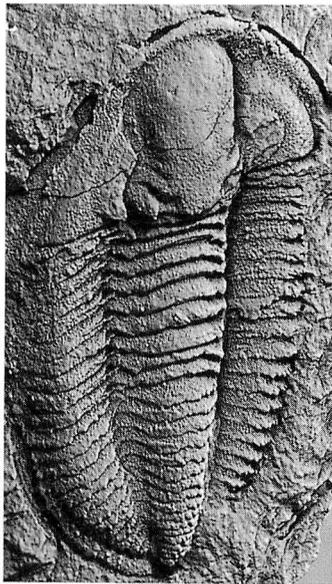


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The fossil on the cover is *Phillipsia ohmorensis* Okubo, an Early Carboniferous trilobite from the Hikoroichi Formation in the Higuchizawa valley, Ofunato City, Iwate Prefecture, northeast Japan (Collected by A. Haga, PA 5766, $\times 3.0$; after Kobayashi and Hamada, 1980, pl. 6, fig. 4).

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

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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;

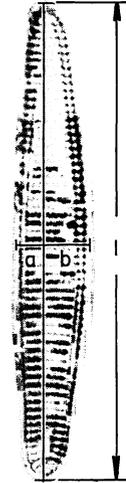


Figure 2. Measurements of valve asymmetry (a/b) and apical length (l).

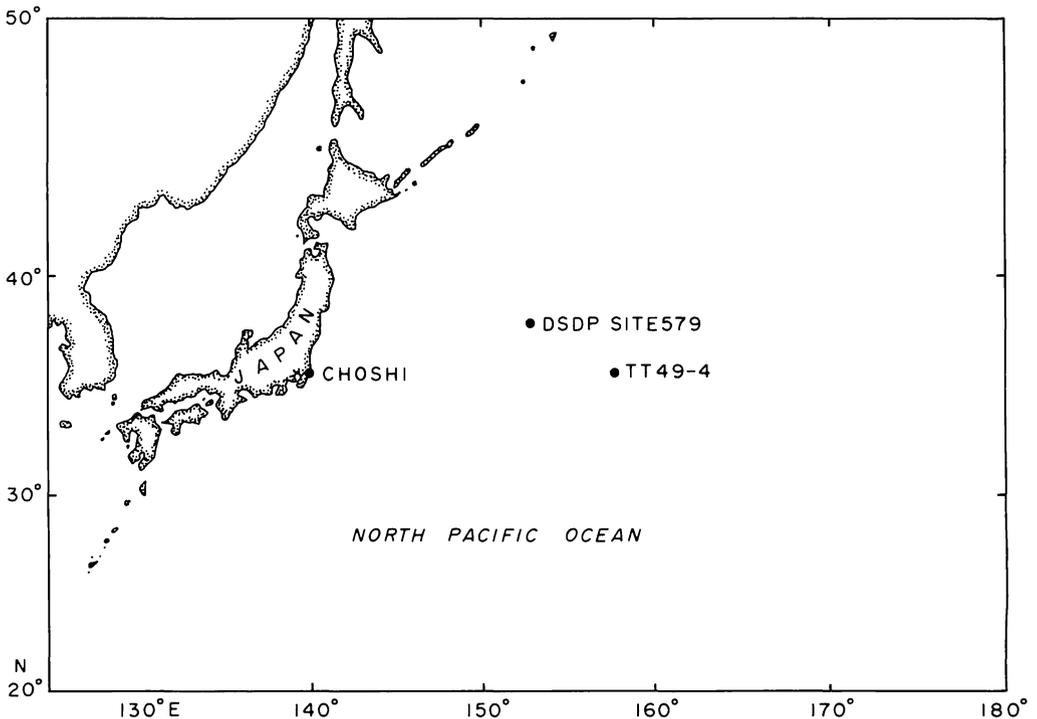


Figure 1. Location of materials used in this study.

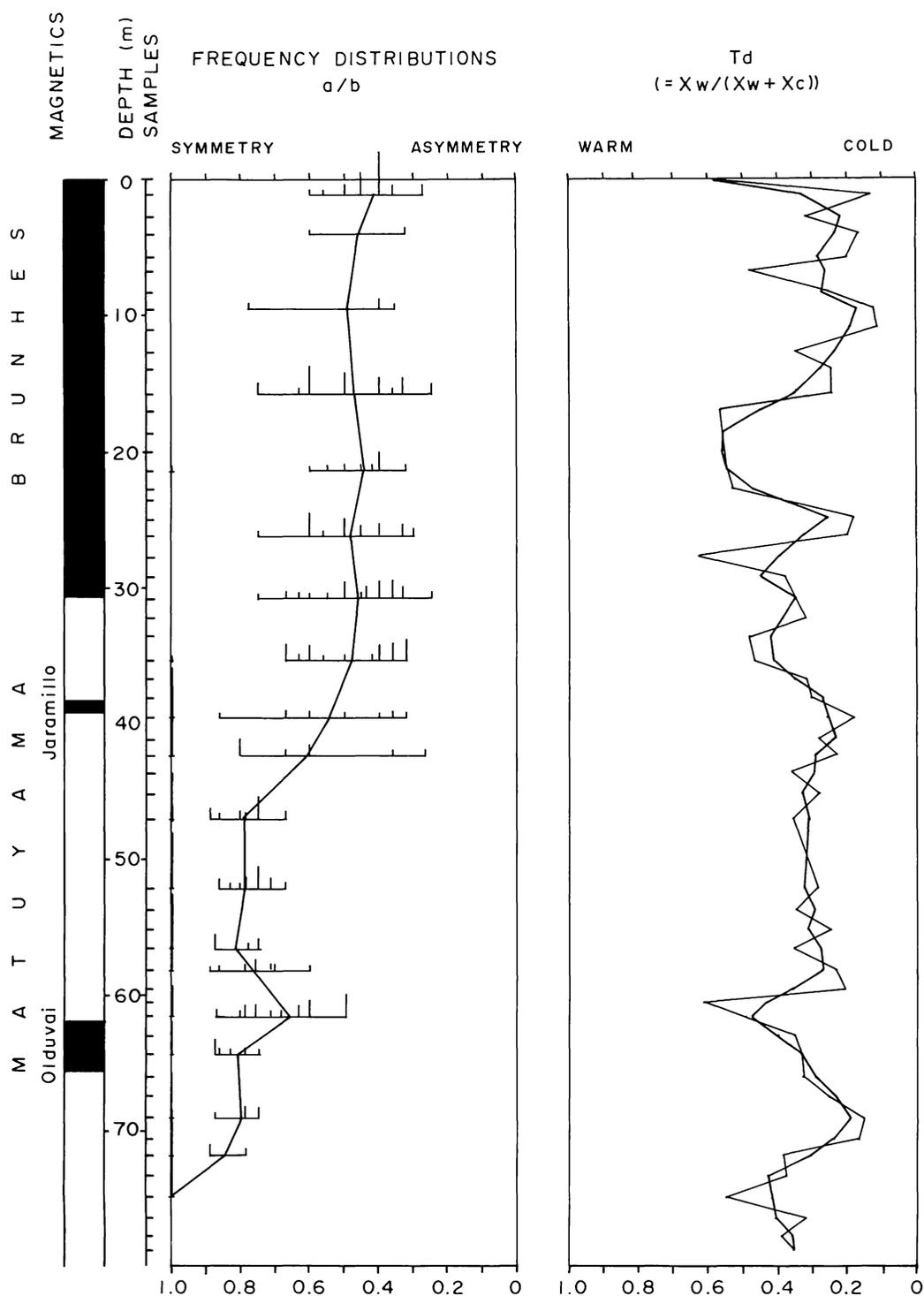


Figure 3. Stratigraphic distribution in frequencies of the asymmetry index (a/b) for *Pseudoeunotia doliolus* and *Nitzschia fossilis*, and T_d values from the DSDP Site 579.

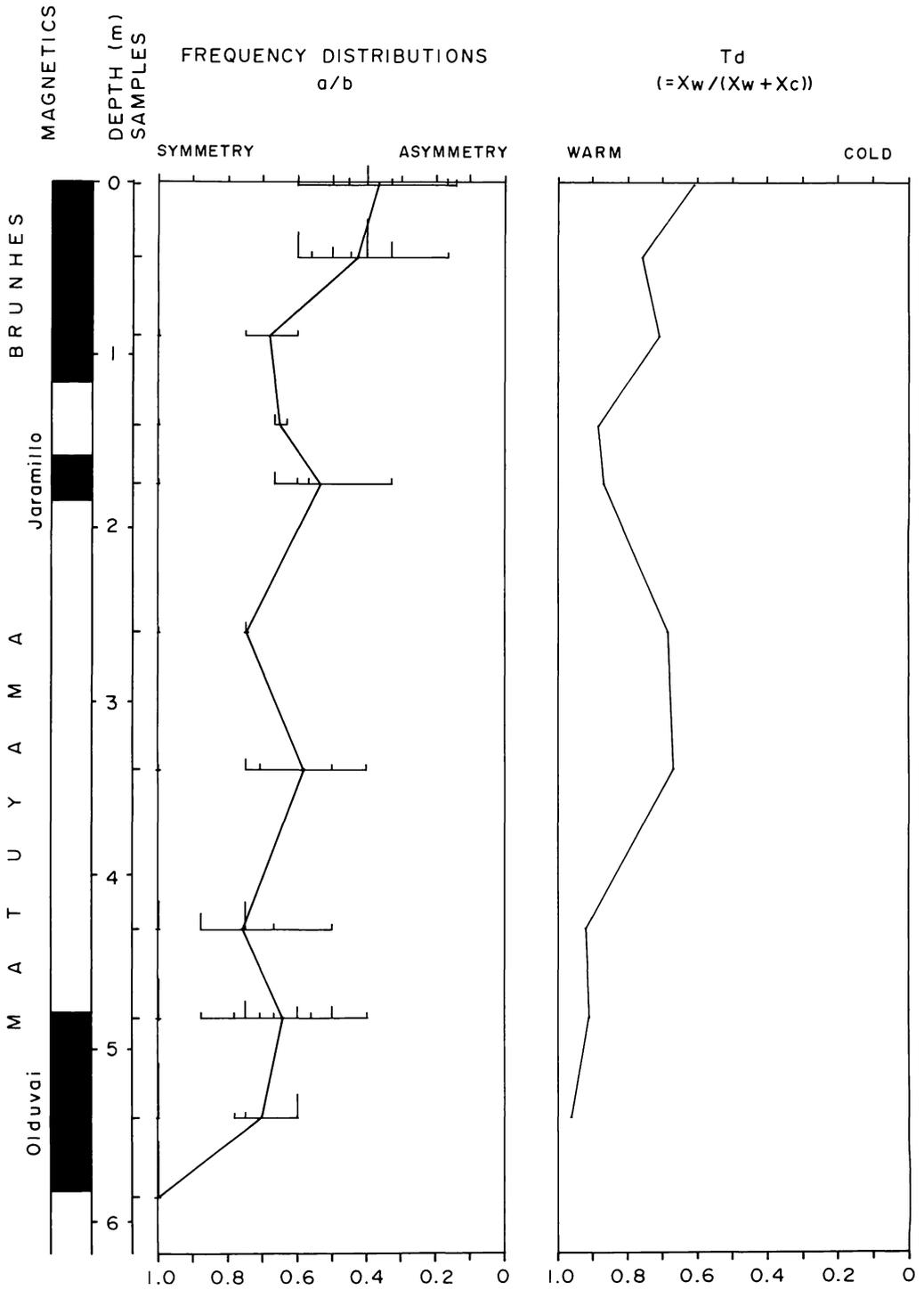


Figure 4. Stratigraphic distribution in frequencies of the asymmetry index (a/b) for *Pseudoeunotia doliolus* and *Nitzschia fossilis*, and Td values from TT 49-4.

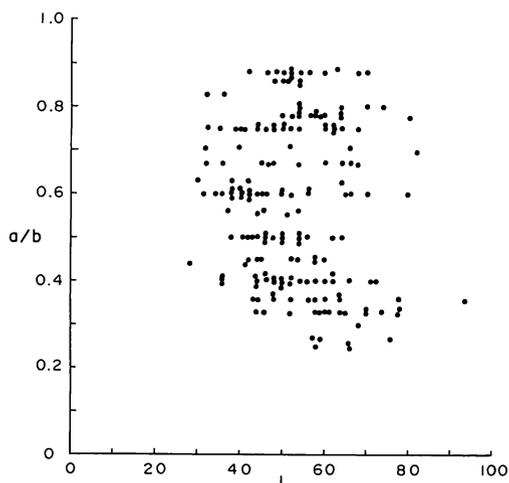


Figure 6. Relationship between the asymmetry index (a/b) and the apical length (l) for *Pseudoeunotia doliolus* from the DSDP Site 579.

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 asym-

metry 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.

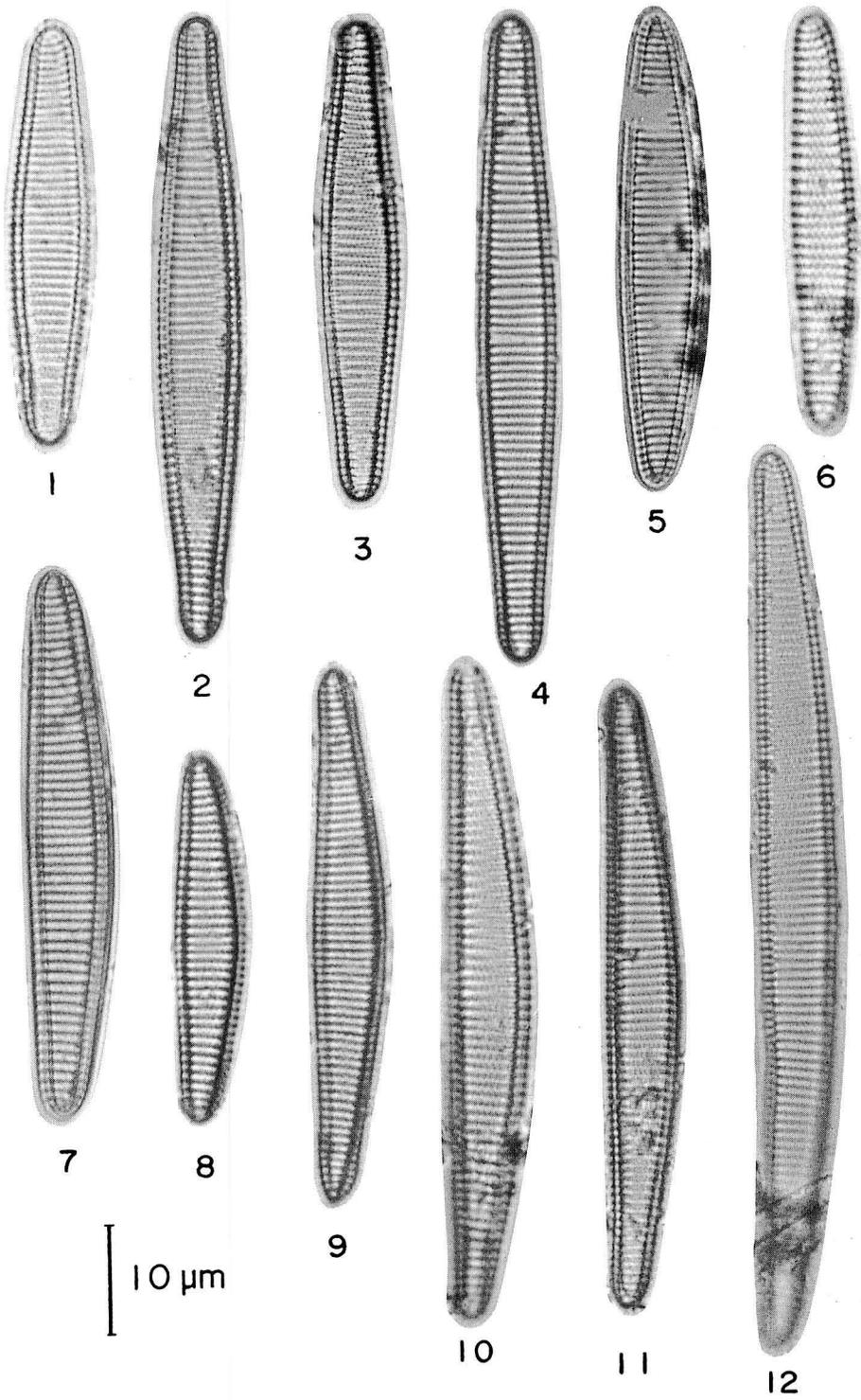
The asymmetry index for *P. doliolus* in the core TT 49-4 traces a zigzag decline (Figure 4). These fluctuations might be due to the smaller numbers of valves measured in each sample. *N. fossilis* disappears in the lower part of the Brunhes Chron.

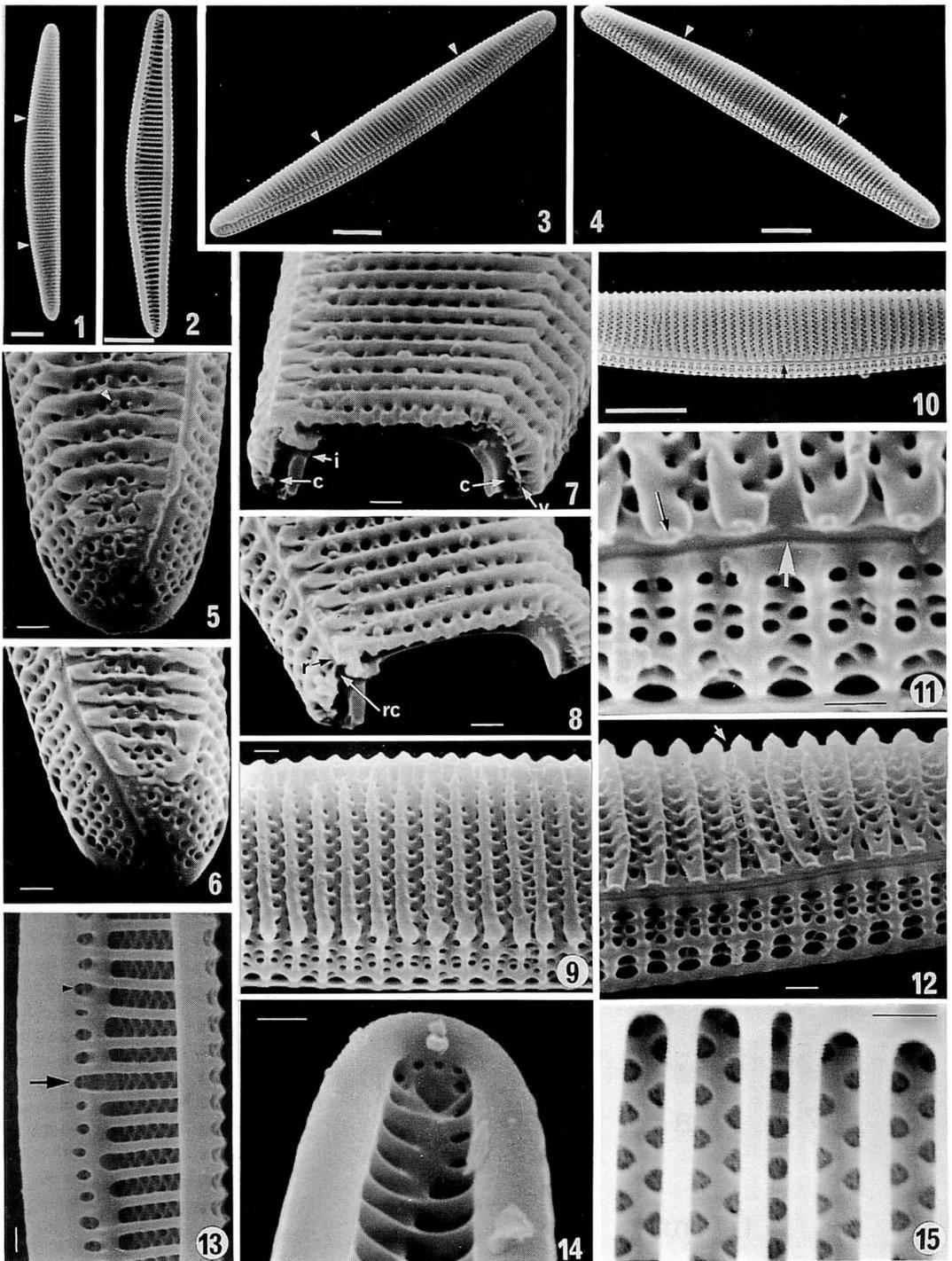
The asymmetry index for *P. doliolus* in the Choshi section covers a wide range in each sample, previously decreasing upwards, especially in the interval from the Olduvai to Jaramillo Events (Figure 5). The last occurrence of *N. fossilis* lies in the lowest part of the Brunhes Chron as in the two sections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

[2] Asymmetry index vs. apical length

The ratio of apical length (l) to asymmetry

→ **Figure 7.** 1–2. *Nitzschia fossilis* (Frenguelli) Kanaya: 1, $a/b=1.00$, TT 49-4 (12); 2, $a/b=1.00$, DSDP 579A (5-1). 3–12. *Pseudoeunotia doliolus* (Wallich) Grunow; 3, $a/b=0.92$, Choshi (A-4); 4, $a/b=0.83$, DSDP 579A (8-1); 5, $a/b=0.77$, Choshi (A-20); 6, $a/b=0.67$, TT 49-4 (9); 7, $a/b=0.57$, DSDP 679A (6-1); 8, $a/b=0.43$, DSDP 579A (3-4); 9, $a/b=0.43$, DSDP 579A (2-7); 10, $a/b=0.33$, DSDP 579A (1-1); 11, $a/b=0.31$, DSDP 579A (1-3); 12, $a/b=0.22$, Choshi (IK 31).





index (a/b) was calculated for 197 valves of *P. doliolus* from the DSDP Site 597 but there is no specific relationship between these two measurements (Figure 6).

[3] SEM observation

Pseudoeunotia 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

← **Figure 8.** *Pseudoeunotia doliolus* (Wallich) Grunow, GH 82-3, RC 226 (cc), bottom sediment of the Sendai Bay, Japan. Broader scale bar equals 10 μ m and narrower one equals 1 μ m. **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**, extexternal surface of apex of valve (Arrow head indicates one of the knobs on the valve face); **7-8**, sections of valve (r, raphe slit; rc, 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.

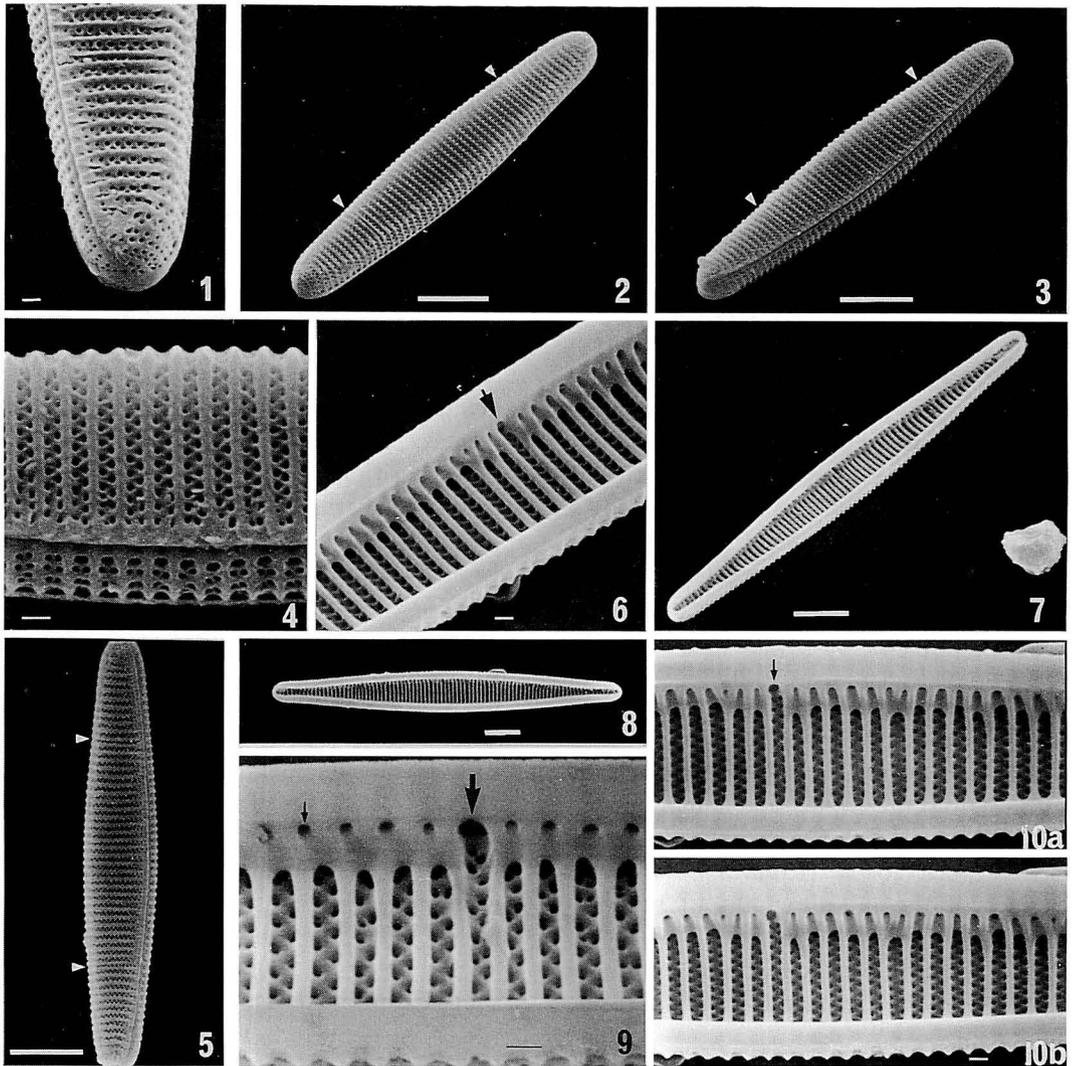


Figure 9. *Nitzschia fossilis* (Frenguelli) Kanaya, TT 49-4, 630-633 cm. Broader scale bar equals 10 μm and narrower one equals 1 μm . **1**, external surface of valve apex; **2, 3**, oblique external view showing narrower irregular spacing of transapical costae (arrow head), **2**, raphe-less side, **3**, raphe-bearing side; **4**, external valve face and mantle; **5**, external valve view showing narrower irregular spacing of transapical costae; **6**, enlargement of Figure 9-7 (Arrow indicates a large interspace at middle point of raphe); **7**, oblique internal view; **8**, internal valve view; **9**, enlargement of Figure 9-10b (Large arrow indicates a large interspace at middle point of raphe. Small arrow indicates one of ordinary small interspace); **10a—b**, internal valve view (Stereoscopic pair. Arrow indicates a large interspace at the middle point of raphe).

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 in 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 Raphidineae

Family Nitzschiaceae Grunow, 1860

Genus *Nitzschia* Hassall, 1845

Nitzschia fossilis (Frenguelli) Kanaya, 1973

Figures 7-1-2; 9

Nitzschia fossilis (Frenguelli) emend. Kanaya in Kanaya et Koizumi ex Schrader. Kanaya and Koizumi, 1970, p. 59 (nomen. invalid): Koizumi, 1972, p. 352, pl. 42, figs. 14a-15c (as *Nitzschia fossilis* Kanaya); Schrader, 1973, p. 707, pl. 4, figs. 9-11, 24, 25; Koizumi, 1973, p. 833; Koizumi and Kanaya, 1976, p. 155, pl. 1, figs. 11-14.

Synonym.- *Pseudonitzschia fossilis* Frenguelli, 1949,

p. 118, pl. 1, fig. 7 (not fig. 6); *Fragilariopsis pliocene* (Brun) Sheshukova-Poretskaya, Kanaya, 1971, p. 556, pl. 40.3, 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 dorsovental ribbons. Ventral girdle band side linear, dorsal girdle band side with slightly convex margins. Valves halves 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 .

Pseudoraphe and central area absent.

Acknowledgments

This paper builds on the fundamental work on diatoms initiated by Dr. T. Kanaya who was formerly Professor of Tohoku University. We would like to thank Professor F.E. Round of the University of Bristol for a critical review of this manuscript.

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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縁は絶滅種 *Nitzschia fossilis* の突出した弧状の縁から約 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* の腹縁の張りみは第四紀更新世を通じて起っ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支持される。

小泉 格・柳沢幸夫

894. A NEW TRILOBITE GENUS *RHINOPHACOPS**

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Abstract. A phacopid genus *Rhinophacops* is proposed on the basis of *Echinophacops schizoloma* Zhou, 1983 described from the Zhusileng Formation (Upper Emsian) of Inner Mongolia. This new genus is characterized by having an anterior opening during enrollment. Material collected from the N₃ Member of the Nakazato Formation, Iwate Prefecture, Northeast Japan was described in detail.

Key words. *Rhinophacops*, trilobite, Devonian, Inner Mongolia, Nakazato Formation, Northeast Japan.

Introduction

The present author already described trilobites from the Nakazato Formation in the Kitakami Mountains, Northeast Japan (Kaneko, 1984, 1985). This paper treats of phacopid specimens collected by Ono from the N₃ Member of the Nakazato Formation exposed in the Higuchi-zawa, Hikoroichi-cho, Ofunato City, Iwate Prefecture. These specimens are identified with *Echinophacops schizoloma* Zhou, 1983 from the Upper Emsian Zhusileng Formation of western Inner Mongolia (Zhou, 1983). Based on this species, a new genus *Rhinophacops* is proposed and the specimens came from the Nakazato Formation are fully described herein.

The geologic age of the Nakazato Formation was collectively regarded as Middle Devonian (*e.g.* Kobayashi and Hamada, 1977; Minato *et al.*, 1979, Murata, 1972 and others). Copper *et al.*, (1982) studied brachiopods from the N₃ Member of the Nakazato and insisted that the brachiopods show a middle to late Eifelian. However, the present trilobite apparently indicates a late Ems-

ian age (Zhou, 1983; Zhan and Ruan, 1983) and this fossil evidence may suggest that the N₃ Member of the Nakazato is close to the Emsian — Eifelian boundary. Furthermore, the occurrence of the present characteristic trilobite species from Inner Mongolia and Kitakami, Northeast Japan shows close faunal similarity between both regions.

Acknowledgments: The present author is greatly indebted to the following persons; Drs. Takashi Hamada (University of Tokyo), Tadao Kamei (Shinshu University), Allen R. Ormiston (Amoco Production Co., U.S.A.), Ivo Chlupáč (Central Geological Survey, Prague, Czechoslovakia), Zhou Zhi-qiang (Xi'an Institute of Geology and Mineral Resources, China), Messrs. Teruo Ono, Hitoshi Koizumi (Kesen Chishitsu Kenkyusho) and Ken Kawanami (Onimaru Quarry).

Systematic paleontology

Family Phacopidae Hawle and Corda, 1847
Genus *Rhinophacops* Kaneko, gen. nov.

Derivation of genus name.— the Greek word *rhin* horn + typical genus *Phacops* Emrich, 1839.

Type-species.— *Echinophacops schizoloma*

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Zhou, 1983.

Generic diagnosis.— A phacopid with anterior opening left between dorsally arched cephalic and pygidial extremities and with short cephalic and pygidial marginal spines. Anterior cephalic doublure gently concave dorsally inside vincular furrow, which is interrupted behind between first pair of cephalic marginal spines. Most anterior pygidial marginal spine represented by broad (trans.) subrectangular lateral process; each of subsequent ones by spinule.

Discussion.— *Rhinophacops*, gen. nov. can be readily distinguished from all other members of the family Phacopidae by having an anterior opening during enrollment (paired photographs shown in Figures 2–1c, 3b; 10d, 14). *Rhinophacops* has a common ancestor with *Echinophacops* Zhou, 1983 based on *E. mirabilis* Zhou from the Zhushileng Formation. They share the following characters: (1) extremely depressed glabellae with wedge-shaped lateral profile, (2) completely reduced 2p lateral glabellar furrows, (3) relatively posteriorly situated 3p lateral glabellar furrows, (4) reduced (sag.) median part of 1p glabellar lobe which almost coalesces into the composite glabellar lobe, (5) small, low lateral nodes of 1p glabellar lobe, (6) unnotched lateral vincular furrows, (7) proportionally elongate (sag.), multisegmented pygidia with marginal spines developed as distal prolongations of the pleural ribs, (8) deep pleural furrows, (9) lack of the interpleural furrow, (10) cephalic and pygidial marginal spines which interlocked

with each other so as to provide an efficient fastening at the completion of enrollment, (11) a tendency of a gap to be left between the cephalon and pygidium.

Echinophacops differs from *Rhinophacops* in not produced anterior opening and much more developed inversely cephalic marginal spines as the anterior vincular furrow, which is completely reduced. The pygidial marginal spines in the former genus are more developed than those of the latter, and the anterior cephalic doublure is not concave with a pair of protuberances.

Distribution.— The Upper Emsian Zhushileng Formation of western Inner Mongolia and the N₃ Member of the Nakazato Formation of Northeast Japan.

Rhinophacops schizoloma (Zhou, 1983)

Figures 2-1-7

1983 *Echinophacops schizoloma* Zhou, p. 646-648, pl. 2, figs. 2-16, text-fig. 3.

