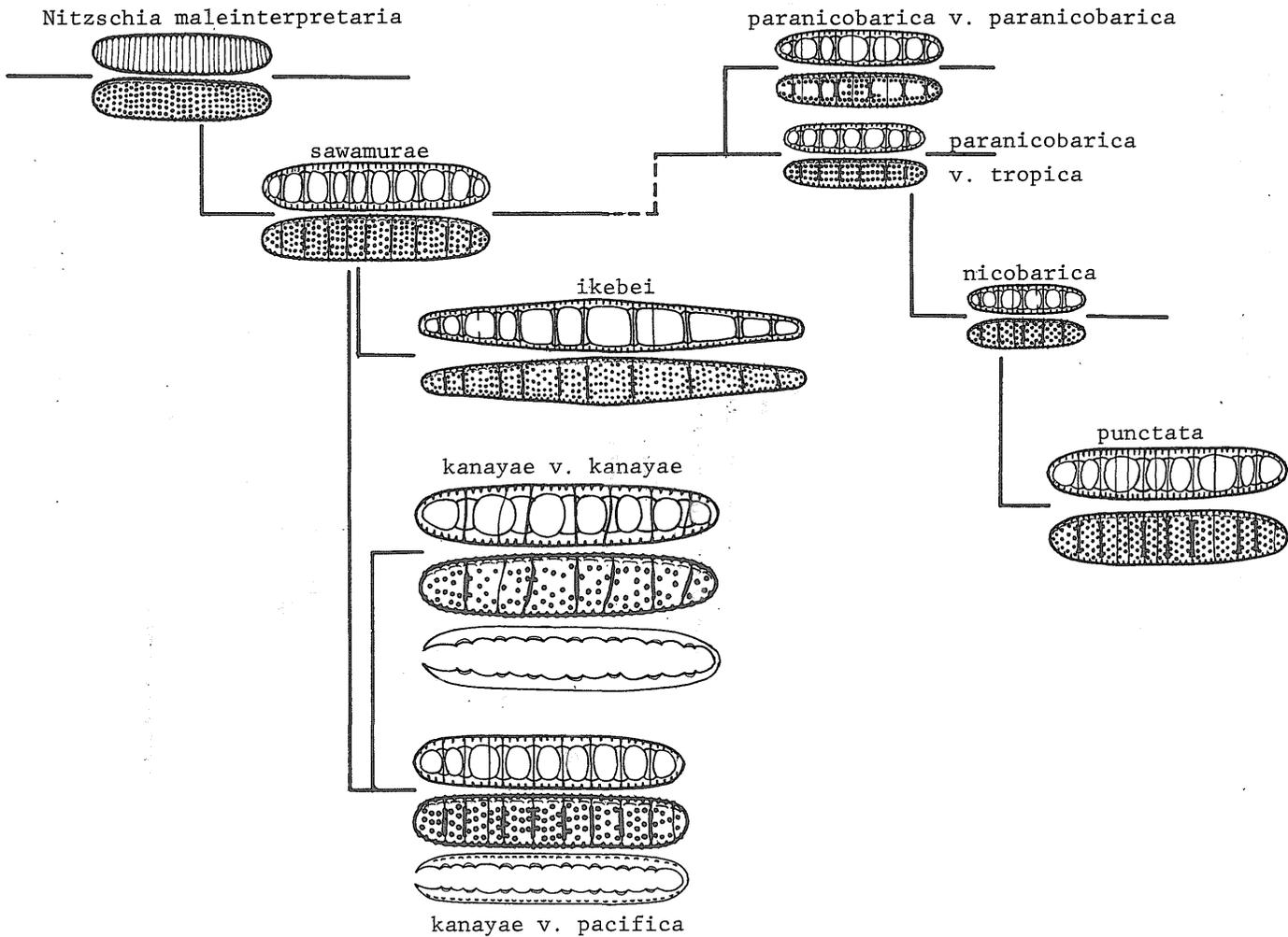


Fig. 14 Evolutionary lineages of the genus *Nitzschia*.

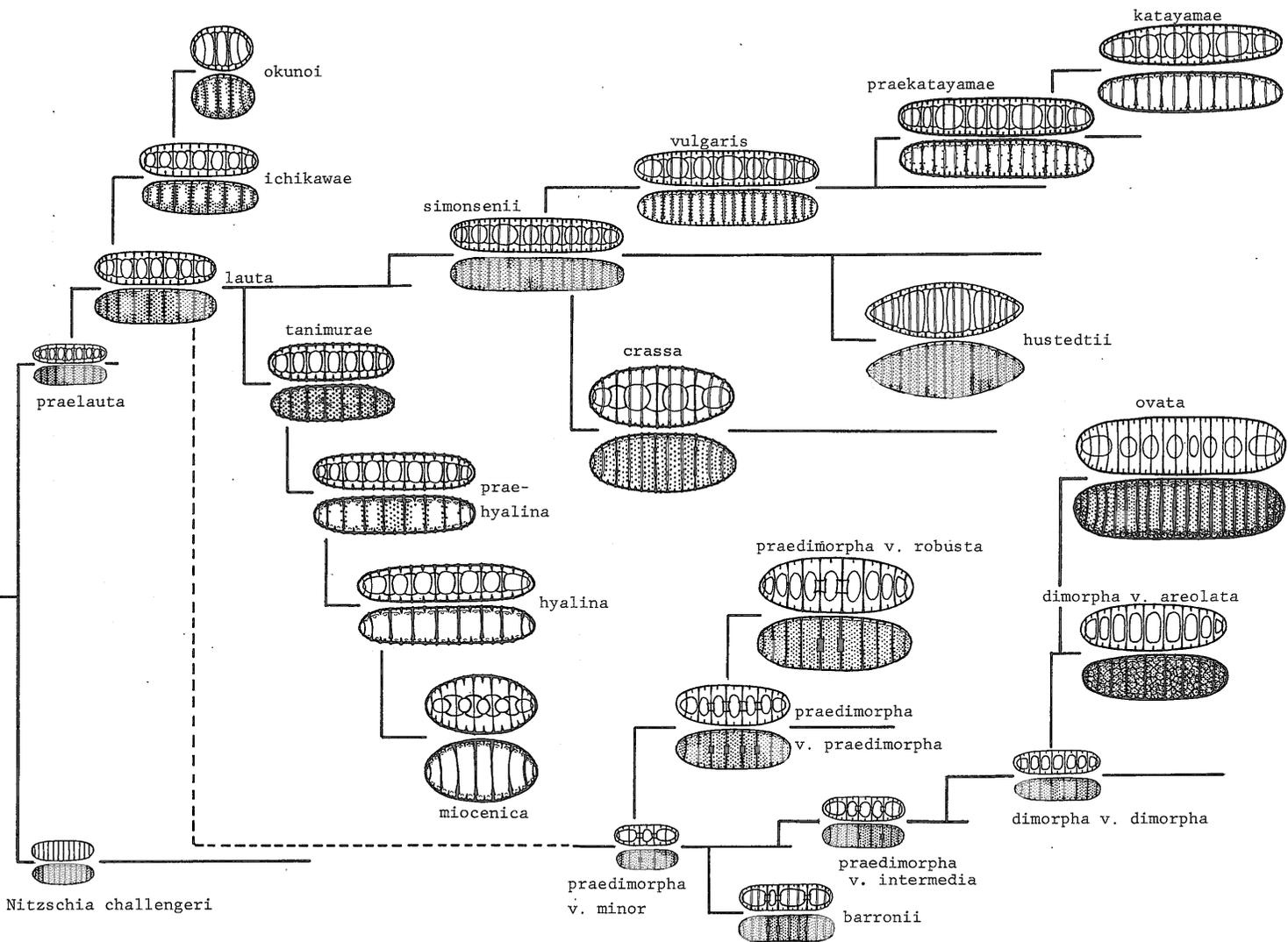


Fig. 15 Evolutionary lineages of the genus *Denticulopsis*. Only Vc type valves are illustrated for *Denticulopsis praedimorpha*, *D. barronii*, *D. dimorpha* and *D. ovata*.

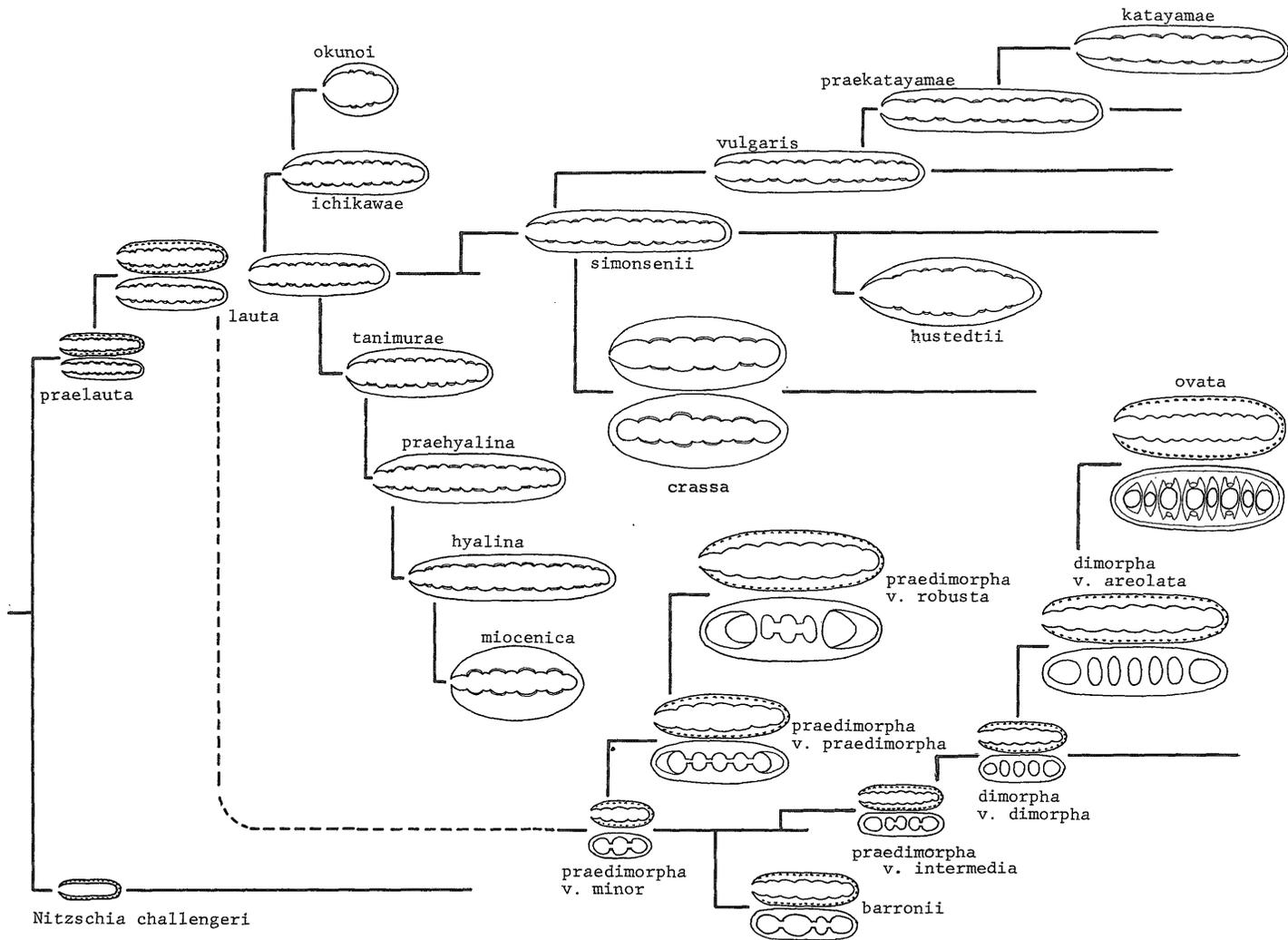


Fig. 16 Evolutionary change in morphology of copula of the genus *Denticulopsis*.

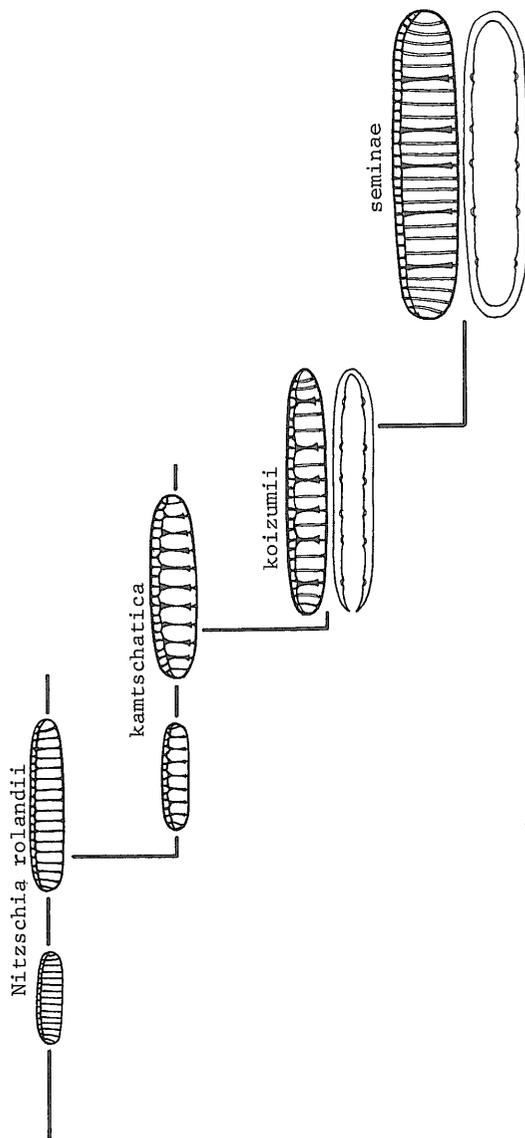


Fig. 17 Evolutionary lineage of the genus *Neodenticula*.

it became established as one of the most common diatom group in the Middle Miocene tropical diatom assemblage. Thus the lineage became a cosmopolitan diatom group distributed both in the high- to middle latitudes and the low-latitude, except for the last member *D. katayamae* which is restricted to

the middle- to high-latitude.

A short lineage from *D. simonsenii* to *D. crassa* is characterized by a morphologic change to oval valve outline, thick silicification and development of closed copula. Another short lineage which led from *D. simonsenii* to *D. hustedtii* shows a phylogenetic trend of changing valve outline from linear to lanceolate form. Both lineages are geographically confined to the middle- to high-latitudes.

The third lineage which has its origin in *D. lauta* is a group of *Denticulopsis praedimorpha*. It appears to have arisen from the primitive form of *D. lauta* by creation of closed copula, although a stratigraphic gap exists between the ranges of the two species. *D. praedimorpha* var. *minor*, the first element of this lineage, appeared in the early Middle Miocene, and rapidly evolved into var. *praedimorpha* through an increase in size and the development of apical thickening of closed copula. The latter variety further developed into var. *robusta* by further enlargement of valve and the partial formation of cross rod in closed copula. On the other hand, *D. barronii* branched off from *D. praedimorpha* var. *minor* by making secondary pseudosepta in Vc type valve. Moreover, with gradual development of cross rods in closed copula, *D. praedimorpha* var. *minor* gave rise to *D. praedimorpha* var. *intermedia*, which is a link to the next *D. dimorpha* lineage. The *D. praedimorpha* lineage is originally and mainly a middle- to high-latitude group, although it includes a tropical species, *D. barronii*.

The next lineage started from *D. dimorpha* var. *dimorpha*. This lineage descended from *D. praedimorpha* var. *intermedia* by developing complete cross rods of closed copula. Stratigraphic and geographic data indicate that *D. dimorpha* lineage was first established in the Southern Ocean during the late Middle Miocene and later migrated to the middle- to high-latitude in the Northern Hemisphere. This evolutionary line consists of *D. dimorpha* var. *dimorpha*, *D. dimorpha* var. *areolata* and

D. ovata. The evolution from *D. dimorpha* var. *dimorpha* to var. *areolata* shows tendencies to increase in size and form double-layered punctation on both valve face and mantle. The last species *D. ovata* evolved from the primitive form of *D. dimorpha* var. *areolata* by development of unequally spaced cross rods of closed copula. All members of this lineage are middle- to high-latitude taxa. *D. dimorpha* is distributed in both the Northern and Southern Hemispheres, but *D. ovata* is endemic in the Southern Ocean.

By the end of the late Late Miocene *D. katayamae* Zone (NPD 6A), all *Denticulopsis* species including the last species *D. katayamae* became extinct. The extinction of the genus *Denticulopsis* coincides with the Late Miocene "ice growth event" (MILLER *et al.*, 1987).

No descendant species of this genus is present in overlying intervals. However, remarkable reworking of many *Denticulopsis* species is recognized in the latest Miocene to Early Pliocene sequences in the North Pacific and the Southern Ocean (Figs. 8,10 ; Table 4).

Genus *Neodenticula*

The evolutionary pattern of the genus *Neodenticula* is rather simple compared with those of *Crucidentricula* and *Denticulopsis*; It is represented by a single lineage from *Nitzschia rolandii* through *Neodenticula kamtschatica* and *N. koizumii* to *N. seminae*. These species are all endemic in the Northern Hemisphere (Fig. 11), especially dominant in the high-latitude North Pacific. This endemic and restricted distribution of *Neodenticula* is attributed to the strong provincialism of diatom assemblage which has developed remarkably since the beginning of the Pliocene.

Nitzschia rolandii, a precursor of the genus *Neodenticula*, first appeared in the late Middle Miocene, though it is sporadic during the Middle to early Late Miocene interval. After the Late Miocene extinction of the genus *Denticulopsis*, *N. rolandii* increased in abundance and occupied the ecological niche which

the genus *Denticulopsis* occupied. After a while, this *Nitzschia* species graded into *N. kamtschatica* by the widening of interval between pseudosepta or transapical costae. Near the end of the Miocene (about 6 Ma), *N. kamtschatica* increased abruptly and became a most important constituent of the North Pacific Pliocene diatom assemblage. This species later gave rise to its descendant *N. koizumii* by creating secondary pseudosepta in the late Pliocene. Near the beginning of the Quaternary, the last species *N. seminae* evolved from *N. koizumii* by the development of closed copula, enlargement of valve and narrowing interval between the pseudosepta. *N. seminae* remains extant as the most important cold water diatom species in the high-latitude North Pacific (KANAYA and KOIZUMI, 1966).

VII. Taxonomic part

VII.1 Genus *Crucidentricula* AKIBA *et* YANAGISAWA, with related species

Nitzschia maleinterpretaria SCHRADER

Plate 1, Figs. 1-4;

Plate 8, Figs. 1-7

SCHRADER, 1976, p. 634, pl. 2, figs. 9, 11-19, 21, 24; BARRON, 1983, pl. 5, figs. 7, 8; BARRON, 1985a, pl. 9, fig. 8; BARRON 1985b, p. 787-788, fig. 13.13; non SCHRADER and FENNER, 1976, pl. 1, fig. 30.

Description: Frustule rectangular with rounded corners in girdle view (Pl. 1, Fig. 2). Valve linear or linear-elliptical with rounded apices, 8-57 μm long, 3-6 μm wide. Smaller valve linear with rounded apices (Pl. 1, Fig. 3), whereas larger valve linear-elliptical with slightly rostrate rounded apices (Pl. 8, Fig. 1). Transapical striae on valve face coarsely punctated, 11-16 in 10 μm , puncta not in quin-cunx arrangement (Pl. 8, Fig. 3). Puncta rounded, 15-16 in 10 μm . Valve mantle low, perforated by a row of puncta (Pl. 8, Fig. 5). Shallow transapical costae between each two

transapical striae, 12-16 in 10 μm , often branching at raphe-bearing margin (Pl. 8, Figs. 6, 7). Transapical costae straight and parallel to transapical axis in the middle of valve, becoming oblique to transapical axis and slightly curved toward apices. Raphe at the edge of valve face, divided into two branches at the middle (Pl. 8, Fig. 3). Portulae of raphe not spaced regularly, about one between two transapical striae on average. A central portula located where raphe is interrupted, larger than other portulae (Pl. 8, Fig. 3). Copula open and punctated by a row of puncta (Pl. 1, Fig. 2).

Stratigraphic occurrence: This species has a long stratigraphic range from the upper part of the *Craspedodiscus elegans* Zone (NTD 2) to the lower part of the *Cestodiscus peplum* Zone (NTD 5) in the equatorial Pacific. It occurs dominantly within the *Triceratium pileus* Zone (NTD 3). In the Southern Ocean, it occurs from the middle part of the *Coscinodiscus rhombicus* Zone (NSD 2) through the *N. maleinterpretaria* Zone (NSD 3). Its last occurrence defines the top of the latter zone (SCHRADER, 1976; WEAVER and GOMBOS, 1981; BARRON, 1985b).

Geographic distribution: The species is distributed in the equatorial Pacific and the Southern Ocean. It is also reported from the Norwegian Sea (SCHRADER and FENNER, 1976) but the illustrated specimen (pl. 1, fig. 30) is not assigned evidently to this species. It has not been reported from the middle- to high-latitude of the North Pacific.

Remarks: The species closely resembles *Crucidentricula sawamurae* in punctation on valve face and valve outline. However, it is easily distinguished from the latter species by the absence of pseudosepta.

Phylogenetic relationship: The species certainly exhibits strong affinities in valve outline and structure with *Crucidentricula sawamurae*. It evidently evolved into *C. sawamurae* by development of pseudosepta. The antecedent of this species can not be traceable at present.

Crucidentricula sawamurae n. sp.

Plate 1, Figs. 5-9

Synonymy: *Denticula punctata* SCHRADER, DZINORIDZE *et al.*, 1978, pl. 20, figs. 3, 4; *Denticulopsis nicobarica* (GRUNOW) SIMONSEN, BARRON, 1981b, pl. 2, fig. 8; BARRON, 1985b, pl. 9, fig. 7; *Denticulopsis* aff. *kanayae* (AKIBA) BARRON, POWERS, 1988, pl. 5, figs. 4, 5; *Denticulopsis kanayae* (AKIBA) BARRON, POWERS, 1988, pl. 5, fig. 6.

Description: Frustule rectangular with rounded corners in girdle view, about 6-7 μm in depth. Valve linear or slightly linear-elliptical with rounded apices, 14-51 μm long, 3.5-5.5 μm wide. Transapical striae on valve face coarsely punctated, 13-16 in 10 μm , puncta not arranged in quincunx and sometimes sporadic. Transapical striae straight and parallel to transapical axis in the middle, becoming curved and oblique to transapical axis toward apices. Puncta rounded, 11-12 in 10 μm . Valve mantle perforated by two rows of puncta, 13-16 puncta in 10 μm . Primary pseudosepta, 3-5 in 10 μm , sometimes oblique to transapical axis and not always equally spaced. Unclear secondary pseudosepta rarely present. Marginal ribs short and numerous, 13-16 in 10 μm between each two transapical striae. Raphe marginal. Copula open, perforated by a row of puncta, 13-14 in 10 μm .

Holotype: Plate 1, Fig. 9; GSJ F12752 deposited in Geological Survey of Japan (Sample DSDP Hole 71, 25-3, 96-98 cm, eastern equatorial Pacific).

Paratype: Plate 1, Fig. 8; GSJ F12751 (Sample DSDP Hole 71, 25-1, 128-130 cm, eastern equatorial Pacific)

Stratigraphic occurrences: The first occurrence of this species marks the base of the A Subzone of the *Denticulopsis nicobarica* Zone (NTD 4) in the equatorial Pacific. Its last occurrence falls within the lower part of the B Subzone of the *D. nicobarica* Zone.

Geographic distribution: *C. sawamurae* occurs dominantly in the equatorial Pacific. It is also found with very rare abundance from

the Early Miocene Kamenoo Formation in Joban Coalfield of Japan (AKIBA, 1985). This species is distributed in the Southern Ocean (BARRON, personal communication, 1988). This geographic distribution indicates that *C. sawamurae* is basically a low-latitude species.

Remarks: This new species is distinguished from *Crucidenticula nicobarica* and *C. punctata* by non-quincunx arrangement of puncta. It differs from *C. paranicobarica* by more robust and wider valve, and from *C. ikebei* by its linear valve outline. The species is easily distinguished from *C. kanayae* by finer punctation. It resembles *Nitzschia maleinterpretaria* in valve outline, the same density of transapical striae, slightly oblique transapical striae and punctated copula, but differs by the presence of pseudosepta.

Phylogenetic relationship: The species is the oldest representative of the genus *Crucidenticula* and may be a basic ancestor of all species included in this genus. It appears that the species evolved from *Nitzschia maleinterpretaria* because of morphologic similarities between the two species. This phylogenetic relationship is also supported by the presence of evolutionary intermediate form between the two species (Pl. 1, Fig. 4), which show close affinity with *N. maleinterpretaria* but has inconspicuous pseudosepta. *C. sawamurae* evolved from *N. maleinterpretaria* through gradual development of pseudosepta from transapical costae. It gave rise to *C. ikebei* and *C. kanayae* var. *pacifica*.

Derivation of name: The species is named in honor of Dr. Konosuke SAWAMURA, one of the pioneers of diatom biostratigraphic study of Japan.

***Crucidenticula ikebei* AKIBA
et YANAGISAWA**

Plate 1, Figs. 10-12;

Plate 8, Figs. 8-13

AKIBA and YANAGISAWA, 1986, p. 485-486, pl. 1, figs. 1, 2; YANAGISAWA *et al.*, 1989, pl. 6, fig. 28.

Synonymy: *Denticula ikebei* AKIBA, 1977, pl. 1, figs. 15a-15c, pl. 2, figs. 1a-3, nom. invalid; *Denticula ikebei* AKIBA ex BARRON, 1980, p. 672, pl. 1, fig. 30, nom. invalid.

Description: Frustule rectangular with rounded corners, sometimes curved in girdle view (Pl. 1, Fig. 12). Valve linear-elliptical, broad in the middle and tapered to apices with elongated rounded apices, 18-67 μm long, 4-7 μm wide. Transapical striae of rounded puncta on valve face coarsely punctated, 12-16 in 10 μm , arranged not in clear quincunx, so that oblique rows obscure. Valve mantle low, perforated by two longitudinal rows of puncta (Pl. 8, Fig. 11). Primary pseudosepta, 3-5 in 10 μm , not equally spaced, with narrow basal ridges (Pl. 8, Fig. 12). Secondary pseudosepta absent. Marginal ribs short and inconspicuous on both sides between transapical striae. Raphe located at valve margin, interrupted at the middle point and divided into two branches of raphe (Pl. 8, Fig. 9). Portulae of raphe rounded and small except for a large central one which is located where raphe is interrupted (Pl. 8, Fig. 13). Portulae irregularly spaced, about one in two transapical striae on average. Copula open with punctated sides (Pl. 1, Fig. 12).

Stratigraphic occurrence: The species occurs rarely within the *C. kanayae* Zone (NPD 3A) in the middle- to high-latitude North Pacific. It is sometimes found with very sporadic occurrence in the overlying *Denticulopsis lauta* Zone (NPD 4A) and the *D. hyalina* Zone (NPD 4B).

Geographic distribution: *C. ikebei* is known only from the middle- to high-latitude North Pacific at present. It is not distributed in the equatorial Pacific. This species has not been reported from the Southern Ocean.

Remarks: The species is very similar to *Crucidenticula sawamurae* and *C. paranicobarica*, but distinguished by the slender linear-elliptical valve outline with elongated apices. It also resembles *Denticula norwegica* SCHRADER (Pl. 1, Fig. 40) in valve outline, but differs fundamentally in shape and structure

of puncta; *C. ikebei* has round puncta occluded by cross-shaped rotae, whereas *D. norwegica* possesses oval puncta occluded by mesh-like cribra (Pl. 8, Fig. 18).

Phylogenetic relationship: *C. ikebei* is considered to be a descendant of *C. sawamurae* because of morphologic similarities between the two species. It evolved from *C. sawamurae* by the change in valve outline from linear to linear lanceolate form. It left no descendant.

***Crucidentricula kanayae* var.
pacifica n. var.**

Plate 1, Figs. 36-38

Synonym: *Denticulopsis* sp. cf. *D. kanayae* (AKIBA) BARRON, 1985a, pl. 9, fig. 4.

Description: Frustule rectangular with rounded corners. Valve heavily silicified, mostly linear with bluntly rounded apices, 20-48 μm long, 5.5-7 μm wide. Transapical striae very coarsely punctated, 10-11 in 10 μm ; puncta not arranged in clear quincunx. Puncta rounded about 6-7 in 10 μm , occluded by cross-shaped rotae. Valve mantle high, perforated with two longitudinal rows of rounded puncta. Primary pseudosepta about 3 in 10 μm , mostly in transapical direction, but sometimes slightly oblique to transapical axis near apices. Secondary pseudosepta absent. Marginal ribs very inconspicuous between each two transapical striae on both sides, 10-11 in 10 μm . Raphe marginal. Copula open and punctated with a row of longitudinal row of puncta.

Holotype: Plate 1, Fig. 38; GSJ F12744 deposited in Geological Survey of Japan (Sample DSDP Hole 71, 22-6, 116-118 cm, eastern equatorial Pacific).

Paratype: Plate 1, Fig. 37; GSJ F12745 (Sample DSDP Hole 71, 23-2, 117-119, eastern equatorial Pacific).

Stratigraphic occurrence: The variety has a short range from the base of the B Subzone of the *Denticulopsis nicobarica* Zone (NTD 4B) to the lowest part of the *Cestodiscus peplum*

Zone (NTD 5) in the equatorial Pacific.

Geographic distribution: The variety is found in the equatorial Pacific but not in the middle- to high-latitude North Pacific.

Remarks: This new variety and *C. kanayae* var. *kanayae* are different mainly in type of copula; the var. *pacifica* has open punctated copulae (Type Cop; Pl. 1, Fig. 38) without any exceptions, whereas the var. *kanayae* has open non-punctated copulae (Type Con; Pl. 8, Fig. 14). This new variety differs from the nominative variety also by slightly denser punctation on valve face and more linear valve outline. *C. kanayae* var. *pacifica* differs from *C. sawamurae* by coarser punctation and from *C. punctata* by both coarser punctation and non-quincunx arrangement of puncta.

Phylogenetic relationship: The stratigraphic range and morphologic similarities suggest that this taxon evolved from *Crucidentricula sawamurae* by enlargement of valve structure. *C. kanayae* var. *pacifica* is probably a geographic variety of *C. kanayae* var. *kanayae* and may be an ancestor of the latter variety.

***Crucidentricula kanayae* AKIBA
et YANAGISAWA var. *kanayae***

Plate 1, Figs. 33-35, 39;

Plate 8, Figs. 14-17

AKIBA and YANAGISAWA, 1986, p. 486, pl. 1, figs. 3-8, pl. 3, figs. 1-6, 9-11.

Synonymy: *Denticula nicobarica* GRUNOW, HATA and HASEGAWA, 1970, pl. 4, figs. 3a-6b, *Denticula punctata* SCHRADER, SCHRADER and FENNER, 1976, pl. 1, figs. 42, 43, non pl. 1, fig. 33; *Denticula kanayae* AKIBA, 1977, pl. 1, figs. 1a-10b, pl. 2, fig. 13, nom. invalid.; *Denticula kanayae* AKIBA ex BARRON, 1980, p. 672, pl. 1, figs. 26-28, nom. invalid.; *Denticulopsis kanayae* (AKIBA) BARRON, 1985b, p. 784, figs. 13.20, 13.21, nom. invalid.

Description: Frustule rectangular with rounded corners, about 9 μm in depth. Valve heavily silicified, mostly linear-oblong, less frequently linear-elliptical with bluntly

rounded apices, 14-43 μm long, 4-8 μm wide. Transapical striae very coarsely punctated, 9-10 in 10 μm ; puncta not always arranged in clear quincunx and sometimes sporadic so that hyaline areas sometimes present on valve face. Puncta rounded about 6 in 10 μm , occluded by cross-shaped rotæ. Valve mantle high, perforated with two longitudinal rows of rounded puncta. Primary pseudosepta 2 in 10 μm , mostly in transapical direction, but sometimes slightly oblique to transapical axis. Secondary pseudosepta absent, but some specimens has shallow incomplete rudimentary pseudosepta. Marginal ribs very inconspicuous between each two transapical striae, 9-10 in 10 μm . Raphe marginal. Copula open and not punctated.

Stratigraphic occurrence: This variety is very abundant in the *C. kanayae* Zone (NPD 3 A) and rare or sporadic in younger horizons up to the *Denticulopsis hyalina* Zone (NPD 4B) in the middle- to high-latitude North Pacific.

Geographic distribution: *C. kanayae* var. *kanayae* occurs in the middle- to high-latitude North Pacific. It is also reported from the Norwegian Sea (SCHRADER and FENNER, 1976). In the equatorial Pacific, it is not found but another variety *C. kanayae* var. *pacifica* is distributed. There has been no information on this taxon in the Southern Ocean.

Remarks: The copula of this variety is an open non-punctated type (Con; Pl. 8, Figs. 14, 15). This is a unique and specialized characteristic among the genus *Crucidentricula* because all other *Crucidentricula* taxa have open punctated copulae (type Cop). The taxon differs from the variety *pacifica* by this open non-punctated copula. The variety resembles *Crucidentricula sawamurae*, but differs by coarser punctation. It is also similar to *Crucidentricula punctata* but differs by both coarser punctation and non-quincunx arrangement of puncta.

