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The fossil on the cover is *Vicarya yokoyamai* Takeyama, an Early Middle Miocene gastropod from the Kurosedani Formation at Kakehata, Yatsuo-cho, Nei-gun, Toyama Prefecture, central Japan (Collected by T. Kotaka and K. Ogasawara, IGPS No. 99075, photo by S. Ohtomo and Y. Kikuchi,  $\times 0.9$ ).

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**PALAEONTOLOGICAL SOCIETY OF JAPAN**

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## 840. THE OSTRACOD GENUS *CYHERE* O.F. MÜLLER, 1785 AND ITS SPECIES\*

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**Abstract.** It has been determined that a total of 17 species in the world belong to the genus *Cythere* s.s. All of these species occur exclusively in the coastal areas of the north-western and northeastern Pacific and the North Atlantic. The genus is restricted to areas north of the Tropic of Cancer. *Cythere* species are most diverse around the Japanese Archipelago and neighbouring areas. *Cythere* first appears in the Miocene, and a total of 12 species, including 9 Recent ones, have been found so far in and around the Japanese Archipelago. On the other hand, only 4 species are found in the northeastern Pacific and only 2 along the northern Atlantic coastal areas. The northeastern Pacific and Atlantic forms are all found in Pliocene or younger deposits.

The *Cythere* species are classified into five species groups on the basis of morphological characteristics. We hypothesize that these groups have been formed in the process of speciation. Members of a group have closer affinities with each other than with a members of any other group. We have re-examined ten species which are already known to science, and we describe 7 new species. The new taxa are *C. cronini*, *C. hanaii*, *C. kamikoaniensis*, *C. nopporoensis*, *C. sanrikuensis*, *C. valentinei*, and an unnamed species.

### Introduction

The genus *Cythere*, established by O.F. Müller in 1785, is the oldest genus of marine ostracods. Since it was proposed a large number of marine forms have been included in the genus. In 1889, Brady and Norman designated *C. lutea* as the type species of the genus *Cythere*. Most species which were once included in the genus *Cythere* have been transferred to other genera. At present in the North Atlantic, only *C. lutea* of the many species assigned by early workers to *Cythere* has remained in the genus *Cythere* sensu stricto.

In 1931, Lucas, who also published under her married name, Smith (1952), identified a variety of forms of living *Cythere* species from Van-

couver Island, British Columbia as *C. lutea*. On the basis of the same material in 1952, she proposed two new species *C. alveolivalva* and *C. uncifalcata* (the latter we believe to be a juvenile of *C. alveolivalva*). Benson (1959), also described a Recent *Cythere* species as *Haplocytheridea maia* from Todos Santos Bay, Baja California, Mexico. In the same year, Hanai (1959) proposed a new species *C. japonica* (not included in *Cythere* in this paper) and two subspecies, *C. lutea uranipponica* and *C. lutea omotenipponica*, from Pliocene and Recent material of Japan, and redefined the concept of the genus *Cythere*, restricting it to the taxa that are closely related to *C. lutea*, the type species. Schornikov (1974) proposed three new species, *C. golikovi*, *C. urupensis*, and *C. boreokurila*, from the littoral zones of the Kuril Islands, and he also promoted one of

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the Hanai's subspecies to a distinct species, *C. uranipponica*. In the next year (Schornikov, 1975), he raised the other subspecies, *C. lutea omotenipponica*, to a species. Okubo (1976) reported *C. nishinipponica* from littoral zones in the Inland Sea of Japan, while Valentine (1976) reported *C. maia* (= *C. sp.* in this paper) and *C. sp. B* (= *C. valentinei*, n. sp.) from the Holocene (subfossil) sediments in the areas from Oregon to California. Hu (1977), in addition, described *C. simplex* (= *C. omotenipponica* of Malz and Ikeya, 1983) from the Pliocene sediments of Taiwan.

Therefore, through the research of a number of workers, new members were slowly added to the genus *Cythere* since it was first proposed more than two centuries ago. The distribution of *Cythere* is known to range from the North Pacific and the North Atlantic Oceans. The list of the species belonging to the genus *Cythere* up to the present study included only one valid species from the North Atlantic, two in the northeastern Pacific, and seven in the northwestern Pacific. In this report, we reorganize and redescribe these known species and, in addition, propose seven new species: *C. cronini* from the late Pleistocene of Northeast America, *C. valentinei* and *C. sp.* from the Pliocene to Recent of the west coast of America, and *C. hanaii*, *C. kamikoaniensis*, *C. nopporoensis* and *C. sanrikuensis* from the Miocene to Recent of Japan.

The 17 species that constitute the genus *Cythere* are described and classified into 5 groups which seem to suggest close affinities between the included species as based on the characteristics of the surface ornamentation of the carapace. The most important characters are the ridges, pits and the distribution patterns of the sieve-type normal pore canals. The principal aim of this paper is to reorganize the systematics of the genus *Cythere* and establish the taxonomic significance of each species. The description of these species is a prerequisite for understanding speciation and evolutionary patterns in the *Cythere* group.

The following abbreviations are used in this paper.

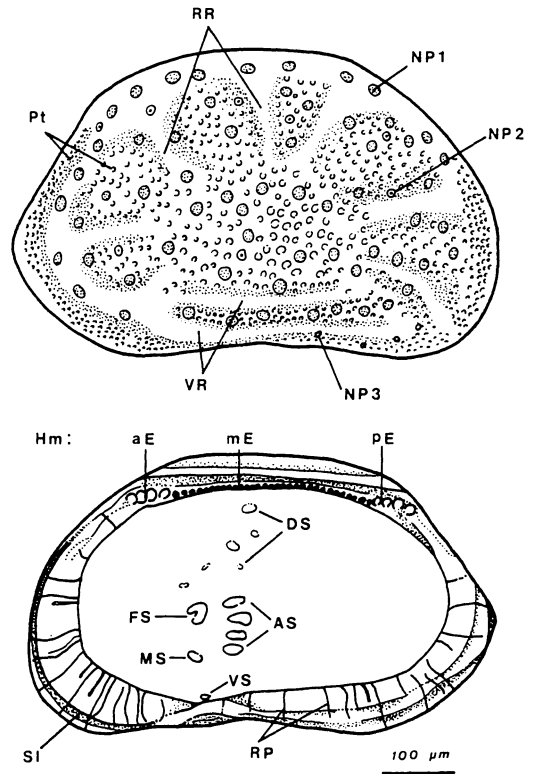
M: male, F: female, C: carapace, RV: right

valve, LV: left valve, L: length of valve, H: height of valve,  $\bar{X}$ : arithmetic mean, OR: observed range, N: number of specimens.

### Carapace morphology of *Cythere*

**Carapace.** Valves heavily calcified. Generally very thick and hard, although some difference is seen between species. Light brown in color when alive.

**Outline.** Viewed dorsally, somewhat compressed elongate-ovate, thickest posteriorly, an-



**Figure 1.** The terms used in the description of the surface features of the carapace in the Cytheridae.

- a) External ornament of RV in *C. valentinei*, n. sp.  
 NP1: normal pores of sieve-type, NP2: normal pores of funnel type, NP3: normal pores of simple type, Pt: pits, RR: radial ridges, VR: ventral ridges
- b) Internal structure of RV in *C. valentinei*, n. sp.  
 Hm: hingement, aE: anterior elements, mE: middle elements, pE: posterior elements, S1: selvage, RP: radial pores, DS: dorsal scars, FS: frontal scars, MS: mandibular scars, AS: adductor scars, VS: ventral scars

terior narrower than posterior, both ends bird-bill shaped and pointed. LV projects over RV. RV overlaps LV in the hingement area, which is the reverse in the ventral view. Viewed anteriorly and posteriorly, ovate, thickest in the middle. RV overlaps LV in the dorsal margin. In the lateral view, LV broad bean-shaped, RV subtrapezoidal. Dorsal margin gently arched; more expensive and gently arched in LV. Ventral margin slightly sinuate, more pronouncedly in RV. Anterior margin shows smooth infracurvature, which crosses the dorsal margin at a relatively gentle angle in RV. Posterior margin has a slight angle in the middle; the lower half gently curved and the upper half more linear, especially in RV.

**Ornamentation.** Generally not many undulations seen on the surface. A weak ridge runs along the ventral region of both valves. In some species this ridge branches into two in the posterior portion. Several blunt radial ridges are developed; expensive intra- and inter-specific variations found in the degree of their development. Numerous small, shallow, circular pits distributed all over the carapace surface; in a few species, however, these pits are restricted to the ventral area. Pits generally larger in the central area of the valve and smaller in the marginal areas, except for the dorsal margin. The diameter of the pits between 1 to 8  $\mu\text{m}$ . Pits are distributed less densely in the center, more densely in the marginal areas. Eye spots very weak by developed.

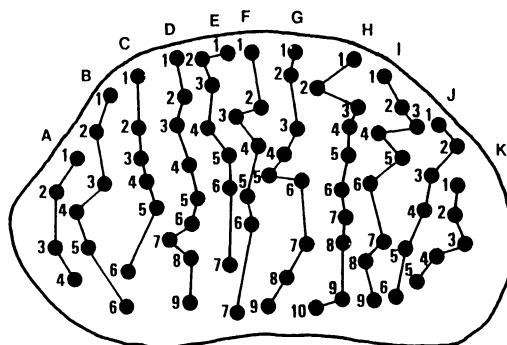
**Size.** The adult carapace measures approximately 0.55–0.85 mm in length, 0.35–0.45 mm in height, 0.31–0.34 mm in width. LV larger than RV in length; the reverse in height.

**Sexual dimorphism.** Length generally greater in males than in females, whereas the height of the two both sexes is about the same. In lateral view, the dorsal and ventral margins curved more gently in male than in female. In the posterior half of male, a prominent swelling observed around the postero-dorsal margin, although almost no difference is seen in width between the two sexes.

**Normal pores.** Single and sieve-types. The former is further classified into two types; simple

(without a lip) and funnel (with a lip). Simple type pores are cone-shaped, the diameter being 2–4  $\mu\text{m}$  at the surface, and the pore opens at the bottom of the cone. Funnel type pores have a lip with a diameter of 4–6  $\mu\text{m}$ , and the pore with a diameter of about 2  $\mu\text{m}$  opens inside the lip. Sieve-type pores have a sieve plate with a diameter of 10–20  $\mu\text{m}$ , and the opening at the carapace surface is cone-shaped. The surface of the sieve plate is crowded with a number of small conical projections. Simple type pores are restricted to the anterior and ventral areas, and the number of them is only 5 to 6 per valve. Funnel type and sieve-type pores are distributed over the valve, and their numbers are 13 and 60–90 per valve, respectively. From each pore canal a seta extends outward, some setae are branched into two. The location of the pore through which the seta comes out is either in the center or close to the edge of the plate. The distribution pattern of the single type pores is fairly stable within the genus as a whole, whereas that of the sieve-type pores is consistent at the species level. The distribution patterns of the sieve-type pores clearly differ among species. Therefore, they are highly important taxonomic characters in taxonomy. In this study the distribution pattern of sieve-type pores on *Cythere uranipponica* (Figure 2) is used as a standard to which the other species are compared with each species.

**Inner lamella.** Marginal areas generally wide, with only a trace of vestibule, widest in the



**Figure 2.** Distribution pattern of sieve-type normal pores on the RV of *C. uranipponica*. Combination of alphabet and arabic numeral shows the reference of each pore.

antero-ventral region, but narrow and twisted in the middle of ventral margin. Selvage narrow, slightly wider in the posterior margin than anterior margin. A flange is weakly developed at the posterior end of RV, forming a weak caudal process.

**Radial pores.** Distributed mainly in the anteroventral area, numbering 30 to 40 in total. About half of them short, and do not reach the outer margin. Mostly straight. In the antero-ventral area, however, a number of radials are either bent or slightly sinuous. Not branched. Somewhat thickened in the middle.

**Hingement.** Hinge line almost straight. Merodont/entomodont. All the elements are crenulated and arranged in a horizontal plane. In RV the anterior element forms four rounded projecting teeth. Two of which at the anterior end are fused. The median element consists of about 30 minute sockets. The posterior element is similar and symmetrical to the anterior element. LV complementary to RV. The teeth of the median element, however, are very fragile and often not preserved. In the upper part of the hingement area of the RV a narrow groove is formed, and above it an eaves-shaped projection is formed in the median element. This projection overlaps the dorsal margin of the LV.

**Muscle scars.** Four adductor scars are aligned namely vertically in a gentle curve convex side to the posterior. The uppermost and the lowest adductor scars are semicircular, whereas the other two between them both are constricted in the middle. Frontal scar is a distorted V-shape located in front of the upper two adductor scars. An elliptical mandibular scar in front and below of the lowest adductor. About 10 dorsal scars are scattered in the upper half of the valve. An elliptical ventral scar located below and posterior to the mandibular scar.

#### Appendages of *Cythere*

**Antennule.** Robust. 5-segmented. The length of each segment decreases in the following order; 2nd, 1st, 4th, 3rd and 5th segment. 2nd segment nearly equal to the combined lengths of 3rd and

4th segments. Costae develop on the anterior and posterior margins of each segment; especially broad in the anterior margin of 2nd, 3rd and 4th segments. 1st segment without seta, wider than the other segments. 2nd segment with plumose setae on the anterior distal end, the anterior proximal end and the posterior middle margin; setae in the first 2 areas longer than those in the last. The anterior margin of 2nd segment covered with numerous short cilia. Third segment has a stout spine on the anterior distal end, and a slightly longer seta with cilia on the posterior proximal end. 4th segment with a long stout spines with curved claw-like tips and a short seta on the ledge in the anterior middle, and with a seta on the posterior middle margin. Furthermore, 4th segment has a very strong claw tipped spine and 3 long setae on the anterior distal end, and covered with numerous short cilia along the entire anterior margin. On the 2 strong claw tipped spines of 4th segment numerous serrations are arranged in 2 rows along the anterior margin. 5th segment with 4 long setae on the distal end, 2 of them relatively stout.

**Antenna.** Broad and stout. 4-segmented. The length of each segment decreases in the following order; 3rd, 1st, 2nd, and 4th segment. Costae in each segment well developed and similar to those of the antennule. Costae especially broad in the anterior margin of 2nd and 3rd segments. First segment with short plumose setae on the posterior middle, 1st segment wider than the other segments. 2nd segment has an very long flagellum extending from the anterior proximal end to near the top of the distal claw of 4th segment, and from the root of the flagellum extends a plumose seta. Furthermore, on the posterior distal end of 2nd segment a long stout seta with cilia is developed. Along the anterior margin, 3rd segment bears a seta or plumose seta on the one fourth from the proximal end, and 2 setae of unequal size on the middle. Along the posterior margin 3rd segment bears 2 stout setae of subequal size and a fine seta in the middle of the ledge. Furthermore, a claw develops on the posterior distal end of 3rd segment. Two terminal claws of 4th segment very well developed, anterior claw

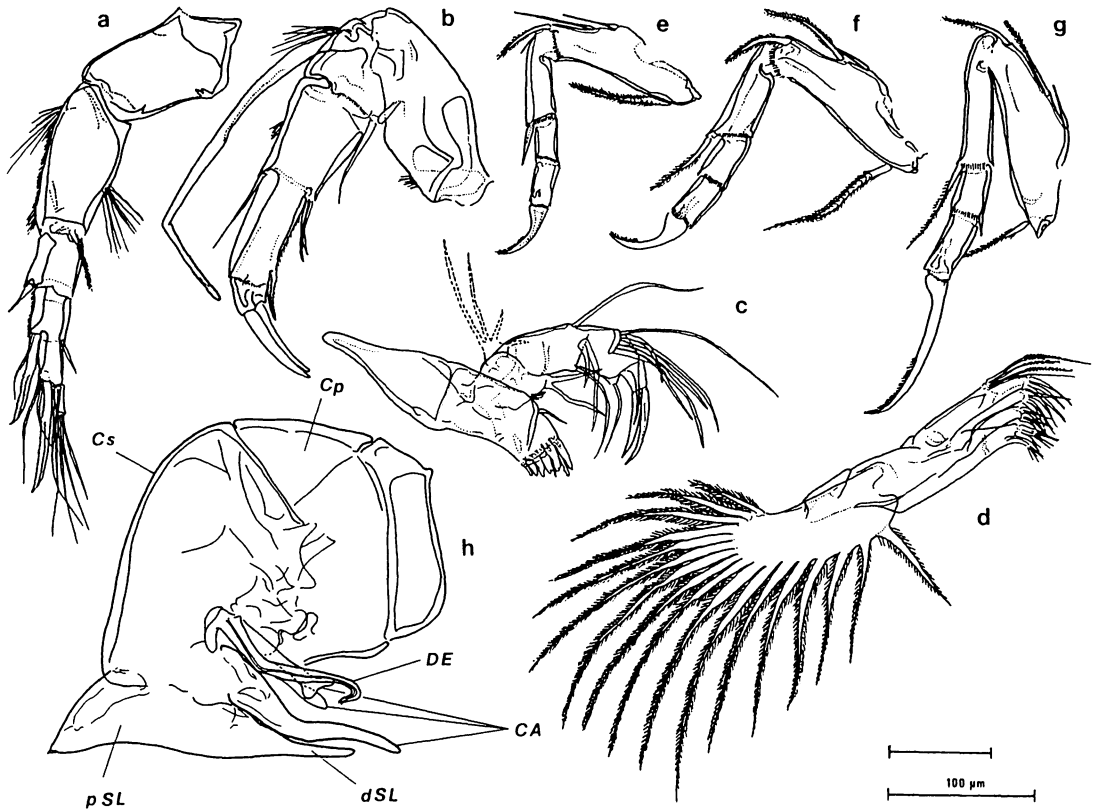


Figure 3. Appendages of *C. sanrikuensis* (Loc. 15. a, b, e–g: IGSU-O-536, c: IGSU-O-553, d, h: IGSU-O-542) a): antennule, b): antenna, c): mandibule, d): maxilla, e): first thoracic leg, f): second thoracic leg, g): third thoracic leg, h): copulatory organ (scale: short bar) Cp: capsule, CS: costa, dSL: distal supporting lobe, pSL: proximal supporting lobe, CA: clasp apparatus, DE: ductus ejaculatorius (ejaculatory duct).

larger than the other.

**Mandible.** Gnathal lobe beak-shaped on the anterior side with well branched teeth on the posterior side. A palp with 3 segments; 1st segment with poorly developed vibratory plate bearing a few setae and processes on the distal part, and 2 long setae on the posterior distal end. 2nd segment with 4 ledges bearing 1 to 6 long setae respectively, and 2 setae on the distal end, the anterior seta being especially stout. 3rd segment with 3 stout setae on the distal end.

**Maxilla.** Branchial plate extremely thin, with 17 long branches along the margin, each branch covered with numerous cilia. Palp slender, 2-segmented. First segment with a somewhat stout seta on the anterior distal end, and a relatively fine longer seta on the posterior distal end.

Second segment composed of 3 masticatory processes, each of which bears on the distal end several stout setae.

**Thoracic legs.** Three legs similar in shape. 3rd leg longest and 1st shortest. Each leg composed of 4 segments whose length decreases in following order; 1st, 2nd, 3rd, and 4th leg, but 2nd and 3rd legs about the same in length. Costae develop in the anterior and posterior margins of each segment; especially broad in the anterior margin of 2nd and 3rd segments. Many short cilia cover the distal margins of each segment. Each 1st segment bears a seta covered with numerous cilia in the proximal, middle, and distal areas of the anterior margin. Each 2nd segment with a slightly stout seta on the anterior distal end. 3rd and 4th segments without seta. Each 4th segment bears on

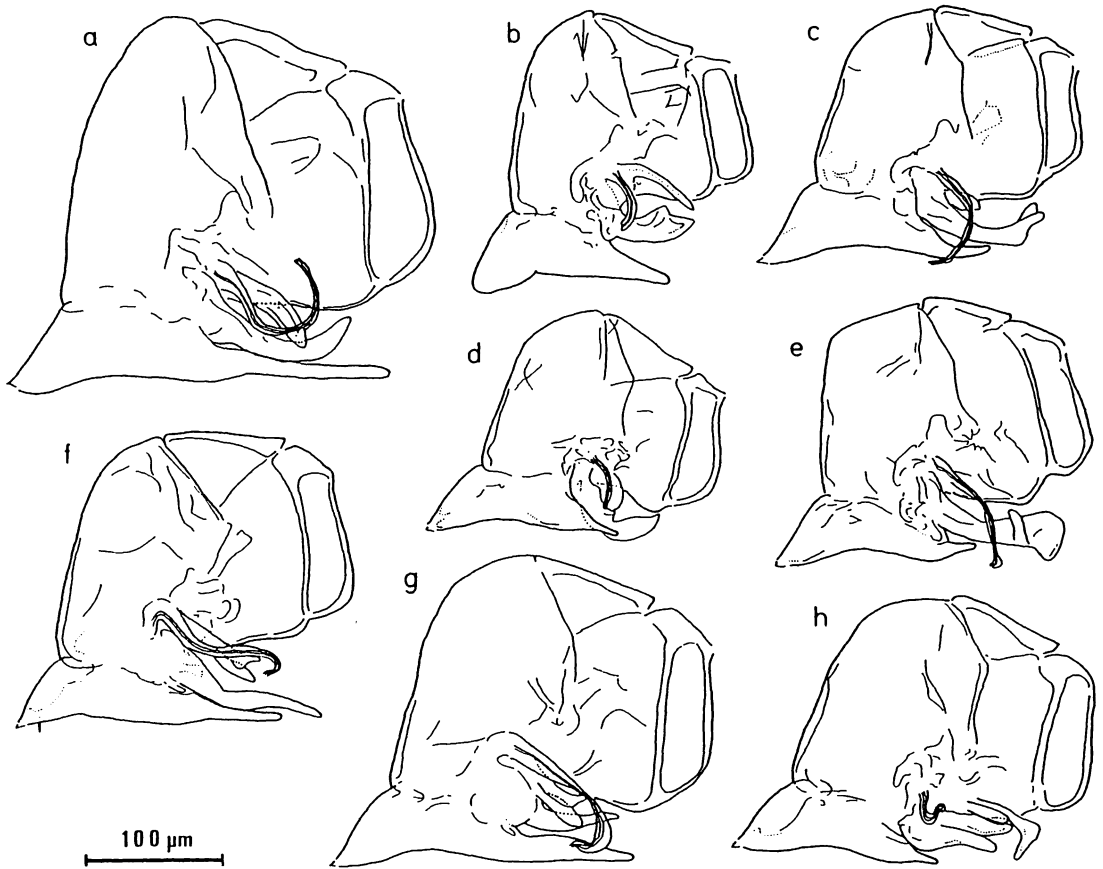


Figure 4. Male copulatory organs of *Cythere* species.

a: *C. alveolivalva* (Loc. 1, IGSU-O-554), b: *C. golikovi* (Loc. 16, IGSU-O-555), c: *C. lutea* (Loc. 6, IGSU-O-556), d: *C. nishinipponica* (Loc. 7, IGSU-O-444), e: *C. omotenipponica* (Loc. 17, IGSU-O-557), f: *C. sanrikuensis* (Loc. 15, IGSU-O-542), g: *C. schornikovi* (Loc. 11, IGSU-O-451), h: *C. uranipponica* (Loc. 12, IGSU-O-433)

the distal end a huge terminal claw which is equal in length to 2nd segment; these claws have a short plumose seta in the distal half of the anterior margin. Sexual dimorphism observed in the claw of 3rd leg; longer in male than in female.

**Copulatory organ of the male.** (Figure 4). Basal capsule with costae in the margin almost rounded quadrangular in the entire shape, with complex appendages attached in the distal part. The complex appendages have a pair of long tongue-like adapters in the distal part. In the right hemipenis, the distal lobe of the right adapter more rounded, and the proximal lobe often projects posteriorly in a long finger-like process. The prehensile hooks vary widely in number

from 1 to 4, and also differ in shape. Ejaculatory duct relatively short; not longer than the adapters.

**Caudal lamella.** A small thumb-like process projects behind the copulatory organ. The process warps dorsally, and bears many setae on the proximal end; the setae longer and stouter on the dorsal side than on the ventral.

#### Species groups of *Cythere*

*Cythere* is divided into five groups of species on the basis of surface ornamentation of the carapace. They are:

(1) *C. nishinipponica*, *C. uranipponica*;



- (2) *C. hanaii*, *C. kamikoaniensis*, *C. noporoensis*  
 (3) *C. alveolivalva*, *C. cronini*, *C. golikovi*, *C. sanrikuensis*, *C. schornikovi*  
 (4) *C. boreokurila*, *C. lutea*, *C. maia*, *C. urupensis*, *C. valentinei*, *C. sp.*  
 (5) *C. omotenipponica*

#### (1) *Cythere uranipponica* group

Several relatively weak radial ridges are developed. Surface of the valve is covered with numerous pits. The number of the sieve-type pores on each valve is approximately 75 to 82. One of these pores that is near the center of the dorsal margin is diagnostic of this group, and is never seen in other *Cythere* species. Detailed comparison of the two species of this group is given in Ikeya and Tsukagoshi (1987).

#### (2) *Cythere kamikoaniensis* group

The carapace is thicker and the Height/Length ratio greater than in other groups. Relatively distinct radial ridges are developed on the carapace surface, and the ventral ridges are also prominent. Numerous distinct pits are scattered all over the carapace. The number of the sieve-type pores is approximately 68 to 75, and their distribution pattern is similar to that of *C. alveolivalva*. The size of the surface pits can be used to distinction between the species of this group.

#### (3) *Cythere alveolivalva* group

The carapace surface is comparatively smooth. Faint radial ridges, if any, are present in the anterior and posterior areas in some individuals. Fairly deep pits are found in large numbers in the postero-ventral area of the valves. However, only very shallow faint pits or no pits at all are found in other areas of the valves. The number of the sieve-type pores varies widely; the number is relatively small (70 to 75) in one subgroup, and relatively greater (78 to 86) in another subgroup. The former includes *C. alveolivalva*, *C. cronini* and *C. schornikovi*, whereas the latter includes *C. golikovi* and *C. sanrikuensis*. Interspecific variation of the number is smaller in this group than in others. Distinction between the species, however, is easily made by the distribution pattern of the sieve-type pores and the copulatory organs.

#### (4) *Cythere lutea* group

Distinct radial ridges develop. The carapace is covered with deep pits. The number of the sieve-type pores is about the same or somewhat less than as in the *C. uranipponica* group. Distinction between the species of this group is made by the degree of development of the radial ridges, distribution pattern of the sieve-type pores, and characteristics of the copulatory organs.

#### (5) *Cythere omotenipponica* group

The carapace is thick and the Height/Length ratio is relatively large. Radial ridges are well developed in the posterior half of the valves. Marginal ridges are developed in the anterior and posterior parts. Gentle swellings exist around the sieve-type pores, and minute shallow pits are present on the surface of these swellings. The number of the sieve-type pores is relatively small (63 to 66). No other species has been found so far that could be included in this group. What has been reported reference as this species from Pleistocene sediments on Chinese coast may be another species belonging to this group.

### Materials and their localities

Listed below are the localities of samples used. References to locations contained in the text are indicated by the index number.

Loc. 1: Recent, algal samples collected in July 18, 1940 (provided by T. Hanai). Tidal zone of west coast of San Juan Island, Strait of Georgia, Washington, U.S.A.

Loc. 2: Fossil, 79TC5 sample collected by T.M. Cronin. "T's" corner (Loc. H-8 of R.B. Mixon), Accomack County, Virginia, U.S.A. (Pleistocene Accomack Member of Omar Formation). (see Mixon, 1985).

Loc. 3: Recent, SUT-7-5 sample (well sorted medium sand) *Zostera* zone (depth 5m) of Sutttsu Bay, Southwest Hokkaido, Japan (42°46.2'N, 140°15.8'E).

Loc. 4: Fossil, 840902-5 sample. An exposure along Hanyu River, about 250m west of Hanyu Village, Sawane-machi, Sado Island, Japan (37°59.4'N, 138°15.9'E). (Middle Pleistocene Kaidate Formation).

Loc. 5: Fossil, TG006 sample collected by S. Itoh. An exposure at the upper most course of Bussha River, about 2.6 km WNW of Kobuchi railroad station of the Aniai Line, Kamikoani-mura, Kita-Akita-gun, Akita Pref., Japan (40°02.5'N, 140°22.6'E). (Late Miocene Kamikoani Formation).

Loc. 6: Recent, algal samples collected in Nov. 28,

1984 (provided by J.W. Neale). Tidal zone of Robin Hood's Bay, North Yorkshire, England, U.K. (54°26'N, 00°32'W).

Loc. 7: Recent, algal samples collected in May 11, 1982 (provided by I. Okubo). Tidal zone of Dezaki, Tamano-shi, Okayama Pref., Setonaikai, Japan (34°30.9'N, 133°54.8'E).

Loc. 8: Fossil, Nop. 3 sample. An exposure behind the "Kyohei" industrial district, about 2.8 km NNW of Kita-Hiroshima railroad station of the Chitose Line, Sapporo-gun, central Hokkaido, Japan (43°00.1'N, 141°33.1'E), (Late Pleistocene Nopporo Formation).

Loc. 9: Recent, St. 2-4 sample (fine to medium sand) collected in May 2, 1983 (provided by H. Kitazato). Surge channel of tidal zone, Omaezaki, Shizuoka Pref., Japan (34°35.4'N, 138°13.8'E). (see Ikeya *et al.*, 1985).

Loc. 10: Recent, 760808-12 sample (fine sand) collected in Aug. 8, 1976. Tidal zone of Kesaiso, Motoyoshi-gun, Miyagi Pref., Japan (38°45.7'N, 141°31.6'E).

Loc. 11: Recent, algal sample 830807-2 collected in Aug. 7, 1983. Tidal zone of Okeneppu, Nemuro Pen., Hokkaido, Japan (43°19.9'N, 145°47.2'E).

Loc. 12: Recent, algal sample 840812-1b collected in Aug. 12, 1984. Tidal zone of rocky shore, Ayukawahama, Ojika Pen., Miyagi Pref., Japan (38°17.2'N, 140°30.7'E).

Loc. 13: Recent, 830805-7 sample (medium sand) collected in Aug. 5, 1983. Sand beach of Nosappumisaki, Nemuro Pen., Hokkaido, Japan (43°22.8'N, 145°47.2'E).

Loc. 14: Fossil, 820829-1a sample, Cape Blanco, Oregon, U.S.A. (42°50.5'N, 124°25.3'W). (Pleistocene, terrace deposits, same as USGS Cenozoic locality M 1450). (see Addicott, 1964).

Loc. 15: Recent, algal sample collected in Jun. 21, 1986. Tidal zone of rocky shore, Toyoura, north coast of Funka Bay, southwest Hokkaido, Japan (42°34.3'N, 140°43.2'E).

Loc. 16: Recent, F 10 sample (silty sand) dredged by the Sedimentological Research Group of Hokkaido University. Near shore bottom (depth 5 m) off Kuroiwa, west coast of Funka Bay, southwest Hokkaido, Japan (42°22.8'N, 140°20.0'E).

Loc. 17: Recent, algal sample collected in Aug. 17, 1984. Tidal zone of rocky shore, Nagasaki-bana, Choshi, Chiba Pref., Japan (35°41.1'N, 139°52.1'E).

### Types

All types of the new species are deposited in the collection of the Institute of Geosciences, Faculty of Science, Shizuoka University (IGSU-O-number). Duplicate paratypes are deposited in the H.V. Howe Collection, Department of Geology, Louisiana State University, Baton

Range, Louisiana, U.S.A.

The following abbreviations refer to the institutions where types are preserved:

BLOSJC: Biological Laboratory, Okayama Shu-jitsu Junior College, Okayama, Japan. UMUT: University Museum, University of Tokyo, Tokyo, Japan. USNM: U.S. National Museum of Natural History, Washington D.C., U.S.A. FESC: Institute of Marine Biology, Far Eastern Scientific Center, Academy of Science, Vladivostok, U.S.S.R.

### Systematic description

Subclass Ostracoda Latreille, 1802  
Order Podocopida G.W. Müller, 1894  
Suborder Podocopa Sars, 1866  
Superfamily Cytheracea Baird, 1850  
Family Cytheridae Baird, 1850  
Subfamily Cytherinae Baird, 1850  
Genus *Cythere* O.F. Müller, 1785

*Type species. Cythere lutea* O.F. Müller, 1785

*Cythere alveolivalva* Smith, 1952

Figures 4a, 5a, 6-1a, b

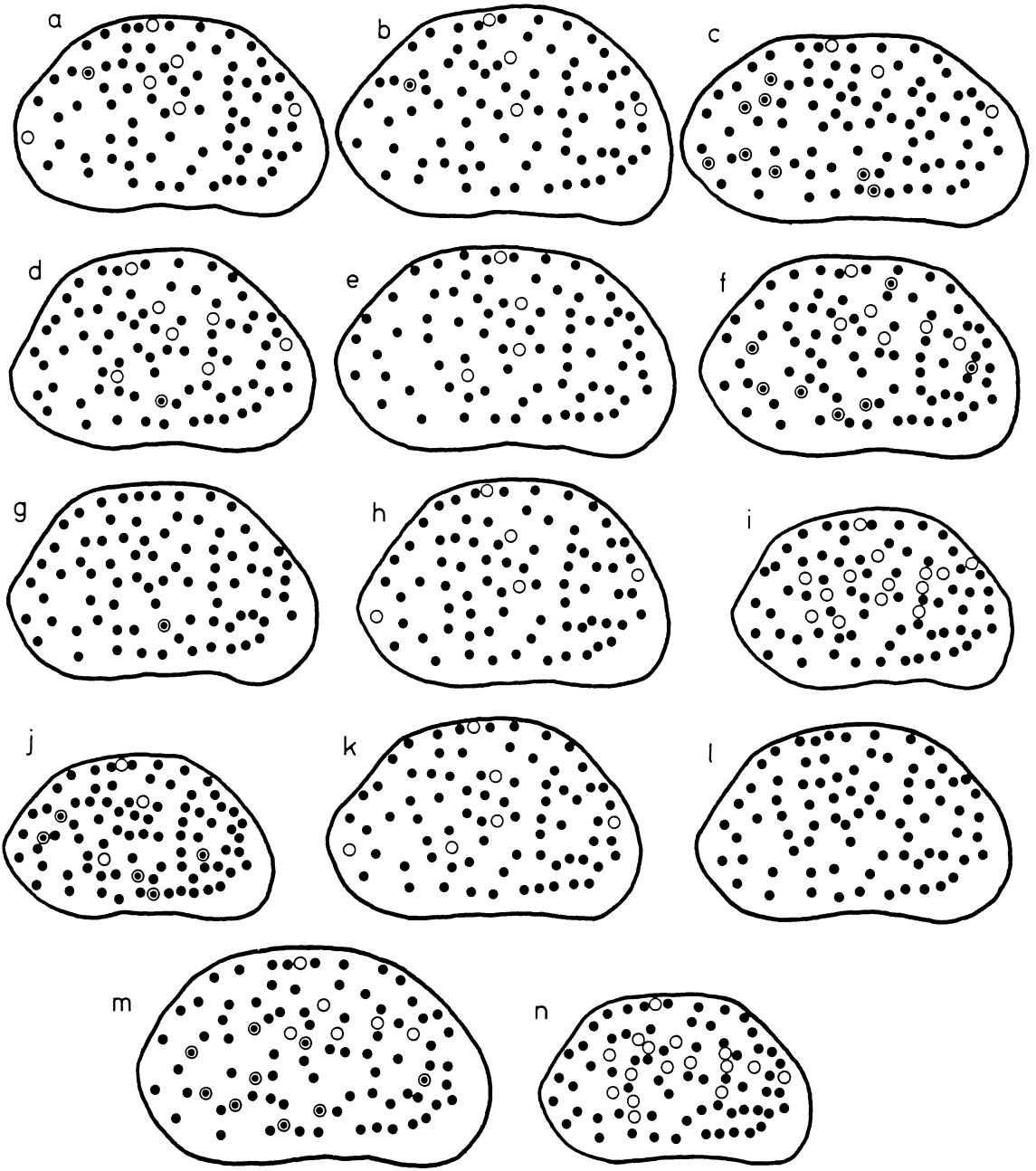
*Cythere alveolivalva* Smith, 1952, p. 23, 24, 26, pl. 4, figs. 1-10; Schornikov, 1974, p. 142, 143, pl. 1, fig. 2, text-fig. 3; (not) Swain, 1969, p. 462, pl. 4, figs. 12a, b, pl. 7, figs. 1a, b, pl. 9, figs. 4a, b, pl. 10, figs. 9a, b, pl. 11, fig. 7; (not) Swain and Gilby, 1974, p. 285, pl. 2, figs. 9, 10, 26a, b, Text-fig. 18.

*Cythere uncifalcata* Smith, 1952, p. 26-28, pl. 5, figs. 1-7. *Cythere* sp. A. Valentine, 1976, pl. 12, figs. 15, 16.

*Types.* Syntypes. Female, LV (pl. 4, fig. 2), L = 0.81 mm; Male, RV (pl. 4, fig. 1) and LV (pl. 4, fig. 3), L = 0.75 mm.

*Types.* Syntypes. Female, LV (pl. 4, fig. 2), L = 0.81 mm; Male, RV (pl. 4, fig. 1) and LV (pl. 4, fig. 3), L = 0.75 mm.

*Diagnosis.* Carapace surface very smooth. However, very shallow pits found in large numbers all over the surface with only a faint ridge in the ventral margin. The number of the sieve-type pores smaller by 5 to 6 in total than that of *C. uranipponica*; the pores with the reference numbers A-3, E-1, E-5, F-2, G-5, and K-1 are missing, whereas a new pore is often added be-



**Figure 5.** Distribution patterns of the sieve-type pores of *Cythere* species (In comparison with *C. uranipponica*, black points: coexisting pores, white circle: missing pores, double circle: additional pores, all figures are the same magnification).

a: *C. alveolivalva*, b: *C. cronini*, c: *C. golikovi*, d: *C. hanaii*, e: *C. kamikoaniensis*, f: *C. lutea*, g: *C. nishinipponica*, h: *C. nopporoensis*, i: *C. omotenipponica*, j: *C. sanrikuensis*, k: *C. schornikovii*, l: *C. uranipponica*, m: *C. urupensis*, n: *C. valentinei*

tween B-2 and C-2 pores. In male, the proximal lobe of adapters remarkably longer. The two hemipenises have two pairs of clasping apparatuses; the outer one gently curves inside, and the inner one outside, respectively. Ejaculatory duct relatively long.

*Distribution.* Recent: Coastal areas of the northern Pacific; northern Kuril Islands, Kamchatka Pen., west of Alaska, and coasts of Washington, Oregon and California. Fossil: Late Pleistocene to Holocene terrace deposits from Oregon to California.

*Remarks.* The distribution pattern of the sieve-type pores very similar to that of *C. schornikovi* and *C. cronini*, but the morphology of the copulatory organ in male greatly differs from that of *C. schornikovi* and *C. sanrikuensis*; *C. schornikovi* and *C. sanrikuensis* have three pairs of clasping apparatuses on the hemipenis, whereas this species has two pairs. Also the proximal lobe of adapters longer than that of *C. schornikovi*, the difference being particularly marked in the right hemipenis. When Smith (1952) proposed this species, she also recognized *C. uncifalcata*, n. sp. as an independent species. However, the clearly younger specimen we consider a juvenile form (A-1 stage) of *C. alveolivalva*. The word "alveolivalva", which really means "pitted shell", is actually not suitable to characterize this species. Judging from her comment "surface pitted with approximately seventy large scattered pits", it seems that she mistook normal pore canals for pits. The number of the sieve-type pores, in fact, corresponds to the number of the "pits" in her description. From the known geographical distribution it is reasonable to assume that this species will be found to inhabit coastal areas of the Aleutian Islands to Bering Sea.

*Cythere boreokurila* Schornikov, 1974

*Cythere boreokurila* Schornikov, 1974, p. 147-148, pl. 1, figs. 4a-d, Text-fig. 6.