Description.— Glabella subpentagonal in outline, wedge-shaped in lateral profile, with short spines on its anterior margin. Glabellar marginal spines directed outwardly and upwardly; the most anterior three (median unpaired and first pair counted from the front) much more prominent than the remainders, of which only second pair is usually somewhat more prominent than glabellar tubercles. 1p glabellar furrow transverse and deep at apodeme but turning forwards and fading away very rapidly medially. 2p lateral glabellar furrow completely reduced. 3p lightly incised, biparted; inner part situated at about posterior one third of glabellar length (sag.), nearly transverse to slightly convex forwards; outer part almost parallel to axial furrow, never reaching axial furrow. 1p glabellar lobe triparted; lateral node small, low, transverse; median part reduced to two tubercles, coalescing into composite glabellar lobe medially. Anterior and lat-

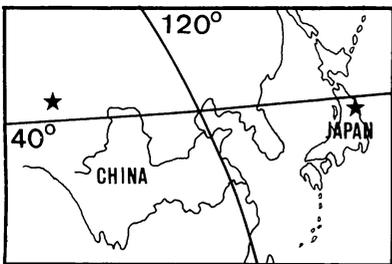
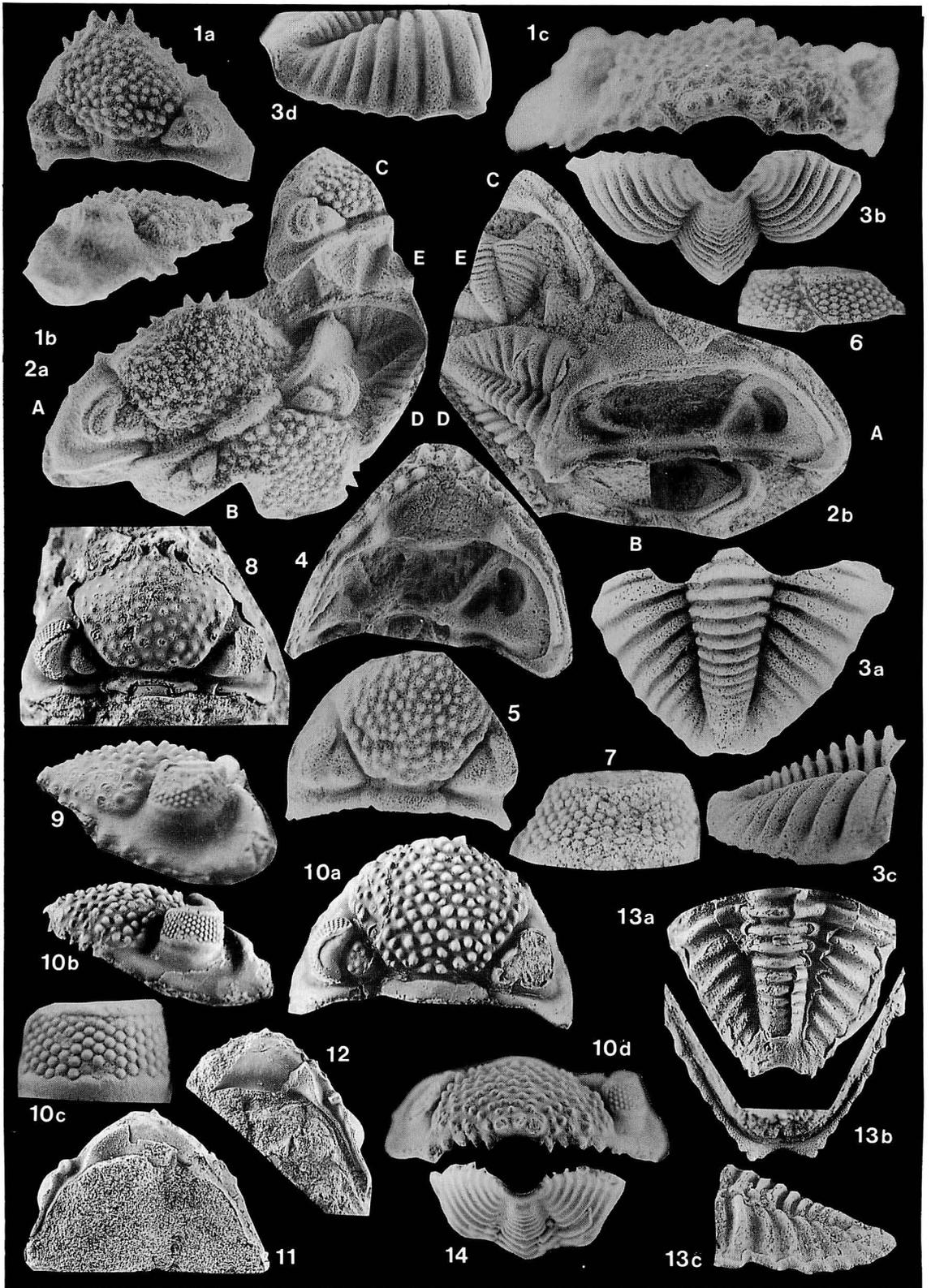


Figure 1. Localities of *Rhinophacops schizoloma* (Zhou, 1983).



eral cephalic margins bearing eight pairs of short cone-like spines, which are directed outwardly and ventrally; first to fourth pairs more prominent than sixth to seventh pairs but less prominent than fifth pair, opposite inwardly indented portion of inner edge of vincular furrow. Antero-medial portion of anterior border furrow developed as a weak transverse incision, which draws a boundary between ventral base of the most anterior and prominent trio of glabellar marginal spines and transverse, very slight swelling between first pair of cephalic marginal spines representing vestigial anterior border; the remainder portion short (exsag.), shallow and indistinct. Occipital ring highly arched transversely, about a half as wide (trans.) as glabella, rising steeply from occipital furrow and then becoming gentler posteriorly in sagittal section; lateral portion semi-isolated by broad (trans.) anterior incision and by narrower (trans.), more lateral posterior incision. Occipital furrow deep, U-shaped in sagittal section, long (sag. and exsag.) behind median part of 1p glabellar lobe but shortening (exsag.) at apodeme. Axial furrow very narrow (trans.) and shallowest at occipital ring, becoming broader (tran.) and more profound between occipital and 1p glabellar furrows; in front of 1p glabellar furrow, axial furrow diverging anteriorly at an angle 30 to 40 degrees from sagittal line, running straight, narrowing (trans.) rapidly and shall-

owing slightly, and then sloping down gently anteriorly, and U-shaped in cross section. Facial suture not distinguishable in front of eye; ϵ almost at posterior border furrow; lateral to ϵ , suture running slightly forward, curving gently backward on lateral border; ω at approximate level of ϵ . Palpebral lobe moderate in width (trans.), subreniform in outline, a little lower than glabella, widest at γ ; outer palpebral rim defined by very weak furrow which runs in parallel with palpebral margin. Palpebral area inflated as highly as palpebral lobe, flat-topped, delimited by palpebral furrow abaxially, with subvertical adaxial and posterior slopes. Palpebral furrow not so narrow (trans.), curving outwards and backwards and cutting up somewhat deeply from axial furrow, becoming slightly shallower as far as level of δ , after there running in parallel with axial furrow and cutting down deeply and steeply. Eye medium-sized; visual surface steeply inclined abaxially at 70 to 80 degrees, with 20 dorso-ventral files, each of which contains up to 6 lenses; lens distribution is shown in Table 1. Vertical concave area well extended beneath visual surface of eye to lateral border furrow, which is represented by very broad (exsag.), weak concavity of gena which is inclined steeply outwardly. Postocular area completely reduced. Lateral border represented by more or less narrow (trans.), slight convexity along lateral cephalic margin, which widens poster-

← **Figure 2.** *Rhinopacops schizoloma* (Zhou, 1983). **1–7**, Material from the Nakazato Formation (specimens figured are all represented by rubber cast). **1a–c**, Cephalon, JP10001; **a**, dorsal view, $\times 2.0$; **b**, right lateral view, $\times 2.65$; **c**, anterior view, $\times 3.8$. **2a**, Three cephalons (A, B and C) and one pygidium (D) contained in a slab together with a dechenelid pygidium (E); cephalon (A), JP10002, $\times 1.8$. **2b**, counter part of **2a**, $\times 1.8$. **3a–d**, Pygidium, JP10003, $\times 2$; **a**, dorsal view; **b**, posterior view; **c**, right lateral view; **d**, dorso-lateral view showing marginal spines. **4**, Cephalon, JP10004, $\times 2.0$; ventral view. **5**, Cephalon, JP10005, $\times 2.0$; dorsal view showing well preserved 1p glabellar lobe. **6, 7**, Right and left eyes, JP10006, PJ10007, $\times 5.0$. **8–14**, Material from Inner Mongolia. **8**, Cephalon, Tr-239 (Zhou, 1983, pl. 2, fig. 5), dorsal view, $\times 1.5$; **9**, cephalon, Tr-237 (*Ibid.*, pl. 2, fig. 3), left lateral view, $\times 4.0$; **10a–d**, cephalon, Tr-240 (*Ibid.*, pl. 2, figs. 7–8); **a**, dorsal view, $\times 2.0$; **b**, left lateral view, $\times 2.0$; **c**, enlargement of left eye shown in **b**, $\times 5.3$; **d**, anterior view, $\times 2.23$. **11**, Cephalon, Tr-242 (*Ibid.*, pl. 2, fig. 11), ventral view, $\times 2$. **12**, Cephalon, Tr-243 (*Ibid.*, pl. 2, fig. 12), ventral view, $\times 2$. **13a–c**, Pygidium, holotype, Tr-244 (*Ibid.*, pl. 2, figs. 13–15), $\times 2.0$; **a**, dorsal view; **b**, ventral view; **c**, left lateral view. **14**, Pygidium, Tr-245 (*Ibid.*, pl. 2, fig. 16), posterior view, $\times 2.43$. Two sets of photographs each showing an anterior opening (**1c** and **3b**; **10d** and **14**). (Photos, **1a–7**, **10d**, **14** by Kaneko; **8–10c**, **11–13c** by Zhou Zhi-qiang).

Table 1. Lens distribution of *Rhinophacops schizoloma* (Zhou, 1983).

	specimen	number of lenses per file (front to rear)							total	maximum number per file
Northeast Japan	Figure 1-6	345	566	555	*** 555	555	554	32	93	6
	Figure 1-7	355	565	** 555	*** 555	555	554	42	94	
Inner Mongolia	Figure 10b	355	565	655	555	545	544	42	93	6

* probable original number

iorly to meet posterior border. Posterior border furrow deep, U-shaped in sagittal section, moderate in length (exsag.) at axial furrow but progressively lengthening (exsag.) abaxially, and then gently curving forwards to meet lateral border furrow. Posterior border short (exsag.) and evenly rounded (exsag.) adaxially; outside fulcrum posterior border curving downwards and becoming progressively flattened and elongate (exsag.). Genal angle well-rounded, with a short spine. Anterior doublure about a half as long (sag.) as cephalon; inside inner edge of vincular furrow anterior doublure broadly depressed dorsally, with steep slope which is narrow (trans.) opposite first cephalic marginal spine but progressively increases in width posteriorly because depressed portion inside the slope inclined dorsally posteriorly; medial portion with weak, broad crescent-shaped concavity along hypostomal suture. Medial part of hypostomal suture slightly convex posteriorly in ventral view, weakly arched in posterior view. Vincular furrow interrupted behind between first pair of cephalic marginal spines, without lateral notches: inner edge somewhat sharp: inner wall of moderate height posterolaterally, but rapidly decreasing in height opposite between fifth and fourth cephalic marginal spines, reduced to weak ridge anterolaterally; inner wall moderately indented opposite at abaxial extremity of hypostomal suture. Hypostome unknown.

Thoracic axial ring with incision from rear, which does not separate lateral axial node. Number of thoracic segments unknown.

Pygidium elongate (sag.) triangular in general outline, moderately convex, with upward deflection of posterior extremity which is also embayed forwards in dorsal view and with marginal spines in prolongation of pleural ribs. Axis slender, highly arched, not constricted, comprising an articulating half-ring, eleven rings and a terminal piece; each ring with axial node on sagittal line; first ring furrow deepest and longest (sag.); subsequent furrows becoming progressively shallower and shorter (sag.) posteriorly. Pleural region with nine ribs each developing a marginal spine as its distal prolongation; the first one represented by a broad subrectangular lateral process; each of the rest by a spinule. Pleural furrow short (exsag.), V-shaped in exsagittal section, moderate in depth; second furrow deepest; subsequent ones becoming progressively shallower posteriorly; first two furrows fading away just before reaching margin; third to ninth furrows flexed backwards before reaching margin, and then continuing to troughs between marginal spines. Interpleural furrow absent. Doublure consisting of very narrow (trans.) outer band just inside marginal spines and much wider, very steep inner band except its most anterior portion on lateral process from the first pleural rib, where the outer band somewhat widens and curves strongly outwardly and then turns rapidly forwards and narrows; the inner band becomes gentler and slightly bulges inwardly at the posterior base of process and then becomes much more gentler at its posterolateral corner.

Glabella covered with coarse tubercles and rest of body apparently smooth.

Remarks.—The present Nakazato specimens are quite identical with Zhou's Inner Mongolian ones in the shape, length, number, position and direction of cephalic, glabellar and pygidial marginal spines, the structures of glabella and cephalic doublure, the outline, degree of deflection of posterior extremity and the number of pleural ribs of pygidium. The distribution of eye lenses, in which the intra-specific variations are usually recognized in the family Phacopidae, is also identical. Slight differences are only recognized in tubercles on the palpebral area and apparent persistence of the most anterior portion of the vinicular furrow in Zhou's specimens.

Occurrence.—Fine- to coarse-grained sandstone beds of the N₃ Member of the Nakazato Formation exposed along the river-side of a small tributary branching from the middle course of the Higuchi-zawa Valley, Hikoroichi-cho, Ofunato City, Iwate Prefecture.

Repository.—All specimens came from the Nakazato Formation are housed in the Institute of Geology and Mineralogy, Faculty of Science, Kyoto University with prefix JP.

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Higuchi-zawa 樋口沢, Hikoroichi 日頃市, Iwate 岩手, Nakazato 中里, Ofunato 大船渡, Zhusileng 珠斯楞。

三葉虫の新属 *Rhinophacops*: 内モンゴルの上部エムス統 Zhusileng Formation (珠斯楞組) から報告された *Echinophacops schizoloma* Zhou, 1983 を模式種として新属 *Rhinophacops* を提唱する。新属は完全に巻き込んだ際に、背方に窪んだ頭部の先端及び重複板と、背方に強くはね上がった尾板後端との間に開口部を形成する。この新属の模式種に同定できる標本が北上山地中里層 N₃ 部層から得られたので詳細に記載した。なお、中里層はこれまで全体として中部デボン系に相当すると考えられてきたが、少なくとも N₃ 部層の一部は下部デボン系最上部の上部エムス統に対比される可能性がでてきた。またこのような特徴的な種が内モンゴルと北上山地から産出することは、両地域の古生物地理区を考察するうえで重要である。

金子 篤

895. GIGANTIC AMMONITES FROM THE CRETACEOUS FUTABA GROUP OF FUKUSHIMA PREFECTURE*

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Abstract. Ten large or gigantic ammonite specimens were obtained by a number of persons from the Upper Cretaceous Futaba Group in the coastal area of Fukushima Prefecture (Northeast Japan). They are more or less incompletely preserved, but complementary with one another in showing characteristic features, which allow us to conclude that they are macroconchs of *Mesopuzosia yubarensis* (Jimbo). They can supplement in some respects the knowledge of this species, which has been recently described on the material from Hokkaido. They occur sporadically in a limited part (silty fine-grained sandstone and sandy mudstone) of the Coniacian Ashizawa Formation, *i.e.* the lower unit of the tripartite Futaba Group. For some reasons no microconch of this species has been found from the same part.

Key words. *Mesopuzosia yubarensis*, macroconch, microconch, Coniacian, Futaba Group.

Introduction

Since 1963 large or huge ammonites have been found from the Upper Cretaceous Futaba Group of Fukushima Prefecture. They numbered ten at the date (1982) when one of us (T.M.) had keen interests in gigantic ammonites. Some of them are so great that a group of persons organized by the Iwaki City Board of Education (IBE) worked for the excavation. Most of them were brought to a workshop for preparation and eventually registered at the Iwaki City Museum of Coal

and Fossils (IMNH) except for one at the Yotsukura Museum of History (YH). After preliminary investigations by several members of the Taira Geologic Society (Yanagisawa *et al.*, 1973; Hashimoto *et al.*, 1981), T. M. was invited by the Board of Education to cooperate with them to complete the palaeontological study. Among a number of persons concerned with these gigantic ammonites, M.N. and C.S. were selected by Ichiro Yanagisawa, the Chief of the Society, to accomplish this research work with T.M. M. N. is especially responsible for the field work to make clear the stratigraphic occurrence of the ammonites.

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Palaeontological description*Mesopuzosia yubarensis* (Jimbo)

Figures 1—8

Synonymy. — See Matsumoto, 1988, p. 68.

Material. — The following ten specimens, in the order of date of acquisition, indicated by the register number at the repository (abbreviated), proprietary (abbr.), finder, year of finding and brief remarks on the state of preservation:

(1) IMNHP402001, IBE, Teruo Sato (as student of Chiba University), 1963, fragmentary piece of middle-aged whorl (Figure 8); (2) IMNHP402002, IBE, Tamiye Yoshida (deceased; donated by Mrs. Yuriko Yoshida to IBE, 1965, secondarily deformed and eroded inner whorls with a piece of outer whorl; (3) YH. P1, YAH, anonym (donated by way of Tadashi Suzuki), 1967, very incomplete four whorls up to the last septum; (4) IMNHP 402003, IBE, Nagayuki Nemoto (as student of Iwaki High School), 1970, nearly entire shell but for several damaged portions of outer whorl (Figure 7); (5) IMNH-P402004, IBE, Kin'ichi Nabana, 1973, nearly entire shell embedded in rock matrix (Figures 1, 2); (6) IMNHP402005, IBE, Toyokazu Yoshida (as school boy), 1974, less deformed phragmocone, without body chamber (Figure 3); (7) No number, C. Suzuki's house, private for the present, Chisato Suzuki, 1979, entire phragmocone, somewhat deformed, with secondarily sharpened venter (Figure 4); (8) IMNHP402006, IBE, Kazuo Hashimoto, Takeo Matsumoto, Tokiji Nagata and Chisato Suzuki, 1980, nearly entire shell, but for so much eroded body chamber that even the overlapped part of the next inner whorl is exposed (Figure 6); (9) IMNHP402007, IBE, Yoshiki Koda, 1981, badly damaged, and secondarily compressed specimen, whose preserved fraction of outer whorl is still septate; (10) IMNHP 402008, IBE, Yoshiki Koda, 1981, secondarily

flattened, large but wholly septate specimen.

The repositories are Iwaki City Museum of Coal and Fossils (IMNH) (*Iwaki-shi Sekitan-Kaseki-Kan* in Japanese) and Yotsukura Museum of History (YH) (*Yotsukura Shigaku-Kan* in Japanese). The official proprietaries which correspond to the above two are Iwaki City Board of Education (IBE) and the Yotsukura Association of History (YAH), respectively.

The technical terms in this paper are currently used ones. Their abbreviated expressions are the same as those in the recently published monograph of the Puzosiidae (Matsumoto, 1988), being briefly explained at the bottom of Table 1. An arrow in a figure indicates the position of the last suture (LS).

Dimensions. — See Table 1.

Observations. — Although the ten specimens are more or less incomplete and secondarily compressed, they are complementary with one another to know the characters. Our observations of individual specimens are given below.

The 5th specimen (Figure 1), among others, is a less deformed, nearly entire shell, but for the lost last portion (about 20°) which should have shown an apertural margin. Its diameter is 790 mm at the preserved end (E in Figure 2) and estimated at 825 mm at the inferred peristome. The body chamber is 220° in spiral length and was originally 240°. It has more convex flanks and a more rounded umbilical shoulder and a moderately rounded (in stead of narrowly arched) venter, as compared with the septate whorls. The surface of the shell on the body chamber is nearly smooth and blunt radial elevations are disposed at each 30° (on an average) on the inner part of flank, fading away outward. The last two of them are broad, giving rise to partial inflation of the flank. In the earliest part of body chamber and the preceding late part of phragmocone (altogether 180°), narrower radial elevations are discernible on the inner flank at each 20° or so. Some of them are extended to the outer flank, showing for-

Table 1. Dimensions of measurable specimens.

Specimen	D	U	H	B	H/B	h	H/h	Inv.	Max.
(1) IMNHP402001, E	—	—	156	77	0.49	—	—	0.52	—
(2) IMNHP402002, LS	~ 540 (1)	207 (.38)	—	—	—	—	—	—	≥ 820
IMNHP402002, LS+30°	—	—	208	101	0.49	—	—	—	—
(3) YH. P1, last 4th	—	—	81	45	0.55	—	—	—	—
(4) IMNHP402003, E	605 (1)	229 (.38)	220 (.36)	~100 (.17)	0.45	156	1.41	0.48	≥ 800
(5) IMNHP402004, E	790 (1)	287 (.36)	295 (.37)	—	—	208	1.42	0.51	~ 825
IMNHP402004, LS+10°	~ 558 (1)	201 (.36)	198 (.35)	131 (.23)	0.66	~159	~1.25	—	—
(6) IMNHP402005, E	540 (1)	~198 (.37)	190 (.35)	~110 (.20)	0.58	~152	~1.25	~0.5	≥ 820
(7) IMNHP402006, E	615 (1)	225 (.37)	240 (.39)	~125 (.20)	0.52	162	1.48	~0.5	≥ 1200
(8) IMNHP402007, E	~1056 (1)	~392 (.37)	~392 (.37)	—	—	~272	1.44	0.55	~1200

D=diameter, U=width of umbilicus, H=whorl-height, B=whorl-breadth, h=whorl-height at a point 180° adapically from H, Inv.=degree of involution (overlapped part/whorl-height of the next inner whorl), Max.=estimated maximum diameter at the end of reconstructed body chamber, ~ = approximate or restored; Measured point: LS=last septum, LS+30°=30° adorally from LS, E=at or near the preserved end. Measurements are in mm.

ward projection and can be interpreted as persisting periodic flares. The inner whorls have, in addition to the periodic constrictions and flares, numerous ribs of unequal length, many of which reach the umbilical margin. About a half (0.51 in height) of the inner whorl is overlapped by the outer whorl. The ratio of whorl expansion is moderate ($H/h=1.42$) and the width of umbilicus is also moderate ($U/D=0.36$).

The 6th specimen (Figure 3), with $D=540$ mm at E, is less deformed but wholly septate, representing a late stage of a phragmocone. Its whorl-section at a late stage (Figure 5A) is suboval, with $B/H=0.58$ and more slender at earlier stages. It has a narrowly arched venter and gently convex, instead of plainly flat, flanks. The umbilicus is of moderate width ($U/D=0.37$), encircled by a subangular to abruptly subrounded shoulder. The inner whorl has numerous, fine ribs, which reach or nearly reach the umbilical margin, and constrictions with flares of moderate frequency. Numerous, projected, fine ribs persist on to the ventral part of an early half of the preserved outer whorl, fading away later, whereas blunt, radial elevations develop on the inner flank roughly at each 30° and tend

to broaden in the otherwise smooth late part. These radial elevations are so blunt that they may not be well shown in the photograph of Figure 3.

The 7th specimen (Figures 4A, B), with $D=615$ mm, is also wholly septate, exhibiting finely and deeply incised sutures on the outer whorl. Therefore, it looks very good in lateral view but actually it is distorted, showing a secondarily sharpened venter and deformed outline of whorl-section, which can be restored to a narrowly suboval shape (Figures 5B, C). Although the outer whorl looks smooth, it has blunt radial elevations at intervals (roughly at each 20°) on the inner flank. The radial elevations must have been more widely spaced (*e.g.* at each 30°) and broadened or inflated on the missing body chamber as in the case of the 5th specimen. On the ventral part, which is secondarily sharpened, numerous, projected riblets remain, as those of the early half of the outer whorl in the 6th specimen. Incidentally, several bivalves stick to the shell of outer whorl. Numerous, somewhat prorsiradiate, long ribs can be seen on the inner half of the inner whorls which are exposed in the umbilicus. They are distinctly impressed on the external mould which is



Figure 1. *Mesopuzosia yubarensis* (Jimbo), macroconch. Lateral view of the 5th specimen, IMNHP402004, from Ashizawa. Arrow : position of the last septum. Scale bar = 100 mm.

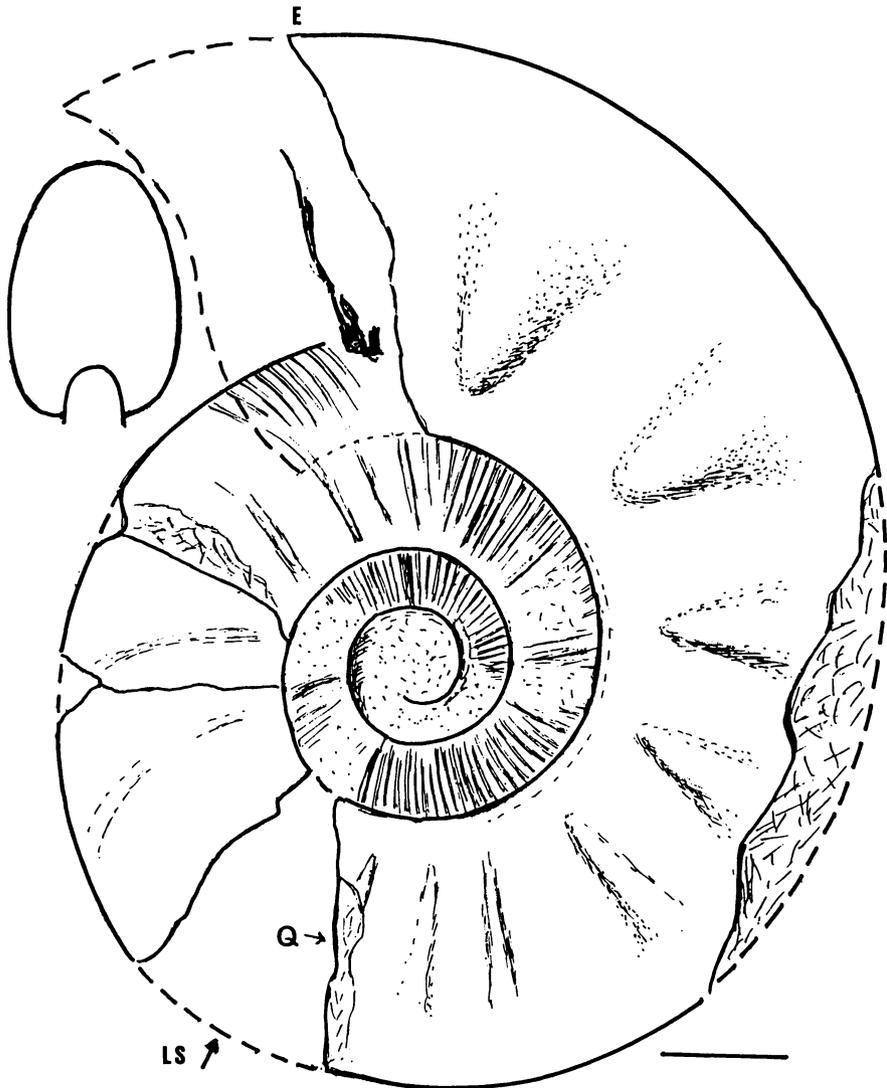


Figure 2. *Mesopuzosia yubarensis* (Jimbo), macroconch. Schematic drawing of IMNHP402004 to supplement Figure 1, with whorl-section (Q) at the beginning of the body chamber. Bar=100 mm.

preserved in the calcareous nodule of silty sandstone. This heavy nodule was carefully brought to the Museum by T. Suzuki. The ribs should curve forward on the outer half of the inner whorl, although that part is overlapped by the outer whorl in this specimen.

The last mentioned is evidenced by the 8th specimen (Figure 6), which exhibits clearly numerous, forward curved ribs on the outer half of the next inner whorl. The outer whorl of this specimen, which includes the

main part of the body chamber, is so much broken that the adequate cleaning has exposed the overlapped outer part of the next inner whorl. The shelly material is preserved on the originally overlapped part of the inner whorl. The diameter of this secondarily compressed specimen is 1050 mm at the preserved end and would be nearly 1200 mm at the inferred peristome.

The 4th specimen (Figure 7), with $D=605$ mm at about the middle of the body chamber

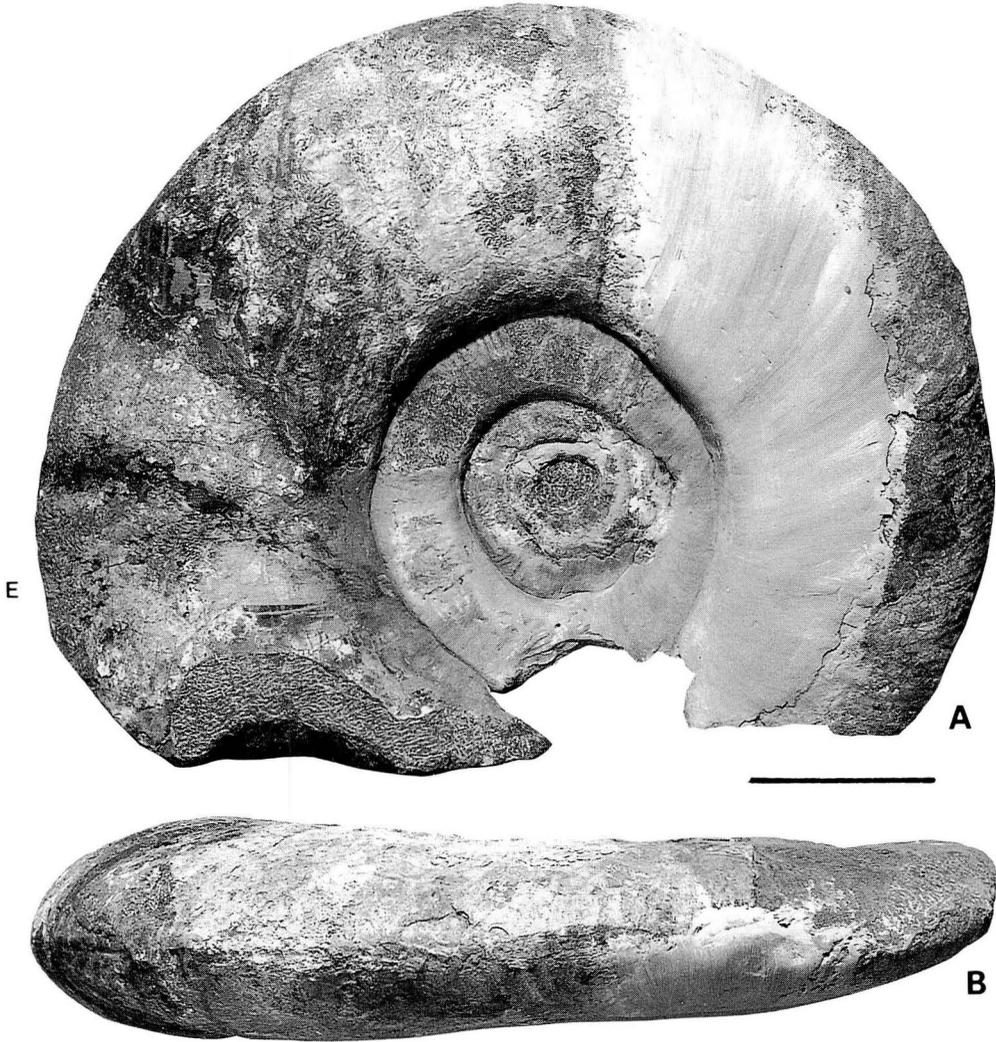


Figure 3. *Mesopuzosia yubarensis* (Jimbo), macroconch. Lateral (A) and ventral (B) views of the 6th specimen, IMNHP402005, from Ashizawa. Scale bar = 100 mm.

(E in Figure 7, 110° adorally from LS), is somewhat crushed and secondarily compressed. It shows, however, the mode of ribbing in the main part of the phragmocone and the change of ornamentation from the last part (about 90°) of the septate whorl to the body-chamber. At the point with $H = 150$ mm, *i.e.* 120° prior to the last septum, there is a narrow but distinct constriction with an accompanied narrow flare. It is somewhat prorsiradiate on the inner half of flank and curved considerably forward on the

outer half, showing a ventral projection. Up to the point with $H = 165$ mm, *i.e.* somewhat ahead of that constriction, there are numerous, crowded, fine ribs which run parallel to the constrictions and may be occasionally gently sigmoidal. They are mostly long, reaching the umbilical margin, but some are intercalary. The periodic constrictions with weak flares are discernible on inner whorls, as far as preservation is favourable. In the last part of the septate whorl the ribs become coarser and are separated by wider inter-



Figure 4. *Mesopuzosia yubarensis* (Jimbo), macroconch. Lateral (A) and ventral (B) views of C. Suzuki's specimen, found loose (but probably derived from the Ashizawa Formation) at Momokizawa. Venter is secondarily sharpened. Scale bar = 50 mm. Dots in A indicate the position of blunt radial bulges.

spaces. At the beginning of the body chamber thick but blunt radial elevations appear, with interspaces somewhat wider than the elevations. On the main part of the body chamber the radial elevations become broader and separated by much wider interspaces (roughly at each 30°), fading away outward. They may be still broader and give inflation as in the 5th specimen in the late part of the

body chamber, but this part is not preserved in the 4th specimen.

The 1st specimen (Figure 8) is a fragmentary piece of an inner whorl, with $H = 156$ mm and $B = 77$ mm. Its outer half is well preserved because it was overlapped by a large outer whorl, showing numerous, projected ribs where shell is preserved, and finely and deeply incised sutures (E and L) where shell is taken

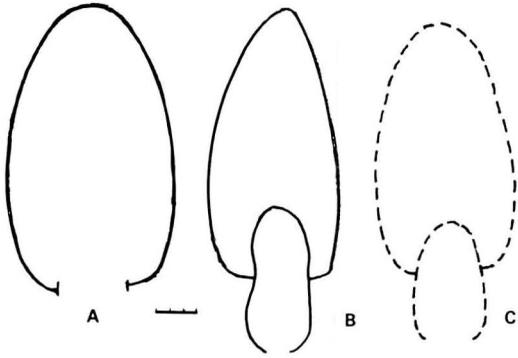


Figure 5. *Mesopuzosia yubarensis* (Jimbo), macroconch. Whorl-sections. **A**: IMNHP402005 at E in Figure 3. **B**: Chisato Suzuki's specimen at Q in Figure 4 (secondarily distorted). **C**: Ditto, restored. Scale bar = 30 mm.

off. Its inner half is much eroded, because of the unprotected condition. The sutural elements are so much eroded that their details are not preserved, but one can see the general configuration of nearly erect U2 and obliquely descending auxiliaries (*i.e.* U3=S). Furthermore, the internal suture is exposed on the dorsal part of this isolated specimen, showing deep I (antisiphonal lobe), erect U1 (by T.M.'s indication) and obliquely descending auxiliaries, *i.e.* suspensive U3=S by T.M.'s way of indication (see Matsumoto, 1954, figs. 2, 3). This specimen is higher than broad, with $B/H=0.49$ and slender or elongated suboval in whorl-section, having gently convex (instead of plainly flat) flanks and a narrowly arched venter.

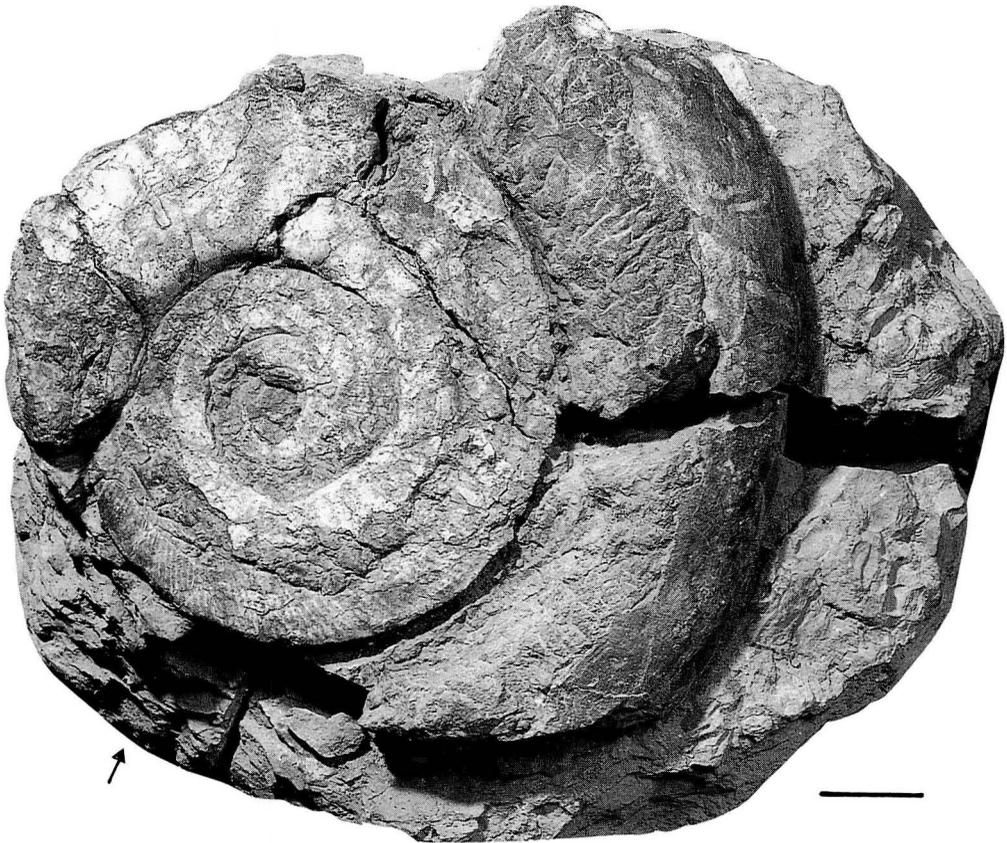


Figure 6. *Mesopuzosia yubarensis* (Jimbo), macroconch. Lateral view of the 8th specimen, IMNHP402006, from Ashizawa. The outer whorl is so much broken that the next inner whorl is wholly exposed. Scale bar = 100 mm.

The 2nd specimen is badly preserved, but the available piece of outer whorl consists of the last portion of phragmocone and the beginning of the body chamber, whose dimensions in somewhat secondarily deformed state are $H=208$ mm, $B=101$ mm, and $B/H=0.49$ and the whorl-section is generally similar to that of the first specimen in having gently convex flanks and a narrowly arched venter. This piece of whorl, roughly 65° in length, is an internal mould but has three weak radial elevations at each 20° on the inner half of flank. The slightly abraded suture is distinctly exposed on the right side showing large, asymmetrically tripartite L, but is much eroded on the left side. The diameter of a restored outline of the shell is roughly 540 mm at LS. This is nearly the same as that of

the 6th specimen.