Phylogenetic relationship: This variety is probably a geographic variety of *C. kanayae* var. *pacifica*; *C. kanayae* var. *pacifica* and var. *kanayae* are distributed mainly in the low-

latitude and the high-latitude, respectively. The var. *kanayae* may be a descendant of the var. *pacifica*, because the former appeared slightly later than the latter variety. *C. kanayae* var. *kanayae* left no descendant.

Crucidentricula paranicobarica

var. *tropica* n. var.

Plate 1, Figs. 17-22

Synonymy: *Denticula nicobarica* GRUNOW, ABBOTT and ERNISSEE, 1983, pl. 13, fig. 7; *Denticulopsis nicobarica* (GRUNOW) SIMONSEN, BARRON, 1983, pl. 5, fig. 2; TANIMURA and SAITO, 1986, pl. 2, fig. 15; *Denticulopsis nicobarica* var. 1, MARUYAMA, 1984a, pl. 16, fig. 12

Description: Frustule rectangular with rounded corners. Valve narrowly linear with bluntly rounded apices, 5-58 μm long, 2-3.5 μm wide. Transapical striae coarsely punctated 16-18 in 10 μm , without reduction of puncta. Primary pseudosepta 5-6 in 10 μm , not always equally spaced. Secondary pseudosepta basically absent but rarely unclear shallow secondary pseudosepta present. Marginal ribs short and numerous, 16-18 in 10 μm . Raphe marginal. Copula open and punctated with a longitudinal row of puncta.

Holotype: Plate 1, Fig. 19; GSJ F12739 deposited in Geological Survey of Japan (Sample DSDP Hole 71, 21-2, 89-91 cm, eastern equatorial Pacific)

Paratype: Plate 1, Fig. 17; GSJ F12740 (Sample DSDP Hole 71, 21-4, 60-62 cm, eastern equatorial Pacific)

Stratigraphic occurrence: The variety has its first occurrence in the middle part of the A Subzone of the *Cestodiscus peplum* Zone (NTD 5A) and its last occurrence near the base of the overlying B Subzone of the *C. peplum* Zone (NTD 5B) in the equatorial Pacific.

Geographic distribution: The variety occurs predominantly in the equatorial Pacific. It is sometimes found from several on-land sequences in Japan which were affected by warm water current during the early Middle Miocene (Pl. 1, Fig. 21). It also

reported from the Atlantic coast of U.S.A. (ABBOTT and ERNISSEE, 1983). These occurrences suggest that this variety is mainly a low-latitude warm water taxon.

Remarks: The variety is characterized by full punctation on valve face, non-quincunx arrangement of puncta and slender valve outline. It is distinguished from its nominative variety by the full punctation on valve face. However, specimens with slightly reduced punctation are rarely encountered in DSDP Hole 71. In this study these specimens are tentatively included in the var. *tropica*. The variety has been confused with *Crucidentricula nicobarica*, but clearly differs by non-quincunx arrangement of puncta. It is also similar to *Crucidentricula sawamurae*, but distinguished by more slender valve outline.

Phylogenetic relationship: The stratigraphic range of this variety is separated from those of preceding *Crucidentricula kanayae* var. *pacifica* and *C. sawamurae* by a short interval where no *Crucidentricula* species occurs. However, morphologic similarities suggest that *C. paranicobarica* var. *tropica* is most probably a descendant of *C. sawamurae*. This variety is a geographic variety of the nominate variety and may be an ancestor of the latter variety because the var. *tropica* occurs slightly earlier than the var. *paranicobarica*. *C. paranicobarica* var. *tropica* gave rise to *C. nicobarica* with development of clear quincunx arrangement of puncta on valve face.

***Crucidentricula paranicobarica* AKIBA
et YANAGISAWA var. *paranicobarica***

Plate 1, Figs. 13-16

AKIBA and YANAGISAWA, 1986, p. 487, pl. 2, figs. 8-14; AKIBA, 1986, pl. 26, fig. 7.

Synonymy: *Denticula nicobarica* GRUNOW, SCHRADER, 1973a, pl. 1, figs. 31-34; *Denticula paranicobarica* AKIBA, 1977, pl. 1, figs. 11a-14b, pl. 2, figs. 7a-9b, nom. invalid; *Denticulopsis paranicobarica* AKIBA, TANIMURA and SAITO, 1986, pl. 2, fig. 14.

Description: Frustule rectangular with

rounded corners in girdle view, 5-8 μm in depth. Valve narrowly linear or rarely linear-elliptical with bluntly rounded apices, 8-32 μm long, 2.5-4.5 μm wide. Puncta on valve face usually sporadic except for two apical rows near both valve margins and several sporadic puncta in or around central chamber, 14-16 in 10 μm . Primary pseudosepta 4-6 in 10 μm , sometimes slightly oblique to transapical axis and not always equally spaced. Secondary pseudosepta rarely present (Pl. 1, Figs. 15, 16). Marginal ribs short and numerous, 14-16 in 10 μm . Raphe marginal. Copula open and punctated with a longitudinal row of puncta.

Stratigraphic occurrence: In the middle- to high-latitude North Pacific, the variety has its first occurrence in the lowest part of the *Denticulopsis lauta* Zone (NPD 4A) and occurs frequently in the middle to upper part of this zone and the lower part of the overlying *Denticulopsis hyalina* Zone (NPD 4B). Its last occurrence, although it is obscure due to sporadic occurrence, is near the top of the *D. hyalina* Zone.

Geographic distribution: The variety is distributed in the middle- to high-latitude North Pacific, but not in the equatorial Pacific. It is not known in the Southern Ocean. Based on these occurrences, this variety seems to be a middle- to high-latitude taxon.

Remarks: *C. paranicobarica* var. *paranicobarica* is characterized by its slender valve outline and non-quincunx arrangement of puncta and reduced sporadic punctation. It is distinguished from *C. paranicobarica* var. *tropica* by the reduced punctation. The variety has been confused with *C. nicobarica* because of similar valve shape, but differs clearly by non-quincunx arrangement of puncta and reduced punctation.

Phylogenetic relationship: *C. paranicobarica* var. *paranicobarica* is mainly distributed in the middle- to high-latitudes, whereas the var. *tropica* occurs in the low-latitude. The two varieties have nearly the same stratigraphic ranges, although the var. *tropica*

appeared slightly earlier than the var. *paranicobarica*. These geographic and stratigraphic evidences suggest that the var. *paranicobarica* is a geographic variation of the var. *tropica* and evolved from the latter variety by reducing of puncta on valve face.

***Crucidenticula nicobarica* (GRUNOW)**

AKIBA et YANAGISAWA

Plate 1, Figs. 23-29

AKIBA and YANAGISAWA, 1986, p. 486-487, pl. 1, fig. 9, pl. 2, figs. 1-7, pl. 5, figs. 1-9; AKIBA, 1986, pl. 26, figs. 1-4; YANAGISAWA *et al.*, 1989, pl. 6, fig. 24.

Synonymy: *Denticula nicobarica* GRUNOW, 1868, p. 97, pl. 1A, figs. 5a, 5b; VAN HEURCK, 1880-1885, pl. 49, fig. 3; SIMONSEN and KANAYA, 1961, p. 503, pl. 1, figs. 11-13; SCHRADER, 1973a, pl. 1, fig. 35; SCHRADER, 1973b, p. 419-420, pl. 1, figs. 25-27; SCHRADER, 1974b, figs. 1:26, 1:27; GOMBOS, 1976, pl. 8, fig. 8; SCHRADER and FENNER, 1976, pl. 1, fig. 32; AKIBA, 1977, pl. 2, figs. 5, 6, 12; ABBOTT, 1980, pl. 1, fig. 18; BARRON, 1980, pl. 1, figs. 22, 23; *Denticulopsis nicobarica* (GRUNOW) SIMONSEN, 1979, p. 65; BARRON, 1981a, pl. 4, fig. 6; AKIBA *et al.*, 1982, pl. 3, figs. 49-52; MARUYAMA, 1984a, pl. 15, figs. 12-13b, pl. 16, fig. 11; BARRON, 1985 b, p. 785, fig. 13.19.

Description: Frustule rectangular with rounded corners in girdle view. Valve narrowly linear to linear-elliptical with bluntly rounded apices, 10-32 μm long, 3.5-4.5 μm wide. Transapical striae on valve face coarsely punctated, about 16 in 10 μm ; puncta in quincunx so that clear oblique rows formed. Puncta rounded, occluded by cross-shaped rotae. Valve mantle perforated by two longitudinal rows of puncta. Primary pseudosepta 4-5 in 10 μm . Secondary pseudosepta absent. Marginal ribs short and numerous, about 16 in 10 μm between transapical striae. Raphe marginal. Copula open and punctated by a row of puncta, 13-14 in 10 μm .

Stratigraphic occurrence: In the middle- to high-latitude North Pacific, the first occur-

rence of this species is in the uppermost part of the Middle Miocene *Denticulopsis lauta* Zone (NPD 4A) and its last occurrence lies in the lower part of the *Denticulopsis praedimorpha* Zone (NPD 5B). However, its abundance is generally rare except within the *C. nicobarica* Zone (NPD 5A) where this species occurs frequently.

In the equatorial Pacific, *C. nicobarica* first occurs in the uppermost part of the A Subzone of the *Cestodiscus peplum* Zone (NTD 5A) and last occurs in the middle part of the *Coscinodiscus gigas* var. *diorama* Zone (NTD 7), occurring very abundantly from the B Subzone of the *C. peplum* Zone through the *Coscinodiscus lewisianus* Zone (NTD 6).

In the Southern Ocean, this species occurs from the middle part of the *Coscinodiscus lewisianus* Zone (NSD 4) to the lower part of the *Nitzschia denticuloides* Zone (NSD 6).

Geographic distribution: This species is a cosmopolitan species with very broad distribution over the world. However, it is most dominant in the equatorial Pacific where it often occupies more than a half of diatom assemblages (Table 6; BARRON, 1985a).

Remark: The diagnostic characteristics of this species are its clear quincunx arrangement of puncta and small size. It is distinguished from *Crucidenticula sawamurae*, *C. ikebei* and *C. paranicobarica* by the clear quincunx pattern of puncta. It resembles *C. punctata*, but differs by smaller size.

Phylogenetic relationship: The most probable ancestor of *C. nicobarica* is *C. paranicobarica* var. *tropica* because of their stratigraphic occurrences and morphologic similarities. The species probably developed from the latter taxon through rearrangement of puncta from non-quincunx to clear quincunx. The descendant form of this species is *C. punctata*.

***Crucidenticula punctata* (SCHRADER)**

AKIBA et YANAGISAWA

Plate 1, Figs. 30-32

AKIBA and YANAGISAWA, 1986, p. 487, pl. 1,

figs. 10-12, pl. 4. figs. 1-9.

Synonymy: *Denticula nicobarica* GRUNOW, KANAYA, 1971, pl. 40.5, figs. 12a, 12b; *Denticula punctata* SCHRADER, 1973a, p. 705, pl. 1, figs. 25-30; SCHRADER, 1973b, p. 420, pl. 1, fig. 19; SCHRADER, 1974b, figs. 1: 22-1: 24; *Denticulopsis punctata* (SCHRADER) SIMONSEN, 1979, p. 65; MARUYAMA, 1984a, pl. 16, fig. 6; *Denticula punctata* f. *hustedtii* SCHRADER, 1973a, p. 705, pl. 1, figs. 23, 24; *Denticulopsis punctata* f. *hustedtii* (SCHRADER) SIMONSEN, 1979, p. 65; BARRON, 1981a, pl. 4, fig. 1; BARRON, 1985a, pl. 9, fig. 11; BARRON, 1985b, p. 785, fig. 13.18; KOIZUMI and TANIMURA, 1985, pl. 1, figs. 9, 10; *Denticula punctata* var. *hustedtii* SCHRADER, 1973b, p. 420, pl. 1, fig. 18; non BARRON, 1980, pl. 1, fig. 29; *Denticulopsis nicobarica* (GRUNOW) SIMONSEN, POWERS, 1988, pl. 5, fig. 7.

Description: Frustule rectangular with rounded corners in girdle view. Valve linear to linear-elliptical with bluntly rounded apices, 20-40 μm long, 5.5-7.5 μm wide. Transapical striae on valve face coarsely punctated, 14-15 in 10 μm ; puncta in clear quincunx so that clear oblique rows formed. Puncta rounded, occluded by cross-shaped rotae. Valve mantle high, perforated by four longitudinal rows of puncta. Primary pseudosepta 3-4 in 10 μm . Secondary pseudosepta 0-2 between each two primary pseudosepta. Marginal ribs short and numerous, 15-16 in 10 μm . Raphe marginal. Copula open and punctated by a row of puncta. Pleurae open, first and third ones narrow and second one broad.

Stratigraphic occurrence: In the middle- to high-latitude North Pacific, this species occurs rarely from the uppermost part of the *Denticulopsis hyalina* Zone (NPD 4B) to the top of the *Denticulopsis praedimorpha* Zone (NPD 5B). In the equatorial Pacific, it is found within the interval from the upper part of the *Coscinodiscus lewisianus* Zone (NTD 6) to the upper part of the *Craspedodiscus coscinodiscus* Zone (NTD 8). In the Southern Ocean, the species has its reported stratigraphic range from the uppermost part of the

Nitzschia maleinterpretaria Zone (NSD 3) to the lower part of the *Nitzschia denticuloides* Zone (NSD 6).

Geographic distribution: *C. punctata* is a cosmopolitan species. It occurs in the middle- to high-latitude of the North Pacific, Norwegian Sea, the equatorial Pacific and the Southern Ocean.

Remarks: This species is characterized by its clear quincunx arrangement of puncta on valve face and relatively large size. It resembles *Crucidentricula nicobarica*, but differs by larger size and more frequent development of secondary pseudosepta. It is also very similar to *C. kanayae* and *C. sawamurae* but distinguished from them by clear quincunx arrangement of puncta.

Phylogenetic relationship: The stratigraphic records and morphologic characteristics indicate that this species evolved from *C. nicobarica* by an increase in size and development of many secondary pseudosepta. *C. punctata* is the last member of the genus *Crucidentricula*. It became extinct without leaving any descendant species before the end of Middle Miocene.

VII. 2 Genus *Denticulopsis* SIMONSEN emend. AKIBA et YANAGISAWA with closely related species

Nitzschia challengerii SCHRADER

Plate 2, Figs. 1, 2, 10;

Plate 9, Figs. 12-16;

Plate 10, Figs. 1, 2

SCHRADER, 1973a, p. 707, pl. 5, figs. 10-14, non pl. 5, fig. 34; BARRON, 1980, pl. 2, fig. 10; BARRON, 1981a, pl. 4, fig. 19; MARUYAMA, 1984b, pl. 11, fig. 18; YANAGISAWA *et al.*, 1989, pl. 6, fig. 32.

Description: Frustule rectangular with rounded corners in girdle view. Valve linear to linear-elliptical with bluntly rounded apices, 10-29 μm long, 3.5-5.5 μm wide. Transapical costae shallow and equally spaced, 9-12 in 10 μm , straight in the middle

and curved near apex. At each apex two or three longitudinal costae running to apex, which are very similar to apical costa of *Denticulopsis* (Pl. 9, Fig. 15). Intercostal area perforated with mostly two or rarely three transapical striae of fine puncta (Pl. 9, Fig. 16). Raphe marginal, divided at the middle into two branches of raphe. Portula between each two transapical costae (Pl. 9, Fig. 15). Copula open and punctated by a row of puncta.

Stratigraphic occurrence: This species occurs rarely but consistently from the latest Early Miocene through the Middle Miocene in the middle- to high-latitude North Pacific. Its first occurrence is in the lowest part of the *Denticulopsis praelauta* Zone (NPD 3B); namely just above the first occurrence of *D. praelauta*, and its last occurrence lies in the uppermost part of the *Denticulopsis praedimorpha* Zone (NPD 5B) or the lower part of the *Thalassiosira yabei* Zone (NPD 5C).

Geographic distribution: The species is found only in the middle- to high-latitude North Pacific.

Remarks: *N. challengerii* is sometimes similar to the primitive form of *D. praelauta* when the spacing of its transapical costae is relatively wide.

Phylogenetic relationship: It is certain that *N. challengerii* shared common ancestry to the genus *Denticulopsis* because of its common valve structures to *Denticulopsis* and its affinity with *D. praelauta*. This species is considered to be derived from an unknown common ancestor with *D. praelauta* in the latest Early Miocene.

Denticulopsis praelauta AKIBA et KOIZUMI

Plate 2, Figs. 3-5, 16-18

AKIBA, 1986, p. 439, pl. 26, figs. 10-14; AKIBA and YANAGISAWA, 1986, p. 490, pl. 7, figs. 1-15, pl. 8, figs. 1-9; YANAGISAWA *et al.*, 1989, pl. 6, figs. 3, 4.

Synonymy: *Denticula* aff. *kamtschatica* ZABELINA, SCHRADER, 1976, p. 632, pl. 4, fig. 18; *Denticula* sp. cf. *D. lauta* BAILEY, BARRON,

1980, p. 672, pl. 1, figs. 13, 14; *Denticulopsis* sp. A, AKIBA *et al.*, 1982, pl. 3, figs. 41-44.

Description: Frustule rectangular with rounded corners in girdle view, 6-7 μm in depth. Valve small, narrowly linear with bluntly rounded apices, 8-16 μm long, 2.5-5.5 μm wide. Transapical striae on valve face finely punctated, 25-30 in 10 μm ; puncta in quincunx so that oblique rows formed. Primary pseudosepta 5-8 (mostly 5-6) in 10 μm , with poorly developed narrow basal ridges. Secondary pseudosepta absent. Marginal ribs absent in primitive form but inconspicuous marginal ribs observed in advanced form. Raphe marginal. Copula open, punctated by longitudinal rows of puncta or non-punctated.

Stratigraphic occurrence: Common to abundant in the Early Miocene *D. praelauta* Zone (NPD 3B) in the middle- to high-latitude North Pacific. Its first occurrence defines the base of this zone and its last occurrence is in the lower part of the overlying *Denticulopsis lauta* Zone (NPD 4A). In the Southern Ocean, the species shows only sporadic occurrence from the uppermost part of the *Nitzschia maleinterpretaria* Zone (NSD 3) to the upper part of the *Denticulopsis lauta*-*D. hustedtii* Zone (NSD 7). This is probably because the interval where *D. praelauta* is expected to occur abundantly (around 16 Ma in age) is missing due to a hiatus at DSDP Site 278 (WEAVER and GOMBOS, 1981).

Geographic distribution: The species is found in the middle- to high-latitude North Pacific and the Southern Ocean but not in the low-latitude.

Remarks: *D. praelauta* resembles *D. lauta*, but differs from the latter by the absence or very poor development of marginal ribs. It is similar to *Nitzschia challengerii* when it has no clear basal ridges, but distinguished by wider intervals of pseudosepta or costae. The older primitive form which occurs in the lower part of the *D. praelauta* Zone is characterized by the absence of marginal ribs and poor development of basal ridges, whereas the younger advanced form found from the upper part of

the *D. praelauta* Zone through the lower part of the *D. lauta* Zone has inconspicuous marginal ribs and moderately developed basal ridges. The latter younger form may be an evolutionary intermediate form to *D. lauta*. *D. praelauta* has two types of copula (Cop and Con) and therefore four types of frustules are formed (Pl. 2, Figs. 16-18).

Phylogenetic relationship: *D. praelauta*, the oldest known member of the genus *Denticulopsis*, is a basic ancestor of all species of this genus. However, a possible ancestor of this species is unknown at present. *Nitzschia challengeri*, which is very similar to *D. praelauta*, may share common ancestry as stated earlier. *D. praelauta* is a direct precursor of *Denticulopsis lauta*.

***Denticulopsis lauta* (BAILLY) SIMONSEN**

Plate 2, Figs. 6-8, 15;

Plate 5, Figs. 1-3;

Plate 9, Fig. 1

SIMONSEN, 1979, p. 64; MARUYAMA, 1984a, pl. 14, figs. 1a-8b, pl. 16, figs. 9, 10; BARRON, 1985b, p. 785; AKIBA, 1986, pl. 26, fig. 15; AKIBA and YANAGISAWA, 1986, p. 489, pl. 7, fig. 29, pl. 9, figs. 2-9, non pl. 9, fig. 1. TANIMURA and SAITO, 1986, pl. 2, figs. 6, 7; YANAGISAWA, *et al.*, 1989, pl. 6, fig. 5; TANIMURA, 1989, pl. 1, figs. 16a-17b.

Synonymy: *Denticula? lauta* BAILEY, 1854, p. 9, figs. 1, 2; *Denticula lauta* BAILEY, SIMONSEN and KANAYA, 1961, p. 500-501, in part, pl. 1, figs. 1, 3, non pl. 1, figs. 2, 6-10.

Description: Frustule rectangular with rounded corners in girdle views. Valve linear to linear-elliptical with bluntly rounded apices, 7-57 μm long, 3.5-8 μm wide. Transapical striae on valve face finely punctated, 20-28 in 10 μm ; puncta in quincunx so that oblique rows formed. Primary pseudosepta 3-5 in 10 μm . Secondary pseudosepta absent. Apical pseudosepta present near apices in some specimens. Marginal ribs present between each two primary pseudosepta on both sides. Raphe marginal. Copula open and

non-punctated but primitive forms with both punctated and non-punctated copulae.

Stratigraphic occurrence: In the middle- to high-latitude North Pacific, the species occurs abundantly in the lower Middle Miocene *D. lauta* Zone (NPD 4A). The first occurrence of this species defines the base of the *D. lauta* Zone and its last consistent occurrence is in the lower part of the *Crucidentricula nicobarica* Zone (NPD 5A).

In the equatorial Pacific, this species is found sporadically in the lower part of the A Subzone of the *Cestodiscus peplum* Zone (NTD 5A).

In the Southern Ocean, the reported stratigraphic range of *D. lauta* is separated into two ranges by a gap in the early Middle Miocene (Fig. 10). Of these two ranges, the lower one from the uppermost part of the *Nitzschia maleinterpretaria* Zone (NSD 3) to the middle part of the *N. grossepunctata* Zone (NSD 5) is considered the true range of *D. lauta*, because it just corresponds to those in the middle- to high-latitude North Pacific and in the equatorial Pacific. However, the upper range from the lower part of the *Nitzschia denticuloides* Zone (NSD 6) to the top of the *D. lauta-D. hustedtii* Zone (NSD 7) may not be a range of *D. lauta* but that of *Denticulopsis dimorpha* s. l. (*D. dimorpha* and *D. praedimorpha*). Since it is not so easy to distinguish the valve of *D. lauta* from those of *D. dimorpha* and *D. praedimorpha* without careful observation as will be discussed in remarks, the valve of *D. dimorpha* and *D. praedimorpha* may have previously been mis identified as *D. lauta*.

Geographic distribution: Although it occurs in the low-latitude, *D. lauta* is basically a middle- to high-latitude species because of its abundant occurrences in the middle- to high-latitude North Pacific and the Southern Ocean.

Remarks: The species resembles *D. ichikawae*, but differs by full punctation on valve face. The more linear valve outline distinguishes *D. lauta* from *D. okunoi* which has more oval outline. *D. lauta* also has similar

characteristics to those of *D. tanimurae* but differs by finer punctation and more weakly silicified valve.

There are sometimes large valves with a central raphe (Pl. 2, Fig. 38 ; Pl. 9, Figs. 10, 11). Although these forms were described as *Yoshidaia divergens* KOMURA (KOMURA, 1976, p. 389-390, Abb. 9, figs 1-3, pl. 40, figs. 6-8), they may possibly be initial valves of *D. lauta* because of similar valve structures. The characteristics of these forms are as follows : (1) A raphe, which is located along valve edge in ordinary vegetative valves, is running along the valve center. (2) The valve face is strongly convex so that valve face and mantle can not be distinguished. (3) The valve is relatively larger than ordinary vegetative valves. (4) Other features are almost the same as those of corresponding vegetative valve. (5) The occurrence of these forms is always very rare. (6) The stratigraphic range of these forms roughly coincides with that of corresponding vegetative valves. Although it is highly possible that *Yoshidaia divergens* may be an initial valve of *D. lauta*, further study is needed to confirm this possibility.

D. lauta, *D. praedimorpha* and *D. dimorpha* are very similar in valve morphology and thus they have been confused and misidentified for a long time (SIMONSEN and KANAYA, 1961 ; KOIZUMI, 1973, 1975 ; BARRON, 1980, 1985b). However, valves of the three species can be clearly distinguished by shape of basal ridge (AKIBA, 1979 ; MARUYAMA, 1984a ; AKIBA and YANAGISAWA, 1986 ; Pl. 5, Figs. 1, 4, 5, 13, 14).

D. lauta possesses distinct basal ridges looking like clear dark bow ties in silhouette in LM (Pl. 5, Fig. 1, right). In contrast the basal ridges of Vc type valve of *D. praedimorpha* are much shorter than those of *D. lauta*, looking like dark small quadrangles in silhouette (Pl. 5, Fig. 4, right), whereas those of Vo type valve are bow tie-shaped, but exhibit very unclear and faint impression because they are very low (Pl. 5, Fig. 5, right). The Vc-type valve of *D. dimorpha* lacks basal ridges (Pl. 5, Fig. 13), while those of Vo type valve have the

same look as those of Vo type valve of *D. praedimorpha* (Pl. 5, Fig. 14).

D. lauta, *D. praedimorpha* and *D. dimorpha* are distinguished more easily in type of copula than in valve morphology. The copula of *D. lauta* is a weakly silicified open band with non-punctated sides (type Con) and short and indistinct pairs of inner extensions (Pl. 5, Fig. 2). In contrast *D. praedimorpha* has two types of closed copulae (types Ccr and Ccm) and one type of open copula (type Cop). The closed copula is strongly silicified with relatively long and sharply truncated pairs of inner extensions (Pl. 5, Fig. 8). The type Ccr copula has a serrate edge (Pl. 5, Fig. 6), whereas the type Ccm copula has a smooth edge (Pl. 5, Fig. 7). The open copula with punctated sides (Cop) is weakly silicified (Pl. 5, Fig. 9) with indistinct pairs of inner extensions. *D. dimorpha* also has two types of closed copula (types Ccr and Ccm) and one type of open copula (type Cop) as *D. praedimorpha* does. However, the closed copula of *D. dimorpha* possesses complete cross rods (Pl. 5, Fig. 15). The open copula of *D. dimorpha* is the same as that of *D. praedimorpha* (Pl. 5, Fig. 16).

Phylogenetic relationship : The species is a descendant of *D. praelauta* because of nearly continuous morphologic series from the younger advanced form of *D. praelauta* to *D. lauta*. *D. lauta* arose from *D. praelauta* by gradually development of marginal ribs. *D. lauta* gave rise to four species ; *D. ichikawae*, *D. tanimurae*, *D. praedimorpha* and *D. simonsenii*.

Denticulopsis ichikawae n. sp.

Plate 2, Figs. 9, 11-13 ;

Plate 9, Figs. 2-4

Synonymy : *Denticula lauta* BAILEY, SIMONSEN and KANAYA, 1961, pl. 1, fig. 2, non pl. 1, figs. 1, 3, 6-10 ; *Denticulopsis lauta* (BAILEY) SIMONSEN, HAJÓS, 1986, pl. 34, figs. 7-16 ; AKIBA and YANAGISAWA, 1986, pl. 9, fig. 1.

Description : Frustule rectangular with rounded corners in girdle view, 6-8 μ m in

depth. Valve linear to linear-elliptical with rounded apices, 9–30 μm long, 4–6 μm wide. Transapical striae on valve face, finely punctated, 20–26 in 10 μm , partly reduced so that the middle part of the interval between pseudosepta is hyaline. Valve mantle finely punctated without reduction of puncta. Primary pseudosepta, 3–5 in 10 μm . Secondary pseudosepta absent. Apical pseudosepta present in some specimens. Between each two primary pseudosepta, short marginal ribs present on both sides. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype: Plate 2, Fig. 12; GSJ F 12813 deposited in Geological Survey of Japan (Sample DSDP Hole 438 A, 79–1, 51–54 cm, north-west Pacific).

Stratigraphic occurrence: The species first occurs in the lower part of the *Denticulopsis lauta* Zone (NPD 4A) and is abundant in the middle part of this zone. It is rare to sporadic in the upper part of this zone and the overlying *Denticulopsis hyalina* Zone (NPD 4B), making its real last occurrence difficult to recognize.

Geographic distribution: The species is distributed in the middle- to high-latitude North Pacific and the Southern Ocean, but not in the equatorial Pacific.

Remarks: This new species resembles *D. lauta* and *D. okunoi*, but differs from the former by its reduced transapical striae or hyaline middle intervals between pseudosepta, and from the latter by its linear valve outline. It is also very similar to *D. praeahyalina* in partly reduced transapical striae, but distinguished by more thinly silicified valve structures, finer punctation and pattern of reduction of puncta on valve face.

Phylogenetic relationship: Morphologic similarities and stratigraphic occurrence indicate that *D. ichikawae* evolved from *D. lauta* through partial reduction of puncta on valve face. *D. ichikawae* developed into *D. okunoi* by change in valve outline from linear to oval form.

Derivation of name: The species is named

in honor of Dr. Wataru ICHIKAWA, one of the pioneers of diatom biostratigraphic research in Japan.

Denticulopsis okunoi n. sp.

Plate 2, Figs. 19–25

Synonymy: *Denticulopsis lauta* (BAILEY) SIMONSEN, AKIBA *et al.*, 1982, pl. 3, figs. 46, 47; *Denticulopsis lauta* BAILEY, ITO, 1986, pl. 1, figs. 1, 2, 5; *Denticulopsis praedimorpha* AKIBA, LEE, 1986, pl. 2, fig. 18.

Description: Frustule rectangular with rounded corners in girdle view. Valve oval with broadly rounded apices, 10–21 μm long, 6–9.5 μm wide. Transapical striae on valve face finely punctated, 22–26 in 10 μm , partly reduced so that the middle part of interval between each two pseudosepta is hyaline. Valve mantle low, finely punctated without reduction of puncta. Primary pseudosepta, 6–7 in 10 μm , curved near apex. Short marginal ribs present between each two pseudosepta on both side. Secondary pseudosepta absent. Apical pseudosepta present in some specimens. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype: Plate 2, Fig. 22; GSJ F12814 deposited in Geological Survey of Japan (Sample JOB 423, Taga Formation, Hirakata, Joban Coalfield, Ibaraki, Japan).

Stratigraphic occurrence: The species has a very short range in the lower part of the *Denticulopsis lauta* Zone (NPD 4A). Its first occurrence is younger than that of *Denticulopsis ichikawae*.

Geographic distribution: The species has been found only from Japan and its environs at present.

Remarks: Reduction of puncta on valve face varies from nearly full punctation (Pl. 2, Fig. 21) to reduction with only two striae near each two pseudosepta (Pl. 2, Fig. 19). This new species is characterized by its oval valve outline, which distinguishes it from its related species *D. ichikawae* and *D. lauta*. Biometric analysis indicates that this species is signifi-

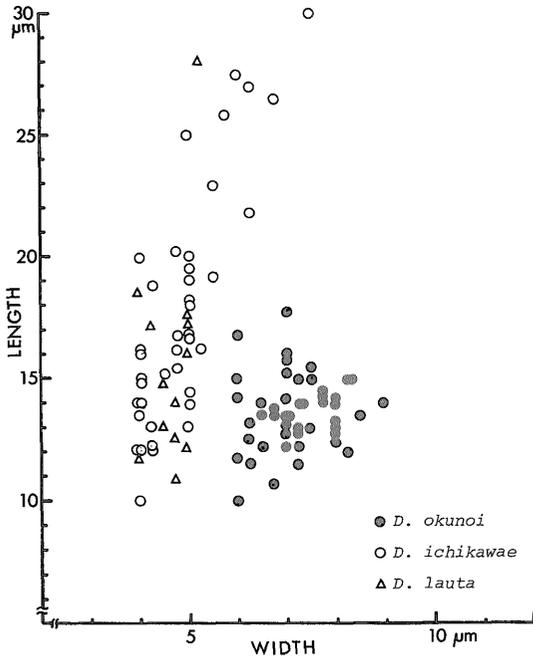


Fig. 18 Plot of width and length in valves of *Denticulopsis okunoi*, *D. ichikawae* and *D. lauta*. Sample JOB 423, Taga Formation, Hirakata, Ibaraki, Joban Coalfield, Japan (*Denticulopsis lauta* Zone, NPD 4A).

cantly different from the latter two species in valve length and width (Fig. 18). It is similar to *D. crassa* in valve outline, but clearly distinguished by the absence of secondary pseudosepta. This species also resembles *D. ovata*, but differs in morphology of copula and stratigraphic range.

Phylogenetic relationship: *D. okunoi* is a descendant of *D. ichikawae* because of its stratigraphic range and morphologic similarities. It evolved from *D. ichikawae* through change in valve outline from linear form to oval one. *D. okunoi* is the last member of the lineage leading from *D. praelauta* via *D. lauta* and *D. ichikawae*.