*Type.* Holotype, a carapace of male, FESC-No. 353-354.

*Type locality.* Recent, Kasharot Bay, Paramushir Island.

*Diagnosis.* Ornamentation of the carapace

generally resembles that of *C. uranipponica*, but the radial ridges similar to that of *C. urupensis* in which several ridges are distinctly developed. Small pits distributed densely all over the carapace except the upper surface of ridges. In males, the proximal lobe of adapters stout and rounded at the tip. The two hemipenises each have two pairs of clasping apparatuses that are curved inside; the outer one branches and the inner one widens in the tip.

*Distribution.* Recent: Known only from the type locality; a few living specimens have been found (littoral zone of Paramushir Island). It is probable that this species occurs along the coasts of the Aleutian Islands and Alaska. Fossil: Unknown.

*Remarks.* This species closely resembles *C. urupensis* but differs in morphology of copulatory organs of the male, especially in the clasping apparatus.

*Cythere cronini*, n. sp.

Figures 5b, 6-2a-d, 10-3a-c

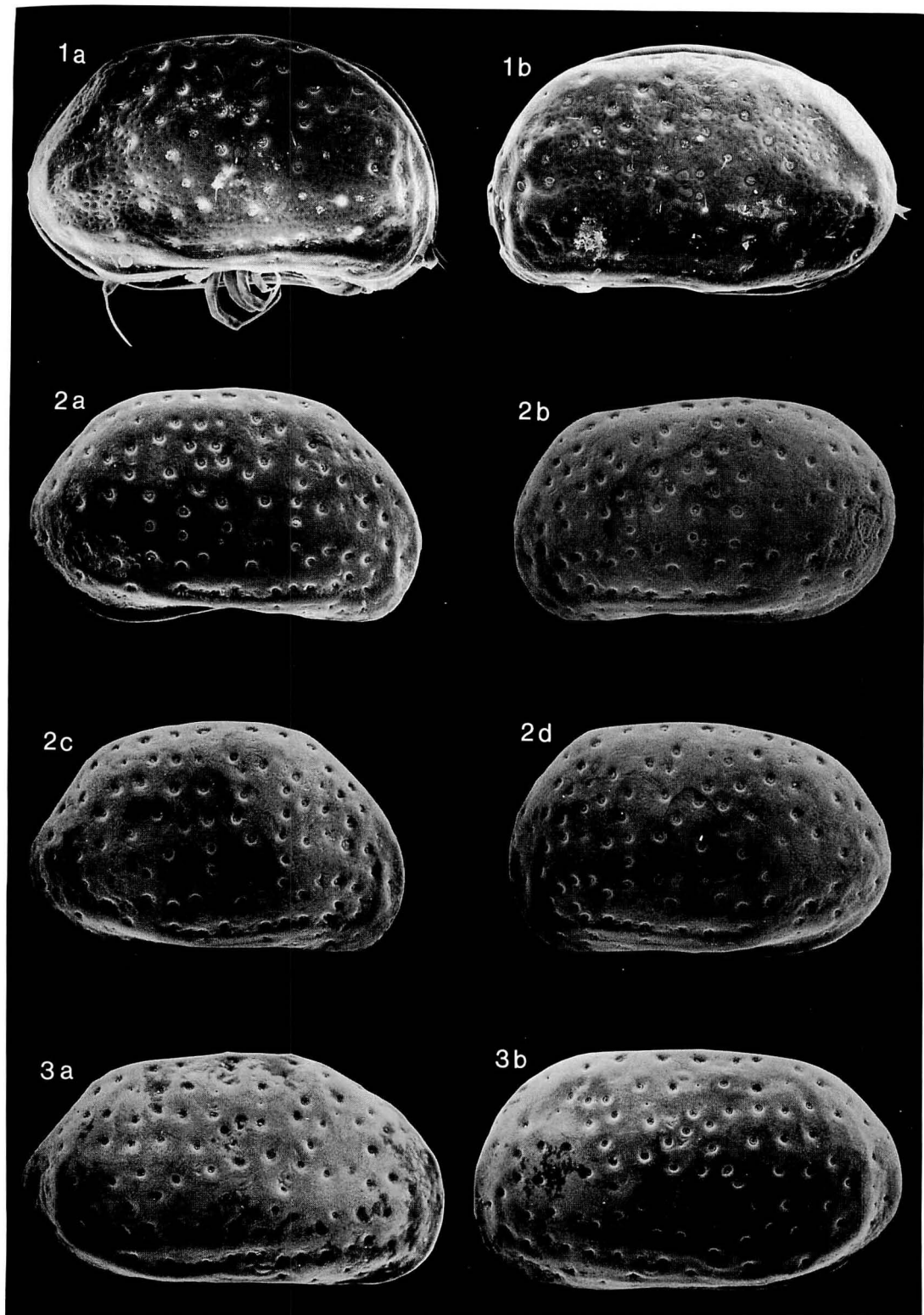
*Types.* Holotype, a carapace of male, IGSU-O-521 (RV, L = 0.71 mm, H = 0.41 mm; LV, L = 0.69 mm, H = 0.41 mm). Paratypes, IGSU-O-522 (a carapace of female, RV, L = 0.68 mm, H = 0.40 mm; LV, L = 0.66 mm, H = 0.40 mm); IGSU-O-523 (RV of female, L = 0.69 mm, H = 0.41 mm); IGSU-O-524 (LV of female, L = 0.69 mm, H = 0.42 mm).

*Type locality.* Loc. 2.

*Etymology.* In honour of Dr. T. M. Cronin, who has provided specimens of this species.

*Diagnosis.* Closely resembles *C. schornikovi* in outline. Carapace surface very smooth, only a weak ridge developed in the ventral margin. No pits found except in areas along the postero-ventral to ventral margin. The number of the sieve-type pores comparatively small (approximately 70 to 75); compared with the distribution pattern in *C. uranipponica*, a few pores are missing, such as E-1, F-2, G-5, K-1, and an additional pore exists between B-2 and C-2, as well as in *C. alveolivalva*.

*Description.* Lateral outline generally bean-



**Figure 6.** (All magnifications  $\times 85$ ) *Cythere alveolivalva* Smith, 1952 (Loc. 1) 1a. Right lateral view of female carapace, IGSU-O-519. Left lateral view of female carapace, IGSU-O-520. *Cythere cronini*, n. sp. (Loc. 2) 2a, b. External lateral view of male R and L valves, holotype, IGSU-O-521. 2c, d. External lateral view of female R and L valves, paratype, IGSU-O-522. *Cythere golikovi* Schornikov, 1974 (Loc. 3) 3a. External lateral view of female RV, IGSU-O-525. 3b. External lateral view of female LV, IGSU-O-526.

shaped, but differs between slightly two valves and between the two sexes. In the RV the dorsal margin gently arched, more gently in male than in female. The dorsal margin joined to the anterior margin at an angle of about  $135^\circ$ , and to the posterior at an angle of about  $120^\circ$ . The posterior margin projects at about the middle whereas the gentle projection in the anterior margin is below to middle, this is especially conspicuous in female valves. Carapace surface very smooth except a weak marginal ridge in the ventral and somewhat small deep pits along the posteroventral to ventral area. Faint shallow pits are sometimes scattered over the surface. The number of the sieve-type pores approximately 70 to 75. On the sieve plates, the pore through which the seta comes out is located close to the edge of the plate in most specimens.

*Dimensions.* Listed below are the length and height measurements of adult specimens from the type locality.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.69	0.66–0.72	0.41	0.40–0.42	7
RV (F)	0.69	0.65–0.72	0.41	0.39–0.44	12
LV (M)	0.72	0.70–0.76	0.42	0.40–0.44	3
LV (F)	0.69	0.65–0.74	0.40	0.38–0.43	9

*Distribution.* Known only from the type locality.

*Remarks.* The presence of this species can be expected from the Pleistocene to Recent at many localities of the north Atlantic coastal area. Brady (1868, p. 395, 396, pl. 28, figs. 47–56) showed *C. lutea* from the coast of U.K. with a smooth surface as an intraspecific variation. These specimens may be included in this species.

*Cythere golikovi* Schornikov, 1974

Figures 4a, 5c, 6-3a, b

*Cythere golikovi* Schornikov, 1974, p. 141, 142, text-fig. 2.

*Cythere lutea lutea*: Ishizaki, 1971, p. 77, pl. 2, fig. 12.

*Cythere lutea uranipponica*: Ishizaki and Matoba, 1985, pl. 2, fig. 20.

*Type.* Holotype, a carapace of a male, FESC No. 355-356.

*Type locality.* Recent, Iturup Island.

*Diagnosis.* Height/Length ratio of carapace smaller than in the other species. Sexual dimorphism in the outline of the carapace not distinct. A weak ventral ridge develops along the margin from posteromedian area to the anteroventral area. Radial ridges and pits are not found on the carapace surface. Number of the sieve-type pores between 80 and 86, which is a relatively large number for the genus. Distribution pattern of the sieve-type pores, compared with that in *C. uranipponica*: the pores E-1, G-2, K-1 are missing, but eight additional pores are found between A-3 and A-4, A-1 and B-3, B-2 and C-2, B-2 and C-3, B-4 and C-6, C-6 and D-7, F-6 and G-9, and G-9 and H-10, respectively. In male the clasping apparatus more stout and round at the tip than that of the other species. The two hemipenises have three pairs of clasping apparatuses; the outer one curves inside and widens in the tip, the middle one heart-shaped, and the inner one slender and curves outside.

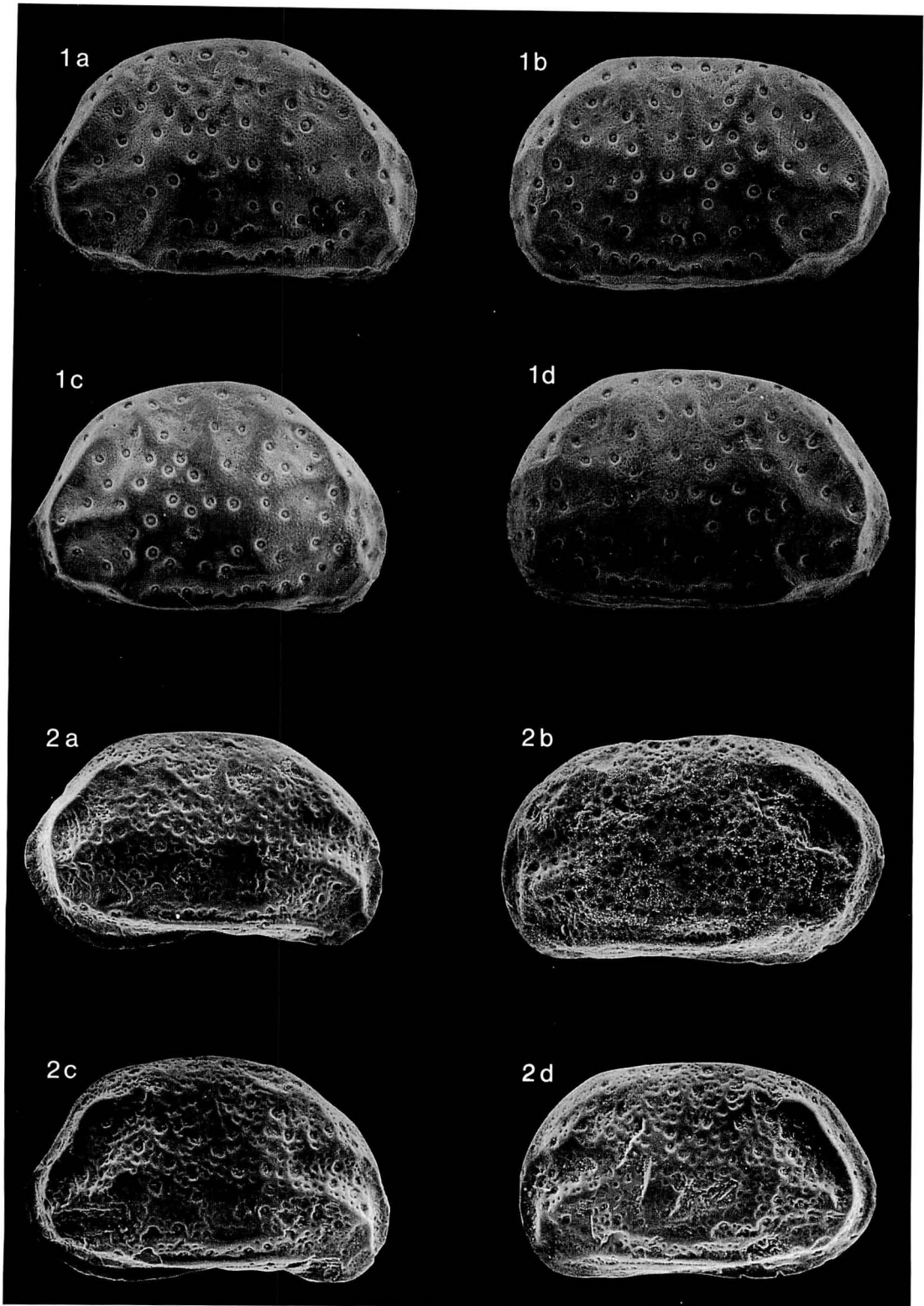
*Distribution.* Recent: Only the terminal area of the "Tsunami Current"; coasts of the south Kuril Islands, coast of Hokkaido. Fossil: Pliocene-Pleistocene formations of northern Honshu to Hokkaido, Japan.

*Remarks.* *Cythere* species generally inhabit the short algae growing in the tidal zones of rocky coasts, but Schornikov (1974) reported that this species was collected on *Phyllospadix* sp., which often grows more than 50 cm in length. This suggests that this species differs ecologically from other *Cythere* species.

*Cythere hanaii*, n. sp.

Figures 5d, 7-1a-d

*Types.* Holotype, RV of male, IGSU-O-527 (L = 0.72 mm, H = 0.44 mm). Paratypes, IGSU-O-528 (LV of male, L = 0.70 mm, H = 0.42 mm); IGSU-O-529 (RV, of female, L = 0.68 mm, H = 0.43 mm); IGSU-O-530 (LV, of female, L = 0.72 mm, H = 0.45 mm).



**Figure 7.** (All magnifications  $\times 85$ ) *Cythere hanaii*, n. sp. (Loc. 4) 1a. External lateral view of male RV, holotype, IGSU-O-527. 1b. External lateral view of male LV, paratype, IGSU-O-528. 1c. External lateral view of female RV, paratype, IGSU-O-529. 1d. External lateral view of female LV, paratype, IGSU-O-530. *Cythere kamikoaniensis*, n. sp. (Loc. 5) 2a. External lateral view of male RV, holotype, IGSU-O-531. 2b. External lateral view of male LV, paratype, IGSU-O-532. 2c. External lateral view of female RV, paratype, IGSU-O-533. 2d. External lateral view of female LV, paratype, IGSU-O-534.

*Type locality.* Loc. 4.

*Etymology.* In honour of T. Hanai, Emeritus Professor of the University of Tokyo who provided specimens of this species with a faunal slide including the topotype of *C. uranipponica*.

*Diagnosis.* Carapace well calcified and very thick. Height relatively large and roundish laterally. Distinct radial ridges and numerous fine shallow pits develop on the carapace surface. The number of the sieve-type pores approximately between 70 and 74. In comparison with the distribution pattern in *C. uranipponica* there is an additional pore between F-6 and G-9, while six pores are not found, namely D-6, E-1, F-2, G-4, H-4, H-7, and K-1.

*Description.* Carapace extremely thick. Lateral outline subreniform; dorsal margin gently arched in RV, but relatively straight in LV. Ventral margin scarcely sinuate in both valves. The Height/Length ratio of the carapace larger than in other species. Sexual dimorphism in the outline of the carapace not clear. The marginal ridge along the venter well developed, and connects with a narrow marginal ridge along the posterior. Radial ridges relatively distinct, forming fan-shaped depressions between them. Numerous fine pits cover the carapace, these pits are denser in the marginal areas and have a diameter of about 1/10 of that of the sieve plates. Number of the sieve-type pores between 70 and 74. On the sieve plates the location of the pore through which the seta comes out is close to the edge of the plate.

*Dimensions.* Listed below are the length and height measurements of adult specimens from the type locality.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.68	0.63–0.72	0.42	0.38–0.44	19
RV (F)	0.67	0.63–0.71	0.42	0.38–0.45	52
LV (M)	0.68	0.65–0.71	0.41	0.40–0.43	12
LV (F)	0.68	0.63–0.72	0.42	0.39–0.45	37

*Distribution.* Recent: Unknown. Fossil: Pliocene Pleistocene formations of northwest Honshu and southwest Hokkaido, Japan.

*Remarks.* The interspecific variation of surface

ornamentation is relatively large.

*Cythere kamikoaniensis*, n. sp.

Figures 5e, 7-2a–d

*Type.* Holotype, RV of male, IGSU-O-531 (L = 0.66 mm, H = 0.39 mm). Paratypes, IGSU-O-532 (LV of male, L = 0.70 mm, H = 0.42 mm); IGSU-O-533 (RV of female, L = 0.65 mm, H = 0.40 mm); IGSU-O-534 (LV of female, L = 0.63 mm, H = 0.38 mm).

*Type locality.* Loc. 5.

*Etymology.* After "Kamikoani", the name of the formation where the species was first discovered.

*Diagnosis.* A strong ridge developed continuously along the margin from posterior to venter. Many deep pits distributed densely all over the carapace. The number of the sieve-type pores between 71 to 75, which is nearly average for the genus. On the distribution pattern of the sieve-type pores, compared with that in *C. uranipponica*, the pores D-6, E-1, F-2, G-5 are missing.

*Description.* Carapace resembles closely the type species of the genus, *C. lutea*, in outline. Radial ridges developed distinctly on the carapace surface, especially in the anterior half. Marginal ridge developed strongly along the posterior to ventral margins, especially in the posterodorsal area. Many deep pits distribute densely all over the carapace, and diameter of the pits larger (about 1/2 to 2/3 of diameter of sieve plate) in the central area and smaller (about 1/3 to 1/5 of diameter of sieve plate) in the marginal areas.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.68	0.65–0.70	0.40	0.37–0.42	4
RV (F)	0.64	0.61–0.66	0.39	0.38–0.41	5
LV (M)	0.70	—	0.42	—	1
LV (F)	0.65	0.63–0.68	0.39	0.38–0.40	4

*Distribution.* Known only from the type locality.

*Remarks.* This species was collected with *C.*



*omotenipponica* from the type locality, and the frequency of adult specimens in the sediment sample is approximately of the ratio of 2 (*C. kamikoaniensis*) to 7 (*C. omotenipponica*).

*Cythere lutea* O.F. Müller, 1785

Figures 4c, 5f, 8-1a, b

*Cythere lutea* O.F. Müller, 1785, p. 65, pl. 7, figs. 3, 4; Brady, 1868, pl. 28, figs. 47–56, pl. 39, fig. 2; Brady *et al.*, 1874, p. 148, pl. 3, figs. 1–6; Sars, 1925, p. 167, 168, pl. 77; Blake, 1931, p. 160, 161, figs. 1b–e; Sylvester-Bradley, 1941, p. 27–33, figs. 15–18; Grekoff, 1956, p. 52, 53, figs. 209–212; Wagner, 1957, p. 47–49, pl. 18; Pokorný, 1958; p. 259, Text-fig. 931; Hanai, 1959, p. 411, 412; Van Morkhoven, 1963, p. 101–103, figs. 135–138; Hanai, 1970, p. 704, text-figs. 5A, B; Ruggieri, 1971, p. 288, fig. 2; Neale and Howe, 1975, p. 424, pl. 4, fig. 11; Siddiqui and Grigg, 1975, p. 377, pl. 1, fig. 15; Load, 1980, pl. 1, fig. 14; Cronin, 1981, p. 403, pl. 4, figs. 7, 8; Siveter, 1982, p. 110, pl. 5, fig. 9; Malz and Ikeya, 1983, p. 141, text-figs. 2, 3.

*Type*. Unknown?

*Type locality*. Recent, North Atlantic (according to Van Morkhoven, 1963).

*Diagnosis*. Somewhat blunt radial ridges developed. Numerous deep pits cover all over the carapace surface; distribution of the pits scatter on the central carapace, dense on the marginal area, and diameter of the pits larger (about 1/2 to 2/3 of diameter of sieve plate) in the center, smaller (about 1/4 to 1/6 of diameter of sieve plate) in the margin. The number of the sieve-type pores is between 74 and 80; compared with their distribution pattern in *C. uranipponica*, seven additional pores exist between B-3 and B-4, B-5 and C-6, C-6 and D-7, D-8 and F-7, F-6 and G-9, G-1 and G-2, I-3 and I-4, respectively, and six pores are missing, E-1, E-5, F-2, G-4, H-4, and I-5. In male the clasping apparatus, the two hemipenises have two pairs of clasping apparatuses; the outer one longer, curves inside, and branches into two in the tip, and the inner one shorter and rounds in the tip.

*Distribution*. Recent: The coasts of North Atlantic, with the range of latitude 30° to 70°N. Fossil: Middle to late Pleistocene of Europe and North America.

*Remarks*. In addition to *C. cronini* proposed

in this paper, it is quite possible that there are other new species that have been assigned to *C. lutea* in the North Atlantic. Elofson (1941) also reported the ecology of this species and stated that *C. lutea* is adapted to the water temperatures of 0° to 20°C, and the depths 4 to 18 m. It is not live in salinities less than 10 to 12‰.

*Cythere maia* (Benson, 1959)

*Haplocytheridea maia* Benson, 1959, p. 48, pl. 3, figs. 1a, b, pl. 9, text-figs. 7, 9; Benson, 1966, p. 745.

(Not) *Cythere maia* (Benson, 1959): Valentine, 1976, pl. 12, figs. 3, 6.

*Type*. Lectotype (LV), USNM 113133 (Benson, 1965).

*Type locality*. Recent, rocky tide pools of the northern side of Todos Santos Bay, Baja California, Mexico.

*Diagnosis*. Carapace surface very smooth. Posteroventral margin slightly curved toward the inside in the both valves. The projection of carapace on the middle of posterior margin weak, and the duplicature in that area narrower than in the other species. The sieve-type normal pore canals distribute with widely spaced prominence.

*Distribution*. Recent: Known only from the rocky tide pools and the shallow waters of the Todos Santos Bay, Baja California, Mexico. Fossils: Unknown.

*Remarks*. Swain and Gilby (1974, p. 285) regarded *Haplocytheridea maia* Benson, 1959 as a synonym of *Cythere alveolivalva* Smith, 1952. However, the specimen of *C. alveolivalva* illustrated by Swain and Gilby, and *H. maia* illustrated by Benson, show greatly different outline and ornamentation from *C. alveolivalva* s. s. Further, *H. maia* Benson, 1959 and *C. alveolivalva* by Swain and Gilby (1974) do not belong to the same species. We consider *C. alveolivalva* of Swain and Gilby (1974) (= *C. maia* by Valentine) belongs to a new species as described in this paper as *C. sp.* Furthermore, *C. maia* of Valentine (1976) differs from Benson's species in having a very different outline of the carapace and by a different pattern of ornamentation.

*Cythere nishinipponica* Okubo, 1976

Figures 4d, 5g, 8-2a, b

*Cythere nishinipponica* Okubo, 1976, p. 113–119, figs. 1a–m, 2a–h', 3a–m; Malz and Ikeya, 1983, p. 141, text-figs. 4, 5; Ikeya and Tsukagoshi, 1987, p. 911–913, pl. 2, figs. a–n, Text-figs. 7E–H.

*Cythere lutea omotenipponica*: Ishizaki, 1969, p. 215, 216, pl. 26, fig. 9.

*Cythere lutea lutea*: Hou *et al.*, 1982, p. 158, 159, pl. 71, figs. 1–3, text-fig. 22.

*Cythere* sp. Cheong *et al.*, 1987, p. 44, pl. 1, fig. 17.

*Type*. Holotype (a carapace of a female), BLOSJC-MO 461.

*Type locality*. Recent intertidal zone, Ozuchi Island, Okayama Pref., Japan (34°20.5'N, 133°55.3'E).

*Diagnosis*. Outline somewhat quadrate on both ends of the dorsal margin. Weak radial ridges developed, as well as strong and relatively wide marginal ridges from anterodorsal to posteroventral. Carapace surface densely covered with deep pits. The number and distribution pattern of the sieve-type pores very similar to those of *C. uranipponica*, except that there is one more pore in the ventromedian area. The two hemipenises of the male have two clasping apparatuses; one of the clasping apparatuses thin and almost circular. Ejaculatory duct thin and extremely short.

*Distribution*. Recent: The southern area of the Tsushima Current (a branch of the Kuroshio Current); the Yellow Sea, southern coast of Korean Peninsula, coast of northern Kyushu to Hokuriku, and coast of the Inland Sea of Japan. Fossil: Pleistocene formations of coastal areas of China, Cheju Island, Korea, and Noto Peninsula, Japan.

*Remarks*. Wide geographical variation is found in surface ornamentation. For example, the population in the Inland Sea of Japan has distinct ridges and pits, whereas that in the Sea of Japan has faint ridges and shallow pits. Detailed description of this species was given in Ikeya and Tsukagoshi (1987).

*Cythere nopporoensis*, n. sp.

Figures 5h, 8-3a–d, 10-4a–d

*Cythere lutea*: Okada, 1979, p. 159, fig. 14b, pl. 21, figs. 1, 4–6.

*Type*. Holotype, RV of male, IGSU-O-537 (L = 0.65 mm, H = 0.38 mm). Paratypes, IGSU-O-538 (LV of male, L = 0.65 mm, H = 0.36 mm); IGSU-O-539 (RV of female, L = 0.71 mm, H = 0.44 mm); IGSU-O-540 (LV of female, L = 0.65 mm, H = 0.42 mm).

*Type locality*. Loc. 8.

*Etymology*. After "Nopporo", the location and the formation where the species was first discovered.

*Diagnosis*. Resembles *C. hanaii* in lateral outline, but height in male smaller than that in female. Ventral ridge well developed, whereas radial ridges indistinct. Faint rised reticulatae found around the sieve-type pores. Deep pits cover most of the surface. The number of the sieve-type pores is approximately 68 to 75, and the pores, A-3, E-1, F-2, G-5, and K-1, which exist in *C. uranipponica*, are not found in this species.

*Description*. Strong sexual dimorphism is found in the carapace morphology. In female, the height greater, the wing-like ventral ridge overhangs the margin in the posteroventral, and the upper branch of the ventral ridge develops strongly, especially in the LV. The pits cover densely around the sieve-type pores and on the marginal areas of the carapace, but less densely on the rised reticulations and the marginal ridge. The diameter of these pits larger (about 1/3 to 1/2 of diameter of sieve plate) in central carapace and smaller (about 1/4 to 1/10 of diameter of sieve plate) in the marginal area. The location of the pore through which the seta comes out is either in the center or close to the edge of the sieve plate.

*Dimensions*. Listed below are the length and height measurements of adult specimens from the type locality.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.64	0.61–0.69	0.37	0.35–0.39	14
RV (F)	0.67	0.61–0.71	0.41	0.38–0.44	32
LV (M)	0.66	0.63–0.67	0.38	0.36–0.38	10
LV (F)	0.68	0.62–0.71	0.42	0.37–0.45	33

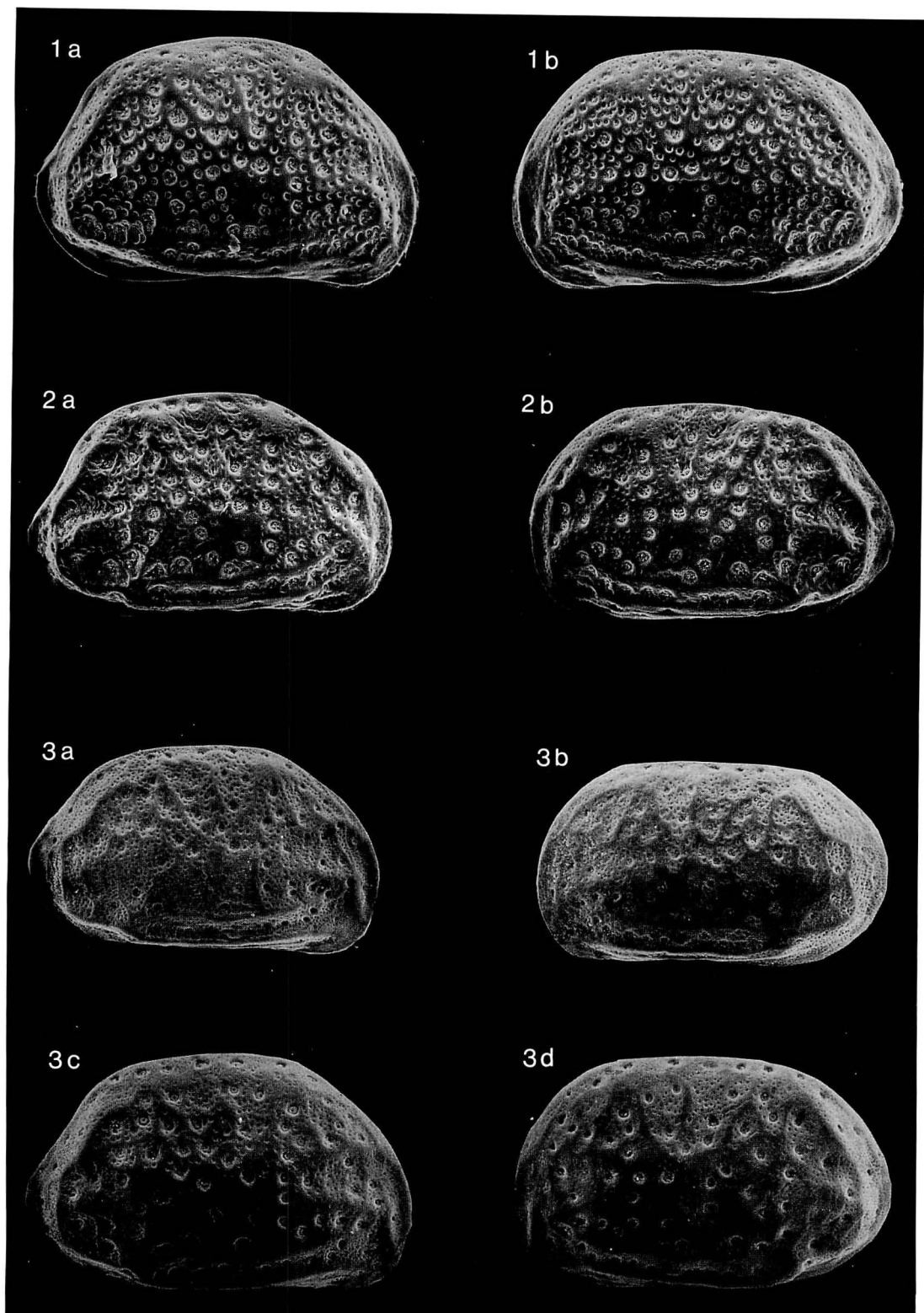


Figure 8. (All magnification  $\times 85$ ) *Cythere lutea* O. F. Müller, 1785 (Loc. 6) 1a, b. External lateral view of female R and L valves, IGSU-O-535. *Cythere nishinipponica* Okubo, 1976 (Loc. 7) 2a, b. External lateral view of female R and L valves, IGSU-O-446. *Cythere nopporoensis*, n. sp. (Loc. 8) 3a. External lateral view of male RV, holotype, IGSU-O-537. 3b. External lateral view of male LV, paratype, IGSU-O-538. 3c. External lateral view of female RV, paratype, IGSU-O-539. 3d. External lateral view of female LV, paratype, IGSU-O-540.

*Distribution.* Recent: Unknown. Fossil: Plio-Pleistocene formations of the northwest Honshu and southwestern Hokkaido, Japan.

*Remarks.* The "well preserved specimens of *C. lutea*", reported by Okada (1979) from the Anden Formation of Oga Pen., correspond to this species.

*Cythere omotenipponica* Hanai, 1959

Figures 4e, 5i, 9-1a, b

*Cythere lutea omotenipponica* Hanai, 1959, p. 413, pl. 28, figs. 5a, b; Ishizaki, 1966, p. 137, pl. 17, figs. 9-12; Ishizaki, 1968, p. 16, pl. 3, figs. 7, 8; (not) Ishizaki, 1969, p. 215, 216, pl. 26, fig. 9; Hanai, 1970, text-figs. 10A-E, 11A, E, J, 12A, A', 13B, D, D', F, H, H'; Cai, 1982, pl. 4, fig. 46.

*Cythere omotenipponica*: Schornikov, 1975, p. 4, 5; Malz and Ikeya, 1983, p. 137-145, pl. 1, figs. 1-8; Ikeya *et al.*, 1985, p. 9, tab. 1, p. 16, 28, tab. 2, pl. 3, fig. 4.

*Cythere lutea*: Okada, 1979, p. 159, fig. 14a, pl. 21, fig. 3.

*Cythere simplex* Hu, 1977, p. 199-201, Fig. 17, Fig. 24-16, 17, 19, 20, 22, 23, 25.

*Cythere simplexia* Hu, 1982, p. 178, 180, pl. 4, figs. 9, 11; Hu, 1984, p. 111, pl. 1, figs. 20, 24-27.

*Type.* Holotype (RV), UMUT-CA 3338. Paratype (LV), UMUT-CA 3339.

*Type locality.* Recent beach sand from the shore behind Hayama Imperial Villa, Hayamachi, Kanagawa Pref., Japan.

*Diagnosis.* Carapace thick and strong. Dorsal half laterally trapezoid with the dorsal margin slightly short and arched. Height/Length ratio larger than in other species. Radial ridges strong in the posterior half, whereas weak in the anterior half. Marginal ridges develop well in both anterior and posterior areas. The carapace surface entirely uneven, sieve-type pores open with deeper holes near bottom of the hollows, fine shallow pits distributed densely on the entire surface of the swellings. Sieve-type pores relatively large in diameter and the number of these pores smaller than that any other species. In comparison with the distribution pattern of the sieve-type pores in *C. uranipponica*, this species lacks 14 pores with the reference numbers C-3, C-5, D-4, D-6, E-1, E-5, F-2, G-4, G-5, H-4, H-5,

H-7, I-4, and J-1. Male has a pair of relatively stout clasping apparatuses, which are slightly curved inside. Ejaculatory duct is very long.

*Distribution.* Recent: Areas under the influence of warm water Kuroshio Current; coast of northern South China Sea, Taiwan, and Kyushu to northern Honshu, Japan. Fossil: Miocene to Pleistocene formations of coastal areas of China, Taiwan, and the Japanese Islands except Ryukyus and Hokkaido.

*Remarks.* No Recent specimens of this species were found throughout our survey between Taiwan and the Japanese Islands. We are doing further research to elucidate the reason for the occurrence of this species from areas that are geographically isolated from each other.

*Cythere sanrikuensis*, n. sp.

Figures 4f, 5j, 9-2a-d

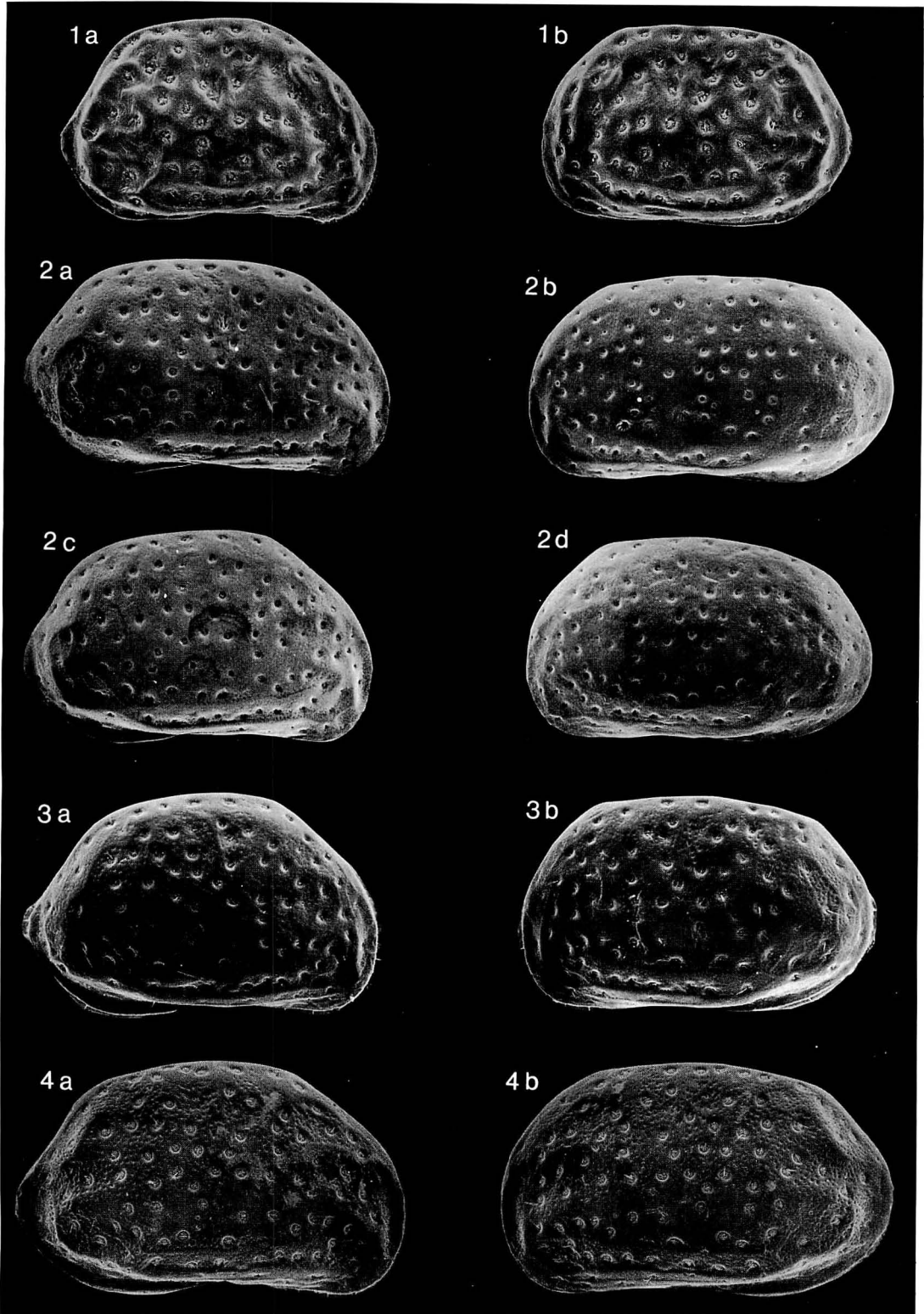
*Types.* Holotype, RV of male, IGSU-O-543 (L = 0.66 mm, H = 0.39 mm). Paratypes IGSU-O-544 (LV of male, L = 0.66 mm, H = 0.37 mm); IGSU-O-545 (RV of female, L = 0.63 mm, H = 0.38 mm); IGSU-O-546 (LV of female, L = 0.63 mm, H = 0.36 mm).

*Type locality.* Loc. 10.

*Etymology.* After "Sanriku" coast, a common name for the northeast coast of Honshu facing the Pacific Ocean, from which the species is found in abundance.

*Diagnosis.* Outline of the carapace closely resembles that of *C. schornikovi* and *C. cronini*. Carapace surface very smooth. Numerous faint shallow pits cover on the ventral margin. The number of sieve-type pores between 78 and 84, relatively large in genus *Cythere*; compared with the distribution pattern in *C. uranipponica*, five additional pores are found between A-1 and B-3, B-2 and C-3, F-6 and G-9, G-9 and H-10, and I-6 and J-5, respectively, and the pores D-6, E-1, and F-2 are not found. In the male the proximal lobe of adapters relatively long. The two hemipenes have three pairs of clasping apparatuses. Ejaculatory duct stout and relatively short.