The 3rd specimen consists of very incomplete pieces of overlapping 4 whorls, of which the outermost one has LS. It shows generally the change of characters mentioned above. The last third whorl is less deformed, whose outline in cross-section is a slender egg-shape, with $H=81$ mm, $B\sim 45$ mm, and $B/H=0.56$.

The 9th and 10th specimens are still septate at the preserved end but huge, about 600 mm and 660 mm, respectively. They are secondarily crushed and only the left side is preserved.

Diagnostic characters.— Summarizing the foregoing observations, the diagnostic characters may be written as follows:

The shell is gigantic, normally somewhat

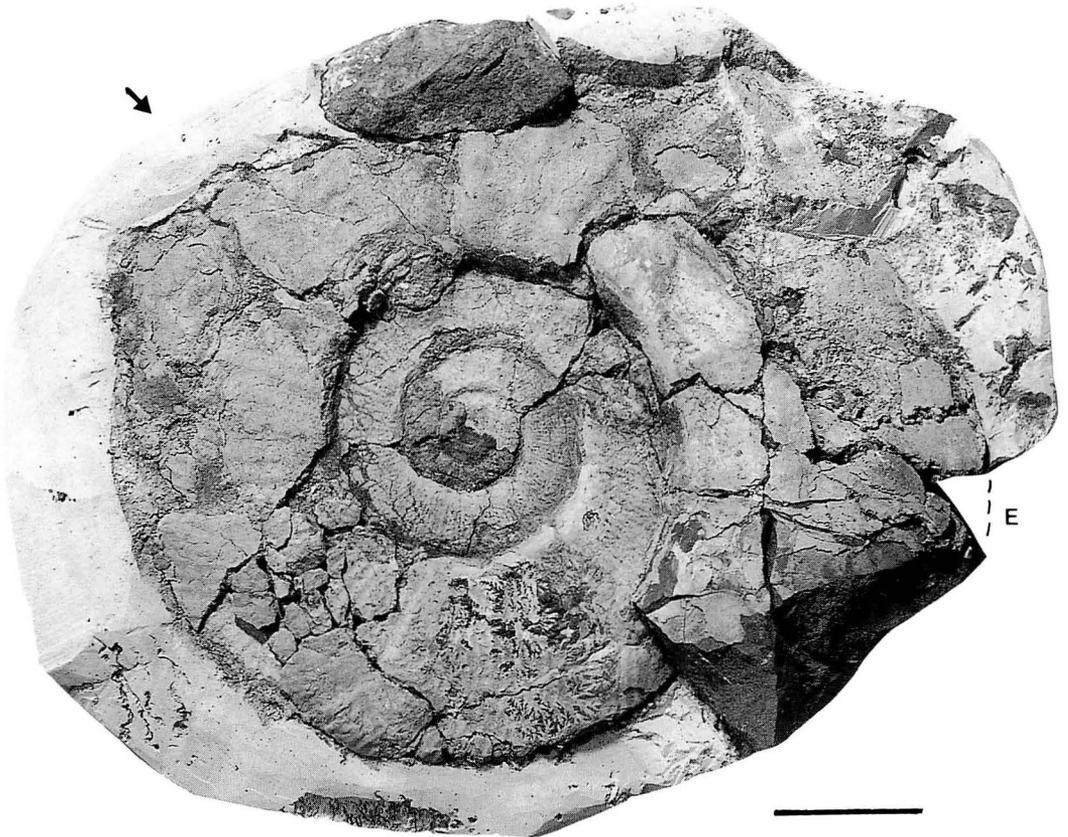


Figure 7. *Mesopuzosia yubarensis* (Jimbo), macroconch. Lateral view of the 4th specimen, IMNHP402003, from the north of Ohhisa. Scale bar = 100 mm.

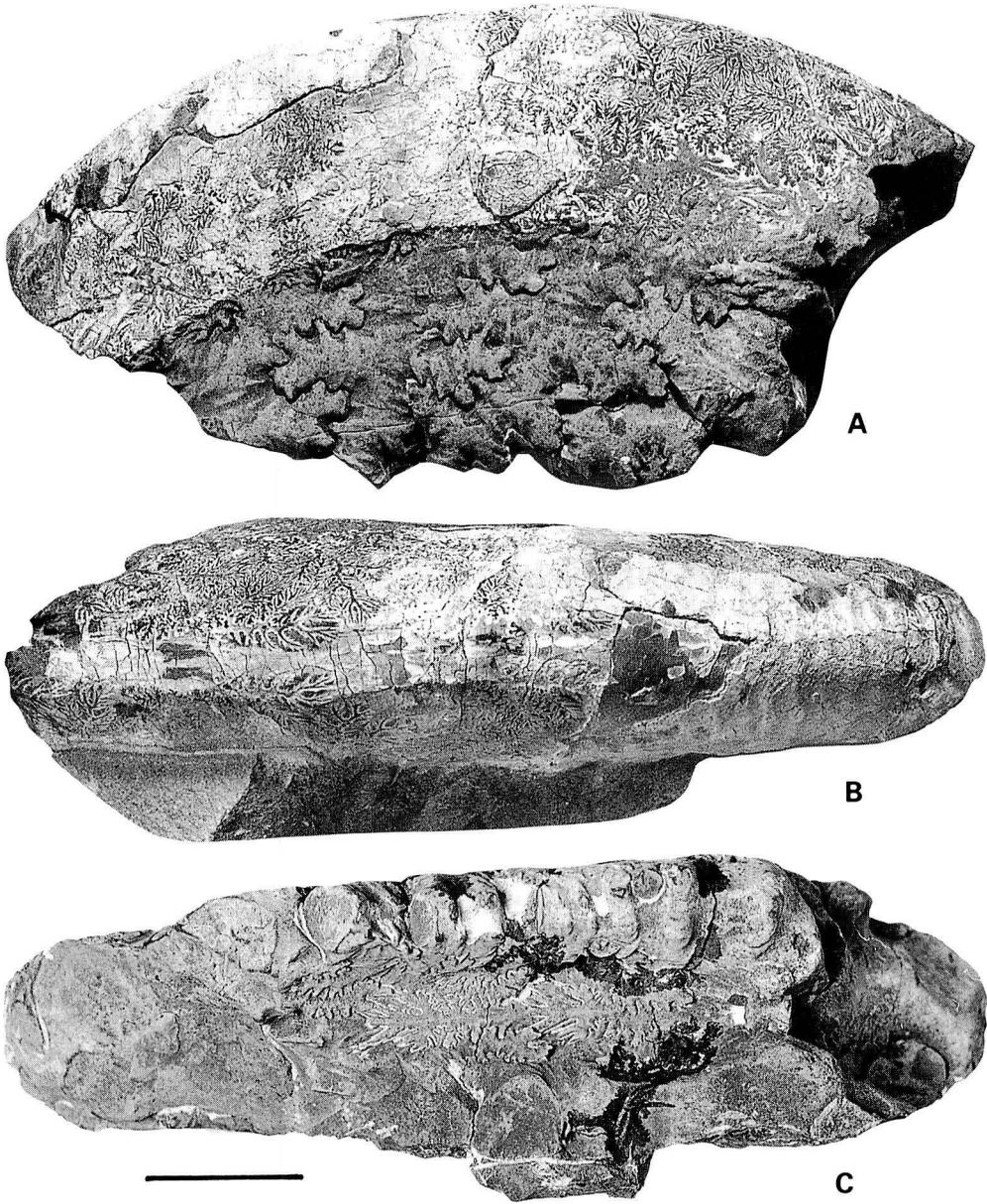


Figure 8. *Mesopuzosia yubarensis* (Jimbo). Lateral (A), ventral (B) and dorsal (C) views of the 1st specimen, IMNHP402001, fragmentary inner whorl of a large shell, from the north of Ohhisa. Scale bar = 50 mm.

over 820 mm at the end of the body chamber, attaining 1200 mm or more in larger examples. The body chamber occupies 240° in spiral angle, nearly smooth on the surface of shell but for blunt major radial elevations at wide intervals (at each 30° on an average),

which develop on the inner part of flank, broadening but fading away outward. The elevations on the late part are generally greater than those on the early part, giving rise to partial inflation of the body chamber.

The body chamber is generally oval in

section, showing a moderately rounded venter, fairly convex flanks and rounded shoulders on the umbilical margin. The outer whorl overlaps about a half (in H) of the next inner whorl and the rate of whorl expansion is moderate or rather low. Hence, the umbilicus is moderately wide.

The inner whorls are much higher than broad, with narrowly suboval cross-section, showing narrowly arched venter, gently convex (instead of plainly flat) flanks, abruptly subrounded umbilical shoulders and low but nearly vertical umbilical walls. They have periodic, weak constrictions, with associated narrow flares, and numerous, dense and fine ribs, which are mostly long, reaching the umbilical margin, with some intercalated shorter ones, subradial or slightly prorsiradiate or occasionally gently flexuous on the inner part of flank and curved forward on the outer part, showing marked ventral projection. The rate of whorl expansion is moderate, involution nearly a half and umbilicus of moderate width.

The last part of the phragmocone, that may form the outer whorl with the body chamber, shows a gradual change in the outline of whorl-section and ornamentation. The fine ribs remain as projected riblets on the ventral part and the periodic flares may persist to some extent, but soon these ornaments disappear and are replaced by blunt radial bulges on the inner part of flank, which are narrower and somewhat more frequent than those on the body chamber.

The sutures are of typical *Puzosia* pattern, showing the disposition of E, L, U2, U3=S, U1, I (by T.M.'s formula; see Matsumoto, 1954, figs. 2-4), large and asymmetrically tripartite L, and much intricate, fine and deep incisions of the elements.

Comparison and discussion.—The above described characters match very well those of macroconchs of *Mesopuzosia yubarensis* (Jimbo), which has been recently redefined on the material from Hokkaido (Matsumoto, Kawashita and Takahashi in Matsumoto

1988, p. 68-76). Examples of macroconchs which preserve the body chamber were not sufficiently numerous in the Hokkaido material. Now the gigantic specimens from the Futaba Group do supplement that weak point, in showing the characters of both the inner and outer whorls, although some of them are secondarily compressed.

The largest specimen from Hokkaido (ditto, fig. 27) is estimated at about 1300 mm in the diameter of the restored entire shell. This is nearly the same dimension as that of the maximum diameter in the restored outline of the 7th and 8th specimens from the Futaba Group (see Table 1). There is, however, some extent of variation in the size of macroconchs. The diameter of 825 mm or so seems to be more common in the Futaba

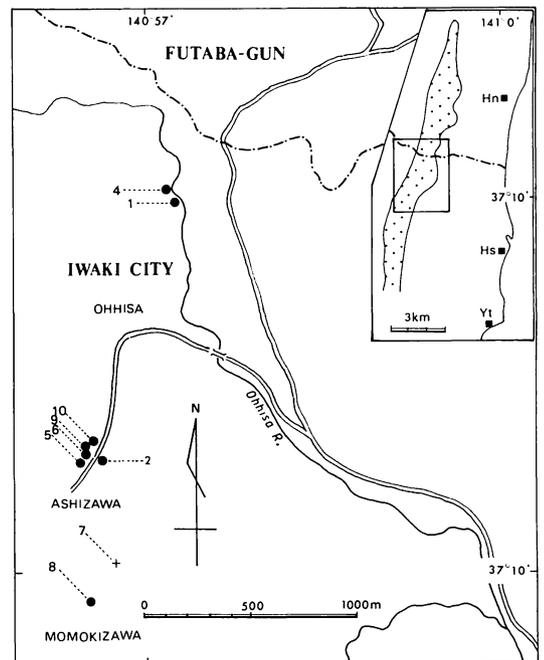


Figure 9. Map showing localities of the gigantic ammonites numbered in the order of acquisition; solid circle in situ; cross: loose. Inset at the upper right corner is the index map, in which outcropping area of the Cretaceous Futaba Group is dotted. Solid square: town — Hn: Hirono, Hs: Hisanohama, Yt: Yotsukura. Chain: administrative boundary of Futaba-gun (north) and Iwaki City (south).

material.

For some reasons, no microconch has been obtained from the macroconch bearing beds of the Futaba Group. A small puzosiid specimen was acquired by Kazuo Hashimoto from the rock close to the bed which contained the 9th and 10th specimens. It is not *M. yubarensis*, because it has coarser ribs which do not show strong ventral projection. It may be juvenile *Pachydesmoceras* cf. *mihoense* (Matsumoto).

Occurrence.—The localities of the described specimens, except for the 3rd without record, are shown in a map of Figure 9. They are north of Ohhisa (1, 4), around Ashizawa (2, 5, 6, 9, 10) and northeastern part of Momokizawa (7 and 8, of which 7 is loose), all in the northern part of Iwaki City by the recent administrative division. In addition to the natural outcrops along the River Ohhisa [sometimes called Ohbisa (*e.g.* the 1st and the 4th specimens), the recent public works to construct a new road and some other private engineering works have brought new exposures of the Cretaceous strata, from which the described gigantic ammonites were found. Stratigraphically these ammonites can be allocated roughly at two levels in the middle member of the Ashizawa Formation, which itself forms the lower unit of the tripartite Futaba Group (Saito, 1960, 1961) or Futaba Beds in the original work of Tokunaga and Shimizu (1926). A bed of orange coloured, probably tuffaceous, coarse- to medium-grained sandstone in the upper part of the Ashizawa Formation is a key to correlate the strata of separated outcrops. The described gigantic ammonites occur in the muddy fine-grained sandstone or sandy siltstone below this key bed. Bioturbation is observable here and there, whereas fine lamination is distinct in other parts. Calcareous nodules are contained at various levels and some of the gigantic ammonites (*e.g.* the 5th, 6th and 7th specimens) are in them, whereas others are embedded directly in the country rock and

compressed secondarily.

Inoceramus uwajimensis Yehara occurs fairly abundantly at various levels in the Ashizawa Formation. Several specimens of *I. uwajimensis* and *I. mihoensis* Matsumoto were obtained and brought to the Museum from the outcrop where the 9th and the 10th gigantic ammonites were excavated. The rock of this outcrop is referred to the higher one of the two levels. A deformed nautiloid specimen of *Cymatoceras* sp. was associated with the 2nd specimen, which is nearly the same level as the 5th and the 6th specimens of the giants. This level is the lower one of the two levels mentioned above. At this level a single, somewhat secondarily deformed specimen of *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine et Thévenin) (Figure 10) was once obtained by Mitsuo Kitago and is now held in the Hirono-Machi Board of Education. This ammonite species and the association of *I. uwajimensis* with *I. mihoensis* suggest the Middle Coniacian age of the middle part of the Ashizawa Formation.

Further remarks

Macroconchs of ammonoids are currently regarded as adult female shells (Lehmann, 1981). In many species of the Puzosiinae the body chamber of a gigantic macroconch is generally broader than its phragmocone as well as its corresponding microconch (Matsumoto, 1988). This is well exemplified by *M. yubarensis*. Furthermore, the body chamber of an adult macroconch of this species has blunt radial elevations at wide intervals (*e.g.* at each 30° on an average) on its otherwise smooth shell-surface, and some of them in the middle to late part of the body chamber are broader or greater than others, giving rise to partial inflation of the flanks. Similar features seem to occur generally in other species of *Mesopuzosia* and *Puzosia*, as one of us (Matsumoto, 1988) has recently shown. Incidentally, *Matsumotoceras donlisteri* van Hoepen, 1968 (p. 157, pl. 1, fig. 1; text-fig.

1a), from South Africa, may be also such an example. Anyhow, the general broadening of the body chamber in a large macroconch may imply an enlargement of the body which must be related to the remarkable growth of the genital and other organs so that the adult female may have exhibited especially vigorous activity in life. The periodic inflations of the body chamber described above suggest the extra capacity afforded to the mantle. One can presume, as a working hypothesis, that adult females of these kinds of ammonite species may have been periodically active in forming and then laying egg-capsules. To find fossil egg-capsules of appropriate size would be required to verify this speculative interpretation.

We agree with Saito (1960, p. 112, fig. 2) in admitting the lateral changes in the sedimentary facies and thickness of the Ashizawa Formation. In the vicinity of Ashizawa, muddy sediments prevail rather than gravels and coarse-grained sands, representing probably the central part of the basin. Such an environment may have been favourable in shallowness and quietude for the adult females of *M. yubarensis* to lay egg-capsules on some suitable substances at the bottom. Should this assumption be warranted, the males of the same species would scarcely come in there. The mating place must have been somewhere else.

Acknowledgements

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Material. Thanks are extended to Professor Ichiro Yanagisawa, Chief of the Taira Geologic Society, for his instructive support to our investigation. The Iwaki Educational and Cultural Corporation took necessary procedures in the excavation, transportation and trimming of the fossil specimens. Mr. Tadashi Suzuki, among others, helped us in the laboratory works as a staff of the Corporation. Photographs of the gigantic ammonites were taken by Mr. Tomoyuki Matsumoto with the aid of Messrs. Tadashi Suzuki, Yoshiki Koda and Keiichi Suzuki; those of *Forresteria* by Dr. Masayuki Noda. Mr. Toshimitsu Watanabe and Dr. Seiichi Toshimitsu kindly helped us in our stratigraphic field work. Miss Akiko Murakami assisted us in preparing the typescript, which was improved with kind suggestions from Dr. Ikuwo Obata and anonymous referees.

Appendix: An ammonite referable to *Forresteria* from the Futaba Group

T. Matsumoto and M. Nemoto

This is a concise systematic description of an ammonite belonging to the genus *Forresteria* mentioned in the main text of this paper.

Family Collignoniceratidae Wright
et Wright, 1951

Subfamily Barroisiceratinae Basse, 1947

Genus *Forresteria* Reeside, 1932

Type species.—*Barroisicerat* (*Forresteria*) *forresteri* Reeside, 1932 (p. 14, original designation) [= *Forresteria alluaudi*; (Boule, Lemoine et Thévenin, 1907)] (see Matsumoto, 1969, p. 306).

Remarks.—In the original definition, Reeside (1932, p. 14) proposed the subgenus *Forresteria* for what he wrote in the same page the group of *Barroisicerat forresteri* and four species were assigned to this subgeneric group. *B. (F.) forresteri* was one of them, being indicated at their top. In other words,

the author (*i.e.* Reeside, 1932) of the new subgeneric name (*i.e.* *Forresteria*) employed this same name (*i.e.* *forresteri*) for one of the included species. That is tautonymy and accordingly the type species can be recognized as an original designation. In the *Treatise* (Wright in Moore, *ed.*, 1957, p. L432) *Forresteria* was ranked up to the genus and *Barroisicerias* (*Forresteria*) *forresteri* Reeside was written as its type species. This is not the subsequent designation (as misprinted in Kennedy *et al.*, 1983, p. 251) and was quite correct on account of the tautonymy (see p. xvi in Editorial Preface of the *Treatise*). At that date Wright (*op. cit.* p. L432, fig. 551.2) did not mention that *F.* (*F.*) *forresteri* is a junior synonym of *F.* (*F.*) *alluaudi* (Boule, Lemoine et Thévenin, 1907). This synonymy was at first pointed out by Matsumoto (1969, p. 311–312) with necessary reasoning and has been confirmed recently by Kennedy *et al.* (1983) on sufficient material of South Africa. They also commented amply the subgeneric taxonomy.

Subgenus *Forresteria* (*Forresteria*)

Reeside, 1932

Forresteria (*Forresteria*) *alluaudi*

(Boule, Lemoine et Thévenin)

Figure 10

1907. *Acanthoceras* (*Prionotropis*) *alluaudi* Boule, Lemoine et Thévenin, p. 12, pl. 1, figs. 6–7, text-fig. 17.

1908–1979. omitted for brevity.

1983. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine et Thévenin); Kennedy *et al.*, p. 267

(with full synonymy list).

1984. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine et Thévenin); Kennedy, p. 46, pl. 8, figs. 4–9.

Material.—HBE-P1, obtained by Mitsuo Kitago from Ashizawa, close to and nearly at the same level as the place where the 5th and 6th huge macroconchs of *Mesopuzosia yubarensis* were contained. It was embedded in the country rock (not in a calcareous nodule) of greenish grey, medium-grained sandstone, but the shelly material is mostly resolved and remains only partially.

Dimensions.—See Table 2. As the specimen is secondarily distorted at the preserved last part of the outer whorl, it is measured on a restored outline.

Description.—Although the specimen is small, one third (120°) of its outer whorl is the body chamber. The less deformed septate part is higher than broad, showing B/H = 0.69. The whorl is moderately involute, about two thirds of the inner whorl is overlapped by the outer one and the umbilicus is narrow, less than 20% of the diameter.

Despite the compressed shell-form, the ribs are moderately coarse and provided with distinct tubercles which strengthen as the shell grows. The clavate tubercles of the outer three rows (on the siphonal line and at the ventrolateral shoulders) are twice as numerous as those of the inner rows (bullate, smaller ones at the umbilical shoulders and nodose or spinose ones at the middle of flanks). The suture is moderately incised, showing roughly subrectangular outlines of

Table 2. Measurements of *F.* (*Forresteria*) *alluaudi* on selected specimens.

Specimen	Position	D	U	H	B	B/H	H/h	UT	VT
HBE-P1	E	~56.0	9.2 (.16)	29.0 (.52)	~21 (.38)	0.72	1.63	11	20
HBE-P1	LS	43.0	7.0 (.16)	22.5 (.52)	15.6 (.36)	0.69	1.67	—	—
SAS Z591*	E	45.4	10.6 (.23)	21.0 (.48)	21.6 (.48)	1.0	1.52	13	?23
GK. H2622**	E	42.0	9.2 (.22)	20.4 (.48)	25.0 (.59)	1.22	1.65	11	21

* Kennedy *et al.*, 1983, fig. 12 C-D; ** Matsumoto, 1969, pl. 40, fig. 1. UT, VT: number of umbilical and ventral tubercles, respectively in outer whorl.

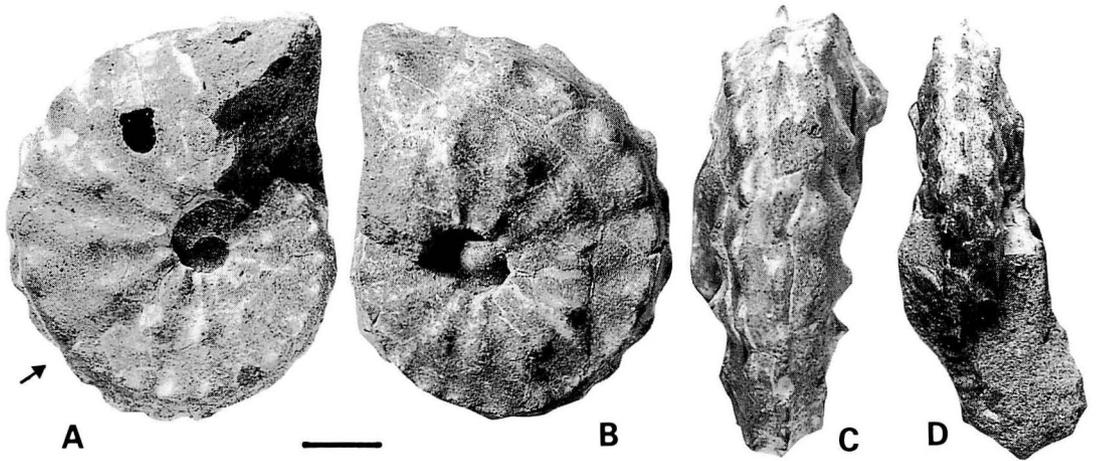


Figure 10. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine et Thévenin). Specimen HBE-P1, from the middle part of the Ashizawa Formation. Two lateral (A, B), back (C) and frontal (up side down) (D) views, $\times 1$. Scale bar = 10 mm.

E, L, U2 and saddles between them.

Comparison and discussion.—Based on a very large collection (over 100 specimens) from a particular zone (Coniacian II) of South Africa, Kennedy *et al.* (1983) have recognized a great variability of *F.* (*F.*) *alluaudi* and placed in synonymy numerous previously described species from South Africa, Madagascar, North America and Japan. They did not, however, state clearly the distinction between the dimorphic pair. Only one example, SAS Z923 (ditto, fig. 28) is explained as “adult? microconch with body chamber”. Any macroconch with completely preserved body chamber does not seem to have been illustrated. They did not indicate the position of the last septum in their numerous figures, except for a few internal moulds with clearly exposed sutures. The early part of our specimen up to D = 30 mm is similar to SAS Z2195 (ditto, fig. 11 A–B) from South Africa, whose B/H = 0.72. In our specimen B/H = 0.6 at the corresponding size (*i.e.* H = 15 mm) and 0.72 at D = 56 mm. In the compressed, involute and narrowly umbilicate shell-form, our specimen may be comparable with what Kennedy *et al.* (1983, figs. 7A–C, D–F) illustrated as “slender variants” of *F.*

(*F.*) *alluaudi*, but quite dissimilar in ornaments. That slender form is feebly and finely ornamented with numerous ventral clavi, whereas our form has as coarse ribs and as strong tubercles as those of normal or typical middle aged shells of *F.* (*F.*) *alluaudi*. For example, as to the ornamentation, our specimen resembles quite well such an example of *F.* (*F.*) *alluaudi* as SAS Z591 (ditto, fig. 12C–D) from South Africa. In addition to the six specimens described by Matsumoto (1969, p. 308, pl. 40, figs. 1–4; text-figs. 5–7) from the Ikushumbets area of Hokkaido, there are now more specimens from the Haboro and other areas of Hokkaido. This is not the place to describe them but they are all what we call normal forms, with some (but not extreme) extent of variation. To sum up, the specimen from the middle part of the Ashizawa Formation of the Futaba Group is identified with *F.* (*F.*) *alluaudi* and probably of middle growth-stage. This species shows a world-wide distribution and occurs in the Middle Coniacian, where accurately dated (Kennedy, 1984, p. 46). That statement conforms with the biostratigraphy of the Futaba Group.

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Ashizawa 芦沢 (地名), 足沢 (層名), Fukuoka 福岡, Fukushima 福島, Haboro 羽幌, Futaba 双葉, Hirono 広野, Hisanohama 久之浜, Hokkaido 北海道, Ikushumbetsu (Ikushunbetsu) 幾春別, Iwaki いわき, Momokizawa 桃木沢, Nishi 西, Ohhisa (sometimes called Oohisa or Ohbisa) 大久, Sakurada 桜田, Shimo-Asamigawa 下浅見川, Taira 平, Yotsukura 四倉

福島県の白亜系双葉層群産巨大アンモナイト；標記は1963年以来10点に達し、その産出の報告もあり、大部分いわき市石炭化石館に展示・保管されているが、学名が未決定であった。保存状態に良否があるが、相互に類似・共通点があり、同一種とみなされる。観察事項を相補的に総括すると特性がわかる。中年までは螺環が狭長だが両側は緩い凸面で、多数の長肋と挿入肋は外側で顕著な前方屈曲を示す。その他の形質も併せ、北海道によく産する *Mesopuzosia yubarensis* (Jimbo) の特性と合う。気房最終部と住房 (約 240°) から成る外の螺環は漸次丸みを帯び横断面は卵形、多数の肋が弱化消失するかわりに鈍い放射状隆起が広い間隔で側面内半に生じ、住房後半では太くなり緩い膨らみを呈する。殻口縁で直径が 82 cm 余り、時には 120 cm を起える。これと同様のものは北海道からも最近報告された。双葉のは生長過程の変化がよくわかる。上記種の二型のマクロコンク (M 殻) と結論される。産地は図示の通り狭い地区内で、層序的には双葉層群下部の足沢層中部に当たる泥質細粒砂岩～砂質泥岩の限られた部分 (厚さ 20 m 中の 2 層準) で、伴う化石種はコアンサン階中砂部を示す。M 殻だけの限定産出の理由について論述した。

松本達郎・根本守・鈴木千里

付録として随伴種 *Forresteria (Forresteria) alluaudi* (Boule, Lemoine et Thévenin) を記載した。

松本達郎・根本守

896. EVOLUTION OF SOME LATE CRETACEOUS DESMOCERATINE AMMONOIDS*

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Abstract. The Cretaceous sediments of Hokkaido accumulated in an island arc setting that was part of a plate convergence margin in the Northwest Pacific. Many differences have been recognized between such sediments and those of epicontinental seas, and there are also faunal differences. A land with a coastline extending to north and south laid to the west of the forearc basin in which lateral changes of lithofacies and biofacies occurred. The desmoceratine taxa *Desmoceras* (*Pseudouhligella*) *ezoanum*, *Desmoceras* (*Pseudouhligella*) *japonicum*, *Tragodesmocerooides subcostatus* and *Tragodesmocerooides matsumotoi*, n. sp. to be described below flourished in this forearc basin sea during Cenomanian and Turonian times. A phylogenetic progression from *D. (P.) japonicum* through *T. subcostatus* to *T. matsumotoi* is proposed, based upon investigations of relative growth, sutural ontogeny, shell ornamentation, stratigraphical ranges and geographical distribution. In this lineage the eastern limit of the habitat moved towards the west with decreasing adult size at each speciation event. The ontogeny of sutural complexity, however, gradually accelerated with time. The details of the evolution of this lineage and *T. matsumotoi* are described and discussed together with the relationship to such events as a marine transgression/regression, oceanic anoxic events and speciation/extinction.

Key words. Late Cretaceous, ammonoids, *Desmoceras*, *Tragodesmocerooides*, evolution, speciation.

Introduction

The Yezo Supergroup (Okada, 1982, 1983) ranging in age from Albian to Maastrichtian is longitudinally distributed from north to

south in central Hokkaido. Sediments of the supergroup have been interpreted by Okada (1983) as forearc basin deposits. A coastline can be distinguished, extending north and south, at the western margin of the forearc basin, and the sea deepened towards the trench in the east through the structural high.

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Sedimentological aspects of this basin, viz: Storm deposits in the west, lateral currents extending from west to east, and north-south axial currents have been well investigated (Ando, 1987; Tanaka, 1963; Tanaka and Sumi, 1981), together with the lateral change of molluscan faunas from the shallower western faunas to the offshore eastern faunas (e.g., Obata and Futakami, 1977; Tanabe, 1979; Futakami, 1986a, b). The sediments are represented by coastal conglomerate, storm-generated sandstone, flysch and offshore mudstone, the ages of which have been determined by ammonoids, inoceramids, foraminifers, radiolarians, nanno-fossils, isotope dating and magnetostratigraphy (e.g., Takayanagi and Matsumoto, 1981).

About two hundred ammonoid species have been described from the Yezo Super-group. The longevity of these species varies from less than two million years to more than ten million years (Hirano, 1984). Among them, most desmoceratine species have a range of one stage, which can be interpreted to mean intermediate longevity. The desmoceratine ammonoids occur fairly abundantly in Cenomanian to Santonian strata but their specific diversity is low. Although the various taxa have been described, used as zonal indices, and preliminarily investigated from the viewpoint of phylogeny at a specific level, nonetheless a detailed case study of their evolution has not yet been published.

Recently, the timing of eustatic transgressions and regressions has been revised (Matsumoto, 1977, 1978; Reymont and Mörner, 1977; Hancock and Kauffman, 1979; Reymont and Bengtson, 1986) and the importance of oceanic anoxic events has been recognized (e.g., William, 1988). The relation between these oceanic events and the evolution of ammonoids is, however, still uncertain. In general, in considering the evolutionary history of the ammonoids, it is believed that ammonoid groups inhabiting offshore waters were able to survive crises and were able to immigrate later into shallower waters where

ecological niches had opened, because the former inhabitants of the shallower waters had died in the crisis (e.g., Wiedmann, 1973). However, this supposition is not always proved by case studies.

The morphological evolution of *D. (P.) ezoanum* and *D. (P.) japonicum* of Cenomanian age and *T. subcostatus* and *T. matsumotoi*, n. sp. of Turonian age is investigated in the current work mainly on the basis of relative growth analyses of population samples, and the relationship between evolution and oceanic events is discussed.

Materials and methods

Materials

Desmoceratine ammonoids studied in this paper were obtained from the Middle and Upper Yezo Group in the Oyubari area, Yubari City and the Obira area, Rumoi County, Hokkaido (Figure 1). Detailed route maps including the locality guide, geological maps, zonation maps and columnar sections of the former have been published by

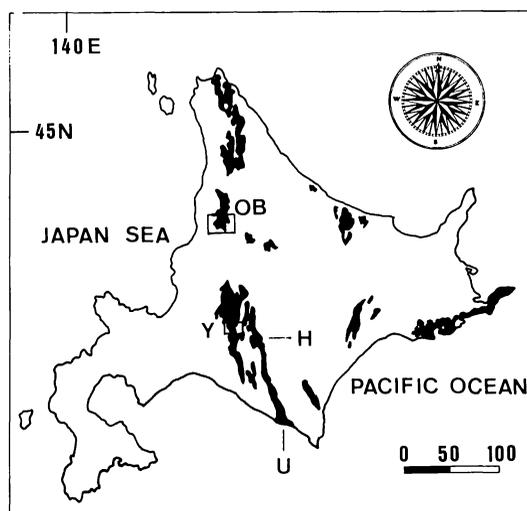


Figure 1. Map showing the areas studied and the distribution of the Cretaceous rocks (black areas) in Hokkaido island. The Obira (OB) and Oyubari (Y) areas of the western Cretaceous belt and the Hidaka (H) and Urakawa (U) areas of the eastern Cretaceous belt are indicated. Scale: km.

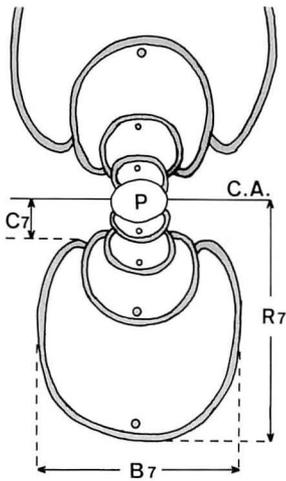


Figure 2. Cross section of an ammonite showing the measured portions. C.A.: Coiling axis, P: Protoconch, B: Whorl-breadth, B7: B at the growth stage of the 3.5 whorls (volution angle: $180^\circ \times 7$), R: Radius-length, R7: R at the same growth stage as above, C: Umbilical radius length, C7: C at the same growth stage as above.

Hirano *et al.* (1977, 1980, 1981, 1989) and Hirano (1982, 1986). A revised locality guide and columnar sections of the Middle and Upper Yezo Group of the latter are given in another paper (Sekine *et al.*, 1985) in addition to geological and zonal maps by Tsuchida *et al.* (1958) and Tanabe *et al.* (1977). Comprehensive biostratigraphical guides for these two areas are now under preparation, and are omitted here for brevity.

Methods

The concepts and methods of relative growth and biostatistics used in this account are the same as those described by Hayami (1969), Hayami and Matsukuma (1971) and Hirano (1975, 1978).

At the beginning of the study, each ammonoid shell was cut and polished to provide a cross section along or across the median plane. Then various portions were measured with a Nikon Profile Projector C-16 (Figure 2; Hirano, 1975, p. 168, fig. 2, Hirano, 1988, p. 516, fig. 3). A regression formula, $\log y = \alpha\theta + \log C$ (where y : radius length, etc., α :

growth ratio, θ : spiral angle of the whorl, C : y -intercept) was obtained from the semilogarithmic plots, and the growth ratio, α in the middle growth stage onward was used to show the characteristics of each population sample, which is defined to be composed of specimens within one and the same calcareous concretion. The whole morphology including surface ornamentation was also observed in advance of and/or in parallel with the biometrical procedure. Sutural ontogeny and variation were studied with a Nikon binocular microscope fitted with drawing equipment. In districts with minimal tectonic disruption, samples are stratigraphically arranged in columnar sections. For dating purposes, statistics of population samples are allocated to *Inoceramus* zones.