Derivation of name: Named in honor of Dr. Haruo OKUNO who first examined fossil *Denticulopsis* species by transmitted electron

microscope.

***Denticulopsis tanimurae* n. sp.**

Plate 2, Figs. 26, 27

Synonymy: *Denticula lauta* var. *valida* (PEDICINO) OKUNO, 1964, p. 41, pl. 505, bottom, non, pl. 505, top; *Denticulopsis praehyalina* TANIMURA, 1989, in part, pl. 1, figs. 5a, 5b, pl. 2, figs. 4a, 4b, non pl. 1, figs. 1-4, 6-9b, pl. 2, figs. 1-3b, 5-7.

Description: Frustule rectangular with rounded corners in girdle view. Valve thickly silicified, linear to linear-elliptical with rounded apices, 10-60 μm long, 4-7.5 μm wide. Transapical striae on valve face relatively coarsely punctated, 20-24 in 10 μm with network of ramified thickening. Valve mantle high with double-layered coarse punctation composed of outer fine and inner chamber-like large punctations. Primary pseudosepta 4-5 in 10 μm . Secondary pseudosepta absent. Marginal ribs present on both side between each two pseudosepta. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype: Plate 2, Fig. 27; GSJ F12819 deposited in Geological Survey of Japan (Sample DSDP Hole 438A, 71-3, 7-11 cm, northwest Pacific).

Stratigraphic occurrence: The species has its first occurrence in the uppermost horizon of the *Denticulopsis lauta* Zone (NPD 4A), slightly prior to the first occurrence of *D. praehyalina*. Its last occurrence is within the upper part of the *Denticulopsis hyalina* Zone (NPD 4B).

Geographic distribution: This species is recognized in the middle- to high-latitude North Pacific but not in the equatorial Pacific.

Remarks: This new species is characterized by the thickly silicified valve and coarser punctation on valve face. It is very similar to *D. lauta*, but distinguished by strongly silicified valve, slightly coarser punctation on valve face and double-layered punctation on valve mantle. The species also resembles *D.*

praehyalina, but differs by the full punctation on valve face.

Phylogenetic relationship: *D. tanimurae* probably evolved from *D. lauta* by development of double-layered punctation on valve mantle associated with strong silicification. *D. tanimurae* evolved into *D. praehyalina* by reduction of puncta on valve face.

Derivation of name: This new species is dedicated to Dr. Yoshihiro TANIMURA, National Science Museum, Tokyo, Japan, who described *Denticulopsis praehyalina*, a descendant species of *D. tanimurae*.

***Denticulopsis praehyalina* TANIMURA
emend.**

Plate 2, Figs. 28-32;

Plate 9, Figs. 5-7

TANIMURA, 1989, p. 172-174, pl. 1, figs. 1-4, 6-9b; pl. 2, figs. 1-3b, 5-7, non pl. 1, fig. 5, pl. 2, figs. 4a, 4b.

Synonymy: *Denticula lauta* BAILEY, SCHRA-
DER, 1973a, pl. 2, figs. 21, 22; SCHRA-
DER, 1973b, pl. 1, fig. 20; *Denticula miocenica* SCHRA-
DER, 1973b, pl. 1, figs. 14, 15; *Denticulopsis* sp. 1,
TANIMURA and SAITO, 1986, pl. 2, figs. 9-12;
YANAGISAWA *et al.*, 1989, pl. 6, fig. 8.

Emended description: Frustule rectangular with rounded corners in girdle view. Valve thickly silicified, linear to linear-elliptical with bluntly rounded apices, 10-40 μm long, 5-9 μm wide. Transapical striae on valve face finely punctated 12-24 in 10 μm , sporadic with variable reduction of puncta. In some specimens with strongly reduced punctation, only one or two striae of sporadic puncta present near primary pseudosepta. Puncta more or less arranged in quincunx. Clusters of puncta arranged in a longitudinal line along raphe-bearing margin, looking like triangular or hexagonal large pores in LM, two in each chamber. Two apically arranged rows of rounded large depressions present on valve face. Valve mantle high, perforated by double-layered punctation composed of outer finely perforated wall, 32-38 puncta in 10 μm , and

inner coarse punctation, 7-10 in 10 μm . Primary pseudosepta 3-5 in 10 μm . Secondary pseudosepta absent. Apical pseudosepta present in some specimens. Marginal ribs present between each two primary pseudosepta. Raphe marginal. Copula open with smooth non-punctated sides.

Stratigraphic occurrence: The first occurrence of this species is observed in the uppermost part of the *D. lauta* Zone (NPD 4A), slightly above the first occurrence of *D. tanimurae* and slightly below that of *D. hyalina*. Its last occurrence is in the uppermost part of the *D. hyalina* Zone (NPD 4B).

Geographic distribution: The species is distributed in the middle- to high-latitude North Pacific, but not in the equatorial Pacific. There is no information on this species in the Southern Ocean so far.

Remarks: The diagnostic features of this species are its thick silicification and partly reduced punctation on valve face. The species resembles *D. tanimurae* and *D. hyalina* in that they are all thickly silicified, but differs from *D. tanimurae* by reduced punctation and from *D. hyalina* by the presence of puncta on valve face. It is also similar to *D. ichikawae* in the partly reduction of puncta, but differs by more thickly silicified valve and the distribution pattern of reduced puncta on valve face. The primitive form of *D. praehyalina* with weakly reduced punctation (Pl. 2, Fig. 28) is rather similar to *D. tanimurae*, whereas the advanced form with sporadic puncta near each pseudoseptum (Pl. 2, Fig. 32) is very close to *D. hyalina*. This graded morphologic series in valve face punctation (Pl. 2, Figs. 26-33) suggests the evolutionary lineage from *D. tanimurae* through *D. praehyalina* to *D. hyalina*.

Phylogenetic relationship: The almost continuous morphologic grading mentioned above indicates that *D. praehyalina* evolved from *D. tanimurae* through reduction of puncta on valve face and developed into *D. hyalina* by further reducing of punctation.

***Denticulopsis hyalina* (SCHRADER)**

SIMONSEN

Plate 2, Figs. 14, 33, 34 ;

Plate 9, Figs. 8, 9

SIMONSEN, 1979, p. 64 ; BARRON, 1981a, pl. 4, figs. 3, 4 ; MARUYAMA, 1984a, pl. 13, figs. 7-10, pl. 16, figs. 7, 8 ; BARRON, 1985b, p. 784, figs. 13, 26, 27 ; AKIBA, 1986, pl. 26, figs. 20-25 ; AKIBA and YANAGISAWA, 1986, p. 488-489, pl. 10, figs. 1-11, 14-16, pl. 11, figs. 1-10, pl. 12, figs. 1-5 ; TANIMURA and SAITO, 1986, pl. 2, figs. 1-4 ; YANAGISAWA *et al.*, 1989, pl. 6, figs. 9-11 ; TANIMURA, 1989, pl. 1, figs. 10-14.

Synonymy : *Denticula lauta* BAILEY, KOIZUMI, 1968, pl. 34, figs. 11a-12b ; *Denticula hyalina* SCHRADER, 1973a, p. 704, pl. 1, figs. 12-22 ; SCHRADER, 1973b, p. 418, pl. 1, figs. 10, 22 ; SCHRADER, 1974b, fig. 1 :25 ; KOIZUMI, 1975a, pl. 1, figs. 21-26 ; AKIBA, 1979, pl. 3, figs. 5, 6 ; BARRON, 1980, pl. 1, fig. 12 ; *Denticula hyalina* var. *hustedtii* SCHRADER, 1973b, pl. 1, figs. 9, 21.

Description : Frustule rectangular with rounded corners in girdle view. Valve thickly silicified, linear to linear-elliptical with bluntly rounded apices, 8-36 μm long, 3.5-7 μm wide. Valve almost hyaline. Clusters of fine puncta arranged in a longitudinal line along raphe-bearing margin, looking like large triangular or hexagonal pores in LM, two between each two primary pseudosepta. Valve mantle high, perforated by double-layered punctation composed of outer finely perforated wall, 32-38 in 10 μm , and inner coarse puncta, 7-10 in 10 μm . Primary pseudosepta 3-4 in 10 μm . Secondary pseudosepta absent. Marginal ribs present between each two primary pseudosepta on both sides. Raphe marginal. Copula open with smooth non-punctated sides.

Stratigraphic occurrence : The first occurrence of this species defines the base of the *D. hyalina* Zone (NPD 4B) in the middle- to high-latitude North Pacific. This species occurs commonly to abundantly through this zone, showing remarkable high abundance in its uppermost part where it occupies 80-90% of

the assemblage. It abruptly decreases in abundance at the base of the *Crucidenticula nicobarica* Zone (NPD 5A) and thereafter it is rare or sporadic in overlying Middle to Late Miocene sequences until the top of the Upper Miocene *D. katayamae* Zone (NPD 6A) in the DSDP Hole 438 A. The species increases again at the base of the *Thalassionema schraderi* Zone (NPD 6B) and shows frequent occurrence through this zone and the overlying *Rouxia californica* Zone (NPD 7A). This occurrence is, however, probably due to reworking related to a hiatus at the base of the *T. schraderi* Zone. Its precise last appearance is, therefore, difficult to recognize.

In the Southern Ocean, this species is found in the uppermost part of the *Coscinodiscus lewisianus* Zone (NSD 4) through the *Nitzschia grossepunctata* Zone (NSD 5).

Geographic distribution : The species is restricted to the middle- to high-latitude in the Northern and Southern Hemispheres.

Remarks : *D. hyalina* is characterized by its almost hyaline valve face. It is distinguished from *D. praehyalina* by the lack of striae on valve face, and from *D. miocenica* by its more slender and linear valve outline. This species bears resemblance to *D. katayamae* in hyaline valve face but differs by the absence of secondary pseudosepta.

A very large valve with linear valve outline, a central raphe and coarse double-layered punctation on whole valve face (Pl. 2, Fig. 45) was described as *Katahiraia oblonga* KOMURA (KOMURA, 1976, p. 386-387, abb. 6, figs. 1-4, pl. 41, fig. 6) or *Katahiraia pauperata* KOMURA (KOMURA, 1976, p. 387-388, abb. 7, pl. 41, fig. 7). However, this form is possibly an initial valve of *D. hyalina* because of morphologic resemblance between them except for differences in valve size and location of raphe. This is also supported by the roughly coincident stratigraphic ranges of these *Katahiraia* species and *D. hyalina*. However, further study is required to confirm their critical relationship.

Phylogenetic relationship : *D. hyalina* is surely a descendant of *D. praehyalina* because

of morphologic continuity between the two species (TANIMURA, 1989). It evolved from *D. praehyalina* by further reduction of puncta, and developed into *D. miocenica* by change in valve outline from linear to oval form.

***Denticulopsis miocenica* (SCHRADER)**

SIMONSEN emend.

Plate 2, Figs. 35-37

SIMONSEN, 1979, p. 65; AKIBA, 1986, pl. 26, figs. 26, 27; AKIBA and YANAGISAWA, 1986, p. 489, pl. 10, figs. 17-23, pl. 12, figs. 6-9.

Synonymy: *Denticula miocenica* SCHRADER, 1973a, p. 705, pl. 2, figs. 26-28; non SCHRADER, 1973b, pl. 1, figs. 14, 15; AKIBA, 1979, pl. 3, fig. 8; *Denticulopsis hyalina* (SCHRADER) SIMONSEN, AKIBA and YANAGISAWA, 1986, pl. 10, figs. 12, 13.

Description: Frustule rectangular with rounded corners in girdle view. Valve thickly silicified, oval with broadly rounded apices, 7.5-38 μm long, 5.5-13 μm wide. Valve face almost hyaline. Clusters of fine puncta arranged in a line along raphe-bearing margin, looking like triangular or hexagonal large pores in LM, two between each two primary pseudosepta. Primary pseudosepta 3.5-5 in 10 μm , curved near apex. Secondary pseudosepta absent. Marginal ribs present between each two primary pseudosepta. Raphe marginal. Deck very broad with small foramina. Copula open with smooth non-punctated sides.

Stratigraphic occurrence: The species is restricted in the uppermost part of the *Denticulopsis hyalina* Zone (NPD 4B) with generally very rare abundance. However it is found very abundantly from exotic blocks in the Chokubetsu Formation of the Kushiro Coalfield, eastern Hokkaido, Japan (Fig. 19; AKIBA and ICHINOSEKI, 1983).

Geographic distribution: This species have been found only from the middle- to high-latitude North Pacific.

Remarks: *D. miocenica* bears resemblance to *D. hyalina*, but differs by more oval valve outline. We have once questioned the tax-

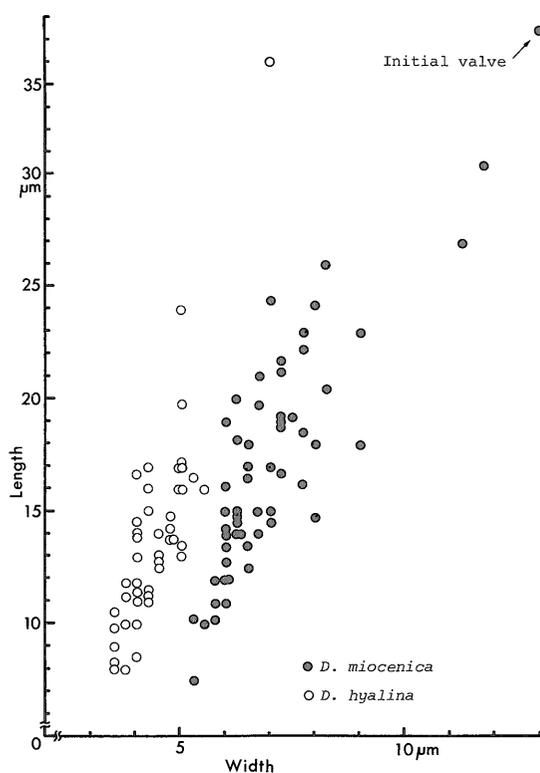


Fig. 19 Plot of width and length in valves of *Denticulopsis miocenica* and *D. hyalina*. Sample JDS 5801, an exotic block in the Chokubetsu Formation, Kushiro Coalfield, eastern Hokkaido, Japan (*Denticulopsis hyalina* Zone, NPD 4B).

onomic status of *D. miocenica* (AKIBA and YANAGISAWA, 1986). However, biometrical measurements show that the two species are significantly different in valve length and width, and thus *D. miocenica* is a distinct species (Fig. 19).

An unusually large valve with oval valve outline, a central raphe and double-layered punctation on the whole valve face is found rarely in the upper part of the *D. hyalina* Zone (NPD 4B) (Pl. 2, Fig. 44; Pl. 10, Figs. 3-9). This form was named *Katahiraia aspera* by KOMURA (1976, p. 385, abb. 5, figs. 1-8, pl.41, figs. 1-5). However, it may possibly be an initial valve of *D. miocenica*.

Phylogenetic relationship : Based on similarity in morphology and stratigraphic occurrences, *D. miocenica* is believed to have evolved from *D. hyalina* by change in valve outline from linear to oval form. *D. miocenica* terminated the lineage leading from *D. tanimurae* through *D. praehyalina* and *D. hyalina*.

***Denticulopsis simonsenii* n. sp.**

Plate 3, Figs. 1-3 ;

Plate 11, Figs. 1, 5

Synonymy : *Denticula hustedtii* SIMONSEN and KANAYA, 1961, in part, pl. 1, figs. 22, 24, 25, non pl. 1, figs. 19-21 ; KOIZUMI, 1968, p. 213, pl. 34, figs. 4a-5b, non pl. 34, figs. 6a, 6b ; SCHRADER, 1974b, fig. 1: 21 ; *Denticulopsis hustedtii* (SIMONSEN and KANAYA) SIMONSEN, MARUYAMA, 1984a, pl. 12, fig. 8, pl. 13, fig. 6, pl. 16, figs. 2, 3 ; AKIBA and YANAGISAWA, 1986, pl. 18, figs. 4, 5 ; YANAGISAWA *et al.*, 1989, pl. 6, fig. 1.

Description : Frustule rectangular with rounded corners in girdle view. Valve linear, not elliptical or oval, 9-49 μm long, 4-8 μm wide. Transapical striae on valve face finely punctated, not reduced, 22-24 in 10 μm , puncta in quincunx arrangement. Valve mantle finely punctated. Pseudosepta (primary or secondary pseudosepta) equally spaced, 5.5-8 in 10 μm , with 1-3 secondary pseudosepta between each two primary pseudosepta. Marginal ribs, very short and sometimes inconspicuous on both sides between each two pseudosepta. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype : Plate 3, Fig. 1 ; GSJ F12818 deposited in Geological Survey of Japan (Sample N 58, Hataya Formation, Matsushima, Japan. Detailed location of the type sample is shown in fig. 3 of AKIBA *et al.*, 1982).

Stratigraphic occurrence : In the middle- to high-latitude North Pacific, this species first occurs in the middle part of the *Denticulopsis hyalina* Zone (NPD 4B), but is in very low abundance until its abrupt increase

at the base of the overlying *Crucidentricula nicobarica* Zone (NPD 5A). Thereafter it maintained its dominance as the most important constituent of the North Pacific diatom assemblage throughout the Middle Miocene. After it gradually decreased in dominance, replaced by its descendant *Denticulopsis vulgaris* at the base or lowest part of the Late Miocene *Denticulopsis dimorpha* Zone (NPD 5D), *D. simonsenii* shows only rare or sporadic occurrence until the top of the *D. katayamae* Zone (NPD 6A). Its recurrent increase at the base of the *Thalassionema schraderi* Zone (NPD 6B) and consistent occurrence through this zone and the overlying *Rouxia californica* Zone (NPD 7A) in DSDP Hole 438 A may be due to reworking from older sediments.

In the equatorial Pacific, *D. simonsenii* has a shorter range than that in the middle- to high-latitude North Pacific. Its consistent occurrence begins near the base of the *Coscinodiscus lewisianus* Zone (NTD 6) which roughly coincides with its abrupt increase in the North Pacific. However, BARRON (1985a) reported its earlier isolated occurrence in the underlying B Subzone of the *Cestodiscus pepulum* Zone (NTD 5B), which closely approximates its first occurrence in the North Pacific. *D. simonsenii* occurs frequently from the middle part of the *C. lewisianus* Zone to the middle part of the *Actinocyclus moronensis* Zone (NTD 9) and then abruptly declined, replaced by *Denticulopsis vulgaris*. It became extinct in the lower part of the *Coscinodiscus yabei* Zone (NTD 10) in the equatorial Pacific.

In the Southern Ocean, *D. simonsenii*, though it has not been differentiated from its related species such as *Denticulopsis vulgaris* and *D. praekatayamae*, occurs from the middle part of the *Nitzschia grossepunctata* Zone (NSD 5) to the top of the *Denticulopsis hustedtii* Zone (NSD 8). The first occurrence datum coincides with that in the middle- to high-latitude North Pacific, but its last occurrence in the lowermost part of the Pliocene is seemingly three million years later than that in the North Pacific. Its sporadic and rare occur-

rence in the middle and upper part of the *D. hustedtii* Zone suggests that the latest Miocene and earliest Pliocene occurrence of *D. simonsenii* may be reworking as it is in the North Pacific.

Geographic distribution : *D. simonsenii* is a cosmopolitan diatom with broad distribution both in the middle- to high-latitudes and the low-latitude. It may be, however, originally a middle- to high-latitude species because of its more abundant occurrence and longer stratigraphic range in the middle to high-latitudes than in the low-latitude. It was introduced to the low-latitude by a major cooling in the Middle Miocene (BARRON, 1986).

Remarks : This new species is characterized by its linear valve outline and full punctation on valve face. It is distinguished from *D. hustedtii* and *D. crassa* by the linear valve outline. The species differs from *D. vulgaris*, *D. praekatayamae* and *D. katayamae* by the full punctation on valve face.

Phylogenetic relationship : A probable ancestor of this species is *Denticulopsis lauta* because there are no other preceding species that have the same pattern of puncta as that of *D. simonsenii*. This is also supported by the presence of a curious specimen that may be interpreted as an evolutionary intermediate form between the two species (AKIBA, 1975, pl. 1, figs. 3a-b). *D. simonsenii* evolved from *D. lauta* by creating secondary pseudosepta. *D. simonsenii* is an ancestral species of *D. vulgaris*, *D. crassa* and *D. hustedtii*.

Derivation of name : The species is named in honor of Dr. Reimer SIMONSEN who first demonstrated the biostratigraphic value of this diatom group with Dr. Taro KANAYA and established the taxonomy of the genus *Denticulopsis*.

***Denticulopsis vulgaris* (OKUNO) n. comb.**

Plate 3, Figs. 4-8 ;

Plate 11, Figs. 2, 6-10

Basionym : *Denticula lauta* var. *vulgaris* OKUNO, 1964, p. 40, pl. 505, top a.

Synonymy : *Denticula hustedtii* SIMONSEN et KANAYA, 1961, in part, pl. 1, fig. 21, non pl. 1, figs. 19, 20, 22, 24, 25 ; KOIZUMI, 1968, pl. 34, figs. 6a, 6b, non pl. 34, figs. 4a-5b ; KANAYA, 1971, pl. 40.5, figs. 14a, 14b ; *Denticula lauta* BAILEY (with reduced structure), SCHRADER, 1973b, pl. 1, fig. 11 ; *Denticulopsis hustedtii* (SIMONSEN et KANAYA) SIMONSEN, MARUYAMA, 1984a, pl. 12, figs. 7, 9a, 9b, pl. 16, fig. 1 ; AKIBA, 1986, pl. 28, fig. 13 ; AKIBA and YANAGISAWA, 1986, pl. 17, fig. 12, pl. 19, figs. 1-3 ; YANAGISAWA *et al.*, 1989, pl. 6, fig. 2.

Description : Frustule rectangular with rounded corners in girdle view. Valve linear with rounded apices, 12-45 μm long, 4-7 μm wide. Transapical striae on valve face, finely punctated and reduced so that only two striae remain near each pseudosepta with a broad hyaline area between each two pseudosepta (Pl. 11, Figs. 2, 6-8). Valve mantle finely punctated without reduction of puncta (Pl. 11, Fig. 8). Punctation on valve mantle usually single-layered but sometimes double-layered in the lower part of *Denticulopsis dimorpha* Zone (NPD 5D). Pseudosepta (primary or secondary) equally spaced, 5.5-8 in 10 μm , with secondary pseudosepta, 1-3 between each two primary pseudosepta. Marginal ribs short and sometimes inconspicuous between each two pseudosepta on both sides. Raphe marginal. Copula open with smooth non-punctated sides.

Stratigraphic occurrence : In the middle- to high-latitude North Pacific, the first occurrence of this species lies within the *Crucidentricula nicobarica* Zone (NPD 5A), but its occurrence remains rare to sporadic until the top of the *Denticulopsis praedimorpha* Zone (NPD 5B). The species became a consistent member of diatom assemblage from the base of the *Thalassiosira yabei* Zone (NPD 5C), and it shows high abundance, dominating over *Denticulopsis simonsenii* in the lower part of the *Denticulopsis dimorpha* Zone (NPD 5D). Thereafter it declined and became a minor element during the remainder of the Late Miocene. Its recurrent increase at the base of

the *Thalassionema schraderi* Zone (NPD 6B) in DSDP Hole 438A may be due to reworking related to a hiatus at this level, making it difficult to recognize its last occurrence.

In the equatorial Pacific, *D. vulgaris* has its first occurrence in the upper part of the *Actinocyclus moronensis* Zone (NTD 9), which roughly coincides with its increasing in the middle- to high-latitude North Pacific. It replaces *D. simonsenii* and occurs frequently within the upper part of this zone. It last occurs in the lowest part of the overlying *Coscinodiscus yabei* Zone (NTD 10).

This species is found from Miocene sediments of Chile (Pl. 11, Figs. 9-10). However, its detailed stratigraphic range is unknown in the Southern Hemisphere at present.

Geographic distribution: *D. vulgaris* is broadly distributed in the North Pacific, the equatorial Pacific and the Southern Ocean. It occurs more dominantly with a longer stratigraphic range in the North Pacific than in the equatorial Pacific. These occurrences indicate that this species is originally and mainly a middle- to high-latitude species.

Remarks: The most characteristic feature of this species is the reduction of puncta on valve face so that only two striae remain near each pseudoseptum. This species is clearly distinguished from *D. simonsenii* by this reduction of puncta. It is very similar to *D. praekatayamae*, but differs by the continuity of the transapical striae and also by a less silicified valve. The species is distinguished from *D. hustedtii* by its linear valve outline. Some specimens from the *D. dimorpha* Zone are thickly silicified with double-layered punctation on valve mantle (Pl. 3, Fig. 6) and show morphologic similarity to *D. praekatayamae*. These forms may be evolutionary transitional forms between the two species.

An unusually large valve with a central raphe (Pl. 3, Fig. 29) is found rarely. This type of valve was described as *Yoshidaia loculata* KOMURA (KOMURA, 1976, p. 391-392, abb. 11, figs. 1-5, pl. 40, fig. 11, pl. 41, fig. 9). However it may possibly be an initial valve of *D. vul-*

garis because of morphologic similarity between them except for a difference in location of raphe.

Discussion: The species was described initially as a variety of *Denticula lauta* by OKUNO (1964) from the Usujiri deposit at Futami, southern Hokkaido, Japan. However, its holotype specimen apparently possesses secondary pseudosepta and therefore it is not a variety of *D. lauta*. SCHRADER (1973b) referred to this taxon but treated it as a synonym of *D. lauta*. He also noticed the reduction of transapical striae in *Denticula hustedtii* and described a specimen that can now be included in *D. vulgaris* (SCHRADER, 1973b, p. 418). Nevertheless, he illustrated this specimen as *Denticula lauta* (with reduced structure). No one has referred to this taxon since then.

Phylogenetic relationship: It is certain that *D. vulgaris* evolved from *D. simonsenii* through reduction of puncta on valve face because of intimate morphologic similarity between the two species. *D. vulgaris* gave rise to *D. praekatayamae* by further reducing of puncta and thick silicification.

***Denticulopsis praekatayamae* n. sp.**

Plate 3, Figs. 9-11, 20;

Plate 11, Figs. 3, 14-16

Synonymy: *Denticulopsis katayamae* MARUYAMA, 1984a, in part, pl. 17, figs. 14, 17, non pl. 17, figs. 1-13, 15, 16, 18-23; AKIBA and YANAGISAWA, 1986, pl. 20, figs. 2, 3, 6.

Description: Frustule rectangular with rounded corners in girdle view. Valve strongly silicified, linear with rounded apices, 15-44 μm long, 5-8 μm wide. Transapical striae strongly reduced so that only two striae of sporadic puncta remain near each pseudoseptum. Valve mantle perforated by double-layered punctation composed of outer fine and inner coarse punctations. Pseudosepta (primary or secondary) equally spaced, 6-7 in 10 μm , with secondary pseudosepta 1-3 between each two primary pseudosepta. Marginal ribs short and sometimes inconspicuous between

pseudosepta on both sides. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype: Plate 3, Fig. 10; GSJ F12817 deposited in Geological Survey of Japan (Sample DSDP Hole 438A, 56 cc, northwest Pacific).

Stratigraphic distribution: In the middle- to high-latitude North Pacific, the first occurrence of this species is in the middle part of the *D. dimorpha* Zone (NPD 5D), slightly prior to that of *D. katayamae*. Its last occurrence is observed in the uppermost part of the overlying *D. katayamae* Zone (NPD 6A). The species shows spot occurrence at the uppermost part of the *Actinocyclus moronensis* Zone (NTD 9) in the equatorial Pacific.

Geographic distribution: The species is found frequently in the middle- to high-latitude North Pacific and the Southern Ocean, but rarely in the equatorial Pacific. This species is mainly a middle- to high-latitude species.

Remarks: Diagnostic characters of this new species are its strongly silicified valve and reduced punctation on valve face with remaining two striae of sporadic puncta near each pseudoseptum. *D. praekatayamae* resembles *D. katayamae*, but is distinguished by the presence of striae on valve face. It is also similar to *D. vulgaris*, but differs by its sporadic puncta of striae and thick silicification.

Phylogenetic relationship: The species evolved from *D. vulgaris* through further reduction of puncta on valve face associated with strong silicification of valve, and it developed into *D. katayamae* by complete reduction of puncta.

***Denticulopsis katayamae* MARUYAMA
emend.**

Plate 3, Figs. 12, 13, 28;

Plate 11, Fig. 4

MARUYAMA, 1984a, p. 158-159, pl. 12, figs. 1a-6, pl. 17, figs. 1-13, 15, 16, 18-23, non pl. 17, figs. 14, 17; KOIZUMI and TANIMURA, 1985, pl.

1, figs. 5, 6; AKIBA, 1986, pl. 28, figs. 1-4; AKIBA and YANAGISAWA, 1986, p. 489, pl. 17, figs. 1-3, 6, pl. 19, figs. 6-9, pl. 20, figs. 1, 4, 5, 7, non pl. 20, figs. 2, 3, 6.

Synonymy: *Denticula hyalina* var. *hustedtii* SCHRADER, 1973b, p. 418, non pl. 1, figs. 9, 21; *Denticulopsis* aff. *hyalina* var. *hustedtii* (SCHRADER) SIMONSEN, ORESHKINA, 1985, pl. 1, figs. 11-13.

Emended description: Frustule rectangular with rounded corners in girdle view. Valve linear with bluntly rounded apices, 7-37 μm long, 4-7 μm wide. Valve face almost hyaline. Cluster of fine puncta arranged in a longitudinal line along raphe-bearing margin, looking like large pores in LM. Valve mantle perforated by double-layered punctation composed of outer fine and inner coarse punctations. Pseudosepta (primary or secondary) equally spaced, 6-7 in 10 μm . Secondary pseudosepta 1-3 between each two primary pseudosepta. Marginal ribs short and inconspicuous between each two pseudosepta. Raphe marginal. Copula open with smooth non-punctated sides.

Stratigraphic occurrence: The species is common to abundant in the Late Miocene *D. katayamae* Zone (NPD 6A) and characterizes this zone. Its first occurrence is recognized in the middle part of the *D. dimorpha* Zone (NPD 5D) and its last occurrence defines the top of the *D. katayamae* Zone.

Geographic distribution: The species is abundantly distributed in the North Pacific but not found in the equatorial Pacific.

Remarks: *D. katayamae* is characterized by hyaline valve face and thickly silicified valve. It is distinguished from *D. praekatayamae* by the absence of transapical striae on valve face. This species resembles *D. hyalina* in having hyaline valve face, but clearly differs by the presence of secondary pseudosepta.

An oval form (Pl. 3, Fig. 28), which is found sporadically in the upper part of the *D. katayamae* Zone, may be a distinct taxon but more stratigraphic data are required to establish a new taxon.

Discussion: In the original description (MARUYAMA, 1984a, p. 158-159), an expression, "in some specimens sparsely punctate" must be omitted because it describes *D. praekatayamae* n. sp.

This species was described correctly by SCHRADER (1973b) as *Denticula hyalina* var. *hustedtii*. However, his holotype specimen (SCHRADER, 1973b, pl. 1, fig. 9) does not fit his description; namely it lacks secondary pseudosepta which is the most distinctive feature that distinguishes the variety from the nominate variety. Consequently, the holotype of *D. hyalina* var. *hustedtii* is undoubtedly *D. hyalina* and SCHRADER's (1973b) taxon is invalid.

Phylogenetic relationship: This species is surely a descendant of *D. praekatayamae* because of common features between the two species. AKIBA and YANAGISAWA (1986) suggested another possible evolutionary change from *D. hyalina* to *D. katayamae*. This possibility is, however, now rejected because of more intimate and graded morphologic change from *D. praekatayamae* to *D. katayamae*. *D. katayamae* is the last species of the lineage composed of *D. simonsenii*, *D. vulgaris*, *D. praekatayamae* and *D. katayamae*.

***Denticulopsis delicata* n. sp.**

Plate 7, Figs. 1-4

Description: Valve delicate, linear and slender, 36-53 μm long, 5.5-6.5 μm wide in observed specimens. Valve face seems hyaline in ordinary LM observation. Pseudosepta (primary or secondary) equally spaced, ca. 7 in 10 μm . Primary pseudosepta with poorly developed narrow basal ridge. Secondary pseudosepta present 1-2 between each two primary pseudosepta. Marginal ribs short and inconspicuous on both sides between pseudosepta. Raphe marginal.

Holotype: Plate 7, Fig. 1; GSJ F12891 deposited in Geological Survey of Japan (Sample DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean).

Stratigraphic occurrence: Not well known at present.

Geographic distribution: The species is found only from the Southern Ocean.

Remarks: The characteristic feature of this species is its delicate valve with seemingly hyaline valve face. It is similar to *D. katayamae* in the hyaline valve face, but differs by a more linear and more thinly silicified valve.

Discussion: The features of this species are just fit with those of *Denticula* aff. *seminae*, a taxon which SCHRADER (1976) recognized in the DSDP Hole 278 in the Southern Ocean, although he presented no illustration of the taxon. According to his occurrence chart, *D. seminae* aff. *seminae* occurs in the lower part of the *D. lauta* - *D. hustedtii* Zone (NSD 7) (Fig. 10). Further biostratigraphic study is needed to establish the stratigraphic distribution and phylogeny of this species.