*Description.* Lateral outline generally broad bean-shaped as in *C. cronini*, the posterior



**Figure 9.** (All magnifications  $\times 85$ ) *Cythere omotenipponica* Hanai, 1959 (Loc. 9) 1a, b. External lateral view of female R and L valves, IGSU-O-541. *Cythere sanrikuensis*, n. sp. (Loc. 10) 2a. External lateral view of male RV, holotype, IGSU-O-543. 2b. External lateral view of male LV, paratype, IGSU-O-544. 2c. External lateral view of female RV, paratype, IGSU-O-545. 2d. External lateral view of female LV, paratype, IGSU-O-546. *Cythere schornikovi* Ikeya and Tsukagoshi, 1987 (Loc. 11) 3a, b. External lateral view of female R and L valves. IGSU-O-454. *Cythere uranipponica* Hanai, 1959 (Loc. 12) 4a, b. External lateral view of female R and L valves, IGSU-O-436.

margin projects in the middle part as that of *C. schornikovi*. Very weak radial ridges develop both in the anterior and posterior halves, a ventral marginal ridge relatively weak. Carapace surface very smooth except the posteroventral area, which is faintly reticulated. Numerous relatively deep pits distributed densely in the ventral margin and inside the reticulations in the posteroventral area. Faint shallow pits are scattered over the carapace. The number of sieve-type pores fluctuates approximately between 78 and 84. The distribution pattern of sieve-type pores in the ventromedian area similar to that of *C. golikovi*. In male the proximal lobe of adapters relatively long. The two hemipenises have three pairs of clasping apparatus; the outer one curves inside and longer, the middle one hammer-shaped, and the inner one club-shaped and with a globular tip. Ejaculatory duct short and bends in an S-shape.

*Dimensions.* Listed below are the length and height measurements of adult specimens from the type locality.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.64	0.60–0.70	0.37	0.35–0.40	22
RV (F)	0.61	0.57–0.64	0.36	0.34–0.38	31
LV (M)	0.66	0.57–0.70	0.37	0.33–0.40	17
LV (F)	0.61	0.55–0.67	0.35	0.31–0.38	18

*Distribution.* Recent: Only the terminal area of the "Tsushima Current"; Pacific coast of northern Honshu and southern Hokkaido. Fossil: Plio-Pleistocene of northeast Honshu to southwestern Hokkaido, Japan.

*Remarks.* Among the *C. alveolivalva* group, this species and *C. golikovi* are adapted to the warm water region, whereas other three species the group live in the cold water region.

*Cythere schornikovi* Ikeya and Tsukagoshi, 1987

Figures 4g, 5k, 9-3a, b

*Cythere uranipponica*: Schornikov, 1974, p. 143–145, text-fig. 4, pl. 1, figs. 1a–c.

*Cythere schornikovi* Ikeya and Tsukagoshi, 1987, p. 913–915, text-figs. 7I–L, pl. 3, figs. a–n.

*Types.* Holotype, a carapace of male, IGSU-O-453. Paratypes, IGSU-O-451, 452, and 454–457.

*Type locality.* Loc. 11.

*Diagnosis.* Carapace surface very smooth with faint uneven ornamentation; blunt radial ridges and a marginal ridge in the anteroventral area. Numerous fine pits cover all over the surface. Number of sieve-type pores between 70 and 74; compared with the distribution pattern in *C. uranipponica*, the pores A-3, D-6, E-1, F-2, G-5, and K-1 are not found. In male the proximal lobe of adapters extremely long. The two hemipenises have two pairs of clasping apparatuses; the outer one gently curves inside, and the inner one outside, respectively. Ejaculatory duct relatively long.

*Distribution.* Recent: Coasts from southern Kuril Islands to eastern Hokkaido. Fossil: Pliocene to Pleistocene formations of northern Honshu and southwestern Hokkaido, Japan.

*Remarks.* Detailed description of this species is given in Ikeya and Tsukagoshi (1987).

*Cythere uranipponica* Hanai, 1959

Figures 4h, 5l, 9-4a, b

*Cythere lutea uranipponica* Hanai, 1959, p. 412, 413, pl. 28, figs. 2, 6a, b, text-figs. 2a, b; Hanai, 1961, p. 366, text-fig. 9, figs. 2a, b; Hanai, 1970, p. 704, text-figs. 5c, d; Ishizaki and Matoba, 1985, pl. 2, fig. 19, (not) fig. 20.

*Cythere lutea*: Ueno and Hanai, 1965, p. 455, figs. 420-1, 2, (not) 3; Hanai, 1970, pl. 107, fig. 6; Okada, 1979, p. 159, Fig. 14c, pl. 21, figs. 2, 7, 8.

*Cythere lutea lutea*: Ishizaki, 1966, p. 137, pl. 17, figs. 1, 2.

*Cythere uranipponica*: (Not) Schornikov, 1974, p. 143–145, pl. 1, figs. 1a–c, text-fig. 4; Ikeya and Tsukagoshi, 1987, p. 909–911, pl. 1, figs. a–n, text-figs. 2b, 7A–D, 8A–F.

*Types.* Holotype, RV, UMUT-CA 3333. Paratypes, LV and RV, CA 3334–3337.

*Type locality.* Pliocene Sawane Formation. The cliff at Mano Bay, Sawane-machi, Sado Island, Niigata Pref., Japan.

*Diagnosis.* Outline slightly rounded at both ends of the dorsal margin. Weak radial ridges developed, as well as narrow marginal ridges in the anterodorsal and posteroventral regions of

the valves. Carapace surface densely covered with small shallow pits. The number of the sieve-type pores averages 78, and fluctuates between 75 and 82. One of these pores which is close to the center of the dorsal margin, as in *C. nishinipponica*, exists in addition to those in other *Cythere* species. Each hemipenis of the male has four clasping apparatuses, the greatest number of all *Cythere* species. Proximal lobe of adapters short, ejaculatory duct very thin and short.

*Distribution.* Recent: The terminal area of Tsushima Current (a branch of Kuroshio Current); Coasts of the Sea of Japan from San-in to southwestern Hokkaido and Pacific coasts from Sanriku to southern Hokkaido. Fossil: Miocene to Pleistocene Formations of Northern Honshu and Hokkaido, Japan.

*Remarks.* Surface ornamentation and the distribution pattern of sieve-type pores are similar to those of *C. nishinipponica*, but this species is distinguished by the lack of one pore in the ventro-median area. Further the morphology of the male copulatory organ is radically different from that of *C. nishinipponica*. This species was described in detail in Ikeya and Tsukagoshi (1987).

*Cythere urupensis* Schornikov, 1974

Figures 5m, 10-1a, b

*Cythere urupensis* Schornikov, 1974, p. 145–147, pl. 1, figs. 3a–d, text-fig. 5.

*Type.* Holotype, a carapace of male, FESC No. 351–352.

*Type locality.* Urup Island.

*Diagnosis.* Several wide radial ridges develop strongly, three of which is especially remarkable and run vertically near the center of carapace. These both side ridges convex to the center, the middle one more distinct in the dorsal half. The sieve-type pores open at the bottom of the cone-shaped depression, and the raised reticulatae developed around the cones. Very deep pits distributed densely over the carapace, except for the upper surface of the ridges and the reticulations. The number of the sieve-type pores approxi-

mately between 78 and 84. The distribution pattern of the sieve-type pores, compared with that in *C. uranipponica*, eight additional pores are found between B-3 and B-4, B-5 and C-6, C-6 and D-7, C-4 and D-4, C-5 and D-6, D-8 and F-7, F-4 and F-5, F-7 and G-8, J-4 and J-5, respectively, but eight pores, such as E-1, E-5, F-2, G-4, H-4, and I-5 are missing. In male the two hemipenises have two pairs of clasping apparatuses; the outer one larger, curves inside, and branches into two in the tip, and the inner one sharp-pointed and curved inside.

*Distribution.* Recent: The southern Kuril Islands to northeastern Honshu, Japan. Fossil: Plio-Pleistocene formations of northeast Honshu to southwestern Hokkaido, Japan.

*Remarks.* This species closely resembles *C. lutea* in the male copulatory organs and the distribution pattern of sieve-type pores. Nevertheless, the two species greatly differ in the morphology of carapace. Their phylogenetical relationship may be very close.

*Cythere valentinei*, n. sp.

Figures 5n, 10-2a–d

*Cythere* sp. B. Valentine, 1976, pl. 12, figs. 9, 13.

*Cythere* cf. *C. lutea*: Swain, 1969, p. 461, pl. 1, fig. 11.

*Cythere alveolivalva*: Swain, 1969, p. 462, pl. 9, figs. 4a, b.

*Cythere lutea*: Swain and Gilby, 1974, p. 284, pl. 2, figs. 7a, b, text-figs. 12a–j.

*Type.* Holotype, RV of male, IGSU-O-549 (L = 0.64 mm, H = 0.37 mm). Paratypes, IGSU-O-550 (LV of male, L = 0.65 mm, H = 0.38 mm); IGSU-O-551 (RV of female, L = 0.64 mm, H = 0.40 mm); IGSU-O-552 (LV of female, L = 0.63 mm, H = 0.37 mm).

*Type locality.* Loc. 14.

*Etymology.* In honour of Dr. P.C. Valentine who illustrated this species and recognized it differs from other *Cythere* species.

*Diagnosis.* Outline and surface ornamentation of the carapace resemble closely those of *C. lutea*. Pits larger in size and smaller in number. The number of the sieve-type pores is approximately between about 60 and 65, and the smallest in the genus *Cythere*; compared with the distribu-

tion pattern of those in *C. uranipponica*, the following 16 pores, C-3, C-5, D-4, D-6, D-8, E-1, E-4, E-5, F-2, F-4, G-4, H-4, H-5, H-7, I-5, and K-1 are missing.

**Description.** In the male Height/Length ratio and curvature in the dorsal margin smaller than those in female. Several wide radial ridges develop, among which the ridges in the posteroventral region form an arc toward the posteroventral margin and continue to the ventral ridge. The upper branch of the ventral marginal ridge develops strongly. The marginal ridges at the anterodorsal and the posterodorsal regions also remarkable. The Numerous deep pits cover the carapace surface; they are smaller and denser on the marginal region, and larger and sporadic on the central region of the carapace.

**Dimensions.** Listed below are the length and height measurements of adult specimens from the type locality.

	Length		Height		N
	$\bar{X}$	OR	$\bar{X}$	OR	
RV (M)	0.64	0.60–0.65	0.38	0.37–0.40	9
RV (F)	0.63	0.60–0.66	0.39	0.36–0.41	11
LV (M)	0.66	0.64–0.68	0.38	0.37–0.39	8
LV (F)	0.63	0.58–0.67	0.37	0.33–0.39	10

**Distribution.** Recent: Living specimens unknown, but Holocene (subfossils) from the west coast of North America; the coastal area of the southern Canada to California. Fossil: Pleistocene to early Pliocene formations of the west coast of North America.

**Remarks.** According to Valentine (1976) this species occurs in the areas from latitude 38° to 48.5°N of the west coast of North America. As a trial estimation of the paleo-temperature from these data, he assumed that this species adapted to the water temperature ranging from 7° to

15°C. Although Lucas = Smith (1931, 1952) reported *C. lutea* from the tidal zone of Vancouver, British Columbia, there are no figures in her reports. Those "*C. lutea*" are tentatively included in this new species based on their geographic distribution. Swain and Gilby (1974) reported *C. sp. aff. C. lutea* which is obviously represented by a juvenile specimen of *C. maia* or *C. valentinei*.

#### *Cythere* sp.

*Cythere alveolivalva*: Swain, 1969, p. 462, pl. 4, figs. 12a, b, pl. 7, figs. 1a, b, pl. 10, figs. 9a, b; Swain and Gilby, 1974, p. 285, pl. 2, figs. 9, 10, 26a, b, text-fig. 18.

*Cythere sp. aff. C. lutea*: Swain and Gilby, 1974, p. 284, 285, pl. 2, figs. 6, 8.

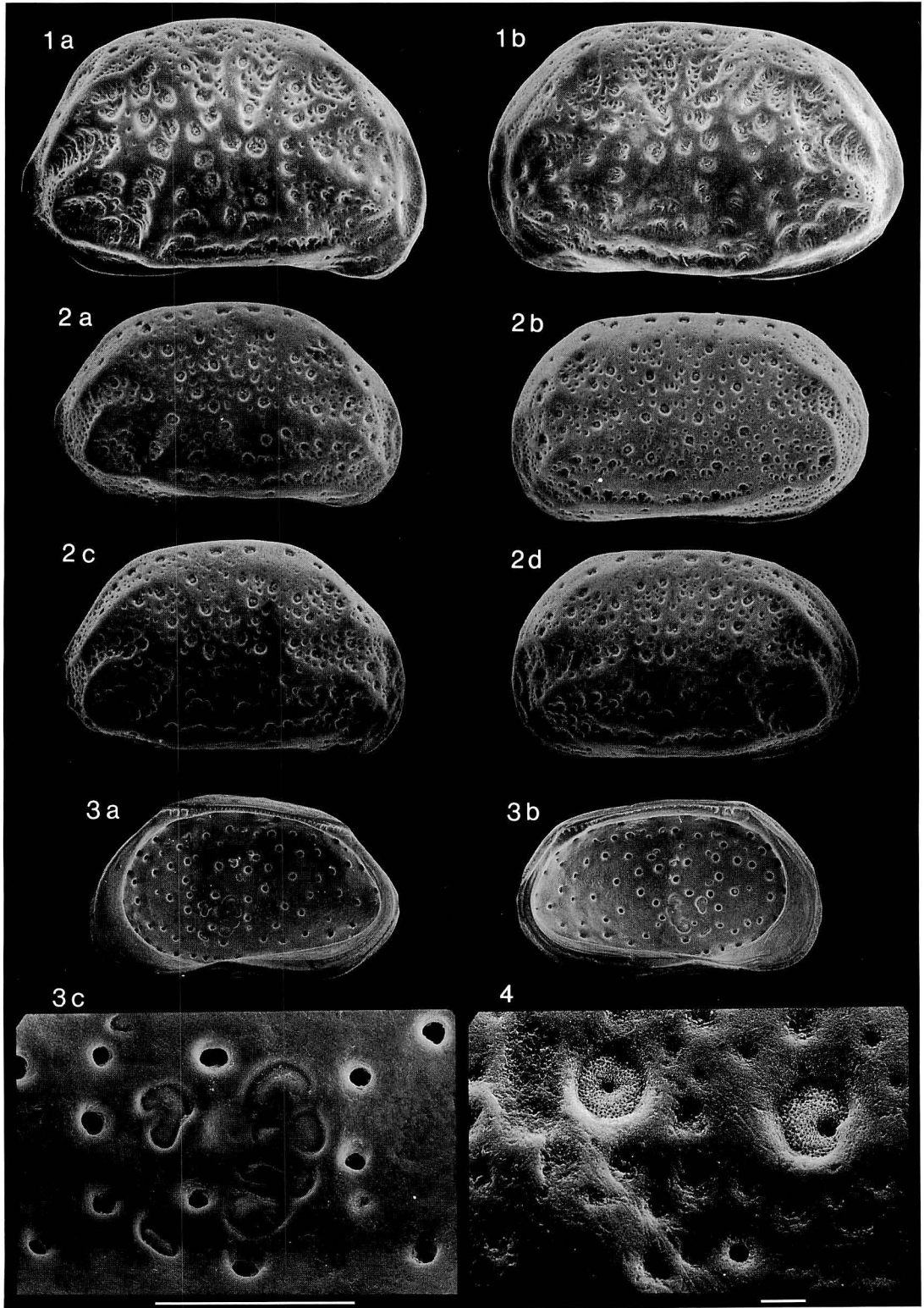
*Cythere maia*: Valentine, 1976, pl. 12, figs. 3, 6.

**Distribution.** Recent: Tide pool of Point Piedras Blancas, California. Holocene (subfossils) the west coast of the California to Baja California, Mexico. Fossil: Early Pleistocene to middle Pliocene formations of the west coast of North America.

**Remarks.** Dorsal margin of the carapace gently arched and connected with both anterior and posterior margins at obtuse angle. Several faint radial ridges found, among which the ridges in the posteroventral region develop strongly, and the shape resembles closely that of *C. valentinei* n. sp. The marginal ridges at the posterodorsal and ventral regions distinctly developed. Small and relatively deep pits cover the carapace; these are denser in the dorsal half of carapace, and the diameter of these pits are about 1/4 to 1/6 of diameter of sieve plates in the central part of the carapace. The number of sieve-type pores is great (approximately 80) for the genus. Valentine (1976) identified the specimens (Valentine, 1976, pl. 12, figs. 3 (= USNM 207982), 6

→ **Figure 10.** *Cythere urupensis* Schornikov, 1974 (x85) (Loc. 13) 1a. External lateral view of female RV, IGSU-O-547. 1b. External lateral view of female LV, IGSU-O-548. *Cythere valentinei*, n. sp. (x85) (Loc. 14) 2a. External lateral view of male RV, holotype, IGSU-O-549. 2b. External lateral view of male LV, paratype, IGSU-O-550. 2c. External lateral view of female RV, paratype, IGSU-O-551. 2d. External lateral view of female LV, paratype, IGSU-O-552. *Cythere cronini*, n. sp. 3a. Internal lateral view of female RV, IGSU-O-553 (x72). 3b. Internal lateral view of female LV, IGSU-O-554 (x72). 3c. Distribution of the adductor, frontal, and mandibular scars of female RV, IGSU-O-553 (x320, scale shows 100  $\mu$ m). *Cythere nopporoensis*, n. sp. 4. Sieve and funnel type normal pore canals of female RV, paratype, IGSU-O-539 (x720, scale shows 10  $\mu$ m).





(= USNM 207983)), collected from a tide pool at Point Piedras Blancas, California (35°40'N, 121°15'W) as *C. maia* (Benson). So far as judged from the illustrated specimens and descriptions, the surface of the carapace of *H. maia* by Benson (1959) appears to be very smooth, whereas that of *C. maia* of Valentine (1976) has well developed ornamentation. We consider that *C. maia* (Benson), as identified by Valentine (1976) differs from *H. maia* Benson, 1959 and belongs to a new species. According to Valentine (1976) this species inhabits the area of latitude 26°45'N to 35°45'N of the water temperature 12° to 24°C in the westcoast of North America. We include *H. maia* Benson in the genus *Cythere* and regard it as an independent species. *C. maia* of Valentine (1976) needs a proper new name, but we need more specimens to fully understand the species.

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Suttu 寿都, Hanyu 羽二生, Sawane 沢根, Sado 佐渡, Kaidate 貝立, Bussha 仏社, Kobuchi 小淵, Aniai 阿仁合, Kamikoani 上小阿仁, Dezaki 出崎, Kita-hiroshima 北広島, Kesaiso 今朝磯, Motoyoshi 本吉, Okenepu 沖根婦, Ayukawahama 鮎川浜, Nosappu-misaki 納沙布岬, Toyoura 豊浦, Funka bay 噴火湾, Kuroiwa 黒岩, Nagasakibana 長崎鼻, Choshi 銚子.

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介形虫 *Cythere* (O. F. Müller, 1785) 属とその種の記載: *Cythere* 属は, 1785年, O. F. Müller によって海生の介形虫類に与えられた最古の属として名高い。本研究は, 全世界の *Cythere* 属の化石および現世標本の徹底した収集を行うと共に, これまでの研究を総括して, 本属に17種が含まれることを明らかにした。分類の基準として, 遺伝的に保存性の高い形質のひとつである殻表面に開口する sieve-type normal pore canals の分布形式を重要視して種の分類を行った。また, 現生種については, soft part (生物体), 特に雄の生殖器官の形態の比較により, これらの種分類の信頼性を確認した。本属は, 北回帰線以北に分布圏をもち, 北大西洋沿岸地域に2種, 北太平洋東部地域に4種, 日本列島を含む北太平洋西部沿岸地域に絶滅種3種を含む12種(一部北太平洋東部沿岸地域との共通種を含む)が産出する。種の多様度は, 日本列島地域で最も高く, また化石記録は日本では, 初期中新世まで遡れるのに対して, ヨーロッパおよび北米東部では, 中期更新世以降, 北米西部では, 中期鮮新世以降に産出する。これらの知見を背景として, 本属の各種間の近縁性を考察し, 5つの種グループを認めた。既知種10種の再記載を行うと共に, 7新種 (*C. cronini*, *C. hanaii*, *C. kamikoaniensis*, *C. nopporoensis*, *C. sanrikuensis*, *C. valentinei*, *C. sp.*) を提唱し, *Cythere* 属の種分化および進化系統を追跡する上での基礎とした。

塚越 哲・池谷仙之

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## 841. *ADNATOCERAS* FROM MIDDLE CARBONIFEROUS OF THE ICHINOTANI FORMATION, FUKUJI DISTRICT, CENTRAL JAPAN\*

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The University of Tokyo, Komaba, Tokyo 153

**Abstract.** *Adnatoceras ichinotaniensis*, sp. nov. is described from a late Bashkirian (Middle Carboniferous) limestone of the Ichinotani Formation in the Fukuji district, central Japan. This species is morphologically characterized by the following features; (1) subcircular cross-section of the shell in early stages, (2) position of the siphuncle shifts ventralwards to some degree from center as the shell grows, and (3) episepal-mural and hyoseptal deposits are well-developed in apical portion. The genus *Adnatoceras* has previously been known only from Western Europe, U.S.S.R. and North America of Middle Devonian to Late Carboniferous time.

### Introduction

The genus *Adnatoceras* was established by Flower in 1939 based on *Orthoceras spissum* Hall, the type species for the genus, from the upper limestone band of the Pompey Member of the Hamilton Group, New York. The genus has been previously identified from Western Europe (Ireland; Belgium?), U.S.S.R. (Armenia; Komi A.S.S.R.: Urals; Kazakhstan; Berkhoynian) and North America (Alaska; Texas; Arkansas; New York). The stratigraphic range of *Adnatoceras* is known from Middle Devonian through Upper Carboniferous.

In the present article, we describe a new species of *Adnatoceras* from the Ichinotani Formation in the middle course of the Ichinotani valley in the Fukuji district, Kamitakara Village, Yoshiki Country, Gifu Prefecture (Figure 1).

We are deeply grateful to Dr. T. Kobayashi of the Japan Academy for critical reading of the manuscript. The authors wish to thank Dr. T. Nishida of Saga University for valuable discussion and also to Dr. H. Igo of the University of Tsukuba for providing informations of the fossil

locality.

The repositories of the described specimens are in the University Museum, The University of Tokyo (UMUT).

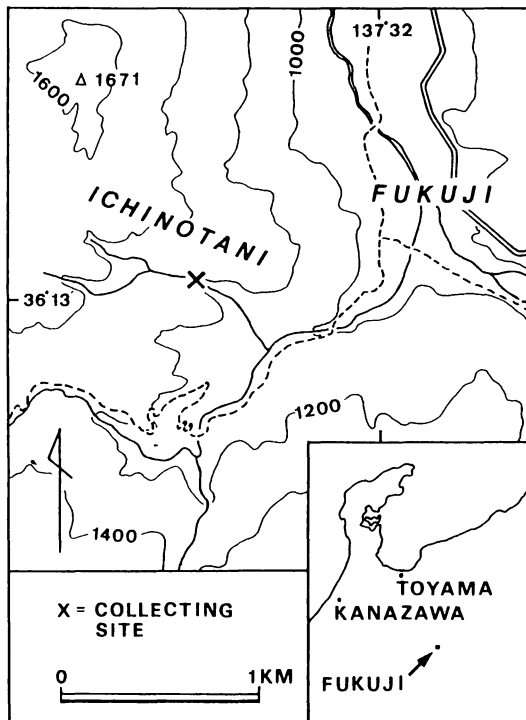


Figure 1. Map showing the fossil locality in the Fukuji district, Gifu Prefecture.

\*Received August 20, 1987; revised manuscript accepted October 26, 1987; Studies on Japanese Trilobites and Associated Fossils—LVII.

### Geological setting

The Ichinotani Formation (late Early Carboniferous to Early Permian age) is exposed in the Ichinotani valley, Mizuboradani valley, and the lower reaches of the Mizuyagadani valley, and comprises about 350 m thick of mostly fossiliferous limestone with subordinate amounts of interbedded terrigenous sediments. It can be subdivided into the Lower, Middle and Upper Members (Igo and Adachi, 1981; Adachi, 1985).

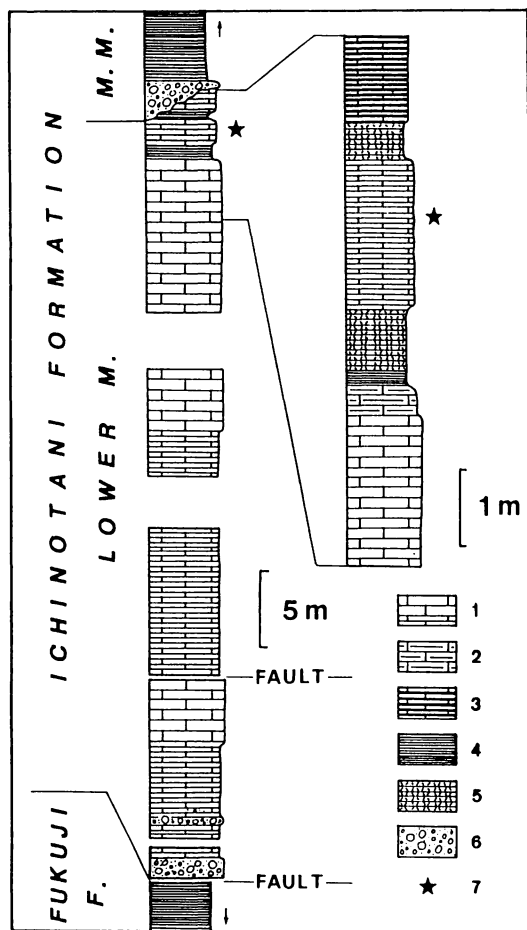


Figure 2. Columnar section showing lithology and stratigraphic position of sample. 1: limestone, 2: impure limestone, 3: alternating beds of limestone and thin shale, 4: shale, 5: tuffaceous shale, 6: conglomerate, 7: *Adnatoceras*.

The Lower and Upper Members are mostly composed of bioclastic wackestone and packstone; the Middle Member consists mainly of bioclastic packstone, wackestone and oolitic grainstone, and is characterized by frequent intercalation of red shale and acidic tuff. A detailed description of these rocks is presented by Adachi (1985).

The cephalopod herein described came from the upper part of the Lower Member (Figure 2). The orthoceratid-bearing bed is in a dark gray limestone (bioclastic wackestone) with thin shale, which contains crinoid fragments, ostracods, foraminifers, bryozoans, brachiopods, gastropods, goniatites, and rugose corals (*Amplexocarinia radricula* Igo and Adachi). This bed did not produce any keen microfauna for age determination except for ill-preserved small archaedisids. However, the occurrence of fusulinid, *Profusulinella fukujiensis* Igo, at a part about 3 m below the orthoceratid-bearing bed may suggest that it probably corresponds to upper Bashkirian.

### Systematic paleontology

Superfamily Pseudorthocerataceae  
Flower and Caster, 1935

Family Pseudorthoceratidae  
Flower and Caster, 1935

Genus *Adnatoceras* Flower, 1939

*Adnatoceras* Flower, 1939, p. 120–121; Balashov and Zhuravleva, 1962, p. 89; Gordon, 1964, p. 125–126; Sweet, 1964, p. K246; Shimansky, 1968, p. 78.

*Type species*:—*Orthoceras spissum* Hall, 1879.

*Diagnosis*:—*Adnatoceras* is applied to smooth orthocone nautiloid with a circular to subcircular cross section being provided with slightly oblique sutures. Siphuncle subcentral, slightly ventral to center. Siphuncular segments are abruptly expanded at the place of septal foramen; parallel-sided, and area of adnation equals at least to width of brim; septal necks cyrtocoanitic to suborthochoanitic. Both cameral and endosiphuncular deposits are well-developed.

*Remarks*:—The generic description given above is essentially the same as that of Flower (1939), which is accepted without any emendation. The morphology of this genus exemplifies the very

close relationship to *Euloxoceras*. The major difference is in the venterward siphuncular position of the former. *Adnatoceras* includes species formerly assigned to *Dolorthoceras*. The distinction between those two genera is based on the difference of width of adnation area and expansion of siphuncular segments at septal foramen. The following Carboniferous species are included in the genus *Adnatoceras*:

*alaskense* Gordon, 1957; Meramecian, Alaska and Arkansas

*ciscoense* (Miller, Dunber and Condra), 1933, (*Dolorthoceras*); Late Pennsylvanian (Cisco), Texas

*ichinotaniensis* Niko and Hamada, sp. nov.; Bashkirian, central Japan (this report)

*kipchakense* Shimansky, 1968; Viséan, Kazakhstan

?*neglectum* (de Koninck), 1880, (*Orthoceras*); Tournaisian, Belgium (Flower, 1939; Gordon, 1964)

*tyrense* Shimansky, 1968; Early Carboniferous, Berkhoynian

*usense* Shimansky, 1968; Viséan, Urals

*variabile* (Foord), 1896, (*Orthoceras*); Early Carboniferous, Ireland and Urals

*Adnatoceras ichinotaniensis*

Niko and Hamada, sp. nov.

Figures 3-1-6

**Material:**—Holotype, UMUT PM 18068 (Figures 3-1-3, 5); paratype, UMUT PM 18069 (Figures 3-4, 6). The studied materials are all the imperfect phragmocones partly replaced by secondary silicate that the microscopic structures are often obliterated.

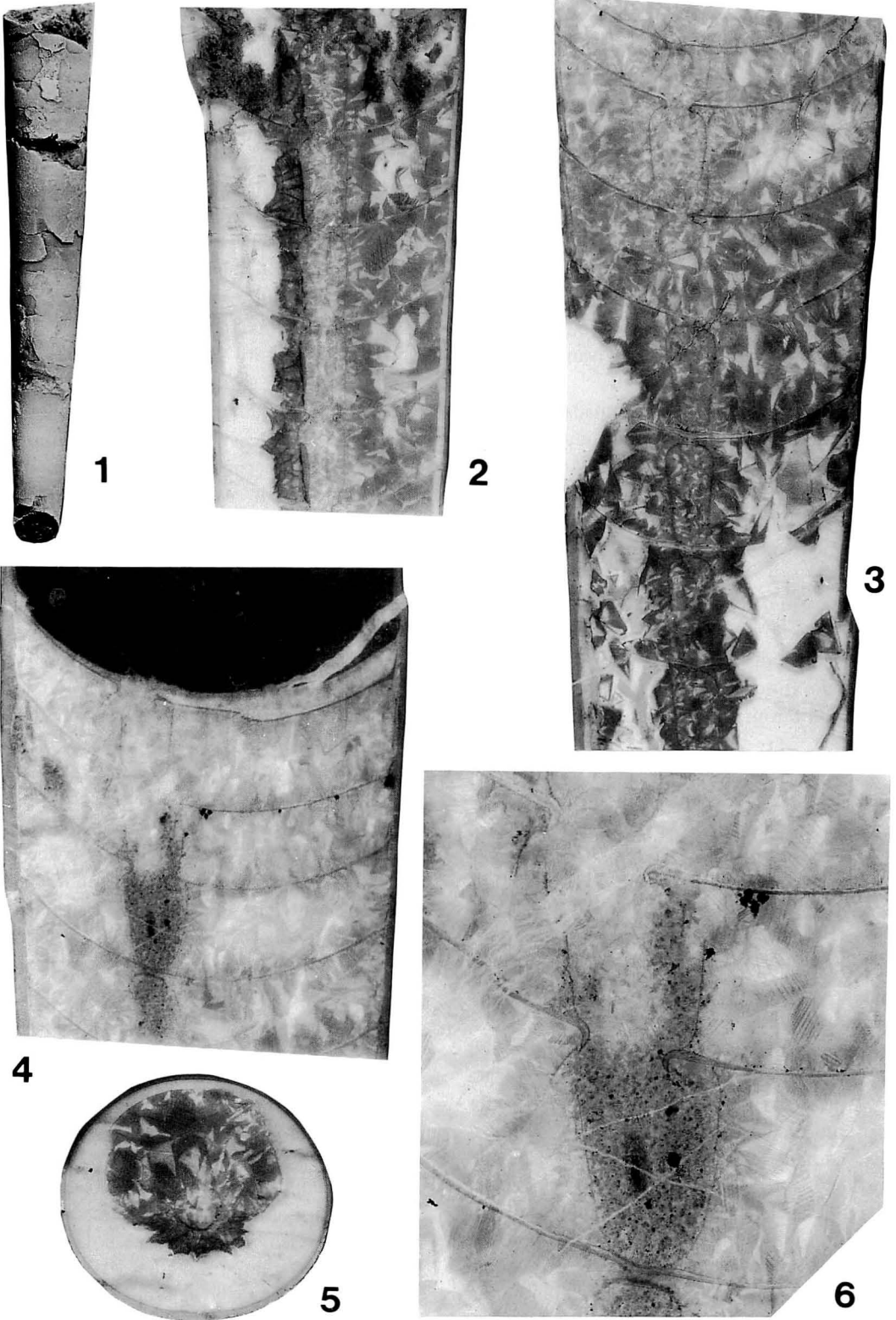
**Diagnosis:**—*Adnatoceras* with smooth shell surface, subcircular cross section in early stages and with relatively shallow septa. Apically, siphuncle subcentral with cyrtochoanitic septal necks; adorally it moves to ventral side, and suborthochoanitic septal necks on ventral side. Cameral deposits episeptal-mural and hyposeptal.

**Description:**—Holotype, UMUT PM 18068: The holotype is a portion of an orthoconic phragmocone, 41 mm long. Cross section of the

shell is subcircular in early stages, later becoming circular. Diameter of the conch is 4 × 3.5 mm at the apical end and expands up to 7 mm at the adoral end. The shell surface is smooth. Sutures are straight and slightly oblique to the long axis of the conch. Apically, two and one-half camerae occupy a length equal to the corresponding conch diameter; adorally this figure increases to three and one-half. Curvature of septa is relatively shallow. The siphuncle is subcentral in early stages, slightly ventral side to the center in later stages. Septal necks are short and cyrtochoanitic, joined by thin rings. Free part of connecting rings is abruptly constricted at septal foramen, and middle part is almost cylindrical. Cameral deposits are found throughout the length of the specimen. On the ventral side of the siphuncle, it can be differentiated into episeptal-mural and hyposeptal deposits. Dorsally, L-shaped episeptal-mural deposits are developed in the apical part. The presence of weak pseudorthoceroid annuli is recognized on the ventral side of the siphuncle wall in the apical 3 camerae.

**Paratype, UMUT PM 18069:** This represents a portion of a phragmocone in more mature stage than the holotype. Over a length of about 14.5 mm the specimen increases in diameter from 7.5 mm to 8.5 mm. Cross section of the shell is circular. About 4 camerae occupy a length equal to the adoral conch diameter. The siphuncle is circular in cross section and removed from the center of the conch by a distance approximately equal to its diameter. Septal necks are short, suborthochoanitic at the ventral side and cyrtochoanitic at the dorsal side, joined by thin connecting rings which are abruptly constricted at septal foramen. The shell wall is thicker in the ventral side than in the dorsal side. No cameral and siphonal deposits are evident.

**Discussion:**—*Adnatoceras ichinotaniensis*, sp. nov. closely resembles *A. kipchakense* Shimansky from Kazakhstan, but has more slender shell than the Russian form. The examined specimens somewhat resemble *A. alaskense* Gordon, but they are different from the latter in having shorter camerae, shallower septa and non-orna-



Figures 3-1-6. *Adnatoceras ichinotaniensis*, sp. nov. 1-3, 5. UMUT PM 18068, holotype. 1, ventral view,  $\times 2.2$ , vertical thin section, apical part, venter on left,  $\times 10.3$ , vertical thin section, adoral part, venter on left,  $\times 8.5$ , cross thin section, near the apical end, venter on down,  $\times 10$ . 4, 6. UMUT PM 18069, paratype. 4, vertical thin section, venter on left,  $\times 8$ . 6, enlargement of vertical thin section, venter on left,  $\times 18$ .



mented shell. *A. ichinotaniensis* differs in general from *A. tyrense* Shimansky and *A. ciscoense* (Miller, Dunbar and Condra) in having more eccentric siphuncle and circular cross section of the shell in later stages. The specimens mark the first occurrence of the genus in East Asia.

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Ichinotani 一ノ谷, Fukuji 福地, Kamitakara 上宝, Yoshiki 吉城, Gifu 岐阜, Mizuboradani 水洞谷, Mizuyagadani 水屋ヶ谷.

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岐阜県福地地域，一ノ谷層の石炭紀中期 *Adnatoceras* : 岐阜県吉城郡上宝村福地地域の一ノ谷層の下部層上部 (late Bashkirian) より産出した *Adnatoceras ichinotaniensis* Niko and Hamada, sp. nov. を記載した。本種は，(1)成長の比較的初期に壱円状の殻断面を示す，(2)体管の位置が成長に伴い殻の中心からやや腹側へ移動する，(3) episepetal-mural 及び hyposeptal の各位置に気房内分泌物が認められることにより特徴づけられる。*Adnatoceras* 属は，従来ヨーロッパ，ソビエト，北米の中部デボン系から上部石炭系にかけてのみその産出が知られていた。

児子修司・浜田隆士

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## 842. EARLY CARBONIFEROUS CORALS FROM THE OMI LIMESTONE, CENTRAL JAPAN\*

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**Abstract.** Corals are abundant in the lowest part of the Omi Limestone, Central Japan. An assemblage of corals obtained from the lowest part in the Fukugakuchi area comprises more than 13 forms, from which the following five species including three new species are herein described and illustrated: *Cyathaxonia* cfr. *C. cornu* Michelin, *Clisiophyllum kurohimense*, sp. nov., *Akiyosiphyllum stylophorum* Yabe and Sugiyama, *Carcinophyllum hasegawai*, sp. nov. and *Hiroshimaphyllum simplex*, sp. nov. This coralline fauna is correlatable with that of the *Nagatophyllum satoi* Zone of the Akiyoshi Limestone, Southwest Japan, and indicates Late Viséan in age.

### Introduction

The Carboniferous coralline faunas of the Omi Limestone distributed in Nishikubiki County, Niigata Prefecture, Central Japan, were described or reported by Hayasaka (1921, 1922, 1924, 1932, 1939), Kawada (1954a, b, c), Minato (1951, 1955), Fujita (1958), Kato *et al.* (1964), Kato (1967), Rowett and Minato (1968) and Kato and Minato (1975).

Recently, one of the authors (Y.Y.) newly collected a number of specimens of corals from the lowest part of the Omi Limestone in the Fukugakuchi area (Figure 1). This locality is referable to the lower part of the *Endothyra* Zone of Hasegawa *et al.* (1969, 1982).

In this paper the fauna is discussed in terms of its affinity, and five species including three new species are described.

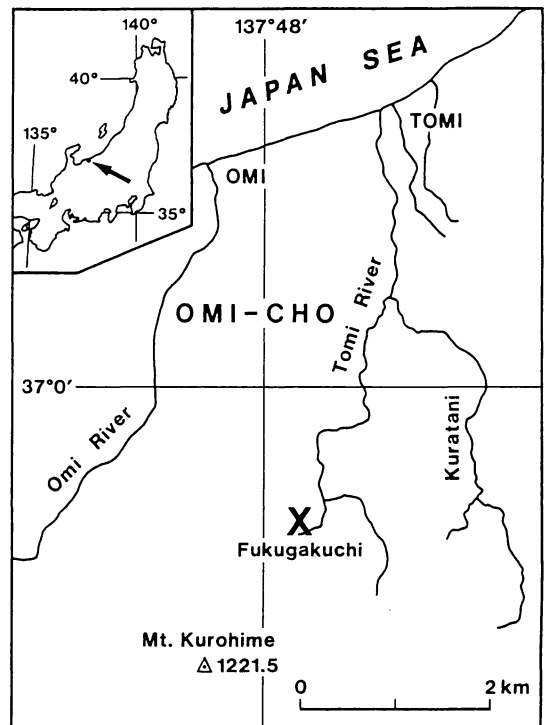


Figure 1. Map showing the fossil locality.