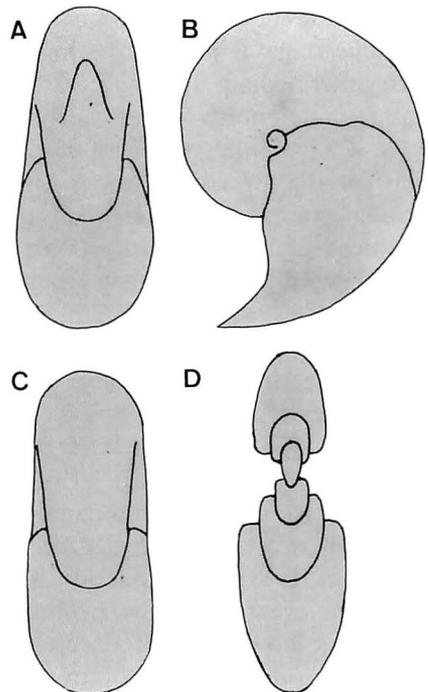


Figure 3. Shell forms of three desmocerate ammonites. A, B: *Tragodesmocerooides subcostatus*, C: *Desmoceras (Pseudouhligella) japonicum*, D: *D. (P.) ezoanum*.

Phylogeny of *Desmoceras (Pseudouhligella) japonicum*

Six species of the genus *Desmoceras* have been recorded from Japan: *D. latidorsatum* (Michelin, 1838); *D. kossmati* Matsumoto, 1942; *D. japonicum* Yabe, 1904; *D. ezoanum* Matsumoto, 1942; *D. poronaicum* Yabe, 1904; *D. dawsoni* Whiteaves, 1900.

Among these *D. japonicum*, *D. ezoanum*,

D. poronaicum and *D. dawsoni* belong to the subgenus *Pseudouhligella* proposed by Matsumoto (1938). The characteristics of the subgenus are that the whorl is compressed, gradumbilicate in the adult stage and that the venter is ornamented with weak subcostae.

D. (P.) japonicum and *D. (P.) ezoanum* are the indices for the Japanese Cenomanian stage, and as they have the same stratigraphical and geographical ranges they are

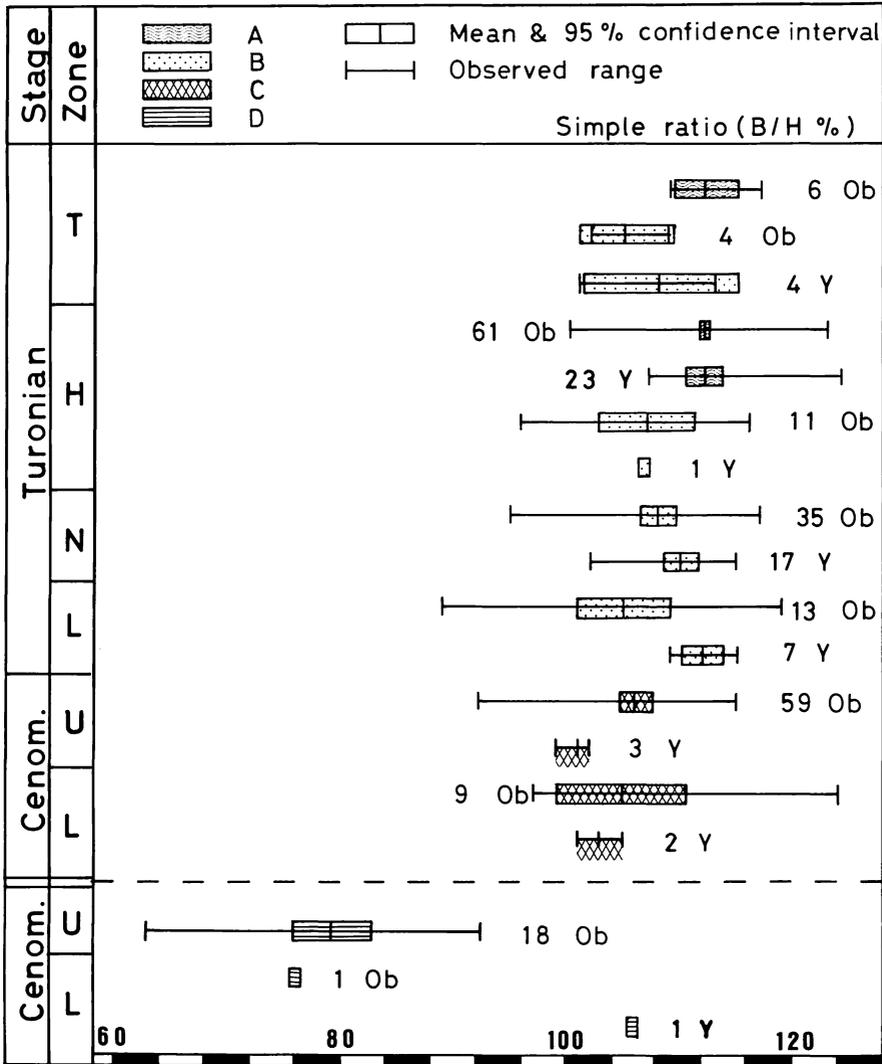


Figure 4. Chronological change of the simple ratio of the whorl-breadth to the whorl-height at the third and a half whorl (volution angle: $180^\circ \times 7$). A: *Tragodesmocerooides matsumotoi*, n. sp., B: *Tragodesmocerooides subcostatus*, C: *Desmoceras (Pseudouhligella) japonicum*, D: *D. (P.) ezoanum*, Y: Oyubari sample, Ob: Obira sample. Each number indicates the number of treated specimens.

thought to be sympatric species. *D. (P.) dawsoni* is recorded from the Albian, and *D. (P.) poronaicum* from the Cenomanian in some limited localities outside of the areas studied.

Relationship between D. (P.) japonicum and D. (P.) ezoanum

D. (P.) japonicum and *D. (P.) ezoanum* are clearly distinguished from each other in several respects: differences in whorl-section being the most obvious. The flanks of *D. (P.) japonicum* are flat and parallel to each other and the venter is rounded and wide (Figure 3). On the other hand, in *D. (P.) ezoanum* the whorl-section is widest at the middle of the preceding whorl and it becomes rapidly narrower outwards, forming an arched venter (Figure 3). This observation of the whorl-section is also biometrically demonstrated by the simple ratio of whorl-breadth to whorl-height, B/H, at the growth point of 7π (the third and a half whorl) (Figure 4), where the observed ranges and 95% confidence intervals of means for two Obira samples of *D. (P.) ezoanum* clearly do not overlap those of *D. (P.) japonicum*. On the other hand, in the growth ratio of the breadth to the volution (Table 1, Figure 5) and the size of the protoconch (Figure 6), the observed values very much overlap with each other, and the two species cannot be distinguished by using these characters. The growth ratio of the radius length of *D. (P.) japonicum* in relation to the volution increases with time (Figure 7) and the growth ratio of the umbilical radius of the species in relation to the volution decreases slightly with time (Figure 8). Therefore, the simple ratio of the umbilicus to the diameter, U/D, at the growth point of 7π also decreases with time (Figure 9). Although the low number of samples is insufficient to state with certainty, *D. (P.) ezoanum* also seems to follow the same trend. Thus, although these two species share many common characters, they can be separated on the basis of some major

characters. Matsumoto (1954) proposed that *D. (P.) ezoanum* was derived from *D. inane* (Stoliczka), via *D. kossmati* and *D. (P.) poronaicum*. However, as the taxa of this lineage are not presently accessible to us, no further mention is possible.

Phylogeny of D. (P.) japonicum

D. (P.) japonicum (Figures 10-1-11; Figure 11-26) was first described by Yabe (1904) under the name of *Desmoceras dawsoni* Whiteaves var. *japonica*. Later it was separated by Matsumoto (1938) as an independent species, *D. (P.) japonicum* Yabe. Matsumoto (1941) proposed that the Albian *D. latidorsatum* (Michelin) was the probable ancestor of *D. (P.) japonicum*, and later on he again pointed out that *D. (s.s.) latidorsatum* was possibly an ancestor of *D. (P.) japonicum* (Matsumoto, 1954).

In both the Obira and the Yubari samples, the growth ratio of the radius length of *D. (P.) japonicum* in relation to the volution increases from the Lower to the Upper Cenomanian (Figure 7). The same trend is seen in the decreasing simple ratio U/D (Figure 9), the increasing protoconch width (Figure 6) and the decreasing growth ratio of the umbilical radius to the volution (Figure 8). The other morphologies such as the simple ratio B/H (Figure 4) and the growth ratio of the whorl-breadth to the volution (Figure 5) are stable throughout the entire range of the species, until its extinction at the end of the Cenomanian.

No species of *D. (Pseudouhligella)* occur in the Turonian of Japan. The most similar Turonian species to the Cenomanian *D. (P.) japonicum* is *Tragodesmoceroides subcostatus*.

Comparison of morphology between the Cenomanian *D. (P.) japonicum* and the Turonian *T. subcostatus* is as follows. There is no clear difference between these two species in protoconch size (Figure 6), nor in the growth ratio of the whorl-breadth to the volution (Table 1, Figure 5), but the youngest

Table 1. Coefficients of difference among four species on two parameters. Right upper: the growth ratio of the radius length to the volution. Left lower: the growth ratio of the whorl-breadth to the volution.

		<i>D. ezoanum</i>	<i>Desmoceras japonicum</i>				<i>Tragodesmocerooides subcostatus</i>							<i>T. matsumotoi</i>		
		UC. Ob	LC.Y	LC.Ob	UC.Y	UC.Ob	L.Y	L.Ob	N.Y	N.Ob	H.Ob	T.Y	T.Ob	H.Y	H.Ob	T.Ob
<i>D.e.</i>	UC. Ob	*	1.23	0.80	0.79	0.91	2.54	1.73	2.24	2.16	2.21	2.15	2.48	4.05	3.91	4.51
<i>D. japonicum</i>	LC. Y	0.27	*	0.47	0.71	0.61	0.31	0.23	0.28	0.32	0.23	0.22	0.36	1.50	1.42	1.63
	LC. Ob	0.48	0.68	*	0.17	0.06	1.14	0.80	1.02	1.02	0.97	0.95	1.16	2.50	2.39	2.76
	UC. Y	0.42	0.64	0.05	*	0.14	1.84	1.17	1.58	1.54	1.54	1.49	1.82	3.69	3.52	4.22
	UC. Ob	0.63	0.89	0.00	0.07	*	1.63	1.04	1.40	1.37	1.36	1.31	1.62	3.46	3.30	3.96
<i>T. subcostatus</i>	L. Y	0.00	0.23	0.41	0.37	0.53	*	0.00	0.00	0.11	0.13	0.12	0.14	2.88	2.65	3.58
	L. Ob	0.07	0.21	0.56	0.50	0.74	0.06	*	0.00	0.07	0.07	0.07	0.08	1.52	1.42	1.70
	N. Y	0.06	0.29	0.37	0.32	0.47	0.05	0.13	*	0.09	0.10	0.10	0.11	2.29	2.12	2.71
	N. Ob	0.00	0.24	0.43	0.38	0.55	0.00	0.07	0.06	*	0.19	0.18	0.00	1.94	1.79	2.25
	H. Ob	0.00	0.28	0.48	0.43	0.65	0.00	0.08	0.06	0.00	*	0.00	0.23	2.50	2.32	2.99
	T. Y	0.19	0.17	0.74	0.68	1.05	0.15	0.10	0.23	0.16	0.19	*	0.22	2.38	2.21	2.82
	T. Ob	0.44	0.00	1.01	0.95	1.54	0.34	0.35	0.44	0.37	0.45	0.34	*	2.47	2.27	3.00
<i>T.m.</i>	H. Y	1.55	1.13	1.81	1.77	2.52	1.28	1.55	1.38	1.34	1.59	1.90	2.09	*	0.15	0.00
	H. Ob	1.32	0.93	1.61	1.58	2.22	1.10	1.30	1.19	1.15	1.36	1.57	1.67	0.21	*	0.18
	T. Ob	1.56	1.06	1.85	1.82	2.77	1.24	1.56	1.36	1.32	1.61	2.03	2.34	0.42	0.13	*

Gothic numerals: Coefficient of difference > 1.28 i.e., Overlap less than 10% of the area. For abbreviation, Ob: Obira area, Y: Oyubari area, LC: Lower Cenomanian, UC: Upper Cenomanian, L: Lower Turonian *Saxonicus-Labiatus* Zone, N: lower Middle Turonian *Hobetsensis nonsulcatus* Zone, H: upper Middle Turonian *Hobetsensis hobetsensis* Zone, T: Upper Turonian *Teshioensis* Zone, *D.e.*: *Desmoceras ezoanum*, *T.m.*: *Tragodesmocerooides matsumotoi*.

T. subcostatus show a significant non-overlap with *D. (P.) japonicum* in the latter ratio due to its slightly decreasing trend throughout the Turonian (Table 1). The simple ratio of breadth to height at the growth point 7π of *T. subcostatus* also mostly overlaps that of *D. (P.) japonicum* (Figure 4). The growth ratios of the radius to the volution of the Upper Cenomanian *D. (P.) japonicum* do not overlap those of *T. subcostatus* (Table 1) because of the increasing growth ratio of *D. (P.) japonicum* mentioned

above. The same is true for the simple ratio, U/D (Figure 9). The growth ratio of the umbilical radius length to the volution of *D. (P.) japonicum* also shows a chronologically decreasing trend, but it mostly overlaps that of *T. subcostatus*, because the variation of the morphology of the latter is fairly large (Figure 8).

Hirano (1988) mentioned an intermediate form of *D. (P.) japonicum*, from the late Upper Cenomanian, which has *T. subcostatus*-type anteriorly projected weak ribs

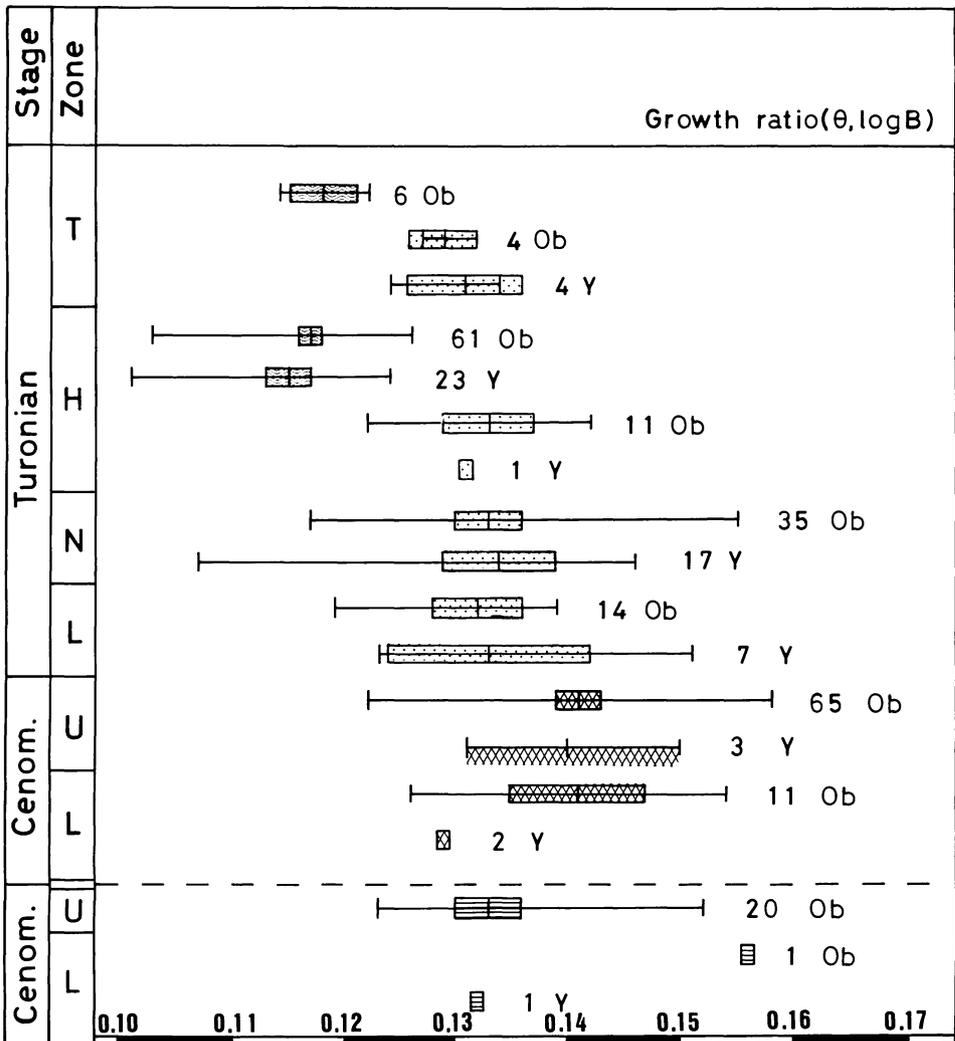


Figure 5. Chronological change of the growth ratios of the whorl-breadth to the volution. Symbols are the same as Figure 4.

on the venter. It occurs at locality R5222 (Matsumoto *et al.*, 1978), and the horizon is slightly higher than that of *Vascoceras* aff. *durandi* and *Fagesia thevestensis*, being regarded as the lower Lower Turonian. The whorl-sections of the two species resemble each other in appearance as well as in the simple ratio, B/H. Later, plain *T. subcostatus* was obtained from some contiguous but slightly lower horizons than that mentioned above. Thus, an intermediate form mentioned in Hirano (1988) is not remarkable at the

present time.

In short, only the strength and the anterior projection of subcostae are different, and the other characters are not always significantly different between *D. (P.) japonicum* and *T. subcostatus*.

Both species occur most abundantly in and around Japan. A time gap between the disappearance of *D. (P.) japonicum* and the appearance of *T. subcostatus* is very short as shown by a columnar section with a range chart of these species (Hirano, 1986, p. 10, fig.

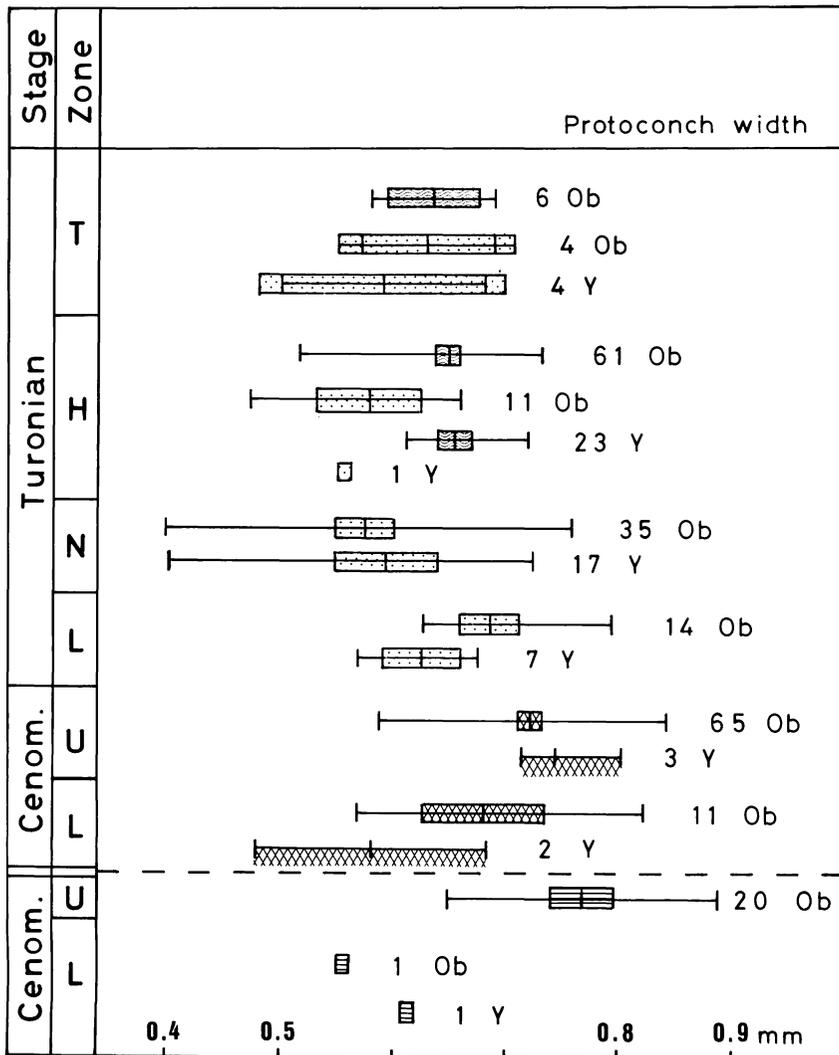


Figure 6. Chronological change of the protoconch width. Symbols are the same as Figure 4.

4).

It could almost be concluded that *T. subcostatus* evolved from *D. (P.) japonicum* on the basis of the information mentioned above. The tempo and mode of evolution seem to be concordant with the punctuated equilibrium hypothesis of Eldredge and Gould (1972), although we cannot make an unequivocal conclusion on this point especially in view of the presence of polymorphic mechanisms, as mentioned by Hayami and Ozawa (1975) and Hirano (1978, 1979).

Speciation of *Tragodesmoceroides subcostatus*

We have elucidated the allopatric speciation from *T. subcostatus* (Figures 11-1-12) to *T. matsumotoi*, n. sp. (Figures 11-16-25) on the basis of numerous specimens obtained from various stratigraphical levels.

Among the six characters (Figures 4-9), the clear differences of these two species in the growth ratios of the radius length (Figure 7) and breadth (Figure 5) to the volution demonstrate this fact. The ranges of these two

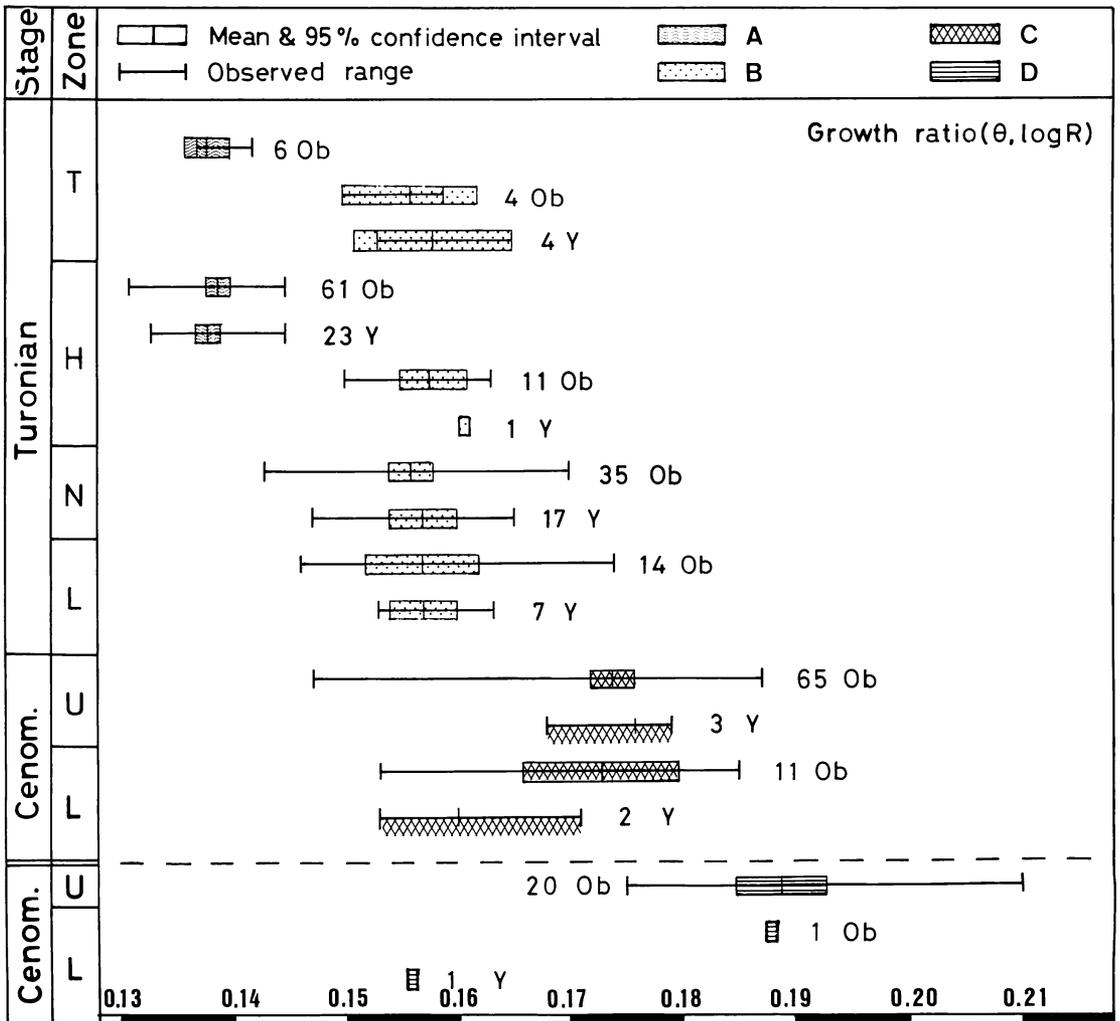


Figure 7. Chronological change of the growth ratios of the radius length to the volution. Symbols are the same as Figure 4.

growth ratios show clearly different values and there is either no overlap or only very slight overlap between these two species (Table 1). It is clearly demonstrated by Tanabe (1979) that the distribution of ammonoid species laterally changes from the west to the east in the Obira area. In addition, many desmoceratine ammonoids studied in these areas in this time contain their aptychi in their body chamber, *in situ*. Thus, it follows that most desmoceratine ammonoids

embedded autochthonously. All of the specimens which belong to *T. matsumotoi*, n. sp. occur only in the district of Takishita (locs. A and C of Figure 12) and Kamikinenbetsu (loc. B of Figure 12) in the Obira area. *T. subcostatus*, which has significantly larger growth ratios, occurs in the east to north-east district of the Obira area (Tanabe *et al.*, 1977), and these two species never co-occur. The same is true in the Oyubari area, where the new species occurs only at one locality

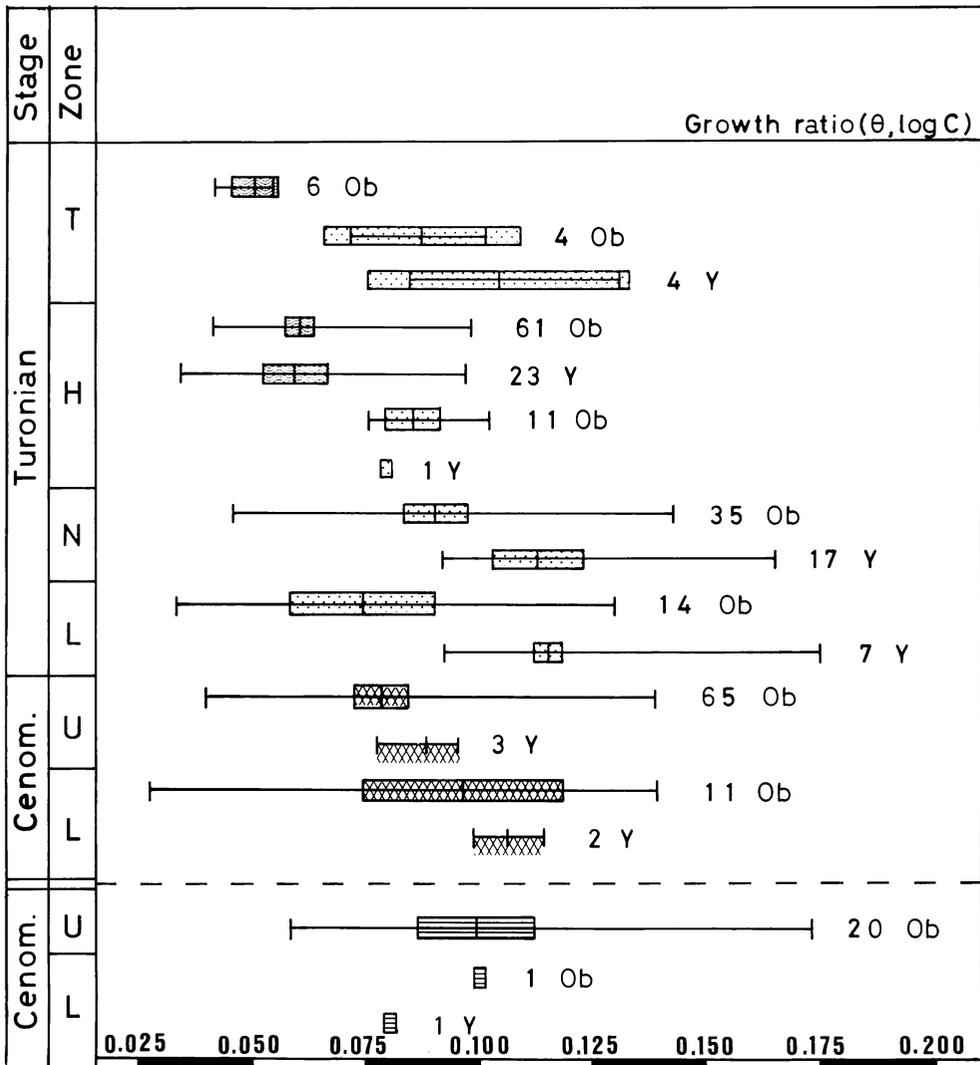


Figure 8. Chronological change of the growth ratio of the umbilical radius length in relation to the evolution. Symbols are the same as Figure 4.

(loc. 2344 of Hirano et al., 1981, fig. 4; a lower stream of the Pankemoyuparo River). The adult size of *T. subcostatus* is also larger than that of *T. matsumotoi*. Thus, the newly recognized species, *T. matsumotoi* is characterized by: (1) it occurs only from the *Hobetsensis* and *Teshioensis* Zones of the Middle-Upper Turonian, (2) it occurs only in the north-west part of the Obira area and from one restricted locality in the Oyubari area, (3) it occurs strictly allopatrically with respect to *T. subcostatus*, (4) the adult size is

smaller than *T. subcostatus* and (5) some biometrical parameters do not overlap those of *T. subcostatus*. On the basis of such differences mentioned above, the new species *T. matsumotoi* is distinguished from the hitherto known *T. subcostatus*. Incidentally, the Cretaceous System of the western part of the Obira area is both empirically and quantitatively known to yield more inshore ammonoids than does the eastern part (Tanabe, 1979). There is scarcely any doubt that these two species were in a relationship

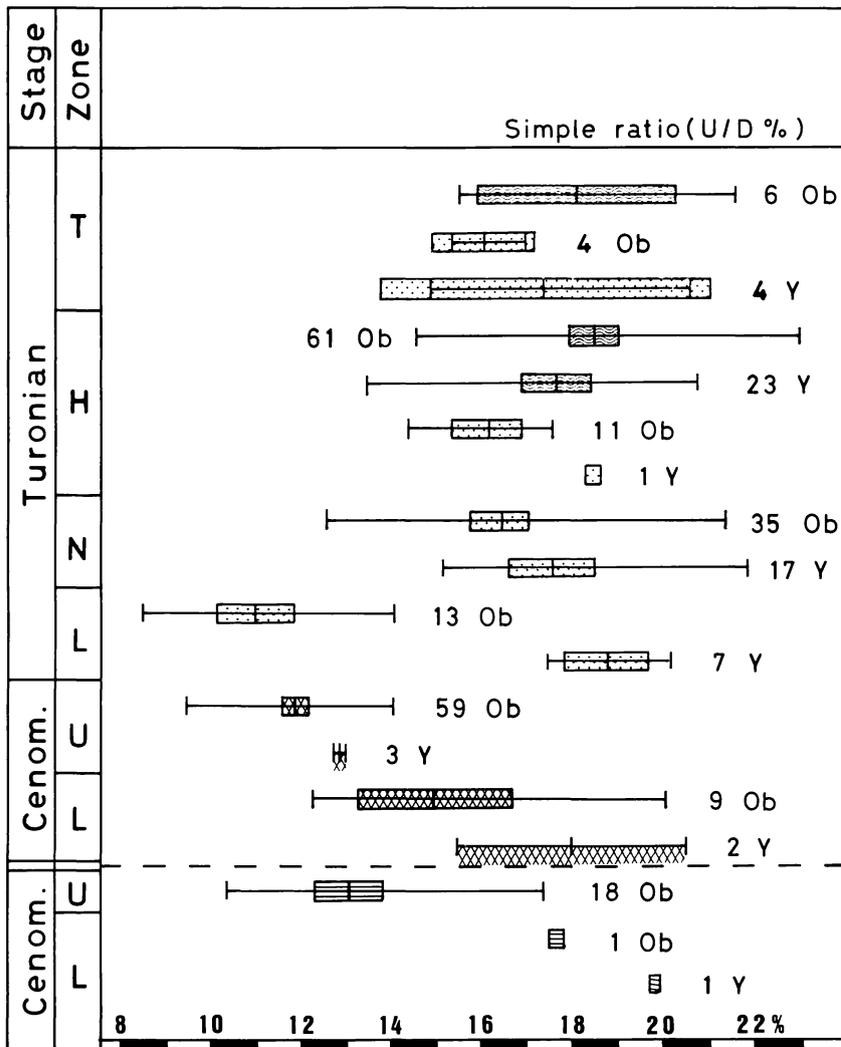


Figure 9. Chronological change of the simple ratios of the umbilical diameter to the whorl diameter at the growth stage of the third and a half whorl. Symbols are the same as Figure 4.

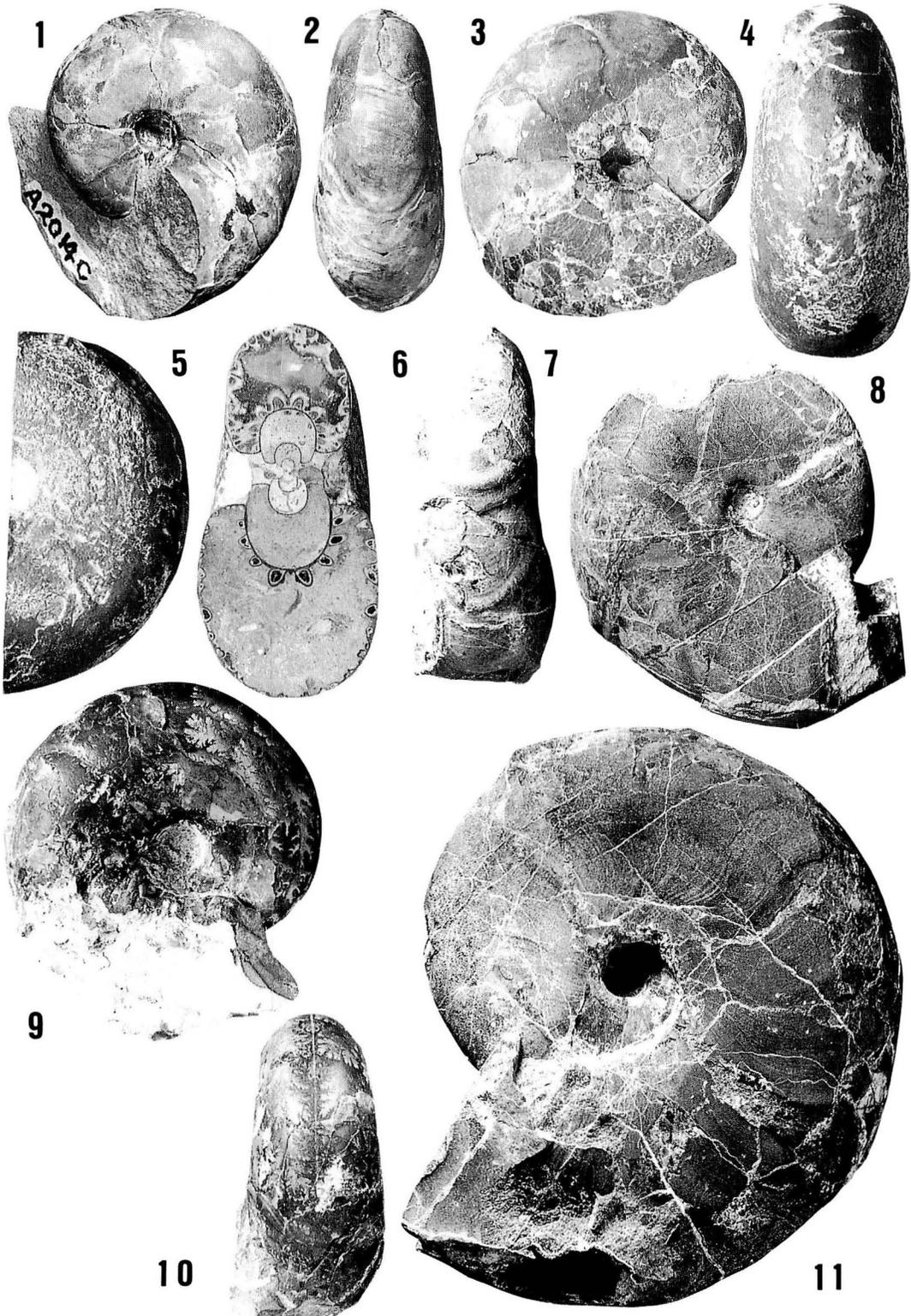


Figure 10. *Desmoceras (Pseudouhligella) japonicum* Yabe. **1, 3** (lateral) and **2** (posterior) from A2014c. **4** (posterior), **5** (lateral) and **6** (cross section) from YC2414. **7** (posterior) and **8** (lateral) from As7018f. **9** (lateral) and **10** (posterior) from T5041. **11** (lateral) from As7018d. All in natural size.

of habitat segregation. Some biometrical parameters show no difference between *T. subcostatus* and *T. matsumotoi*, and for this reason the two species are considered to be very closely related to each other. *Tragodesmocerooides matsumotoi* most likely speciated from *T. subcostatus*. No morphological change in *T. subcostatus* is detected throughout its range, either in an observational or a biostatistical view.