***Denticulopsis hustedtii* (SIMONSEN et KANAYA) SIMONSEN emend.**

Plate 3, Figs. 14-19;

Plate 11, Figs. 11-13.

SIMONSEN, 1979, p. 64.

Synonymy: *Denticula lauta* BAILEY, GRUNOW in VAN HEURCK, 1880-1885, pl. 49, figs. 1, 2; *Denticula hustedtii* SIMONSEN and KANAYA, 1961, in part, pl. 1, fig. 19, non pl. 1, figs. 20-22, 24, 25; BARRON, 1973, pl. 1, fig. 6; SCHRADER, 1974b, fig. 1:20; BARRON, 1975, pl. 8, fig. 9, non pl. 8, fig. 10; AKIBA, 1979, pl. 3, fig. 2; *Denticula hustedtii* SIMONSEN and KANAYA var. 1, BARRON, 1976, p. 55, pl. 2, figs. 27, 34; *Denticulopsis hustedtii* (SIMONSEN and KANAYA) SIMONSEN (elliptical form), MARUYAMA, 1984a, pl. 13, figs. 1a-3, pl. 16, figs. 4, 5. *Denticulopsis hustedtii* (SIMONSEN and KANAYA) SIMONSEN, AKIBA, 1986, pl. 28, figs. 16, 17; *Denticulopsis hustedtii* SIMONSEN et KANAYA, ITO, 1986, pl. 1, fig. 14.

Emended description: Frustule rectangular with rounded corners in girdle view. Valve elliptical or lanceolate with acutely rounded

apices, 9–37 μm long, 6–10 μm wide. Transapical striae, finely punctated, 22–26 in 10 μm , in quincunx arrangement. Punctuation on valve face full in some specimens, or reduced in part in other specimens so that only two striae remain near each pseudoseptum. Valve mantle low, punctated finely without reduction of puncta. Pseudosepta (primary or secondary) equally spaced, 6–8 in 10 μm , with secondary pseudosepta 1–3 between each two primary pseudosepta. Marginal ribs very short on both sides between each two pseudosepta. Raphe marginal. Copula open with smooth non-punctated sides.

Holotype: SIMONSEN and KANAYA, 1961, pl. 1, fig. 19 (Plate 3, Fig. 15).

Stratigraphic occurrence: This species is restricted within the late Middle Miocene *Thalassiosira yabei* Zone (NPD 5C) and characteristic of this zone. Its first occurrence is slightly above the base of this zone and its last occurrence lies just below the top of this zone.

Geographic distribution: The species is found in the North Pacific and the Southern Ocean, but not distributed in the equatorial Pacific.

Remarks: *D. hustedtii* whose taxonomic concept is emended here is characterized by its elliptical or lanceolate valve outline which distinguishes the species from other *Denticulopsis* species. Reduction of puncta on valve face varies from almost full punctation (Pl. 3, Fig. 15) to partly reduction with only two striae (Pl. 3, Figs. 14, 17–18). The species has resemblance to *D. simonsenii* and *D. vulgaris*, but differs by the lanceolate valve outline and the narrower interval between pseudosepta. Biometrical analysis indicates that this species differs significantly from the latter two species in valve length and width (Fig. 20). It resembles *D. crassa*, but differs by the lanceolate valve outline with more acutely rounded apices, a less silicified valve, a narrower deck and more slender basal ridges.

Discussion: MARUYAMA (1984a) first noticed the stratigraphic value of this species. He described this species as *D. hustedtii* (ellip-

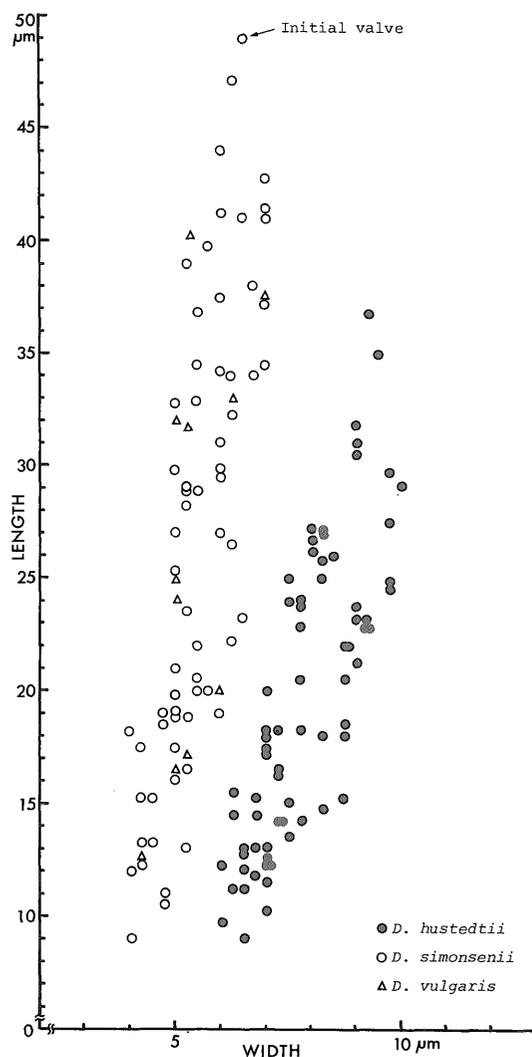


Fig. 20 Plot of width and length in valves of *Denticulopsis hustedtii*, *D. simonsenii* and *D. vulgaris*. Sample WK 205, Nakayama Formation, Sado Island, Japan (*Thalassiosira yabei* Zone, NPD 5C).

tical form) and showed that it was a useful marker of the *T. yabei* Zone (NPD 5C) in the North Pacific.

The taxonomic concept of *Denticulopsis hustedtii* in SIMONSEN and KANAYA (1961) and SIMONSEN (1979) is too broad in variation of valve shape and punctuation pattern. This

Table 9 Classification of *Denticulopsis simonsenii* group.

Punctuation	Valve outline		
	Linear	Oval	Lanceolate
Full	<i>D. simonsenii</i>		<i>D. hustedtii</i>
Reduced	<i>D. vulgaris</i>	<i>D. crassa</i>	
Sporadic	<i>D. praekatayamae</i>		
Hyaline	<i>D. katayamae</i> <i>D. delicata</i>		

study divided this species group into seven species including *D. katayamae* and *D. vulgaris* based on the differences in valve outline and punctuation on valve face (Table 9). As the type specimen of *D. hustedtii* is included in a group of lanceolate valve outline, the species name *D. hustedtii* is retained for these lanceolate group.

Phylogenetic relationship: *D. hustedtii* apparently branched off from *D. simonsenii* by change in valve outline from linear form to lanceolate form. This species did not leave any descendants.

***Denticulopsis crassa* n. sp.**

Plate 3, Figs. 21-27 ;

Plate 12, Figs. 1-8

Synonymy: *Denticula hustedtii* SIMONSEN and KANAYA, SCHRADER, 1973a, pl. 2, figs. 29, 30 ; *Denticulopsis hustedtii* (SIMONSEN and KANAYA) SIMONSEN, AKIBA, 1986, pl. 28, figs. 5, 9, 14, 15, 18 ; AKIBA and YANAGISAWA, 1986, pl. 17, figs. 9, 10, 20.

Description: Frustule rectangular with rounded corners in girdle view. Valve thickly silicified, ovate with broadly rounded apices, 10-32 μ m long, 5.5-11 μ m wide. Transapical striae on valve face, 12-15 in 10 μ m with puncta slightly reduced in quincunx arrangement. Valve mantle more finely and densely punctated than valve face. Pseudosepta (primary or secondary) equally spaced, 5-6 in 10 μ m, with secondary pseudosepta, 1-2 between

each two primary pseudosepta. Basal ridge short and broad. Marginal ribs short on both sides between each two pseudosepta. Deck broad with small foramina. Copula open or closed with smooth non-punctated sides. Apical thickening not developed in closed copula.

Holotype: Plate 3, Fig. 23 ; GSJ F12893 deposited in Geological Survey of Japan (Sample DSDP Hole 438A, 65-7, 17-18 cm, north-west Pacific).

Stratigraphic occurrence: In the middle- to high-latitude North Pacific, the first occurrence of this species roughly coincides with the base of the *D. praedimorpha* Zone (NPD 5B) and its last occurrence lies in the lower part of the *D. dimorpha* Zone (NPD 5D). This species has two abundance peaks: one in the middle part of the *D. praedimorpha* Zone and the other in the middle part of the *Thalassiosira yabei* Zone (Table 4, Fig. 8).

Geographic distribution: This species is distributed both in the middle- to high-latitude North Pacific and the Southern Ocean but not found in the equatorial Pacific. It is, therefore, a middle- to high-latitude species.

Remarks: *D. crassa* is distinguished from *D. simonsenii*, *D. vulgaris*, *D. praekatayamae* and *D. katayamae* by its oval shape, a broader deck with smaller foramina, short and robust basal ridges and the presence of closed copula. Biometrical measurement indicates that *D. crassa* differs significantly from *D. simonsenii* and *D. vulgaris* in width and length (Fig. 21). This species is similar to *D. hustedtii* when the valve outline is not so oval, but differs by a more thickly silicified valve, broader basal ridges, a broader deck and more rounded apices.

D. crassa is also very similar to *D. ovata* in valve outline. In particular, the valve of *D. ovata* combined with its closed copula (Pl. 5, Fig. 19) is hardly distinguishable from the valve of *D. crassa* (Pl. 3, Fig. 23). Nevertheless, careful observation can distinguish the two species; In *D. ovata*, the suture line between the basal ridge and the pair of inner

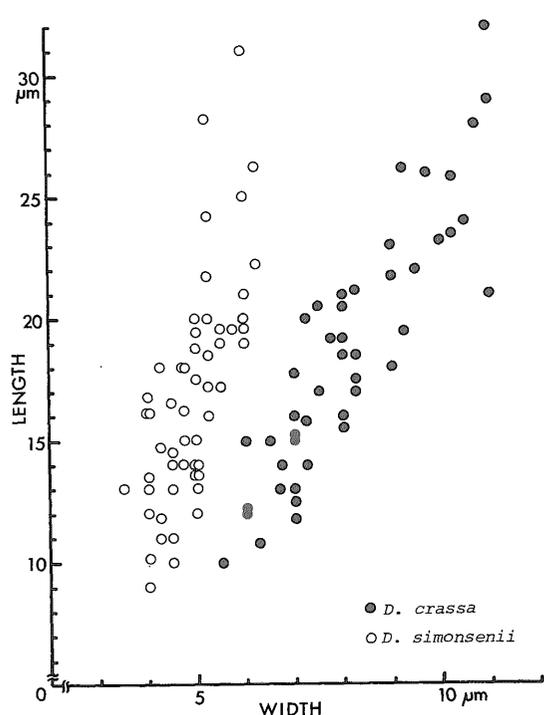


Fig. 21 Plot of width and length in valves of *Denticulopsis crassa* and *D. simonsenii*. Sample DSDP Hole 438A, 65-7, 17-18 cm (*Denticulopsis praedimorpha* Zone).

extensions are not present (the right figure of Fig. 19 in Plate 5), whereas *D. crassa* clearly possesses this suture line (Pl. 12, Fig. 3).

The closed copula of *D. crassa* resembles that of *D. praedimorpha* but is distinguished by the following characteristics: (1) *D. crassa* is more ovate in outline than *D. praedimorpha*. (2) *D. crassa* has no silicified apical thickening in its closed copula, while *D. praedimorpha* has well developed apical thickenings except for its small form.

Phylogenetic relationship: This species is an evolutionary offshoot of *D. simonsenii*. It evolved from the latter species by change in valve outline to oval form, thick silicification and development of closed copula. *D. crassa* left no descendant.

***Denticulopsis praedimorpha* var. *minor* n. var.**

Plate 4, Figs. 1, 2, 8, 9, 11, 21-24;

Plate 7, Figs. 5, 6, 10;

Plate 12, Fig. 9

Synonymy: *Denticulopsis praedimorpha* (AKIBA) BARRON, 1981a, pl. 4, figs. 9, 10; *Denticulopsis* cf. *dimorpha* (SCHRADER) SIMONSEN, AKIBA, 1982, pl. 10, fig. 19; *Denticulopsis praedimorpha* AKIBA, MARUYAMA, 1984a, pl. 15, fig. 1, pl. 18, fig. 11, *Denticulopsis praedimorpha* (AKIBA) BARRON ex AKIBA, BARRON, 1985b, fig. 13.24; *Denticulopsis praedimorpha* BARRON ex AKIBA, ORESHKINA, 1985, pl. 1, fig. 4; AKIBA and YANAGISAWA, 1986, pl. 13, figs. 3, 4, 16, 24.

Description: Valve linear with rounded apices, small, 6-19 μm mostly 6-13 μm long, 2.5-4 μm wide. Pseudosepta 6-7 in 10 μm . Silicified inner apical thickening of closed copula absent. Other features are nearly the same as those of the nominative variety.

Holotype: Plate 4, Fig. 8 (closed copula); GSJ F12815 deposited in Geological Survey of Japan (DSDP Hole 438 A, 66-1, 121-123 cm, northwest Pacific)

Stratigraphic occurrence: The variety occurs from the base of the *D. praedimorpha* Zone (NPD 5B) to the top of this zone.

Remarks: The variety differs from *D. praedimorpha* var. *praedimorpha* and var. *robusta* by the absence of apical thickening of closed copula and smaller size (less than 4 μm in width, Fig. 22). It is distinguished from *D. praedimorpha* var. *intermedia* by the lack of partially developed cross rod of closed copula.

Phylogenetic relationship: This variety is the most primitive form of *D. praedimorpha*. It is very similar to the primitive form of *Denticulopsis lauta* in small valve size, full punctation on valve face and the presence of two types of copula. There is a stratigraphic gap between the last abundant occurrence of *D. lauta* and the first occurrence of this variety in the North Pacific. However, the morphologic similarities mentioned above sug-

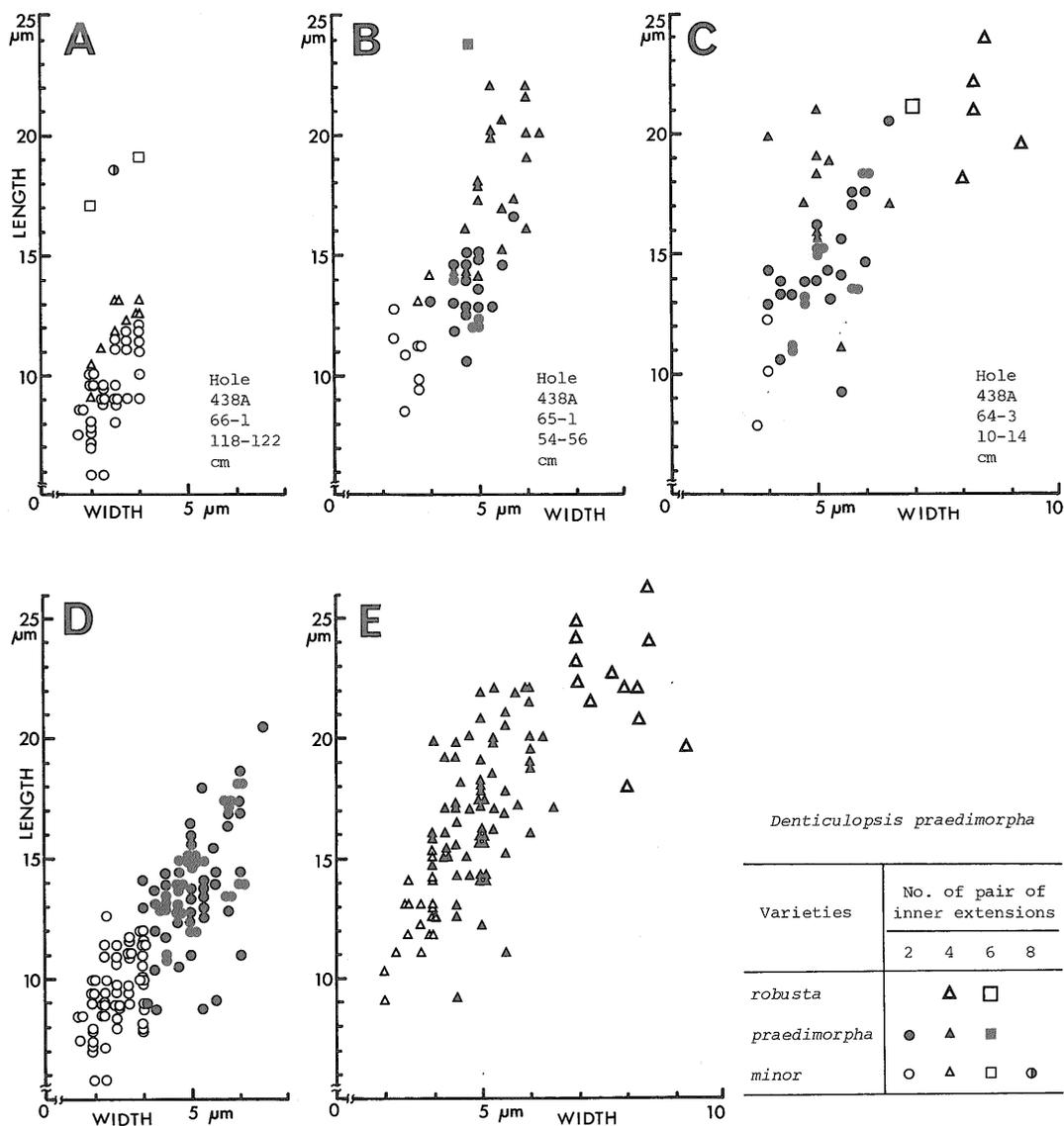


Fig. 22 Plot of width and length in closed copulae of *Denticulopsis praedimorpha*. A: lower part of *Denticulopsis praedimorpha* Zone (NPD 5B); B: middle part of the zone; C: upper part of the zone; D: specimens with two pairs of inner extensions, samples DSDP Hole 438A, 66-1 (118-122 cm), 65-3 (100-103 cm), 65-1 (54-56 cm), 64-5 (30-32 cm), 64-3 (10-14 cm); E: specimens with four pairs of inner extensions, samples are the same as those used for Figure D.

gests that *D. praedimorpha* var. *minor* evolved from the primitive form of *D. lauta* by acquiring a closed-copula with well-developed pair of inner extensions.

This variety is an ancestor of *D. praedimorpha* var. *praedimorpha*, var. *intermedia* and *D. barronii*.

***Denticulopsis praedimorpha* BARRON ex
AKIBA var. *praedimorpha***

Plate 4, Figs. 3-5, 10, 12-17, 39;

Plate 5, Figs. 4-12

AKIBA, 1982, p. 46-48, pl. 11, figs. 9a-16, 18-27b; ORESHKINA, 1985, pl. 1, fig. 3; AKIBA, 1986, pl. 27, figs. 15-26; AKIBA and YANAGISAWA, 1986, p. 489-490, pl. 13, figs. 1, 2, 5-15, 17-23, 25-28, pl. 14, figs. 1-12; YANAGISAWA *et al.*, 1989, pl. 6, fig. 6.

Synonymy: *Denticula lauta* BAILEY, KANAYA, 1959, p. 112-116, in part, pl. 10, figs. 7-9, 16, non pl. 10, figs. 10a-15; SIMONSEN and KANAYA, 1961, pl. 1, figs. 6-10, non pl. 1, figs. 1-5; *Denticula?* sp., KANAYA, 1959, p. 116, pl. 10, figs. 17a-20b; *Denticula praedimorpha* AKIBA, 1979, pl. 1, figs. 11a-19, pl. 2, figs. 1a-5, 7a-8b, 11-21b, nom. invalid; BARRON, 1980, p. 672, pl. 1, figs. 18-20; *Denticulopsis praedimorpha* (AKIBA) BARRON, 1981a, p. 529, pl. 4, fig. 8, non pl. 4, figs. 9, 10; *Denticulopsis praedimorpha* (AKIBA ex BARRON) BARRON, AKIBA *et al.*, 1982, pl. 3, figs. 58-62; *Denticulopsis praedimorpha* AKIBA, MARUYAMA, 1984a, pl. 15, figs. 2-7, pl. 18, figs. 1-6, 10, pl. 19, figs. 1-15; *Denticulopsis praedimorpha* (AKIBA) BARRON ex AKIBA, BARRON 1985b, p. 785, fig. 13.25.

Description: Frustule rectangular with rounded corners in girdle view. Valve linear to linear elliptical with bluntly rounded apices, 9-24 μm long, 4-6.5 μm wide. Transapical striae on valve face finely punctated, 24-26 in 10 μm , arranged in quincunx. Valve mantle high perforated by fine puncta. Primary pseudosepta, about 5 in 10 μm . In Vc valve, primary pseudosepta with high and short basal ridges, about 5 in 10 μm , with 2 or 3 apical pseudosepta near each apex. In Vo valve, primary pseudosepta with low and indistinct basal ridges, about 4-5 in 10 μm . Secondary pseudosepta absent. Marginal ribs between each two pseudosepta on both sides. Raphe marginal. Copula closed or open. Closed copula with serrate edge (Ccr) or with smooth edge (Ccm), combined with Vc valve.

In closed copula, apical thickening well developed. Open copula with punctated sides (Cop), combined with Vo valve.

Stratigraphic occurrence: The variety first occurs in the lower part of the *D. praedimorpha* Zone (NPD 5B) and last at the top of this zone in the middle- to high-latitude North Pacific. In the Southern Ocean, *D. praedimorpha* is found in the middle part of the *Nitzschia denticuloides* Zone (NSD 6).

Geographic distribution: *D. praedimorpha* occurs in the middle- to high-latitude North Pacific, the Norwegian Sea and the Southern Ocean. It is not distributed in the equatorial Pacific. Hence, *D. praedimorpha* is a middle- to high-latitude species.

Remarks: *D. praedimorpha* var. *praedimorpha* differs from the var. *minor* by the presence of apical thickening of closed copula and a larger valve (4-6.5 μm wide, Fig. 22). It is distinguished from the var. *robusta* by a relatively smaller and slender valve (less than 6.5 μm wide, Fig. 22) and the absence of partially developed cross rod of closed copula. The variety *praedimorpha* differs from the var. *intermedia* by the lack of partially developed cross rods of closed copula.

D. praedimorpha is different from *D. dimorpha* and *D. ovata* in that it lacks complete cross rods of closed copula. *D. praedimorpha* differs from *D. barronii* mainly by the absence of secondary pseudosepta in Vc valve. The two species also differ in geographic distribution: *D. praedimorpha* is a middle- to high-latitude species, while *D. barronii* is distributed in the low-latitude.

Because of close resemblance, the valve of *D. praedimorpha* have been confused with the valve of *D. lauta* by many previous studies. However, the valves of the two species are clearly distinguished by the length and height of basal ridge: basal ridges of Vc valve of *D. praedimorpha* are shorter and higher than those of *D. lauta*, whereas basal ridge of Vo valve of *D. praedimorpha* are lower and more indistinct than those of *D. lauta* (Compare Figures 1 and 5 in Plate 5). More detailed

morphologic differences between *D. lauta*, *D. praedimorpha* and *D. dimorpha* are discussed in remarks of *D. lauta* (p. 236).

The three types of copulae of *D. praedimorpha* might theoretically form nine (3×3) combinations in frustule (Table 3), but we have observed only seven combinations as it follows:

Cop/Cop: Pl. 4, Fig. 5.

Cop/Ccr: Pl. 4, Fig. 17; AKIBA and YANAGISAWA, 1986, pl. 14, fig. 12.

Cop/Ccr: Pl. 5, Fig. 10.

Ccr/Ccr: Pl. 4, Fig. 35.

Ccr/Ccm: Pl. 5, Fig. 11.

Ccm/Ccr: not illustrated.

Ccm/Ccm: Pl. 5, Fig. 12; Pl. 4, Fig. 16; Pl. 4, Fig. 24; AKIBA and YANAGISAWA, 1986, pl. 14, fig. 11.

(In each combination, the left indicates epicopula and the right indicates hypocopula.) We have not yet recognized combinations of Ccr/Cop and Ccm/Cop.

Phylogenetic relationship: *D. praedimorpha* var. *praedimorpha* evolved from its variety *minor* through development of apical thickening of closed copula and an increase in size.

***Denticulopsis praedimorpha* var.
robusta n. var.**

Plate 4, Figs. 6, 7, 18-20, 34, 35;

Plate 12, Figs. 10-14

Synonymy: *Denticula praedimorpha* AKIBA, 1979, pl. 2, figs. 9, 10; *Denticulopsis praedimorpha* BARRON ex AKIBA, 1982, pl. 11, fig. 11; AKIBA, 1986, pl. 27, fig. 14; *Denticulopsis praedimorpha* AKIBA, MARUYAMA, 1984a, pl. 18, figs. 7-9.

Description: Valve robust, linear-elliptical with rounded apices, 18-25 μm long, 7-9 μm wide. Valve mantle perforated with double-layered punctation composed of outer fine and inner coarse perforations. Pseudosepta 4-5 in 10 μm . Closed copula robust, sometimes with cross rods. Apical thickening of closed copula well developed. Other features are almost the

same as those of the nominative variety.

Holotype: Plate 4, Fig. 19 (closed copula); GSJ F12816 deposited in Geological Survey of Japan (DSDP Hole 438A, 64-3, 10-14 cm, northwest Pacific)

Stratigraphic occurrence: The variety occurs in the upper part of the *D. praedimorpha* Zone (NPD 5B).

Remarks: The variety differs from varieties *praedimorpha* and *minor* in a robust larger valve (more than 7 μm in width, Fig. 22), double-layered punctation on valve mantle and its robust closed copula which sometimes has partially developed cross rods.

Phylogenetic relationship: It is certain that the variety *robusta* is a descendant of the var. *praedimorpha* because of morphologic continuity between them. The var. *robusta* evolved from the var. *praedimorpha* by an increase in size and partially developed cross rods of closed copula. It did not leave any descendants.

***Denticulopsis praedimorpha* var.
intermedia n. var.**

Plate 7, Figs. 7-9, 11-13

Synonym: *Denticulopsis* cf. *dimorpha* (SCHRADER) SIMONSEN, AKIBA, 1982, pl. 10, fig. 12.

Description: Valve linear with bluntly rounded apices, small 13-27 μm long, 5-6 μm wide. Vc valve has two types of primary pseudosepta; one with a short basal ridge and the other without basal ridge. The latter type looks like a secondary pseudoseptum in valve view. Copula open or closed. Closed copula with truncated pairs of inner extensions and some partially developed cross rods. Apical thickening not developed.

Holotype: Plate 7, Fig. 13 (Closed copula); GSJ F12892 deposited in Geological Survey of Japan (Sample DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean).

Stratigraphic occurrence: This variety is found only from DSDP Hole 266 (this study) and JDS 15775 (the Southern Ocean; AKIBA,

1982) at present.

Geographic distribution: The variety is known from the Southern Ocean but not found in the middle- to high-latitude North Pacific and the low-latitude.

Remarks: This form differs from *D. praedimorpha* var. *minor* by partial development of cross rods in closed copula. It is very similar to *D. praedimorpha* var. *robusta* in that both have partially developed cross rods. However, the var. *intermedia* differs from the var. *robusta* by smaller size and the absence of apical thickening in the closed copula, as well as by the different distribution pattern of cross rods. The cross rods of the var. *robusta* are always located just near each apices (Pl. 4, Figs. 19, 20), while the location of cross rods is not fixed in the var. *intermedia* (Pl. 7, Figs. 11-13).

The Vc valve of var. *intermedia* (Pl. 7, Figs. 7-9) is hardly distinguishable from that of *D. barronii* (Pl. 4, Fig. 31). However, the two taxa differ in morphology of closed copula (Pl. 7, Figs. 11-13; Pl. 4, Figs. 26-30). *D. praedimorpha* var. *intermedia* resembles *D. dimorpha* var. *dimorpha* but differs by partial development of cross rods and the presence of basal ridge.

Phylogenetic relationship: Although its precise stratigraphic range is not known at present, *D. praedimorpha* var. *intermedia* is probably an evolutionary intermediate form between *D. praedimorpha* and *D. dimorpha*. The var. *intermedia* descended from the var. *minor* by partial development of cross rods of closed copula and evolved into *D. dimorpha* var. *dimorpha*.

***Denticulopsis barronii* n. sp.**

Plate 4, Figs. 25-33, 36-38

Synonymy: *Denticulopsis praedimorpha* (AKIBA) AKIBA, BARRON, 1985a, pl. 9, figs. 9, 10 (Closed copula).

Description: Valve linear with rounded apices, 10-28 μm long, 3.5-5 μm wide. Transapical striae finely punctated, 24-26 in 10 μm .

Puncta arranged in quincunx, so that oblique rows formed. Pseudosepta, 7.5-10 in 10 μm . Two types of valves present. One type Vc has both primary and secondary pseudosepta, each primary pseudoseptum with a short and distinct basal ridge (Pl. 4, Fig. 31). The other type Vo has only primary pseudosepta with low and indistinct basal ridges. (Pl. 4, Fig. 25). Between each two pseudosepta, short and indistinct marginal ribs present. Raphe marginal. Copula closed or open. Closed copula not punctated, with serrate edge (Ccr, Pl. 4, Fig. 32) or smooth edge (Ccm, Pl. 4, Fig. 33). Silicified apical thickening of closed copula absent or very poorly developed. Open copula (Cop) punctated with one row of puncta (Pl. 4, Fig. 38). Closed copula (Ccr and Ccm) connected with Vc valve, whereas open copula (Cop) with Vo valve.

Holotype: Plate 4, Fig. 37 (Vc valve connected with closed copula); GSJ F12803 deposited in Geological Survey of Japan (Sample DSDP Hole 77B, 20-6, 38-40 cm, eastern equatorial Pacific).

Stratigraphic occurrence: The species occurs from the uppermost part of the *Coscinodiscus gigas* var. *diorama* Zone (NTD 7) to the lower part of the *Craspedodiscus coscinodiscus* Zone (NTD 8) in the equatorial Pacific.

Geographic distribution: This new species is found only in the eastern equatorial Pacific and not in the middle- to high-latitude North Pacific.

Remarks: No complete frustule is observed in this study, but the species probably has dimorphic or polymorphic frustules as *D. praedimorpha* does.

This species bears close resemblance to *D. praedimorpha*, but differs by the presence of secondary pseudosepta of Vc valve. Closed copulae of *D. barronii* and *D. praedimorpha* are very similar to each other, but the number of pairs of teeth-like inner extensions distinguishes the two species; both odd and even numbers are permitted in *D. barronii*, whereas only odd numbers are observed in *D. praedi-*

morpha. The V_o valve of *D. barronii* also resembles *D. simonsenii* in that both have secondary pseudosepta, but *D. barronii* differs from *D. simonsenii* by the shorter basal ridges of primary pseudosepta.

Phylogenetic relationship: This species is probably a descendant of *D. praedimorpha* because of close morphologic similarities and stratigraphic range. Of the four varieties of *D. praedimorpha*, the var. *minor* is the most similar to *D. barronii* in the lack of apical thickening of closed copula, the absence of partial cross rods and relatively small size. Hence, *D. barronii* may have evolved from *D. praedimorpha* var. *minor* through development of secondary pseudosepta. This species left no descendant.

Derivation of name: The species is dedicated to Dr. John A. BARRON of U.S. Geological Survey, who first illustrated this species as *D. praedimorpha*.

***Denticulopsis dimorpha* (SCHRADER)**

SIMONSEN var. *dimorpha*

Plate 4, Figs. 42-49;

Plate 7, Figs. 14-16

SIMONSEN, 1979, p. 64; BARRON, 1981a, pl. 4, fig. 7; AKIBA, 1982, pl. 11, figs. 1, 5-6a; AKIBA *et al.*, 1982, pl. 3, figs. 63-65; MARUYAMA, 1984a, pl. 15, figs. 8-11; pl. 18, figs. 12-33; pl. 20, figs. 1-3, 5-18; AKIBA, 1986, pl. 27, figs. 3, 4, 7-9, 11-13; AKIBA and YANAGISAWA, 1986, p. 488, pl. 15, figs. 2-4, 17, 18, 20, 23-25; YANAGISAWA *et al.*, 1989, pl. 6, fig. 7.

Synonymy: *Denticula dimorpha* SCHRADER, 1973a, p. 704, pl. 1, figs. 37-44, 46; SCHRADER, 1973b, p. 418, pl. 1, figs. 16, 17; SCHRADER, 1974b, fig. 1: 15; KOIZUMI, 1975a, pl. 1, figs. 27, 28; KOIZUMI, 1975c, pl. 1, fig. 10; BARRON, 1975, pl. 8, fig. 7; BARRON, 1976, pl. II, figs. 25, 33; AKIBA, 1979, pl. 1, figs. 1a, 1b, 4, 9a-10b; *Denticula lauta* BAILEY, KOIZUMI, 1973, pl. 5, figs. 26-28.

Description: Frustule rectangular with rounded corners in girdle view. Valve linear with rounded apices, relatively small, 8-21.5

μm long, 3-5 μm wide. Valve face and mantle perforated with single-layered punctation to form transapical striae, 24-26 in 10 μm. In V_c valve, primary pseudosepta without basal ridges, 6-7 in 10 μm. In V_o valve, primary pseudosepta with low and indistinct basal ridges, 6-7 in 10 μm. Secondary pseudosepta absent. Marginal ribs between each two pseudosepta on both sides. Raphe marginal. Copula closed with serrate edge (Cr) or closed with smooth edge (Ccm), open with punctated sides (Cop). Closed copula with complete cross rods and with no or poorly developed apical thickenings. Closed copula combined with V_c valve and open copula with V_o valve.