\*Received August 20, 1987

### Stratigraphy and age of the coralline fauna

The lowest part of the Omi Limestone is characterized by the greenish or purplish, basic pyroclastic rocks with bioclastic and tuffaceous limestone clasts of various size, intercalating the oolitic limestone layers near its uppermost part

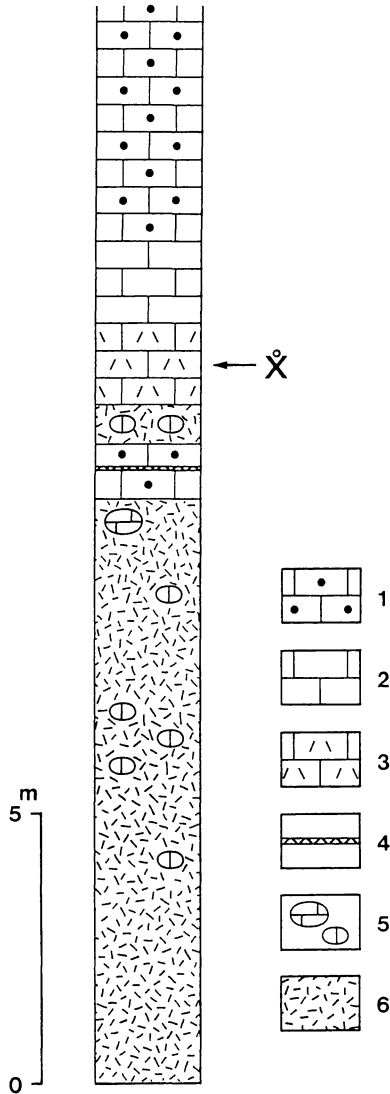


Figure 2. Columnar section of the lower part of the Omi Limestone in the Fukugakuchi area, showing the stratigraphic position of the fossil locality shown on index map, see Figure 1. 1: oolitic limestone; 2: bioclastic packstone; 3: bryozoan-crinoidal packstone-rudite; 4: basic tuff; 5: clasts of limestone; 6: pyroclastic rocks.

(about 14 m in total thickness). The coral specimens were obtained from the uppermost part consisting of bryozoan-crinoidal packstonerudite with basic tuffaceous matrices (1.5 m in thickness) followed by massive bioclastic and oolitic limestone (Figure 2).

The following is a list of identified corals from the above mentioned locality and horizon (Numerals show the examined specimen-number).

* <i>Cyathaxonia</i> cfr. <i>C. cornu</i> Michelin	8
<i>Neaxon</i> sp.	1
<i>Zaphrentoides</i> spp.	7
" <i>Polycoelia</i> " <i>japonica</i> Ozawa	12
<i>Plerophyllum</i> spp.	2
<i>Pentaphyllum</i> sp.	1
* <i>Clisiophyllum kurohimense</i> , sp. nov.	9
* <i>Akiyosiphyllum stylophorum</i> Yabe and Sugiyama	67
* <i>Carcinophyllum hasegawai</i> , sp. nov.	30
* <i>Hiroshimaphyllum simplex</i> , sp. nov.	5
<i>Pseudofavosites</i> sp.	1
<i>Pseudoromingeria kotoi</i> (Yabe and Hayasaka)	9
Metriophyllidae, gen. et sp. indet.	1
*Species herein described. Total	153

The coralline fauna, besides, is associated with such smaller foraminifers and primitive fusulinaceans as *Endothyra spinosa* Chernysheva, *E. gigantea* (Okimura), *E. masanae* (Okimura), *E. spp.*, *Globivalvulina* sp., *Palaeotextularia* spp., *Tetrataxis* spp., *Endostaffella* sp., *Mediocris mediocris* (Vissarionova), *M. breviscula* (Ganelina), and this foraminiferal assemblage is closely referred to those of the Middle to Late Viséan *Endostaffella delicata* Zone and the lower part of the *Mediocris mediocris* Zone of the Akiyoshi Limestone, Southwest Japan (Okimura, 1966).

Two species described in this paper, *Cyathaxonia* cfr. *C. cornu* and *Akiyosiphyllum stylophorum*, and "*Polycoelia*" *japonica*, are well known as the important faunal elements of the Middle to Late Viséan *Nagatophyllum satoi* Zone of the Akiyoshi Limestone (Ota, 1977). In addition to the occurrences of common species between the Akiyoshi and this area, it is noteworthy that the lithologic characters described by Ota (1977)

show the close affinity to those in the locality of Fukugakuchi.

Recently, Tazawa *et al.* (1983) described some Late Viséan brachiopod species from basic tuff in the lowermost part of the Omi Limestone cropping out in the east side of the Omi River. Stratigraphically, the brachiopod bearing horizon may be slightly lower than the impure limestone bed yielding the present corals.

According to the viewpoints mentioned above, the present authors estimate this coralline fauna to be of Late Viséan age.

### Systematic Description

All the specimens described and illustrated in the present study are stored in the Institute of Geology and Mineralogy, Faculty of Science, Hiroshima University, Hiroshima. The registered numbers of the type specimens (IGSH-YY No.) and the illustrated specimen-numbers (OM No.) are shown in the brackets of explanation of Figures.

Family Cyathaxoniidae Milne-Edwards and Haime, 1850

Genus *Cyathaxonia* Michelin, 1847

*Type species* (by subsequent designation of Milne-Edwards and Haime, 1850):—  
*Cyathaxonia cornu* Michelin, 1847

*Cyathaxonia* cfr. *C. cornu* Michelin

Figures 4-1a-3

*Compare*:—

- 1847 *Cyathaxonia cornu* Michelin, p. 258, pl. 59, figs. 9a-b.  
1909 *Cyathaxonia cornu*; Faurot, p. 75 (7).  
1913 *Cyathaxonia cornu*; Carruthers, p. 53, pl. 3, figs. 4-7.  
1940 *Cyathaxonia cornu*; Hill, p. 195.  
1960 *Cyathaxonia cornu*; Vassiljuk, p. 157, pl. 12, fig. 8.  
1964 *Cyathaxonia cornu*; Vassiljuk, p. 87, pl. 7, fig. 1.  
1968 *Cyathaxonia cornu*; Fedorowski, p. 210, pl. 1, figs. 4a-d.  
1977 *Cyathaxonia cornu*; Khoa, p. 319, pl. 1, figs. 1, 2, 3a-b, 4-6.  
1978 *Cyathaxonia cornu*; Poty in Kimpe *et al.*, pl. 5,

fig. 5.

1978 *Cyathaxonia cornu*; Yü *et al.*, p. 14, pl. 1, figs. 11a-b, 12a-b.

1981 *Cyathaxonia cornu*; Poty, p. 17, pl. 2, figs. 2-5.

1986 *Cyathaxonia* cf. *C. cornu*; Haikawa, pl. 3, figs. 1, 2.

*Material*:—Eight fragmental corallites, from which twelve thin sections were prepared.

*Description*:—Corallum is solitary, ceratoid and small in size. The length of the corallum is unknown, owing to the lack of its proximal end.

In transverse section, corallite has round and smooth configuration, and is 3.3 mm in diameter in the largest corallite. The peripheral stereozone formed by lateral fusion of septa is prominent. No dissepiments are developed. Septa are thick and in two orders, major and minor respectively. Fossula is not observed. Major septa are long, reaching a columella. The axial ends of septa are bluntly terminated and occasionally slightly clavate. Counter septum is somewhat thinner than other major septa. Minor septa, which are a little thinner than and alternate with the major, show a contratingent nature. They attain usually 1/2 to 2/3 the length of the major, and sometimes they are longer and join the major at the periphery of the columella. Minor septa on both sides of the counter septum are longer than the rest and may be connected with the columella. Septal fine structure is trabecular. The sides of septa are smooth and not vepreculate. As many as 28 septa occur in the 3.3 mm diameter corallite. Relationship between the number of septa and the diameter of corallite is shown in Figure

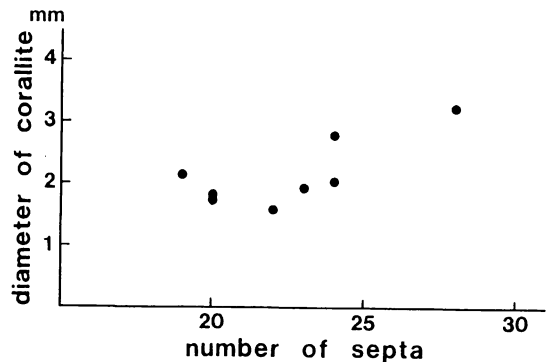


Figure 3. Relationship between number of septa and diameter of corallite in *Cyathaxonia* cfr. *C. cornu* Michelin.

3. Columella is round in outline, occupies 1/5 to 1/3 of the diameter of corallite. In one corallite (OM 10003), it merely reaches 1/7 of the diameter. The columella is solid and compact, in which calcite fibres are radially arranged from the centre. No concentric growth lines can be seen in the columella.

Only one longitudinal section is available, which is cut through the centre of the septa so that the features of tabulae are not observable. Wall is thick and smooth, as far as preserved. Columella is wide and stout, with the fibres directed upwards and outwards from the axis. Calice is deep, with a distinct calicular boss.

*Remarks:*—The present form is almost identical with *Cyathaxonia* cf. *C. cornu* figured by Haikawa (1986), which was obtained from the Viséan of Akiyoshi, Southwest Japan. Concentric growth lines are said to be present in *Cyathaxonia cornu* (e.g. Carruthers, 1913, p. 54). This character is not found in the present form.

*Cyathaxonia rushiana* Vaughan (1906) is clearly distinguished from the present form in having larger corallite.

Family Aulophyllidae Dybowski, 1873

Subfamily Clisiophyllinae Nicholson, 1889

Genus *Clisiophyllum* Dana, 1846

*Type species* (by subsequent designation of Dingwall, 1926):—*Clisiophyllum keyserlingi* McCoy, 1849

*Clisiophyllum kurohimense*, sp. nov.

Figures 4-4a-6

*Derivation of the specific name:*—After the Mt. Kurohime in the Omi district, Niigata Prefecture, Japan.

*Material:*—Nine solitary corallites, from which 24 transverse and longitudinal sections were obtained. Holotype IGSH-YY 10001, Paratypes IGSH-YY 10002-10006.

*Specific diagnosis:*—Medium sized *Clisiophyllum* having fairly long minor septa and a weak axial structure with a long and sinuous median plate, septal lamellae which tend to degenerate

and tent shaped axial tabellae. Caninomorphic corallites may occur.

*Description:*—Corallum is solitary, ceratoid, and medium in size. Surface characters are unknown.

In transverse section, corallite is round in outline, but its peripheral parts are often eroded. It is 17 mm in diameter in the largest corallite, and internally consists of wall, dissepimentarium, tabularium and axial structure. Wall is thin and with smooth external surface, and no trace for the presence of ridges or grooves is detectable. Dissepimentarium is comparatively narrow, occupying 1/4 to 1/3 of the radius of corallite. It is composed of regularly or irregularly arranged concentric or angulo-concentric dissepiments. Lateral dissepiments are frequently developed in the peripheral part. Herringbone dissepiments occur in the places in which minor septa are short or intermittent. Only occasionally pseudoherringbone dissepiments are observed between major and minor septa. Lonsdaleoid dissepiments are absent. Inner wall is indistinct. The boundary between dissepimentarium and tabularium is not very clear. Tabularium is wide, where cut edges of tabulae are seen between septa. Septa are in two orders, major and minor respectively. They are straight or slightly flexuous, relatively thin, but somewhat thickened in the tabularium. Major septa are long, extending towards axial structure, and some of them are intruded in the latter structure. Minor septa alternate with the major septa and are a little thinner than the major. They are in general fairly long, protruded into the tabularium, but uncommonly short, confined in the dissepimentarium. Septal fine structure is trabecular. The number of major septa is counted as 39 in a corallite of 16 mm in diameter. Relationship between the number of major septa and the diameter of corallite is shown in Figure 5. Cardinal fossula may be marked by a slight contraction of dissepimentarium or the shortening of the cardinal septum. Axial structure is usually large, occupying 1/4 to 1/3 of the diameter of corallite, but is not well differentiated from the tabularium. In early growth stage a complicated axial column is

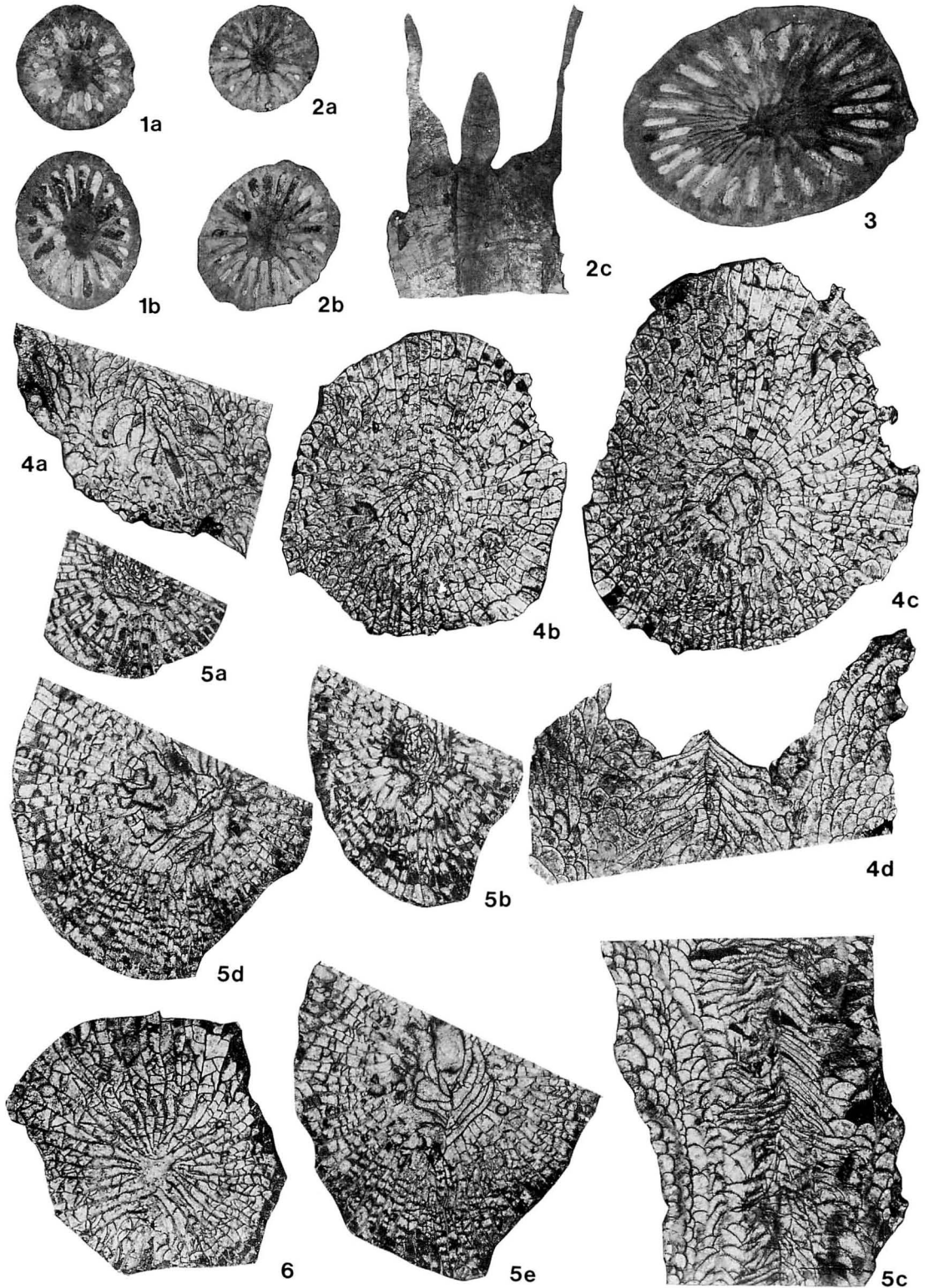


Figure 4. 1–3 *Cythaxonia* cfr. *C. cornu* Michelin, all  $\times 10$ . 1a–b. Transverse sections (OM 10001), 2a–c. Transverse (2a–b) and longitudinal (2c) sections (OM 10002), 3. Transverse section (OM 10003). 4–6. *Clisio-phyllum kurohimense*, sp. nov., all  $\times 3$ . 4a–d. Longitudinal (4a, 4d) and transverse (4b, 4c) sections (Holotype: IGSH-YY 10001), 5. Serial transverse (5a–b, 5d–e) and longitudinal (5c) sections (Paratype: IGSH-YY 10002), 6. Transverse section (Paratype: IGSH-YY 10003).

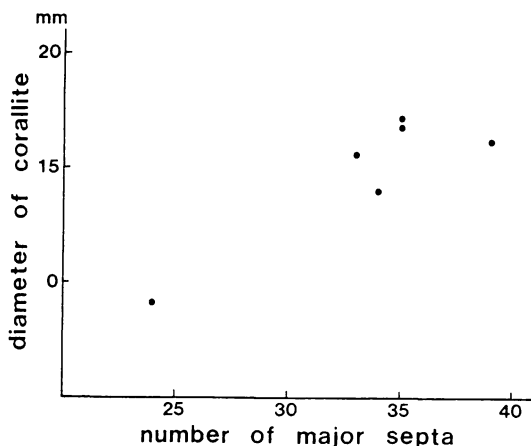


Figure 5. Relationship between number of major septa and diameter of corallite in *Clisiophyllum kurohimense*, sp. nov.

developed, which is composed of a long median plate, slightly sinuous, discontinuous and radially arranged septal lamellae -approximately equal in number to the major septa-, and thin, small, numerous and outwardly convex axial tabellae (Figure 4-5a). It is mostly separated from the axial ends of the major septa, but with some septal lamellae joined to the major. As the growth proceeds the median plate becomes thinner and septal lamellae gradually degenerate (Figure 4-5b). In the mature stages axial structure is loosely constructed by a thin, long and flexuous median plate which is reinforced by rings of axial tabellae, and a few or no septal lamellae (Figures 4-4b-c, -5d-e). Median plate is mostly connected with the cardinal septum in early growth stages, but becomes almost separated from it in the mature stages. Caninomorphs occur in a few corallites in which no axial structure is present (Figure 4-6).

In longitudinal section, wall is thin and weakly undulated. Dissepimentarium is comparatively narrow, with 3 to 6 rows of irregular globose dissepiments of various size. Dissepiments are large and steeply inclined in the periphery and small, vertical near the tabularium. Differentiation between the dissepimentarium and tabularium is clear. Tabularium is wide, and is occupied by incomplete, vesicular and upwardly convex peripheral tabellae which are steeply ascending

towards the axial structure in early growth stage (Figure 4-4a), but more or less horizontally disposed in the mature stages (Figures 4-4d, 5c). Axial structure is not well differentiated from the tabularium, consists of a thin, sinuous median plate and tent shaped axial tabellae ascending towards the median plate and resting on each other on the periphery of the axial structure. A few vesicular tabellae may appear axially.

*Remarks:*—No previously described species of *Clisiophyllum* is similar to the present form. The present form is characterized by fairly long minor septa and a weakly constructed axial structure in which septal lamellae tend to degenerate and axial tabellae are tent shaped in longitudinal section. These features serve to distinguish it from any other species of the same genus.

Family Lithostrotionidae d'Orbigny, 1852

Subfamily Lithostrotioninae d'Orbigny, 1852

Genus *Akiyosiphyllum* Yabe and Sugiyama, 1942

*Type species* (by Monotopy):—*Akiyosiphyllum stylophorum* Yabe and Sugiyama, 1942

*Akiyosiphyllum stylophorum* Yabe and Sugiyama

Figures 7-1a-15b

- 1942 *Akiyosiphyllum stylophorum* Yabe and Sugiyama, p. 574, figs. 1, 2.  
 1955 *Akiyosiphyllum stylophorum*; Minato, p. 167, pl. 16, fig. 3; pl. 19, fig. 2; pl. 26, fig. 1; pl. 30, fig. 3; pl. 37, figs. 5a-c.  
 1986 *Akiyosiphyllum stylophorum*; Haikawa, pl. 2, figs. 3a-b.

*Material:*—Sixty-seven coralla, from which 146 thin sections have been prepared and examined.

*Description:*—Corallum is compound, fasciculate and dendritic. Corallites are cylindrical and subparallel, closely arranged and are often in contact with each other. Surface characters are unknown.

In transverse section, corallite has round and comparatively smooth configuration, and is

12.8 mm in diameter in the largest corallite. Internally it consists of wall, dissepimentarium, tabularium and axial column. Wall is moderately thick. In some corallites the peripheral stereozone formed by lateral fusion of septa is present and already developed even in relatively early growth stages. It becomes gradually thickened as the coral grew upward, but is never constantly developed. In the mature stages it is prominent in a part of corallite, but indistinct in other part, so that the thickness of the wall is variable even within one corallite. The width of the dissepimentarium is narrow to comparatively wide, but less than 1/2 of the radius of corallite, and is frequently so reduced as to be replaced by a thick stereowall. It is composed of regularly or irregularly arranged concentric to angulo-concentric dissepiments when minor septa are well developed. Dissepiments become inosculating to herringbone in case of weakly developed minor septa. Lateral dissepiments occur in the periphery of the dissepimentarium in some corallites. Sometimes, when corallites are relatively large, dissepiments show pseudoherringbone pattern in the place between major and minor septa. Only occasionally, lonsdaleoid dissepiments may be developed, but they are small and only indicated by discontinuous minor septa. Intrathecal dilation on the septa and the internal surface of the dissepimentarium may form a distinct inner wall. The boundary between dissepimentarium and tabularium is clear. Tabularium is wide, where cut edges of tabulae are seen between septa. Septa are in two orders, major and minor respectively. Fossula is usually indistinct. Septa are almost straight, or slightly sinuous in the dissepimentarium. Major septa are long, extend towards axial column and directly unite with it in early growth stages, but become separated from it in the mature stages in some corallites. They are more or less dilated in the tabularium, but attenuated in the dissepimentarium. However, in some corallites some of them may be very thick at their bases, forming a stereozone as above stated, and rapidly attenuating towards axis. The axial ends of major septa are sharply tapering or bluntly terminated, and often slightly clavate.

Minor septa alternate with the major, and extremely variable in length. They are fairly long, intruding into the tabularium in some corallites, but very short, confined in the dissepimentarium in the others. Septa are in general radially arranged, but show somewhat pinnate arrangement when some short major septa are newly inserted. Fine structure of septa is trabecular. As many as 29 major septa are counted in the 11.5 mm diameter corallite. Relationship between the number of major septa and the diameter of corallite is shown in Figure 6. Axial column is large, variable in size and construction, and its morphological and ontogenetic trends correspond to the series from type a to type d of Kato (1963, text-fig. 18). In very early growth stages it is represented by an elongation of the cardinal septum, with which the axial ends of other major septa are confluent (Figure 7-6). Subsequently, it is dilated to form a round, solid and compact columella, in which calcite fibres are radially arranged around a median plate in counter-cardinal plane (Figures 7-1a, 3a-c). With the growth, the columella becomes split into bundles by grouping of calcite fibres to form contiguous septal lamellae which correspond to both major and minor septa, showing an appearance of typical amygdalophylloid axial column (Figure 7-1b). In some corallites such a column still persists or is only sporadically replaced by a few axial tabellae even in the mature stages (Figures 7-1d-e, 2a-b, 10, 13, 14). However, in other corallites as septal lamellation proceeds axial tabellae become also considerably differentiated to achieve echigophylloid (or "clisaxophylloid") axial column (Figures 7-3d-f, 4, 5, 7, 11, 12, 15a). This tendency towards differentiation of septal lamellae and axial tabellae leads in the extreme case to reticulo-vesicular pattern in which axial tabellae are dominant and septal lamellae are weakly developed (Figure 7-9b). Outline of axial column is round, subelliptical or fusiform.

In longitudinal section, triareal arrangement of skeletal elements is very clear. Wall is moderately thick and feebly undulated. Dissepimentarium is occupied by 4 to 8 rows of small globose



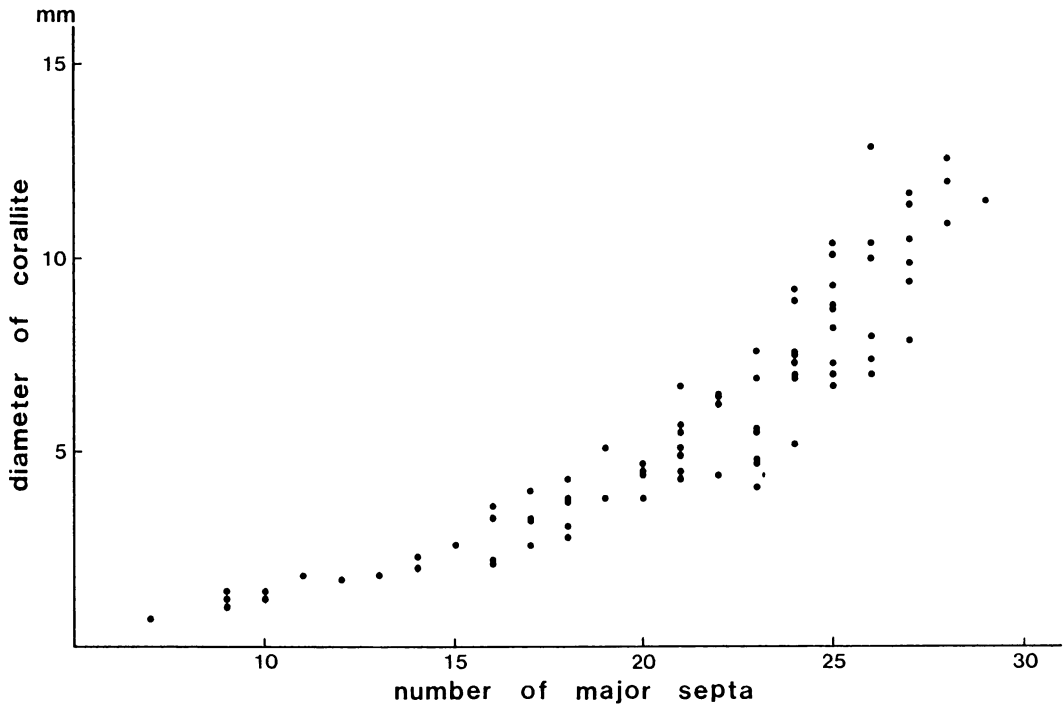


Figure 6. Relationship between number of major septa and diameter of corallite in *Akiyosiphillum stylophorum* Yabe and Sugiyama.

and large flattened dissepiments, which are steeply inclined in the periphery and almost vertical near the tabularium. Elongate dissepiments are present. Intrathecal dilation may occur on the internal surface of the dissepimentarium, forming an inner wall. Tabularium is wide, clearly differentiated from the dissepimentarium, composed of vesicular, arched and upwardly convex tabulae which are gently or steeply ascending towards the axial column. They are mostly incomplete, but may be locally complete. A few horizontal accessory plates occur in the peripheral part. Axial column is also well differentiated from the tabularium, wide and stout with no, a few or numerous axial tabellae steeply inclined against the median plate. Calice is deep, with prominent calicular boss.

*Remarks:*—The present form shows great variability in its skeletal construction in the mature stages, and it may be morphologically divided into at least three types as the following:

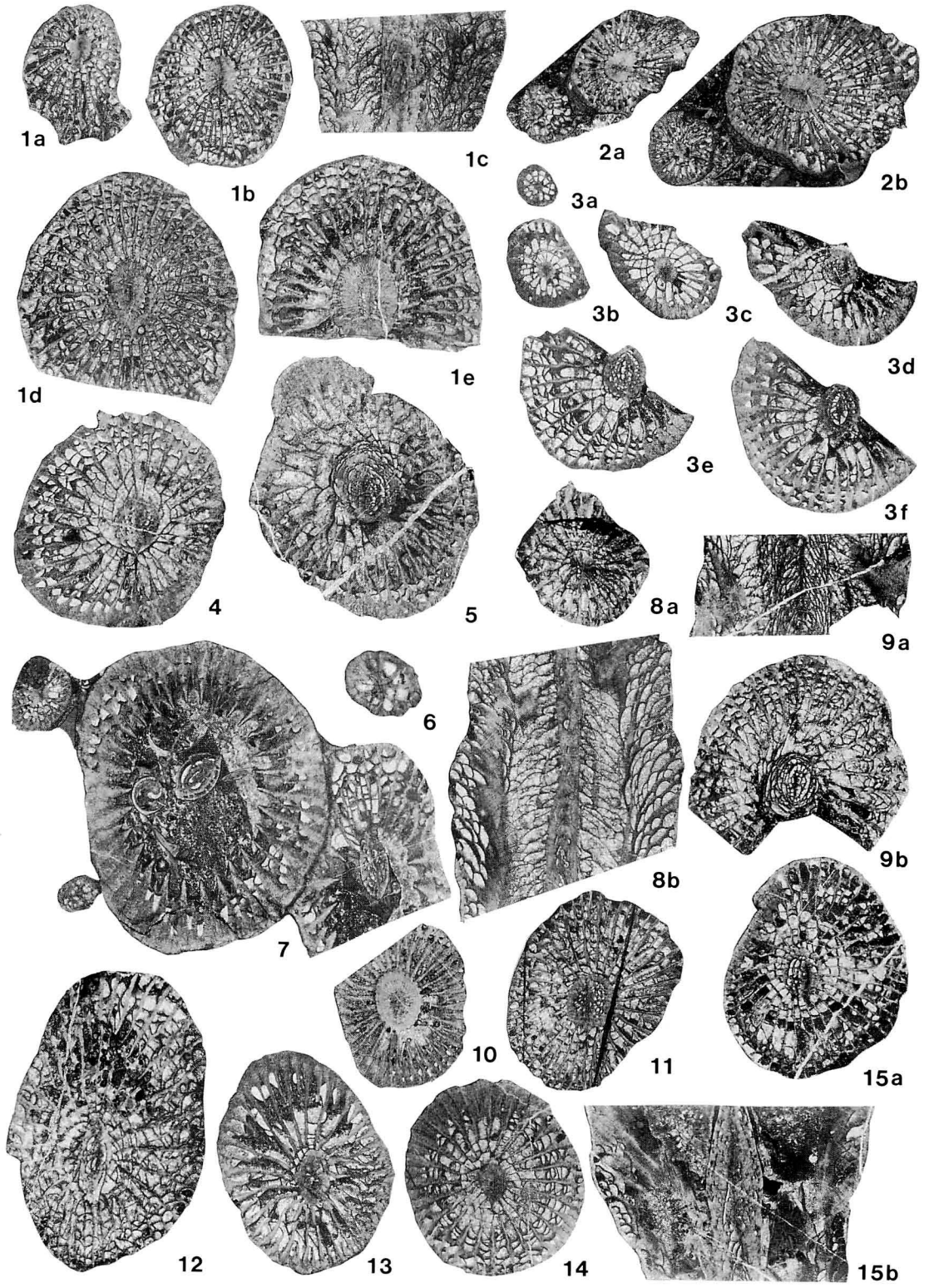
Type 1—With no stereozone, concentric to

anglo-concentric dissepiments, bluntly terminated or slightly clavate axial ends of major septa which are mostly in contact with columella, fairly long minor septa and amygdalophylloid axial column (e.g. OM 10004, 10005).

Type 2—With imperfect stereozone, concentric to anglo-concentric and herringbonal dissepiments, rapidly tapering axial ends of major septa which are almost isolated from axial column, short minor septa and echigophylloid (or “clisaxophylloid”) axial column in which axial tabellae become distinct (e.g. OM 10006-10008, 10010, 10011).

Type 3—With the skeletal elements similar to type 2, except for having reticulo-vesicular pattern of echigophylloid (or “clisaxophylloid”) axial column (e.g. OM 10012).

Thus these types may be apt to be treated as representing three different species. However, as shown in Figures 7-10-15b, there are further gradational forms between these types, especially between type 1 and type 2. Moreover, these



morphological variations occur together at the same locality and even in a single specimen. Therefore they are best considered as intraspecific variations.

As a whole the present form is almost identical with the variable species, *Akiyosiphillum stylophorum* Yabe and Sugiyama (1942).

The present form also has some similarity with *Lithostrotion stanvellense* described by Benson and Smith (1923, p. 168, pl. 9, figs. 3, 6), which is not identical with *L. ? stanvellensis* (sic) proposed by Etheridge (1900, p. 20, pl. 1, fig. 5; pl. 2, figs. 7, 8) but may be congeneric with *Akiyosiphillum* as Minato (1955, p. 168) pointed out. However the latter has smaller axial column compared to the present form, and is provided with sharply bent tabulae in the periphery of the tabularium in longitudinal section.

#### Family Carcinophyllidae Fomitchev, 1953

##### Genus *Carcinophyllum* Thomson and Nicholson, 1876

*Type species* (by subsequent designation of Thomson, 1880):—*Carcinophyllum Kirsopiana* (sic) Thomson, 1880

*Remarks*:—The possible synonymy between *Carcinophyllum* and *Axophyllum* Milne-Edwards and Haime (1850), has been accepted by many authors (Hill, 1940, 1956, 1981; Wang, 1950; Perret and Semenoff-Tian-Chansky, 1971; Semenoff-Tian-Chansky, 1974; Poty, 1981, 1982). However, the definite conclusion of the problem should be reserved, because the lectotype of the type species of *Axophyllum*, *A. expansum* Milne-Edwards and Haime (1950), has not yet been fully redescribed by any authors. In the present state of our knowledge, the authors would like to consider *Carcinophyllum* as an independent

genus.

##### *Carcinophyllum hasegawai*, sp. nov.

Figures 9-1a-5, 10-1a-3c

*Derivation of the specific name*:—After Prof. Yoshiyuki Hasegawa, who greatly advanced our knowledge on the foraminiferal biostratigraphy of the Omi Limestone.

*Material*:—Thirty solitary corallites, from which 78 transverse and longitudinal sections have been prepared. Holotype IGSH-YY 10007, Paratypes IGSH-YY 10008–10016.

*Specific diagnosis*:—Medium sized *Carcinophyllum* having well developed dissepiments, narrow tabularium with steeply inclined clinotabulae, rhopaloid axial ends of major septa, long minor septa and thick septal lamellae which are curving or sometimes irregularly twisted in the most advanced stage.

*Description*:—Corallum is solitary, trochoid to conico-cylindrical, and medium in size. Sometimes, two corallites belonging to different individuals are observed to grow parallel to and appressed with each other, so as to give a false impression of a compound corallum (Figures 10-3a-c). Surface characters are unknown.

In transverse section, corallite is round in outline, and 25 mm in diameter in the largest corallite. Internally it consists of wall, dissepimentarium, tabularium and axial structure. Wall is moderately thick, comparatively smooth or marked only by faint septal grooves and interseptal ridges in outer configuration. But it is crenulated inside, corresponding to the position of septa, except in early growth stages in which lateral fusion of peripherally dilated septa produces a pronounced stereozone. Dissepimentarium is wide, varies in its diameter from 1/3 to

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← **Figure 7.** 1–15. *Akiyosiphillum stylophorum* Yabe and Sugiyama, all  $\times 3$  except 6, which is  $\times 10$ . 1a–e. Serial transverse (1a–b, 1d–e) and longitudinal (1c) sections (OM 10004), 2a–b. Transverse sections (OM 10005), 3a–f. Serial transverse sections (OM 10006), 4. Transverse section (OM 10007), 5. Transverse section (OM 10008), 6. Transverse section (OM 10009), 7. Transverse section (OM 10010), 8a–b. Transverse (8a) and longitudinal (8b) sections (OM 10011), 9a–b. Longitudinal (9a) and transverse (9b) sections (OM 10012), 10 Transverse section (OM 10013), 11. Transverse section (OM 10014), 12. Transverse section (OM 10015), 13. Transverse section (OM 10016), 14. Transverse section (OM 10017), 15a–b. Transverse (15a) and longitudinal (15b) sections (OM 10018).

2/3 of the radius of corallite. It is composed of large and irregular lonsdaleoid dissepiments and narrow, small concentric ones. Lonsdaleoid dissepiments are already developed even in relatively early growth stages, though partially or rudimentarily (Figure 9-2a), and soon come to occupy a peripheral zone external to the septal cycle in the midst of the young growth stages. Intrathecal dilation is often very distinct and inner wall is clear in that instance. Tabularium is narrow, where cut edges of tabulae are seen between septa. Septa are moderately thick and in two orders, major and minor respectively. Fossula is indistinct. Septa are interrupted from the wall by the development of lonsdaleoid dissepiments, which leave only spiny projections on vesicles. They are commonly straight in the tabularium, however slightly sinuous in the dissepimentarium. Major septa are long, extend

near to the axial structure but never connected with it except in very early growth stage, in which only the cardinal septum is firmly united with the median plate in the axial structure (Figure 10-1a). The axial ends of major septa are clavate and rhopaloid. Minor septa alternating with the major are also fairly long, intruded into the tabularium, with bluntly terminated axial ends. Septa are in general radially arranged, but show a somewhat pinnate arrangement in some corallites. Septal fine structure is stout trabecular. As many as 41 major occur in the 25 mm diameter corallite. Relationship between the number of major septa and the diameter of corallite is shown in Figure 8. Axial structure is round to subelliptical in outline, occupies 1/5 to 2/5 of the diameter of corallite. It is constructed by a thick, slightly undulating median plate with thick, irregular, curved and anastomosing septal

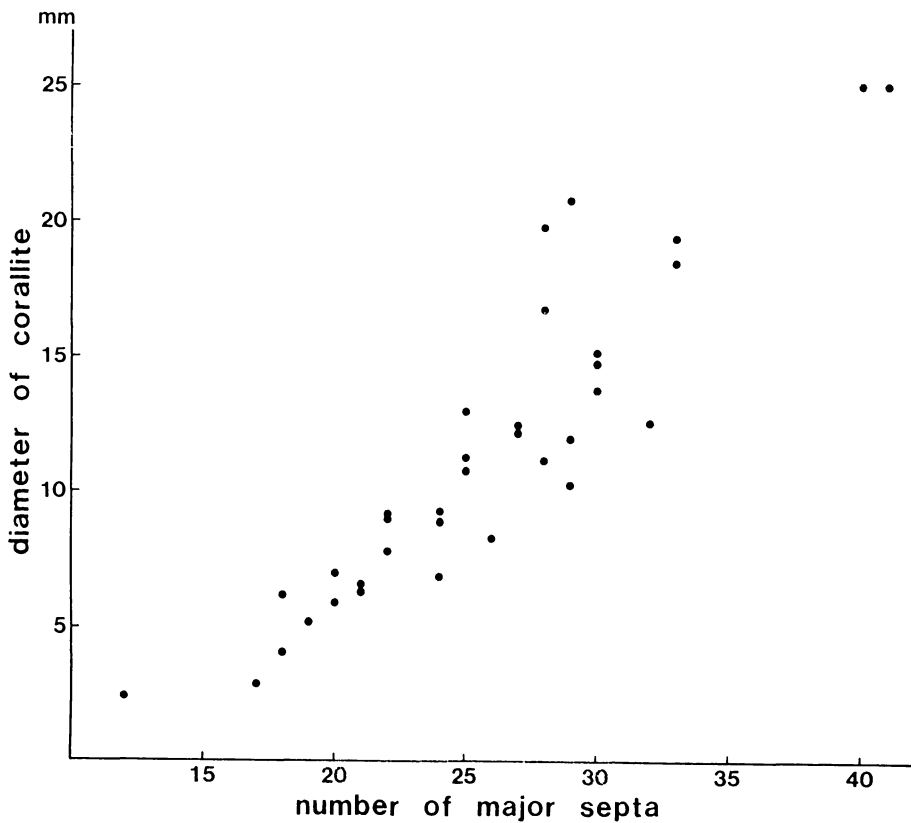


Figure 8. Relationship between number of major septa and diameter of corallite in *Carcinophyllum hasegawai*, sp. nov.

lamellae-approximately equal in number and the thickness to the major septa-, and thin, straight or inwardly convex axial tabellae which are sparsely disposed. Median plate is relatively long in early growth stages, becoming shortened in the mature. Sometimes, in the most advanced stage of larger corallites it becomes indistinguishable from septal lamellae, the feature presenting somewhat an appearance of gangamophylloid axial structure, in which septal lamellae are irregularly twisted (Figures 9-1e-f). Other different type of axial structure is observable in one corallite, in which slightly flexuous septal lamellae are radially arranged in a regular manner around a short median plate (Figure 9-3b). Simple budding is discernible in the holotype (Figures 9-1e-f) and in one of the paratype specimens (IGSH-YY 10016): one or two small offsets arise in the lonsdaleoid dissepimentarium of the mother corallite, and these offsets correspond in morphology to comparable ontogenic stages of a mature corallite. In transverse sections of some corallites laterally projecting parts of the corallite probably indicate the presence of talon (Figure 9-4).