Both species died out at the end of the Turonian, and no descendants are detected among the Coniacian desmoceratids.

Systematic description

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Desmocerataceae Zittel, 1895

Family Desmoceratidae Zittel, 1895

Subfamily Desmoceratinae Zittel, 1895

Genus *Tragodesmocerooides* Matsumoto, 1942

Type-species: *Tragodesmocerooides subcostatus* Matsumoto, 1942.

Generic diagnosis: Matsumoto, 1942 (p. 25, p. 28, figs. 1-d1 and d2) described the generic diagnosis with illustration, and later he (Matsumoto, 1954, p. 262, pl. 4) fully described it with a photograph. According to the latter the generic diagnosis is as follows: Relatively small desmoceratids characteristically ornamented with sharp and narrow ribs which covers the ventral half of the mature shell. Similar to *Desmoceras* in shell-form, but with a very narrow crater-like umbilicus. Apertural margin provided with strongly projected sinuses. Suture-line similar to that of *Desmoceras* in general pattern, with fine

and deep incisions. Arkell *et al.* (1957) summarized the generic diagnosis based upon Matsumoto (1942, 1954), and it is as follows: Very involute, moderately inflated; falcooid constrictions and sharp, dense falcooid ribs or striae on outer part of side, and strongly projected on venter, mid-line of which tends to be raised.

Tragodesmocerooides matsumotoi, sp. nov.

Figures 11–16—25

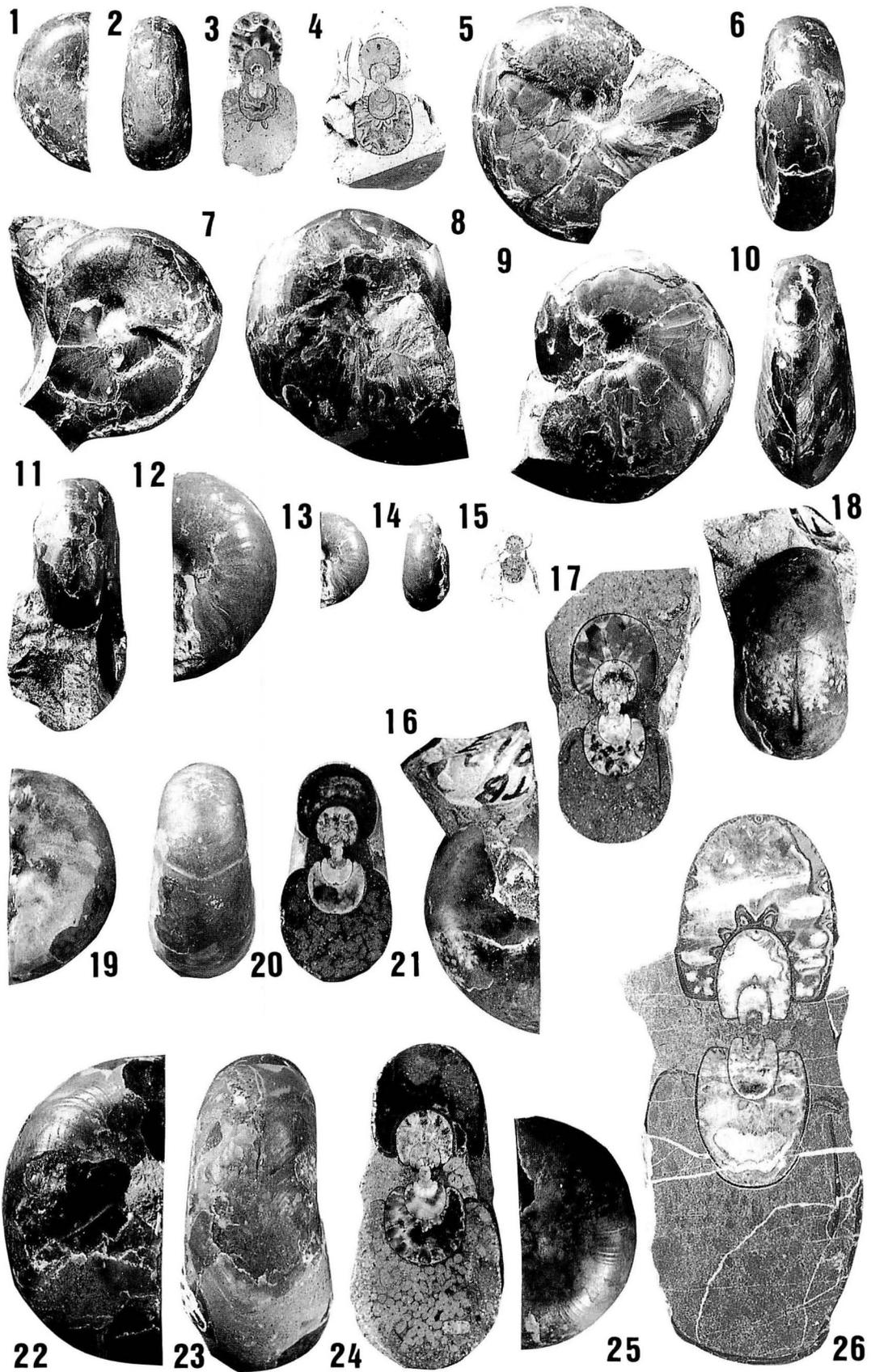
1988 *Tragodesmocerooides* sp.: Hirano, In Wiedemann and Kullman *eds.*, p. 513–523.

Types: WEA103T (Figures 11–22–24) is designated here as the holotype, which was obtained at locality A, Takishita, Obira area (Figure 12; same as loc. R6072 of Tanabe *et al.*, 1977). Two specimens, WEA101T (Figures 11–16–18) and WEA102T (Figures 11–19–21) are designated as paratypes, both of which were also obtained from the same exposure as the holotype.

Materials: Sixty-one specimens from Middle Turonian *Inoceramus hobetsensis hobetsensis* zone at locality A, the River Obirashibe and six from Upper Turonian *Inoceramus teshioensis* zone at locality B, the River Kamikinenbetsu of the Obira area (Figure 12), and twenty-three from *Inoceramus hobetsensis hobetsensis* zone at locality YC2357, the River Pankemoyuparo (Hirano *et al.*, 1981) of the Oyubari area are used in this study. All the specimens including types mentioned above are curated in the Type-collections, Institute of Earth Science, School of Education, Waseda University.

Etymology: Dedicated to Tatsuro Matsu-

→ **Figure 11.** 1–15: *Tragodesmocerooides subcostatus* Matsumoto. 1 (lateral), 2 (posterior), 3 (cross section) from YE2009b. 4 (cross section) from YE2009b. 5 (lateral), 6 (posterior), 7 (lateral) from 2YC3050X. 8, 9 (lateral), 10 (posterior), 11 (anterior) from YA6037. 12 (lateral, ×2 of 13), 13 (lateral), 14 (posterior), 15 (cross section) from R5222=T6044a–84. 16–25: *Tragodesmocerooides matsumotoi*, n. sp. 16 (lateral), 17 (section), 18 (posterior) from loc. A, Paratype (WEA101T). 19 (lateral, ×3), 20 (posterior, ×3), 21 (cross section, ×3) from loc. A, Paratype (WEA102T). 22 (lateral, ×3), 23 (posterior, ×3), 24 (cross section, ×3) from loc. A, Holotype (WEA103T). 25 (lateral, ×3) from loc. A. 26: *Desmoceras (Pseudouhligella) japonicum* Yabe. 26 (cross section) from As7018f. All in natural size unless otherwise mentioned.



moto, a noted investigator of cephalopods and historical geology.

Specific diagnosis: A species of *Tragodesmoceroides*, which is characterized by and distinguished from other species in clearly smaller growth ratios of the radius length and the whorl-breadth in relation to volution and somewhat smaller growth ratio of the umbilical radius length in relation to the volution.

Description: The shell is small and mostly less than 2 cm in the adult diameter. The whorl-section is rounded and the height is nearly the same as the breadth in the early stage, but the height increases more rapidly than the breadth. The growth ratio of the radius length in relation to the volution is small (Figure 7). The growth ratio of the breadth in relation to the volution is also characteristically small (Figure 5). Thus, flanks are nearly parallel to each other beyond the middle growth stage, although they are somewhat inflated. The umbilicus is narrow and deep through the development as shown by the small growth ratio of the umbilical radius in relation to the volution (Figure 8). The shell surface is ornamented with numerous falcoïd lirae in the middle growth stage and subcostae in the adult stage, which strongly project anteriorly in the ventral area. There are a few falcoïd constrictions, which are mostly parallel to lirae or subcostae, on one whorl. The ontogenetic development of a suture-line is characterized by that of Desmoceratidae (Figures 13-16), and is $ELU2U3U4=S, U1vU1dI$ (Figures 15-16) in terms of the sutural formula of Kullmann and Wiedmann (1970). The sutural patterns of *T. subcostatus* (Matsumoto, 1954, p. 264, figs. 8-9; Figure 14) are substantially the same as those of the present species, but the formula can be different whether the differentiation of the U1 after the formation of U2 is considered as U1vU1d or U3. The adult sutural pattern is accomplished beyond the third whorl.

Comparison: The present species is very

similar to ancestral *T. subcostatus* (Figure 4). In relative growth analyses, the present species is clearly distinguishable from *T. subcostatus* in the smaller growth ratios of the radius length and the breadth in relation to the volution (Table 1). The growth ratio of the umbilical radius of the present species in relation to the volution is somewhat smaller than that of *T. subcostatus* (Figure 8).

Although statistical comparison is impossible at the present because of the lack of apertural margin of the shell, the adult size of the present species is clearly much smaller than that of *T. subcostatus* in 183 specimens.

There is no significant difference in the sutural pattern between *T. subcostatus* and the present species (Figures 14-16), but $ELU2U3U4=S, U1vU1dI$ is accomplished at the second and a half whorl in *T. subcostatus* and beyond the third whorl in the present species. These two species of *Tragodesmoceroides* have deeper lobes and more complex incisions than *D. (P.) japonicum* (Figure 13).

Occurrence: The present species occurs in the Turonian *Inoceramus hobetsensis hobetsensis* and *Inoceramus teshioensis* zones, with acanthoceratacean ammonoids in the western nearshore shallower facies, where hummocky cross-stratification of medium-grained sandstone deposited at the bottom shallower than intense storm wave base is preserved, and never co-occur with *T. subcostatus*. Incidentally *T. subcostatus* occurs in the eastern outer intermediate facies of the Western Cretaceous belt, where turbidites predominated, but does not occur in areas as far as the Hidaka (Obata et al., 1973) and Urakawa (Kanie, 1966) of the Eastern Cretaceous belt, where offshore mudstone predominated.

T. subcostatus of North America was described by Matsumoto (1959), but the occurrence of the present species is still unknown there.

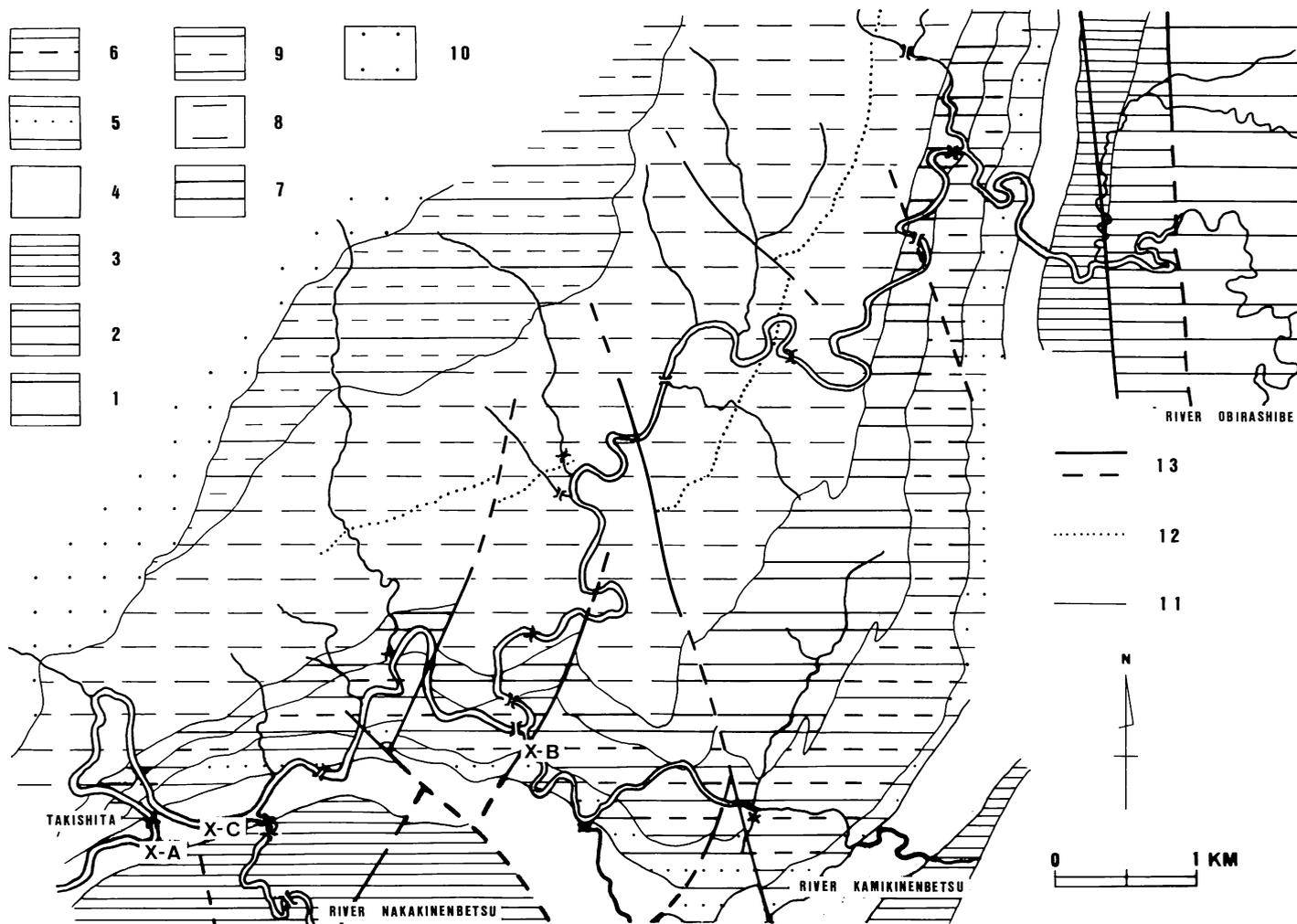


Figure 12. Map showing the fossil localities A, B and C of *T. matsumotoi*, n. sp. and *Inoceramus* zonation of the Obira area. 1: Cenomanian formations, 2: Lower Turonian *Inoceramus labiatus* zone, 3: lower Middle Turonian *I. hobetsensis nonsulcatus* zone, 4: upper Middle Turonian *I. hobetsensis hobetsensis* zone, 5: Upper Turonian *I. teshioensis* zone, 6: Lower Coniacian *I. uwajimensis* zone, 7: Upper Coniacian *I. mihoensis* zone, 8: Lower Santonian *I. amakusensis* zone, 9: Upper Santonian *I. japonicus* zone, 10: Tertiary, 11: Boundary of zone, 12: Local key-marker tuff bed, 13: Fault.

Discussion

1. Migration to shallower water.

Tsushima *et al.* (1958) showed that the Upper Cretaceous sediments become coarser westward and finer eastward, and Tanabe (1979) demonstrated that acanthoceratacean ammonoids occur abundantly westward. These results are in agreement with the results of Tanaka (1963) and Tanaka and Sumi (1981) on palaeocurrent analyses of the whole area of the Cretaceous Yezo Supergroup. The sedimentary facies which transect the

Yezo Supergroup were schematically illustrated by Matsumoto and Okada (1973), Okada (1982) and Hirano (1982), which show the western inshore and eastern offshore facies.

In such a basin setting, *T. matsumotoi* is allopatric to *T. subcostatus* and occurs only in the nearshore area. *T. matsumotoi* often co-occurs with acanthoceratacean ammonoids in the localities. The peculiar faunal composition of *T. matsumotoi* at Takishita, Obira has already been discussed by Tanabe (1979, p. 619, Table 2 for locality R2003) from a

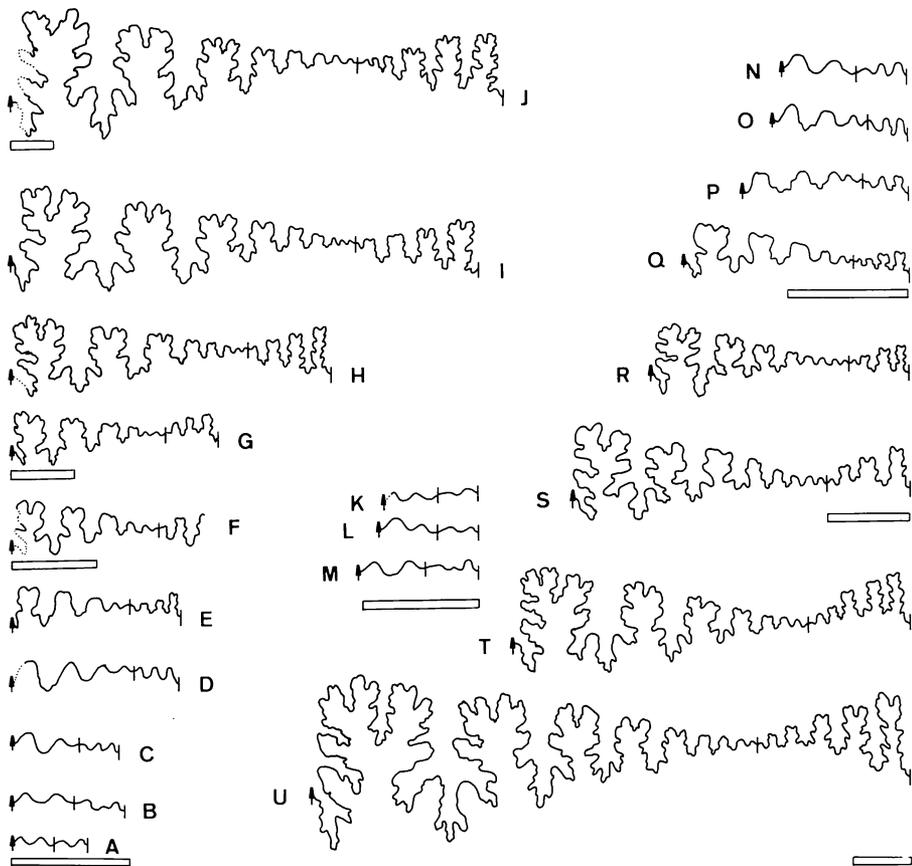


Figure 13. Sutural ontogeny of *Desmoceras (Pseudouhligella) japonicum* Matsumoto represented by two specimens from the Obira area. A—J: T6311-12x85-1, A: primary suture (0.157), B: 1/2 whorl, C: 1 whorl (0.236), D: 1+1/3 whorl (0.420), E: 1+1/2 whorl (0.484), F: 2 whorls (0.865), G: 2+1/2 whorls (1.187), H: 3 whorls (1.675), I: 3+1/2 whorls (2.270), J: 4 whorls (3.467), K—U: T6311-12x85-2, K: probably primary suture (0.167), L: probably 2nd suture, M: 1/3 whorl (0.230), N: 1/2 whorl (0.287), O: 1 whorl (0.400), P: 1+1/3 whorl (0.470), Q: 1+1/2 whorl (0.609), R: 2 whorls (1.050), S: 2+1/2 whorls (1.440), T: 3 whorls (2.202), U: 3+1/2 whorls (3.529). Height of the whorl in mm in parentheses. Bar scale: 1 mm, A—E, G—I, K—M, N—Q, R—S and T—U are in the same scale, respectively.

different view, although the species was not yet been recognized at that time. We recognized hummocky cross-stratification, which indicates a shallower condition than storm wave base, in some medium-grained sandstone beds and obtained such bivalves as

Acila sp., *Nanonavis* sp. and ostoreid, gastropods, simple corals, fish bones, floating wood and plant leaves in addition to some acanthoceratids at the type-locality of *T. matsumotoi*. It is of no doubt that these two species of *Tragodesmoceroidea* inhabited

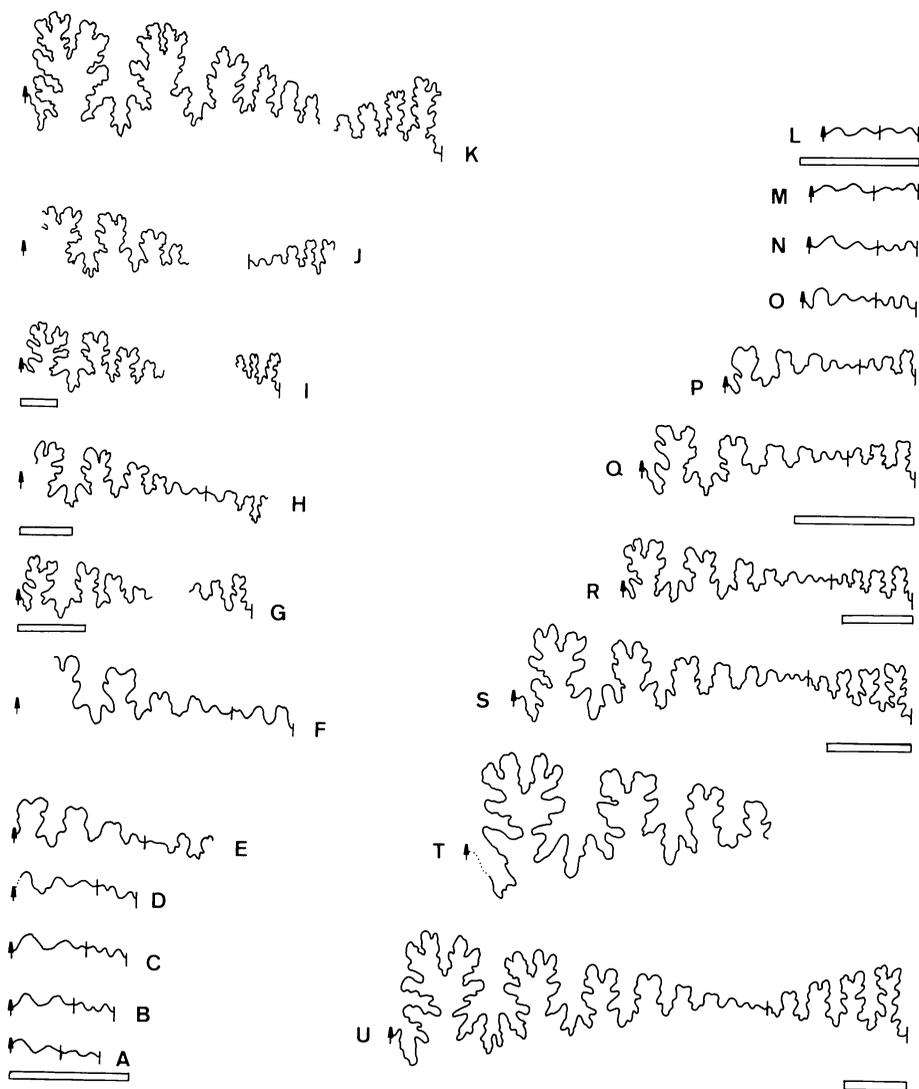


Figure 14. Sutural ontogeny of *Tragodesmoceroidea subcostatus* represented by two specimens from the Obira area. **A—K:** T6039-0-85-1. **A:** primary suture (0.159), **B:** 4th suture, **C:** 1/2 whorl (0.228), **D:** 1 whorl (0.351), **E:** 1+1/2 whorl (0.559), **F:** 2 whorls (0.800), **G:** 2+1/2 whorls (1.115), **H:** 3 whorls (1.720), **I:** 3+1/2 whorls (2.531), **J:** 4 whorls (3.200), **K:** 4+1/2 whorls (5.230). **L—U:** T6039-0-85-2. **L:** primary suture (0.157), **M:** 2nd suture, **N:** 1/2 whorl (0.288), **O:** 1 whorl (0.359), **P:** 1+1/2 whorl (0.465), **Q:** 2 whorls (0.755), **R:** 2+1/2 whorls (1.107), **S:** 3 whorls (1.383), **T:** 3+1/2 whorls (1.716), **U:** 4 whorls (2.671). Height of the whorl in mm in parentheses. Bar scale: 1 mm, **A—F, I—K, L, P, Q** and **T—U** are in the same scale, respectively.

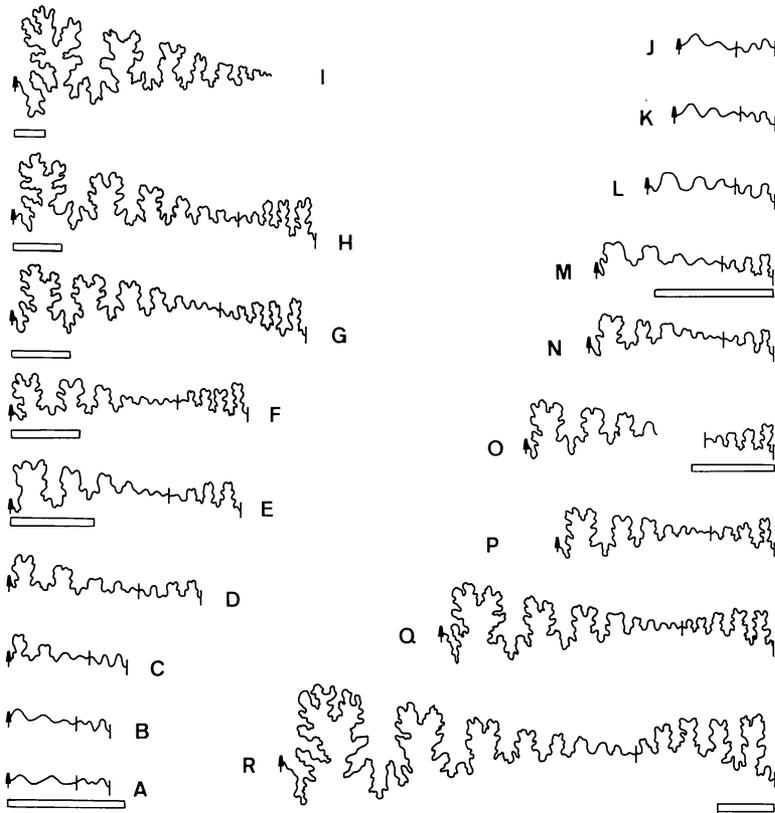


Figure 15. Sutural ontogeny of *Tragodesmoceroides matsumotoi*, n. sp. represented by two specimens from the Obira area. **A—I:** T1012y1-85. **A:** 2nd suture, **B:** 1 whorl (0.299), **C:** 1+1/2 whorl (0.403), **D:** 2 whorls (0.491), **E:** 2+1/2 whorls (0.626), **F:** 3 whorls (0.958), **G:** 3+1/2 whorls, **H:** 4 whorls (1.975), **I:** 5 whorls (3.990). **J—R:** T1012h8-85. **J:** 1/2 whorl (0.219), **K:** 1 whorl (0.249), **L:** 1+1/2 whorl (0.305), **M:** 2 whorls (0.421), **N:** 2+1/2 whorls (0.587), **O:** 3 whorls (0.798), **P:** 3+1/2 whorls (1.104), **Q:** 4 whorls (1.553), **R:** 4+1/2 whorls (2.039). Height of the whorl in mm in parentheses. Bar scale: 1 mm. **A—D, J—M, N—O** and **P—R** are in the same scale, respectively.

different waters of conditions; *T. matsumotoi* shallower nearshore water and *T. subcostatus* deeper offshore water.

D. (P.) japonicum, the ancestor of *T. subcostatus*, occurs in the western and eastern belts of the Cretaceous Yezo Supergroup which is distributed longitudinally north to south in central Hokkaido. However, *T. subcostatus*, does not occur in the deeper eastern belt, being limited in the outer intermediate facies of the western belt, where turbidites predominate. *T. matsumotoi* exclusively occurs in the western nearshore facies of the western belt, where stormbeds predominate. Thus, the lineage of *T. matsumotoi*

via *T. subcostatus* from *D. (P.) japonicum* changed habitat toward western shallower water at each speciation episode.

2. Size decreasing strategy.

Evolutionary size increase has already been discussed by many authors on various taxa (e.g., Hallam, 1978; Hayami, 1978). The present lineage shows the reverse, size decrease.

Even in the Yezo Supergroup which yields exceptionally well preserved shells, it is not so frequent to see completely preserved adult specimens with a peristome and an undeformed body chamber. The approximation of the final septum which indicates the close of growth is not always confirmed. Although

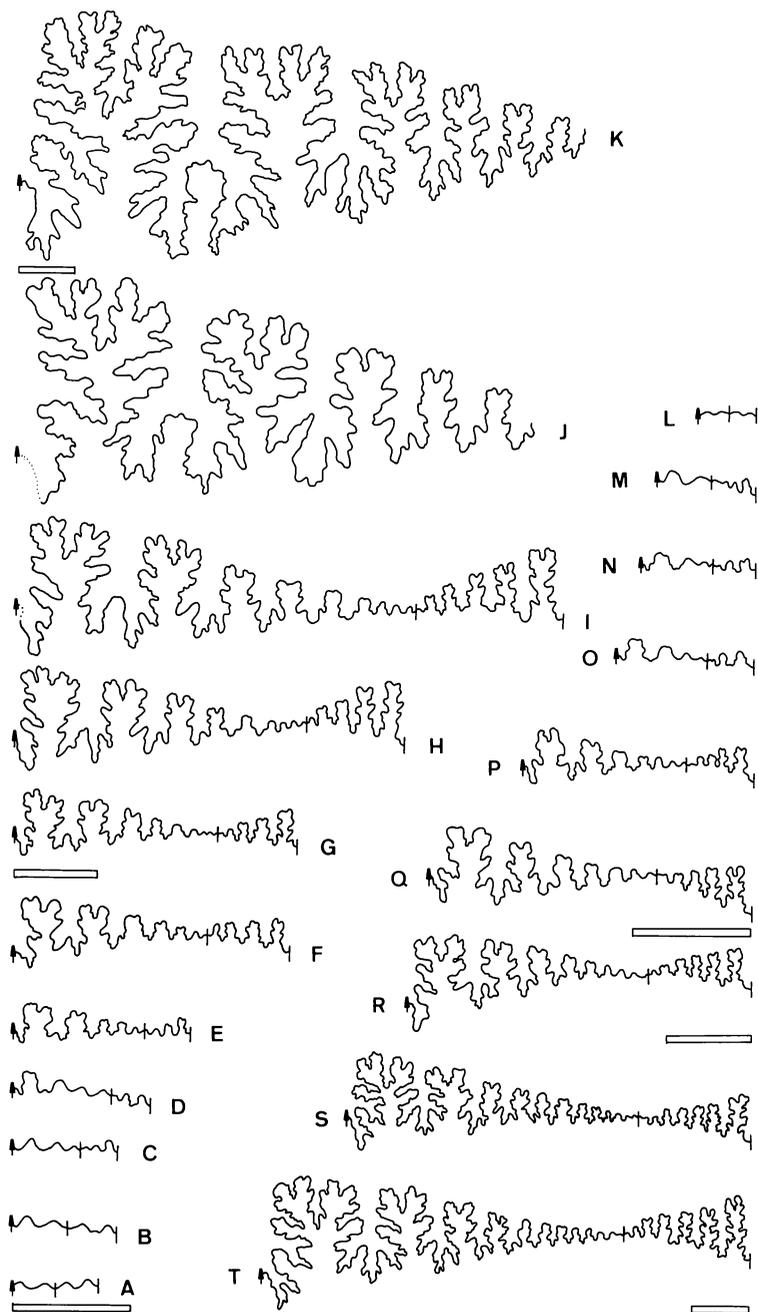


Figure 16. Sutural ontogeny of *Tragodesmocerooides matsumotoi* and *Damesites damesi* for comparison. A—K: *T. matsumotoi* (Y090009a-85) from the Oyubari area. A: primary suture (0.128), B: 2nd suture, C: 1 whorl (0.273), D: 1+1/2 whorl (0.352), E: 2 whorls (0.506), F: 2+1/2 whorls (0.716), G: 3 whorls (1.026), H: 3+1/2 whorls (1.412), I: 4 whorls (1.998), J: 4+1/2 whorls (2.998), K: 5 whorls (4.594). L—T: *D. damesi* (K1007g-82) from Santonian *I. amakusensis* zone in the Kotanbetsu area, north of the Obira area. L: primary suture (0.101), M: 1/2 whorl (0.116), N: 1 whorl (0.311), O: 1+1/2 whorl (0.424), P: 2 whorls (0.624), Q: 2+1/2 whorls (0.910), R: 3 whorls (1.301), S: 3+1/2 whorls (1.799), T: 4 whorls (2.459). Height of the whorl in mm in parentheses. Bar scale: 1 mm. A—F, G—J, L—Q and S—T are in the same scale, respectively.

we cannot show quantitatively the change of adult size in the present lineage under such conditions, we can recognize a trend of size decrease in the description of Matsumoto (1938, 1942, 1954) and Figures 10–11 of this paper: Specimens of *D. (P.) japonicum* which exceed 10 cm in diameter are very common; *T. subcostatus* has a maximum diameter of 4 cm, and *T. matsumotoi* does not grow over 3 cm maximum diameter. This conclusion does not come from a few specimens of some limited areas, but from several hundred specimens of various localities in the Yezo Supergroup which is distributed in the area of some 50 km in the width of east and west and of some 200 km in the length of north and south. Therefore this conclusion is not biased by current sorting or other sedimentological factors.

These lines of evidence indicate that the evolutionary lineage of *T. matsumotoi* via *T. subcostatus* from *D. (P.) japonicum* migrated into shallower water step by step with a decreasing trend of the adult shell size. It is not yet clarified that the population sizes of these species increased with the change over of these strategies, but *T. matsumotoi* seems to occur most abundantly.