Stratigraphic occurrence: The total range of this variety defines the *D. dimorpha* Zone (NPD 5D) in the middle- to high-latitude North Pacific. In the Southern Ocean, the species, though this variety and var. *areolata* are not distinguished, first occurs at about 11.1 Ma (BARRON, personal communication, 1988). It last occurs at the top of the *Denticulopsis lauta*-*Denticulopsis hustedtii* Zone (NSD 7).

Geographic distribution: The species is found in the middle- to high-latitude North Pacific, the Norwegian Sea and the Southern Ocean, but not in the equatorial Pacific.

Remarks: This nominative variety of *D. dimorpha* is distinguished from the var. *areolata* by its single-layered punctation and smaller size (less than 5 μm in width, Figs. 23, 24). A transitional form between the two varieties with poorly developed double-layered punctation on the valve face (Pl. 4, Fig. 47) occurs prior to the first occurrence of the typical form of *D. dimorpha* var. *areolata* (Table 4). This form is tentatively included in the var. *dimorpha* in this paper.

D. dimorpha is distinguished from *D. praedimorpha* and *D. barronii* by the presence of completely developed cross rods of closed copula and the absence of basal ridge of V_c valve. Differences between *D. lauta*, *D. praedimorpha* and *D. dimorpha* are discussed in remarks of *D. lauta* (p. 236).

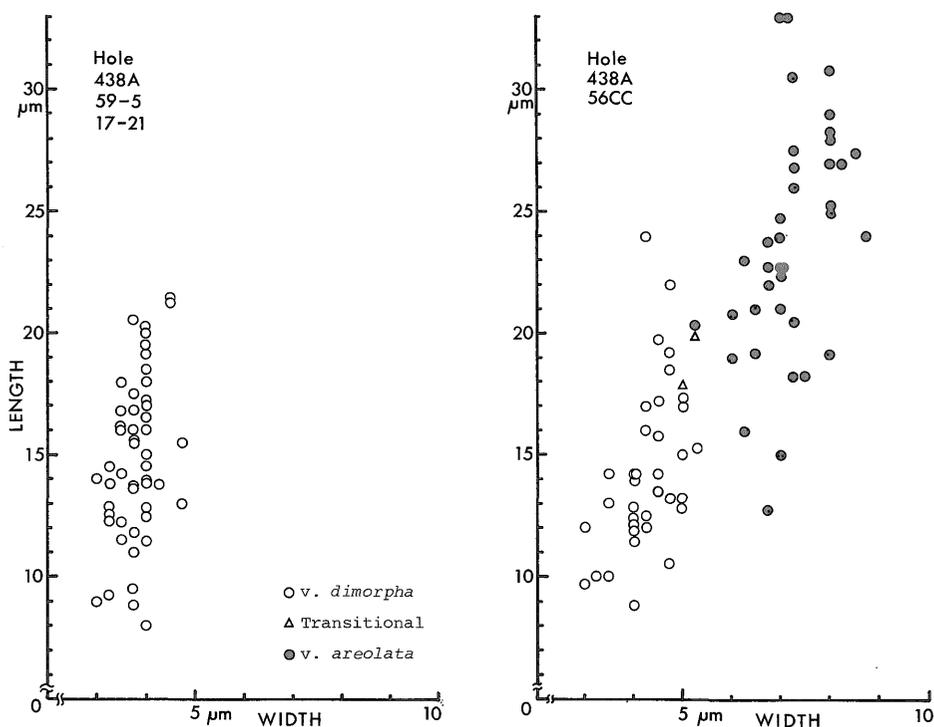


Fig. 23 Plot of width and length in valves of *Denticulopsis dimorpha*. Left: lower part of *D. dimorpha* Zone (NPD 5D); Right: upper part of the zone.

Phylogenetic relationship: As stated by MARUYAMA (1984a) and AKIBA and YANAGISAWA (1986), it is evident that *D. dimorpha* has very close relationship to *D. praedimorpha* on the basis of morphologic similarity between the two species. The variety shows intimate similarity to *D. praedimorpha* var. *intermedia* and var. *minor*, in small valve size, lack of apical thickening of closed copula. Hence *D. dimorpha* var. *dimorpha* must have been derived from *D. praedimorpha* var. *minor* through *D. praedimorpha* var. *intermedia* by forming complete cross rods of closed copula.

The stratigraphic range of *D. dimorpha* var. *dimorpha* overlaps with that of *D. praedimorpha* in the Southern Ocean (BARRON, personal communication, 1988), whereas the range of these two taxa are seemingly separated by an interval represented by the *Thalassiosira yabei* Zone (NPD 5C) in the middle- to high-latitude

North Pacific (Fig. 8). Moreover, the first occurrence of *D. dimorpha* var. *dimorpha* in the Southern Ocean is clearly older than that in the North Pacific. These occurrences suggest that *D. dimorpha* var. *dimorpha* established in the Southern Ocean and later migrated in the middle- to high-latitude of the northern Hemisphere. This is also supported by the fact that *D. praedimorpha* var. *intermedia*, a probable direct evolutionary precursor of *D. dimorpha* var. *dimorpha*, is geographically confined in the Southern Ocean and not distributed in the middle- to high-latitude of the Northern Hemisphere.

D. dimorpha var. *dimorpha* evolved into *D. dimorpha* var. *areolata*.

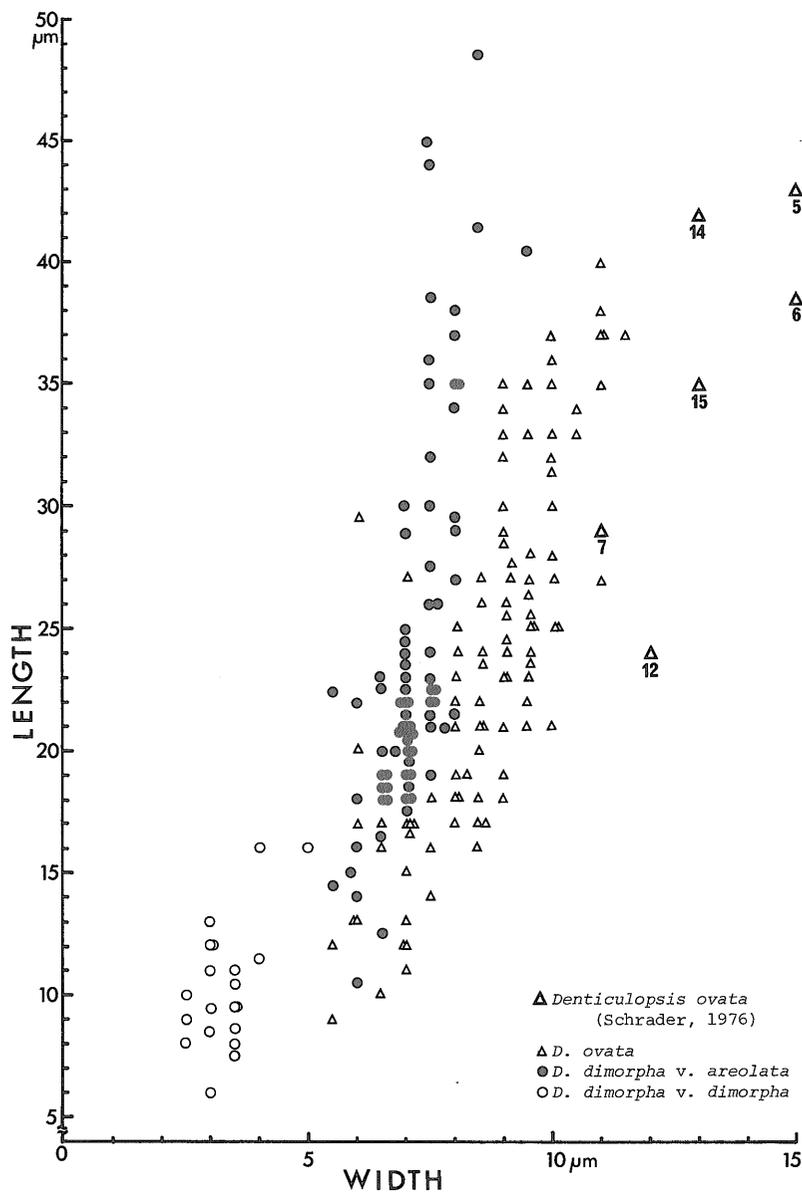


Fig. 24 Plot of width and length in copulae of *Denticulopsis dimorpha* var. *dimorpha*, *D. dimorpha* var. *areolata* and *D. ovata*. Sample DSDP Hole 266, 10-1, 80-83 cm. Numbers under large open triangles indicate figure numbers in plate 8 of SCHRADER (1976). 5 : holotype of *Denticula hustedtii* var. *ovata* SCHRADER, 1976 ; 6 : paratype of the same variety ; 7 : holotype of *Denticula lauta* var. *ovata* SCHRADER, 1976.

***Denticulopsis dimorpha* var.
areolata n. var.**

Plate 4, Figs. 40, 41, 50-54 ;

Plate 5, figs. 13-17 ;

Plate 6, Figs. 1-5, 15-23 ;

Plate 12, Figs. 15, 16.

Synonymy: *Denticula lauta* BAILEY, KOIZUMI, 1973, pl. 5, figs. 24, 25 ; KOIZUMI, 1975c, pl. 1, fig. 8 ; *Denticula dimorpha* SCHRADER, 1973a, pl. 1, fig. 45 ; AKIBA, 1979, pl. 1, figs. 2a-3, 5-8 ; BARRON, 1980, pl. 1, fig. 21 ; *Denticulopsis dimorpha* (SCHRADER) SIMONSEN, AKIBA, 1982, pl. 11, figs. 2-4, 7, 8 ; MARUYAMA, 1984a, pl. 18, fig. 34, pl. 20, fig. 4 ; BARRON, 1985b, p. 784, figs. 13.22, 13.23 ; AKIBA, 1986, pl. 27, figs. 1, 2, 5, 6, 10 ; AKIBA and YANAGISAWA, 1986, pl. 15, figs. 1, 5-16, 19, 21, 22, pl. 16, figs. 1-16.

Description: Valve linear-elliptical with bluntly rounded apices, 11-33 μm long, 5-8.5 μm wide. Valve face and mantle perforated by double-layered punctation. Outer fine puncta form transapical striae, 22-25 in 10 μm , rarely reduced. Inner coarse puncta form network of ramified thickenings. In Vc valve primary pseudosepta without basal ridges, 4-5 in 10 μm . Secondary pseudosepta absent. Marginal ribs on both sides between each two primary pseudosepta. Raphe marginal. Copula closed with serrate edge (Ccr) or closed with smooth edge (Ccm), open with punctated sides (Cop). Closed copula has no or poorly developed apical thickenings. Some copulae from the Southern Ocean have partly or completely discontinuous cross rods (Pl. 6, Figs. 16, 18, 21). Other features are nearly the same as those of the nominative variety.

Holotype: Plate 4, Fig. 54 ; GSJ F12812 deposited in Geological Survey of Japan (Sample DSDP 438A, 56 cc, northwest Pacific).

Stratigraphic occurrence: This variety occurs in the uppermost part of the *D. dimorpha* Zone (NPD 5D) in the middle- to high-latitude North Pacific. The stratigraphic range is not well known at present in the Southern Ocean.

Geographic distribution: This variety is

distributed in the middle- to high-latitude North Pacific and the Southern Ocean, but not in the equatorial Pacific.

Remarks: *D. dimorpha* var. *areolata* differs from *D. dimorpha* var. *dimorpha* mainly by its double-layered punctation. It is larger than the latter variety (the var. *areolata* more than 5 μm in width, whereas the var. *dimorpha* less than 5 μm in width ; Figs. 23, 24). *D. dimorpha* var. *areolata* resembles *D. ovata*, but is distinguished by equally spaced cross rods of closed copula, and by more slender outline (Fig. 24).

Phylogenetic relationship: It is certain that this variety evolved from *D. dimorpha* var. *dimorpha* because of the presence of transitional form and its stratigraphic range. This evolutionary change was accompanied by the development of double-layered punctation on the valve face and mantle. *D. dimorpha* var. *areolata* evolved into *D. ovata*.

***Denticulopsis ovata* (SCHRADER) n. comb.**

Plate 6, Figs. 6-14, 24-32

Basionym: *Denticula hustedtii* var. *ovata* SCHRADER, 1976, p. 632, pl. 4, figs. 5, 6, 12, 14, 15.

Synonymy: *Denticula lauta* var. *ovata* SCHRADER, 1976, p. 632, pl. 4, fig. 7 ; *Denticula lauta* BAILEY, SCHRADER, 1976, pl. 4, fig. 13 ; *Denticula hustedtii* (?) SIMONSEN and KANAYA, GOMBOS, 1976, pl. 8, fig. 5 ; *Denticula* cf. *dimorpha* SCHRADER, GOMBOS, 1976, pl. 8, figs. 9, 10 ; *Denticulopsis hustedtii* var. *ovata* (SCHRADER) SIMONSEN, 1979, p. 64 ; *Denticulopsis lauta* var. *ovata* (SCHRADER) SIMONSEN, 1979, p. 65 ; AKIBA, 1982, pl. 10, fig. 18.

Description: Frustule rectangular with rounded corners in girdle view. Valve robust, linear to oval with broadly rounded apices, 9-43 μm long, 5.5-15 μm wide. Transapical striae on valve face finely punctated 22-26 in 10 μm , in quincunx arrangement, double-layered in part near valve margin. Valve mantle perforated by double-layered punctation. Primary pseudosepta without basal ridges, 5-6.5 in 10 μm . Secondary pseudo-

septa absent. Marginal ribs present on both sides between each two pseudosepta. Raphe marginal. Deck broad with small foramina. Copula open or closed. Closed copula robust, very thickly silicified, with serrate edge (Ccr) or smooth edge (Ccm). Cross rods unequally spaced, with large and small foramina. At the large foramina, truncated pairs of inner extensions present. Distinct impressions which correspond to deck and pseudosepta of valve present at advalver side of closed copula (Pl. 6, Figs. 24, 26). Apical thickening absent or poorly developed. Open copula perforated on both sides by a row of puncta (Cop, Pl. 6, Fig. 14). When closed copula and valve are found combined, it seems as if the species had secondary pseudosepta (Pl. 6, Figs. 6, 10, 11, 13), because the primary pseudosepta which are not correspond to cross rod seem like secondary pseudosepta.

Stratigraphic occurrence: This species occurs from the middle part of the *Nitzschia denticuloides* Zone (NSD 6) to the lower part of the *D. lauta*-*D. hustedtii* Zone (NSD 7) in the Southern Ocean.

Geographic distribution: *D. ovata* is an endemic species in the Southern Ocean.

Remarks: *D. ovata* differs from *D. dimorpha* (varieties *dimorpha* and *areolata*) by its unequally spaced cross rods of closed copula and broader valve outline (Fig. 24). When its valve and closed copula are found combined (Pl. 5, Figs. 16, 19), the species has a very similar look to that of *D. crassa* (Pl. 3, Figs. 23, 24). However, the lack of suture lines between the basal ridge and the inner extensions of copula distinguish *D. ovata* from *D. crassa*.

Discussion: This taxon was described as a variety of *D. hustedtii* (SCHRADER, 1976) because of the presence of secondary pseudosepta. However, the "secondary pseudosepta" of this taxon is merely an optical illusion, as noted in the description. This taxon is, therefore, not a variety of *D. hustedtii*, but a distinct species close to *D. dimorpha*.

Denticula lauta var. *ovata*, another taxon

described by SCHRADER (1976) from the Southern Ocean, is a synonym of *D. ovata*, because the holotype specimen of *D. lauta* var. *ovata* is undoubtedly identical to the Vo valve of *D. ovata*.

Phylogenetic relationship: The ancestor of *D. ovata* must be a primitive form of *D. dimorpha* var. *areolata*. This presumption is based on the similarity in valve face punctation between the two taxa, both of which have partly developed double-layered punctation on valve face. *D. ovata* evolved in the Southern Ocean in the early Late Miocene, but did not migrate to the middle- to high-latitude of the Northern Hemisphere as its ancestors *D. dimorpha* var. *dimorpha* and var. *areolata* did. *D. ovata* became extinct without leaving any descendants.

VII.3 Genus *Neodenticula* AKIBA et YANAGISAWA with its related species

Nitzschia rolandii SCHRADER

Plate 7, Figs. 17-26

SCHRADER, 1973a, p. 708, pl. 5, figs. 31, 42 (?), pl. 26, figs. 3, 4; SCHRADER, 1974b, figs. 6-22, 6-24, 6-26, 6-27; BARRON, 1981a, pl. 4, fig. 18; ORESHKINA, 1985, pl. 1, figs. 14, 15; *Nitzschia rolandii* SCHRADER emend. HARPER, 1977, p. 89-90, pl. 3, figs. 9-11, pl. 5, figs. 5-7; *Nitzschia rolandii* SCHRADER emend. KOIZUMI, 1980, p. 396, pl. 2, figs. 15-20; AKIBA, 1986, pl. 25, figs. 1-6; AKIBA and YANAGISAWA, 1986, pl. 21, figs. 1-6; YANAGISAWA *et al.*, 1989, pl. 6, fig. 22.

Synonymy: *Denticula seminae* f. *fossilis* KOIZUMI, SCHRADER, 1973a, pl. 5, figs. 30, 37, 38; *Denticula* sp. cf. *D. kamtschatica* ZABELINA, BARRON, 1980, p. 672, pl. 1, figs. 15-17; *Neodenticula kamtschatica* (ZABELINA) AKIBA and YANAGISAWA, 1986, pl. 21, figs. 9-12, 20; Akiba, 1986, pl. 25, figs. 7-14.

Description: Valve linear to linear-elliptical with rounded apices, 10-47 μm long, 2-5 μm wide. Primitive form sometimes asymmetric. Transapical costae branching at

raphe-bearing margin, straight in the middle, becoming slightly curved and oblique to transapical axis toward apex. Transapical costae 11-15 in 10 μm in primitive form, and 8.5-10.5 in 10 μm in advanced form. Transapical striae very fine, not visible in ordinary LM observation. Raphe marginal with portulae between marginal branching of transapical costae.

Stratigraphic occurrence: The species occurs consistently from the middle part of the Late Miocene *Thalassionema schraderi* Zone (NPD 6B) to the middle part of the Early Pliocene *Neodenticula kamtschatica* Zone (NPD 7B). It also occurs very sporadically in the underlying Middle to Late Miocene interval, the oldest occurrence being in the uppermost part of the Middle Miocene *Denticulopsis praedimorpha* Zone (NPD 5B).

Geographic distribution: This species is an endemic diatom in the middle- to high-latitude North Pacific.

Remarks: The species shows a remarkable morphologic variation in both spacing of transapical costae and valve outline. In this paper, it is divided tentatively into the following three forms:

- (1) primitive asymmetric form (Pl. 7, Figs. 17-19)
- (2) primitive symmetric form (Pl. 7, Figs. 20-22)
- (3) advanced form (Pl. 7, Figs. 23-26)

The primitive asymmetric form is characterized by a narrower interval of transapical costae (11-15 in 10 μm) and an asymmetric lanceolate valve outline. This form mainly occurs sporadically from the Middle Miocene *D. praedimorpha* Zone (NPD 5B) to the Late Miocene *Thalassionema schraderi* Zone (NPD 6B).

The primitive symmetric form has a linear symmetric outline and a narrower interval of costae (11-15 in 10 μm), occurring from the middle part of the Late Miocene *T. schraderi* Zone (NPD 6B) to the middle part of the *Neodenticula kamtschatica* Zone (NPD 7B).

The advanced form is distinguished from

the primitive ones by a broader interval of costae (8.5-10.5 in 10 μm), but this separation is not always easy (See Fig. 25). It occurs from the upper part of the *T. schraderi* Zone (NPD 6B) to the upper part of the *N. kamtschatica* Zone (NPD 7B). The advanced form of *N. rolandii* shows very close affinity to *N. kamtschatica* as pointed out by previous authors (HARPER, 1977; KOIZUMI, 1980; BARON, 1980; AKIBA and YANAGISAWA, 1986), but it differs from the latter species by a narrower spacing of transapical costae or pseudosepta (8.5-10.5 versus 5-8 in 10 μm , Fig. 25).

Discussion: SCHRADER (1973a) originally gave about 10 for the number of transapical costae of *N. rolandii* per 10 μm . Later HARPER (1977) expanded the number to 7-10 and KOIZUMI (1980) emended it 10-12. Our biometric analysis shows that the number of transapical costae per 10 μm varies 8.5-14.5 (Fig. 25).

Phylogenetic relationship: This species is evidently the ancestor of the genus *Neodenticula*. It evolved into *Neodenticula kamtschatica* by widening of space between transapical costae or pseudosepta and an increase in size.

Neodenticula kamtschatica (ZABELINA)

AKIBA et YANAGISAWA

Plate 7, Figs. 27-37

AKIBA and YANAGISAWA, 1986, p. 490-491, pl. 21, figs. 7, 8, 13-19, 21, pl. 22, figs. 1-12; AKIBA, 1986, pl. 25, figs. 15-27; YANAGISAWA *et al.*, 1989, pl. 6, figs. 18-20.

Synonymy: *Denticula kamtschatica* ZABELINA, 1934, p. 16, figs. 7-9; SIMONSEN and KANAYA, 1961, p. 503, pl. 1, figs. 14-18; SHESHUKOVA-PORETSUKAYA, 1967, p. 300, pl. 47, figs. 9a, 9b, pl. 48, figs. 4a-4e; KOIZUMI, 1968, p. 213, pl. 34, figs. 7-10; KOIZUMI, 1972, pl. 42, figs. 12, 13; KOIZUMI, 1973, p. 832, pl. 5, figs. 14-17; SCHRADER, 1973a, p. 705, pl. 2, figs. 1-13; SCHRADER, 1973b, p. 418, pl. 1 figs. 7, 8; KOIZUMI, 1975a, pl. 1, figs. 13-20; KOIZUMI, 1975b, pl. 4, fig. 47; KOIZUMI, 1975c, pl. 1, fig.

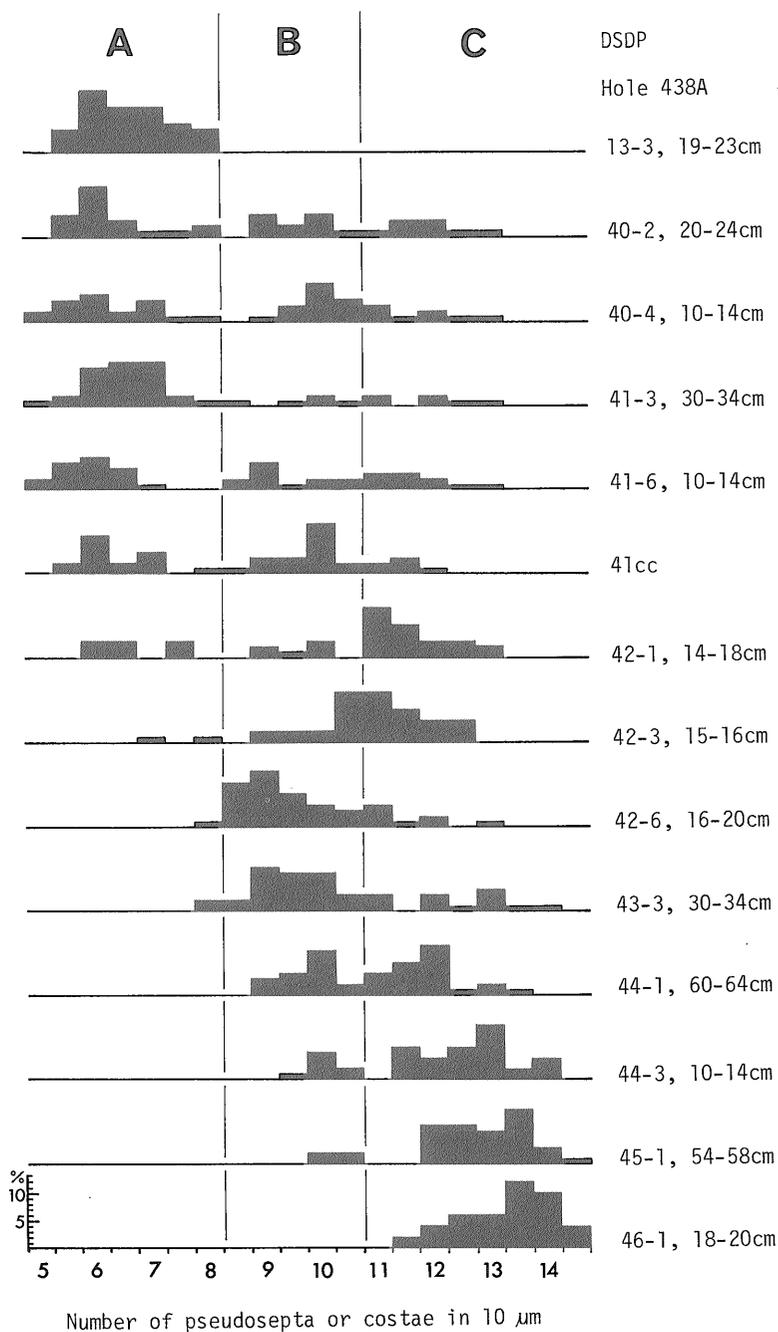


Fig. 25 Frequency distribution of number of pseudosepta or transapical costae (per 10 μ m) in *Neodenticula kamtschatica* and *Nitzschia rolandii*. A: *N. kamtschatica*; B: *N. rolandii* (advanced form); C: *N. rolandii* (primitive form).

5; BARRON, 1976, pl. II, fig. 32; HARPER, 1977, p. 89, pl. 3, figs. 1-4, pl. 5, figs. 1-4, 8; DZINORIDZE *et al.*, 1978, pl. 20, fig. 7; BARRON, 1980, p. 672, pl. 1, figs. 5-8; *Denticula seminae* var. *fossilis* SCHRADER, 1973 b, pl. 1, figs. 5, 6; *Denticulopsis kamtschatica* (ZABELINA) SIMONSEN, 1979, p. 64; AKIBA *et al.*, 1982, pl. 3, figs. 66-68; ORESHKINA, 1985, pl. 1, figs. 16-20; BARRON, 1985b, p. 784, fig. 13.16; *Denticula kamtschatica* ZABELINA emend. KOIZUMI, 1980, p. 396, pl. 2, figs. 1-10.

Description: Frustule rectangular with rounded corners in girdle view. Valve linear or linear-elliptical with sometimes protracted, broadly rounded apices, 9-35 μm long, 3-6.5 μm wide. Transapical striae on valve face very finely punctated, about 42-44 in 10 μm , not discernible in ordinary LM observation, visible only in oblique illumination (Pl. 7, Figs. 30, 37) or in SEM observation. Puncta arranged in clear quincunx. Valve mantle perforated by very fine puncta of the same density as those on valve face. Primary pseudosepta with more and less developed basal ridges, 5-8 in 10 μm , branching at raphe-bearing margin. Secondary pseudosepta absent. Apical pseudosepta sometimes present only shortly just near apex. Marginal ribs formed by branching of pseudosepta at raphe-bearing margin, 9-10 in 10 μm , absent at raphe-less margin. Raphe marginal with portula between marginal ribs. Raphe slit continuous, not interrupted at the middle. Copula open with smooth non-punctated sides. Pleurae open.

Stratigraphic occurrence: The species occurs commonly to abundantly from the *N. kamtschatica* Zone (NPD 7 B) to the *Neodenticula koizumii*-*N. kamtschatica* Zone (NPD 8). It first occurs near the base of the underlying *Rouxia californica* Zone (NPD 7A), but it is rare or sporadic until its sudden great increase at the base of the *N. kamtschatica* Zone. Its last occurrence defines the top of the *N. koizumii*-*N. kamtschatica* Zone. According to BURCKLE and OPDYKE (1985), the first occurrence of this species is diachronous; this species appeared earlier in the high-lati-

tudes than in the middle-latitudes.

Geographic distribution: *N. kamtschatica* is an endemic species in the middle- to high-latitude Northern Hemisphere, especially dominant in the high-latitude North Pacific. It occurs in the Norwegian Sea with rare abundance (DZINORIDZE *et al.*, 1978).

Remarks: The species is distinguished from *N. koizumii* by the absence of secondary pseudosepta. It closely resembles *Nitzschia rolandii* SCHRADER (advanced form) but differs by the broader spacing of pseudosepta or costae (5-8 versus 8.5-10.5 in 10 μm), the development of basal ridge, more frequent branching of pseudosepta on raphe side and the relatively wider valve.

Discussion: Various definitions have been made concerning the spacing of pseudosepta in this species. ZABELINA (1934) originally described 4-8 for the number of pseudosepta in 10 μm . Later SIMONSEN and KANAYA (1961) and Harper (1977) gave 5-6 for it. KOIZUMI (1980) expanded it to 5-8 again. In our previous paper (AKIBA and YANAGISAWA, 1986), we wrote that the number of pseudosepta in 10 μm varies from 5 to 10. However, frequency distributions in number of pseudosepta per 10 μm for *N. kamtschatica* and *Nitzschia rolandii* overlap slightly but clearly differ, showing two distinct clusters separated by a gap around 8-8.5 (Fig. 25). KOIZUMI's (1980) definition for *N. kamtschatica* (5-8 pseudosepta in 10 μm) therefore is the most appropriate.

Phylogenetic relationship: Morphologic similarities and stratigraphic ranges indicate without doubt that *N. kamtschatica* evolved directly from *Nitzschia rolandii* through widening of the spacing of pseudosepta, an increase in size, further branching of pseudosepta and development of basal ridges (HARPER, 1977; AKIBA and YANAGISAWA, 1986). *N. kamtschatica* developed into *N. koizumii* by forming secondary pseudosepta.

***Neodenticula koizumii* AKIBA
et YANAGISAWA**

Plate 7, Figs. 38-41, (42-44)

AKIBA and YANAGISAWA, 1986, p. 491, pl. 21, figs. 22-28, pl. 23, figs. 1-12, pl. 24, fig. 19; YANAGISAWA *et al.*, 1989, pl. 6, fig. 17.

Synonymy: *Denticula seminae* SIMONSEN et KANAYA, KOIZUMI, 1972, p. 350, pl. 42, figs. 5a-6; KOIZUMI, 1973, p. 832, in part, pl. 5, figs. 7-9, 10-13, non pl. 5, figs. 1-6; SCHRADER, 1973a, pl. 1, figs. 7-11, non pl. 1, figs. 1-8, 36, 47; *Denticula seminae* var. *fossilis* SCHRADER, KOIZUMI, 1975a, p. 802, pl. 1, figs. 4-12; KOIZUMI, 1975b, pl. 4, figs. 44-46; KOIZUMI, 1975c, pl. 1, figs. 3, 4; HARPER, 1977, pl. 3, fig. 5; AKIBA, 1979, pl. 3, fig. 7; BARRON, 1980, pl. 1, figs. 2-4; *Denticulopsis seminae* var. *fossilis* (SCHRADER) SIMONSEN, BARRON, 1985b, p. 785, fig. 13.15; *Denticulopsis seminae* (SIMONSEN et KANAYA) SIMONSEN, ORESHKINA, 1985, pl. 1, figs. 21-23; *Neodenticula* sp. A, AKIBA and YANAGISAWA, 1986, p. 492, pl. 21, figs. 29-31, pl. 24, figs. 12-18, pl. 25, figs. 1-6; YANAGISAWA *et al.*, 1989, pl. 6, figs. 15, 16; non *Denticula seminae* f. *fossilis* KOIZUMI ex SCHRADER, 1973a, p. 705, pl. 5, figs. 30, 37, 38; non *Denticula seminae* var. *fossilis* SCHRADER, 1973b, p. 420, pl. 1, figs. 5, 6.

Description: Frustule rectangular with rounded corners. Valve linear to linear-elliptical with bluntly rounded apices, 10-42 μm long, 3-6 μm wide. Transapical striae on valve face very finely punctated, 42-44 in 10 μm , arranged in quincunx, not discernible in ordinary LM observation, visible only in oblique illumination or SEM observation. Valve mantle low, perforated by very fine puncta of the same density as those on valve face. Pseudosepta (primary or secondary) straight throughout valve face, spaced equally, 6-7 in 10 μm . Secondary pseudosepta 1-3 between each two primary pseudosepta. Pseudosepta branching to form marginal ribs at raphe-bearing margin. No marginal ribs present at raphe-less margin. Raphe marginal with continuous raphe slit. Portula

between each two marginal ribs. Copula open with smooth non-punctated sides.

Stratigraphic occurrence: The species is common to abundant in the interval from the base of the *N. koizumii*-*N. kamtschatica* Zone (NPD 8) through the overlying *N. koizumii* Zone (NPD 9). KOIZUMI and TANIMURA (1985) indicated that the first occurrence of this species is slightly diachronous in the North Pacific.