In longitudinal section, trizonal arrangement of skeletal elements is very clear. The wall is moderately thick and weakly undulated. Dissepimentarium is wide, with inner series of small and vertical dissepiments and outer series of large, flattened and steeply inclined ones. Large elongate dissepiments are developed. Intrathecal dilation may occur on the internal surface of the dissepimentarium. Tabularium is narrow, well differentiated from the dissepimentarium, and occupied by deeply dipping clinotabulae and horizontal or sagging transverse tabulae. In one corallite transverse tabulae are gently inclined inward (Figure 10-2b). All the tabulae are fairly distantly spaced. Axial structure is also differentiated from the tabularium, consists of a thick, sinuous median plate, cut edges of thick, flexuous septal lamellae and thin, steeply ascending axial tabellae which are straight or inwardly convex. Calice is spreading and moderately deep, with prominent calicular boss.

*Remarks:*—The present form falls in the group

of *Carcinophyllum* with well developed lonsdaleoid dissepiments and a typical carcinophylloid axial structure, but is different from the hitherto described species of the genus in having long minor septa.

On the other hand, the present form has some similarity with *Hiroshimaphyllum toriyamai* (Minato, 1955), but the latter is a fasciculate and dendritic form, and has smaller corallites having less numerous septa and more dense skeletal elements compared to the present form.

Family Pseudopavonidae Yabe, Sugiyama and Eguchi, 1943

Subfamily Pseudopavoninae Yabe, Sugiyama and Eguchi, 1943

Genus *Hiroshimaphyllum* Kato and Minato, 1974

*Type species* (by original designation):—*Lonsdaleoides toriyamai* Minato, 1955

*Hiroshimaphyllum simplex*, sp. nov.

Figures 10-4a-7

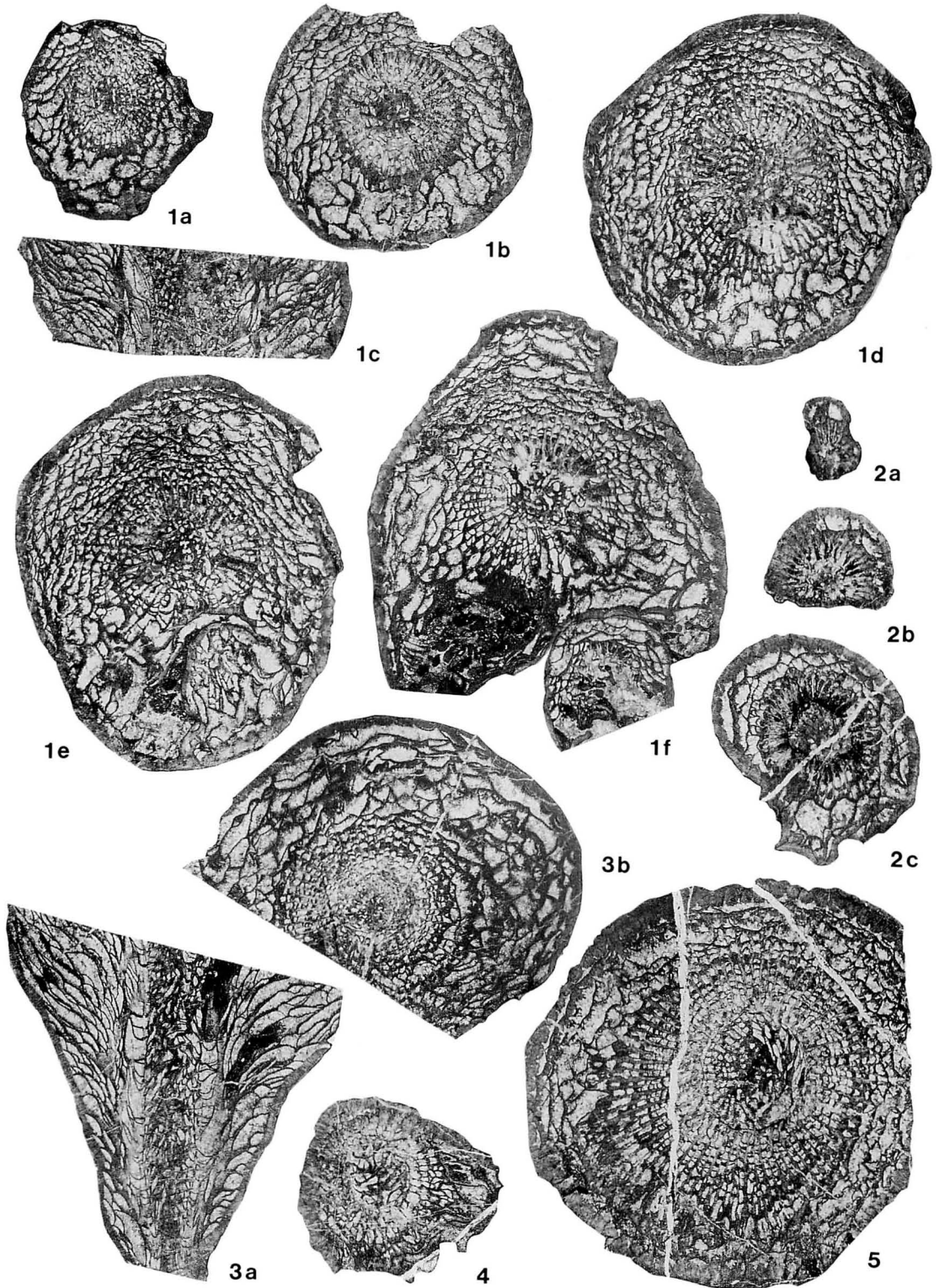
*Derivation of the specific name:*—After the feature of corallum having simply constructed axial structure. Latin *simplex*-simple.

*Material:*—Four fasciculate colonies and single fragmental corallite, from which eleven sections are available for study. Holotype IGSH-YY 10017, Paratypes IGSH-YY 10018-10020.

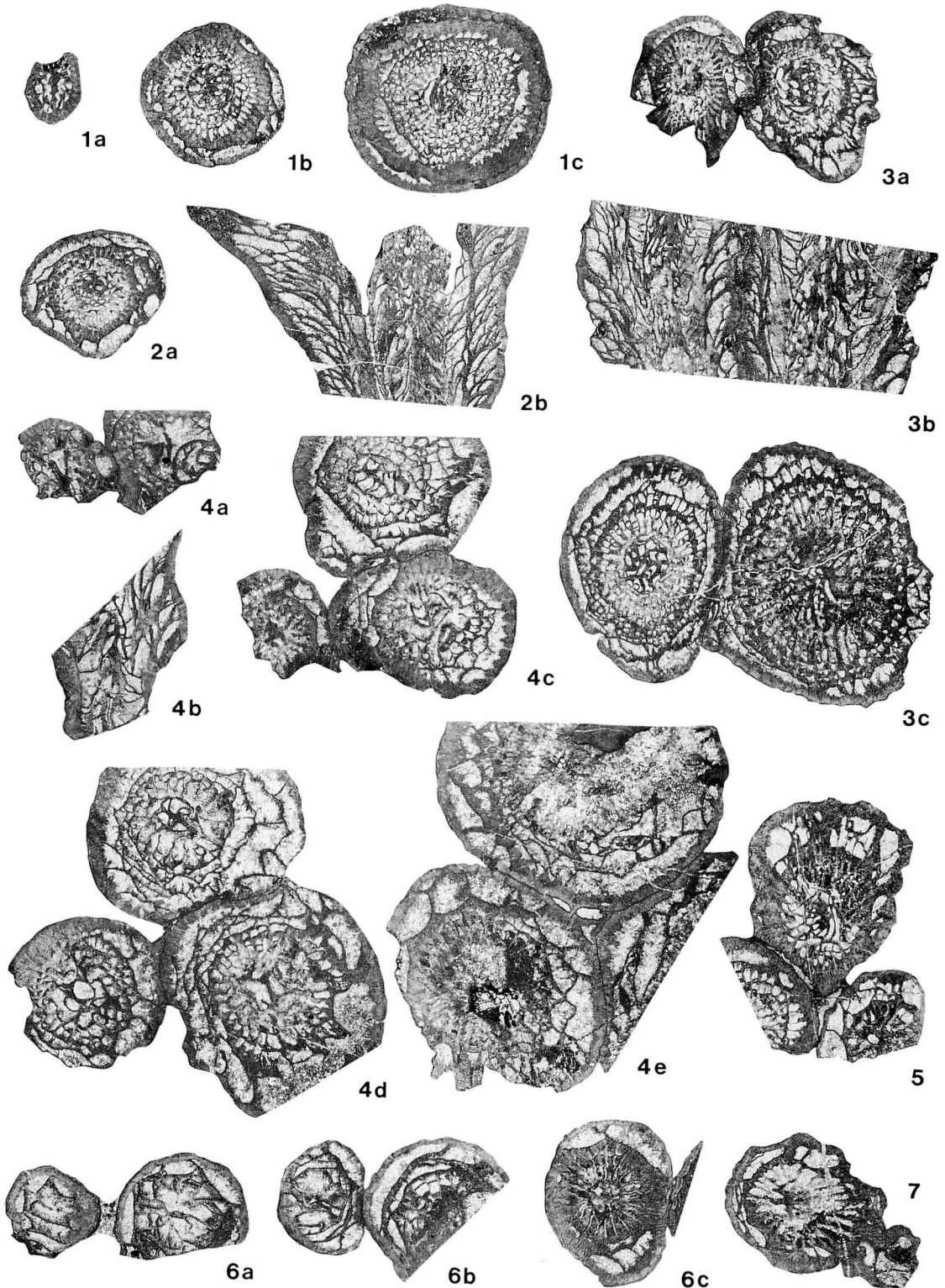
*Specific diagnosis:*—Small sized *Hiroshimaphyllum* with less dilated internal skeleton. Axial structure is relatively simple in construction.

*Description:*—Corallum is compound, fasciculate and dendritic. Corallites are trochoid and subparallel, closely situated and are often in contact with each other. Surface characters are unknown.

In transverse section, corallite has round and comparatively smooth outer configuration, and internally consists of wall, dissepimentarium, tabularium and axial structure. Corallite diameter reaches up to 10.0 mm in the largest corallite, but commonly it measures 4 to 7 mm in the mature stages. Wall is moderately thick and cre-



**Figure 9.** 1–5. *Carcinophyllum hasegawai*, sp. nov., 1, 3, 5 are  $\times 2.5$ ; 2, 4 are  $\times 3$ . 1a–f. Serial transverse (1a–b, 1d–f) and longitudinal (1c) sections (Holotype: IGSH-YY 10007), 2a–c. Serial transverse sections (Paratype: IGSH-YY 10008), 3a–b. Longitudinal (3a) and transverse (3b) sections (Paratype: IGSH-YY 10009), 4. Transverse section (Paratype: IGSH-YY 10010), 5. Transverse section (Paratype: IGSH-YY 10011).



**Figure 10.** 1–3. *Carcinophyllum hasegawai*, sp. nov., 1, 3 are  $\times 3$ ; 2 is  $\times 2.5$ . 1a–c. Serial transverse sections (Paratype: IGSH-YY 10012), 2a–b. Transverse (2a) and longitudinal (2b) sections (Paratype: IGSH-YY 10013). 3a–c. Transverse (3a, 3c) and longitudinal (3b) sections (Paratype: IGSH-YY 10014). 4–7. *Hiroshimaphyllum simplex*, sp. nov., all  $\times 4.5$ . 4a–e. Serial transverse (4a, 4c–e) and longitudinal (4b) sections (Holotype: IGSH-YY 10017), 5. Transverse section (Paratype: IGSH-YY 10018), 6a–c. Serial transverse sections (Paratype: IGSH-YY 10019), 7. Transverse section (Paratype: IGSH-YY 10020).

nulated inside, corresponding to the position of septa. Dissepimentarium is wide, varies in its width from 1/4 to 1/2 of the radius of corallite. It is composed of one to several rows of lonsdaleoid dissepiments of various size and one to three rows of narrow, small, concentric ones. Lonsdaleoid dissepiments are sometimes so reduced as to be replaced by a thick stereowall which is formed by lateral fusion of peripherally dilated septa. Slight intrathecal dilation on the internal surface of the dissepimentarium marks a distinct inner wall. Tabularium is wide, where straight cut edges of tabulae are seen between septa. Septa are in two orders, major and minor respectively. Fossula is indistinct. Septa are moderately thick, somewhat sinuous and become discontinuous in the lonsdaleoid dissepimentarium where they are represented by spiny projections on the dissepimental vesicles. Major septa fall short to the axial structure except in early growth stages, in which the prolongation of axial end of the cardinal septum makes an axial structure. In one corallite (IGSH-YY 10019), however, the cardinal septum is firmly connected with the median plate in the axial structure through the growth. The axial ends of major septa are bluntly terminated and occasionally slightly clavate. Minor septa alternating with the major are fairly long, intruded into the tabularium. They attain 1/2 to 2/3 the length of the major. Septa are in general radially arranged, but show a somewhat pinnate arrangement in some corallites. Fine structure of septa is trabecular. The number of major septa is counted as many as 21 in a corallite of 8.7 mm in diameter. Relationship between the number of major septa and the diameter of corallite is shown in Figure 11. Axial structure is a mere elongation of the cardinal septum in early growth stages as above described. In the mature stages axial structure is round to subround in outline, occupies 1/5 to 1/3 of the diameter of corallite. It is simply made up of a thick and somewhat undulating median plate, several, irregular and curving septal lamellae and one to two rows of thin, straight or inwardly convex axial tabellae. In two corallites (IGSH-YY 10019,

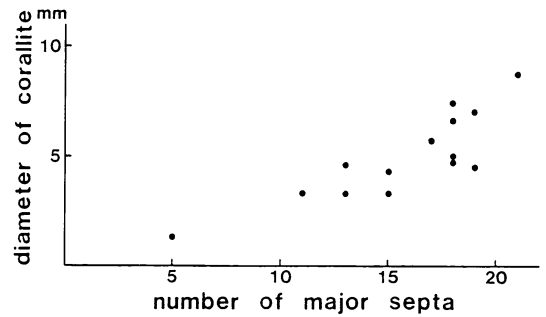


Figure 11. Relationship between number of major septa and diameter of corallite in *Hiroshimaphyllum simplex*, sp. nov.

10020) no axial tabellae are developed. Two modes of increase are observable, namely peripheral and lateral. In the peripheral increase, one small offset arises in the dissepimentarium of the mother corallite (Figure 10-4a), while in the lateral increase, it is sprung out from the side-wall of the mother corallite in a form of raindrop (Figure 10-7).

In longitudinal section, trizonal arrangement of skeletal elements of a corallite is clearly recognizable. Wall is moderately thick and wavy. Dissepimentarium is absent in early growth stage, but well developed in the mature stages, with large, flattened and steeply inclined dissepiments in the periphery and small, vertical ones near the tabularium. Intrathecal dilation occurs on the internal surface of the dissepimentarium. Tabularium is wide, well differentiated from the dissepimentarium in the mature stage. It consists of mostly complete transverse tabulae which are horizontal or slightly sagging and sometimes gently ascending towards axis. They may be locally incomplete. Clinotabulae may be present in the mature stage. In vertical distance of 2 mm, 3 to 5 tabulae are counted. Axial structure is also well differentiated from the tabularium, composed of a thick, sinuous median plate, cut edges of thick septal lamellae and thin, steeply ascending axial tabellae which are sparsely disposed.

*Remarks:*—Five species have been ascribed to the genus *Hiroshimaphyllum*, namely *H. enorme* (Ozawa, 1925), *H. toriyamai* (Minato, 1955), *H.*



*shikokuense* (Yamagiwa, 1961), *H. compactum* Wu and Zhang (1979) and *H. crassithecum* Wu and Zhang (1979). However, the present form is different from the above listed species in having smaller corallites, less dense skeletal elements and less complicated axial structure.

On the other hand, the present form has some similarity with *Carcinophyllum hasegawai*, sp. nov. described in this paper, but the latter is a solitary form, and has larger corallite compared to the present form.

### Acknowledgments

The authors would like to express their appreciation to Professor Emeritus Akira Hase of Hiroshima University for his leading and encouragement. Acknowledgement is also due to Professor Yoshiyuki Hasegawa and Dr. Isao Niikawa of Niigata University for their instructive advices and suggestions in various ways. The authors are much indebted to the Myojo Cement Co., Ltd. for every facility in the field. Thanks are extended to Messrs. Hideo Takahashi and Akito Magai of Hiroshima University for preparing thin sections. This study was partly financed by the Grant in Aid for Scientific Researches from the Ministry of Education.

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青海石灰岩産の前期石炭紀サンゴ化石：新潟県青海石灰岩の最下部から豊富なサンゴ化石を産出した。このサンゴ化石群集の構成要素は、秋吉石灰岩の *Nagatophyllum satoi* 帯のそれと類似し、後期ビゼー世を指示している。同定されたサンゴ化石のうち、多産するだけでなく、分類、対比のうえで重要と考えられる2種および3新種を記載する：*Cyathaxonia* cfr. *C. cornu* Michelin, *Clisiophyllum kurohimense*, sp. nov., *Akiyosiphyllum stylophorum* Yabe and Sugiyama, *Carcinophyllum hasegawai*, sp. nov., *Hiroshimaphyllum simplex*, sp. nov.

吉田 靖・沖村雄二・加藤 誠

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## 843. MIOCENE MOLLUSCS FROM THE KOZONO FORMATION, SAITAMA PREFECTURE, CENTRAL JAPAN\*

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**Abstract.** A molluscan assemblage composed of twelve species occurs in the Miocene Kozono Formation, near Yorii, Oosato-gun, northern Saitama Prefecture. This assemblage is considered to have lived in a tidal sandflat near to an estuary and is comparable to the estuarine tidal flat community, characterized by arcids and potamidids, of the early middle Miocene Kadonosawa-type Fauna. The four species of Potamididae, *Tateiwaia tateiwai* (Makiyama), *T. yamanarii* (Makiyama), *Vicaryella atukoe* (Otuka) and *V. ishiana* (Yokoyama) are described for the first time from the Kozono Formation.

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### Introduction

Miocene estuarine tidal flat molluscs have been reported from Saitama Prefecture by Watanabe *et al.* (1950) and Hatai and Masuda (1962), but those workers did not describe or illustrate the fauna. During the spring of 1987, the authors collected a small molluscan assemblage from the Miocene Kozono Formation that is exposed in a cliff along the left bank of the Arakawa River, near Yorii, Oosato-gun, Saitama Prefecture, central Japan (Figure 1). This assemblage is comparable to the estuarine tidal flat community of the early middle Miocene Kadonosawa-type Fauna (Otuka, 1939; Chinzei, 1978) known from scattered localities elsewhere in Japan.

### Location and stratigraphic setting

Fossil locality is in a cliff on the left bank of

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the Arakawa River, about 80 m upstream of the Tamayodo-Oohashi Bridge, about 1500 m ENE of Yorii, at lat. 36°7'6"N., long. 139°7'51"E., in Oosato-gun, northern Saitama Prefecture, central Japan (Figure 1).

The present assemblage occurs in a stratigraphic interval about 4 m thick, which is composed of dark yellowish brown, fine-grained sandstone (A in Figure 2) of the Miocene Kozono Formation. The sandstone grades laterally into conglomerate and is overlain by poorly sorted sandstone that contains abundant plant fragments (Figure 2).

The Kozono Formation is the stratigraphically lowest among the Neogene formations exposed along the Arakawa River, near Yorii and consists of conglomerates, sandstones, mudstones and tuff. Along the Arakawa River, the Kozono Formation lies in fault contact with pre-Neogene sedimentary rocks and crystalline schists, and is divided into two outcrop areas, the Tachigase (west) and Kozono (east) areas, by NW-SE

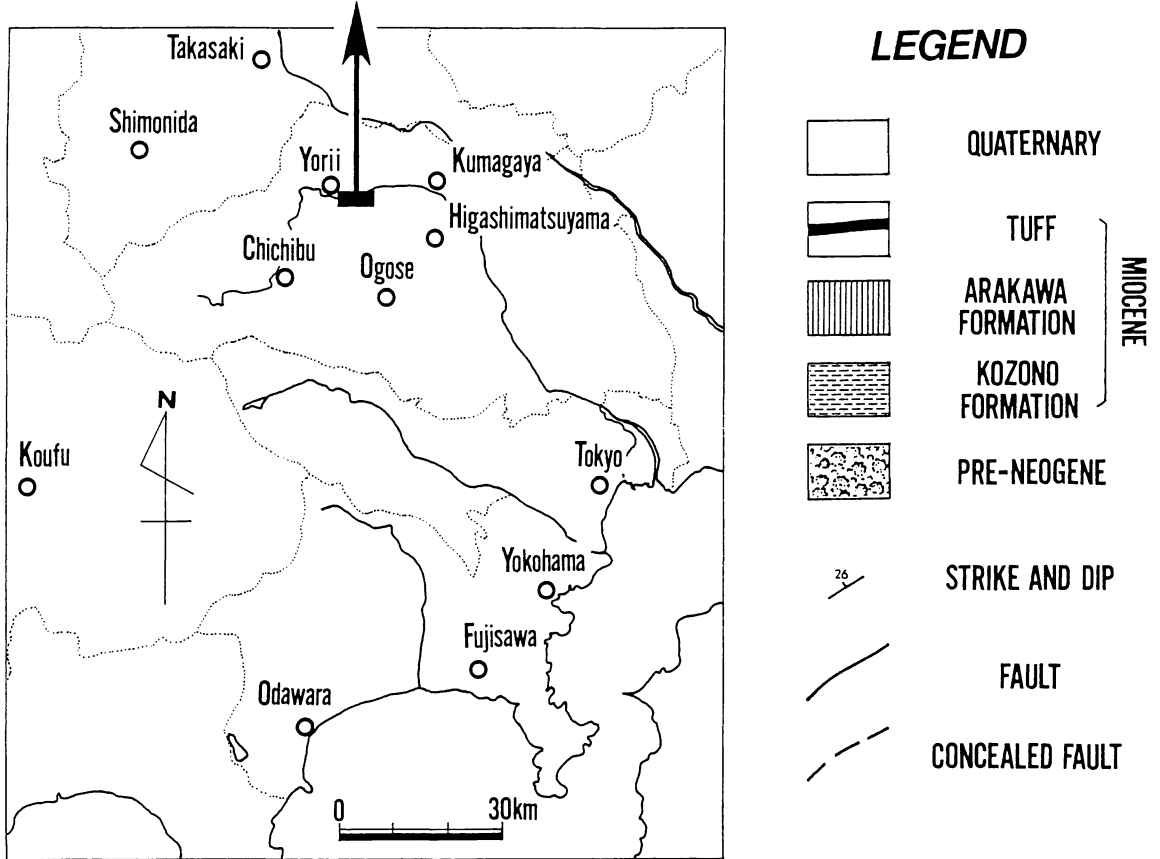
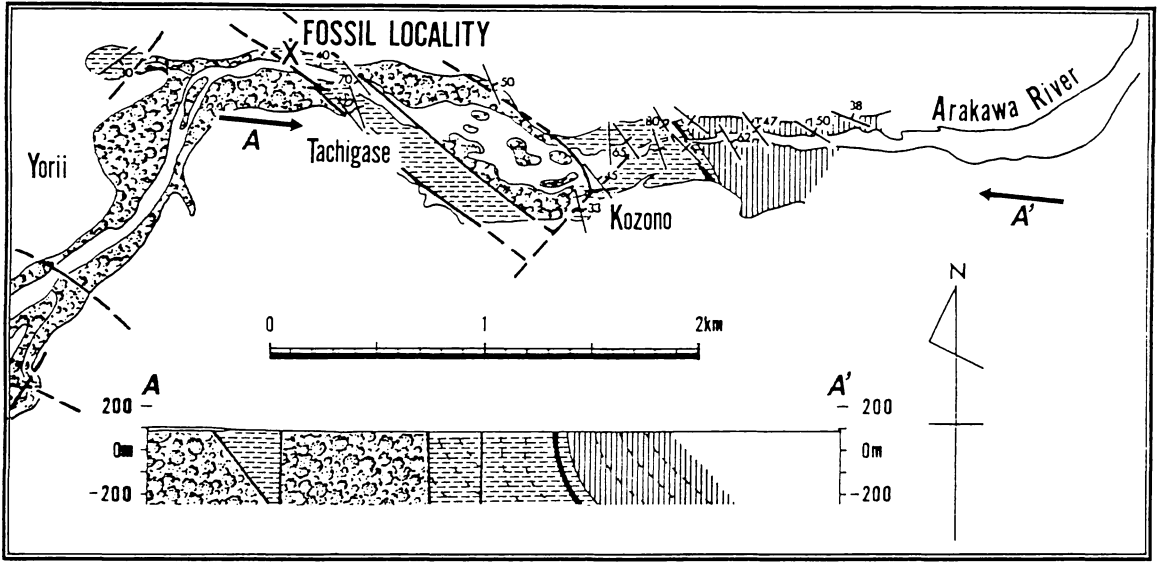


Figure 1. Fossil locality and geology along the Arakawa River, Yorii-machi, northern Saitama Prefecture. Geologic map modified from Majima (1978MS).

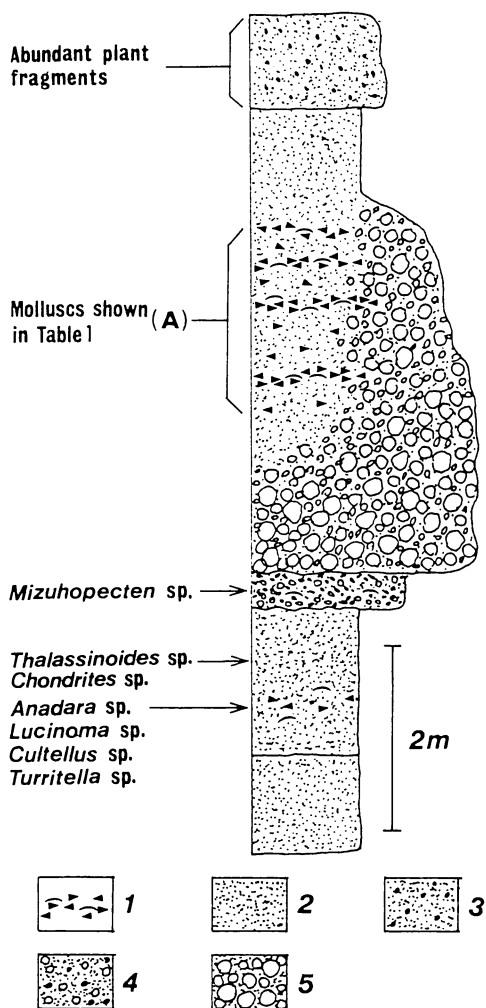


Figure 2. Columnar section of fossil locality (Figure 1). The estuarine intertidal molluscs occur in fine-grained sandstone (A). 1: Molluscan fossils. 2: Fine-grained sandstone. 3: Poorly sorted sandstone. 4: Conglomeratic sandstone. 5: Conglomerate. All the beds are a lower part of the early middle Miocene Kozono Formation.

faults (Figure 1). The Kozono Formation in the Tachigase area, which yielded the present molluscan assemblage, is complexly folded and faulted and the sequence of strata is unclear. The Kozono Formation of the Tachigase is lithologically comparable to that of the lower part of the Kozono Formation in the Kozono area where the formation dips northeast. The

lower part of the Kozono Formation is characterized by abundant conglomerates, sandstones and rare tuff. The upper part of the Kozono Formation is characterized by abundant mudstones with frequent intercalations of tuff. The Kozono Formation is conformably overlain by the Arakawa Formation that is composed of alternating sandstone and mudstone (Figure 1).

#### Modes of occurrence

Fossils are aggregated in lenticular beds less than 5 cm thick, and may occur sporadically (A in Figure 2). Modes of fossil occurrences in shell-aggregated lenticular beds are given in Figures 4-9a-10b in stereopairs.

Fossils are preserved as casts or molds. Gastropods are usually well preserved, but most specimens of *Vicaryella ishiiiana* are generally secondarily depressed (Figures 3-19-22) except for juveniles (Figure 3-17) and one adult (Figure 3-18). Bivalves are usually poorly preserved. They are secondarily deformed and bear many fractures (Figures 4-5, 7, 8).

#### Fauna

Twelve species of molluscs, consisting of eight gastropods and four bivalves, have been identified. Their relative abundance in the sample is summarized in Table 1. *Tateiwaia yamanarii* is the most abundant species in the collection. More than 50 specimens were obtained. The other species occur at much lower densities. With the exception of *Tateiwaia tateiwai* and *Vicaryella ishiiiana*, none are represented by more than 10 specimens.

The abundant occurrence of potamidids (*Cerithidea* sp., *Tateiwaia tateiwai*, *T. yamanarii*, *Vicaryella atukoae* and *V. ishiiiana*) suggests that the assemblage may have lived in an intertidal sandflat near to an estuary, and in a tropical to subtropical habitat. The family Potamididae typically occurs in great abundance in mangrove swamps of brackish-water bays and estuaries.

The present molluscan assemblage clearly indicates an early middle Miocene age. The

Table 1. Faunal list and relative abundance of species in the collection from the Kozono Formation. A = more than 25 specimens; C = 11–25 specimens; F = 5–10 specimens; and R = fewer than 5 specimens.

Species	Relative abundance	Illustrations
Gastropoda		
<i>Margarites</i> ? sp.	F	
<i>Cerithidea</i> sp.	R	Figure 3-1
<i>Tateiwaia tateiwai</i> (Makiyama)	C	Figure 3-2–8
<i>Tateiwaia yamanarii</i> (Makiyama)	A	Figure 3-10–16
<i>Vicaryella atukoae</i> (Otuka)	R	Figure 3-9
<i>Vicaryella ishiiiana</i> (Yokoyama)	C	Figure 3-17–22
<i>Pollia</i> sp.	F	Figure 4-1a–3
<i>Hemifusus</i> ? sp.	R	Figure 4-4
Bivalvia		
<i>Striarca</i> sp.	F	Figure 4-6
<i>Saxolucina</i> cf. <i>khataii</i> (Otuka)	F	Figure 4-5
<i>Clementia</i> sp.	R	Figure 4-8
<i>Dosinia</i> sp.	R	Figure 4-7

age of the assemblage is evaluated in terms of the molluscan faunal characteristics of the Japanese Neogene (Chinzei, 1978; Tsuchi and Shuto, 1984). The present assemblage is comparable with a tropical to subtropical estuarine tidal flat community, which is characterized by the co-occurrence of arcids (*Striarca uetsukiensis* and *Anadara (Hataiarca)* spp.) and potamidids (*Vicarya* spp., *Vicaryella* spp., *Tateiwaia* spp. and others) (the "Arcid-Potamidid fauna" of Tsuda, 1965), of the early middle Miocene Kadonosawa-type Faune (Otuka, 1934; Chinzei, 1978).

#### Systematic paleontology

Phylum Mollusca

Class Gastropoda

Order Mesogastropoda

Family Potamididae

Genus *Tateiwaia* Makiyama, 1936

*Type species.* — By original designation, *Batillaria tateiwai* Makiyama, 1926.

*Tateiwaia tateiwai* (Makiyama, 1926)

Figures 3-2–8

*Batillaria tateiwai* Makiyama, 1926, pp. 147–148, pl. 12, figs. 5, 6; ? Otuka, 1934, p. 624, pl. 49, fig. 71; Nomura, 1935, p. 228, pl. 17, figs. 30–33.

*Batillaria (Tateiwaia) tateiwai* Makiyama, Makiyama, 1936, p. 219; Fujie and Uozumi, 1957, p. 502, pl. 24, fig. 6; Okamoto *et al.*, 1978, pl. 1, fig. 10.

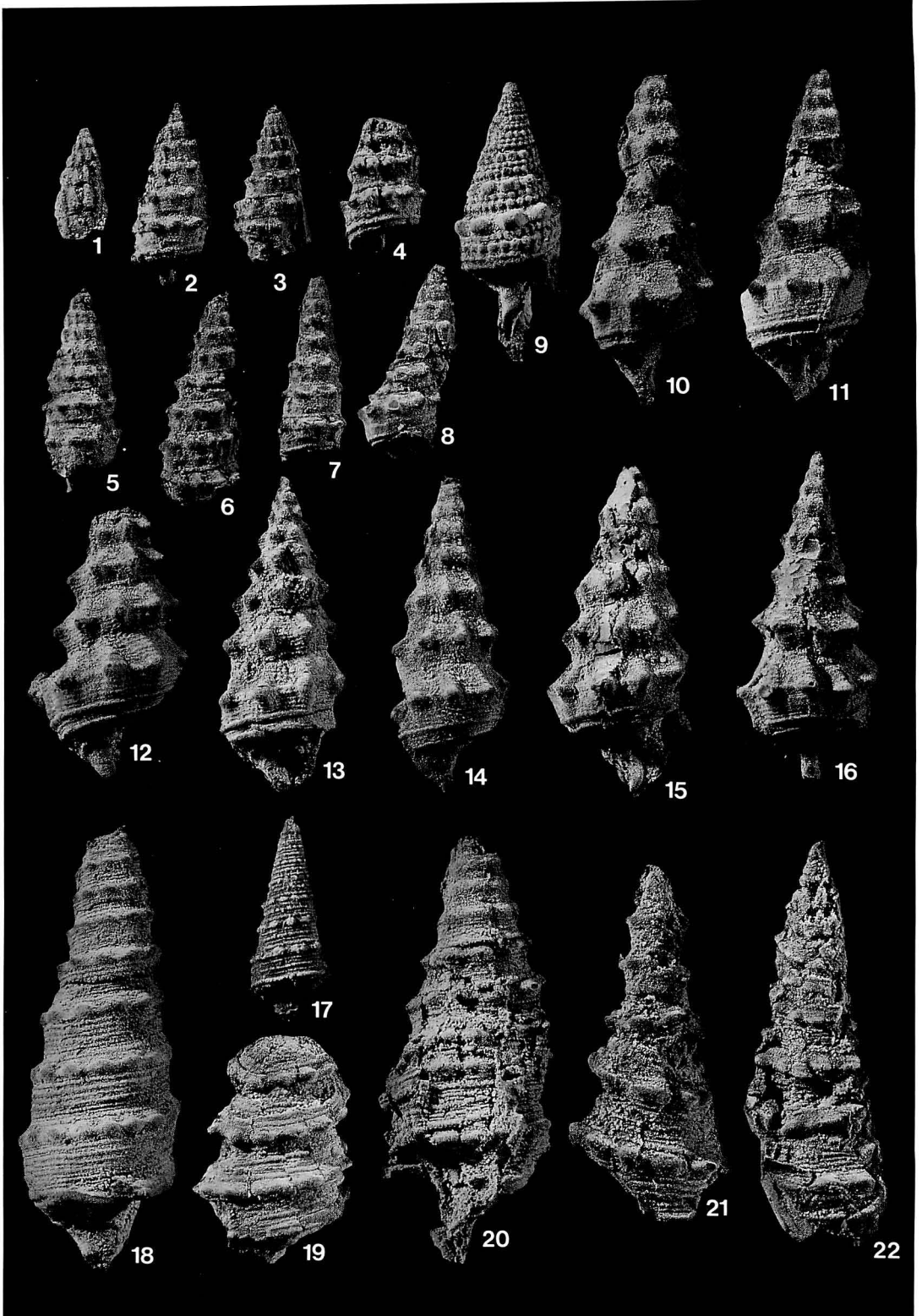
*Tateiwaia tateiwai* (Makiyama), Itoigawa, 1978, pl. 2, fig. 5; Taguchi *et al.*, 1979, pl. 3, figs. 24–26; Takayasu, 1981, p. 92, pl. 1, figs. 6, 7; Taguchi, 1981, pl. 4, fig. 11; Takahashi, 1984, pl. 1, fig. 7; Itoigawa and Shibata, 1986, pl. 16, fig. 3.

*Cerithium sakamotoi* Yokoyama, 1929, p. 367, pl. 70, fig. 4.

*Measurements.*—Largest specimen, height 18.8 mm (incomplete), diameter 7.1 mm (incomplete) [IGUT 11116-5: Figure 3-6].

*Discussion.*—Eleven specimens were examined. All lack protoconchs and apertural parts. The whorls are weakly shouldered and their sides are flattened. The whorl sculpture shows a pronounced change during ontogeny. The preserved early whorls have eleven well-defined axial ribs. On the later whorls, the axial ribs become weak or disappear, and three weak but distinct spiral threads appear. The upper thread bears eleven well-defined spines per whorl, the middle thread has twenty-two nodes, and the lower thread is nearly smooth.

The characters of the present specimens are





nearly identical with Makiyama's (1926) original description of the species, except for finer sculpture that is not preserved in the present specimens and for the presence of sculpture on the middle threads of the later whorls in present specimens. The observed specimens bear twenty-two nodes per whorl on the middle thread of the later whorls whereas Makiyama's specimens have a smooth middle thread. This difference in sculpture is an individual variation of the species.

*Tateiwaia yamanarii* (Makiyama, 1926)

Figures 3-10-16

*Batillaria yamanarii* Makiyama, 1926, pp. 148-149, pl. 12, fig. 4; Otuka, 1934, p. 624, pl. 49, figs. 80, 81; Nomura, 1935, p. 228, pl. 17, figs. 27, 28; ? Kanno and Ogawa, 1964, pl. 2, fig. 17; Mizuno, 1964, pl. 1, figs. 1-3.

*Batillaria (Tateiwaia) yamanarii* Makiyama, Makiyama, 1936, pp. 219-220; Fujie and Uozumi, 1957, pp. 502-503, pl. 24, figs. 5, 7; Okamoto and Terachi, 1974, pl. 47, fig. 12; Sasaki and Ogasawara, 1986, pl. 6, figs. 6a-b.

*Tateiwaia yamanarii* (Makiyama), Itoigawa *et al.*, 1974, pp. 134-135, pl. 40, figs. 23-24b; Itoigawa and Nishikawa, 1976, pl. 35, fig. 15; Itoigawa, 1978, pl. 2, fig. 4; Taguchi *et al.*, 1979, pl. 3, figs. 27, 28; Takayasu, 1981, pp. 92-93, pl. 1, figs. 8, 9; Itoigawa *et al.*, 1981, pl. 30, figs. 10a-b; Taguchi, 1981, pl. 4, fig. 12; Itoigawa *et al.*, 1982, p. 173; Okamoto *et al.*, 1983, pl. 23, figs. 10-11; Okumura, 1983, pl. 50, figs. 2a-b; Takahashi, 1984, pl. 1, figs. 9-11; Nakagawa and Takeyama, 1985, pl. 15, figs. 7, 8; Ozawa *et al.*, 1986, pl. 12, fig. 3; Itoigawa and Shibata, 1986, pl. 16, fig. 4.

*Cerithium proavitum* Yokoyama, 1929, p. 336, pl. 70, fig. 3.

*Measurements.*—Largest specimen, height 20.5 mm (incomplete), diameter 12.4 mm (incomplete) [IGUT 11118-3: Figure 3-12].