3. Sutural complexity.

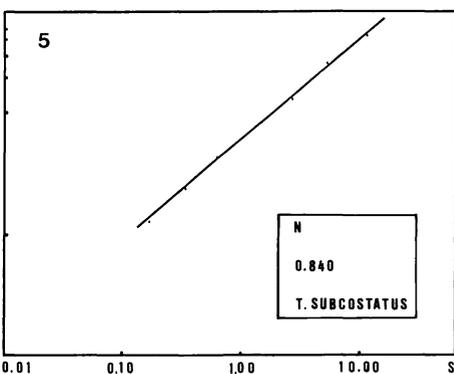
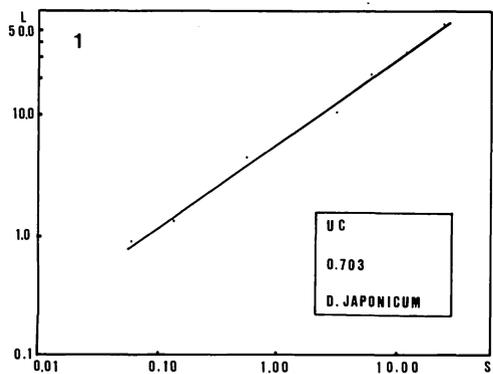
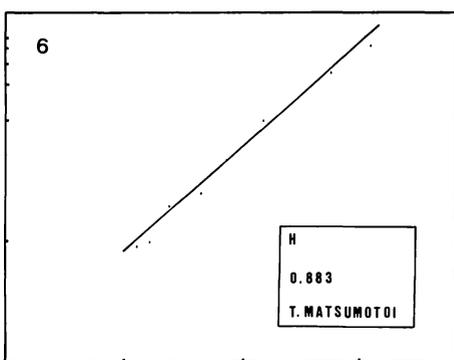
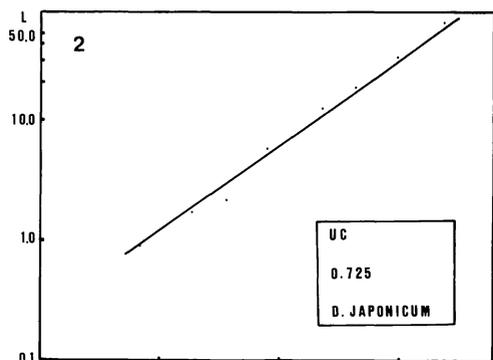
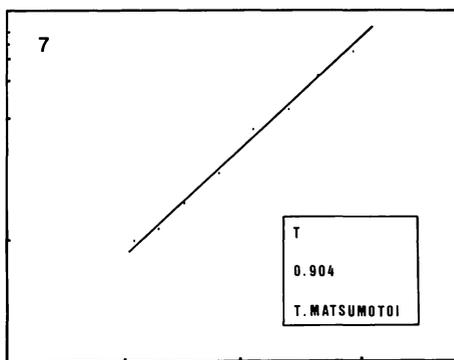
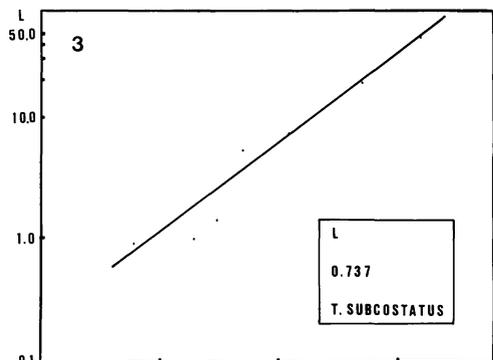
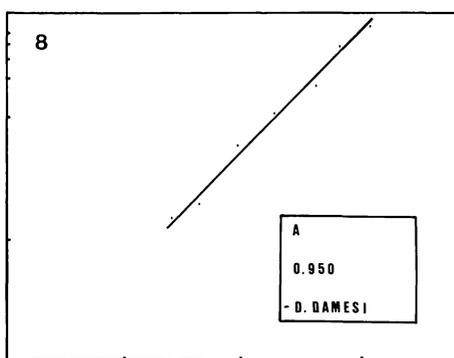
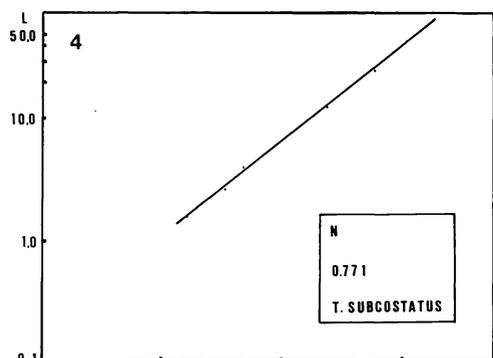
In spite of the fact that the present lineage changed its habitat from deeper water to shallower water at each episode of speciation, the sutural complexity increased. We measured the rate of ontogenetic development of a half length of the suture line in relation to the area of the whorl section in the growth stage from the middle of the second whorl to the fourth whorl for each species (Figure 17). The result indicates us that the growth rate of

the sutural length consistently accelerated in relation to the area of the whorl section, that is, the suture historically became more complex for a same area. The function of sutural part is regarded as hydrostatic apparatus to protect the whorl against water pressure with least amount of shell material (economy of calcium carbonate) and provision for muscle attachment (Westermann, 1971; Hirano, 1975; Seilacher, 1975; Kennedy and Cobban, 1976; Bayer, 1977; Henderson, 1984). The phylogenetical increase of sutural complexity is not explained only from this view, because the present lineage immigrated into shallower waters. Thus the mode of life and the depth of the water column where these ammonoids inhabited are important topics, and pleiotropy may have played a key role in relationship to changes of other characters.

4. Relation to oceanic events.

Many conditions which control the rise and decline of marine animals have been recognized. It has also been recognized that times of marine regression coincide with major boundaries of geological ages which are defined by extinctions/appearances of marine animals. Wiedmann (1973), for example, advocates that the renewal of ammonoid faunas at each age boundary of Late Cretaceous is due to the effects of marine regressions at each boundary. However, Matsumoto (1977) and Hancock and Kauffman (1979) have shown that eustatic sea level changes do not necessarily coincide with age boundaries in the Cretaceous. Therefore, the renewal of ammonoid faunas at each age boundary has to be investigated for each age in each area. For such a study a probabilistic contemporaneous extinction

→ **Figure 17.** Acceleration in the ontogeny of sutural complexity of the lineage from *D. (P.) japonicum* through *T. subcostatus* to *T. matsumotoi*. A few specimens for these species are chosen, and ontogenetic development of sutural length (half length) in relation to the area of whorl (half area of the whorl section) in each specimen are plotted. Santonian *Damesites damesi*, which shows the concordant value in the trend of the Cenomanian-Turonian lineage, is also shown for comparison. In inlet, UC: Upper Cenomanian, L: Lower Turonian *Inoceramus labiatus* zone, N: lower Middle Turonian *Inoceramus hobetsensis nonsulcatus* zone, H: upper Middle Turonian *I. hobetsensis hobetsensis* zone, T: Upper Turonian *Inoceramus teshioensis* zone, A: Lower Santonian *Inoceramus amakusensis* zone. 0.703–0.950: growth rate of sutural length in relation to the area of the whorl section.



(Raup *et al.*, 1973) has to be considered. But it is also necessary to consider whether or not such a contemporaneous extinction is a result of a deterministic process. Even if Cretaceous age boundaries do not coincide with eustatic sea level changes, changes in marine morphology caused by local tectonic movements are still important factors causing changes in local marine faunas. Species-area hypotheses as advocated by Schopf (1974) and Simberloff (1974), and as discussed by Gould (1977), can also be applied on various scales ranging from world-wide to local. Also, eustatic extinction/speciation models (Hallam, 1978, 1984, 1987) are applicable for various scales.

Comparison of the sedimentary and faunal successions in the Yezo Supergroup with the factors mentioned above reveals the importance of the oceanic anoxic event at the Cenomanian/Turonian boundary and the regression and transgression at the Turonian/Coniacian boundary.

Black shale beds of 5 m in thickness at the Cenomanian/Turonian boundary are widely recognized in the Yezo Supergroup (*e.g.*, Obira=Tappu, Kotanbetsu, Ashibetsu, Iku-shunbetsudake and Oyubari areas) by us. Upper Cenomanian inoceramids are obtained from calcareous concretions in the underlying grey mudstone beds which are frequently intercalated by sandstone beds. In the black shale beds, however, there are neither calcareous concretions nor marine molluscs. The black shale beds are overlain by alternating grey mudstone with sandstone beds, from which Turonian ammonoids and inoceramids bearing calcareous concretions occur at about the 50 m higher level than the black shale. Although more detailed investigation is under progress, in the meantime the presence of this black shale is interpreted to indicate the oceanic anoxic event (OAE) at the Cenomanian-Turonian boundary. Therefore, we regard that the Cenomanian *D. (P.) japonicum* died out at the OAE and *T. subcostatus* phyletically speciated in the surviv-

ing small populations. At the time of speciation the habitat of the lineage became limited to the western shallower waters. It is uncertain whether *T. subcostatus* evolved through immigration of surviving populations from offshore to nearshore waters or from isolated small populations which were left in the shallower waters.

Late Turonian is the age of a world-wide regression, which is recognized also in the sedimentary succession of the Yezo Supergroup. Sedimentation of the Middle Yezo Group ceased at about the Turonian-Coniacian boundary and that of the Upper Yezo Group began with the Coniacian transgression.

T. matsumotoi speciated from isolated small populations which were left in the shallower waters in the phase of a world-wide regression. The habitat of *T. matsumotoi* is in the shallower waters of which bottom is shallower than the intense storm wave base. *T. matsumotoi* and *T. subcostatus* which inhabited offshore waters never co-occur and thus allopatric. At the present we regard both two species died out at the end Turonian. Some *Damesites* species which may be related to these two species occur in the Coniacian onward, and the phylogenetical relation between them will be the subject for future next investigations.

Conclusions

1. *Desmoceras (Pseudouhligella) japonicum* existed throughout the Cenomanian, during which the protoconch size and growth ratio of the radius length in relation to the volution increased. On the other hand, the simple ratio U/D and the growth ratio of the umbilical radius in relation to the volution decreased. The growth ratio of breadth in relation to the volution and the simple ratio B/H did not change, and was stable.

2. There is an overlap of biometric characters between *D. (P.) japonicum* of the Upper Cenomanian and *T. subcostatus* of the

Lower Turonian. The comparatively stronger ribbing, the ventral anterior projection of subcostae and the smaller adult size are unique to *T. subcostatus*. Both species have their main distribution in and around Japan, and *T. subcostatus* most likely evolved from *D. (P.) japonicum* at about the Cenomanian/Turonian boundary.

3. *Tragodesmoceroides subcostatus*, following its evolution from *D. (P.) japonicum*, was morphologically stable in qualitative and biometric terms throughout the duration of the Turonian. The speciation of *T. subcostatus* from *D. (P.) japonicum* seems to have been in harmony with the punctuated equilibrium hypothesis.

4. Speciation occurred in *T. subcostatus* by the Middle Turonian, and *T. matsumotoi* arose. These taxa were clearly allopatric, and the latter inhabited shallower waters, which is characterized by some storm deposits in the Obira and Oyubari areas. Growth ratios of the radius length and the breadth in relation to the volution are different between the two species, and the adult size of *T. matsumotoi* is smaller than that of *T. subcostatus*.

5. *T. subcostatus* was morphologically stable throughout, with no temporal fluctuation around an average, except for one parameter (a simple ratio, U/D) mentioned earlier and there is no transitional form between the two species of *Tragodesmoceroides*. There is a small possibility of polymorphism because of the habitat segregation of these two species. Thus migration from offshore to shallower waters took place instantaneously in the geological sense.

6. The timing of speciation of *T. subcostatus* from *D. (P.) japonicum* and that of *T. matsumotoi* from the former is in accordance with oceanic events, with an oceanic anoxic event for the former and a marine regression for the latter.

7. The lineage of *T. matsumotoi* via *T. subcostatus* from *D. (P.) japonicum* has an increasing rate of the sutural length in rela-

tion to the area of the whorl section. That is, the sutural complexity accelerated with time.

8. The present lineage also shows a decreasing adult size with time. In accordance with this trend the habitat changed from deeper waters to changeable shallower waters step by step.

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後期白亜紀デスメセラス亜科アンモナイト類の進化：後期白亜紀の北太平洋には、デスメセラス亜科のアンモナイト類が繁栄した。北西太平洋の白亜紀前弧海盆堆積物の一代表とされる蝦夷累層群からは、このデスメセラス亜科のものが多数産出する。これらのうち、産出頻度の高いセノマニアン期の *D. japonicum*, *D. ezoanum*, チューロニアン期の *T. subcostatus* について、主として大夕張および小平地方のサンプルを用いて、相対成長解析を主たる方法として、各種の形態進化および各種間の関係を考察した。すなわち、*D. japonicum* と *D. ezoanum* は、各々生存期間を通じて形態の有意の変化はない。*T. subcostatus* は、*D. japonicum* と一二の形質を除いて差はなく、後者から進化したものと考えられる。また、*T. subcostatus* もその生存期間を通じて形態に有意の変化は無いが、チューロニアン期中頃までに種分化し *T. matsumotoi*, n. sp. を生じた。*D. japonicum*, *T. subcostatus*, *T. matsumotoi* の進化系統を通じて、縫合線の長さの螺環断面積に対する相対成長は、漸次加速されているが、種分化のつど成体のサイズが減少し、生息域の東方限界が西方の陸より移動した。また、これらの種の分化や絶滅は、海退・海進や海洋無酸素事変とタイミングが一致することから、このような海洋環境との関係についても論じた。

平野弘道・岡本 隆・服部幸司

Appendix

The statistics on which the description, figures (Figures 5—11) and discussion in the text based are shown in the following tabular forms (Tables 2—7).

Table 2. Protoconch width of studied desmoceratine ammonites. Number of specimens (N), 95% confidence interval (C.I.), standard deviation (S.D.), coefficients of variability (C.V.) and observed range (O.R.) are shown for each species of each zone.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	.634±.041	.040	6.42	.579-.688
<i>T. matsumotoi</i>	H	61	.650±.011	.041	6.32	.516-.689
<i>T. subcostatus</i>	T	4	.629±.077	.048	7.66	.571-.689
<i>T. subcostatus</i>	H	11	.578±.045	.068	11.8	.474-.660
<i>T. subcostatus</i>	HN	35	.573±.025	.074	12.9	.397-.757
<i>T. subcostatus</i>	S	14	.685±.027	.046	6.77	.626-.794
<i>D. japonicum</i>	C	65	.765±.011	.045	5.88	.625-.880
<i>D. japonicum</i>	CN	11	.682±.053	.080	11.7	.566-.821
<i>D. ezoanum</i>	C	20	.767±.028	.059	7.75	.647-.887
<i>D. ezoanum</i>	CN	1	.557	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	.655±.013	.031	4.73	.610-.720
<i>T. subcostatus</i>	T	4	.590±.109	.078	13.3	.500-.680
<i>T. subcostatus</i>	H	1	.599	—	—	—
<i>T. subcostatus</i>	HN	17	.594±.045	.088	14.7	.401-.722
<i>T. subcostatus</i>	S	7	.624±.034	.038	6.04	.566-.674
<i>D. japonicum</i>	C	3	.744	—	—	.714-.803
<i>D. japonicum</i>	CN	2	.580	—	—	.478-.681
<i>D. ezoanum</i>	CN	1	.614	—	—	—

For abbreviation of zones, T: *Teshioensis* Zone, H: *Hobetsensis hobetsensis* Zone, HN: *Hobetsensis nonsulcatus* Zone, S: *Saxonicus-Labiatus* Zone, C: Upper Cenomanian, CN: Lower Cenomanian. C. I. = $\bar{x} \pm t_{0.05} \cdot S.D. / \sqrt{N}$

Table 3. Relative growth ratios of whorl-radius in relation to the evolution of studied desmoceratine ammonites. For abbreviations see Table 2.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	.138±.002	.002	1.42	.137-.142
<i>T. matsumotoi</i>	H	61	.139±.001	.004	2.50	.131-.145
<i>T. subcostatus</i>	T	4	.156±.006	.004	2.59	.150-.159
<i>T. subcostatus</i>	H	11	.158±.003	.005	3.00	.150-.163
<i>T. subcostatus</i>	HN	35	.156±.002	.006	3.84	.143-.170
<i>T. subcostatus</i>	S	14	.157±.005	.009	5.86	.146-.174
<i>D. japonicum</i>	C	65	.174±.002	.007	4.06	.147-.187
<i>D. japonicum</i>	CN	11	.173±.007	.011	6.21	.153-.185
<i>D. ezoanum</i>	C	20	.189±.004	.009	4.90	.175-.210
<i>D. ezoanum</i>	CN	1	.188	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	.138±.001	.003	2.39	.133-.145
<i>T. subcostatus</i>	T	4	.158±.007	.005	3.23	.153-.165
<i>T. subcostatus</i>	H	1	.161	—	—	—
<i>T. subcostatus</i>	HN	17	.157±.003	.005	3.16	.147-.165
<i>T. subcostatus</i>	S	7	.157±.003	.003	2.10	.153-.163
<i>D. japonicum</i>	C	3	.176	—	—	.168-.179
<i>D. japonicum</i>	CN	2	.162	—	—	.153-.171
<i>D. ezoanum</i>	CN	1	.156	—	—	—

Table 4. Relative growth ratios of whorl-breadth in relation to the volution of studied desmoceratine ammonites. For abbreviation see Table 2.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	.118±.003	.003	2.17	.144-.122
<i>T. matsumotoi</i>	H	61	.117±.001	.005	4.41	.103-.126
<i>T. subcostatus</i>	T	4	.129±.003	.002	1.60	.127-.132
<i>T. subcostatus</i>	H	11	.133±.004	.007	5.07	.122-.142
<i>T. subcostatus</i>	HN	35	.133±.003	.009	6.61	.117-.155
<i>T. subcostatus</i>	S	14	.132±.004	.006	4.82	.119-.139
<i>D. japonicum</i>	C	65	.141±.002	.006	4.03	.122-.158
<i>D. japonicum</i>	CN	11	.141±.006	.010	6.95	.126-.154
<i>D. ezoanum</i>	C	20	.133±.003	.007	5.28	.123-.152
<i>D. ezoanum</i>	CN	1	.156	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	.115±.002	.005	3.98	.101-.124
<i>T. subcostatus</i>	T	4	.131±.005	.004	2.88	.126-.134
<i>T. subcostatus</i>	H	1	.131	—	—	—
<i>T. subcostatus</i>	HN	17	.134±.005	.009	6.83	.107-.146
<i>T. subcostatus</i>	S	7	.133±.009	.010	7.17	.123-.151
<i>D. japonicum</i>	C	3	.140	—	—	.131-.150
<i>D. japonicum</i>	CN	2	.129	—	—	.123-.134
<i>D. ezoanum</i>	CN	1	.132	—	—	—

Table 5. Relative growth ratios of whorl-umbilical radius in relation to the volution of studied desmoceratine ammonites. For abbreviations see Table 2.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	.050±.005	.005	9.72	.041-.054
<i>T. matsumotoi</i>	H	61	.060±.003	.011	18.5	.041-.098
<i>T. subcostatus</i>	T	4	.087±.022	.016	18.1	.071-.101
<i>T. subcostatus</i>	H	11	.085±.006	.008	9.74	.075-.102
<i>T. subcostatus</i>	HN	35	.090±.007	.019	21.2	.045-.143
<i>T. subcostatus</i>	S	14	.074±.016	.029	38.7	.033-.130
<i>D. japonicum</i>	C	65	.078±.006	.024	30.3	.039-.148
<i>D. japonicum</i>	CN	11	.096±.022	.034	34.9	.027-.139
<i>D. ezoanum</i>	C	20	.099±.013	.029	29.1	.058-.173
<i>D. ezoanum</i>	CN	1	.100	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	.059±.007	.016	27.3	.034-.097
<i>T. subcostatus</i>	T	4	.104±.029	.021	20.0	.084-.131
<i>T. subcostatus</i>	H	1	.079	—	—	—
<i>T. subcostatus</i>	HN	17	.113±.010	.020	18.1	.091-.165
<i>T. subcostatus</i>	S	7	.115±.003	.029	24.8	.092-.175
<i>D. japonicum</i>	C	3	.088	—	—	.077-.095
<i>D. japonicum</i>	CN	2	.106	—	—	.098-.114
<i>D. ezoanum</i>	CN	1	.080	—	—	—

Table 6. Simple ratios of breadth to height of whorl at the fourth whorl of studied desmoceratine ammonites. For abbreviations see Table 2.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	1.12±.029	.029	2.57	1.09-1.17
<i>T. matsumotoi</i>	H	61	1.12±.001	.039	3.44	1.00-1.23
<i>T. subcostatus</i>	T	4	1.05±.042	.031	2.90	1.02-1.09
<i>T. subcostatus</i>	H	11	1.07±.043	.065	6.12	.957-1.16
<i>T. subcostatus</i>	HN	35	1.08±.016	.048	4.45	.948-1.17
<i>T. subcostatus</i>	S	13	1.05±.041	.069	6.57	.889-1.19
<i>D. japonicum</i>	C	59	1.06±.014	.055	5.17	.923-1.15
<i>D. japonicum</i>	CN	9	1.05±.058	.078	7.41	.970-1.24
<i>D. ezoanum</i>	C	18	.792±.034	.068	8.62	.627-.923
<i>D. ezoanum</i>	CN	1	.760	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	1.12±.016	.036	3.21	1.07-1.24
<i>T. subcostatus</i>	T	4	1.08±0.68	.049	4.54	1.01-1.13
<i>T. subcostatus</i>	H	1	1.07	—	—	—
<i>T. subcostatus</i>	HN	17	1.10±.016	.032	2.90	1.02-1.15
<i>T. subcostatus</i>	S	7	1.12±.019	.021	1.91	1.09-1.15
<i>D. japonicum</i>	C	3	1.01	—	—	.992-1.02
<i>D. japonicum</i>	CN	2	1.03	—	—	1.01-1.05
<i>D. ezoanum</i>	CN	1	1.06	—	—	—

Table 7. Simple ratios (%) of umbilical radius to whorl radius at the fourth whorl of studied desmoceratine ammonites. For abbreviations see Table 2.

Species	Zone	N	C.I.	S.D.	C.V.	O.R.
[Obira area]						
<i>T. matsumotoi</i>	T	6	18.0±2.19	2.19	12.2	15.4-21.5
<i>T. matsumotoi</i>	H	61	18.4±.53	2.08	11.3	14.5-22.9
<i>T. subcostatus</i>	T	4	16.0±1.11	0.80	5.01	15.3-16.9
<i>T. subcostatus</i>	H	11	16.1±.76	1.14	7.08	14.3-17.5
<i>T. subcostatus</i>	HN	35	16.4±.61	1.79	10.9	12.5-21.3
<i>T. subcostatus</i>	S	13	10.9±.83	1.38	12.7	8.4-14.0
<i>D. japonicum</i>	C	59	11.8±.30	1.14	9.69	9.4-14.0
<i>D. japonicum</i>	CN	9	14.9±1.77	2.35	15.7	12.2-20.0
<i>D. ezoanum</i>	C	18	13.0±.76	1.53	11.8	10.3-17.3
<i>D. ezoanum</i>	CN	1	17.6	—	—	—
[Oyubari area]						
<i>T. matsumotoi</i>	H	23	17.6±.74	1.72	9.77	13.4-20.7
<i>T. subcostatus</i>	T	4	17.3±3.61	2.61	15.1	14.8-20.5
<i>T. subcostatus</i>	H	1	18.4	—	—	—
<i>T. subcostatus</i>	HN	17	17.5±.94	1.84	10.5	15.1-21.8
<i>T. subcostatus</i>	S	7	18.7±.90	1.00	5.35	17.4-20.1
<i>D. japonicum</i>	C	3	12.8	—	—	12.7-12.9
<i>D. japonicum</i>	CN	2	17.9	—	—	15.4-20.4
<i>D. ezoanum</i>	CN	1	19.7	—	—	—

897. MIOCENE ISOCRINIDAE (STALKED CRINOIDS) FROM JAPAN AND THEIR BIOGEOGRAPHIC IMPLICATION*

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Abstract. Three isocrinids, *Teliocrinus springeri* (Clark), *Isocrinus* sp. and *Issellicrinus* sp., are described from the late Early to early Middle Miocene of Japan, and their biogeographic implications are discussed. *Teliocrinus* had been represented only by a living species distributed in the Indian Ocean, and this discovery not only extends its stratigraphic record back to the Miocene but also widens its geographic distribution to the western Pacific region. *Isocrinus* sp. is based on many disarticulated columnals and is very similar to Oligocene *Isocrinus oregonensis* and *I. nehalemensis* from western Oregon. *Issellicrinus* sp. is based on fragmentary columnals, representing one of the latest occurrences of this genus.

A relatively striking turnover of the isocrinid fauna is presumed to have occurred in the western Pacific during the period between the late Early Miocene and Recent. This turnover includes the disappearance of *Teliocrinus*, *Isocrinus* and *Issellicrinus* from the western Pacific, and the introduction of *Metacrinus* and *Saracrinus* into this area. As a possible explanation for this, the northwestward movement of oceanic plates and a collision of a part of Gondwana (Australia/New Guinea) to the Eurasia continent are considered, which probably brought *Metacrinus* to the western Pacific region and an appearance of a barrier separating the deep-water isocrinid fauna into two provinces. Shallow water dwellers like many species of comasterid comatulids in the Indo-Pacific region are less subjected to such faunal separation.

Key words. Crinoidea, Miocene, paleobiogeography.

Introduction

Miocene marine deposits are widely distributed in many local areas of Japan. Recent paleontological work has focused mostly on biostratigraphy based on planktonic foraminifers and other microfossils, or paleoenvironmental and ecological analysis based on molluscan fossils from intertidal to shelf environments. These investigations have revealed precise spatio-temporal distributions of several molluscan assemblages in and around the Japanese Islands (Itoigawa, 1981, Chinzei, 1986, among others). In deposits representing deeper environments, such as bathyal zones or continental slopes,

invertebrates generally are very scarce, and paleoecological studies of benthic faunas for the most part remain to be conducted. Within such deep environments, echinoderms are sometimes proportionally dominant with respect to molluscs. However, because of their comparatively low preservation potential, fossil echinoderms from deeper environments have not yet been adequately investigated.

The present paper presents systematic descriptions of three species of Isocrinidae (*Teliocrinus springeri*, *Isocrinus* sp., and *Issellicrinus* sp.) from four different Japanese Miocene localities, and their biogeographic and evolutionary significances are also assessed in some detail.

Thus far, *Pentacrinus ariakensis* Yoko-

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yama is the only stalked crinoid so far described from the Tertiary of Japan (Yokoyama, 1911; Nagao, 1928). Sieverts (1932) described *Balanocrinus* sp. and *Metacrinus* sp. from the upper Miocene of Borneo and from the Pliocene of Sulawesi, respectively. Wanner (1938) described *Balanocrinus sundaicus* from the lower Miocene of Madura Island, north of Java. Klikushin (1977a) subsequently assigned the above two species of *Balanocrinus* to *Isselocrinus*; the revision seems appropriate owing to the diagnostic features of the columns. Klikushin (1977a) further pointed out a possibility that *Pentacrinus ariakensis* Yokoyama from the Paleogene of western Japan be placed in a species of *Isselocrinus*. Nevertheless, the data on Tertiary Isocrinidae from the western Pacific region remain scarce. Though still speculative, the new occurrence of Miocene isocrinids from Japan will provide important data on the biogeography of the Isocrinidae in this region.

The Recent isocrinid faunas of the Pacific show clear differences from those of the Indian Ocean. Each ocean is inhabited by an almost independent generic and species composition: *Metacrinus* in the Pacific and *Teliocrinus* in the Indian Ocean. It is important to consider how and when such characteristic faunas of each ocean became established, with respect to paleobiogeography and past plate movements. Previous discussions on paleobiogeography of marine invertebrates, including those of the stalked crinoids, have tended to emphasize origin and migration or dispersal rather than the concept of vicariance. Among the paleobiogeographic interpretations of stalked crinoids, Roux (1979, 1987) proposed that western Pacific and Atlantic Isocrinidae originated from a common Mesozoic Tethyan ancestral fauna ("faune Mesogée"), and migrated toward the present distributions. A comparison of the fossil records of the Tertiary Isocrinidae with the distribution of Recent species provides data that help to determine the relative merits

of the two concepts, dispersal and vicariance.

Recently, the paleobiogeography of South-east Asia has attracted increasing attention with respect to plate tectonics. The classic work by Wallace on the biogeography of the Malay archipelago has been reviewed in relation to continental movement and collision of Australia/New Guinea with Eurasia, and "Wallace's Line" has been reinterpreted as a remnant of an ancient suture between the continents (Audley-Charles, 1981; Hayami, 1987). The interpretation of Wallace's Line as a faunal boundary was based mostly on land animals and plants. Shallow-water marine invertebrates are thought to have enjoyed relatively free interchange between the western Pacific and the Indian Ocean. For example, Ekman (1953) showed many examples of marine animals that possess wide distribution both in the western Pacific and the Indian Ocean. Thus, the distribution pattern of the marine invertebrates is thought to exhibit less pronounced faunal boundaries in this region.

Material and occurrence

Three isocrinid species were collected from four different areas; Morozaki, Shobara, Ichishi and Hota in Honshu Island (Figure 1); each area was in a sedimentary basin that was separated from the others by topographic basement relief. Stratigraphic studies based on planktonic foraminifers, diatoms and pteropods (Shibata and Ishigaki, 1981; Koizumi, 1981; Ito, 1982; Doi, 1983; Watanabe, 1988), as well as paleomagnetic polarity (Hayashida and Ito, 1984; Hayashida, 1985, 1986) indicate that crinoid-bearing formations of Morozaki and Ichishi are late Early Miocene in age (N. 7-8 and N. 8 of subdivision by Blow (1969), respectively). The crinoid-bearing horizon of the Bihoku Group in Shobara has not yet been correlated precisely with microfossils, but the occurrence of Kadonosawa-type molluscs such as *Geloina yamanei* and *Vicarya callosa japonica* from a

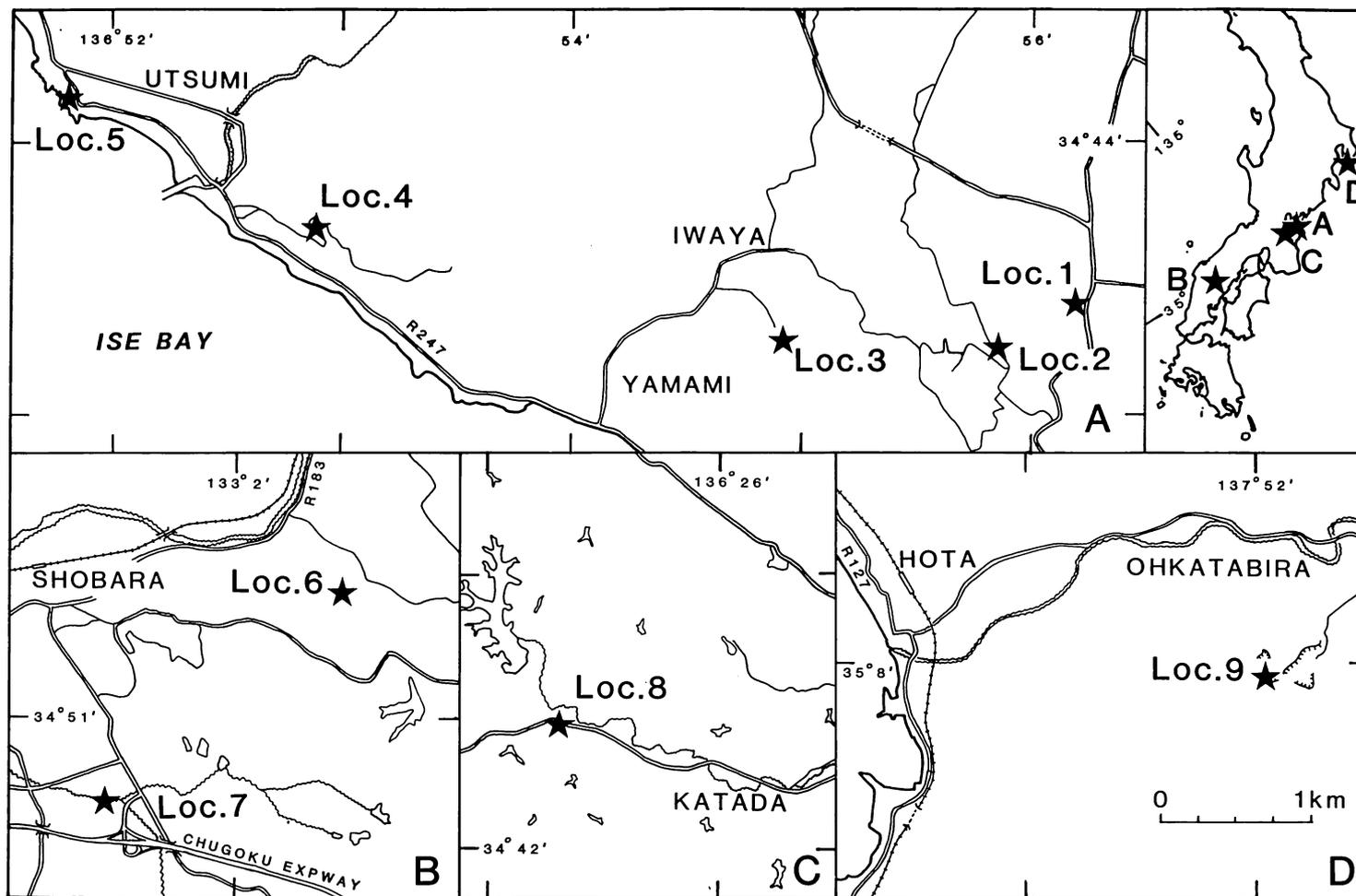


Figure 1. Localities of the Miocene crinoids from Japan. **A.** *Teliocrinus springeri* from the Yamami Formation, Morozaki Group (Locs. 1-5). **B.** *Isocrinus* sp. from the upper member of the Bihoku Group (Locs. 6, 7). **C.** *Isselocrinus* sp. from the Yakuoji Member, Katada Formation, Ichishi Group (Loc. 8). **D.** *Isselocrinus* sp. from the Ohkatabira Formation, Awa Group (Loc. 9).

slightly lower horizon (Okamoto and Terauchi, 1974) suggests that the age would be N. 8–N. 9; *i.e.*, late Early to early Middle Miocene. The fossil locality at Ohkatabira (Loc. 9) was previously assigned to an unnamed subdivision of the Hota Group (Mitsunashi *et al.*, 1984). More recently, it has been correlated to the Ohkatabira Formation of the Awa Group; early Middle Miocene, N. 9–10 (Watanabe, 1988). This horizon is stratigraphically equivalent to the lower part of the Amatsu Formation which is widely distributed in the southern part of Boso Peninsula.

The specimens described in this study are housed in the following institutions: Mizunami Fossil Museum (with prefix MFM), and University Museum, University of Tokyo (UMUT), except for the specimens of *Isoocrinus* sp. from Shobara which are partly housed in the University Museum (UMUT CE 18692–18699) and the private collection of S. Hirose.

1. *Teliocrinus springeri* (A.H. Clark) — Eight specimens were collected from the Yamami Formation of the Morozaki Group (Figure 1A). This formation is characterized by mudstone-dominated turbidites and mudstone, and is thought to represent an offshore environment (Shikama and Kase, 1976; Shibata, 1977).

Specimen 1 (MFM 38051) occurred within a thin fossiliferous layer, 15 cm above the base of a thick turbiditic siltstone (2 m) of the lower part of the Yamami Formation (Loc. 1). The turbidite bed consists mostly of silt-sized acid volcanoclasts, with graded bedding at the base. The crinoid specimen occurred associated with unidentified irregular sea urchins, mostly fragmentary. Fossils are restricted to this thin layer.

Specimen 2 (UMUT CE 18691) occurred in conglomeratic sandstone exposed at a road cut near Hajikami (Loc. 2). This horizon is correlated to the lower part of the Yamami Formation. The sandstone is poorly-sorted, containing intraclasts of pebble- to granule-

sized mudstone, fragments of ophiuroids, and indeterminate echinoderm ossicles.

Specimen 3 (MFM 38052) occurred at the base of a thick turbidite bed (4 m) exposed at a large cut beside a farm in Yamami (Loc. 3). The horizon is correlated to the middle part of the Yamami Formation. The turbidite bed consists of white pumiceous fine-grained tuff. At the locality, several beds of this tuff show graded bedding, with distinct parallel lamination near the base, and are interbedded with massive gray mudstone. These tuffaceous turbidites flowed into a deep environment under high-energy conditions, and were deposited rapidly. The fossil horizon consists of many plant fragments, associated sporadically with well-preserved fish skeletons, small ophiuroids and asteroids.

Specimen 4 (MFM 38053) occurred near the base of a turbiditic sandstone bed (15 cm), associated with abundant fragmentary molluscan shells, in the upper part of the Yamami Formation (Loc. 4). The sandstone is coarse- to medium-grained, contains intraclasts of mudstone, and shows conspicuous load casts at the base. All fossils were poorly preserved; the shells were completely dissolved, and concentrated in the lowermost part of the turbidite bed. They consist of *Dentalium* (*Fissidentalium*) *yokoyamai* and indeterminate gastropods.