Geographic distribution: The species is distributed only in the middle- to high-latitude Northern Hemisphere, especially dominant in the high-latitude North Pacific.

Remarks: This species is similar to *N. kamtschatica*, but is easily distinguishable from the latter by the presence of secondary pseudosepta. It differs from *Neodenticula seminae* mainly by the absence of closed copula and more slender valve outline. The valve of *N. koizumii* is distinguished from that of *N. seminae* in that pseudosepta near apex are not so curved but nearly parallel to transapical axis and that branchings of pseudosepta at raphe side are very conspicuous. The two species are also differ in punctuation on the valve face: *N. koizumii* has full punctuation whereas *N. seminae* has reduced punctuation (AKIBA and YANAGISAWA, 1986, pl. 23, fig. 4; pl. 26, fig. 5).

N. koizumii is similar to *Denticulopsis simonsenii* group (Compare Pl. 7, Fig. 38 and Pl. 3, Fig. 1), but differs by the absence of marginal ribs at raphe-less margin and very fine puncta that are not visible in ordinary LM observation.

Discussion: *Neodenticula* sp. A of AKIBA and YANAGISAWA (1986) (Pl. 7, Figs. 42-44) is tentatively included in *N. koizumii* in this paper, because *N. sp. A* has an open copula as *N. koizumii* does (*N. seminae* has a closed copula). However, the reduced punctuation on valve face of *N. sp. A* shows that it bears more intimate resemblance to *N. seminae* as described by AKIBA and YANAGISAWA (1986). Thus it is apparent that *N. sp. A* is an intermediate form between *N. koizumii* and *N.*

seminae. The formal description of this form will be made after its precise stratigraphic range is well investigated.

Further taxonomic problems of *N. koizumii* are discussed in detail in AKIBA and YANAGISAWA (1986).

Phylogenetic relationship: *N. koizumii* evolved from *N. kamtschatica* with development of secondary pseudosepta and gave rise to *N. seminae* via *N. sp. A*.

***Neodenticula seminae* (SIMONSEN et KANAYA) AKIBA et YANAGISAWA**

Plate 7, Figs. 45-49

AKIBA and YANAGISAWA, 1986, p. 491-492, pl. 24, figs. 1-11, pl. 26, figs. 1-10; AKIBA, 1986, pl. 25, figs. 28-32.

Synonymy: *Denticula marina* SEMINA, 1956, p. 82, figs. 1-2b; *Denticula seminae* SIMONSEN et KANAYA, 1961, p. 503, pl. 1 figs. 26-30; SHESHUKOVA-PORETSUKAYA, 1967, p. 301-302, pl. 47, figs. 11a-11c; HASLE, 1972, fig. 3, 4, 8; SCHRADER, 1973a, p. 705, pl. 1, figs. 1-6, 36, 47; 1973b, p. 420, pl. 1, figs. 1-4; KOIZUMI, 1973, p. 832, pl. 5, figs. 1-6; KOIZUMI, 1975a, p. 802, pl. 1, figs. 1-3; KOIZUMI, 1975c, pl. 1, figs. 1,2; DZINORIDZE *et al.*, 1978, pl. 20, figs. 5, 6; BARON, 1980, pl. 1, fig. 1; *Denticulopsis seminae* (SIMONSEN et KANAYA) SIMONSEN, 1979, p. 65; SEMINA, 1981, p. 180-182, pl. 1, figs. 1-4, pl. 2, figs. 5-9, pl. 3, figs. 10-14; SANCETTA, 1982, p. 230-231, pl. 3, figs. 1-3; ORESHKINA, 1985, pl. 1, figs. 24-28.

Description: Frustule rectangular with rounded corners. Valve linear to linear-elliptical with sometimes protracted bluntly rounded apices, 10-60 μm long, 4-9 μm wide. Transapical striae on valve face very finely punctated, not discernible in ordinary LM observation, only visible in oblique illumination or SEM observation. Some transapical striae near pseudosepta reduced so that only one to three striae remain on valve face between pseudosepta. Valve mantle low, perforated by very fine puncta without reduction of puncta. Pseudosepta (primary or second-

dary) equally spaced, 7-9 in 10 μm , with 2-6 secondary pseudosepta between primary pseudosepta, or between primary pseudosepta and apex. Pseudosepta branching at raphe-bearing margin so that fork-like structure formed. Pseudosepta straight in the middle part of valve, becoming gradually curved toward apex. Marginal ribs formed by branching of pseudosepta at raphe-bearing margin, but absent at the other margin. Raphe marginal with each portula between each two marginal ribs. Raphe slit continuous. Copula closed with smooth non-punctated sides.

Stratigraphic occurrence: The species is common to abundant in the Quaternary to the Recent. The first occurrence of this species is in the upper part of the *N. koizumii* Zone (NPD 9).

Geographic distribution: The species is mainly and dominantly distributed in the middle- to high-latitude North Pacific. SANCETTA (1982) found this species to be very abundant in the northeast Pacific and a good tracer of water of the Alaskan Stream. She also showed that the species is lower in abundance in the northwest Pacific than in the northeast Pacific. The species is rarely found in the Norwegian Sea (DZINORIDZE *et al.*, 1978; BALDAUF, 1987). KANAYA and KOIZUMI (1966) regarded the species as the most representative cold water species in the North Pacific. HASLE (1976) stressed that this species was not reported from other part of the world oceans. However, SEMINA (1981) found *N. seminae* living, though very rarely, in the low-latitude areas (the tropical Pacific, Indian and Atlantic Oceans), and consequently she classified this species as a tropical-boreal species in all three Oceans.

Remarks: The species differs from *N. koizumii* by the presence of closed copula and broader valve outline. It also differs from the latter in having curved pseudosepta near apex, lacking conspicuous branching of pseudosepta at raphe side margin and larger number of secondary pseudosepta between primary pseudosepta.

N. seminae is very similar to *N. sp. A* of AKIBA and YANAGISAWA (1986) but differs from the latter by more linear valve outline and the presence of closed copula.

Discussion : HASLE (1972) observed an open copula of this species (HASLE, 1972, fig. 4). Some specimens might possess open copulae, although we could not find this type of copula in this study.

Phylogenetic relationship : *N. seminae* evolved from *N. koizumii* and remains extant.

VII. 4 Other species

"Denticula" norwegica SCHRADER in SCHRADER et FENNER

Plate 1, Fig. 40 ; Plate 8, Fig. 18

Denticula norwegica SCHRADER and FENNER, 1976, p. 978, pl. 1, fig. 38 ; AKIBA and YANAGISAWA, 1986, p. 487, pl. 2, figs. 15-21, pl. 6, figs. 1-9.

Synonymy : *Denticula punctata* SCHRADER, 1973a, pl. 3, figs. 16, 17 ; *Denticulopsis norvegica* (SCHRADER) SIMONSEN, 1979, p. 65 ; MARUYAMA, 1984a, pl. 16, fig. 13 ; *Denticulopsis norvegica* SCHRADER, POWERS, 1988, pl. 5, fig. 8.

Description : Valve lanceolate with acutely rounded apices, 35-64 μm long, 6-15 μm wide in the middle of valve. Transapical striae on valve face coarsely punctated, 12-18 in 10 μm , not arranged in quincunx; puncta, 10-16 in 10 μm , oval, elongated in transapical direction, occluded by mesh-like cribra. Valve mantle low, perforated by two longitudinal rows of coarse puncta. Primary pseudosepta with unclear basal ridges, unequally spaced, 3-5 in 10 μm . Secondary pseudosepta rarely present between primary pseudosepta. Marginal ribs numerous but inconspicuous. Raphe marginal with interrupted raphe slit. Portula, 7-8 in 10 μm or two between primary pseudosepta. Central portula larger and apically elongated.

Stratigraphic occurrence : This species rarely occurs in the *C. kanayae* Zone (NPD 3A) and *D. praelauta* Zone (NPD 3B) in the middle

- to high-latitude North Pacific. SCHRADER and FENNER (1976) reported this species from the *Denticula nicobarica* Zone of their diatom zonation at DSDP Site 338 in the Norwegian Sea.

Geographic distribution : The species is found in the Norwegian Sea and the middle- to high-latitude North Pacific, and also in the low-latitude Pacific.

Discussion : SIMONSEN (1979) transferred this species to the genus *Denticulopsis* SIMONSEN. However, it cannot surely be assigned in the genera *Crucidentacula*, *Denticulopsis* nor *Neodenticula*, because the valve structure of this species is fundamentally different from those of the three genera ; This species has peculiar oval areolae with mesh-like cribra (Pl. 8, Fig. 18), which is unique to this species and never present in any species of *Crucidentacula*, *Denticulopsis* nor *Neodenticula* (AKIBA and YANAGISAWA, 1986). "*Denticula*" *norwegica* probably has no phylogenetic relationship to these three genera.

"Denticulopsis" maccollumii SIMONSEN

Plate 2, Figs. 39-41

Denticulopsis maccollumii SIMONSEN, 1979, p. 65 ; BARRON, 1985b, p. 785, figs. 14.10, 14.11.

Synonym : *Denticula antarctica* MCCOLLUM, 1975, p. 527, pl. 8, figs. 6-10 ; SCHRADER, 1976, p. 631, pl. 4, figs. 3, 22, 23, 25 ; DEFELICE and MILLER, 1978, p. 115, figs. 1-8.

Description : Valve weakly silicified, elliptical to linear-elliptical with broadly rounded apices, 14-60 μm long, 4-8 μm wide. Primary pseudosepta ca. 6 in 10 μm with marginal ribs on both sides between pseudosepta. Secondary pseudosepta absent. On valve face, lanceolate hyaline central area present. On both sides double rows of pores present, one row on valve face and the other on mantle. The pores 4-8 in 10 μm , one or two between pseudosepta. Raphe marginal between the double rows of pores. Copula open with non-punctate sides.

Stratigraphic occurrence : The species occurs from the uppermost part of the *Nitzs-*

chia maleinterpretaria Zone (NSD 3) to the upper part of the *N. denticuloides* Zone (NSD 6) in the Southern Ocean.

Geographic distribution: "*Denticulopsis*" *maccollumii* is an endemic diatom in the Southern Ocean.

Remarks: The species is very similar to *Denticulopsis hyalina* in valve view (SCHRADER, 1976), but differs by the valve mantle structure. *D. hyalina* has double-layered punctation in the valve mantle, whereas "*Denticulopsis*" *maccollumii* has a row of large pores in the valve mantle.

Discussion: This species has probably no phylogenetic relationship to the genera *Denticulopsis*, *Crucidentricula* nor *Neodenticula*, because of the fundamental difference in the valve mantle structure. The species is rather similar to *Nitzschia denticuloides* SCHRADER (Pl. 2, Figs. 42, 43), as suggested by DEFELICE and MILLER (1978).

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海生珪藻属 *Crucidentricula*, *Denticulopsis* 及び *Neodenticula* 属の分類と系統

柳沢幸夫・秋葉文雄

要 旨

後期新生代海生珪藻化石層序区分の指標種を多く含む *Crucidentricula*, *Denticulopsis* 及び *Neodenticula* 属について、走査型電子顕微鏡及び光学顕微鏡を用いて形態観察と統計的な計測を行い、被殻の詳しい構成・構造及び変異の幅を明らかにした。その結果に基づいて分類学的再検討を行い、新たに15種の新タクサを識別し、2タクサについて分類階級の変更を行った。さらに、*Crucidentricula* 属の7タクサ、*Denticulopsis* 属の23タクサ、*Neodenticula* 属の3タクサ、及び近縁の *Nitzschia* 属の3種と、“*Denticula*” *norwegica* 及び “*Denticulopsis maccollumii*” の2種について、詳しい記載を行った。

深海掘削計画で得られた DSDP Hole 438A 及び 438B (北西太平洋, 八戸沖) と DSDP Hole 71 及び 77B (東赤道太平洋) の試料を分析して、北太平洋中-高緯度地域及び低緯度地域における3属の層序的分布を明らかにするとともに、これまでに公表されているデータを基に南氷洋におけるこれらの属の層序的分布をまとめた。また、これまでの産出報告を総括して、3属の地理的分布特性を明らかにした。そして、形態的類似性・層序的分布及び地理的分布に基づいて、3属の進化・系統関係を推定した。

Crucidentricula, *Denticulopsis* 及び *Neodenticula* 属は、形態的に一見非常に類似しているが、側肋の配置、縦溝間隙の配置及び点紋の大きさ等、被殻の基本的な構造に大きな違いがある。また、化石記録からみて、これら3属は、近縁の *Nitzschia* 属からそれぞれ異なった時期に独立に進化したものであり、互いに直接的な系統関係は認められない。従って、3属の形態的類似性は、典型的な進化的収斂であると言える。

3属の進化パターンは、後期新生代における海洋及び気候の変化と密接に関連している。基本的に低緯度地域(熱帯地域)に主たる分布域を持つ *Crucidentricula* 属は、全世界的に温暖であった前期中新世の中頃、*Nitzschia maleinterpretaria* から進化し、最も温暖であった17-16Ma頃中-高緯度地域にも分布域を拡大した。しかし、中期中新世以降寒冷化が進む中で次第に衰え、中期中新世末には絶滅した。*Denticulopsis* 属は、中期中新世が始まる頃、*Nitzschia challengerii* に類似した未知の小型の *Nitzschia* から進化し、多くの系統に分化した。本属は起源的には寒流系であるが、14Ma頃に起こった急激な寒冷化に伴って赤道地域にも進出・定着し、汎世界的な分布を持つようになった。しかし、後期中新世には全ての種が絶滅した。一方、*Neodenticula* 属は、*Denticulopsis* 属の消滅後、*Nitzschia rolandii* から次第に進化し、6Ma頃急激に優勢となって現在に至っている。この属は、北半球高緯度、特に北太平洋高緯度に分布が限定されており、南半球には分布しない。

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Appendix 1: List and index of diatom taxa treated in this paper
(genera arranged in the order treated, and species in alphabetical order)

Genus *Crucidenticula* AKIBA et YANAGISAWA 1986

1. *C. ikebei* AKIBA et YANAGISAWA 1986 p. 228
2. *C. kanayae* AKIBA et YANAGISAWA 1986 var. *kanayae* p. 229
3. *C. kanayae* var. *pacifica* YANAGISAWA et AKIBA 1990 n. var. p. 229
4. *C. nicobarica* (GRUNOW) AKIBA et YANAGISAWA 1986 p. 232
5. *C. paranicobarica* AKIBA et YANAGISAWA 1986 var. *paranicobarica* p. 231
6. *C. paranicobarica* var. *tropica* YANAGISAWA et AKIBA 1990 n. var. p. 230
7. *C. punctata* (SCHRADER) AKIBA et YANAGISAWA 1986 p. 232
8. *C. sawamurae* YANAGISAWA et AKIBA 1990 n. sp. p. 227

Genus *Denticulopsis* SIMONSEN 1979 emend. AKIBA et YANAGISAWA 1986

9. *D. barronii* YANAGISAWA et AKIBA 1990 n. sp. p. 253
10. *D. crassa* YANAGISAWA et AKIBA 1990 n. sp. p. 248
11. *D. delicata* YANAGISAWA et AKIBA 1990 n. sp. p. 246
12. *D. dimorpha* (SCHRADER) SIMONSEN 1979 var. *dimorpha* p. 254
13. *D. dimorpha* var. *areolata* YANAGISAWA et AKIBA 1990 n. var. p. 257
14. *D. hustedtii* (SIMONSEN et KANAYA) SIMONSEN 1979 emend. YANAGISAWA et AKIBA 1990 p. 246
15. *D. hyalina* (SCHRADER) SIMONSEN 1979 p. 240
16. *D. ichikawae* YANAGISAWA et AKIBA 1990 n. sp. p. 236
17. *D. katayamae* MARUYAMA 1984 emend. YANAGISAWA et AKIBA 1990 p. 245
18. *D. lauta* (BAILEY) SIMONSEN 1979 p. 235
19. *D. miocenica* (SCHRADER) SIMONSEN 1979 emend. YANAGISAWA et AKIBA 1990 p. 241
20. *D. okunoi* YANAGISAWA et AKIBA 1990 n. sp. p. 237
21. *D. ovata* (SCHRADER) YANAGISAWA et AKIBA 1990 n. comb. p. 257
22. *D. praedimorpha* BARRON ex AKIBA 1982 var. *praedimorpha* p. 251
23. *D. praedimorpha* var. *minor* YANAGISAWA et AKIBA 1990 n. var. p. 249
24. *D. praedimorpha* var. *robusta* YANAGISAWA et AKIBA 1990 n. var. p. 252
25. *D. praedimorpha* var. *intermedia* YANAGISAWA et AKIBA 1990 n. var. p. 252
26. *D. praehyalina* TANIMURA 1989 p. 239
27. *D. praekatayamae* YANAGISAWA et AKIBA 1990 n. sp. p. 244
28. *D. praelauta* AKIBA et KOIZUMI in AKIBA 1986 p. 234
29. *D. simonsenii* YANAGISAWA et AKIBA 1990 n. sp. p. 242
30. *D. tanimurae* YANAGISAWA et AKIBA 1990 n. sp. p. 238
31. *D. vulgaris* (OKUNO) YANAGISAWA et AKIBA 1990 n. comb. p. 243

Genus *Neodenticula* AKIBA et YANAGISAWA 1986

32. *N. kamtschatica* (ZABELINA) AKIBA et YANAGISAWA 1986 p. 259
33. *N. koizumii* AKIBA et YANAGISAWA 1986 p. 262
34. *N. seminae* (SIMONSEN et KANAYA) AKIBA et YANAGISAWA 1986 p. 263

Genus *Nitzschia* HASSALL 1845

35. *N. challengeri* SCHRADER 1973 p. 233
36. *N. maleinterpretaria* SCHRADER 1976 p. 226
37. *N. rolandii* SCHRADER 1973 emend. HARPER 1977 p. 258

Other species

38. "*Denticula*" *norwegica* SCHRADER in SCHRADER et FENNER 1976 p. 264
39. "*Denticulopsis*" *maccollumii* SIMONSEN 1979 p. 264

Appendix 2: Key to species

(Characteristics of each species are summarized in Tables A-1—3.)

Genus *Crucidentricula*

- 1a. Pseudosepta absent *Nitzschia maleinterpretaria*
1b. Pseudosepta present 2
2a. Puncta on valve face arranged in non-quincunx 3
2b. Puncta on valve face arranged in clear quincunx 8
3a. Valve linear or linear-elliptical 4
3b. Valve narrowly linear and slender 7
4a. Valve robust with very large puncta 5
4b. Valve not so robust with large puncta 6
5a. Copula not punctated *C. kanayae* var. *kanayae*
5b. Copula punctated *C. kanayae* var. *pacifica*
6a. Valve outline linear-elliptical *C. ikebei*
6b. Valve outline linear *C. sawamurae*
7a. Puncta not reduced *C. paranicobarica* var. *tropica*
7b. Puncta reduced partly *C. paranicobarica* var. *paranicobarica*
8a. Valve narrow (3.5–4.5 μ m wide) mostly without secondary
pseudosepta *C. nicobarica*
8b. Valve broad (5.5–7.5 μ m wide) mostly with secondary pseudosepta *C. punctata*

Genus *Denticulopsis*

- 1a. Pseudosepta absent *Nitzschia challengeri*
1b. Pseudosepta present 2
2a. Marginal ribs absent or poorly developed *D. praelauta*
2b. Marginal ribs developed 3
3a. Only one type of valve present 4
3b. Two types of valves present 16
4a. Secondary pseudosepta absent 5
4b. Secondary pseudosepta present 11
5a. Valve not thickly silicified 6
5b. Valve thickly silicified 8
6a. Puncta on valve face not reduced *D. lauta*

6b. Puncta on valve face reduced partly	7
7a. Valve outline linear or linear-elliptical	<i>D. ichikawae</i>
7b. Valve outline oval	<i>D. okunoi</i>
8a. Puncta on valve face not reduced	<i>D. tanimurae</i>
8b. Puncta on valve face reduced	9
9a. Puncta on valve face reduced partly	<i>D. praehyalina</i>
9b. Puncta on valve face reduced completely (hyaline)	10
10a. Valve outline linear or linear-elliptical	<i>D. hyalina</i>
10b. Valve outline oval	<i>D. miocenica</i>
11a. Valve outline linear	12
11b. Valve outline not linear	15
12a. Puncta on valve face not reduced	<i>D. simonsenii</i>
12b. Puncta on valve face reduced	13
13a. Valve not thickly silicified	<i>D. vulgaris</i>
13b. Valve thickly silicified	14
14a. Puncta on valve face present	<i>D. praekatayamae</i>
14b. Valve face hyaline	<i>D. katayamae</i>
15a. Valve outline oval	<i>D. crassa</i>
15b. Valve outline lanceolate	<i>D. hustedtii</i>
16a. Apical thickening of closed copula present	17
16b. Apical thickening of closed copula absent	18
17a. Valve width 4-6.5 μm	<i>D. praedimorpha</i> var. <i>praedimorpha</i>
17b. Valve width more than 7 μm	<i>D. praedimorpha</i> var. <i>robusta</i>
18a. Secondary pseudosepta present	<i>D. barronii</i>
18b. Secondary pseudosepta absent	19
19a. Cross rods absent	<i>D. praedimorpha</i> var. <i>minor</i>
19b. Cross rods present	20
20a. Cross rods partly developed	<i>D. praedimorpha</i> var. <i>intermedia</i>
20b. Cross rods completely developed	21
21a. Double-layered punctation absent	<i>D. dimorpha</i> var. <i>dimorpha</i>
21b. Double-layered punctation present	22
22a. Cross rods regularly spaced	<i>D. dimorpha</i> var. <i>areolata</i>
22b. Cross rods irregularly spaced	<i>D. ovata</i>

Genus *Neodenticula*

1a. Secondary pseudosepta absent	2
1b. Secondary pseudosepta present	3
2a. Pseudosepta (costae) more than 8.5 in 10 μm	<i>Nitzschia rolandii</i>
2b. Pseudosepta less than 8 in 10 μm	<i>N. kamtschatica</i>
3a. Closed copula absent	<i>N. koizumii</i>
3b. Closed copula present	<i>N. seminae</i>

Table A-1 Characters useful in distinguishing taxa within the genus *Crucidentricula* and its related species.

Taxa	Outline	Length (μm)	Width (μm)	Punctuation on valve face			Rows on mantle	Spacing of pseudosepta	Secondary pseudosepta	Type of copula
				Q	Striae	Distribution				
<i>Nitzschia maleinterpretaria</i>	Linear, linear-elliptical	8-57	3-6	-	11-16	Full	1	Absent	-	Cop
<i>Crucidentricula sawamurae</i>	Linear	14-51	3.5-5.5	-	11-12	Full	2	3-5	Unclear	Cop
<i>C. kanayae</i> var. <i>pacifica</i>	Linear	20-48	5.5-7	-	10-11	Full	2	3-4	-	Cop
<i>C. kanayae</i> var. <i>kanayae</i>	Linear-oblong	14-43	4-8	-	9-10	Sporadic	2	ca. 3	-	Con
<i>C. ikebei</i>	Linear-elliptical	18-67	4-7	-	12-16	Full	2	3-5	-	Cop
<i>C. paranicobarica</i> var. <i>tropica</i>	Narrowly Linear	5-38	2-3.5	-	16-18	Full	2	5-6	-	Cop
<i>C. paranicobarica</i> var. <i>paranicobarica</i>	Narrowly linear	8-32	2.5-4.5	-	14-16	Reduced	2	4-6	Rare	Cop
<i>C. nicobarica</i>	Linear, linear-elliptical	10-32	3.5-4.5	+	ca. 16	Full	2	4-5	-	Cop
<i>C. punctata</i>	Linear, linear-elliptical	20-40	5.5-7.5	+	14-15	Full	4	3-4	0-2	Cop

Q; Quincunx arrangement; Striae: numbers in 10 μm ; Spacing of pseudosepta: numbers in 10 μm ; Secondary pseudosepta: numbers between each two primary pseudosepta; +: present; -: absent.

Table A-2 Characters useful in distinguishing taxa within the genus *Neodenticula* and its related species.

Taxa	Outline	Length (μm)	Width (μm)	Punctuation		Spacing of pseudosepta	Secondary pseudosepta	Type of copula
				Striae	Distribution			
<i>Nitzschia rolandii</i>	Linear, linear-elliptical	10-47	2-5	?	Full	8.5-15	-	?
<i>Neodenticula kamtschatica</i>	Linear, linear-elliptical	9-35	3-6.5	42-44	Full	5-8	-	Con
<i>N. koizumii</i>	Linear, linear-elliptical	10-42	3-6	42-44	Full	6-7	1-3	Con
<i>N. seminae</i>	Linear, linear-elliptical	10-60	4-9	42-44	Reduced	7-9	2-6	Ccm, (Con)

Striae: numbers in 10 μm ; Spacing of pseudosepta: numbers in 10 μm ; Secondary pseudosepta: numbers between each two primary pseudosepta; -: absent.

Table A-3 Characters useful in distinguishing taxa within the genus *Denticulopsis* and its related species.

Taxa	Outline	Length (μm)	Width (μm)	Punctuation on valve face			Punctuation on mantle
				Type	Striae	Distribution	
<i>Nitzschia challengerii</i>	Linear, linear-elliptical	10-29	3.5-5.5	Single	18-24	Full	Single
<i>Denticulopsis praelauta</i>	Narrowly Linear	6-16	2.5-5.5	Single	25-30	Full	Single
<i>D. lauta</i>	Linear, linear-elliptical	7-57	3.5-8	Single	20-28	Full	Single
<i>D. ichikawae</i>	Linear, linear-elliptical	9-30	4-6	Single	20-26	Reduced	Single
<i>D. okunoi</i>	Oval	10-21	6-9.5	Single	22-26	Reduced	Single
<i>D. tanimurae</i>	Linear, linear-elliptical	10-60	4-7.5	(Single)	20-24	Full	Double
<i>D. praehyalina</i>	Linear, linear-elliptical	10-40	5-9	Single	12-24	Reduced	Double
<i>D. hyalina</i>	Linear, linear-elliptical	8-36	3.5-7	—	—	Hyaline	Double
<i>D. miocenica</i>	Oval	7.5-38	5.5-13	—	—	Hyaline	Double
<i>D. simonsenii</i>	Linear	9-49	4-8	Single	22-24	Full	Single
<i>D. vulgaris</i>	Linear	12-45	4-7	Single		Reduced	Single
<i>D. prae katayamae</i>	Linear	15-44	5-8	Single		Reduced sporadic	Double
<i>D. katayamae</i>	Linear	7-37	4-7	—	—	Hyaline	Double
<i>D. delicata</i>	Linear and slender	36-53	5.5-6.5	—	—	Seemingly hyaline	Single
<i>D. hustedtii</i>	Elliptical, lanceolate	9-37	6-10	Single	22-24	Full or reduced	Single
<i>D. crassa</i>	Oval	10-32	5.5-11	Single	12-15	Reduced	Double
<i>D. praedimorpha</i> var. <i>minor</i>	Linear	6-19	2.5-4	Single	24-26	Full	Single
<i>D. praedimorpha</i> var. <i>praedimorpha</i>	Linear, linear-elliptical	9-24	4-6.5	Single	24-26	Full	Single
<i>D. praedimorpha</i> var. <i>robusta</i>	Linear-elliptical	18-25	7-9	Single	24-26	Full	Double
<i>D. praedimorpha</i> var. <i>intermedia</i>	Linear	13-27	5-6	Single	24-26	Full	Single
<i>D. barronii</i>	Linear	10-28	3.5-5	Single	24-26	Full	Single
<i>D. dimorpha</i> var. <i>dimorpha</i>	Linear	8-21.5	3-5	Single	24-26	Full	Single
<i>D. dimorpha</i> var. <i>areolata</i>	Linear-elliptical	11-33	5-8.5	Double	22-25	Full	double
<i>D. ovata</i>	Linear, oval	9-43	5.5-15	Single	23-26	Full	Double

Striae : numbers in 10 μm .

Table A-3 continued

Taxa	Spacing of pseudosepta	Basal ridge	Secondary pseudosepta	Marginal ribs	Type of copula	Cross rod	Other features
<i>Nitzschia challengerii</i>	9-12	Absent	—	—	Cop	—	
<i>Denticulopsis praelauta</i>	5-8	Narrow	—	—, (+)	Cop, Con	—	
<i>D. lauta</i>	3-5	Broad	—	+	Con, (Cop)	—	
<i>D. ichikawae</i>	3-5	Broad	—	+	Con	—	
<i>D. okunoi</i>	6-7	Narrow	—	+	Con	—	
<i>D. tanimurae</i>	4-5	Broad	—	+	Con	—	Silicified
<i>D. praeahyalina</i>	3-5	Broad	—	+	Con	—	Silicified
<i>D. hyalina</i>	3-4	Broad	—	+	Con	—	Silicified
<i>D. miocenica</i>	3.5-5	Very broad	—	+	Con	—	Silicified
<i>D. simonsenii</i>	5.5-8	Broad	1-3	+	Con	—	
<i>D. vulgaris</i>	5.5-8	Broad	1-3	+	Con	—	
<i>D. praekatayamae</i>	6-7	Broad	1-3	+	Con	—	Silicified
<i>D. katayamae</i>	6-7	Broad	1-3	+	Con	—	Silicified
<i>D. delicata</i>	7	Narrow	1-2	+	?	—	
<i>D. hustedtii</i>	6-8	Narrow	1-3	+	Con	—	
<i>D. crassa</i>	5-6	Very broad	1-2	+	Con, Ccm	—	
<i>D. praedimorpha</i> var. <i>minor</i>	6-7	Vc High, short Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	— —	No apical thickening
<i>D. praedimorpha</i> var. <i>praedimorpha</i>	5	Vc High, short Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	— —	Apical thickening
<i>D. praedimorpha</i> var. <i>robusta</i>	4-5	Vc High, short Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	Partial —	Apical thickening
<i>D. praedimorpha</i> var. <i>intermedia</i>	5-6	Vc High, short Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	Partial —	No apical thickening
<i>D. barronii</i>	7.5-10	Vc High, short Vo Low, indistinct	1-2 —	+ +	Ccr, Ccm Cop	— —	No apical thickening
<i>D. dimorpha</i> var. <i>dimorpha</i>	6-7	Vc Absent Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	+ —	
<i>D. dimorpha</i> var. <i>areolata</i>	4-5	Vc Absent Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	+ —	
<i>D. ovata</i>	5-6.5	Vc Absent Vo Low, indistinct	— —	+ +	Ccr, Ccm Cop	+ —	Cross rods unequally spaced

Spacing of pseudosepta : numbers in 10 μm ; Secondary pseudosepta : numbers between each two primary pseudosepta ; + : present ; — : absent.Diatom genera *Crucidentricula*, *Denticulopsis* and *Neodenticula* (Y. Yanagisawa and F. Aiba)

Plate 1 Transmitted light micrographs. Scale bar equals 10 μ m for all figures.

- 1-4 *Nitzschia maleinterpretaria* SCHRADER
1, 3, outer valve views; 2, girdle view of frustule; 4, inner valve view of intermediate form to *Crucidentricula sawamurae* with very poorly developed pseudosepta (1, 3, 4, DSDP Hole 71, 26-2, 70-72 cm; 2, DSDP Hole 71, 26-4, 70-72 cm).
- 5-9 *Crucidentricula sawamurae* n. sp.
9, holotype; 8, paratype; 5, 7-9, outer valve views; 6, girdle view of frustule (5, 7, 9, DSDP Hole 71, 25-3, 96-98 cm; 6, 8, DSDP Hole 71, 25-1, 128-130 cm).
- 10-12 *Crucidentricula ikebei* AKIBA et YANAGISAWA
10, 11, outer valve views; 12, girdle view of frustule (Sample 70-B49-1a, calcareous concretion dredged from the Bering Sea).
- 13-16 *Crucidentricula paranicobarica* AKIBA et YANAGISAWA var. *paranicobarica*
Outer valve views (13, Sample JOB 487, Shimotezuna Formation, North Takahagi Section, Joban Coalfield, Ibaraki, Japan; 14, DSDP Hole 438A, 73-5, 9-11 cm; 15, DSDP Hole 438A, 72-3, 15-17 cm; 16, Sample JDS-4685, Masuporo Formation, Tenpoku area, northern Hokkaido, Japan).
- 17-22 *Crucidentricula paranicobarica* var. *tropica* n. var.
19, holotype, 17, paratype; 17-21, outer valve views, 22, girdle view of frustule (17, DSDP Hole 71, 21-4, 60-62 cm; 18-20, 22, DSDP Hole 71, 21-2, 89-91 cm; 21, Ab-11, Nishimyo Formation, Sumon area, Niigata, Japan).
- 23-29 *Crucidentricula nicobarica* (GRUNOW) AKIBA et YANAGISAWA
23-27, 29, outer valve views; 28, girdle view of frustule (23, DSDP Hole 77B, 22-6, 35-37 cm; 24, DSDP Hole 77B, 24-6, 20-22 cm; 25, 27, 28, Sample NKW 166, Taga Formation, Shinkawa Section, Katta area, Ibaraki, Japan; 26, DSDP Hole 438A, 72-3, 15-17 cm; 29, DSDP Hole 77B, 22-6, 35-37 cm).
- 30-32 *Crucidentricula punctata* (SCHRADER) AKIBA et YANAGISAWA
30, 31, outer valve views of valve; 32, inner valve view of valve (30, DSDP Hole 77B, 20-6, 38-40 cm; 31, DSDP Hole 438A, 64-3, 10-14 cm; 32, DSDP Hole 77B, 22-2, 35-37 cm)
- 33-35 *Crucidentricula kanayae* AKIBA et YANAGISAWA var. *kanayae*
33, 35, outer valve views; 34, inner valve view (Sample 70-B49-1a, calcareous concretion dredged from the Bering Sea).
- 36-38 *Crucidentricula kanayae* var. *pacifica* n. var.
38, holotype; 37, paratype; 36, outer valve view; 37, inner valve view; 38, girdle view of valve with punctated copula (36, 38, DSDP Hole 71, 22-6, 116-118 cm; 37, DSDP Hole 71, 23-2, 117-119 cm).
- 39 *Crucidentricula kanayae* AKIBA et YANAGISAWA var. *kanayae*
Girdle view of valve (Sample 70-B49-1a, calcareous concretion dredged from the Bering Sea)
- 40 "*Denticula*" *norwegica* SCHRADER
Outer valve view (Sample JOB 423, Taga Formation, Hirakata, Joban Coalfield, Ibaraki, Japan).