*Discussion.*—More than fifty specimens were examined. Protoconchs of all specimens are

missing. *Tateiwaia yamanarii* is characterized by medially angulate whorls; angularly depressed sutural part; eight or nine axial ribs per whorl, the axial ribs slightly prosoclinal, becoming coarser spines where they override the angulation, and not aligned from whorl to whorl; spiral sculpture of twelve to thirteen threads, with the spiral threads coarsest and crossed by the spines at the median whorl angle. The base is circumscribed by two spiral cords.

Like *Vicarya* spp. and *Vicaryella* spp., *Tateiwaia yamanarii* is among the morphologically most distinct and most common species in the estuarine tidal flat community of the early middle Miocene Kadonosawa-type Fauna. So, this species is one of the best indicators for the faunas of Kadonosawa age.

Genus *Vicaryella* Yabe and Hatai, 1938

*Type species.*—By original designation. *Vicaryella tyosenica* Yabe and Hatai, 1938.

*Vicaryella atukoae* (Otuka, 1934)

Figure 3-9

*Batillaria atukoae* Otuka, 1934, pp. 623-624, pl. 49, figs. 69, 70; ? Nomura, 1935, p. 228, pl. 17, fig. 23; ? Fujie and Uozumi, 1957, p. 503, pl. 24, fig. 8.

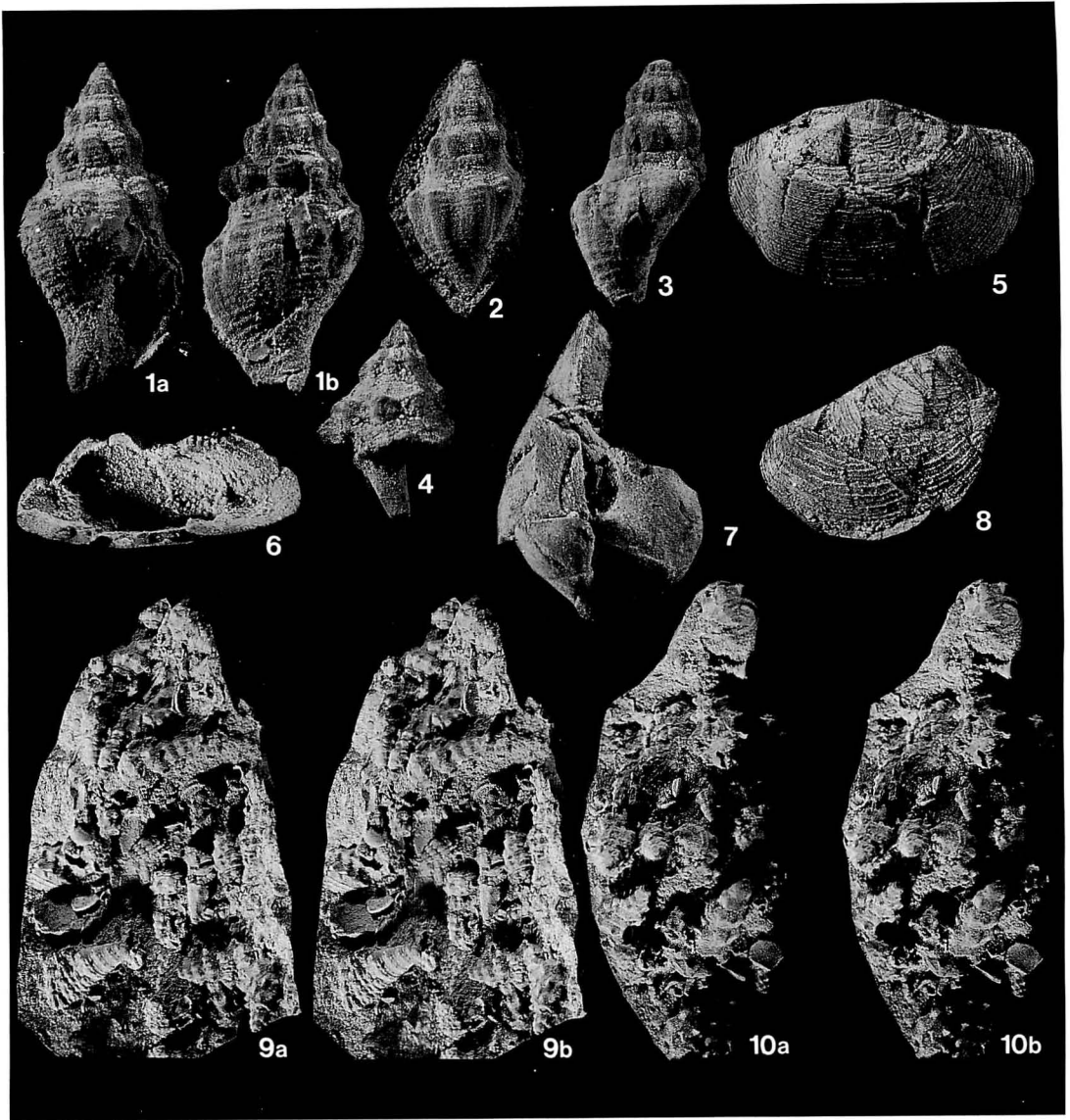
*Cerithium (Proclava) ancisum* (Yokoyama), Otuka, 1938, p. 42, pl. 4, fig. 36 [not *Potamides ancisum* Yokoyama, 1929].

*Measurements.*—Height, 21.4 mm (incomplete), diameter, 9.8 mm (incomplete).

*Discussion.*—Only one specimen was examined. Eight whorls are preserved but the protoconch and apertural parts are missing. The whorls are sculptured with three well-defined spiral cords bearing granular tubercles. In the early whorls, tubercles on the three cords are approximately equal in strength and eighteen in

← **Figure 3.** Fossil potamidids collected from the Kozono Formation. All figures are x2, unless otherwise stated. All specimens are rubber casts made from the external molds.

1. *Cerithidea* sp. IGUT 11115. 2-8. *Tateiwaia tateiwai* (Makiyama). 2, IGUT 11116-1; 3, IGUT 11116-2; 4, IGUT 11116-3; 5, IGUT 11116-4; 6, IGUT 11116-5; 7, IGUT 11116-6; 8, deformed, IGUT 11116-7. 9. *Vicaryella atukoae* (Otuka). IGUT 11117. 10-16. *Tateiwaia yamanarii* (Makiyama). 10, IGUT 11118-1; 11, IGUT 11118-2; 12, IGUT 11118-3; 13, IGUT 11118-4; 14, IGUT 11118-5; 15, IGUT 11118-6; 16, IGUT 11118-7. 17-22. *Vicaryella ishihana* (Yokoyama). 17, juvenile, IGUT 11119-1, x2.8; 18, IGUT 11119-2; 19, deformed, IGUT 11119-3; 20, deformed, IGUT 11119-4; 21, deformed, IGUT 11119-5; 22, deformed, IGUT 11119-6.



**Figure 4.** Fossil gastropods and bivalves collected from the Kozono Formation. All figures are  $\times 2$ , unless otherwise stated. All specimens are rubber casts made from the external molds. 1a–3. *Pollia* sp. 1a–b, IGUT 11120-1; 2, IGUT 11120-2; 3, IGUT 11120-3. 4. *Hemifusus* ? sp. Later whorls missing, IGUT 11121. 5. *Saxolucina* cf. *khataii* (Otuka). IGUT 16127. 6. *Striarca* sp. Interior view, IGUT 11123. 7. *Dosinia* sp. Dorsal view, showing a distinct lunule, IGUT 11124,  $\times 1.7$ . 8. *Clementia* sp. IGUT 11125. 9a–b. Stereopair, showing mode of fossil occurrence. IGUT 11126,  $\times 0.7$ . The block contains *Cerithidea* sp., *Tateiwaia tateiwai* (Makiyama), *T. yamanarii* (Makiyama), *Vicaryella ishiana* (Yokoyama) and bivalve fragments. 10a–b. Stereopair, showing mode of occurrence of *Tateiwaia yamanarii* (Makiyama). IGUT 11127,  $\times 0.7$ .

number on each cord of a whorl. The granular tubercles of the upper cord develop gradually into spinose tubercles during growth, and become fewer in number than tubercles on other spiral cords on the same whorl. On the last whorl, the spinose tubercles of the upper cord are nine in number, whereas tubercles of the other two cords are twenty-seven in number. The base is circumscribed by two spiral cords, the upper of which is weakly granulated. The columella is weakly but distinctly folded.

*Vicaryella atukoae* is similar to *Potamides ancisus* Yokoyama, 1929 in whorl sculpture, but the whorl sculpture of the former is coarser than that of the latter, and the former's columella is distinctly folded. *Potamides ancisus* Yokoyama has no columnar fold (Masuda, 1967).

#### *Vicaryella ishiana* (Yokoyama, 1926)

Figures 3-17–22

*Cerithium baculum* Yokoyama, Yokoyama, 1925, p. 12, pl. 2, fig. 6 [not *Cerithium baculum* Yokoyama, 1924].

*Vicaryella bacula* (Yokoyama) [not *Cerithium baculum* Yokoyama, 1924], Okamoto and Terachi, 1974, pl. 47, fig. 10; Taguchi *et al.*, 1979, pl. 3, figs. 29, 30.

*Cerithium ishianum* Yokoyama, 1926, p. 218, pl. 28, figs. 11, 12.

"*Vicaryella*" *ishiana* (Yokoyama), Yabe and Hatai, 1938, p. 169.

*Vicaryella ishiana* (Yokoyama), Oyama and Saka, 1944, pp. 139–140, pl. 14, figs. 5–8b; Kamada, 1960, p. 284, pl. 31, figs. 4a–b, 8, 9; Kamada, 1962, p. 152, pl. 18, figs. 15, 16; Masuda, 1967, pp. 1–2, pl. 1, figs. 1a–2b; Ogasawara, 1973, pl. 13, fig. 22; Itoigawa *et al.*, 1974, p. 137, pl. 42, figs. 5a–b; Kim *et al.*, 1974, pp. 279–280, pl. 39, fig. 2; Yoon, 1976, p. 64, pl. 1, figs. 5, 6; Yoon, 1979, p. 22, pl. 5, fig. 10; Itoigawa *et al.*, 1981, pl. 30, figs. 11a–b, 12a–b; Itoigawa *et al.*, 1982, pp. 171–172; Okamoto *et al.*, 1983, pl. 23, figs. 1–3; Nakagawa and Takeyama, 1985, pl. 15, fig. 9; Okamoto *et al.*, 1986, pl. 19, figs. 1, 2; Itoigawa and Shibata, 1986, pl. 16, fig. 9.

*Measurements*.—Largest specimen, height 33.5 mm (incomplete), diameter, 13.0 mm (incomplete) [IGUT 11119-2: Figure 3-18]

*Discussion*.—Twenty specimens were examined. Whorls have flat sides and are sculptured with several beaded or smooth spiral cords. Primary spirals are four in number, equidistant

and much narrower than their interspaces. They are all beaded except a suprasutural one that has a flat-topped surface. A subsutural beaded row develops into spinose tubercles, numbering 14 or 15 on average, although one specimen (IGUT 11119-2: Figure 3-18) has 18. Secondary interstitial spirals appear in the middle of the shell, and tertiary ones occur rarely on the later whorls. Base weakly concave, set off from the whorl sides by an acute angle, ornamented with several fine and smooth spiral threads, and circumscribed by two flat-topped, smooth spirals. Outer lip is broken. Inner lip is smooth, covered with a thick callous forming a semicircular plate. Siphonal canal is short.

This species is characterized by its highly turreted shell with many spiral cords that have a smooth or somewhat granular surface, of which the subsutural cord is the strongest and has about 14–15 spinose tubercles.

*Vicaryella notoensis* Masuda (1956, pp. 161–162, pl. 26, figs. 2–4) is quite similar to the present species, but differs by having 24–25 spinose tubercles on the subsutural spiral cord and secondary spirals that often become as strong as primary ones.

*Vicaryella atukoae* (Otuka) differs from the present species by having three granular spiral cords per whorl, and about ten strong spinose tubercles on the subsutural spiral cord of the last whorl.

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Arakawa 荒川, Kozono 小園, Tachigase 立ヶ瀬, Yorii 寄居.

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中部日本，埼玉県の小園層産中新世貝化石：埼玉県大里郡寄居付近の荒川流域に発達する中新統小園層から12種よりなる軟体動物群集が産出する。この群集は河口付近の潮汐砂底に生息していたと考えられ，中期中新世前期の門ノ沢型動物群内のフネガイ類やウミナ類の産出によって特徴づけられる潮間帯河口群集に比較される。ウミナ科の4種，*Tateiwaia tateiwaia* (Makiyama), *T. yamanarii* (Makiyama), *Vicaryella atukae* (Otuka) および *V. ishiana* (Yokoyama) は，小園層から初めて記載される。

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間嶋隆一・高橋宏和

## 844. TRIASSIC AND JURASSIC RADIOLARIA FROM THE NADANHADA RANGE, NORTHEAST CHINA\*

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**Abstract.** Triassic Radiolaria from bedded chert and Jurassic Radiolaria from siliceous shale in the Nadanhada Range, Northeast China are described; they are *Capnodoce traversi*, *Eucyrtidiellum ptyctum*, *E. unumaense*, *Guexella nudata*, *Livarella validus*, *Parahsuum(?)* sp. A, *Pentactinocarpus* sp. A, *Poulpus curvispinus*, *Pseudostylosphaera japonica*, *P. cf. hellenica*, *P. cf. tenue*, *P. sp. A*, *P. sp. B*, *P. sp. C*, *P. sp. D*, *P. sp. E*, *Stichocapsa convexa*, *Triassocampe deweveri*, *T. sp. A*, *Tricolocapsa(?) fusiformis*, *T. plicarum*, *T. tetragona*, *T. cf. ruesti*, *Yeharaia annulata*, *Y. japonica* and *Y. sp. A*. Other genera (species undetermined) are also illustrated. Ages of the bedded chert and siliceous shale are assigned to middle to late Triassic (late Anisian to Ladinian; late Carnian to Norian), and to middle Jurassic (Bathonian to Callovian), respectively.

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### Introduction

Recent progress in Mesozoic radiolarian biostratigraphy has made a profound contribution to the geology of Mesozoic and Paleozoic sedimentary complexes distributed in western North America, Japan and Europe, and the results have a great influence on the tectonic interpretations of these regions. For example, the Mino terrane in central Japan is composed of greenstone, limestone, bedded chert, sandstone and shale, and these rocks were long believed to be late Paleozoic in age based on fusulinaceans and corals in limestone. Recently, however, Triassic and Jurassic Radiolaria have been obtained from chert and shale. This fact indicates that the rocks in the Mino terrane are not Paleozoic, but mostly Mesozoic in age (*e.g.*, Mizutani *et al.*, 1981; Kojima, 1982, 1984). The radiolarian biostratigraphy also revealed that the geologic structure of Mesozoic and Paleozoic sedimentary complexes of the Mino terrane was exceedingly complicated. In many areas of the

terrane, chaotic and incoherent sedimentary complexes called olistostrome or mélange are distributed; they comprise blocks of various sizes (from a few centimeters to several kilometers in thickness), a wide ranging ages (Carboniferous to late Jurassic) and varying rock-types (limestone, greenstone, bedded chert, shale, etc.) which are enclosed in the Jurassic to earliest Cretaceous clastic matrix. A lithologic association of the same kind of rocks, radiolarian assemblages and geologic structure are traceable to the Tamba area in the west and to the Ashio area in the east; thus, the geologic body of these areas is collectively called the Tamba-Mino-Ashio terrane.

The northern part of the mainland of China is underlain by the Sino-Korean paraplatform, the Inner Mongolian-Great Khingan fold system, the Jilin-Heilong Jiang fold system and so forth (Ren *et al.*, 1980), where few bedded chert formations have been reported to occur. Even when descriptions of chert are presented, most of them are concerned with chert concretions contained in limestone beds and are of secondary origin. Fossil-bearing cherts or siliceous rocks, particularly of Mesozoic age, are extremely rare and almost absent except for the northeastern

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extremity, the Nadanhada area. Mesozoic formations of north and northeast China are mostly characterized by terrestrial deposits and subaerial volcanic rocks.

As early as the 1950's, the Radiolaria-bearing cherts are known to be distributed in the Nadanhada Range (Yabe, 1959; Yabe and Ohki, 1957). They noted that sandstone, chert, slate, conglomerate and a lesser amount of limestone occurred in the area. Most of these rocks were considered to be Jurassic in age. (e.g., Chinese Academy of Geological Science, 1976), although no reliable index fossils had been found. Li *et al.* (1979) reported the occurrence of Carboniferous and Permian fossils together with Radiolaria from the Nadanhada Range. Furthermore, Feng and Yang (1984) pointed out the distribution of sedimentary complex having a chaotic nature in the northeastern margin of the Chinese mainland. Recently, Wang *et al.* (1986) have disclosed the occurrence of late Triassic formation in the Nadanhada area, and discussed the possibility of widespread distribution of the Triassic rocks. From these lines of evidence, it is presumed that the Nadanhada Range was a northern extension of the Tamba-Mino-Ashio terrane, prior to the opening of the Sea of Japan, and that a superterrane, consisting of the Nadanhada terrane, part of Sikhote Alin, and Tamba-Mino-Ashio terrane, represents an ancient accretion complex formed during a time period from the Jurassic to the beginning of Cretaceous at the continental margin of East Asia (Mizutani, 1986, 1987).

Terrane analysis has made a fruitful advance since 1975 in the circum-Pacific region, especially in western North America (e.g., Coney *et al.*, 1980; Monger and Irving, 1980; Howell *et al.*, 1985). A tectonostratigraphic terrane is defined as "a fault-bounded package of rocks of regional extent characterized by a geologic history which differs from that of neighboring terranes" (Howell *et al.*, 1985). Intraterrane stratigraphy and structure have been examined by utilizing microfossils, such as Radiolaria and foraminifers in addition to the ordinary field investigations. Interterrane relationship, on the other hand, is inferred from paleomagnetism, paleogeography

and paleobiogeography. Wrangellia is one of the best examples investigated by these methods in the early stage of the development of terrane concept (Jones *et al.*, 1977). The Tamba-Mino-Ashio terrane and its probable extension, the Nadanhada Range, play an important role as a key terrane to reconstruct the East Asian collage, as Wrangellia does.

Following our preliminary report (Mizutani *et al.*, 1986), this paper describes in detail the occurrence of the characteristic species of Radiolaria collected from the Nadanhada Range and discusses ages of Radiolaria-bearing rocks and Jurassic radiolarian paleobiogeography.

### Geologic setting

The Nadanhada Range in Northeast China forms part of the Nadanhada eugeosyncline fold belt of Ren *et al.* (1980) or of the Nadanhada ophiolite belt of Li *et al.* (1982) and Zhang *et al.*

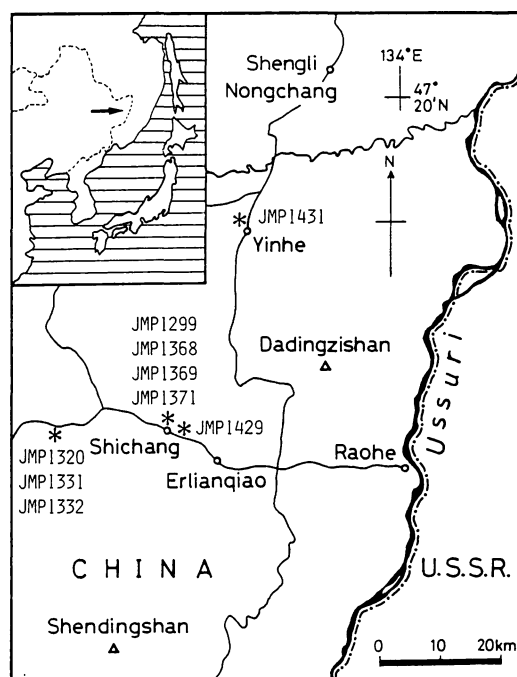


Figure 1. Index map of the Nadanhada Range, Northeast China. Numbers (JMP1331 etc.) are localities of samples treated in this paper.

(1984). To the south of the Nadanhada area there distributed is the late Proterozoic Khanka massif, and to the east and north of the area there is the Sikhote Alin fold belt. To the west there occurs the Jiamusi microcontinent composed of the Precambrian basement covered with an Upper Proterozoic formation with the Ediacara fauna (Zhang *et al.*, 1984). Serpentinite and glaucophane-schist found between the Nadanhada Range and the Jiamusi microcontinent (Zhang *et al.*, 1984) might be indicative of a suture zone between them.

The Nadanhada area is underlain by the Paleozoic and Mesozoic sedimentary complexes made up of greenstone, limestone, bedded chert, sandstone and shale, which crop out sporadically in quarries and roadside cuttings. Lenticular bodies of limestone, about 10 meters thick, are seen at Erlianqiao (Figure 1), embedded as olistolith together with blocks of basic lava in weakly sheared sandstone and shale. The limestone is massive, homogeneous and gray in color. Middle Carboniferous fusulinaceans (*Profusulinella* sp., *Fusulinella eopulchra* Rauser, *F. subpulchra submesopachis* Putrja) and corals (*Donophyllum* sp., *Koninckocarinia* sp.) are reported from this limestone by Li *et al.* (1979). They also described the occurrence of Carboniferous fusulinaceans (*Eostaffella*, *Fusulinella*, etc.) and Permian fusulinaceans (*Schwagerina*, *Chalartoschwagerina*, *Paraschwagerina*, *Pseudoschwagerina*, *Neoschwagerina*, *Pseudodoliolina*, *Kahlerina*, *Verbeekina*, *Reichelina*, *Rausarella*, etc.) fusulinaceans from other limestone bodies and radiolarian fossils (*Dictyomitra*, *Theocampe*, *Cenosphaera*, *Hemicryptocapsa*, etc.) from red shales in the Nadanhada Range. Later, Han (1982, 1985) described the fusulinaceans in detail. Pillow basalts, amygdaloidal and considerably altered, are well exposed at a road cut about 10 km east of Erlianqiao. Other varieties of greenstone including basic tuff, gabbro and diabase dyke are also found. Although the size of the mass of greenstone is unclear, Mt. Dadingzishan, 5 km across, consists of a greenstone complex of an ophiolitic succession partly containing komatiite as was reported by Cui (1986).

Bedded chert formations, invariably displaying an intraformational fold, are distributed in some quarries near Shichang, Yinhe and Shengli Nongchang (Figure 1). They seem to comprise isolated blocks enclosed in clastic matrix. Sandstone and shale make no good exposures, because they are no more resistant to weathering and economically less important than bedded chert or limestone. A sandstone block about 2 m in diameter, gray medium-grained quartzo-feldspathic wacke, occurs to the east of an exposure of bedded chert at Shichang (JMP1429 in Figure 1). A heavily weathered gray and reddish brown siliceous shale with faint fissility crops out at a site about 15 km west of Shichang (the point of JMP1320, etc. in Figure 1). Black manganese nodules of 10 to 20 cm in diameter occur in association with the shale.

All the rock specimens, except for JMP1299, treated for micropaleontological examination in this paper were collected by the present authors in the summer of 1986. Registered numbers of rock specimens (JMP-) and sample numbers recorded in the field are listed below (see Figure 1 for localities of the samples).

- JMP1299 (A-5-3): reddish brown bedded (?) chert offered by Dr. Shao Ji An (Beijing Univ.). She informed us that this specimen is collected from the quarry near Shichang. (in the same location of JMP1368 etc.)
- JMP1320 (SM86080905): reddish brown siliceous shale with faint fissility. (west of Shichang)
- JMP1331 (SM86080906): greenish gray siliceous shale with faint fissility. (west of Shichang)
- JMP1332 (SM86080910): gray siliceous shale with faint fissility. (west of Schichang)
- JMP1368 (SK86080708A): gray bedded chert. (Shichang)
- JMP1369 (SK86080708B): reddish brown bedded chert. (Shichang)
- JMP1371 (SK86080708D): reddish brown bedded chert. (Shichang)
- JMP1429 (SM86080901): reddish brown bedded chert. (Shichang)
- JMP1431 (SK86080603A): gray bedded chert. (Yinhe)

### Descriptions of Radiolaria

Since study of Mesozoic Radiolaria is still in its infancy, the phylogeny and classification, especially at the suprageneric level, have not been





established so far. In this paper, we describe the Radiolaria in alphabetical order of the genus name for convenience. All the species described herein are illustrated in Figures 2–5. The fossil individuals used in the description and figures are numbered, for example, as (12345/6789); the numerator represents a sequential number of SEM photograph and the denominator indicates that of the rock specimen (JMP numbers shown in Figure 1 and Table 1) from which a given fossil was extracted. Both of these numbers are registered in the Rad File, Department of Earth Sciences, Nagoya University.

Genus *Capnodoce* De Wever, 1979

*Capnodoce traversi* Pessagno, 1979

Figure 3-13

*Capnodoce traversi* Pessagno, 1979, p. 176, 177, pl. 1, figs. 11, 12; Blome, 1983, p. 36, pl. 8, figs. 4, 16; Blome, 1984, p. 35, pl. 4, fig. 19.

Genus *Eucyrtidiellum* Baumgartner, 1984

*Eucyrtidiellum ptyctum* (Riedel and Sanfilippo, 1974)

Figures 4-12, 13

*Eucyrtidium ptyctum* Riedel and Sanfilippo, 1974, p. 778, pl. 5, fig. 7, pl. 12, fig. 14; Baumgartner and Bernoulli, 1976, p. 617, figs. 11e, g; Baumgartner *et al.*, 1980, p. 53, pl. 3, fig. 13; Aita, 1982, pl. 2, figs. 8–9b; Nishizono *et al.*, 1982, pl. 2, fig. 12; Yao, 1984, pl. 2, fig. 30.

*Eucyrtidiellum ptyctum* (Riedel and Sanfilippo), Baumgartner, 1984, p. 764, pl. 4, figs. 1–3; Matsuoka, 1986a, pl. 2, fig. 10; Nagai, 1986, p. 14, 15, pl. 2, fig. 7.

*Eucyrtidium(?) ptyctum* Riedel and Sanfilippo, Pessagno, 1977, p. 94, pl. 12, fig. 7; Mizutani, 1981, p. 182, pl. 64, figs. 1a–2; Adachi, 1982, pl. 3, figs. 7, 8; Mizutani *et al.*, 1982, p. 57, pl. 4, fig. 5; Ishida, 1983, pl. 9, fig. 4; Nishizono and Murata, 1983, pl. 4, fig. 7; Yamamoto, 1983, pl. 1, fig. 4; Takashima and Koike, 1984, pl. 2, fig. 5; Aita, 1985, fig. 7-14; Ishida, 1985a, pl. 3, fig. 15; Matsuoka and Yao, 1985, pl. 2, fig. 8; Matsuoka and Yao, 1986, pl. 2, fig. 10; Tanaka *et al.*, 1985, pl. 1, fig. 16; Aita and Okada, 1986, p. 109, pl. 6, figs. 14–17, pl. 7, figs. 3a, b.

*"Eucyrtidium" ptyctum* Riedel and Sanfilippo, Pessagno *et al.*, 1984, p. 30, 31, pl. 4, figs. 12–14.

*Eucyrtidiellum unumaense* (Yao, 1979)

Figure 4-16

*Eucyrtidium(?) unumaensis* Yao, 1979, p. 39, pl. 9, figs. 1–11; Sugano *et al.*, 1980, pl. 4, fig. 3; Kido *et al.*, 1982, pl. 4, fig. 9; Kojima, 1982, pl. 1, fig. 11; Matsuoka, 1982, pl. 1, fig. 15; Owada and Saka, 1982, pl. 2, fig. 8; Sashida *et al.*, 1982, pl. 2, fig. 3; Wakita, 1982, pl. 3, fig. 1; Wakita and Okamura, 1982, pl. 8, fig. 7; Yao *et al.*, 1982, pl. 3, fig. 7; Saka, 1983, pl. 5, figs. 6, 7; Aita, 1985, figs. 7-15, 16; Yamamoto, 1985, pl. 2, fig. 4.

*Eucyrtidiellum unumaense* (Yao), Baumgartner, 1984, p. 765, pl. 4, fig. 6; Yamamoto *et al.*, 1985, p. 35, pl. 4, fig. 6; Ishida, 1986, pl. 1, fig. 6; Nagai, 1986, p. 13, 14, pl. 1, figs. 1a–c, pl. 2, fig. 1.

*Stichocorys* sp. Ichikawa and Yao, 1973, pl. 1, figs. 3–4b.

*Eucyrtidium(?) unumaense* Yao, Mizutani *et al.*, 1984, pl. 1, fig. 8; Ishida, 1985b, pl. 2, fig. 27; Matsuoka, 1985, pl. 1, fig. 9.

Genus *Guexella* Baumgartner, 1984

*Guexella nudata* (Kocher, 1980)

Figures 4-9, 10

*Lithocampe nudata* Kocher in Baumgartner *et al.*, 1980, p. 55, pl. 6, fig. 3.

*Guexella nudata* (Kocher), Baumgartner, 1984, p. 766, 767, pl. 5, figs. 5–7; Yamamoto *et al.*, 1985, p. 35, pl. 4, fig. 7; Kishida and Hisada, 1986, fig. 8-3; Matsuoka, 1986a, pl. 3, figs. 15a, b.

*Lithocampe(?) nudata* Kocher, Aita, 1982, pl. 1, figs. 19a–c; Matsuoka, 1982, pl. 2, figs. 1, 2; Yao *et al.*, 1982, pl. 4, figs. 1, 2; Koike and Takashima, 1983, pl. 1, fig. 7; Matsuoka, 1983a, p. 27, pl. 9, figs. 12–14; Matsuoka, 1983b, fig. 4-10; Takashima and Koike, 1984, pl. 1, fig. 20; Yao, 1984, pl. 2, fig. 1; Aita, 1985, fig. 7-17; Ishida, 1985a, pl. 3, fig. 13.

Genus *Livarella* Kozur and Mostler, 1981

*Livarella validus* Yoshida, 1986

Figures 3-18a, b

*Livarella validus* Yoshida, 1986, p. 14, pl. 3, figs. 1–3.

Genus *Parahsuum* Yao, 1982

*Parahsuum(?)* sp. A

Figure 3-10

*Description*:—Test conical and cylindrical distally. Cephalis trapezoidal, poreless, without

apical horn. Proximal one-third to one-fifth of the test poreless, the rest covered by irregularly pored meshwork.

*Remarks*:—*Parahsuum* Yao (1982) was originally described as follows: "Shell multisegmented, conical to spindle-shaped lacking well-developed strictures. Cephalis conical to dome-shaped, poreless with or without apical horn. Thorax trapezoidal in outline with sparse irregularly displaced pores. Abdomen and post-abdominal segments with continuous edged costae. Single row of square pore frames with circular, primary pores between costae." We tentatively treat this form under the genus *Parahsuum* based on the external features of the test. Although none of our six specimens has apical horn, this species might originally have had an apical horn, judging from the abrupt termination and the irregular upper surface of the cephalis.

Genus *Pentactinocarpus* Dumitrica, 1978

*Pentactinocarpus* sp. A

Figure 2-13

*Description*:—Shell spherical with hexagonal pore frames. Pore frames with small nodes at vertices. Apical spine short, and basal spines connected at their proximal parts with pore frames.

Genus *Poulpus* De Wever, 1979

*Poulpus curvispinus* Dumitrica, Kozur and Mostler, 1980

Figure 2-16

*Poulpus curvispinus* Dumitrica et al., 1980, p. 22, pl. 2, fig. 1, pl. 15, figs. 5, 6.

*Poulpus* sp. aff. *P. curvispinus* Dumitrica et al., Yao, 1982, pl. 1, fig. 18.

*Remarks*:—Although the internal cephalic structure of this specimen cannot be observed because of secondary fillings, this specimen seems to be assignable to *P. curvispinus*, judging from characteristic shape of cephalis and feet.

Genus *Pseudostylosphaera* Kozur and

Mostler, 1981

*Remarks*:—*Archaeospongoprimum* Pessagno (1973) is originally described as a spongurid with spongy meshwork shell and two triradiate or tetraradiate polar spines, and De Wever et al., (1979), and Nakaseko and Nishimura (1979) included some Triassic spumerallian Radiolaria in this genus. Subsequently, Kozur and Mostler (1981) proposed a new genus *Pseudostylosphaera*, and included in it some species which were described under the genus *Archaeospongoprimum*. We use this new generic name in this paper, although it is not clear whether our specimens have the inner structure characteristic of the genus.

*Pseudostylosphaera japonica* (Nakaseko and Nishimura, 1979)

Figure 2-1

*Archaeospongoprimum japonicum* Nakaseko and Nishimura, 1979, p. 67, 68, pl. 1, figs. 2, 4, 9; Mizutani and Koike, 1982, pl. 3, fig. 3; Yao, 1982, pl. 1, fig. 21; Adachi and Kojima, 1983, pl. 13, fig. 10; Yoshida, 1986, pl. 9, figs. 1, 2.

*Pseudostylosphaera japonica* (Nakaseko and Nishimura), Lahm, 1984, p. 34, pl. 4, figs. 9, 10; Kishida and Hisada, 1986, fig. 3-4.

*Stylosphaera*(?) *japonica* (Nakaseko and Nishimura), Kishida and Sugano, 1982, pl. 1, figs. 10-15;

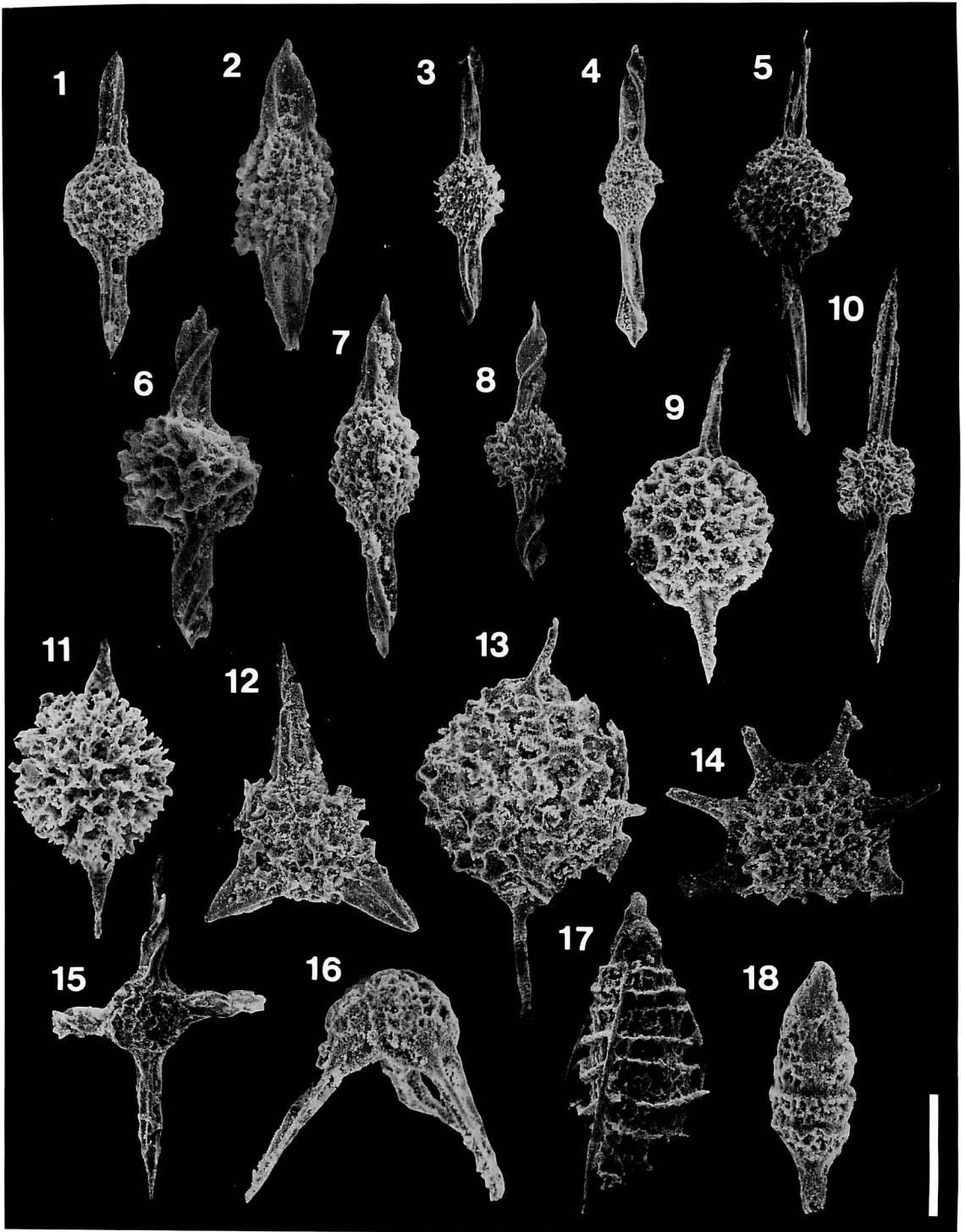
*Remarks*:—The holotype of *Pseudostylosphaera japonica* (Nakaseko and Nishimura) (1979, pl. 1, fig. 2) and that of *P. japonica* of Lahm (1984, pl. 4, figs. 9, 10) slightly differ from our present specimen in having more constricted polar spines in their proximal portions. Other examples of *P. japonica* of Nakaseko and Nishimura (1979, pl. 1, figs. 4, 9), however, are very similar to our specimen, and we tentatively assigned this form to *P. japonica*.

*Pseudostylosphaera* sp. cf. *P. hellenica* (De Wever, 1979)

Figure 2-4

*Archaeospongoprimum hellenicum* De Wever?, 1982, p. 179, 180, pl. 10, fig. 5.

cf. *Archaeospongoprimum*(?) *hellenicum* De Wever et al., 1979, p. 78, pl. 1, fig. 8.



cf. *Archaeospongoprimum hellenicum* De Wever, 1982, p. 179, 180, pl. 10, fig. 4.

cf. *Stylosphaera?* cf. *hellenica* (De Wever), Kozur and Mostler, 1979, p. 55, pl. 1, fig. 4, pl. 17, fig. 4.

cf. *Pseudostylosphaera hellenica* (De Wever), Lahm, 1984, p. 35, pl. 5, figs. 1, 2.

*Pseudostylosphaera* sp. cf. *P. tenue*  
(Nakaseko and Nishimura, 1979)

Figure 2-5

cf. *Archaeospongoprimum tenue* Nakaseko and Nishimura, 1979, p. 68, 69, pl. 1, figs. 8, 10; Mizutani and Koike, 1982, pl. 3, fig. 2; Adachi and Kojima, 1983, pl. 13, fig. 11.

cf. *Pseudostylosphaera tenue* (Nakaseko and Nishimura); Lahm, 1984, p. 36, pl. 5, figs. 5, 6.

*Pseudostylosphaera* sp. A

Figure 2-2

*Description*:—Shell elliptical with spongy meshwork. Two opposite polar spines short, wide, equal in length and triradiate in cross section; three wide grooves alternating with three narrow ridges.

*Remarks*:—The present specimen differs from other species of *Pseudostylosphaera* in having wide polar spines.

*Pseudostylosphaera* sp. B

Figure 2-3

*Description*:—Shell subglobular with two polar spines. These spines have three narrow ridges alternating with relatively wide grooves, and are twisted distally. The width of the spines is constant in much of the length and decreases

abruptly near the terminations.

*Pseudostylosphaera* sp. C

Figure 2-7

*Description*:—Shell slender, ellipsoidal with meshwork, and has a circumferential sulcus. Polar spines sturdy, triradiate in cross section, and slightly twisted.

*Pseudostylosphaera* sp. D

Figure 2-8

*Description*:—Shell subspherical to ellipsoidal with spongy meshwork. Two opposite polar spines triradiate in cross section, three wide grooves alternating with three narrow ridges displaying a strong torsion.

*Pseudostylosphaera* sp. E

Figure 2-10

*Description*:—Shell cylindrical, covered by polygonal meshwork with small nodes. Two opposite polar spines unequal in length; shorter one twisted and triradiate in cross section, whereas longer one not twisted and tetradiate.

