893. EVOLUTIONARY CHANGE IN DIATOM MORPHOLOGY
——AN EXAMPLE FROM NITZSCHIA FOSSILIS
TO PSEUDEUNOTIA DOLIOLUS*——

ITARU KOIZUMI
Department of Geology and Mineralogy, Faculty of Science,
Hokkaido University, Sapporo 060

and

YUKIO YANAGISAWA
Geological Survey of Japan, 1–1–3 Higashi, Tsukuba, Ibaraki 305

Abstract. Pseudoeunotia doliolus gradually developed its convex dorsal margin from the Nitzschia fossilis morphology during the course of time since 2.00 m.y. B.P. This development corresponds with the general trend of the diatom temperature (Td) curve observed in the same sedimentary sections. However, the development of the convex dorsal margin is considered to have likely been caused by a genetic character rather than the effect of surface water temperature decline, because this evolutionary process does not correspond strictly with the climatic deterioration during the Pleistocene. Our SEM examination of the diatom valves of P. doliolus and N. fossilis shows that they have the same valve structure except for the valve symmetry. It is concluded that P. doliolus evolved from N. fossilis at the beginning of the Pleistocene and that these two species persisted for a period of about one m.y. until the disappearance of the latter species at 0.6 m.y. B.P. Therefore, this evolutionary change occurred during a time interval of 10^6 or more years.

Key words. Diatom, evolution, Nitzschia fossilis, Pseudoeunotia doliolus.

Introduction

From the morphology and structure of diatom valves, and from the stratigraphic occurrence of the species, it is possible to judge the evolutionary relationships between some diatom species.

Pseudoeunotia doliolus (Wallich) Grunow seems to have developed its curved apical axis during its evolution from Nitzschia fossilis (Frenguelli) Kanaya which is a symmetrical form present at the beginning of the Pleistocene age. The stratigraphic data show that more than 10^6 years elapsed before the former replaced the latter completely in the North Pacific planktonic population (Koizumi and Kanaya, 1976).

The disappearance of N. fossilis is remarkably synchronous at 0.6 m.y. B.P. in the middle- to high-latitudes of the North Pacific (Koizumi and Tanimura, 1985). This datum level was first proposed by Koizumi and Kanaya (1976) at the lower part of the Brunhes Chron (about 0.65 m.y. B.P.) in the Choshi section of Choshi Peninsula, central Japan. This species also disappears at an identical time in the equatorial region (Burckle and Trainer, 1979). P. doliolus is broadly distributed over the tropical and middle-latitudes, so it is an important element

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of both tropical and subtropical diatom assemblages. Its first occurrence is slightly earlier in the low-latitudes (2.00 m.y. B.P.) than in the middle-latitudes (1.89 m.y. B.P.) (Koizumi and Tanimura, 1985).

The purposes of this paper are two-fold, namely: (1) to present the stratigraphic development of the convex dorsal margin in *P. doliolus* from *N. fossilis*, and (2) to describe the fine valve structures of these two species based on SEM observations in order to confirm their evolutionary relationship.

**Materials and methods**

The occurrence of both *Pseudoeunotia doliolus* and *Nitzschia fossilis* were counted until 20 valves per one sample, except some samples containing very rarely these species, in the previously reported samples from the DSDP Site 579 (Koizumi and Tanimura, 1985) and the Choshi section (Koizumi and Kanaya, 1976). In addition, samples from a piston core recovered by the R/V Thomas G. Thompson cruise 49 were also examined (TT 49-4: Lat. 35°40.96′N. Long, 157°45.73′E; [Figure 2](#fig2)).