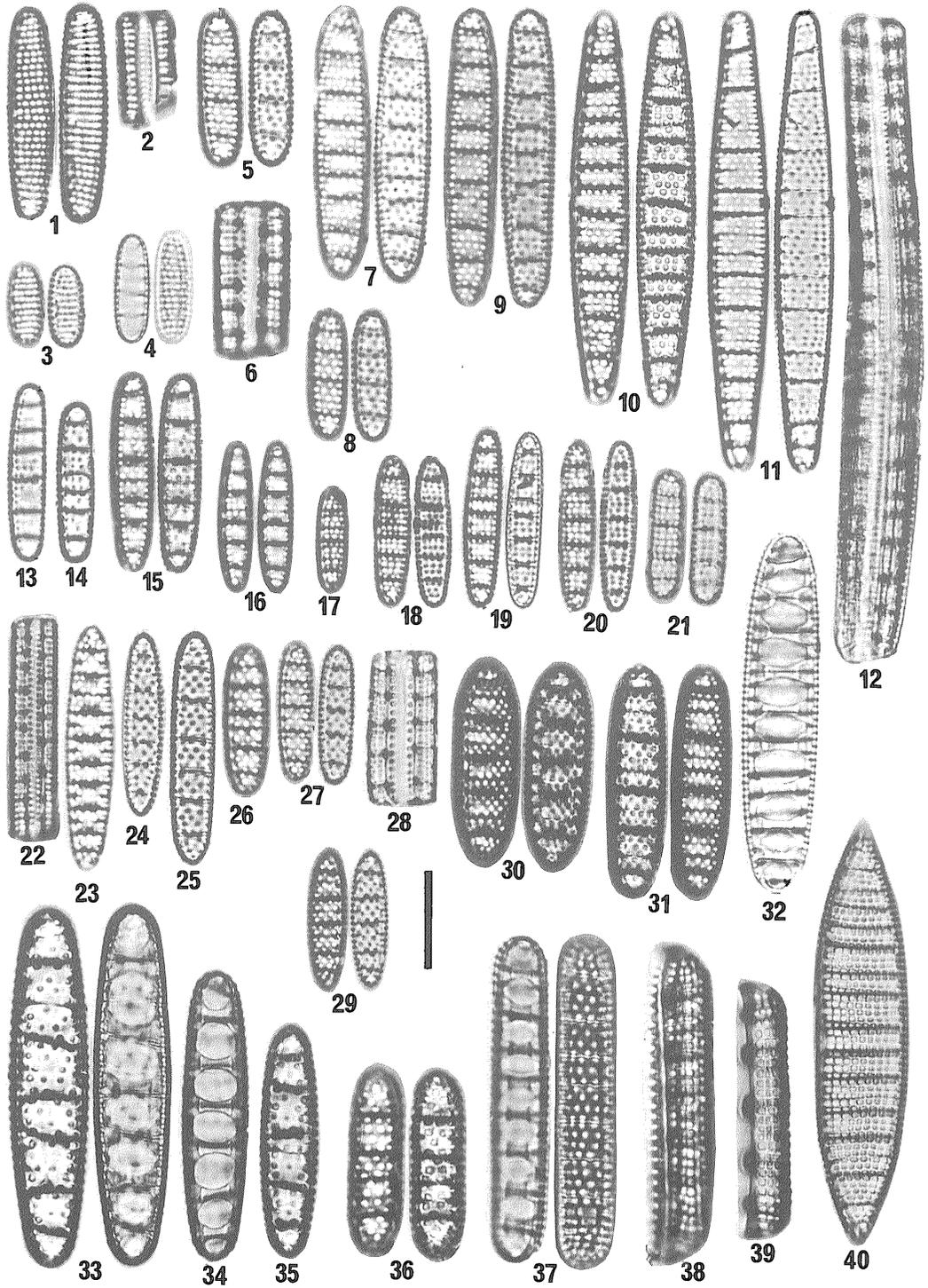


Plate 2 Transmitted light micrographs. Scale bar equals 10 μ m for all figures.

- 1, 2, 10 *Nitzschia challenger* SCHRADER
1, girdle view of frustule; 2, 10, outer valve views (1, DSDP Hole 438A, 67-1, 112-113 cm; 2, Sample JOB 423, Taga Formation, Hirakata, Joban Coalfield, Ibaraki, Japan; 10, Sample N 58, Hataya Formation, Matsushima area, Miyagi, Japan).
- 3-5 *Denticulopsis praelauta* AKIBA et KOIZUMI
3, 4, outer valve views of primitive form with no marginal rib; 5, outer valve view of advanced form with indistinct marginal ribs (3, DSDP Hole 438B, 8-1, 90-92 cm; 4, 5, Sample N 575, Otsuka Formation, Matsushima area, Miyagi, Japan).
- 6-8 *Denticulopsis lauta* (BAILEY) SIMONSEN
Outer valve views (6, DSDP Hole 71, 22-2, 88-90 cm; 7, Sample N 665, Otsuka Formation, Matsushima area, Miyagi, Japan; 8, JDS 15816 = GC 803-9, Southern Ocean).
- 9, 11-13 *Denticulopsis ichikawae* n. sp.
12, holotype; all outer valve views (9, Sample N 665, Otsuka Formation, Matsushima area, Miyagi, Japan; 11-13, DSDP Hole 438A, 79-1, 51-54 cm).
- 14 *Denticulopsis hyalina* (SCHRADER) SIMONSEN
Girdle view of frustule (DSDP Hole 438A, 71-3, 7-11 cm).
- 15 *Denticulopsis lauta* (BAILEY) SIMONSEN
Girdle view of frustule (Sample NKW 14, Genjigawa Formation, Zuiryu Section, Hitachi-ota, Ibaraki, Japan).
- 16-18 *Denticulopsis praelauta* AKIBA et KOIZUMI
Girdle views of frustule; 16, heterovalvate frustule with an open non-punctated copula (Con) and an open punctated copula (Cop); 17, homovalvate frustule with two open punctated copulae (Cop); 18, homovalvate frustule with two open non-punctated copulae (Con) (16, DSDP Hole 438B, 7-1, 128-130 cm; 17, DSDP Hole 438B, 8-1, 90-92 cm; 18, Sample N 575, Otsuka Formation, Matsushima area, Miyagi, Japan).
- 19-25 *Denticulopsis okunoi* n. sp.
22, holotype; 19-24, outer valve views; 25, inner valve view (19, 24, Sample JOB 422; 20-23, 25, Sample JOB 423, Taga Formation, Hirakata, Joban Coalfield, Ibaraki, Japan).
- 26, 27 *Denticulopsis tanimurae* n. sp.
27, holotype; outer valve views (26, DSDP Hole 438A, 72-3, 15-17 cm; 27, DSDP Hole 438A, 71-3, 7-11 cm).
- 28-32 *Denticulopsis praehyalina* TANIMURA
Outer valve views (28, DSDP Hole 438A, 71-3, 7-11 cm; 29, DSDP Hole 438A, 70-7, 5-7 cm; 30, 32, DSDP Hole 438A, 70-3, 49-53 cm; 31, DSDP Hole 438A, 69 cc).
- 33, 34 *Denticulopsis hyalina* (SCHRADER) SIMONSEN
Outer valve views (33, DSDP Hole 438A, 72-1, 14-18 cm; 34, DSDP Hole 438A, 71-3, 7-11 cm).
- 35-37 *Denticulopsis miocenica* (SCHRADER) SIMONSEN
35, 37, outer valve views; 36, inner valve view (Sample JDS-5801, an exotic block in the Chokubetsu Formation, Kushiro Coalfield, eastern Hokkaido, Japan).
- 38 *Yoshidaia divergens* KOMURA
Outer valve view of valve (This form is possibly an initial valve of *Denticulopsis lauta* (BAILEY) SIMONSEN; DSDP Hole 438A, 79-1, 51-54 cm).
- 39-41 "*Denticulopsis*" *maccollumii* SIMONSEN
39, outer valve views of valve; 40, possibly outer valve view of initial valve; 41, inner valve view (ETL PC-16, 36-16, 588-560 cm, Southern Ocean).
- 42, 43 *Nitzschia denticuloides* SCHRADER
42, outer valve view of valve with weakly developed transapical costae; 43, outer valve view of valve with well developed transapical costae (ETL PC-16, 36-16, 588-560 cm).
- 44 *Katahiraia aspera* KOMURA
Outer valve view of valve (This form is possibly an initial valve of *Denticulopsis miocenica* (SCHRADER) SIMONSEN; JDS-5801, an exotic block in the Chokubetsu Formation, Kushiro Coalfield, eastern Hokkaido, Japan).
- 45 *Katahiraia oblonga* KOMURA
Outer valve view of valve (This form is possibly an initial valve of *Denticulopsis hyalina* (SCHRADER) SIMONSEN; DSDP Hole 438A, 70-3, 49-53 cm).

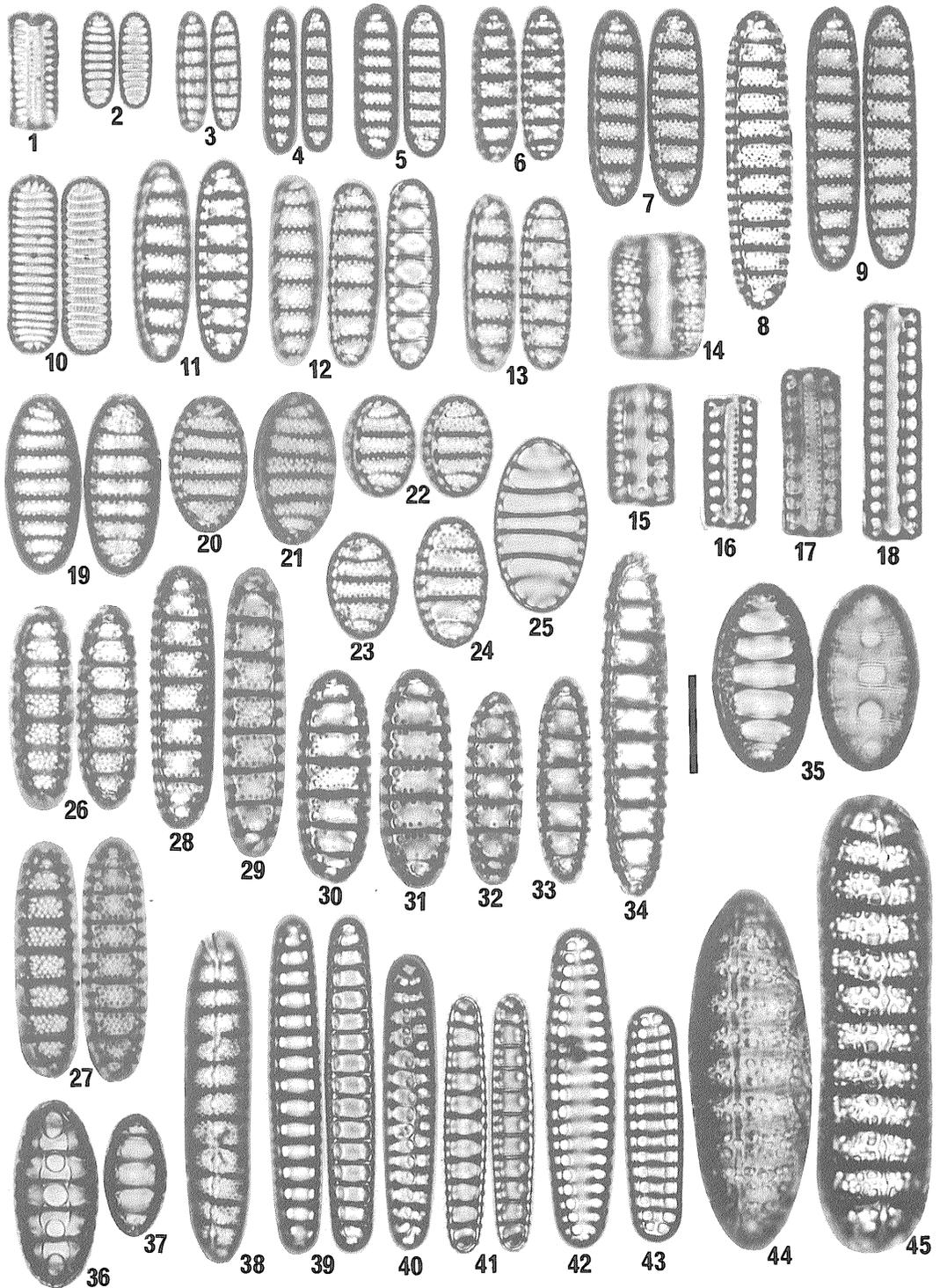


Plate 3 Transmitted light micrographs. Scale bars equal 10 μ m. Bar B for Fig. 15 and bar A for all other figures.

- 1-3 *Denticulopsis simonsenii* n. sp.
1, holotype; all outer valve views (1, 2, Sample N 58, Hataya Formation, Matsushima area, Miyagi, Japan; 3, DSDP Hole 77B, 20- 6, 38-40 cm).
- 4-8 *Denticulopsis vulgaris* (OKUNO) n. comb.
Outer valve views (4, Bore hole A-1, 86.00-86.15m in YANAGISAWA *et al.*, 1989, Futaba area, Fukushima, Japan; 5, 7, 8, DSDP Hole 438A, 57-4, 59-60 cm; 6, DSDP Hole 438A, 59-4, 17-21 cm).
- 9-11 *Denticulopsis praekatayamae* n. sp.
10, holotype; all outer valve views (9, JDS 15775 = GC801-5, Southern Ocean; 10, DSDP Hole 438A, 56 cc; 11, DSDP Hole 77B, 18-2, 23-25 cm).
- 12, 13 *Denticulopsis katayamae* MARUYAMA
Outer valve views (12, DSDP Hole 438A, 56 cc; 13, DSDP Hole 438A, 53-1, 77-81 cm).
- 14-18 *Denticulopsis hustedtii* (SIMONSEN and KANAYA) SIMONSEN
15, holotype; all outer valve views (14, DSDP Hole 226, 10-5, 87-90 cm; 15, Sample 23 of SIMONSEN and KANAYA, 1961, Del Monte, Monterey County, California; 16, 17, DSDP Hole 438A, 61 cc; 18, DSDP 438A, 62-1, 20-24 cm).
- 19 *Denticulopsis hustedtii* (SIMONSEN et KANAYA) SIMONSEN
Copula (DSDP Hole 266, 10-5, 87-90 cm).
- 20 *Denticulopsis praekatayamae* n. sp.
Girdle views of frustule (DSDP Hole 77B, 18-2, 23-25 cm).
- 21-27 *Denticulopsis crassa* n. sp.
23, holotype; 21, open copula; 22, 25, closed copulae; 23, 24, 26, 27, outer valve views (21, 22, 24, DSDP Hole 438A, 62-1, 20-24 cm; 23, DSDP Hole 438A, 65-7, 17-18 cm; 25, DSDP Hole 438A, 64-5, 30-32 cm; 26, DSDP Hole 266, 10-1, 80-83 cm; 27, DSDP Hole 438A, 59-5, 17-21 cm).
- 28 *Denticulopsis katayamae* MARUYAMA (oval form)
Outer valve view (DSDP Hole 438A, 53-1, 77-81 cm).
- 29 *Yoshidaia loculata* KOMURA
Outer valve view of valve (This form is possibly an initial valve of *Denticulopsis vulgaris* (OKUNO) n. comb.; Wk 205, Nakayama Formation, Sado Island, Japan).

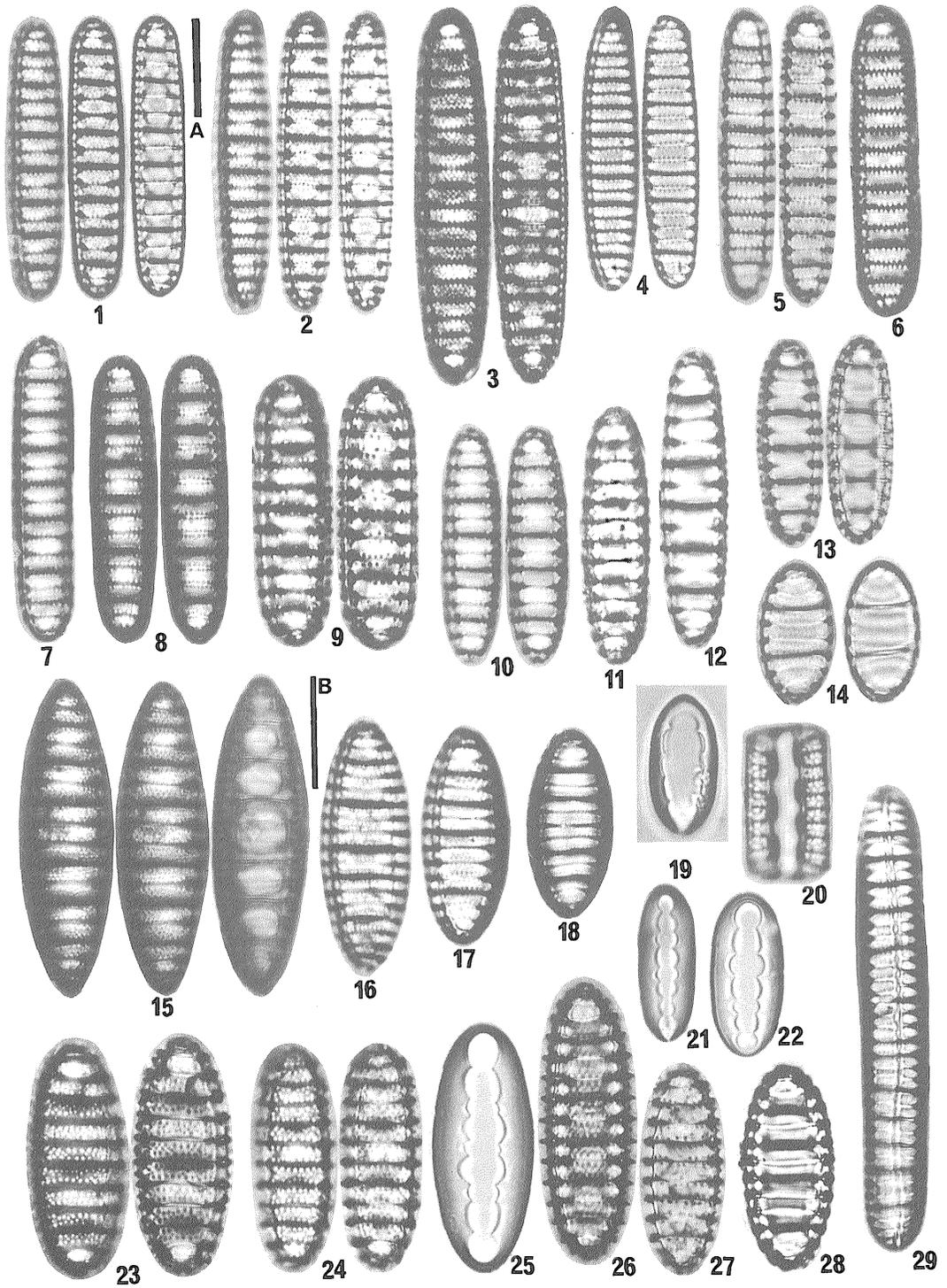


Plate 4 Transmitted light micrographs. Scale bar equals 10 μ m for all figures.

- 1, 2 *Denticulopsis praedimorpha* var. *minor* n. var.
1, outer valve view of Vc valve with a closed copula ; 2, outer valve view of Vo valve (DSDP 438A, 66-1, 118-122 cm).
- 3-5 *Denticulopsis praedimorpha* BARRON ex AKIBA var. *praedimorpha*
3, outer valve view of Vc valve ; 4, outer valve view of Vo valve ; 5, girdle view of frustule with two Cop copulae (3, 4, JDS 8865, Masuura Formation, Abashiri area, eastern Hokkaido, Japan ; 5, DSDP Hole 438A, 65-3, 100-103 cm).
- 6, 7 *Denticulopsis praedimorpha* var. *robusta* n. var.
6, outer valve view of Vc valve ; 7, outer valve view of Vc valve with a closed copula (DSDP Hole 438A, 64-3, 10-14 cm).
- 8, 9, 11 *Denticulopsis praedimorpha* var. *minor* n. var.
8, holotype ; 8, 9, valve views of closed copulae ; 11, girdle view of closed copula with smooth edge (Ccm) (8, DSDP Hole 438A, 66-1, 121-123 cm ; 9, 11, JDS-8865, Masuura Facies, Abashiri Formation, Abashiri area, eastern Hokkaido, Japan).
- 10,12-17 *Denticulopsis praedimorpha* BARRON ex AKIBA var. *praedimorpha*
10, girdle view of closed copula with serrate edge (Ccr) ; 12-14, valve views of closed copulae ; 15, girdle view of Vo valve with a Cop copula ; 16, girdle view of frustule with two Ccm copulae ; 17, girdle view of frustule with Ccr and Cop copulae (JDS-8865, Masuura Facies, Abashiri Formation, Abashiri area, eastern Hokkaido, Japan).
- 18-20 *Denticulopsis praedimorpha* var. *robusta* n. var.
19, holotype ; valve views of closed copulae (DSDP Hole 438A, 64-3, 10-14 cm).
- 21-24 *Denticulopsis praedimorpha* var. *minor* n. var.
21, girdle view of Vc valve with a Ccr copula, also with a Cop copula of epitheca ; 22, girdle view of Vc valve with a Ccr copula ; 23, girdle view of frustule with Ccr and Cop copulae ; 24, girdle view of frustule with two Ccm copulae (21, 22, DSDP Hole 438A, 66-1, 118-122 cm ; 23, 24, JDS-8865, Masuura Facies, Abashiri Formation, Abashiri area, eastern Hokkaido, Japan).
- 25-33 *Denticulopsis barronii* n. sp.
25, outer valve view of Vo valve ; 26-30, valve views of closed copulae ; 31, outer valve view of Vc valve ; 32, girdle view of Vc valve with a Ccr copula ; 33, girdle view of Vc valve with a Ccm copula (DSDP Hole 77B, 20-6, 38-40 cm).
- 34, 35 *Denticulopsis praedimorpha* var. *robusta* n. var.
34, girdle view of frustule with Cop and Ccr copulae ; 35, girdle view of frustule with two Ccr copulae (DSDP Hole 438A, 64-3, 10-14 cm).
- 36-38 *Denticulopsis barronii* n. sp.
37, holotype ; 36, 37, valve views of Vc valve with a closed copula ; 38, valve view of open copula with punctated sides (Cop) (DSDP Hole 77B, 20-6, 38-40 cm).
- 39 *Denticulopsis praedimorpha* BARRON ex AKIBA var. *praedimorpha*
Valve view of open copula with punctated sides (Cop). (JDS-8865, Masuura Facies, Abashiri Formation, Abashiri area, eastern Hokkaido, Japan).
- 40, 41 *Denticulopsis dimorpha* var. *areolata* n. var.
40, valve view of closed copula ; 41, girdle view of closed copula with serrate edge (Ccr) (DSDP Hole 438A, 56 cc).
- 42-49 *Denticulopsis dimorpha* (SCHRADER) SIMONSEN var. *dimorpha*
42, girdle view of closed copula with smooth edge (Ccm) ; 43, valve view of closed copula ; 44, outer valve view of Vo valve ; 45, girdle view of frustule with Ccr and Cop copulae ; 46, girdle view of frustule with Ccr and Ccm copulae ; 47, outer valve view of transitional form to var. *areolata* (Note slightly developed double-layered punctation on valve face.) ; 48, outer valve view of Vc valve ; 49, outer valve view of Vc valve with a closed copula (42, 47, DSDP Hole 438A, 57-4, 59-60 cm ; 43, 44, 46, 48, 49, DSDP Hole 438A, 59-5, 17-21 cm ; 45, DSDP Hole 438A, 56 cc).
- 50-54 *Denticulopsis dimorpha* var. *areolata* n. var.
54, holotype ; 50, outer valve view of Vc valve ; 51, 54, girdle view of frustule with Ccr and Cop copulae ; 52, valve view of open copula with punctated sides (Cop) ; 53, girdle view of Vc valve with a Ccr copula (DSDP Hole 438A, 56 cc).

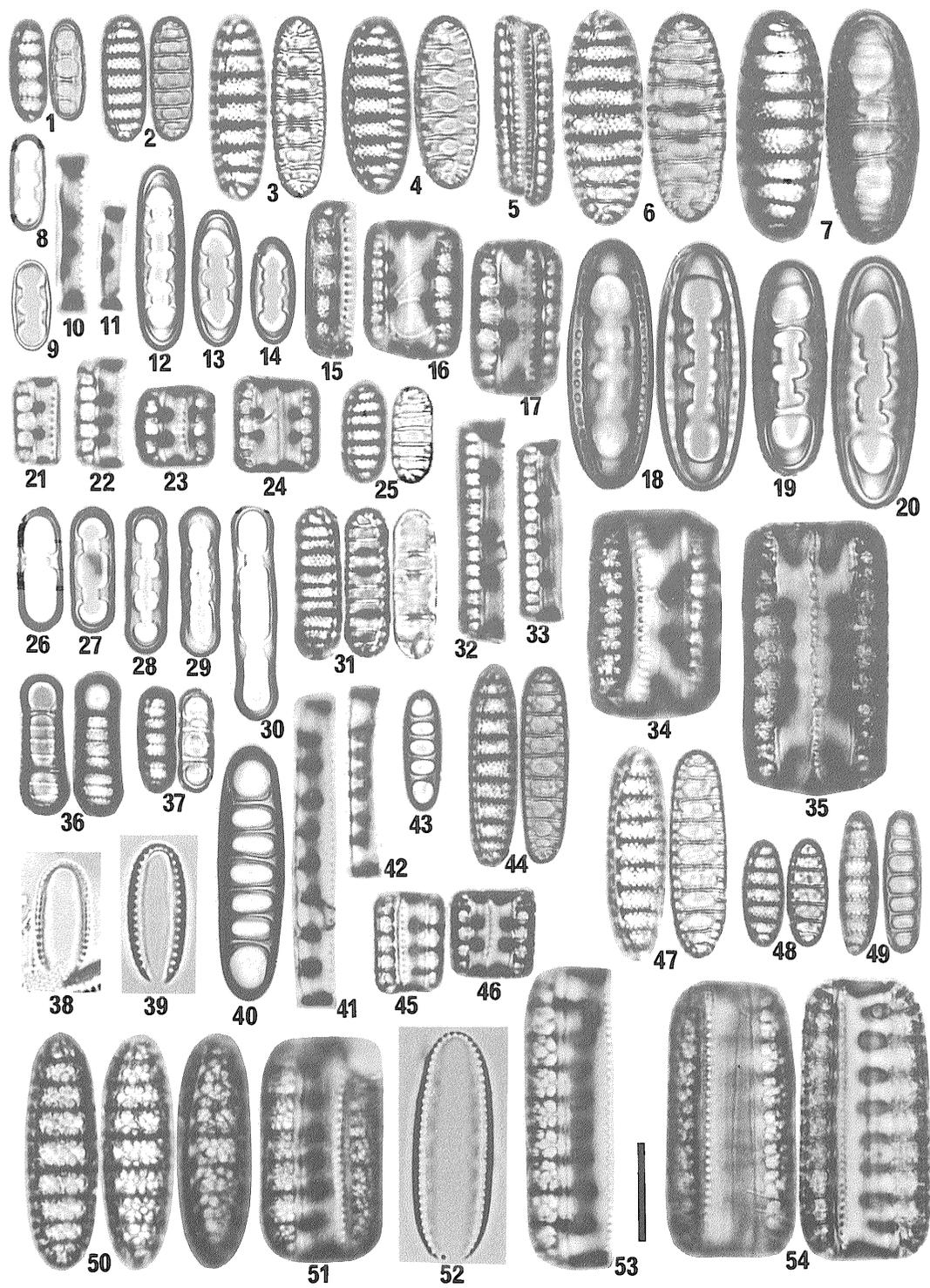


Plate 5 Transmitted light micrographs. Scale bar equals 10 μ m for all figures.

- 1-3 *Denticulopsis lauta* (BAILEY) SIMONSEN
(Sample N 665, Otsuka Formation, Matsushima area, Japan)
- 4-12 *Denticulopsis praedimorpha* BARRON ex AKIBA var. *praedimorpha*
(JDS-8865, Masuura Facies, Abashiri Formation, Abashiri area, eastern Hokkaido, Japan)
- 13-17 *Denticulopsis dimorpha* var. *areolata* n. var.
(DSDP Hole 438A, 56cc)
- Vc : Vc valve (Valve connecting with closed copula)
Vo : Vo valve (Valve connecting with open copula)
Con : open copula with non-punctated sides
Cop : open copula with punctated sides
Ccr : closed copula with serrate edge
Ccm : closed copula with smooth edge
Cc : closed copula

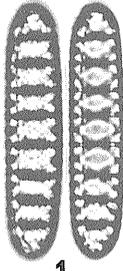
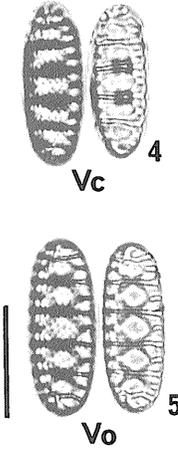
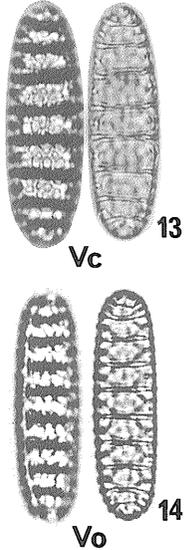
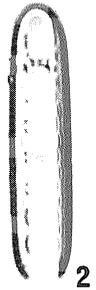
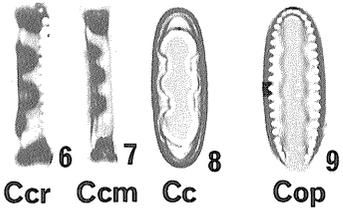
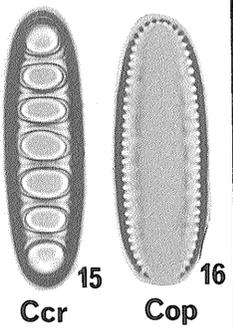
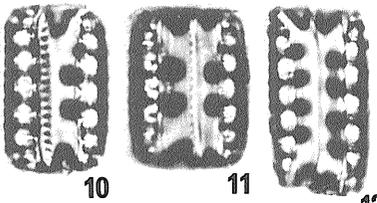
	<i>D. lauta</i>	<i>D. praedimorpha</i> v. <i>praedimorpha</i>	<i>D. dimorpha</i> v. <i>areolata</i>
Valve	 <p>1</p>	 <p>4 Vc 5 Vo</p>	 <p>13 Vc 14 Vo</p>
Copula	 <p>2 Con</p>	 <p>6 Ccr 7 Ccm 8 Cc 9 Cop</p>	 <p>15 Ccr 16 Cop</p>
Frustule	 <p>3</p>	 <p>10 11 12</p>	 <p>17</p>

Plate 6 Transmitted light micrographs. Scale bar equals 10 μ m for all figures.

1-5 *Denticulopsis dimorpha* var. *areolata* n. var.

1, 4, outer valve views of valve ; 2, outer valve view of Vc valve with a closed copula ; 3, inner valve view of Vc valve with a closed copula ; 5, open copula with punctated sides (Cop) (DSDP Hole 266, 10-1, 80-83 cm, Southern Ocean)

6-14 *Denticulopsis ovata* (SCHRADER) n. comb.

6, 10, 11, outer valve views of Vc valve with a closed copula ; 7-9, outer valve views of Vo valve ; 12, possibly outer valve view of initial valve ; 13, inner valve view of Vc valve with a closed copula with serrate edge (Ccr) ; 14, open copula with punctated sides (Cop)(DSDP Hole 266, 10-1, 80-83 cm, Southern Ocean)

15-23 *Denticulopsis dimorpha* var. *areolata* n. var.