Genus *Stichocapsa* Haeckel, 1881

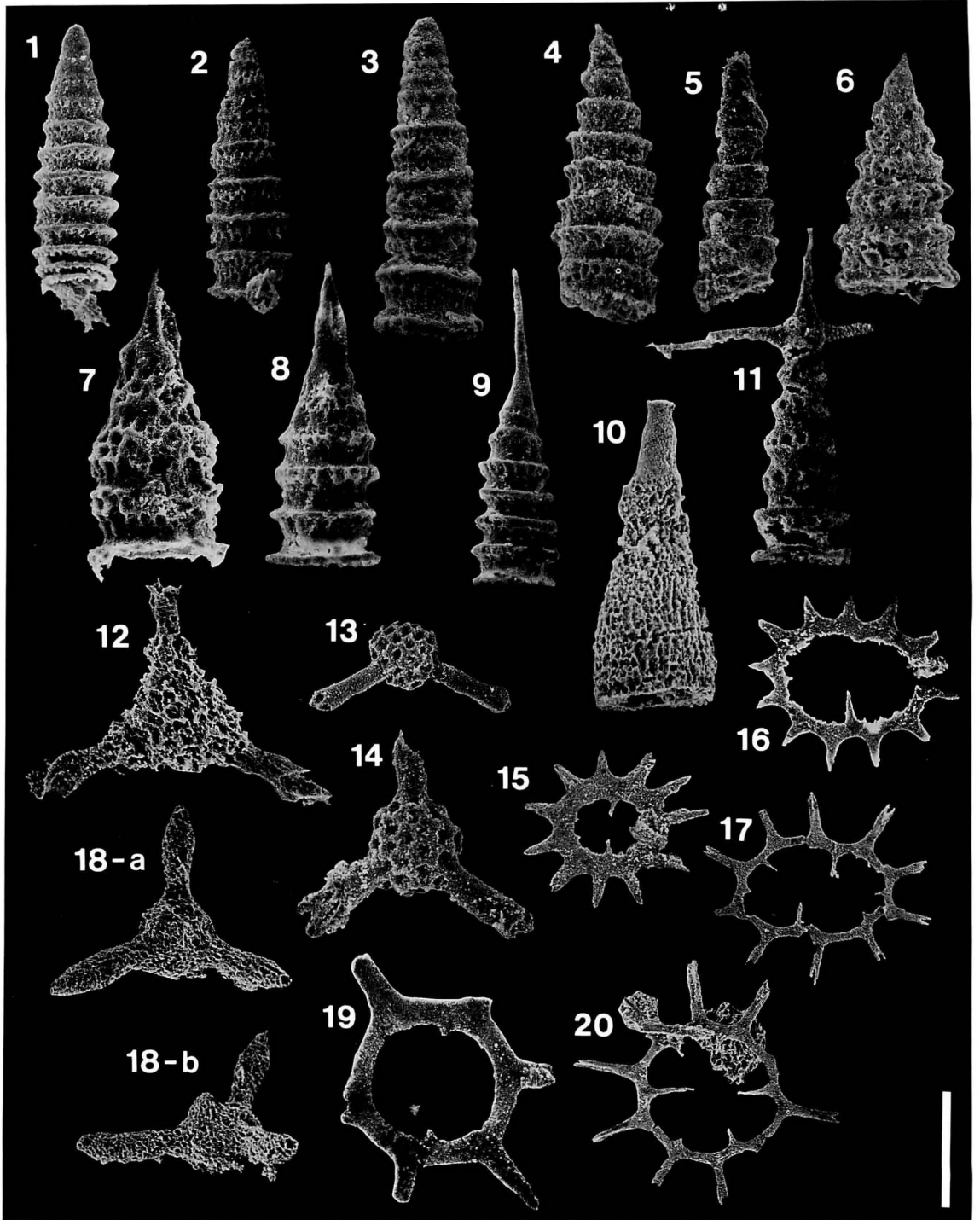
*Stichocapsa convexa* Yao, 1979

Figure 4-2

*Stichocapsa convexa* Yao, 1979, p. 35, 36, pl. 5, figs. 14–16, pl. 6, figs. 1–7; Aita, 1982, pl. 1, figs. 6-7b; Wakita, 1982, pl. 3, fig. 7; Koike and Takashima, 1983, pl. 1, fig. 12; Nishizono and Murata, 1983, pl.

← **Figure 2.** Middle Triassic Radiolaria from the Nandanhada Range.

1. *Pseudostylosphaera japonica* (Nakaseko and Nishimura) (40278/1368) scale bar = 110  $\mu\text{m}$ .
2. *Pseudostylosphaera* sp. A (42219/1368) scale bar = 120  $\mu\text{m}$ .
3. *Pseudostylosphaera* sp. B (41992/1368) scale bar = 210  $\mu\text{m}$ .
4. *Pseudostylosphaera* sp. cf. *P. hellenica* (De Wever) (40275/1368) scale bar = 180  $\mu\text{m}$ .
5. *Pseudostylosphaera* sp. cf. *P. tenue* (Nakaseko and Nishimura) (42215/1368) scale bar = 210  $\mu\text{m}$ .
6. *Pseudostylosphaera* (?) sp. (42220/1368) scale bar = 120  $\mu\text{m}$ .
7. *Pseudostylosphaera* sp. C (42213/1368) scale bar = 120  $\mu\text{m}$ .
8. *Pseudostylosphaera* sp. D (42216/1368) scale bar = 210  $\mu\text{m}$ .
9. *Pseudostylosphaera* (?) sp. (40319/1369) scale bar = 77  $\mu\text{m}$ .
10. *Pseudostylosphaera* sp. E (40286/1368) scale bar = 180  $\mu\text{m}$ .
11. *Xiphosphaera* (?) sp. (40345/1369) scale bar = 77  $\mu\text{m}$ .
12. *Eptingium* sp. (40325/1369) scale bar = 110  $\mu\text{m}$ .
13. *Pentactinocarpus* sp. A (40340/1369) scale bar = 110  $\mu\text{m}$ .
14. *Pseudoheliodiscus* sp. (40266/1368) scale bar = 110  $\mu\text{m}$ .
15. *Plafkerium* sp. (42000/1368) scale bar = 210  $\mu\text{m}$ .
16. *Poulpus curvispinus* Dumitrica et al. (40332/1369) scale bar = 77  $\mu\text{m}$ .
17. *Silicarmiger* sp. (42008/1368) scale bar = 120  $\mu\text{m}$ .
18. *Eucyrtis* (?) sp. (40288/1368) scale bar = 77  $\mu\text{m}$ .



4, fig. 5; Baumgartner, 1984, p. 785, pl. 8, fig. 19; Matsuoka, 1985, pl. 1, fig. 8; Yamamoto *et al.*, 1985, p. 38, pl. 7, fig. 4; Takemura, 1986, p. 55, pl. 7, figs. 9, 10; Yokota and Sano, 1986, pl. 1, fig. 4.

"*Stichocapsa*" sp. B, Ichikawa and Yao, 1973, pl. 3, figs. 3-5.

*Stichocapsa* sp. J, Aita, 1982, pl. 1, figs. 8-9b.

Genus *Triassocampe* Dumitrica, Kozur and Mostler, 1980

*Triassocampe deweveri* (Nakaseko and Nishimura, 1979)

Figures 3-2, 3

*Dictyomitrella deweveri* Nakaseko and Nishimura, 1979, p. 77, pl. 10, figs. 8, 9.

*Triassocampe deweveri* (Nakaseko and Nishimura, 1979), Mizutani *et al.*, 1982, p. 55, 56, pl. 4, fig. 1; Yao, 1982, pl. 1, figs. 1-3; Yao *et al.*, 1982, pl. 1, fig. 1; Yao, 1983, fig. 2-1; Kishida and Hisada, 1986, fig. 3-2.

*Triassocampe scalaris* Dumitrica *et al.*, 1980, p. 26, pl. 9, figs. 5, 6, 11, pl. 14, fig. 2; Mizutani and Koike, 1982, pl. 4, fig. 4.

*Remarks*:—*Triassocampe scalaris* (Dumitrica *et al.*, 1980) has common characteristics with *Triassocampe deweveri* (Nakaseko and Nishimura), and is regarded as a synonym. Although Nakaseko and Nishimura (1979, p. 77) remarked that the *Dictyomitrella deweveri* "appears to be identical with *Dictyomitrella* sp. A of De Wever (1979, p. 90, pl. 5, figs. 12, 16)", the latter is distinguished from the former by having only one row of pores below circumferential ridges.

*Triassocampe* sp. A

Figure 3-1

*Dictyomitrella* sp. A De Wever *et al.*, 1979, p. 90, pl. 5, figs. 12, 16.

*Remarks*:—This form is different from *T. deweveri* in having one row of pores below each circumferential ridge.

Genus *Tricolocapsa* Haeckel, 1887

*Tricolocapsa*(?) *fusiformis* Yao, 1979

Figures 4-3, 4

*Tricolocapsa*(?) *fusiformis* Yao, 1979, p. 33, 34, pl. 4, figs. 12-18, pl. 5, figs. 1-4; Kido *et al.*, 1982, pl. 5, fig. 3; Matsuoka, 1982, pl. 1, figs. 17-19; Wakita, 1982, pl. 3, fig. 4; Wakita and Okamura, 1982, pl. 7, fig. 10; Adachi and Kojima, 1983, pl. 16, fig. 5; Kashima, 1983, pl. 8; fig. 4; Matsuoka, 1983a, p. 19, pl. 2, fig. 11, pl. 8, fig. 1; Takashima and Koike, 1984, pl. 1, fig. 12; Ishida, 1985a, pl. 5, fig. 13; Matsuoka, 1985, pl. 1, fig. 3; Yamamoto, 1985, pl. 2, fig. 6; Ishida, 1986, pl. 1, fig. 7; Takemura, 1986, p. 54, pl. 7, fig. 6; Yokota and Sano, 1986, pl. 1, fig. 7.

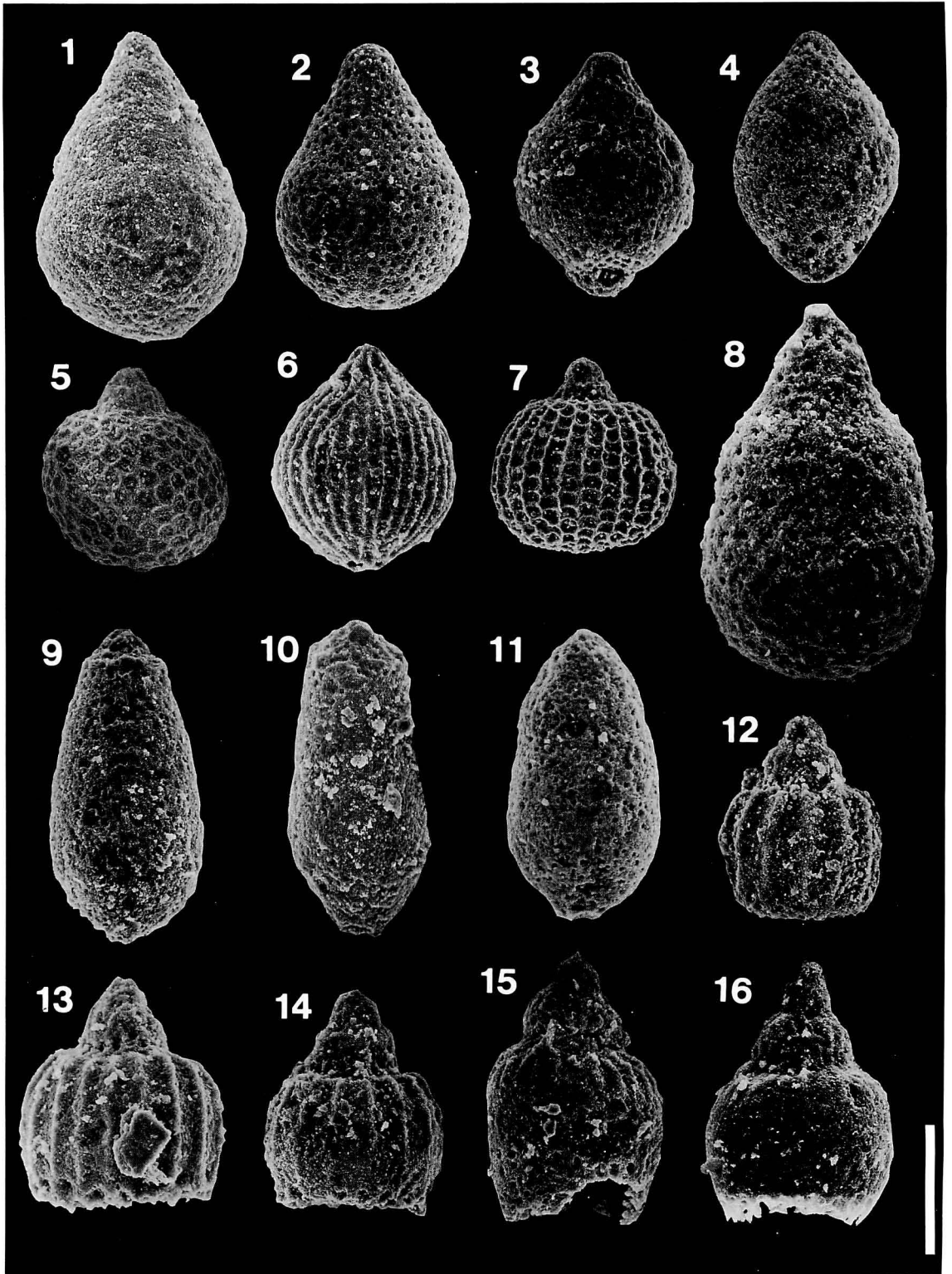
*Tricolocapsa plicarum* Yao, 1979

Figure 4-6

*Tricolocapsa plicarum* Yao, 1979, p. 32, 33, pl. 4, figs. 1-11; Aita, 1982, pl. 1, fig. 17; Kido *et al.*, 1982, pl. 5, fig. 1; Kishida and Sugano, 1982, pl. 12, figs. 1, 2; Kojima, 1982, pl. 2, fig. 1; Nishizono *et al.*, 1982, pl. 2, fig. 16; Sashida *et al.*, 1982, pl. 2, fig. 1; Wakita, 1982, pl. 3, fig. 3; Wakita and Okamura, 1982, pl. 7, fig. 9; Yao *et al.*, 1982, pl. 3, fig. 12; Adachi and Kojima, 1983, pl. 16, fig. 7; Kashima, 1983, pl. 9, fig. 1; Matsuoka, 1983a, p. 20, pl. 3, figs. 1, 2; Nishizono and Murata, 1983, pl. 4, fig. 4; Saka, 1983, pl. 6, figs. 2-4; Takashima and Koike, 1984, pl. 1, fig. 9; Yao, 1984, pl. 2, figs. 11, 12; Ishida, 1985a, pl. 3, fig. 12; Matsuoka, 1985, pl. 1, figs. 1, 2; Yamamoto, 1985, pl. 2, fig. 8; Yamamoto

← **Figure 3.** Middle and Upper Triassic Radiolaria from the Nandanhada Range.

1. *Triassocampe* sp. A (42221/1368) scale bar = 120  $\mu$ m.
2. *Triassocampe deweveri* (Nakaseko and Nishimura) (42224/1369) scale bar = 120  $\mu$ m.
3. *Triassocampe deweveri* (Nakaseko and Nishimura) (42225/1369) scale bar = 84  $\mu$ m.
4. *Triassocampe* sp. (41501/1431) scale bar = 77  $\mu$ m.
5. *Triassocampe* sp. (41499/1431) scale bar = 110  $\mu$ m.
6. *Triassocampe* (?) sp. (40262/1368) scale bar = 77  $\mu$ m.
7. *Yeharaia* sp. (41921/1369) scale bar = 84  $\mu$ m.
8. *Yeharaia japonica* Nakaseko and Nishimura (41943/1369) scale bar = 84  $\mu$ m.
9. *Yeharaia annulata* Nakaseko and Nishimura (41919/1369) scale bar = 120  $\mu$ m.
10. *Parahsuum* (?) sp. A (38972/1299) scale bar = 110  $\mu$ m.
11. *Yeharaia* sp. A (41950/1369) scale bar = 84  $\mu$ m.
12. *Capnuhosphaera* (?) sp. (38929/1299) scale bar = 110  $\mu$ m.
13. *Capnodoce traversi* Pessagno (41479/1429) scale bar = 180  $\mu$ m.
14. *Capnodoce* sp. (41480/1429) scale bar = 110  $\mu$ m.
15. *Acanthocircus* sp. (38920/1299) scale bar = 180  $\mu$ m.
16. *Acanthocircus* sp. (38967/1299) scale bar = 110  $\mu$ m.
17. *Pseudoheliodiscus* sp. (38971/1299) scale bar = 180  $\mu$ m.
- 18a. *Livarella validus* Yoshida (38950/1299) scale bar = 110  $\mu$ m.
- 18b. *Livarella validus* Yoshida (38951/1299) scale bar = 110  $\mu$ m.
19. *Acanthocircus* sp. (40409/1371) scale bar = 120  $\mu$ m.
20. *Pseudoheliodiscus* sp. (38990/1299) scale bar = 180  $\mu$ m.





*et al.*, 1985, p. 39, pl. 8, fig. 8; Ishida, 1986, pl. 1, fig. 9; Matsuoka, 1986b, figs. 3-a-c; Sato *et al.*, 1986, fig. 17-12; Yokota and Sano, 1986, pl. 1, fig. 5.

"*Artocapsa*" sp. A, Ichikawa and Yao, 1973, pl. 5, figs. 1a, b.

*Tricolocapsa tetragona* Matsuoka, 1983

Figure 4-7

*Tricolocapsa tetragona* Matsuoka, 1983a, p. 22, 23, pl. 3, figs. 8-12, pl. 8, figs. 4-10; Takashima and Koike, 1984, pl. 1, fig. 11; Sato *et al.*, 1986, fig. 17-18.

*Tricolocapsa* sp. N, Matsuoka, 1982, pl. 2, figs. 13, 17.

*Tricolocapsa* sp. E, Aita, 1982, pl. 2, fig. 4

*Tricolocapsa* sp. cf. *T. ruesti* Tan Sin Hok, 1927

Figure 4-5

*Tricolocapsa* sp. cf. *T. rüsti* Tan Sin Hok, Yao, 1979, p. 30, 31, pl. 3, figs. 8-20; Adachi and Kojima, 1983, pl. 16, fig. 8; Kashima, 1983, pl. 9, fig. 10; Ujiie and Hashimoto, 1983, fig. 5-5; Matsuoka, 1985, pl. 1, fig. 5; Yamamoto *et al.*, 1985, p. 39, pl. 9, fig. 1; Ishida, 1986, pl. 1, fig. 10; Yokota and Sano, 1986, pl. 1, fig. 6.

"*Hemicryptocapsa*" sp. Ichikawa and Yao, 1973, pl. 4, figs. 7a, b.

*Tricolocapsa yaoi* (Kozur), Takemura, 1986, p. 54, pl. 7, figs. 5, 7, 8.

cf. *Tricolocapsa rüsti* Tan Sin Hok, 1927, p. 50, pl. 9, fig. 65.

Genus *Yeharaia* Nakaseko and Nishimura, 1979

*Yeharaia annulata* Nakaseko and  
Nishimura, 1979

Figure 3-9

*Yeharaia annulata* Nakaseko and Nishimura, 1979, p. 82, 83, pl. 10, figs. 1, 7, pl. 12, fig. 5; Kido, 1982, pl. 1,

fig. 10; Kojima, 1982, pl. 2, fig. 5; Adachi and Kojima, 1983, pl. 13, fig. 4, Ishida, 1984, pl. 1, figs. 13-15.

*Triassocampe*(?) *annulata* (Nakaseko and Nishimura), Yao, 1982, pl. 1, fig. 11; Yao *et al.*, 1982, pl. 1, fig. 8; Yao, 1983, fig. 2-5.

*Yeharaia japonica* Nakaseko and  
Nishimura, 1979

Figure 3-8

*Yeharaia japonica* Nakaseko and Nishimura, 1979, p. 83, pl. 10, figs. 6, 10, pl. 12, fig. 9; Ishida, 1984, pl. 1, figs. 17-19.

*Triassocampe*(?) *japonica* (Nakaseko and Nishimura), Yao, 1982, pl. 1, fig. 12.

*Yeharaia* sp. A

Figure 3-11

*Triassocampe*(?) sp. A, Mizutani *et al.*, 1982, p. 56, pl. 4, fig. 2.

*Triassocampe*(?) sp. F, Yao, 1982, pl. 1, fig. 10; Yao *et al.*, 1982, pl. 1, fig. 9.

*Description*:—Test conical to cylindrical with seven to eight, sometimes more, segments. Cephalis hemispherical with apical horn and two laterally extending spines in the same plane. Thorax, abdomen and three post abdominal chambers, all trapezoidal in external form, have broad ridges between them; the chambers have one row of pore on their ridges. Distal segments have more prominent and narrow ridges.

*Remarks*:—This form is distinct from other species of *Yeharaia* in having cephalis with two laterally extending spines.

← **Figure 4.** Middle Jurassic Radiolaria from the Nandanhada Range.

1. *Stichocapsa* (?) sp. (40015/1331) scale bar = 51  $\mu$ m. 2. *Stichocapsa convexa* Yao (42066/1331) scale bar = 84  $\mu$ m. 3. *Tricolocapsa* (?) *fusiformis* Yao (40024/1331) scale bar = 51  $\mu$ m. 4. *Tricolocapsa* (?) *fusiformis* Yao (39862/1320) scale bar = 56  $\mu$ m. 5. *Tricolocapsa* sp. cf. *T. ruesti* Tan Sin Hok (40054/1331) scale bar = 77  $\mu$ m. 6. *Tricolocapsa plicarum* Yao (42211/1331) scale bar = 84  $\mu$ m. 7. *Tricolocapsa tetragona* Matsuoka (40038/1331) scale bar = 77  $\mu$ m. 8. *Stichocapsa* (?) sp. (39983/1331) scale bar = 42  $\mu$ m. 9. *Guexella nudata* (Kocher) (40059/1331) scale bar = 51  $\mu$ m. 10. *Guexella nudata* (Kocher) (40030/1331) scale bar = 51  $\mu$ m. 11. Unnamed Nassellaria (40053/1331) scale bar = 51  $\mu$ m. 12. *Eucyrtidiellum ptyctum* (Riedel and Sanfilippo) (39996/1331) scale bar = 51  $\mu$ m. 13. *Eucyrtidiellum ptyctum* (Riedel and Sanfilippo) (40060/1331) scale bar = 40  $\mu$ m. 14. *Eucyrtidiellum* sp. (40037/1331) scale bar = 51  $\mu$ m. 15. *Eucyrtidiellum* sp. (40043/1331) scale bar = 51  $\mu$ m. 16. *Eucyrtidiellum unumaense* (Yao) (42015/1331) scale bar = 56  $\mu$ m.

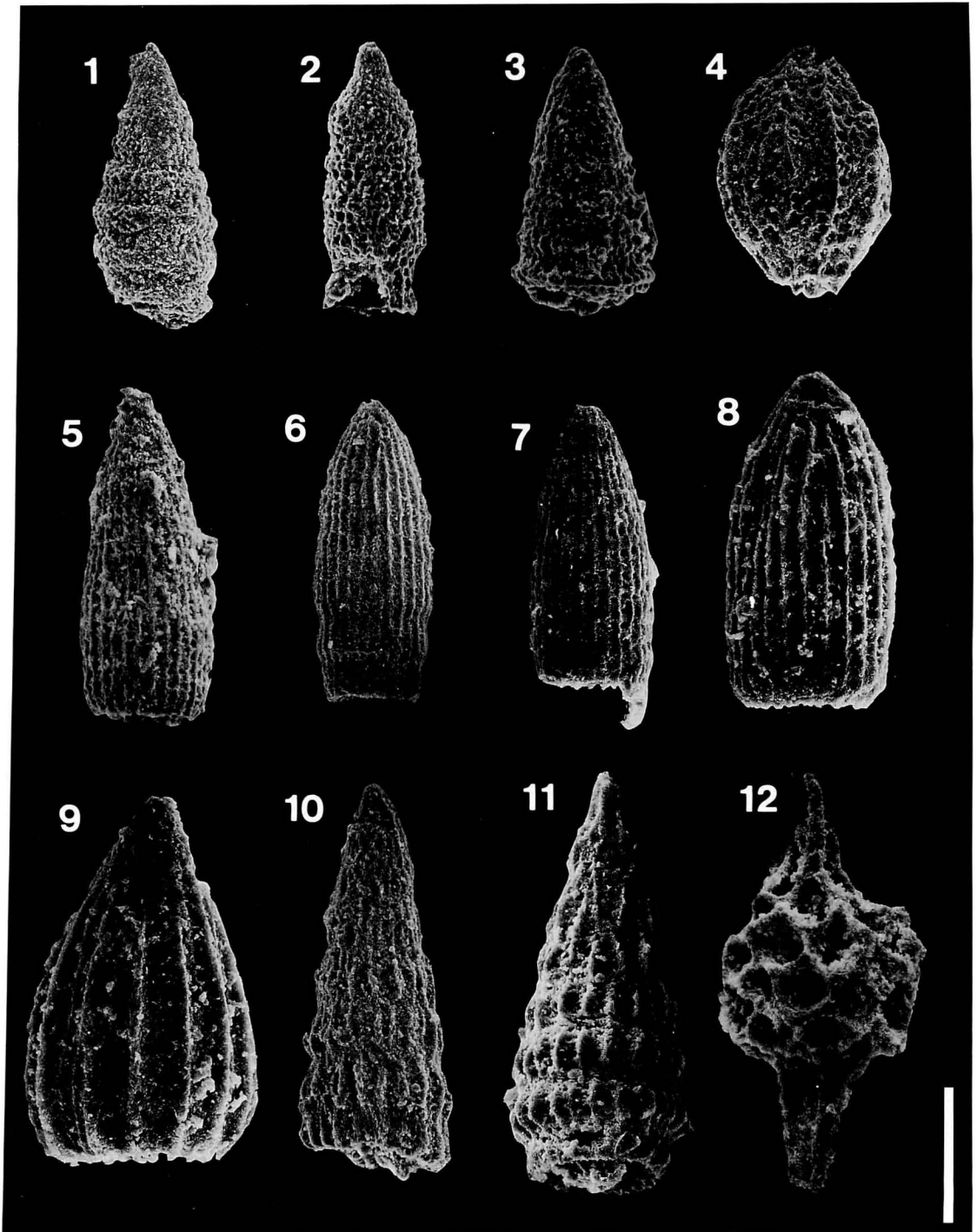


Figure 5. Middle Jurassic Radiolaria from the Nandanhada Range.

1. *Canoptum* sp. (40016/1331) scale bar = 110  $\mu$ m. 2. *Ristola* (?) sp. (40046/1331) scale bar = 77  $\mu$ m. 3. *Dic-tyomitrella* (?) sp. (40044/1331) scale bar = 77  $\mu$ m. 4. *Protunuma* sp. (39848/1320) scale bar = 84  $\mu$ m. 5. *Archaeo-dictyomitra* sp. (39984/1331) scale bar = 84  $\mu$ m. 6. *Archaeodictyomitra* sp. (40040/1331) scale bar = 77  $\mu$ m. 7. *Archaeodictyomitra* sp. (42027/1331) scale bar = 84  $\mu$ m. 8. *Archaeodictyomitra* sp. (42013/1331) scale bar = 56  $\mu$ m. 9. *Thanarla* (?) sp. (42016/1331) scale bar = 56  $\mu$ m. 10. *Hsuum* sp. (40071/1332) scale bar = 77  $\mu$ m. 11. *Hsuum* sp. (42036/1331) scale bar = 84  $\mu$ m. 12. *Pantanellium* sp. (39840/1320) scale bar = 56  $\mu$ m.

## Discussion

### (A) Age of Radiolaria-bearing rocks in the Nadehada Range

The bedded chert sequence in the Nadehada Range (JMP1299, 1368, 1369, 1371, 1429 and 1431, Table 1) yields Triassic Radiolaria. Sample of JMP1369 (Figure 1, Table 1) bears *Eptingium* sp., *Poulpus curvispinus*, *Pseudostylosphaera japonica*, *Triassocampe deweveri*, *Yeharaia annulata*, *Y. elegans*, *Y. japonica*, *Y. sp. A*, etc. These species are characteristic of the *Triassocampe deweveri* Assemblage of Yao (1982), which is assigned to Ladinian (late Ladinian and earlier) based on such coexisting conodonts as *Gladigondolella tethydis* (Huckriede) and *Carinella hungarica* (Kozur and Vegh). *Pseudostylosphaera japonica* was also reported by Lahm (1984) from the upper Anisian to Ladinian section in the Recoaro area, northern Italy. *Poulpus curvispinus* was described from the middle Triassic Buchenstein Formation (probably near the boundary of Anisian and Ladinian) by Dumitrica *et al.* (1980). Sample JMP1368 seems to be approximately of the same age with JMP1369, judging from the occurrence of *Poulpus curvispinus*, *Pseudostylosphaera japonica* and *Triassocampe deweveri*; but JMP1369 yields several species of *Yeharaia*, whereas JMP1368 is characterized by carrying many species of *Pseudostylosphaera*. The above-mentioned evidence indicates that samples JMP1368 and 1369 are middle Triassic in age, probably late Anisian to Ladinian. Triassic age of sample JMP1431 might be indicated by the occurrence of *Triassocampe* sp. (Figures 3-4, 5), although most of Radiolaria from the sample are too poorly preserved to be identified.

Sample JMP1299 yields *Capnodoce* sp., *Capnuhosphaera*(?) sp., *Livarella validus* and *Pseudoheliodiscus* sp. The two genera, *Capnodoce* and *Capnuhosphaera* were first described by De Wever *et al.* (1979) from Carnian to Norian formations in Greece, Sicily and Turkey. Pessagno *et al.* (1979), Blome (1983) and Blome (1984) have studied a late Triassic radiolarian biostratigraphy in western North America, and limited the occurrence of the above-mentioned

two genera within the upper Triassic (from upper Carnian to upper middle Norian). Yoshida (1986) examined a bedded chert sequence of Triassic to Jurassic age in the Mino terrane, Southwest Japan, and subdivided it into seven radiolarian zones. *Livarella validus* is recognized in his *Livarella-Canoptum* Zone, which is supposed to be early to middle Rhaetian in age by comparing with the radiolarian zonation by Yao (1982) and Blome (1984) and the data of Kozur and Mostler (1981). Taking these lines of evidence into account, age of the rock, JMP1299, is correlative with a zone between Carnian to Rhaetian, and probably late Carnian to Norian. Sample JMP1429 also bears *Capnodoce*, and is of late Triassic age.

Jurassic Radiolaria are obtained from a siliceous shale (JMP1320, 1331 and 1332, Table 1) distributed to the west of Shichang (Figure 1). Sample JMP1331 yields well-preserved Radiolaria, such as *Eucyrtidiellum ptyctum*, *E. unumaense*, *Guexella nudata*, *Ristola*(?) sp., *Stichocapsa convexa*, *Tricolocapsa plicarum*, *T. tetragona* and *T. (?) fusiformis*. Baumgartner (1984) reviewed many radiolarian biostratigraphic works, including his own, on the Tethyan middle Jurassic to early Cretaceous. In his range chart *Guexella nudata* and *Eucyrtidiellum ptyctum* occur from late Bathonian to early Oxfordian and middle Callovian to late Tithonian, respectively. Matsuoka and Yao (1986) examined a Jurassic radiolarian biostratigraphy of Southwest Japan, and proposed eight radiolarian zones bounded by biohorizons based on the first (or last) appearance or the first evolutionary appearance of characteristic radiolarian species. Coexistence of *Tricolocapsa tetragona*, *Guexella nudata* and *Eucyrtidiellum ptyctum* is restricted to the middle part of the *Tricolocapsa conexa* Zone assigned to the late Middle Jurassic according to their zonation. Yamamoto *et al.* (1985) examined middle Callovian Radiolaria in a deep-sea core sample recovered from the Atlantic ocean bottom of the Blake Bahama Basin (Leg 76-534A-126-1). The age of this sample was determined by nanofossils and dinoflagellates. The Radiolaria from that core have some genera and

species common to those of sample JMP1331; they are *Canoptum* sp., *Eucyrtidiellum unumaense*, *Guexella nudata*, *Stichocapsa convexa*, *Tricolocapsa plicarum* and *T. cf. ruesti*. All these data suggest that sample JMP1331 is of middle Jurassic age, and probably Bathonian or Callovian. Samples of JMP1320 and 1332 contain Radiolaria common to sample JMP1331 and seem to be middle Jurassic in age, although they lack diagnostic species.

#### (B) *Pantanellium* deficiency problem

Faunal realms and provinces of middle and late Jurassic Radiolaria are discussed by Pessagno and Blome (1986) and Pessagno *et al.* (1986, 1987) in the course of their Jurassic radiolarian biostratigraphic works in western North America and Mexico. They differentiated the radiolarian assemblage of the Tethyan Realm from that of the Boreal Realm; these realms are verified by the realms of calpionellids, ammonites and *Buchia*. Among the Radiolaria which characterize the faunal realms, pantanelliid abundance/diversity conspicuously declines from the Tethyan Realm to the Boreal Realm.

Although about 350 radiolarian individuals were extracted from the siliceous shale of JMP1331 and examined under the SEM, this sample is lacking in pantanelliids completely. From the Nadeh Range, more than 700 middle Jurassic Radiolaria are picked up for the SEM study, and the only one skeleton of *Pantanellium*, shown in Figure 5-12, was extracted from sample JMP1320. Pessagno *et al.* (1987, p. 5–7) recommended to use the radiolarian fauna extracted from limestones, when comparative studies of radiolarian provincialities have been done. It is thought, however, that pantanelliid have tests sufficiently sturdy to be preserved not only in limestones but also in siliceous shales. The radiolarian fauna in sample JMP1331 is so abundant and well-preserved that *Pantanellium*, if present, must be preserved in the rock record. There is little possibility that the pantanelliid tests were selectively removed from the site of sedimentation, because shales in the Mino terrane with similar lithology and sedimen-

tary structure with that in the Nadeh Range terrane have abundant pantanelliid Radiolaria. Thus, the pantanelliid deficiency in the specimens in the Nadeh Range terrane results not from selective destruction of pantanelliid tests but from the provinciality of pantanelliid Radiolaria.

Middle Jurassic siliceous shales widely distributed in the Mino terrane of Japan contain abundant and diversified pantanelliids. According to Hirooka *et al.* (1983), paleomagnetic inclinations indicate that middle Jurassic siliceous shales in the Mino terrane were originally laid down within 12° north or south of the Jurassic paleo-equator. Although we have no paleomagnetic evidence on the Radiolaria-bearing rocks in the Nadeh Range at present, middle Jurassic siliceous shale (JMP1331 etc.) might have been deposited considerably far north from the site of deposition of coeval rocks in the Mino terrane, or the radiolarian fauna in the shales might be strongly controlled by an ancient ocean current which effectively linked the Nadeh Range as far away as to the Brooks Range of Alaska.

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(\* Chinese name)

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中国東北地方, 那丹哈達地域より三疊紀, ジュラ紀放射虫化石の産出: 中国東北部那丹哈達地域の層状チャートより三疊紀放射虫化石, また珪質頁岩よりジュラ紀放射虫化石の産出を記載した。それらは, *Capnodoce traversi*, *Eucyrtidiellum ptyctum*, *E. unumaense*, *Guezella nudata*, *Livarella validus*, *Parahsuum*(?) sp. A, *Pentactinocarpus* sp. A, *Poulpus curvispinus*, *Pseudostylosphaera japonica*, *P.* cf. *hellenica*, *P.* cf. *tenuis*, *P.* sp. A, *P.* sp. B, *P.* sp. C, *P.* sp. D, *P.* sp. E, *Stichocapsa convexa*, *Triassocampe deweveri*, *T.* sp. A, *Tricolocapsa*(?) *fusiformis*, *T. plicarum*, *T. tetragona*, *T.* cf. *ruesti*, *Yeharaia annulata*, *Y. japonica*, *Y.* sp. A. である。層状チャートと珪質頁岩の時代は, それぞれ, 三疊紀中期および後期 (late Anisian から Ladinian および late Carnian から Norian), ジュラ紀中期 (Bathonian から Callovian) である。小嶋 智・水谷伸治郎

## 845. *ATTENUATELLA* (BRACHIOPODA) FROM THE UPPER PERMIAN OF NORTHEAST JAPAN AND ITS BIPOLAR DISTRIBUTION\*

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**Abstract.** *Attenuatella bandoi*, sp. nov. is described from the Upper Permian (Djulfian beds) of the lower Toyoma Formation of Ishihama, Utatsu district, southern Kitakami Mountains, northeast Japan. The genus *Attenuatella* is distributed in Middle Carboniferous (Moscovian) to Upper Permian (Dorashamian) strata of Spitzbergen, Soviet Arctic, Siberia, Urals, northern Yukon, west Texas, northern Mexico, eastern Australia, New Zealand, New Caledonia, northern Thailand, northern China and northeast Japan, mostly in the Lower and Middle Permian of the Boreal and Gondwana Provinces.

### Introduction

*Attenuatella* is a small, very distinctive spiriferid belonging to the family Ambocoeliidae George, 1931. This genus was established by Stehli in 1954, with *Attenuatella texana* Stehli, 1954 from the Bone Spring Formation of the Sierra Diablo Mountains, west Texas as type species. At that time Stehli assigned *Crurithyrus attenuata* Cloud, 1944 from the Middle Permian of Coahuila, northern Mexico to the new genus. Since then it has been described from Middle Carboniferous to Upper Permian strata of Russia (Ustritsky and Tschernjak, 1963; Zavadowsky, 1968; Zavadowsky and Stepanov, 1970; Solomina, 1978; Kalashnikov, 1980; Kalashnikov and Ustritsky, 1981; Abramov and Grigorjeva, 1983), North America (Bamber and Waterhouse, 1971; Cooper and Grant, 1976), Australia (Waterhouse, 1967; Armstrong, 1968; Armstrong and Brown, 1968; Armstrong and Telford, 1970; Waterhouse *et al.*, 1983), New Zealand (Waterhouse, 1964, 1968; Landis and Waterhouse, 1966), New Caledonia (Landis and Waterhouse, 1966), Thailand (Waterhouse, 1983) and China (Lee *et al.*, 1980, 1982). In addition, some Russian species have been transferred from

other genera to *Attenuatella* (see Armstrong, 1968, p. 786).

The present paper indicates the first occurrence of *Attenuatella* in Japan. The specimens described here as *Attenuatella bandoi*, sp. nov. were collected by myself and Dr. M. Ehiro from

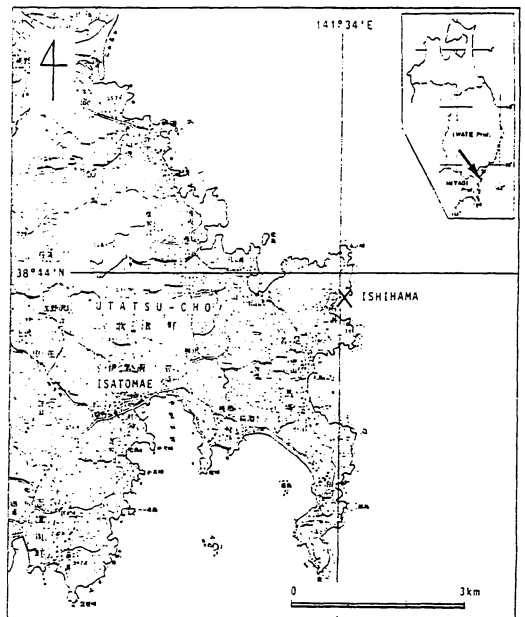


Figure 1. Map showing the fossil locality (using the topographical map of "Tsuya" scale 1:50,000 published by Geographical Survey Institute of Japan).