**Figure 2.** Measurements of valve asymmetry (a/b) and apical length (l).

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**Figure 1.** Location of materials used in this study.
Figure 3. Stratigraphic distribution in frequencies of the asymmetry index \((a/b)\) for *Pseudoenuotia dolichus* and *Nitzschia fossilis*, and \(T_d\) values from the DSDP Site 579.
Figure 4. Stratigraphic distribution in frequencies of the asymmetry index (a/b) for *Pseudoemunotia doliolus* and *Nitzschia fossilis*, and Td values from TT 49-4.
Figure 5. Stratigraphic distribution in frequencies of the asymmetry index \((a/b)\) for *Pseudoeunotia doliolus* and *Nitzschia fossilis*, and \(T_d\) values from the Choshi section, Choshi Peninsula.
water depth 4003 m; core length 744 cm) (Figure 1).

The valve symmetry was measured by the asymmetry index \(a/b\) defined as a ratio of width in a ventral side (a) and a dorsal side (b) of the transapical axis in a valve (Figure 2). In the case of a symmetrical valve, e.g. of \(N.\) fossilis, the ratio \(a/b\) is equal to 1. With the progressing asymmetry of the valve in \(P.\) doliolus, however, the ratio \(a/b\) decreases toward 0. The relationship between the asymmetry index \(a/b\) and the apical length \(l\) was also calculated for \(P.\) doliolus.

SEM observation was carried out for valves of these two species which were picked up and mounted on sample stages from processed materials with a tiny paint brush.

**Results**

[1] Asymmetry index \(a/b\)

The frequency distributions of the asymmetry index \(a/b\) for \(P.\) doliolus are shown by a cluster of bars with a thicker line connecting the arithmetical average in each sample (Figures 3—5). The distributions of the asymmetry index gradually change in time without a break, because the ranges overlap one another in the stratigraphy. The stratigraphic distributions of the index for \(N.\) fossilis are also shown as thicker bars.

The frequency distribution of the asymmetry index for \(P.\) doliolus obtained from the DSDP Site 579 are within the range from \(a/b=0.89\) to \(0.25\) (Figure 3). The general trend in the distributions of this index is toward smaller values in more recent period, from \(a/b=0.85\) at the lowermost sample below the Olduvai Event to \(a/b=0.42\) at the uppermost sample near the sea floor. The large decreases in the index, however, occur at two horizons; i.e. at the upper boundary of Olduvai Event and below the Jaramillo Event. \(N.\) fossilis virtually disappears in the earliest part of the Brunhes Chron; a few sporadic occurrences being noted after the Jaramillo Event.

The asymmetry index for \(P.\) doliolus in the core TT 49–4 traces a zigzag decline (Figure 4). These fluctuations might be due to the smaller numbers of valves measured in each sample. \(N.\) fossilis disappears in the lower part of the Brunhes Chron.

The asymmetry index for \(P.\) doliolus in the Choshi section covers a wide range in each sample, previously decreasing upwards, especially in the interval from the Olduvai to Jaramillo Events (Figure 5). The last occurrence of \(N.\) fossilis lies in the lowest part of the Brunhes Chron as in the two sections previously described.

[2] Asymmetry index vs. apical length

The ratio of apical length \(l\) to asymmetry
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index (a/b) was calculated for 197 valves of *P. doliolus* from the DSDP Site 579 but there is no specific relationship between these two measurements (Figure 6).

[3] SEM observation

*Pseudoenunotia doliolus* (Figure 8): The areolae of this species are rounded to triangular in shape, with finely perforated cribra (Figures 8–7, 15). They are arranged in two transapical rows with quincunx pattern between each two transapical costae (Figure 8–15). The transapical costae are equally spaced but sometimes more narrowly with only one row of areolae between them (Figures 8–1–4, 12). The external costa has a terminal extension with a small depression on its top (Figures 8–9,10). The internal costae often branch at raphe-bearing side so that fork-like structures are formed (Figure 8–13). The small knobs are distributed over the valve face (Figures 8–5, 6). The raphe slit is not interrupted at its middle point (Figures 8–10, 11). The raphe canal, a circular tube running below the raphe slit, communicates with the valve interior through small interspaces between costae (Figures 8–7, 8). An interspace at the middle point of raphe is larger than others (Figure 8–13). The chamber-like hollow spaces are present under both side between each two transapical costae (Figure 8–7).