Specimens 5 through 8 (MFM 38054A–38054D) occurred on a single slab of fine-grained sandstone exposed on the Utsumi coast (Loc. 5). These specimens are well preserved and the skeletons are almost intact, although the calcareous parts were entirely dissolved. This slab is thought to have originated from the sandstone of the same lithology exposed on the coast; the horizon is in the upper part of the Yamami Formation.

All the well-preserved specimens except for those from Locs. 2 and 5 were collected near the base of turbidite beds. The outcrop at Loc. 5 consists of massive fine-grained sandstone and a small amount of mudstone. The

slab from the Loc. 5 may also have been derived from a turbiditic sandstone layer, because the lithology is very similar and the stratigraphic position is correlatable to those of the locality of Specimen 4. The excellent state of preservation, despite their occurrence in turbiditic layers, suggests that these fragile crinoid skeletons were not subjected to substantial transport or disturbance. The specimens were probably subjected to rapid burial by turbidity flow while they were still alive, because they suffered almost no post-mortem disarticulation. Most notably, specimen 1 shows several arms disarticulated only at the cryptosyzygial articulations (Figures 4-4; 5-D), strongly suggesting that the specimen was buried while still alive, and autotomized its arms at the articulations.

2. *Isocrinus* sp.—318 specimens, all consisting entirely of fragmentary columns and columnals, were collected from a road cut at Shinchiku, Shobara, Hiroshima Prefecture (Figure 1B, Loc. 6). Several disarticulated columns of the same species occurred from gray massive siltstone exposed on the river floor of Togo-gawa (Loc. 7), 2.2 km southwest of Loc. 6.

The Bihoku Group in Shobara lies unconformably on a basement of acidic tuff, and consists of lower (approx. 26 m) and upper (more than 13 m) members (Okamoto, 1987). *Isocrinus* sp. occurred in the upper member. The lower member consists of poorly-sorted conglomeratic sandstone, and contains intertidal to shallow-water molluscs and other fossils, including *Vicarya callosa japonica* Yabe and Hatai, *Tateiwaia yamanarii* (Makiyama), *Glycymeris* sp., *Crassostrea* sp., *Geloina yamanei* Oyama and *Astryclypeus* sp. These fossils include Kadonosawa-type tropical and subtropical molluscs, characteristic of tidal flat and intertidal environment in the early Middle Miocene. The upper member consists predominantly of dark gray silty shale, with intercalations of fine-grained sandstone. It is less fossiliferous than the lower member, and contains disarticulated colum-

nals and columns of *Isocrinus* sp., *Dentalium* (*Fissidentalium*) *yokoyamai*, *Acila* sp., *Lucinoma* sp., turrid gastropods, a foraminifer *Dentalina* sp., galatheid crustaceans, and an ostracod *Cytherella* sp. (Yajima, 1988). Columns of *Isocrinus* were especially abundant in a patch near the base of the lower part. Of the species present, *Dentalium yokoyamai*, also lives in Recent waters around Japan, and is regarded as an occupant of the "bathynetric zone (from 100–120 to 200–250 m)" in the outer shelf to upper bathyal slope in southern Japan (Oyama, 1973). *Cytherella* sp. is considered a warm-water species and currently lives along the Pacific coast of southwest Japan (Yajima, 1988). Probably rapid transgression had occurred during the deposition of the lower and/or the upper parts.

3. *Isselocrinus* sp.—Two fragmentary columns (MFM 38055 and 38056), were collected from bioturbated siltstone in an abandoned quarry in Katada (Figure 1C, Loc. 8). The horizon is correlated to the Yakuoji Member, Katada Formation, Ichishi Group (Shibata, 1970). The Yakuoji Member consists mostly of alternating beds of sandstone and siltstone, and slump deposits of the alternating beds and intraclasts. Sandstone beds of the alternating beds are mostly turbidites, showing graded bedding at the bases.

Five fragmentary columnals (UMUT CE 18700—18704) were also collected from fossiliferous mudstone at a quarry in Ohkatabira, Kyonan-cho, Chiba Pref. (Figure 1D, Loc. 9). The most dominant fossils at Loc. 9 are disarticulated but well-preserved *Glycymeris cisshuensis*, and a small number of *Flabellum* sp. Crinoid columnals are scattered in gray mud with granules of chert.

Interpretation of paleozoogeography of the Pacific Cenozoic Isocrinidae

Information about the distribution of Isocrinidae during the Cenozoic time continues to be insufficient. However, important infor-

- ★ *Metacrinus & Saracrinus*
- * *Endoxocrinus*
- ☆ *Hypalocrinus*
- ⊗ *Teliocrinus*
- ⊕ *Issellicrinus*
- *Isocrinus*

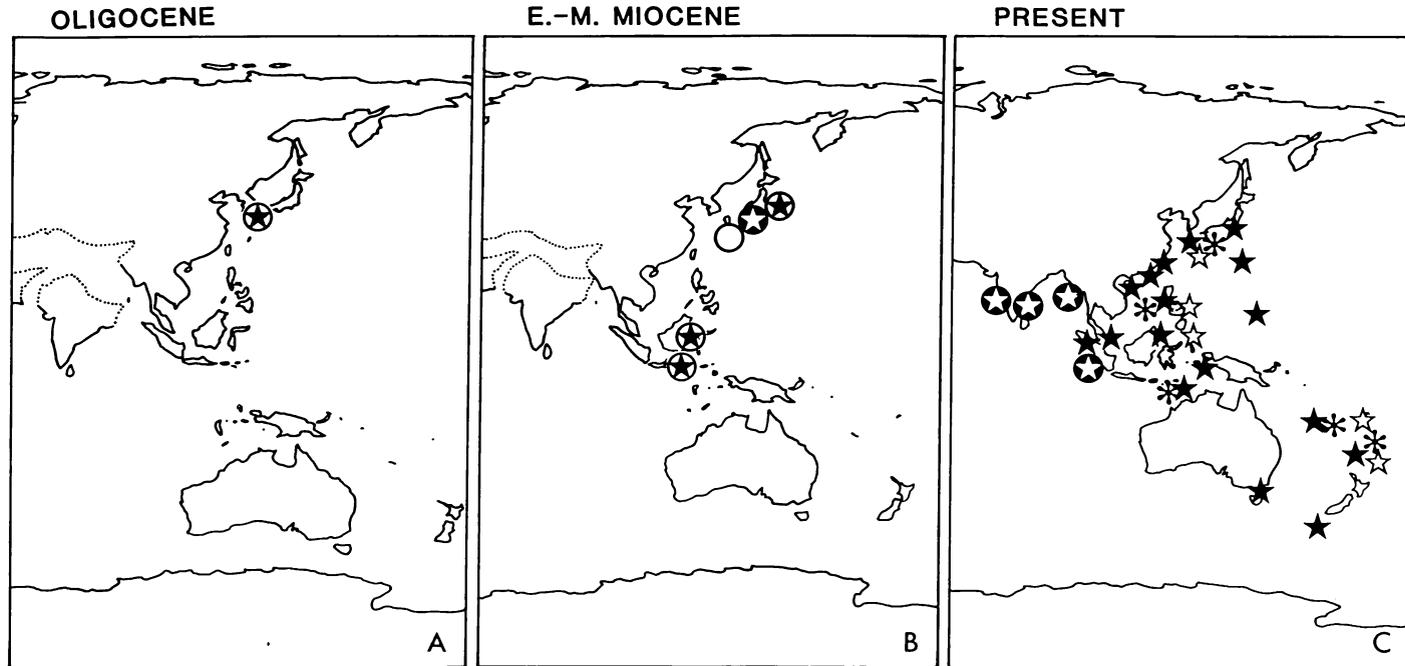


Figure 2. Occurrence of the Cenozoic Isocrinidae and the approximate position of continents at each time. Paleogeographic maps were based on Smith, Hurley and Briden (1981), with slight modification. **A:** Oligocene. **B:** Early to Middle Miocene. **C:** Recent. Note clear faunal separation of isocrinid fauna between today's Pacific and the Indian Ocean.

mation on the biogeography of isocrinids is nevertheless contained in several scattered records of occurrences of isocrinids from the Tertiary. These records include recent discoveries of Tertiary isocrinids that have extended the stratigraphic records of three genera back to the Tertiary. These genera had previously been considered only as Recent representatives in the Indo-Pacific regions.

Teliocrinus is the only isocrinid genus found in the tropical area of the Indian Ocean, and it is not distributed in other oceans. Species of *Metacrinus* and *Saracrinus* characterize tropical to warm-temperate area of the western Pacific, distributed dominantly from southern Japan to eastern Australia and New Caledonia (Figure 2C). There are, however, a few exceptional distributions reported outside this area. *Saracrinus nobilis* was reported off the western coast of Sumatra, (Döderlein, 1912). *Saracrinus nobilis*, *Saracrinus angulatus* and *Metacrinus varians* were recorded near the southern tip of Timor Island (Döderlein, 1907, Clark, 1932). Although species of *Metacrinus* and *Saracrinus* have also been reported from a few stations facing the Indian Ocean, they are restricted to the area along the southern coast of the Greater and Lesser Sundas. Therefore, *Metacrinus* and *Saracrinus* are principally regarded as Pacific elements, whereas *Teliocrinus* is an element of the Indian Ocean.

During the Miocene, however, a considerably different generic composition of Isocrinidae is recognized in the western Pacific region (Figure 2B). In Japan, *Teliocrinus* was found in deep environments, based on its representation in turbidite sequences and its association with other deep-sea fauna. Other isocrinids, including *Isocrinus* sp. and *Issellicrinus*, probably occupied shallower environments, such as the shelf-edge and upper slope. Species of *Issellicrinus* were also found in the Miocene of Borneo and the Madura Islands, suggesting a wide distribution at that time.

During the Miocene, there was presumably no *Metacrinus* and *Saracrinus*, which are the most dominant genera in the Japanese waters today (Oji, 1989). Therefore, a clear change of isocrinid faunal composition must have occurred after the late Early Miocene.

Although of different age, three other records of isocrinids from the Tertiary provide important data for the reconstruction of isocrinid paleobiogeography. The first is an occurrence of *Metacrinus* from the Eocene of Seymour Island, Antarctic Peninsula (Rasmussen, 1979; Meyer and Oji, 1988). This occurrence indicates that *Metacrinus* already existed as early as the Eocene, although it presumably was not distributed in the Pacific at that time. This genus has probably migrated to the Pacific and has diversified after the Middle Miocene. Secondly, there is an occurrence of two species of *Isocrinus*, *I. oregonensis* and *I. nehaemensis*, in the Oligocene near the Pacific coast of Oregon, USA (Moore and Vokes, 1953). *Isocrinus* sp. from Shobara described here is morphologically very similar, suggesting a strong relationship to the *Isocrinus* species from Oregon. These *Isocrinus* species existed during the Oligocene to Miocene, but have since disappeared from the Pacific. Finally, an excellent specimen of Isocrinidae, which is similar to *Hypalocrinus*, was recently discovered from the Eocene of northwest Washington, USA (Franzén-Bengtson in preparation). *Hypalocrinus* had also been represented only by a recent deep-water Pacific species, *H. naresianus*.

Figure 3 summarizes isocrinid occurrences from the Indo-Pacific region in the Cenozoic. Comparison of the distribution of isocrinid faunas at different times leads to the following three hypotheses:

(1) *Teliocrinus* has disappeared from the Pacific, and is now found only in the Indian Ocean. *Isocrinus* also disappeared from the Pacific after Middle Miocene. *Issellicrinus* had a wide distribution in the Miocene of the western Atlantic, western Tethys (Italy) and

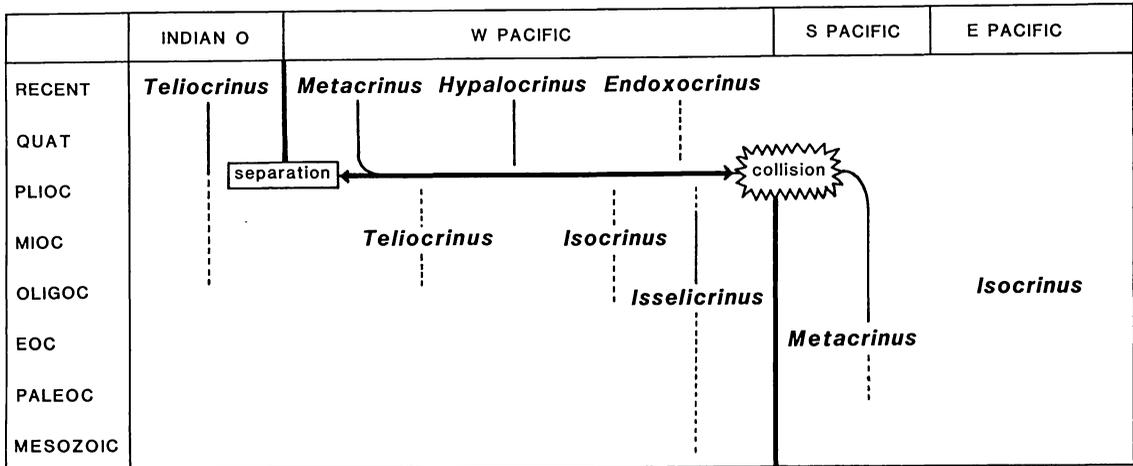


Figure 3. Schematic spatio-temporal distribution of Isocrinidae of the Pacific. A collision of Australia/New Guinea has probably brought *Metacrinus* into the Pacific region, and it has also established wide epicontinental seas between the Pacific and the Indian Oceans, which has become a barrier to the isocrinid faunas.

western Pacific (Borneo, Madura and Japan), whereas it has disappeared entirely since the Miocene.

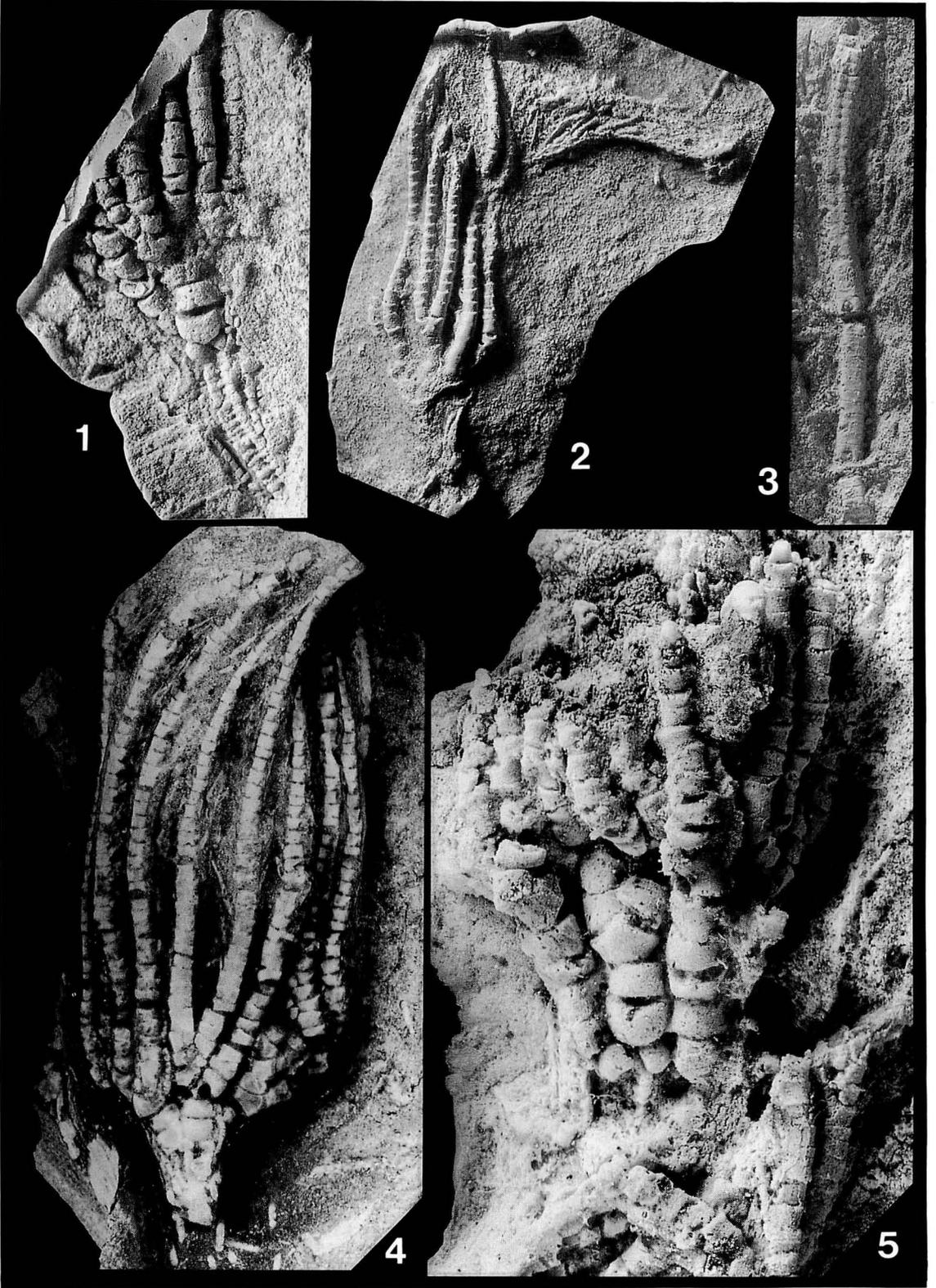
(2) *Metacrinus* already lived in the marginal seas of the Gondwana during the Eocene, at least in an area of Antarctic Peninsula, and entered the western Pacific after the Miocene.

(3) The recent distribution patterns of Isocrinidae show that there are almost no common species between the Pacific and the Indian Oceans. A significant barrier seems to exist along the archipelago in Indonesia.

According to a reconstruction of paleogeographic distribution of lands and oceans in the Eocene to Miocene (Smith, Hurley and Briden, 1981), there was a wide opening of ocean, forming a part of the eastern Tethys, between Eurasia and a part of Gondwana, connecting the present Pacific and the Indian Oceans. Therefore, there was no distinct barrier between the Pacific and the Indian Oceans (Figure 2A). Such a wide passage may have enabled the interchange of deep-sea faunas like crinoids along its northern coast. *Teliocrinus* had probably inhabited both the Pacific and the Indian Oceans since the Miocene. Subsequently, because of the

northward movement of Australia/New Guinea to Eurasia, this seaway has gradually interrupted to form an archipelago (Audley-Charles, 1981) and probably created a large shallow shelf in this area. After the establishment of the archipelago and shallow seas between the two oceans, and following immigration of *Metacrinus*, interchange of isocrinids may have become interrupted by this barrier; *Teliocrinus* was replaced by *Metacrinus* in the Pacific and a characteristic fauna has been formed in each ocean.

As for the comatulid (stalkless) crinoids, A. H. Clark (1937) pointed out a strong similarity between the western Pacific and the Indian Ocean, noting: "The crinoid fauna of the Indian Ocean is simply the progressively depauperate western extension of the very rich fauna that has its centre in the region of the large Malayan islands." (Clark, 1937, p. 103). According to the compilation of comatulids of Japan by Utinomi and Kogo (1968), more than 30% of comasterid species of Japanese water are also found in the Indian Ocean. This figure clearly contrasts with the lack of isocrinid species living widely in the both oceans. Many of the comatulids live in much shallower water, and consequently, the



Indonesian and Malayan archipelagos and wide shelf area do not constitute a significant barrier for such comatulids. The different distribution patterns of isocrinids and comatulids imply that such an archipelago can be a barrier for only the deep sea fauna, whereas it might not be a barrier for the shallow water fauna. Other than crinoids, Ekman (1953) presented that many vertebrates and invertebrates living in shallow waters have their distributions both in the Pacific and the Indian Ocean. Further investigation on the deep-sea faunas in this region will provide more information whether they possess different patterns of distribution in the both oceans or not.

Systematic description

Family Isocrinidae, Gislén, 1924

Genus *Teliocrinus* Döderlein, 1912

Synonym: *Comastrocrinus* A.H. Clark, 1912.

Type species: *Hypalocrinus springeri* A.H. Clark, 1909.

Diagnosis: An isocrinid with cryptosyzygial articulation in primibrachials and frequently with synarthry between first and second secundibrachials. First pinnule on first secundibrachial of outer division and on second secundibrachial of inner division. Relatively long and slender cirri.

Remarks: *Teliocrinus* was firstly introduced as a monospecific genus for a species of Isocrinidae from the Indian Ocean. Döderlein (1912) thought that this species, *Teliocrinus asper*, was a new species. In the same year, A.H. Clark (1912) proposed *Comastrocrinus* for three species, one of which was pre-described species, *C. springeri* (type species *Hypalocrinus springeri*, A.H. Clark, 1909), and two of which he thought were new,

from the Indian Ocean; *C. liliaceus* and *C. ornatus*. Later, A.H. Clark (1923) assigned *T. asper* as the same species to *T. springeri*. Therefore *Comastrocrinus* was replaced by *Teliocrinus*.

According to a compilation of isocrinid species by A.H. Clark (1923), *Teliocrinus* consists of three species, all of which came from the Indian Ocean. A.H. Clark (1912) discriminated *Teliocrinus ornatus* from *T. springeri* only by its small size. Four specimens assigned to *T. ornatus* by A.H. Clark were collected from the same station at which *T. springeri* was also collected. *T. ornatus* should be regarded as relatively young individuals of *T. springeri*. *T. liliaceus* was collected at two stations off Burma. Because of the wide distribution of *T. springeri* from the west coast of India to Burma and off the west coast of Sumatra Island, the distribution of *T. liliaceus* is included entirely in that of *T. springeri*. *T. liliaceus* was distinguished from *T. springeri* by its less prominent eversion of the distal end of the proximal brachials. This character may be considered as intraspecific variation, because such variation is often observed in a population of a single species. H.L. Clark (1928) proposed another species, *Teliocrinus monarthrus*, based on a single specimen from an unknown locality (off the northern coast of Australia?). According to H.L. Clark, this species is distinguished by "having fewer internodals, much more spiny cirri, and only a single segment in the IIIBr series". The number of internodal plates usually shows considerable variation within a species of Isocrinidae, and this can not be a good criterion. As for the number of tertibrachials, as long as there are further divisions distally, specimens of *Teliocrinus* kept in the Smithsonian Institution have four (one case in the specimen USNM 35995, one case in USNM 36068), or three

← **Figure 4.** *Teliocrinus springeri* (A.H. Clark) from the Morozaki Group. 1: Specimen 4 (MFM 38053) from Utsumi, Loc. 4. ×2.4. 2: Specimen 7 (MFM 38054C) from Utsumi coast, Loc. 5. ×1.7. 3: Specimen 2 (UMUT CE18691) from Hajikami, Loc. 2. ×1.65. 4: Specimen 1 (MFM 38051) from Loc. 1. ×1.8. 5: Specimen 5 (MFM 38054A) from Utsumi coast, Loc. 5. ×3.8.

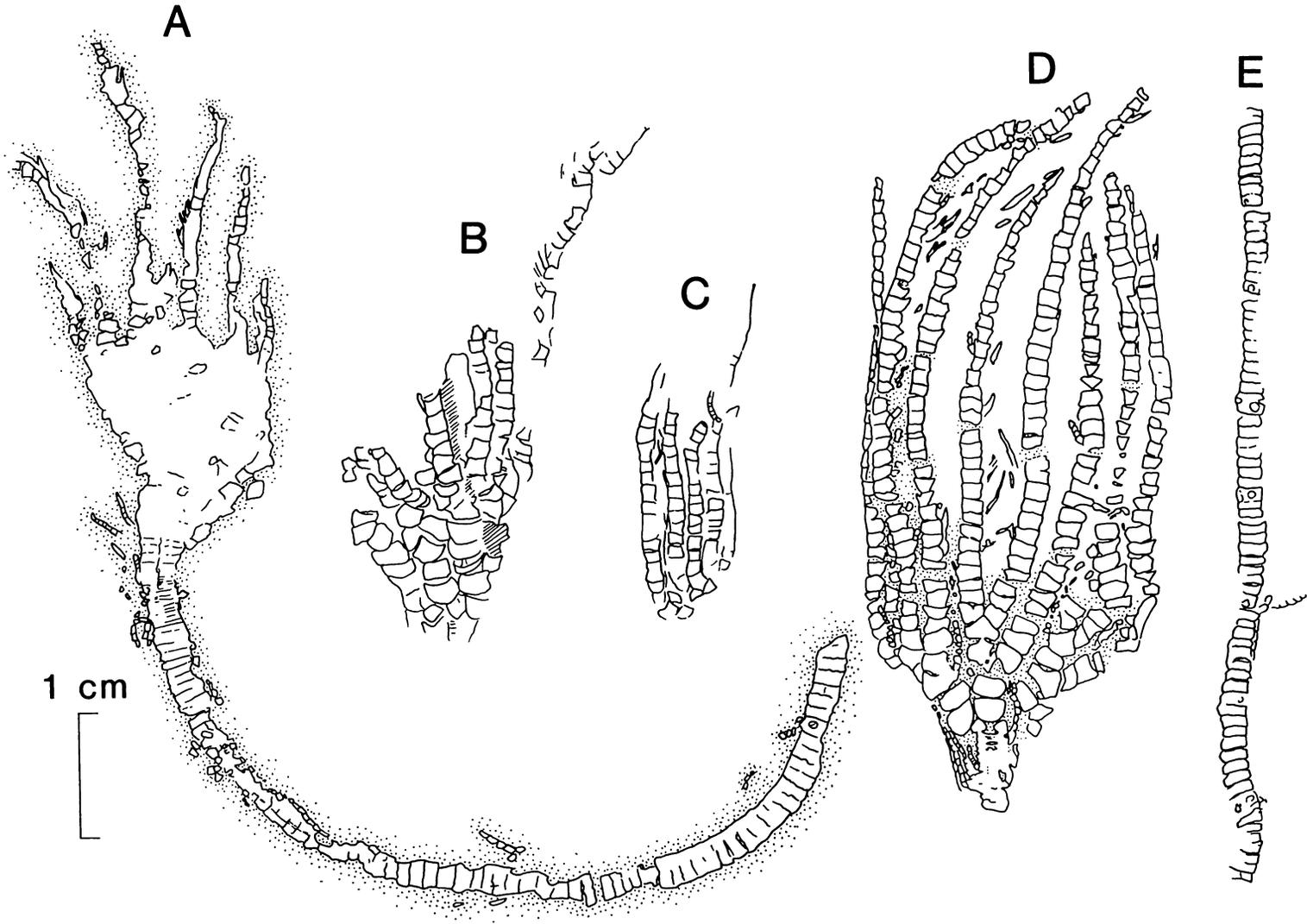


Figure 5. Camera lucida drawings of *Teliocrinus springeri* (A.H. Clark) from the Yamami Formation, Morozaki Group. **A:** Specimen 3 (MFM 38052) from Yamami (Loc. 3). **B:** Specimen 5 (MFM 38054A) from Utsumi coast (Loc. 5). **C:** Specimen 6 (MFM 38054B) from Utsumi coast (Loc. 5). **D:** Specimen 1 (MFM 38051) from Loc. 1. **E:** Specimen 8 (MFM 38054D) from Utsumi coast (Loc. 5).

(three cases in USNM 35995) tertibrachials. Six specimens collected by the Siboga Expedition (Döderlein, 1912) shows wider variation in the number of tertibrachials: one (three cases), two (four cases), three (three cases) and four (two cases). In the other species like *Endoxocrinus parrae* where intraspecific variation is recognizable owing to a large number of specimens, the number of plates in a brachitaxis shows rather wide variation. *T. monarthrus* would therefore be better treated as a synonym of *T. springeri*.

From the viewpoint of ligamentary articulation between the brachials, *Teliocrinus* is included as a member of the new group (Oji, 1985), which is characterized by having cryptosyzygy instead of synarthry in primibrachials. However, at least some of the proximal ligamentary articulations are synarthrial, especially in IIBr1-2. The common presence of a synarthry within species of the new group suggests that *Teliocrinus*, as *Nielsenicrinus*, has features intermediate between the two groups.

Geographic and stratigraphic distribution: Late Early Miocene (Japan) and Recent (Indian Ocean, from the west coast of Indian Peninsula through Burma to the southern coast of Sumatra).

Teliocrinus springeri (A.H. Clark, 1909)

Figures 4-1-4; 6-1-3

Hyalocrinus springeri A.H. Clark, 1909

Teliocrinus asper Döderlein, 1912

Comastrocrinus springeri A.H. Clark, 1912

Comastrocrinus liliaceous A.H. Clark, 1912

Comastrocrinus ornatus A.H. Clark, 1912

Teliocrinus springeri, Roux, 1977

Teliocrinus springeri, Rasmussen, 1978

Diagnosis: As for the generic diagnosis.

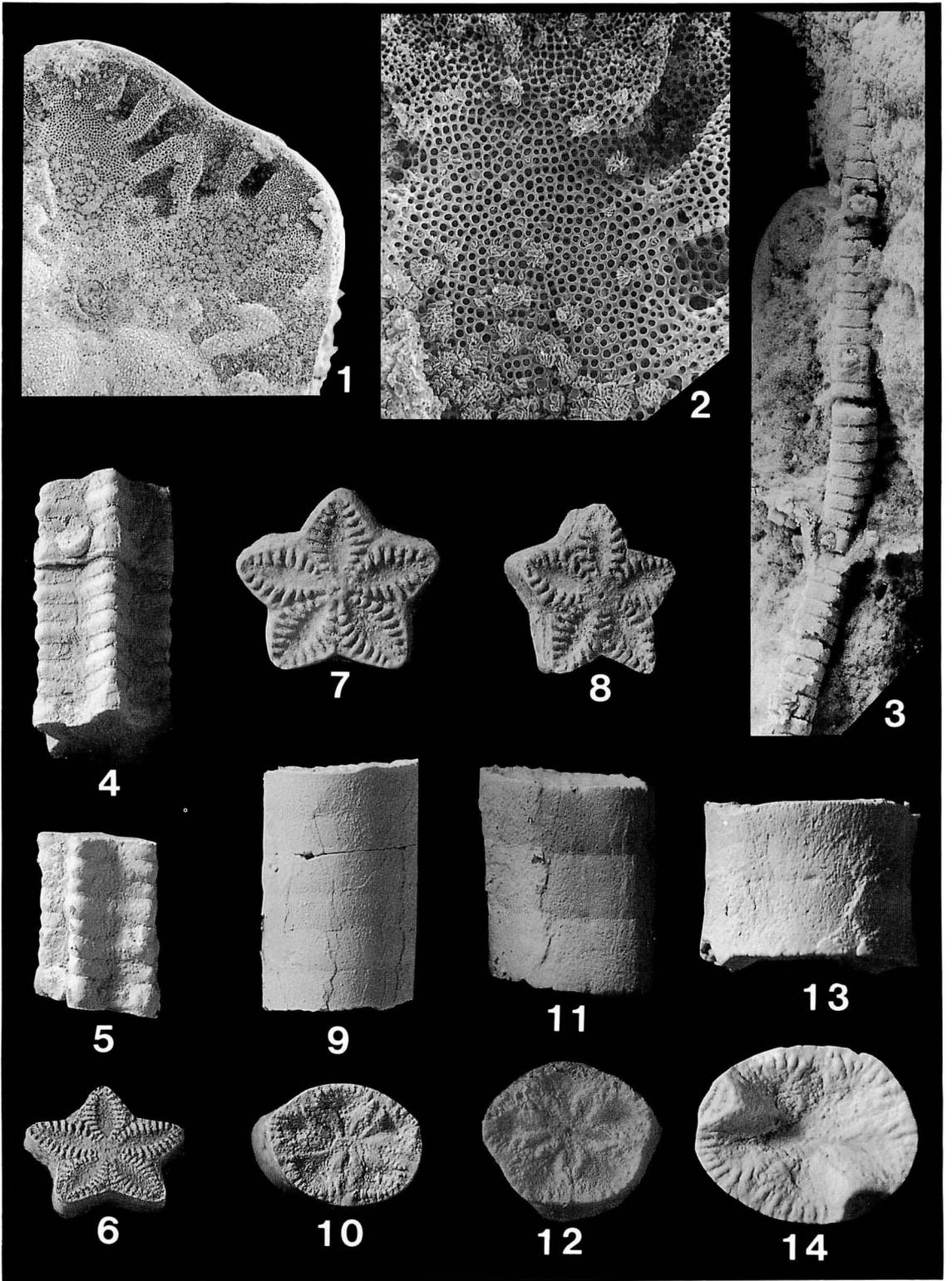
Description: Specimen 1: Basals are small, rounded and separated on dorsal surface. Radials are high, three fourth as high as width. First primibrachial (IBr1) is wider than high, showing cryptosyzygial articula-

tion with second primibrachial (IBr2). IBr2 is first axillary, modified pentagonal on dorsal surface. In three rays, secundibrach consists of two brachials in IIBrT ray on dorsal view, and they give rise to tertibrachs, whereas secundibrach on right side shows no branching. Secundibrachs on right side presumably have synarthry (at least in two rays). Secundibrachs on right side have cryptosyzygy between third and fourth brachials. No other division is observed. Finales taper gradually toward tips. Cryptosyzygies are distributed at an approximately regular interval. Most cryptosyzygies are disarticulated, and hypozygal and epizygal are detached slightly. Only very proximal part of column is preserved. This part is very cirriferous, some cirri reach as far as secundibrach.

Specimen 2: This specimen consists only of a long column. Proximal column has radial pores. Most proximal columnals are very thin and pentalobate in section. Medium to distal portion of column is smooth on surface, rounded pentagonal in section. Nodals are slightly higher than internodals. Cirral socket is large, occupying almost entire height of nodal and interfering hypozygal as a depression. Number of internodals is 2+, 10?, 11, 11, 12 and 9+ from proximal to distal internodals. Columnal articulation shows typical symplexy with distinct crenulae. There is gradual transition in size of crenulae from adradial to marginal position. Total number of crenulae is four to five around one petal. There is no conspicuous radial groove. Petal is subguttiform and it possesses galleried stereom with rounded mesh.

Specimen 3: This specimen consists of a crown and column. Detailed character and morphology of proximal crown are unknown because of the poor state of preservation. Number of distal arms is at least six, probably more. Internodals are presumably seven or eight, according to the distribution of fragmentary cirri. Cirri are short and slender.

Specimen 4: This specimen consists of a



calyx, proximal arms and a proximal column. Basals are relatively large and rounded, separated on surface. Radials are large, three fourths as high as width, pentagonal in dorsal surface. Distal edge of radial is smooth and slightly convex, giving straight muscular articulation with first primibrachial. First primibrachial (IBr1) is cylindrical, slightly narrower than radial. IBr2 is axillary. Articulation IBr1-2 is presumably cryptosyzygial, giving straight suture on dorsal surface. There are two secundibrachs, each possessing two brachials. At least one IIBr1-2 is possibly synarthrial. IIBr2 is axillary. No further division is observable. Proximal columnals are alternating in height and width, and stellate in section. Radial pores between columnals are observable at least up to fifth internode.

Specimen 5: This specimen consists of a calyx, proximal arms and a distal arms. Basals are moderate in size, rounded rhombic and separated on dorsal surface. Radials are large, with rounded proximal and convex distal edges. IBr1 is cylindrical and slightly narrower than radial. IBr2 is axillary, pentagonal in dorsal surface. Articulation IBr1-2 is presumably cryptosyzygial. Most distal arms are at least 11 in number.

Specimen 6: Only poorly-preserved small specimen with five arms impressed as a mold on sandstone. Arms are undivided except for a pair of arms, which fork from primaxillary.

Specimen 7: Small-sized specimen with proximal to distal arms. Basals and radials are scarcely preserved. IBr1 is cylindrical, wider than high. IBr2 is axillary, low tri-

angular on dorsal surface. IIBr1-2 is presumably muscular. IIBr2-3 is cryptosyzygial. Other cryptosyzygies are observed at IIBr10-11 in one arm, IIBr13-14 in the other. Distal arms have long and fine pinnules.

Specimen 8: Only long column, consists of eight noditaxes. Number of internodals in each noditaxis is 8 or more, 7, 9, 7, 9, 8, 8 and 7 or 8 from proximal to distal internodes.