Closed copulae (note serrate edge of Fig. 17, and smooth edge of Fig. 19) (15, DSDP Hole 266, 10-5, 87-90 cm ; 16-23, DSDP Hole 266, 10-1, 80-83 cm, Southern Ocean)

24-32 *Denticulopsis ovata* (SCHRADER) n. comb.

Closed copulae (Note serrate edge of Fig. 27) (DSDP Hole 266, 10-1, 80-83 cm, Southern Ocean)

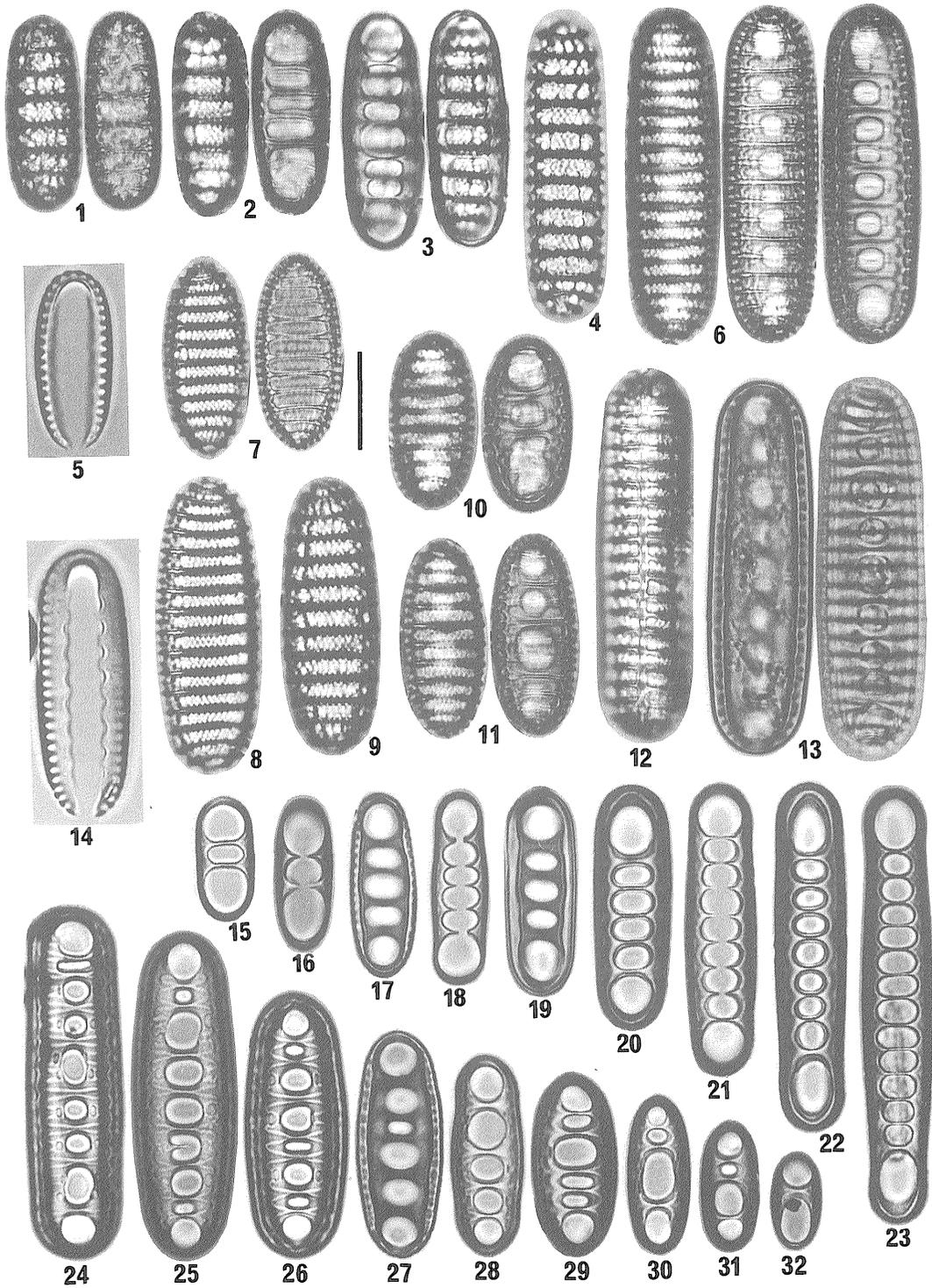


Plate 7 Transmitted light micrographs. Scale bar equals 10 μm for all figures.

- 1-4 *Denticulopsis delicata* n. sp.
Outer valve views; 1, holotype (DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean)
- 5, 6 *Denticulopsis praedimorpha* var. *minor* n. var.
Outer valve views (DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean)
- 7-9 *Denticulopsis praedimorpha* var. *intermedia* n. var.
Outer valve views (7, DSDP Hole 266, 10-5, 87-90 cm; 8, 9, DSDP Hole 266, 10-1, 80-83 cm, Southern Ocean)
- 10 *Denticulopsis praedimorpha* var. *minor* n. var.
Closed copula (DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean)
- 11-13 *Denticulopsis praedimorpha* var. *intermedia* n. var.
Closed copulae; 13, holotype (DSDP Hole 266, 10-5, 87-90 cm, Southern Ocean)
- 14-16 *Denticulopsis dimorpha* (SCHRADER) SIMONSEN var. *dimorpha*
Closed copulae (DSDP Hole 266, 10-3, 77-80 cm, Southern Ocean)
- 17-19 *Nitzschia rolandii* SCHRADER (primitive asymmetric form)
Outer valve views of valve (17, 18, Bore hole A-1, 86.00-86.15 m, Futaba area, Fukushima Prefecture, Japan, *Thalassiosira yabei* Zone, 19, DSDP Hole 438A, 42-1, 14-18 cm)
- 20-22 *Nitzschia rolandii* SCHRADER (primitive symmetric form)
Outer valve views of valve (20, 22, DSDP Hole 438A, 40-6, 10-14 cm; 21, DSDP Hole 438A, 41cc)
- 23-26 *Nitzschia rolandii* SCHRADER (advanced form)
Outer valve views of valve (23, DSDP Hole 438A, 43-1, 59-63 cm; 24, DSDP Hole 438A, 41-6, 10-14 cm; 25, DSDP Hole 438A, 42-6, 16-20 cm; 26, DSDP Hole 438A, 41cc)
- 27-37 *Neodenticula kamtschatica* (ZABELINA) AKIBA et YANAGISAWA
27, 28, 30, 33-37, outer valve views of valve; 29, girdle view of frustule; 31, open copula with non-punctated sides (Con); 32, inner valve view of valve (27, DSDP Hole 438A, 42-1, 14-18 cm; 28, DSDP Hole 438A, 41 cc; 29, JDS-8659, Atsunai Formation, Atsunai area, eastern Hokkaido, Japan; 30, 31, DSDP Hole 438A, 13-3, 19-23 cm; 32, DSDP Hole 438A, 41 cc; 33, JDS-8623, Atsunai Formation, Atsunai area, eastern Hokkaido, Japan; 34, JDS-8629, Atsunai Formation, Atsunai area, eastern Hokkaido, Japan; 35-37, DSDP Hole 438A, 13-3, 19-23 cm). Note very fine puncta on valve face in Figs. 30 and 37. The two figures were photographed with oblique illumination.
- 38-41 *Neodenticula koizumii* AKIBA et YANAGISAWA
38-40, outer valve views of valve; 41, open copula with non-punctated sides (Con) (38-40, JDS-8869, Atsunai Formation, Atsunai area, eastern Hokkaido, Japan; 41, DSDP Hole 438A, 5 cc)
- 42-44 *Neodenticula koizumii* AKIBA et YANAGISAWA (oval form) = *Neodenticula* sp. A of AKIBA and YANAGISAWA (1986)
Outer valve views (42, 44, DSDP Hole 438A, 5 cc; 43, JDS-8634, Shiranuka Formation, Atsunai area, eastern Hokkaido, Japan)
- 45-49 *Neodenticula seminae* (SIMONSEN et KANAYA) AKIBA et YANAGISAWA
45, possibly outer valve view of initial valve; 46, 48, outer valve views of valve; 47, inner valve view of valve; 49, closed copula with smooth edge (Ccm) (Sample 1954. 4. 20, a net sample collected off Kuril Islands by Dr. H. TAKANO)

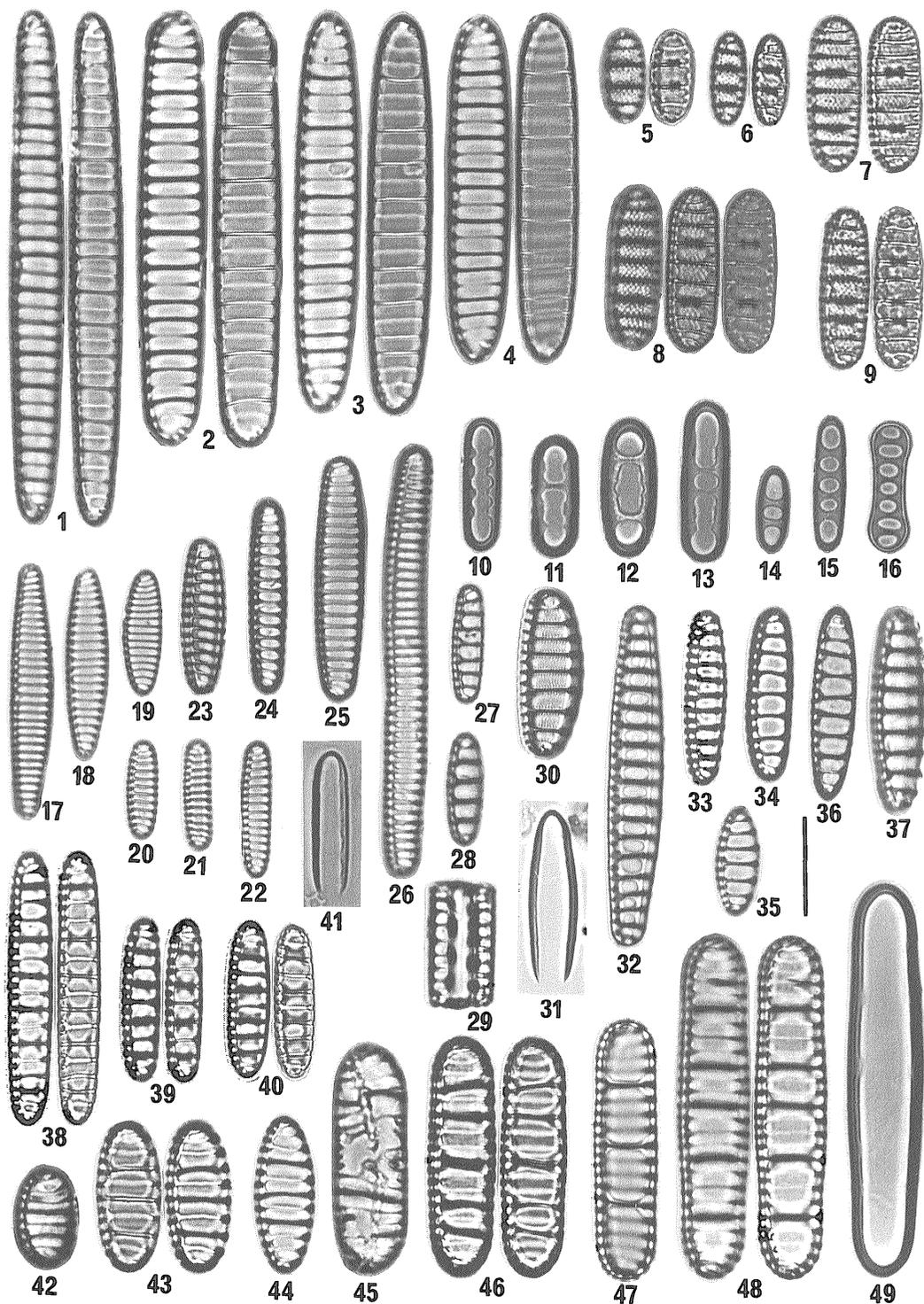


Plate 8 Scanning electron micrographs. White scale bars equal 5 μm and a black bar equals 0.1 μm .

- 1-7 *Nitzschia maleinterpretaria* SCHRADER
1, outer valve view ; 2, enlargement of Fig. 1 showing apical part of valve ; 3, enlargement of Fig. 1 showing central part of valve (Arrow indicates interruption of raphe slit) ; 4, inner valve view ; 5, oblique girdle view ; 6, 7, inner valve views (stereoscopic pair) (Sample P 225, 7-20, eastern equatorial Pacific, the *Triceratium pileus* Zone).
- 8-13 *Crucidentacula ikebei* AKIBA et YANAGISAWA
8, outer valve view ; 9, enlargement of Fig. 8 showing central part of valve ; 10, enlargement of Fig. 8 showing apical part of valve ; 11, girdle view ; 12, inner oblique view of valve apex ; 13, inner oblique view of central part of valve (Note a large central portula) (Sample 70-B49-1a, calcareous concretion dredged in the Bering Sea).
- 14-17 *Crucidentacula kanayae* AKIBA et YANAGISAWA var. *kanayae*
14, oblique view of frustule ; 15, narrow girdle view of frustule ; 16, isolated deck of valve ; 17, oblique view of broken valve (Sample 70-B49-1a, calcareous concretion dredged from the Bering Sea).
- 18 "*Denticula*" *norwegica* SCHRADER
Oval areolae occluded by mesh-like cribra (Sample JDS-11171, Matsushima Formation, Shiogama area, Miyagi, Japan).

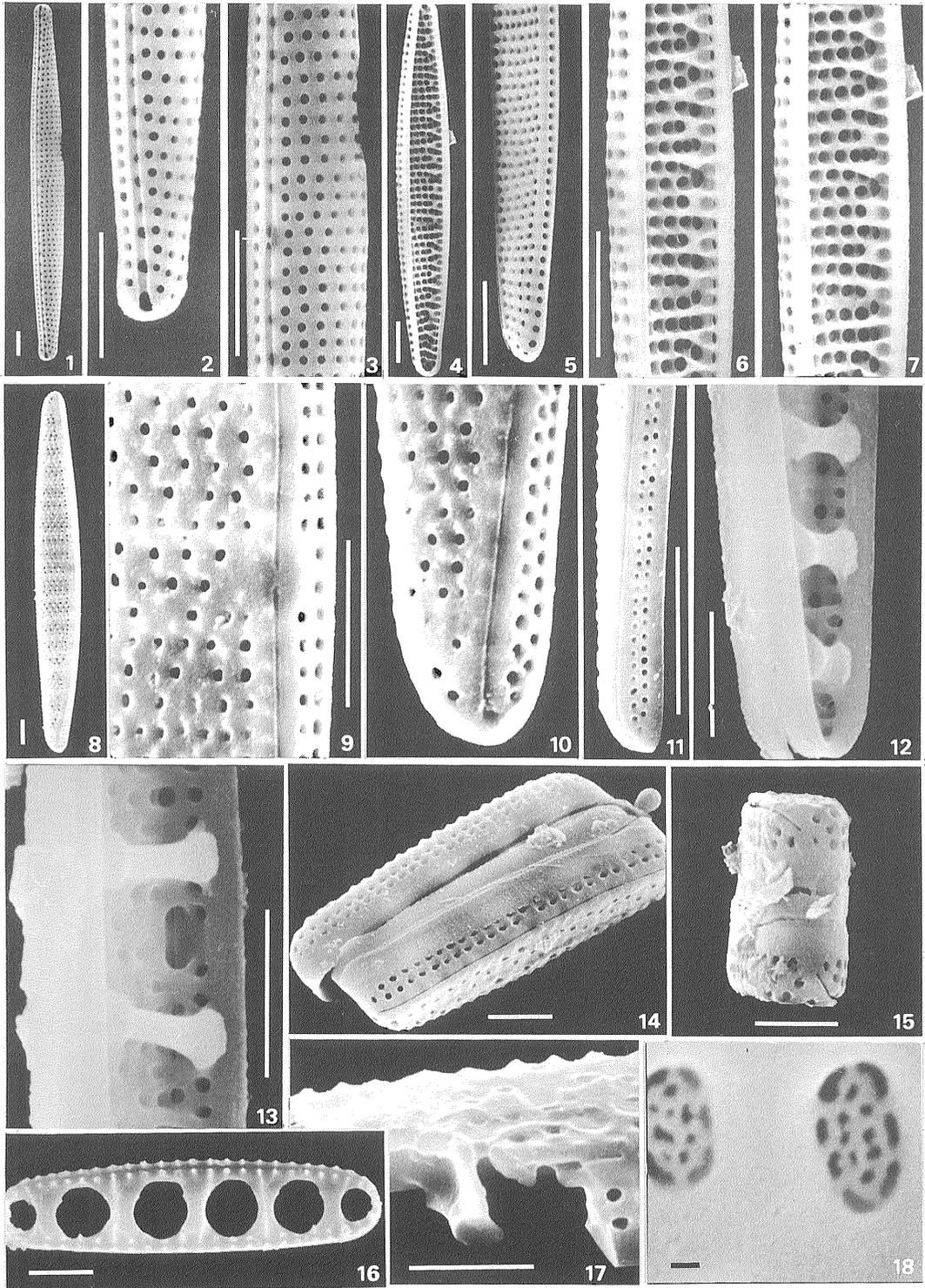


Plate 9 Scanning electron micrographs. Scale bars equal 5 μm .

- 1 *Denticulopsis lauta* (BAILEY) SIMONSEN
Outer valve view (DSDP Hole 438A, 73-3, 27-31 cm).
- 2-4 *Denticulopsis ichikawae* n. sp.
2, 4, outer valve views ; 3, inner valve view (Sample N 665, Otsuka Formation, Matsushima area, Miyagi, Japan).
- 5-7 *Denticulopsis praehyalina* TANIMURA
5, 6, outer valve views ; 7, oblique view of frustule (DSDP Hole 438A, 70-5, 23-27 cm).
- 8, 9 *Denticulopsis hyalina* (SCHRADER) SIMONSEN
Outer valve views (DSDP Hole 438A, 70-5, 23-27 cm).
- 10, 11 *Yoshidaia divergens* KOMURA
Outer valve view of frustule (This form is possibly an initial valve of *Denticulopsis lauta* (BAILEY) SIMONSEN ; DSDP Hole 438A, 73-3, 27-31 cm).
- 12-16 *Nitzschia challengerii* SCHRADER
12, oblique view of two valves attached on valve faces ; 13, enlargement of Fig. 12 showing central part of valve ; 14, inner valve view ; 15, enlargement of Fig. 14 showing apical part of valve ; 16, enlargement of Fig. 14 showing central part of valve (Sample N 575, Matsushima Formation, Matsushima area, Miyagi, Japan).

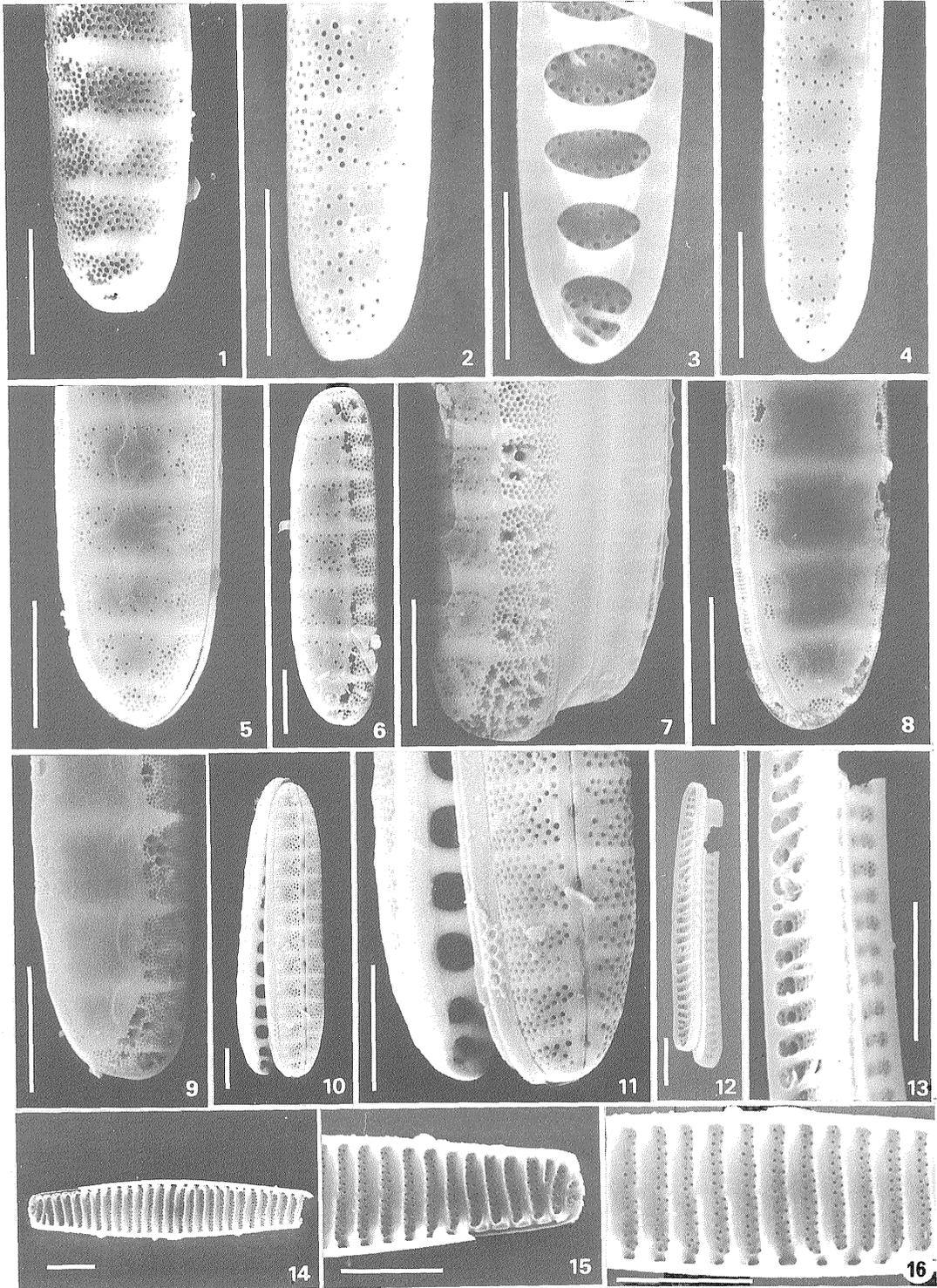


Plate 10 Scanning electron micrographs. Scale bars equal 5 μm .

1, 2 *Nitzschia challengerii* SCHRADER

Outer valve views (Sample N 575, Otsuka Formation, Matsushima area, Miyagi, Japan)

3-9 *Katahiraia aspera* KOMURA

This form is possibly an initial valve of *Denticulopsis miocenica* (SCHRADER) SIMONSEN ; 3, oblique outer valve view 4, outer valve view ; 5, enlargement of Fig. 4 showing central part of valve and interrupted slit of raphe ; 6, oblique narrow girdle views ; 7, 8, inner valve views ; 9, broad girdle view (Sample JDS-5801, an exotic block in Chokubetsu Formation, Atsunai area, eastern Hokkaido, Japan)

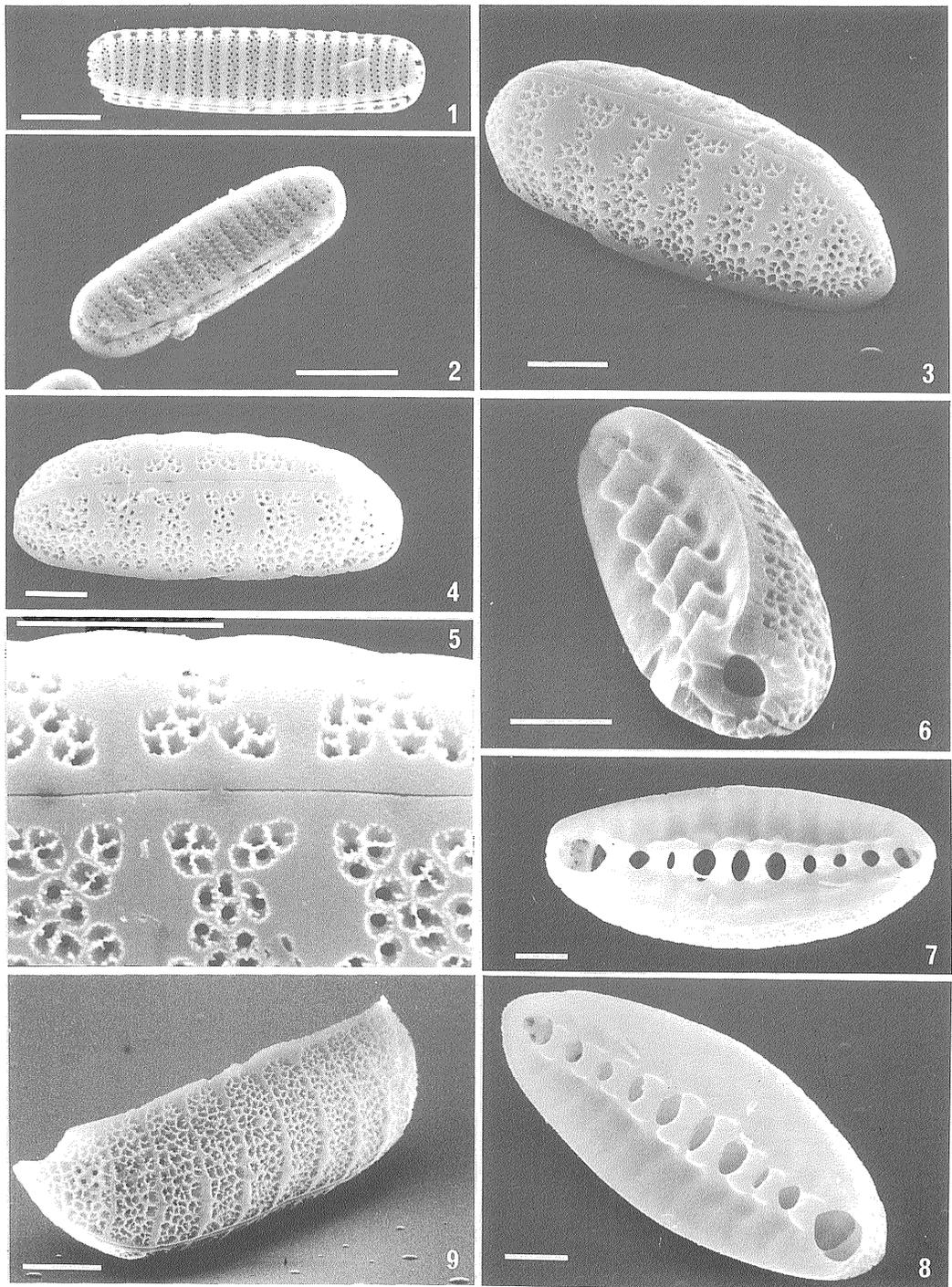


Plate 11 Scanning electron micrographs. Scale bars equal 10 μ m.

- 1 *Denticulopsis simonsenii* n. sp.
Outer valve view (Sample N 58, Hataya Formation, Matsushima area, Miyagi, Japan).
- 2 *Denticulopsis vulgaris* (OKUNO) n. comb.
Outer valve view (DSDP Hole 438A, 57-4, 59-60 cm).
- 3 *Denticulopsis praekatayamae* n. sp.
Outer valve view (DSDP Hole 438A, 56cc).
- 4 *Denticulopsis katayamae* MARUYAMA
Outer valve view (DSDP Hole 438A, 56cc).
- 5 *Denticulopsis simonsenii* n. sp.
Outer valve view (Sample N 58, Hataya Formation, Matsushima area, Miyagi, Japan).
- 6-10 *Denticulopsis vulgaris* (OKUNO) n. comb.
6, outer valve view ; 7, 8, inner valve views ; 9, 10, outer valve views (6-8, DSDP Hole 438A, 57-4, 59-60 cm ; 9, 10, Sample Mj 151-2 from Miocene deposits of Chile collected by Dr. K. SAWAMURA).
- 11-13 *Denticulopsis hustedtii* (SIMONSEN et KANAYA) SIMONSEN
Inner valve views (DSDP Hole 438A, 62-1, 20-24 cm).
- 14-16 *Denticulopsis praekatayamae* n. sp.
Outer valve views (DSDP Hole 438A, 56cc).

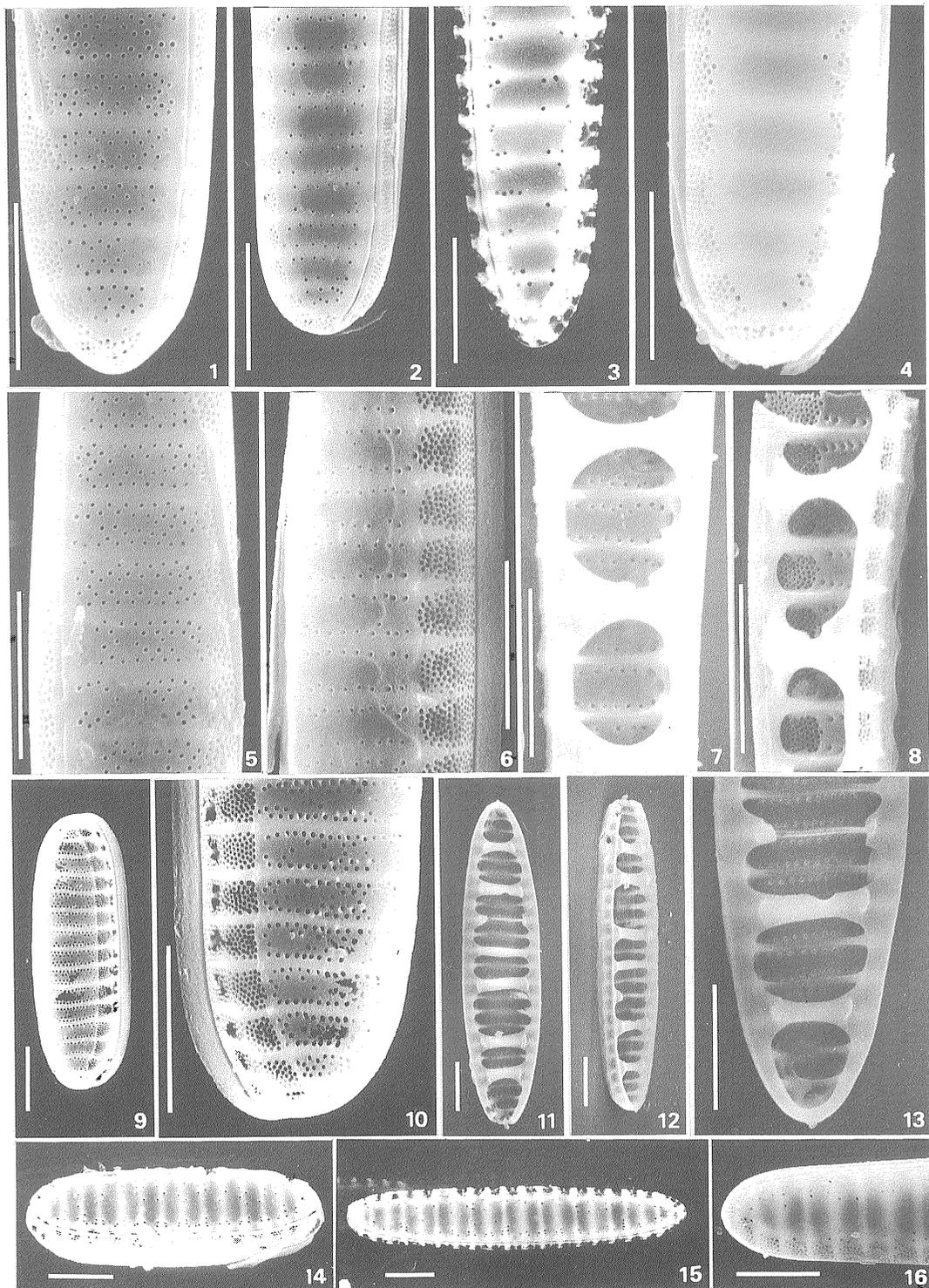


Plate 12 Scanning electron micrographs. Scale bars equal 10 μm .

- 1-8 *Denticulopsis crassa* n. sp.
1, 2, outer valve views ; 3, 4, inner valve views ; 5, inner oblique view ; 6, outer oblique view ;
7, closed copula ; 8, open copula (1-7, DSDP Hole 438A, 65-7, 17-18 cm ; 8, DSDP Hole
438A, 62-1, 20-24 cm).
- 9 *Denticulopsis praedimorpha* var. *minor* n. var.
Closed copula (DSDP Hole 438A, 66-1, 118-122 cm).
- 10-14 *Denticulopsis praedimorpha* var. *robusta* n. var.
10, 11, closed copula ; 12, 13, inner valve views of Vc valve ; 14, inner oblique view of Vc
valve (DSDP Hole 438A, 64-3, 10-14 cm). Note double-layered punctuation on the mantle of
valve in Fig. 14.
- 15, 16 *Denticulopsis dimorpha* var. *areolata* n. var.
Outer oblique views of partly dissolved valve showing double-layered punctuation on valve
face and mantle (DSDP Hole 438A, 56cc).