*Nitzschia fossilis* (Figure 9): The microstructures of this species observed by SEM is just the same as those of *P. doliolus*. The two rows of areolae between costae (Figure 9–4), the branching of internal costae at raphe side (Figures 9–10a, b), and a large interspace at the middle point of raphe (Figure 9–9) are also present in *N. fossilis* as in *P. doliolus*. Furthermore, the irregular narrow spacing of transapical costae is also observed (Figures 9–2, 3, 5).

**Discussion**

The spatial distributions of diatom events, defined by first and last appearances in sedimentary sequences, are influenced by the paleo-position of the subarctic front or the change of surface water temperature in the unstable oceanic environment of the North Pacific (Koizumi, 1986b). It is considered, therefore, that the stratigraphic distributions of the asymmetry index for *P. doliolus* and *N. fossilis* are also dependent principally upon the change of Td value (Kanaya and Koizumi, 1966), which is a correlative of the surface water temperature.

The Td values in the DSDP Site 579 generally decrease upwards with some sharp fluctuations (Koizumi, 1986b). The first Td minimum, which has an equivalent degree to the low Td values during the Brunhes Chron, occurs below the Olduvai Event. Another sharp drop in Td value occurs slightly above the Olduvai Event. The Td curve is relatively stable during the interval between the Olduvai and Jaramillo Events. Large and rhythmic Td fluctuations during the upper

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**Figure 8.** *Pseudoenunotia doliolus* (Wallich) Grunow, GH 82–3, RC 226 (ec), bottom sediment of the Sendai Bay, Japan. Broader scale bar equals 10 μm and narrower one equals 1 μm. 1, external valve view (Arrow heads indicate narrower irregular spacing of transapical costae); 2, internal valve view; 3–4, external oblique views (Arrow heads indicate narrower irregular spacing of transapical costae; 3, raphe-bearing side; 4, raphe-less side); 5–6, external surface of apex of valve (Arrow head indicates one of the knobs on the valve face); 7–8, sections of valve (r, raphe slit; r, raphe canal; i, interspace; c, chamber-like hollow space of both mantle; v, cribra of areolae); 9, oblique external view of raphe-less side; 10, external valve face (Arrow indicates middle point of raphe slit); 11, enlargement of Figure 8–10 (Large arrow indicates middle point of raphe. Note raphe slit is continuous at this point. Small arrow indicates a small depression on the top of extension of costa); 12, oblique external view showing narrower irregular spacing of transapical costae (arrow); 13, internal valve view (Arrow indicates a large interspace at the middle point of raphe. Arrow head indicates one of the ordinary small interspace. 14, internal view of valve apex; 15, internal view showing cribra of areolae.
Pleistocene begin near the Jaramillo Event. Nine Td minima are recognized during the Brunhes Chron. These Td fluctuations are certainly correlated with the cycles of glacial interglacial stages.

The development of the convex dorsal margin of the valve of *P. doliolus* might be affected by the decrease of surface water temperature. However, no strict correlation can be recognized between the change of the asymmetry index of *P. doliolus* and the fluctuations of Td values in the DSDP Site.
579 (Figure 3).

The general decline of the Td curve during the Pleistocene in the Choshi section (Koizumi and Kanaya, 1976) can be correlated with the gradual decrease of asymmetry index of *P. doliolus* (Figure 5).

The disappearance of *N. fossilis* in the lower part of the Brunhes Chron seems to be related to the climatic deterioration as shown by the lowest Td value which is correlated with the stage 16 of the oxygen isotope record in the equatorial Pacific (Koizumi, 1986a) (Figure 3–5).

The SEM observation shows that *P. doliolus* and *N. fossilis* are quite identical in valve structures, except that they differ merely in valve symmetry. This confirms the evolutionary relationships between the two species, but presents a problem for the generic separation of *Pseudoeunotia* from the genus *Nitzschia*, a situation already noted by Simonsen (1974).