Remarks: Specimens from the Morozaki Group are safely assigned to *Teliocrinus* Döderlein 1912 because they have smooth columns with slender and short cirri, relatively long internods, ramification patterns and possession of both cryptosyzygial and synarthrial articulations. Difference in arm ramification among Morozaki specimens may well be attributed to the different growth stages they belong to. *T. springeri* was previously known only from the present Indian Ocean. Although they are ca. 16 Ma apart, the Morozaki specimens show no essential differences from the Recent specimens of *T. springeri*, in morphology of column, columnal articulations, slender cirri, arm branching pattern including the number of arms, arrangement of ligamentary articulations, and morphologies of brachials. Therefore, I am of the opinion that Morozaki specimens should be assigned to *T. springeri*.

Genus *Isocrinus* von Meyer, 1836

Isocrinus sp.

Figures 6-4-8

Description: Columnals are slightly alter-

← **Figure 6.** 1-3: *Teliocrinus springeri* (A.H. Clark) from the Morozaki Group. 1, 2: Scanning electron micrographs of articular facet of a columnal, specimen 2 (UMUT CE18691) from Hajikami, Loc. 2. $\times 27$ and $\times 91$. 3: Specimen 8 (MFM 38054D) from Utsumi coast, Loc 5. $\times 3.4$ 4-8: *Isocrinus* sp. from a road cut at Shinchiku (Loc. 6), the Bihoku Group. 4, 5: Part of columns (UMUT CE18692 and CE18693). $\times 3.0$. 6-8: Columnals (CE 18694-CE18696). $\times 3.0$, $\times 2.9$ and $\times 2.9$. 9-14: *Isselicrinus* sp. 9, 10: A part of column and articular facet (MFM 38055) from Yakuoji (Loc. 8), Ichishi Group. $\times 3.3$ 11, 12: A part of column and articular facet (CE 18701) from Ohkatabira (Loc. 9), Awa Group. $\times 5.0$. 13, 14: A part of column with nodal, and articular facet of the distal facet of nodal (CE 18702) from Ohkatabira (Loc. 9), Awa Group. $\times 4.7$.

nating in height and degree of inflation in most columns, and eminently alternating in proximal columns. Internodals are stellate and nodals pentalobate in section. Lateral surface of internodals is almost flat or a little inflating, and large columnals show lateral horizontal crests. Cirrus socket is always five in number, large in small specimens, occupying almost entire height of the nodal, and it is also large, but proportionally slightly smaller in large specimens. Distal articulation of nodals is synostiosial, and it is concave, surrounded by raised edge. Articular facet of internodals have nine to ten crenulae, and there is gradual transition in size from adradial to marginal crenulae, attaining their greatest length in the middle. Petal is lanceolate.

Remarks: The generic assignment of this species to *Isocrinus* is tentative, because the diagnostic features of *Isocrinus*, *i.e.* combination of the arm articulation types (synarthrial articulation between primibrachials and IIBr1-2, and cryptosyzygial or symmorphial articulation in IIBr3-4) are not observed in the present collection. This species is presumably closely related to *Isocrinus oregonensis* and *Isocrinus nehalemensis* from the Oligocene or Eocene of Oregon (Moore and Vokes, 1953), because (1) external morphology of columnals are quite similar, *i.e.* general size of columns, tumidity of a columnal, not so rounded pentagonal transverse section of column, and height of a columnal, (2) number of internodals is similar (dominantly 7, sometimes 8, rarely 6 or 9 in the present species). Most specimens were subjected to deformation because of post-burial compaction. This is probably related to the argillaceous and soft lithology of the bed. Of the specimens with at least one complete noditaxis, the number of internodals is five to nine: 5 (one case), 6 (two cases), 7 (58), 8 (14), 9 (5). Of the 318 columns and columnals, five specimens show tetragonal outline. Klikushin (1977b) reported similar abnormality for a Paleogene species *Cainocrinus gorbachae*.

This abnormality probably originated from four instead of five basal plates in the calyx. The present specimens show higher frequency of such an abnormality (5/318) than *Cainocrinus gorbachae* (2/1076).

Genus *Issellicrinus* Rovertó 1914
emend. Rasmussen 1954

Remarks: Among isocrinid genera, *Issellicrinus* is defined by the following characteristics: less than five, usually two to three cirral bases on the lower edge of the nodal, long internode, and conspicuous and uniform peripheral crenulae and adradial ridges on the articular facet of columnals (Rasmussen, 1978, Klikushin, 1977a). Many species from the Maastrichtian, Danian to Eocene, and rarely from Oligocene and Miocene are included in this genus (Klikushin, 1977a). Maastrichtian to Paleogene species show relatively wide distribution, especially well-known in Europe, whereas *Issellicrinus* has declined and presumably extinct in the Neogene (probably Miocene). Miocene species have hitherto been described from Italy (Noelli, 1900), Haiti (Springer, 1925), Madura Island, north of Java (Wanner, 1938) and Borneo (Sieverts, 1932). Morphology of columnals of the Japanese species is most similar to *Issellicrinus sundaicus* (Wanner) from Madura Island, although reliable identification of the Japanese species is difficult because of its fragmentary state of preservation. Isocrinids generally show considerable variation in stalk morphology, and the species of *Issellicrinus* must be reviewed from the viewpoint of intraspecific variation. Klikushin (1977a) proposed a subdivision of this genus into three subgenera, *Praeissellicrinus*, *Buchicrinus* and *Issellicrinus*, mainly on the basis of the degree of crenulation or its absence on articular facet below nodal plate. Most of the Recent species of Isocrinidae like *Metacrinus rotundus* show relatively well-defined crenulation on a facet below nodal of the proximal part of the column, whereas it becomes flattened toward the distal part.

Therefore, careful review of this character will be needed.

Isselicrinus sp.

Figures 6-9—14

Description: Specimens from Yakuoji, Ichishi: Larger specimen (MFM 38055) has six internodals, smaller specimen (MFM 38056) has three internodals. Outline of columnals is elliptical, because of post-burial compaction. Lateral surface of column is smooth and with no conspicuous inflation or depression in larger specimen (MFM 38055), whereas it is slightly depressed at suture between columnals in smaller specimen (MFM 38056). Suture is almost straight on surface. Articular facet of columnals shows distinct marginal crenulae, 7-8 in number in larger specimen and 8-9 in smaller specimen. Crenulae becomes longer toward radial direction. Adradial ridges are conspicuous and they are broadest in the middle.

Specimens from Ohkatabira, Awa: Outline of columnals is elliptical, also due to post-burial compaction. Most specimens consist of two columnals, and lateral surface of columnals are smooth but depressed toward suture between columnals. One nodal plate (UMUT CE 18700) possesses two cirral bases. They are directed obliquely downward. Several internodal plates below nodal possess longitudinal depressions on lateral surface of columnals, corresponding presumably down-directed cirri. Facet below nodal is concave, having conspicuous marginal crenulae. Articulation between internodals is similar to that of the specimens from Yakuoji.

Remarks: The present species shows rather conspicuous crenulation on the articular facet of the columnals, a nodal with two cirral bases, and thus classified under the subgenus *Isselicrinus*, if we follow Klikushin's classification. These were obtained from two slightly different horizons

of two areas, Yakuoji of the Ichishi Group (N. 7-8) and Ohkatabira of the Awa Group (N. 9-10). All specimens show considerable similarity of columnal morphologies, such as smooth lateral surface of columnals and distribution of crenulation on the columnal articulation. Several specimens from Ohkatabira show weak but prominent periodic constrictions at the suture of two adjacent columnals.

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日本産中新世ゴカクウミユリ科とその生物地理的意義; ゴカクウミユリ科3種を日本の中新統より記載し, その生物地理的意義を考察する。師崎層群産 *Teliocrinus* は従来インド洋の現生種によってのみ知られていた同属の記録を中新世に溯らせた。備北層群産 *Isoocrinus* sp. は西部オレゴン州産の種に酷似する。一志層群, 安房層群産 *Isselicerinus* sp. は, この属の最後の代表者の1つである。顕著な種構成の入れ替りが中新世と現在の間に西太平洋地域に認められる。この変化は *Teliocrinus*, *Isoocrinus*, *Isselicerinus* 各属が同地域より姿を消し, *Metacrinus* と *Saracrinus* が同地域にもたらされたことである。この説明として, ゴンドワナの一部(オーストラリアとニューギニア)とユーラシアの衝突が考えられる。この衝突により *Metacrinus* が西太平洋地域にもたらされ, また衝突によって生じた浅海域が障壁となり, 両大洋のゴカクウミユリ科を分けるに至ったと解釈される。 大路樹生

SHORT NOTES

**23. A NEW METHOD TO EVALUATE DISSOLUTION OF CaCO_3
IN THE DEEP-SEA SEDIMENTS***

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Introduction

The most part of CaCO_3 stored in deep-sea sediments is produced in the sea-surface by planktonic foraminifers and calcareous nannoplanktons. The CaCO_3 sinks down to the sea floor through water column and is deposited there. Accumulation of CaCO_3 is affected by its dissolution in the deep-sea as well as production in the sea-surface. While the CaCO_3 production reflects environment of the sea-surface, its dissolution does that of the deep-sea. Evaluation of the degree of dissolution is essentially important to analyze the change in deep-sea paleoenvironment.

Three methods have been generally employed to evaluate degree of CaCO_3 dissolution: (1) Solution Index (Berger, 1968); (2) the ratio of planktonic to benthic foraminifers; and (3) the ratio of fragmented to perfect tests of planktonic foraminifers. The Solution Index is based on the difference of dissolution among species of planktonic foraminifers; ratio of species more resistant to dissolution and those less resistant. However, fossil assemblage content of planktonic foraminifers is effected by the initial assemblage as well as dissolution. It is impossible to estimate accurately the degree of dissolution from the Solution Index. The other two methods are also insufficient because the initial ratio of planktonic to benthic for-

aminifers or the initial composition of planktonic foraminiferal assemblage is not always definite.

Oba (1969) divided a planktonic foraminifer, *Globorotalia menardii*, into three types with respect to preservation of the tests (the perfect, damaged, and fragmented) and evaluated the degree of dissolution from the ratio among the three types. This method using only *G. menardii* is better than the other methods, because it is expected to be affected by dissolution but not environmental changes. In spite of that this method was developed to estimate the amount of CaCO_3 dissolution (Oba and Ku, 1977; Ku and Oba, 1978), works employing the method were so far only a few (Oba, 1983).

Several papers have reported on selective dissolution of calcareous nannofossils (McIntyre and McIntyre 1971; Berger, 1973; Roth and Coulbourn, 1982), but, unlike foraminifers, calcareous nannofossils are rarely used to evaluate CaCO_3 dissolution in the deep-sea sediments. It was difficult to not only observe them in detail under a light microscope for their small size but also to express their degree of dissolution objectively.

The purpose of this paper is to propose a new method to evaluate the degree of CaCO_3 dissolution in deep-sea sediments by calcareous nannofossils and then to substantiate its usefulness by comparing with the other method by a planktonic foraminifer (*G. menardii*).

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Method and samples

A calcareous nannofossil, *Calcidiscus leptoporus* has two shields (distal and proximal) which are connected with a central column. Schneidermann (1977) investigated selective dissolution of nannoflora in core-top sediments and showed a distinctive pattern of dissolution in *C. leptoporus*. The two shields of well-preserved *C. leptoporus* are connected each other. When dissolution proceeds, however, either the proximal shield tends to dissolve along the suture line or the central column is dissolved to separate two shields. Only distal shields tend to occur in intensively dissolved samples.

In this work the manner of preservation in *C. leptoporus* dissolution is adopted to evaluate CaCO_3 dissolution. Fossil coccoliths of *C. leptoporus* is divided into two types, the perfect one with two shields and the broken one with only distal shield (Figure 1); a

coccolith with distal shield and a part of proximal shield is included in perfect coccolith. The ratio of the two types is employed as a criterion to evaluate degree of CaCO_3 dissolution.

The piston core "KH84-1, St. 21" was recovered from the deep-sea floor at west-flank of the West Mariana Ridge (19°55.8'N, 142°22.3'E; water depth of 3512 m) during KH84-1 cruise of R/V Hakuho-Maru of Ocean Research Institute, University of Tokyo (Figure 2). The core is 916 cm long, essentially composed of olive calcareous ooze and intercalates thin layers of tephra and sandy silt (Kobayashi, 1985). The base of Brunhes Epoch is located at 498 cm (sub-bottom depth) and the top and base of the Jaramillo event at 620 cm and 670 cm, respectively from paleomagnetic measurement (Kobayashi *et al.*, personal comm.). The sedimentation rate of the core is to be about 0.7 cm/Ky. Two major biostratigraphic

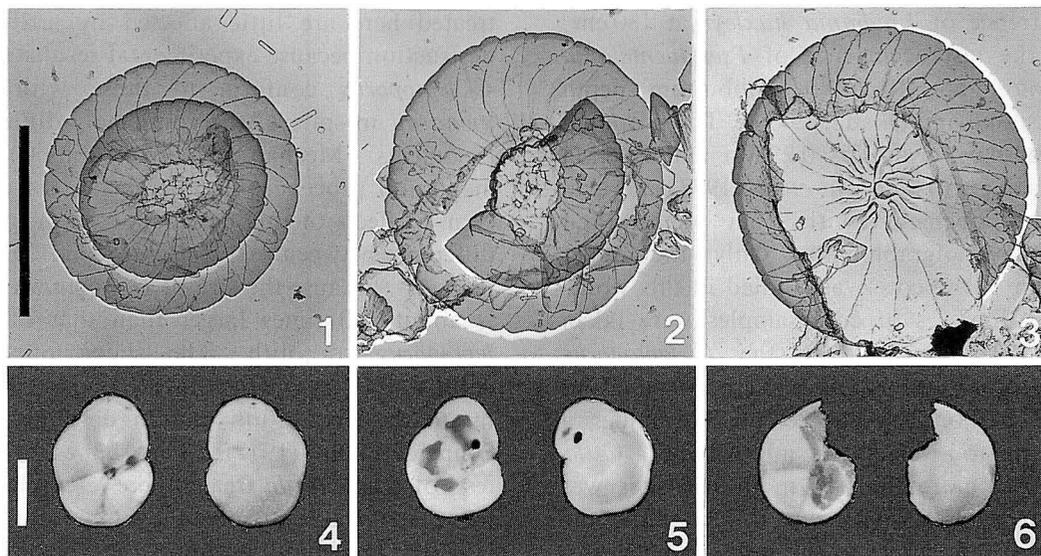


Figure 1. Photographs 1, 2 and 3 are electron micrographs and the scale bar in photograph 1 represents 5 μm . Photographs 4, 5 and 6 are optical micrographs and the scale bar in photograph 4 represents 500 μm . 1-3, *Calcidiscus leptoporus* (Murray and Blackman), Sample at 90 cm (subbottom depth): 1, proximal view of perfect coccolith (distal and proximal shield); 2, proximal view of perfect coccolith (distal shield and a part of proximal shield); 3, proximal view of broken coccolith (distal shield). 4-6, *Globorotalia menardii* (Parker, Jones and Brady), Sample at 1 cm (subbottom depth): 4, perfect test; 5, damaged test; 6, fragmented test.

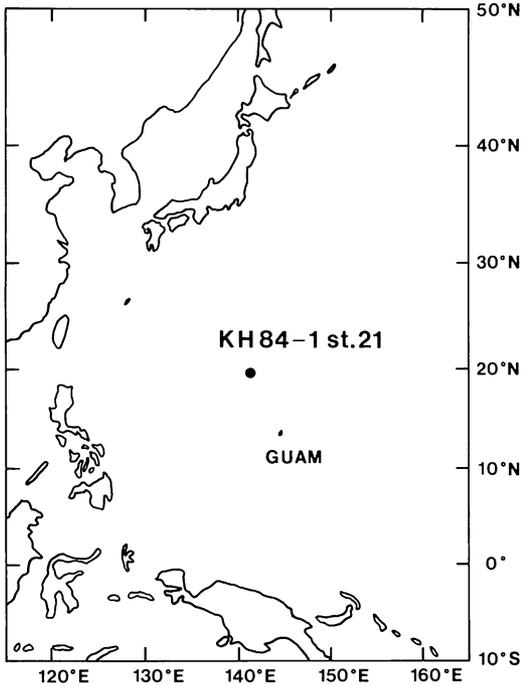


Figure 2. Locality of Core KH84-1 St. 21.

events of nannofossils are founded: the first occurrence of *Emiliana huxleyi* at 180 cm; and the last occurrence of *Pseudoemiliana lacunosa* at 310 cm in subbottom depth (Matsuoka and Okada, 1989). The proposed age of these events is 0.27 Ma and 0.46 Ma respectively (Thierstein *et al.*, 1977) and is in good agreement with that determined magnetostratigraphically. Only the upper 600 cm of the core was studied in this work.

Small pieces of core samples were taken with 10 cm-interval for the *C. leptoporus* analysis. These samples were prepared to make carbon replicas to observe under a transmission electron microscope. *C. leptoporus* more than 5 μm in diameter was counted to 50 specimens to determine the ratio of the perfect to the broken coccoliths. Between 210 cm and 320 cm in the subbottom depth, however, the samples of *C. leptoporus* were counted to 100 specimens with smear slide under a light microscope because of its scarcity.

About 3 g core samples were taken with 5

cm-interval for *G. menardii* analysis. The samples were disaggregated in water and wet-sieved at 63 μm in diameter. Tests of *G. menardii* larger than 250 μm in diameter were collected to determine the ratio of perfect tests. They are divided into three groups (Figure 1) based on the criteria of Oba (1969). While 50 to 100 tests of *G. menardii* were secured from most of the examined intervals, certain intervals yielded less than 30 tests, so that the latter was excluded from the following discussion.

Result and discussion

Figure 3 shows that the curve of change in CaCO_3 dissolution as determined by the method with *C. leptoporus* well correlates with that by *G. menardii*. It might be doubted that destruction of coccoliths and foraminiferal tests is caused from mechanical disintegration during separation procedure but not from chemical dissolution. The specimens of *C. leptoporus* and *G. menardii* treated here are little affected by artificial destruction because experimental results with *C. leptoporus* conform to those with *G. menardii* in spite of the completely different treatments. Mechanical destruction in sedimentation process is another matter of concern. Effects of this destruction seem to be different between *G. menardii* and *C. leptoporus*, because the size of *G. menardii* test is about 100 times larger than that of *C. leptoporus* coccolith. The shape of coccoliths of *C. leptoporus* observed here is similar to the dissolution pattern described by Schneidermann (1977). The shapes of the tests of *G. menardii* treated here resemble the those artificially dissolved by Oba and Ku (1977). These findings imply that the observed destruction of coccoliths and foraminiferal tests is essentially attributable to CaCO_3 dissolution.

The dissolution curve of *C. leptoporus* in Figure 3 indicates that the dissolution tends to advance with increase of the subbottom

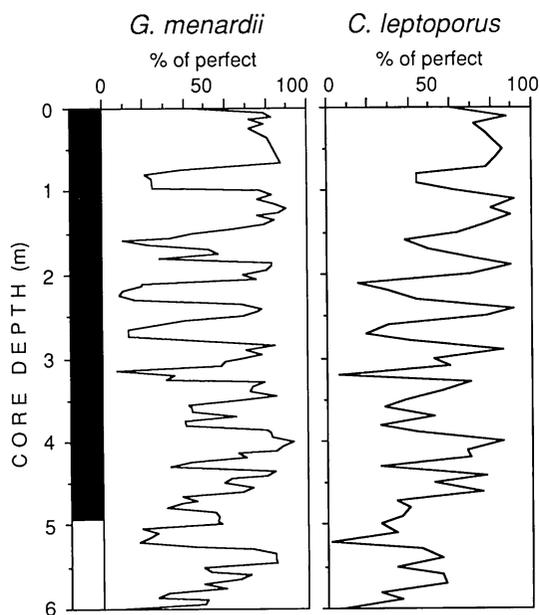


Figure 3. Correlation of percentage of the perfect test of *G. menardii* (left column) with that of *C. leptopus* (right column).

depth, whereas that of *G. menardii* does not indicate the same trend. Two causes may be attributed to this tendency: (1) *C. leptopus* continues to dissolve after deposition; and (2) *C. leptopus* tends to be damaged with compaction of sediment. Although it can not be determined which cause is responsible to the tendency, at present, it appears to be interesting with respect to diagenesis of calcareous nannofossils.

The 8 cycles are recognized in the CaCO_3 dissolution curve between the core top and the Brunhes-Matuyama boundary and they appear to agree chronologically with the cycles of glacial-interglacial stages. This find supports the opinion that dissolutions increased during interglacials but decreased during glacials in the Pacific Ocean. The oxygen isotope ratio of planktonic foraminifers from this core is being determined to discuss the CaCO_3 dissolution in more detail.

Even if the dissolution is intense, it is possible to evaluate CaCO_3 dissolution by the

method with *C. leptopus*, because it has intensive resistance to dissolution. *C. leptopus* is widely and abundantly distributed and the perfect coccoliths are easily distinguished from the broken ones under a light microscope. This method with *C. leptopus* should be convenient and time-saving tool for paleo-oceanographic studies to evaluate the degree of CaCO_3 dissolution.

Conclusions

Conclusions are as follow: (1) it is a useful method to measure the ratio of the perfect to the broken coccoliths of *C. leptopus* in order to evaluate degree of CaCO_3 dissolution in deep-sea sediments and (2) the method based on the percentage of perfect tests of *G. menardii* (Oba, 1969) appears to be verified as a valid and reliable tool for evaluating CaCO_3 dissolution.

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PROCEEDINGS OF THE PALAEOONTOLOGICAL
SOCIETY OF JAPAN

日本古生物学会 1990 年年会・総会

日本古生物学会年会・総会が 1990 年 2 月 2 日～4 日に早稲田大学大隈講堂・早稲田大学教育学部で開催された(参加者 265).

国際学術集会出席報告

Third International Conference on Paleo-oceanography
(Cambridge; 1989 年 9 月 10 日～16 日) 出席報告
……………齊藤常正

特別講演

本邦新第三系貝類化石群の生物地理とその成立過程
……………小笠原憲四郎

総会

シンポジウム

第 29 回 IGC (Kyoto, 1992) 開催に向けて

世話人: 齊藤常正・鎮西清高・棚部一成

第 28 回 IGC (Washington, D.C., 1989) の報告

……………棚部一成・前田晴良

第 29 回 IGC (Kyoto, 1992) の準備状況 ……齊藤常正
古生物関連のシンポジウム案について

A. Disciplinary Symposia

- (1) Functional morphology and morphogenetic constraints: Constructional and theoretical approaches in evolutionary biology
……………鎮西清高・郡司幸夫
- (2) Structure, formation and evolution of fossil hard tissues ……小林敏雄・後藤仁敏
- (3) Tempo and modes of morphologic evolution in fossil lineages ……小澤智生・池谷仙之
- (4) Evolution and migration of marine vertebrates in the Pacific realm ……長谷川善和・岡崎美彦
- (5) Taphonomy with special reference to sedimentological and geochemical approaches
……………近藤康生・下山正一

B. Interdisciplinary Symposia

- (1) Paleobiogeography of Phanerozoic biota in view of plate tectonics
……………速水 格・田沢純一・小笠原憲四郎

- (2) Causal factors of global mass-extinctions: Biotic and abiotic ……平野弘道・海保邦夫
- (3) Sea-level changes through geological times
……………小西健二・増田富士雄

個人講演

Glanta — 有殻の ceratohiscids (放散虫類)

……………杉山和弘・若松尚則・古谷 裕
前期ジュラ紀 *Nassellaria* (*Radiolaria*) の頭室内部骨格と底足の関係について……………松岡 篤
Unuma echinatus 群集 (ジュラ紀中世放散虫) の群集組成 [その 3] ……八尾 昭
瀬戸川層群からの “*Lacazopsis*” について ……松丸国照
白亜紀アンモナイト属 *Cunningtoniceras* について
……………松本達郎

An interesting pachydiscid ammonite from Hokkaido, with remarks on relevant taxa……………Matsumoto, T.
白亜紀蝦夷果層群から産出する鞘形類について

その 1 形態と分類

……………平野弘道・小島郁夫・浮島 都・早川浩司
白亜紀蝦夷果層群から産出する鞘形類について

その 2 古環境 ……早川浩司・平野弘道

Notes on a Cretaceous bivalve *Inoceramus* (*Platyceramus*) *mantelli* Mercey (Barrois) from Japan

……………Noda, M. and Toshimitsu, S.
山口県西部地域の三疊系より初めて発見されたアンモナイト 3 種…石橋 毅・橋本恭一・野原政典・吉田浩一
後期石炭紀アンモナイト *Faqingoceras* 属と *Dunbarites* 属の類縁関係について……………西田民雄・久間裕子
現生甲殻類の巣穴研究の現状について

……………大森昌衛・生痕研究グループ
生痕化石 *Zoophycos* をつくる生物の摂食メカニズム

……………小竹信宏
掛川型動物群より産するツツガキ類 (二枚貝) の産状と分類……………間嶋隆一
鮮新統池子層のシロウリガイ化石の産状

……………鎮西清高・近藤康生・堀越増興
瀬戸川層群の古環境特性……………鈴木明彦
新潟県上越市西部の鮮新世貝化石群集

……………天野和孝・菅野三郎
中部～上部中新統荒川層群における貝類群集の時間的変

- 遷……………高井勇二
掛川層群宇刈累層の軟体動物化石群集の変遷…延原尊美
コケムシの群体形と生息環境 — 沖縄本島の琉球層群に
ついて — ……兼子尚知
リモートセンシングによるサンゴ礁浅海域の底質の判別
と水深の推定……………中森 亨・菅井由利子
与那国島の琉球層群にみられる *Halimeda* 石灰岩の堆積
環境……………鈴木 淳・井龍康文
琉球弧海溝斜面の底生有孔虫群集中に認められる cos-
mopolitan elements ……氏家 宏
安定同位体組成からみた現生浮遊性有孔虫の生息深度
……………魚本和典・大場忠道
同位体からみた黒潮域の古環境……………大場忠道
南北大東島産サンゴ化石のウラン系列年代……………
大村明雄・岩田秀樹・太田陽子・木庭元晴・河名俊男
東インド洋古第三系の底生有孔虫群集 — Ocean Drilling
Program, Leg. 121 の成果の一環として — ……野村律夫
突道湖・中海における珪藻遺骸の運搬・堆積過程
……………鹿島 薫
対馬・三根湾の完新統中の渦鞭毛藻シスト……………松岡数充
内湾域における有孔虫の環境指標種群の設定と古環境解
析……………小杉正人・片岡久子・長谷川四郎
富山湾における堆積物中の Bathyal Ostracoda の分布
……………石崎国熙・入月俊明
庄原市明賀の中新世備北層群の貝化石および *Tateiwaia*
species と底質との関係
……………岡本和夫・林 八重子・勝原雅人
広島県の中新統備北層群より産したオキナワアナジャコ
……………柄沢宏明・西川 功
現生アナジャコ *Upogebia major* (甲殻類) の巢孔構造
……………高塚 潔
松島湾における現生有孔虫の現存量の周年変化
……………沼田志貴子・斉藤常正
サンゴ礁域の底生有孔虫の分布と生態 — 沖縄県石垣島
白保海域を例として — ……小林万里子・斉藤常正
沖縄トラフ熱水性堆積物中の現生底生有孔虫群集
……………秋元和實・田中武男・堀田 宏
相模湾初島沖シロウリガイコロニー周辺の現生底生有孔
虫群集……………秋元和實・田中武男・堀田 宏
ツノガイ類の殻形態と生態の関係について; ヤカドツノ
ガイ (*Dentalium octangulatum*) を例として
……………沢田洋海
中部更新統二宮層群産 *Limopsis* 属二枚貝 2 種の初期生
活史……………棚部一成
巻貝の形態形成に対する生息姿勢の影響……………森田利仁
手取層群産の非海生二枚貝化石群集の古生態学的解析
……………井戸和彦・松川正樹
- 堆積学的観点からみた芦屋動物群の古生態……………早坂竜児
有明海中部海域における潮間帯から浅海帯にかけての貝
類遺骸集団の変化……………下山正一
Sphenoceramus schmidti の産状と形態について
……………加納 学・利光誠一・田代正之
北海道上部蝦夷層群産の「ソテツ綱に属すると考えられ
る材化石」……………大花民子・木村達明
下部白亜系銚子層群産 *Cupressinocladus* 枝条の表皮構
造……………大久保敦・木村達明
北海道上部白亜系産の「スギ科に属すると考えられる球
果化石」の細胞組織学的研究……………斎木健一・木村達明
古第三系野田層群から *Pseudotorellia* 属の産出
……………堀内順治
西南日本の白亜紀車軸藻化石について
……………岩崎泰顕・田村 實
山口県美祢層群平原層産植物化石
……………内藤源太郎・高橋文雄・石田英夫
北海道下川町産の中新世化石植物群……………西田治文
石垣島のサンゴ礁に生育する *Spongites* 属 (紅藻綱・サ
ンゴモ科) の 1 新種について……………松田伸也・井龍康文
Rhizolamellia (紅藻, サンゴモ科) の分類上の位置につ
いて……………非龍康文・松田伸也・鈴木 淳
Motile cell-like cyst of *Gyrodinium instriatum* Freudent-
thal et Lee (Dinophyceae)
……………Kojima, N., Kobayashi, S., and Matsuoka, K.
石灰質ナノプランクトン *Cyclicargolithus* 属の形態変化
と系統分類……………山崎正道・岡田尚武
富山県八尾地域の中新統複合浮遊性微化石層序
……………長谷川四郎・丸山俊明・小笠原憲四郎・
酒井豊三郎・茂林俊宏・高橋宏利・田中裕一郎
本邦 K/T 境界の放散虫群変遷 — 常呂帯サロマ層群と四
万十帯 “有岡層” について —
……………岡村 真・秋山達志・山本浩士
南極海地域, 古第三紀放散虫生層序について……………竹村厚司
埼玉県飯能市正丸峠~東吾野地域の前期ジュラ紀放散虫
群集……………指田勝男
秋田県男鹿半島の台島植物群: その組成と層序的考察
……………藤岡一男・植村和彦
仙台層群の地質年代 — 珪藻化石層序による再検討 —
……………柳沢幸夫
飛騨外縁帯福地地域一重ヶ根の碎屑岩層から産出した
Encrinurus とその層位学的意義
……………田沢純一・金子 篤
Cythere 属 (介形虫) における種分化・地理的分布の成立
……………塚越 哲・池谷仙之
The most primitive living balanomorphan from the
North Fiji Basin Abyssal Hydrothermal Field

-Yamaguchi, T. and Newman, W.A.
 カタマイマイの生物地理.....千葉 聡
 腕足類フォーナによる南部北上帯の後期古生代生物地理
田沢純一
 スピッツベルゲン島, Kapp Starostin 層から産出するベ
 ルム紀サンゴ化石.....江崎洋一・加藤 誠
 インド—太平洋地域の新生代ゴカクウミユリ類の生物
 地理.....大路樹生
 ニューゼーランド産ベルム紀紡錘虫類とその古生物地理
 学的意義について
小澤智生・Hornibrook, N. de B.・Bradshaw, J.D.
 Gigantic beaver [*Youngofiber*] from the late Early
 Miocene Mizunami Group of central Japan and its
 implications on paleogeographyTomida, Y.
 関門層群の白亜紀カメ化石.....岡崎美彦
 富山県八尾層群黒瀬谷累層からの魚類耳石群集
大江文雄
 房総半島鋸山南側の千畑累層から *Zoila* (Gastropoda:
 Cypracidae) の発見とその意義.....富田 進
 大桑動物群の変遷.....北村晃寿
 大桑—万願寺動物群の時代の石灰質ナンノ化石による
 再評価とその意義
松居誠一郎・高山俊昭・菅原晴美・
 山口寿之・田吹亮一
 北海道北西部, チェボツナイ層及び鬼鹿層の中新世貝化
 石群集.....野田芳和
 鹿児島県種子島の茎永層群産の軟体動物化石群集
井上恵介
 海生介形虫類の殻構造.....湯本道明
 マルオミナエシガイ(二枚貝)の生殻外表面におけるア
 ラゴナイトの生成.....大野照文
 カキの固着部にみられる殻構造の特徴.....山口啓子
Baffinicythere 属(介形虫)の網状裝飾配列パターンに
 ついて.....入月俊明
 中新世珪藻 *Denticulopsis dimorpha* のバイオメトリー
丸山俊明・岩井雅夫
 フーリエ記述を用いた形態判別の試み.....佐々木 理
 Comparative functional morphology of Recent and Silur-
 ian myodocope Ostracoda (Crustacea)
Vannier, J. and Abe, K.
 遊泳する現生・化石イタヤガイ類の流体力学的考察
速水 格
 河口湖畔産中新世サンゴ化石.....門田真人・末包鉄郎
 日本産の古生代軟骨魚類化石の新資料について
後藤仁敏・大倉正敏
 大分県玖珠郡九重町竜門の更新世コイ科魚類化石
籾本美孝・上野輝彌・北林栄一
- 福井県勝山市産の恐竜群
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東 洋一・長谷川善和・山ロー男・
 伊佐治鎮司・竹山憲市
 十二町層(更新世前期)産化石群集の示す海進・海退の
 記録.....荒井晃作・北村晃寿・小西健二
 Eocene *Calyplogena* and "*Bathymodiolus*," (Bivalvia,
 Mollusca), from the Bear River, southwest Washin-
 gton, U.S.A.Kanno, S. and Danner, W.R.
 Dinosaur tracks and radial cracks: unusual footprint
 features
Matsukawa, M., Obata, I., and Lockley, M.G.
 岐阜県白川村手取層群から発見された恐竜の足跡化石
国光正宏・鹿野勘次・杉山政広・長谷川善和
 千葉県鋸山産新第三紀のネズミザメ科魚類イスルス・ハ
 スタリスの歯群と脊椎骨
上野輝彌・近藤康生・井上浩吉
 カモノハシ竜 *Edomontosaurus* の腿の構造と機能
福田芳生
 異常巻きアンモナイトの生息形態に関する基礎的研究
内田繁比郎
 ノストセラス科(異常巻きアンモナイト)の成長末期にお
 けるフックの形成機構.....岡本 隆・結城仁夫
 堆積物中における現生底生有孔虫のサイズ分布
西 弘嗣
 雄は右足で雌を回す—VTRによる観察で得られた介形
 虫の交尾行動に関する新発見...阿部勝巳・Vannier, J.
 Molluscan fossils from the Ryukyu islands, Southwest
 Japan; Part 3. Gastropoda and Pelecypoda from the
 Yonabaru Formation in the southwestern part of
 Okinawa-jimaNoda, H.
 中部エゾ層群三笠層(白亜紀セノマニアン~チューロニ
 アン)の海進—海退サイクルとタフォノミー
安藤寿男
 手取層群岐阜県荘川地域の汽水生・淡水生二枚貝につ
 いて.....清水克己
- ポスターセッション
- Gephyrocapsa* 属(石灰質ナノプランクトン)の第四紀
 を通しての形態変化.....松岡裕美
 古環境変動と地磁気永年変化—別府湾における20 m
 ピストンコアリングの結果—
 岡村 真・山口智香・小川光明・大野正夫・島崎邦彦・
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CONTENTS

TRANSACTIONS

893. Itaru Koizumi and Yukio Yanagisawa: Evolutionary change in diatom morphology — An example from *Nitzschia fossilis* to *Pseudoeunotia doliolus* —347
894. Atsushi Kaneko: A new trilobite genus *Rhinophacops* 360
895. Tatsuro Matsumoto, Mamoru Nemoto and Chisato Suzuki: Gigantic ammonites from the Cretaceous Futaba Group of Fukushima Prefecture 366
896. Hiromichi Hirano, Takashi Okamoto and Khoji Hattori: Evolution of some Late Cretaceous desmoceratine ammonoids 382
897. Tatsuo Oji: Miocene Isocrinidae (stalked crinoids) from Japan and their biogeographic implication 412
- SHORT NOTES
23. Hiromi Matsuoka: New method to evaluate dissolution of CaCO₃ in the deep-sea sediments 430
- PROCEEDINGS 435