Kolbe (1954) pointed out the morphological similarity between *P. doliolus* and *Nitzschia marina*. However, the valve microstructure of *N. marina* revealed by Akiba and Yanagisawa (1986) is quite different from that of *P. doliolus*.

**Systematic paleontology**

Class Bacillariophyceae
Order Pennales
Suborder Raphidinaceae
Family Nitzschiaeae Grunow, 1860
Genus *Nitzschia* Hassall, 1845
*Nitzschia fossilis* (Frenquelli) Kanaya, 1973

Figures 7–1—2; 9


*Synonym.* *Pseudonitzschia fossilis* Frenquelli, 1949,

p. 118, pl. 1, fig. 7 (not fig. 6); *Fragilariopsis plicocene* (Brun) Sheshukova-Poretskaya, Kanaya, 1971, p. 556, pl. 40, figs. 7, 8 (not Sheshukova-Poretskaya, 1976, p. 305–306, pl. 47, fig. 13, pl. 48, fig. 7).

**Emended description** (Schrader, 1973).–
Valves elliptical with slightly convex margins and broadly rounded apices, the middle sometimes more strongly convex, 22–45 μm long, 6–8 μm wide. Transapical costae about 11 in 10 μm. Intercostal membranes with two transapical rows of puncta, about 22 in 10 μm. Rows punctate, puncta in decussate arrangement forming oblique rows. Transapical rows and costae near the apices curved. Puncta near the costae, margin strong, raphe marginal (Orthographic errors are corrected).

**Genus Pseudoeunotia** Grunow, 1865

*Pseudoeunotia doliolus* (Wallich)

Grunow, 1880

Figures 7–3—12; 8

*Pseudoeunotia doliolus* (Wallich) Grunow. Hustedt, 1932, p. 259–260, fig. 737; Cupp, 1943, p. 190–191, fig. 140; Lohman, 1941, pl. 17, figs. 12, 13; Kolbe, 1954, p. 43–44, pl. 3, fig. 41; Schrader, 1973, pl. 4, figs. 1–3, 6–8, not 4, 5; Simonsen, 1974, p. 56; Koizumi and Kanaya, 1976, p. 155, pl. 1, figs. 9, 10.

**Full description** (Hustedt, 1932 translated in English by Jensen, 1985 with description of colony formation and girdle view from the genus description). Valve side of cells bound into dorsoventral ribbons. Ventral girdle band side linear, dorsal girdle band side with slightly convex margins. Valves half lanceolate with bluntly rounded ends; straight, slightly concave or rarely slightly convex ventral margin and strongly convex dorsum, gradually sloping from the middle toward the ends and often somewhat retracted, 30–70 μm long, 5–8 μm wide. Transapical ribs 9–14 in 10 μm, in between which are found double rows of delicate areolae in quincunx, about 22 oblique rows in 10 μm.
Pseudoraphic and central area absent.

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References cited


珪藻殻の形態変異にもとづく進化系列 — Nitzschia fossilis から Pseudoeunotia doliolus
への一例：現生珪藻種 Pseudoeunotia doliolus にみられるゆるやかな弧状ないし直線状腹
線は急減種 Nitzschia fossilis の突出した弧状の線から約 200 万年前以降 100 万年以上の時
間をかけて徐々に発達して来た P. doliolus の殻面観にみられる殻の非対称の変化は一般
的な傾向として珪藻温度 (Td) 指数の変化と同調しているが、両者の変化は細部において
一致していない。すなわち P. doliolus の腹線の脇らみは第四紀更新世を通じて見られた表層
海水温の低下によって減少したのではなく、発生学的な原因によって減少したと考えられ
る。このことは P. doliolus と N. fossilis との珪藻殻を走査型電子顕微鏡によって観察した
結果、両者の殻における対称性の違いを除き、両者が全く同じ殻の構造を持っていること
からも支持される。