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shale or calcareous shale in the lower part of the lower Toyoma Formation (lower conglomeratic beds of the Suenosaki Formation of Ehiro and Bando, 1985) in the eastern coast of Ishihama, Utsu district, southern Kitakami Mountains, northeast Japan (Figure 1). Age of the fossiliferous shales of Ishihama is estimated to be early Djulfian on the basis of some ammonoids, *Araxoceras* and *Prototoceras* (Ehiro and Bando, 1985).

The Upper Permian Toyoma Formation is characterized by its fauna bearing several Tethyan elements, such as *Colaniella*, *Palaeofusulina*, *Tschernyshewia*, *Oldhamina* and *Araxoceras*, and associated with only a few Boreal elements, *Megousia* (Murata and Bando, 1975; Tazawa, 1975, 1982; Ishii *et al.*, 1975; Ehiro and Bando, 1985). *Attenuatella* is considered to be a cool or cold-water element, judging from the bipolar distribution, *i.e.*, the Boreal and Gondwana Provinces (Figure 2, Table 1). The nature of the Toyoma fauna suggests that the sea covering the southern Kitakami region in late Permian time occupied the boundary area between the Boreal

and Tethyan Provinces.

### Distribution of *Attenuatella*

The genus *Attenuatella* is distributed in the Middle Carboniferous (Moscovian) to the Upper Permian (Dorashamian) of Spitzbergen, Soviet Arctic (Novaya Zemlya, Taimyr), Siberia (Verkhoyansk, Kolyma-Omolon), Urals, northern Yukon, west Texas, northern Mexico, eastern Australia, New Zealand, New Caledonia, northern Thailand, north and northeast China (Nei Mongol, Jilin, Heilongjiang) and northeast Japan (Figure 2). The following 23 species are known at present, and most of them occur in the Lower and Middle Permian of the Boreal and Gondwana Regions (Table 1):

*Attenuatella acutirostrus* (Krotov, 1885), from the Lower Permian (Artinskian beds) of the Ural Mountains, U.S.S.R. (Krotov, 1885).

*Attenuatella stringocephaloides* (Tschernyschew and Licharew, 1939), from the Lower Permian (Spirifer Limestone and Brachiopod Chert) of Spitzbergen; Lower Permian (Sokolovskaya Formation) of Novaya Zemlya, U.S.S.R.;

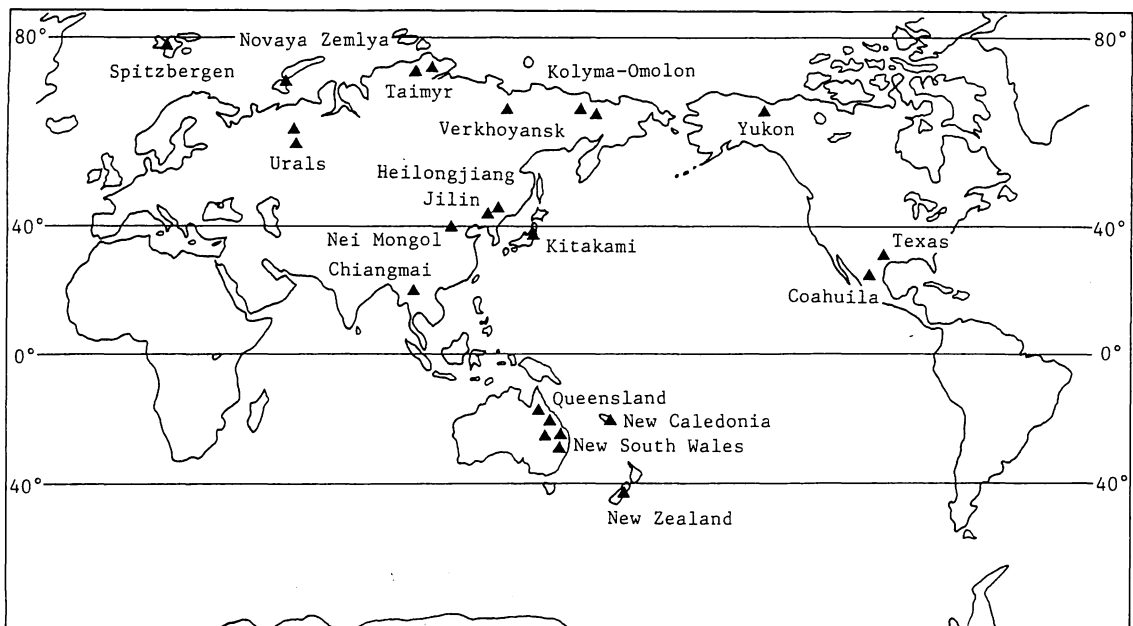


Figure 2. Geographical distribution of *Attenuatella* (modified from Armstrong, 1968 to incorporate the data of Siberia, northern Canada and East Asia).

Lower to Middle Permian (Birrangsky Horizon) of Taimyr (Tschernyschew and Licharew in Licharew and Einor, 1939; Ustritsky and Tschernjak, 1963; Kalashnikov and Ustritsky, 1981).

*Attenuatella attenuata* (Cloud, 1944), from the Middle Permian (*Waagenoceras* Zone or *Polydixodina* Zone) of Coahuila, northern Mexico (Cloud, 1944; Cooper and Grant, 1976).

*Attenuatella texana* Stehli, 1954, from the Lower Permian (Bone Spring Formation) of the Sierra Diablo Mountains, west Texas, U.S.A. (Stehli, 1954; Cooper and Grant, 1976).

*Attenuatella taimyrica* Tschernjak, 1963, from the Middle Permian (Baikursky Horizon) of Taimyr, U.S.S.R. (Ustritsky and Tschernjak, 1963).

*Attenuatella incurvata* Waterhouse, 1964, from the Middle Permian (Arthurton and Kuriwao Groups) of New Zealand; Middle Permian (Chhidruan beds) of New Caledonia; Middle Permian of Heilongjiang, northeast China (Waterhouse, 1964; Landis and Waterhouse, 1966; Lee *et al.*, 1980).

*Attenuatella* sp. cf. *A. incurvata* Waterhouse, 1964, from the Middle Permian (Barfield Formation) of Queensland, eastern Australia (Armstrong, 1968).

*Attenuatella multispinosa* Waterhouse, 1967, from the Middle Permian (Gilgurry Mudstone) of New South Wales, eastern Australia (Waterhouse, 1967; Armstrong and Telford, 1970).

*Attenuatella australis* Armstrong and Brown, 1968, from the Lower Permian (Gigoomgan

Table 1. Stratigraphical and geographical distributions of *Attenuatella*.

Species	Carbon.		Permian			R e g i o n
	M	U	L	M	U	
<i>A. acutirostrus</i>			+			U.S.S.R. (Ural Mts.)
<i>A. stringocephaloides</i>			+	+		U.S.S.R. (Novaya Zemlya, Taimyr), Spitzbergen
<i>A. attenuata</i>				+		Mexico (Coahuila)
<i>A. texana</i>			+			U.S.A. (Texas)
<i>A. taimyrica</i>				+		U.S.S.R. (Taimyr)
<i>A. incurvata</i>				+		New Zealand, New Caledonia, China (Heilongjiang)
<i>A. cf. incurvata</i>				+		Australia (Queensland)
<i>A. multispinosa</i>				+		Australia (New South Wales)
<i>A. australis</i>			+			Australia (Queensland)
<i>A. cf. australis</i>			+			Australia (New South Wales)
<i>A. convexa</i>			+			Australia (Queensland, New South Wales)
<i>A. sp. A</i> (Armstrong, 1968)				+		Australia (Queensland)
<i>A. sp.</i> (Armstrong, 1968)				+		Australia (Queensland)
<i>A. altilis</i>			+			New Zealand
<i>A. omolonensis</i>	+	+	+			U.S.S.R. (Verkhoyansk Mts., Kolyma-Omolon Mts.)
<i>A. cf. omolonensis</i>			+			Canada (Yukon Territory)
<i>A. dorogoyi</i>				+		U.S.S.R. (Omolon River Basin)
<i>A. sp.</i> (Bamber & Waterhouse, 1971)			+			Canada (Yukon Territory)
<i>A. uralica</i>	+					U.S.S.R. (Ural Mts.)
<i>A. paraincurvata</i>				+		China (Jilin, Nei Mongol)
<i>A. xiujumqinqiensis</i>				+		China (Nei Mongol)
<i>A. piyasini</i>					+	Thailand (Chiangmai)
<i>A. bandoi</i>					+	Japan (Kitakami Mts.)

Limestone) of Queensland, eastern Australia (Armstrong and Brown, 1968).

*Attenuatella* sp. cf. *A. australis* Armstrong and Brown, 1968, from the Lower Permian (Farley Formation) of New South Wales, eastern Australia (Armstrong and Telford, 1970).

*Attenuatella convexa* Armstrong, 1968, from the Lower Permian (Tiverton Formation) of Queensland, eastern Australia; Lower Permian (Farley Formation) of New South Wales, eastern Australia (Armstrong, 1968; Armstrong and Telford, 1970; Waterhouse *et al.*, 1983).

*Attenuatella* sp. A, from the Middle Permian of Queensland, eastern Australia (Armstrong, 1968).

*Attenuatella* sp., from the Middle Permian (Flat Top Formation) of Queensland, eastern Australia (Armstrong, 1968).

*Attenuatella altilis* Waterhouse, 1968, from the Lower Permian (Wesney Siltstone and Takitimu Group) of New Zealand (Landis and Waterhouse, 1966; Waterhouse, 1968).

*Attenuatella omolonensis* Zavodowsky, 1968, from the Middle and Upper Carboniferous (Siederskaya and Khaldanskaya Formations) of the northern Verkhoysk Mountains, U.S.S.R.; Upper Carboniferous to Lower Permian of the Kolyma-Omolon Massif, U.S.S.R. (Zavodowsky, 1968; Zavodowsky and Stepanov, 1970; Solomina, 1978; Abramov and Grigorjeva, 1983).

*Attenuatella* sp. cf. *A. omolonensis* Zavodowsky, 1968, from the Lower Permian (*Attenuatella-Tomiopsis* Zone) of northern Yukon Territory, Canada (Bamber and Waterhouse, 1971).

*Attenuatella dorogoyi* Zavodowsky, 1970, from the Middle Permian (Omolon Horizon) of the Omolon River Basin, U.S.S.R. (Zavodowsky and Stepanov, 1970).

*Attenuatella* sp., from the Lower Permian (*Attenuatella* Zone) of northern Yukon Territory, Canada (Bamber and Waterhouse, 1971).

*Attenuatella uralica* Kalashnikov, 1980, from the Middle Carboniferous (Moscovian beds) of the Ural Mountains, U.S.S.R. (Kalashnikov, 1980).

*Attenuatella paraincurvata* Lee and Su, 1980,

from the Middle Permian (Wujiatun Formation) of Jilin, northeast China; Middle Permian of Nei Mongol, north China (Lee *et al.*, 1980).

*Attenuatella xiujumqinqiensis* Lee, Gu and Li, 1982, from the Middle Permian (Jisu Formation) of Nei Mongol, north China (Lee *et al.*, 1982).

*Attenuatella piyasini* Waterhouse, 1983, from the Upper Permian (Huai Tak Formation) of Chiangmai, northern Thailand (Waterhouse, 1983).

*Attenuatella bandoi* Tazawa, sp. nov., from the Upper Permian (lower Toyoma Formation) of the southern Kitakami Mountains, northeast Japan.

### Systematic descriptions

Order Spiriferida Waagen, 1883

Suborder Delthyrididina Ivanova, 1972

Superfamily Martiniacea Waagen, 1883

Family Ambocoeliidae George, 1931

Genus *Attenuatella* Stehli, 1954

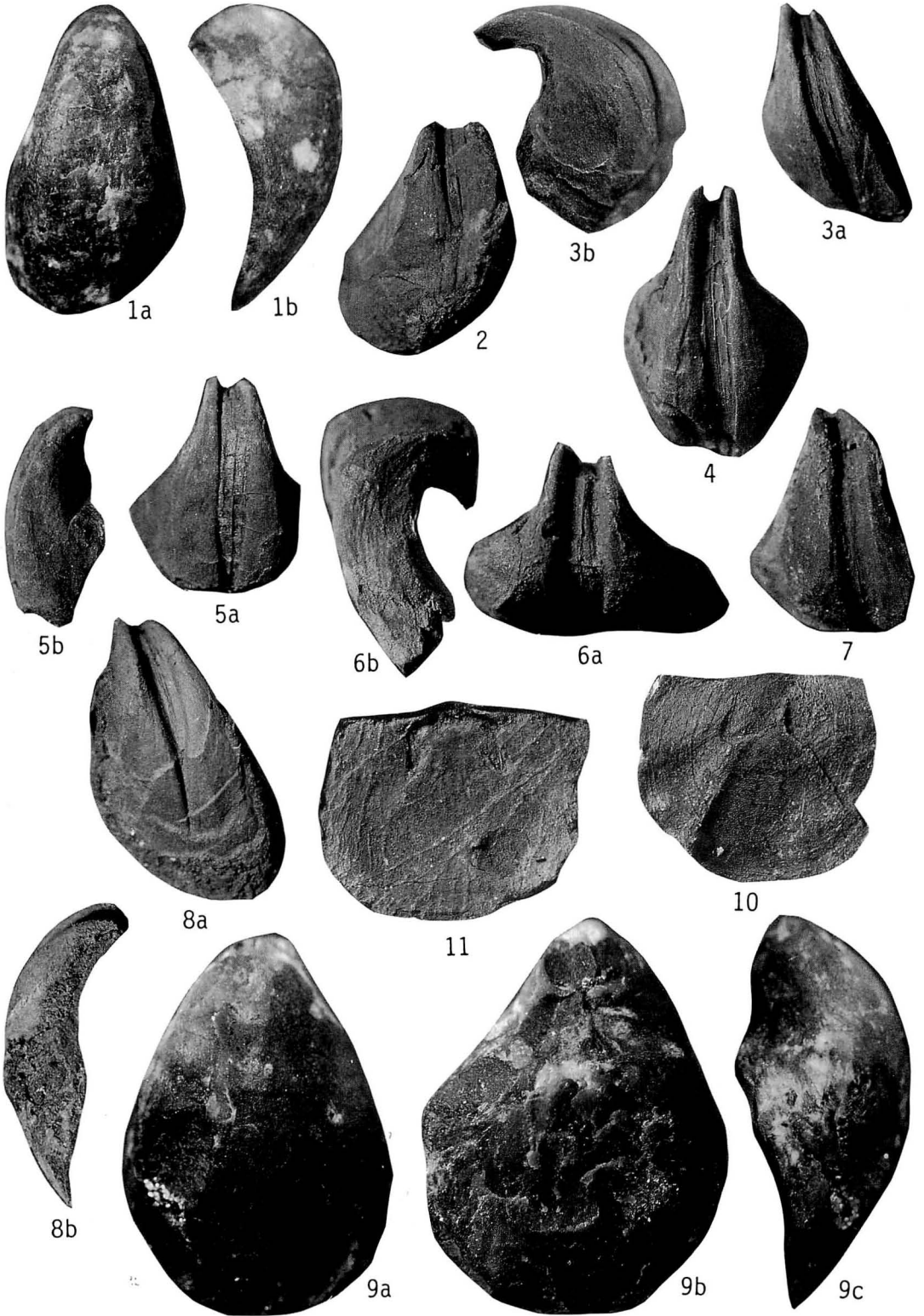
*Attenuatella* Stehli, 1954, p. 343; Waterhouse, 1964, p. 108; Armstrong, 1968, p. 786, Cooper and Grant, 1976, p. 2131.

non *Attenuatella* Winkler Prins, 1970, p. 538; Jin *et al.*, 1979, p. 120.

*Type species*:—*Attenuatella texana* Stehli, 1954, p. 343, pl. 25, figs. 31–33.

*Diagnosis*:—Small to medium, nearly planoconvex and narrowly elongate Ambocoeliidae. Ventral umbo greatly attenuated and strongly incurved. External surface of both valves ornamented by numerous, very fine spine bases. Pedicle valve interior with a long median ridge, on which adductors and diductors attached. Brachial valve having a large, tuberculate cardinal process and massive crura; spiralia absent.

*Remarks*:—The description of the type species by Stehli was based on a single pedicle valve specimen, so that the external and internal features of the brachial valve have long been unknown until the redescription by Cooper and Grant (1976, p. 2132). The dorsal internal structures of *Attenuatella* species were described



in detail by Waterhouse (1964) and Armstrong (1968), using materials of New Zealand and Australia. The peculiar, loop-like brachial skeleton was reconstructed and illustrated by Armstrong (1968, text-fig. 2).

Armstrong (1968, p. 786–788, text-fig. 3) summarized the stratigraphical and geographical distributions of *Attenuatella*, and gave the range of the genus as lower Artinskian (Aktastinian) to Kazanian or Wordian. But afterwards, its Middle Carboniferous and Upper Permian occurrences were disclosed: *A. uralica* from the Moscovian beds of the Urals (Kalashnikov, 1980), and *A. piyasini* from the lower Dorashamian beds of northern Thailand (Waterhouse, 1983).

Both of the species, *A. aff. frechi* (Schellwien) from the Upper Carboniferous of northeast Spain (Winkler Prins, 1970) and *A. bisulcata* (Ustritsky) from the Lower Permian of northeast China (Jin *et al.*, 1979) cannot be assigned to *Attenuatella* because of their massive ventral umbo.

*Attenuatella bandoi*, sp. nov.

Figures 3-1–11, 4

**Material:**—Forty-six specimens, from the lower part of the lower Toyoma Formation in the eastern coast of Ishihama, Utatsu-cho, Motoyoshi-gun, Miyagi Prefecture, northeastern Honshu: (1) two conjoined valves, NU-B 1 (holotype, Figures 3-9a–c), 2; (2) one pedicle valve, NU-B 3; (3) external and internal moulds of eight pedicle valves, NU-B 4–11; (4) external moulds of five pedicle valves, NU-B 11–16; (5) internal mould of a pedicle valve with some shell remains, NU-B 17; (6) internal moulds of twenty-seven

pedicle valves, NU-B 18–44; (7) external mould of a brachial valve, NU-B 45; (8) internal mould of a brachial valve, NU-B 46.

All the specimens are stored in the Department of Earth Sciences, Faculty of General Education, Niigata University.

**Diagnosis:**—Large, elongate *Attenuatella*, lacking ventral sulcus and dorsal fold. Micro-ornament of numerous spine bases which occurring with a density of 8–9 per mm on pedicle valve, 9–10 per mm on brachial valve.

**Description:**—Shell of large size for genus, elongate oval in outline and plano-convex in profile; greatest width at slightly anterior to midvalve; length of pedicle valve 16 mm, width of pedicle valve 12 mm, hinge width 11 mm, length of brachial valve 10 mm, height of shell 8 mm in the holotype.

Pedicle valve strongly inflated, with a narrow and incurved umbo; lateral slopes steep; sulcus absent. Delthyrium open and high; width of bottom 2.7 mm, height 3.8 mm in the holotype. External surface of pedicle valve ornamented by numerous, very fine spine bases, which occurring with a density of 8–9 per mm at about midvalve (Figure 4). Brachial valve semicircular in outline and almost flat, but slightly swollen in umbonal region. Surface ornament consisting of concentric, fine growth lines and numerous spine bases; the latter occurring with a density of 9–10 per mm at about midvalve.

Internally, pedicle valve having a long median ridge, on which muscle scars sited. Median ridge extending over posterior three-quarters of shell length, separated by a narrow median groove through its length and tapering towards anterior portion; maximum width 1.2 mm in an average-sized specimen (NU-B 10, Figures 3a, b). Teeth

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← **Figure 3.** *Attenuatella bandoi* Tazawa, sp. nov., from the lower part of the lower Toyoma Formation of Ishihama, southern Kitakami Mountains, northeast Japan. (All figures are x4). 1a, b: ventral and lateral views of pedicle valve, NU-B 3; 2: ventral view of internal mould of pedicle valve, NU-B 20; 3a, b: ventral and lateral views of internal mould of pedicle valve, NU-B 10; 4: ventral view of internal mould of pedicle valve, NU-B 19; 5a, b: ventral and lateral views of internal mould of pedicle valve, NU-B 31; 6a, b: ventral and lateral views of internal mould of pedicle valve, NU-B 6; 7: ventral view of internal mould of pedicle valve, NU-B 32; 8a, b: ventral and lateral views of internal mould of pedicle valve, NU-B 39; 9a, b, c: ventral, dorsal and lateral views of conjoined valve, NU-B 1 (holotype); 10: dorsal view of external mould of brachial valve, NU-B 45; 11: dorsal view of internal mould of brachial valve, NU-B 46.

not observed. Brachial valve having a large, tuberculate cardinal process and a pair of prominent, wide sockets which bounded by robust inner socket ridges. Crural bases fused with inner socket ridges; the former being sessile and strongly developed. Both of brachidia and muscle scars not observed.

*Remarks:*—*Attenuatella bandoi*, sp. nov. may be the largest one among known species of the genus. This species is named in honour of the late Dr. Yuji Bando, who contributed to the knowledges on Permian and Triassic ammonoids of Japan, and who first described some Upper Permian ammonoids from the present locality of Ishihama. In size and outline, the Kitakami species is close to *A. incurvata* Waterhouse, originally described from the Middle Permian (Kazanian beds) of New Zealand. But this new species is distinguished from *incurvata* by its slightly larger and more elongate shell and more sparse spine bases (10–14 per mm in *A. incurvata*, after Waterhouse, 1967, p. 171).

*A. altilis* Waterhouse from the Lower Permian (upper Sakmarian to lower Artinskian beds) of New Zealand differs from the present species in its smaller shell, and in having a low fold and costae on brachial valve.

An Upper Permian form, *A. piyasini* Waterhouse from the Huai Tak Formation of northern Thailand is readily distinguished from the present species by its much smaller and less elongate

shell.

The type species, *A. texana* Stehli is characterized by its small size and elongate outline, and is clearly distinguished from the Kitakami species.

#### Acknowledgments

I thank Dr. M. Ehiro, Department of Earth Science, College of General Education, Tohoku University, for providing specimens he collected and information on stratigraphic data of the fossil locality; Prof. Y. Hasegawa, Dr. I. Niikawa and Dr. A. Matsuoka, Department of Earth Sciences, Faculty of General Education, Niigata University, for critical reading of the manuscript.

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Figure 4. Spine bases over the external surface of pedicle valve, NU-B 14 (x10).



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東北日本の上部ペルム系産腕足類 *Attenuatella* および同属の両極性分布: 南部北上山地, 宮城県本吉郡歌津町石浜東方海岸に露出する上部ペルム系 (ズルファー階) 下部登米層下部の頁岩と石灰質頁岩から, 我が国では初めての腕足類 *Attenuatella* が採集された。これを *Attenuatella bandoi* と命名し, 記載する。*Attenuatella* はスピッツベルゲン・ソ連邦北極地方・シベリア・ウラル山脈・ユーコン北部・テキサス西部・メキシコ北部・オーストラリア東部・ニュージーランド・ニューカレドニア・タイ北部・中国北部および東北日本の中部石炭系 (モスコ階) から上部ペルム系 (ドラシャム階) に分布するが, 特にボレアル地域とゴンドワナ地域の下部~中部ペルム系に集中している。

田沢純一

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## 846. TAPHONOMY OF AMMONITES FROM THE CRETACEOUS YEZO GROUP IN THE TAPPU AREA, NORTHWESTERN HOKKAIDO, JAPAN\*

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**Abstract.** Taphonomy of ammonites in the Cretaceous Yezo Group has been discussed on the basis of field and laboratory observations of many specimens from the Tappu area, northwestern Hokkaido. The Cretaceous deposits in the study area are represented mainly by monotonous, off-shore muddy sequence attaining several thousand meters thick, and yield numerous ammonites and other molluscan fossils at various horizons. Ammonite fossils are preserved in both calcareous concretions and surrounding mudstone. Most specimens from a well-laminated mudstone of the lower stratigraphic levels [lower to middle Cenomanian] are large-sized, and have been suffered compaction and dissolution, even they are preserved in calcareous concretions. On the contrary, ammonites including immatures, are quite well preserved in spherical or mushroom-shaped calcareous concretions, embedded in intensely bioturbated mudstone of the upper stratigraphic levels [middle Turonian to upper Santonian]. Such concretions might have consolidated in earlier stage than those of the lower stratigraphic levels before ammonite shells suffered diagenetic damage. Intermediate preservational features are observable in the uppermost Cenomanian to the lower Turonian.

Large ammonites, occurring solitarily in mudstone are generally much poorly preserved than the moderate-sized ones. Several interesting mode of preservation: for example, “half-ammonite” and “ventral-tire”, are observable at various horizons in the area surveyed. Because of preservational uniformity of “half-ammonites” belonging various taxa and occurring from various horizons, the mode of preservation may be originated from partial sedimentary filling in phragmocone, prescribed by position of septal neck, and diagenetic compaction and shell-dissolution after complete burial.

Ammonite shells and plant remains were drifted similarly and accumulated at the same places as patches on the sea floor. In some cases, they are concentrated in lower umbilical void of horizontally laid large ammonite shell. Large ammonite shells might probably trigger off such accumulations, acting as a “trap” on the sea floor. Some spatangoids, preserved regularly in the umbilical void of large ammonite, might assemble to eat organic matter accumulated there.

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### Introduction

Post-Aptian marine Cretaceous deposits are widely distributed in the central zone of Hokkaido and Sakhalin (Figure 1). Those in Hokkaido have long been lithostratigraphically subdivided into the Lower, Middle, Upper Yezo Groups and Hakobuchi Group in upward sequence, but they are now summarized as the Yezo Group or Yezo Supergroup (Okada, 1979, 1983). The

Yezo Group and contemporaneous deposits in Sakhalin yield numerous well-preserved ammonites at various horizons. These ammonite fossils have been studied from the various points of view since last century (*e.g.*, Yokoyama, 1890, Jimbo, 1892; see Matsumoto, 1975). Ammonite and inoceramid biostratigraphy of the group has already been well established (Matsumoto, 1942, 1943, 1959, 1977 *etc.*), and more than two hundred ammonite species have hitherto described from the Yezo Group during this century. In addition to the biostratigraphic and taxonomic

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\*Received September 9, 1987.

approach, paleoecological studies of ammonites were made recently (e.g., Tanabe, 1979; Tanabe and Ohtsuka, 1985).

In contrast to these works, little has been done for the detailed analysis on the mode of ammonite occurrence and preservation. Extinct animals without any allied recent animals such as ammonites should be at first investigated on their mode of occurrence. It may involve many informations on their mode of life and depositional environments.

During the course of paleontological studies of Cretaceous ammonites from Hokkaido, I have recognized interesting mode of occurrence and preservation in many specimens from the selected areas. In this paper, I describe the mode of occurrence and preservation of several ammonite

specimens from the Cretaceous deposits in Hokkaido and Sakhalin as the basis for further research on the ammonite taphonomy and paleoecology. I also discuss the probable taphonomic history of ammonites from the Yezo Group on the basis of the observed results. The material utilized is UMUT. (University Museum, University of Tokyo) and KSG. (Geological Department, Kochi University) specimens collected by myself and other paleontologists since last century.

### Geological setting

The Cretaceous System in the meridional zone of Hokkaido and Sakhalin (Figure 1) is a thick clastic sequence attaining several thousand meters thick. Off-shore facies characterized by thick, monotonous, dark-colored mudstone predominates in central region of the Cretaceous outcropping zone; e.g. Abeshinai, Tappu and Oyubari areas (Figure 1). Similar mudstone facies extends laterally, particularly in N-S direction. The sediments tend to coarse in grain and thinner toward the western marginal area (e.g., Ikushumbetsu and Bibai areas; Figure 1).

In this paper, the Cretaceous succession in the Tappu (=Obira) area where the more or less off-shore mudstone facies is well-developed, is discussed (Figure 1). Figure 2 shows a generalized columnar section of the Cretaceous in the area. It attains more than 6000 m thick, and lithostratigraphically divided into the Middle and Upper Yezo Groups which correspond to the lower Cenomanian to upper Santonian. Both groups consist mainly of thick, dark-colored mudstone, except in the lowest part of the Middle Yezo. Such mudstone intercalates turbiditic sandstone beds, slump deposits, and acidic tuff beds at several stratigraphic levels.

Although monotonous mudstone predominates throughout the Yezo Group, detailed sedimentary features of the mudstone are fairly variable at different horizons (Maeda, in preparation). Roughly speaking, the following four mudstone units can be recognized in upward sequence (Figure 2).

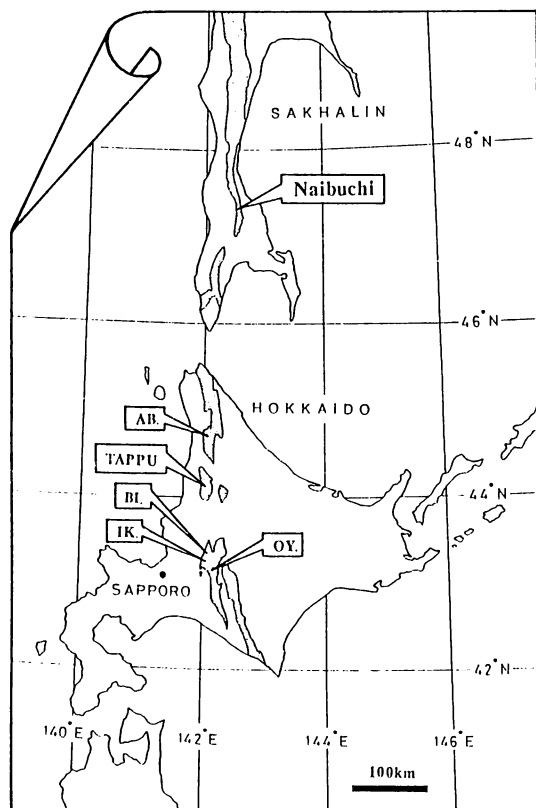
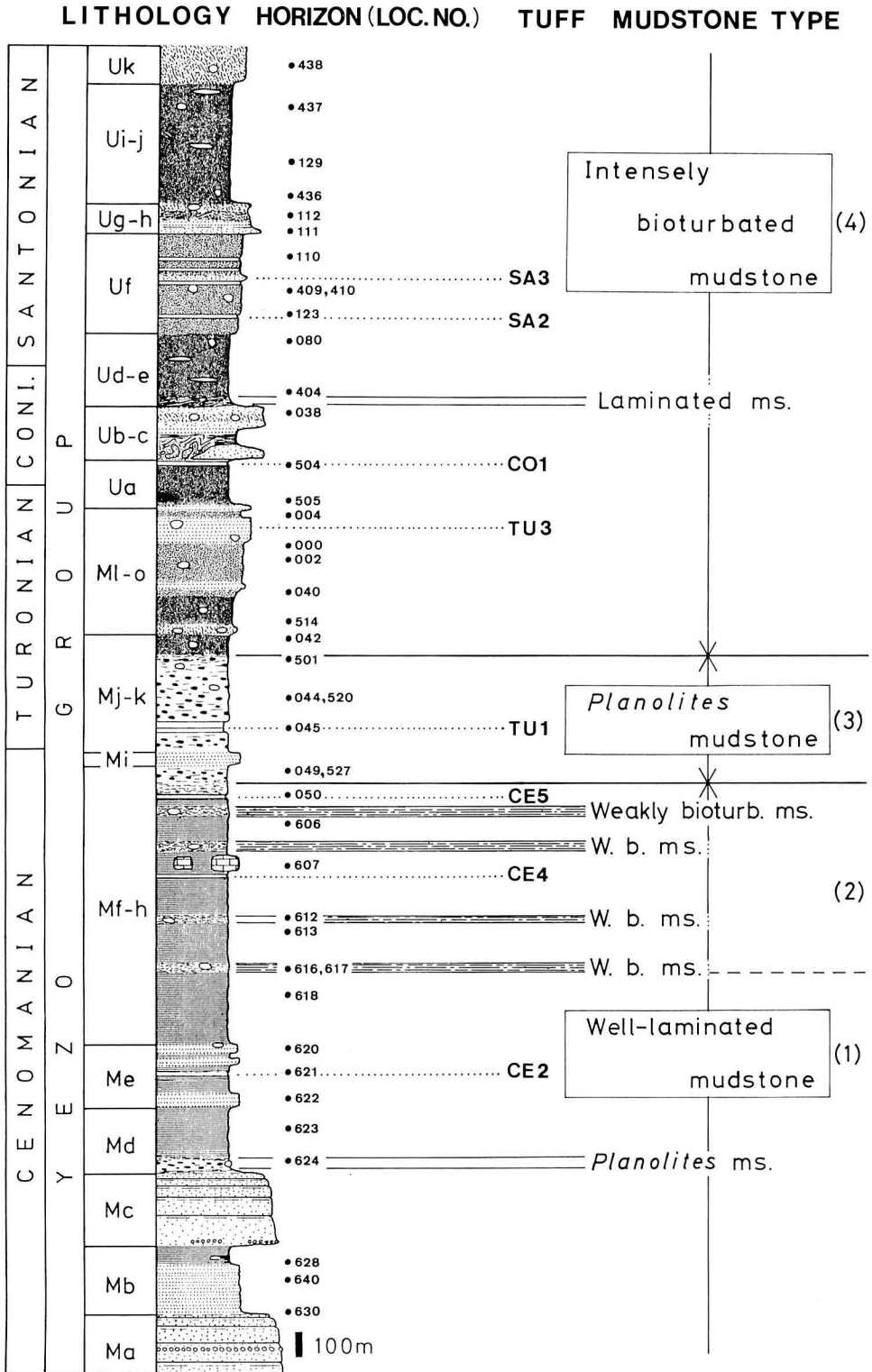


Figure 1. Distribution of the Cretaceous deposits in the meridional zone of Hokkaido and Sakhalin. AB: Abeshinai; BI: Bibai; IK: Ikushumbetsu; OY: Oyubari (modified from Matsumoto, 1954).



**Figure 2.** Generalized columnar section of the Cretaceous System in the Tappu area. Exact locations should be made reference to Maeda (in preparation).

- (1) Well-laminated mudstone unit [lower Cenomanian].
- (2) Well-laminated mudstone unit with intercalations of weakly-bioturbated mudstone [middle to upper Cenomanian].
- (3) *Planolites* mudstone unit [uppermost Cenomanian to lower Turonian].
- (4) Intensely bioturbated mudstone unit [middle Turonian to upper Santonian].

The upper part of the Yezo Group is generally much intensely bioturbated than the lower part. The same evidence is also confirmed in other areas of Hokkaido (e.g. Bibai area: Maeda, 1986; Figure 1). Muddy deposits contain calcareous concretions of various size and shape. Numerous ammonites occur from both calcareous concretions and surrounding mudstone.

#### Mode of ammonite occurrence and preservation in calcareous concretion

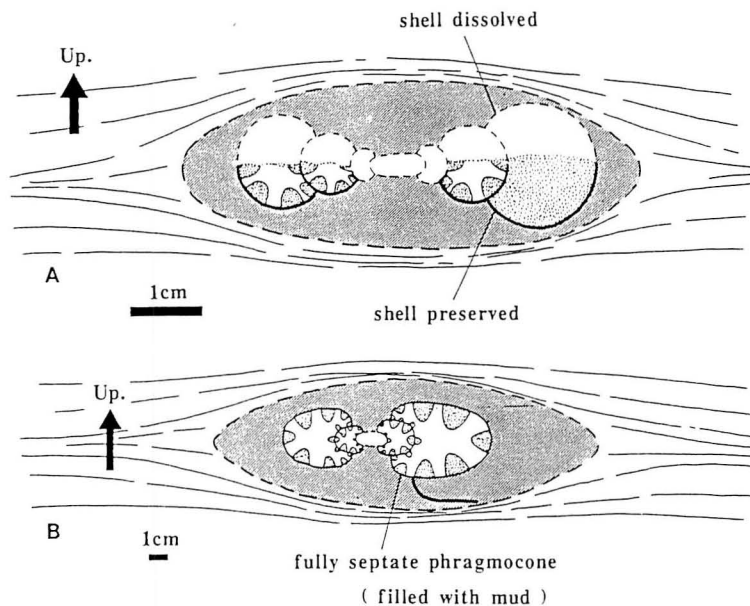
Ammonite fossils from the Cretaceous Yezo Group in Hokkaido are mostly found in calcareous concretions embedded in muddy deposits. In the Tappu area, their detailed mode of occurrence is, however, fairly variable at different stratigraphic horizons. Detailed observations for the moderate-sized ammonites (ca. 2 to 15 cm in diameter) in calcareous concretions are summarized as below.

**Occurrence in the Cenomanian:** Dark-gray (N3) to medium gray (N4), well-laminated mudstone predominates in the Cenomanian (Mb to the middle part of Mf-h in Figure 2). *Desmoceras* (*Pseudouhligella*) *japonicum*, *Anagaudryceras sacya* and *Calycoceras orientale* are dominant in the sequence. They are found individually in flat, lenticular-shaped calcareous concretions ranging from 5 to 30 cm in diameter, where size and shape are strongly controlled by the ammonites contained. Most specimens contained in the calcareous concretions are mature or in middle-growth stage, and lay horizontally. Small immature shells, less than 1 cm in diameter, are scarcely found. Figure 3 shows a typical example of such preservation of ammonite in a lenticular calcareous concretion embedded in well-lami-

nated mudstone at Loc. TP-613 (Mf-h member; middle Cenomanian; see also Figure 2). The shell of *Anagaudryceras sacya* is only preserved its lower half, and the upper flank and the inner whorls have been dissolved away (Figure 3A). Figure 3B shows another example of the similar ammonite preservation in a calcareous concretion. In the case, the fully septate phragmocone of *Desmoceras* (*Pseudouhligella*) *japonicum* is preserved in its original shell-geometry, but its inner whorl, siphuncle and original shell materials have been dissolved away. As described above, ammonites in well-laminated mudstone of the lower stratigraphic levels are generally poorly preserved. Many of them are collapsed or have suffered shell dissolution during diagenetic process, even in case found in the calcareous concretions. Plant remains are usually few in the ammonite-bearing calcareous nodules, although large drifted wood particles are occasionally seen. Ammonites are rare in the surrounding mudstone.

It is noticeable that the mode of preservation of ammonite within the calcareous nodules is variable within the Cenomanian mudstone sequence. Figure 4 is a diagrammatic sketch showing the mode of preservation in weakly bioturbated mudstone at Loc. TP-617 (Mf-h member; middle Cenomanian; Figure 2). In this case, both living chamber and septate phragmocone of an adult shell of *Desmoceras* (*Pseudouhligella*) *japonicum* has been collapsed horizontally during diagenesis, but, shell wall and septa have still remained except for the inner whorls. In general, ammonite specimens found in calcareous concretions embedded in weakly bioturbated mudstone occur more abundantly and more well preserved than those in well-laminated mudstone.

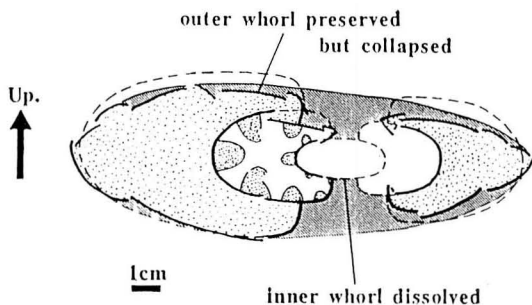
**Occurrence in the uppermost Cenomanian to the lower Turonian:** The uppermost part of the member Mf-h and the member Mj-k [uppermost Cenomanian to lower Turonian] exhibit intermediate features between the lower members and upper members for the mode of fossil preservation. Mudstone in these strata is occasionally moderately or weakly bioturbated, and in such horizons abundant *Planolites* burrows are ob-



**Figure 3.** Modes of ammonite occurrence and preservation in lenticular calcareous concretions embedded in well-laminated mudstone at Loc. TP-613, Mf-h member [middle Cenomanian] in the Tappu area. Thick line: preserved shell; thin, dashed line: dissolved shell; shadow: calcareous concretion (same as in Figure 4).

A: *Anagaudryceras sacya*.

B: *Desmoceras (Pseudouhligella) japonicum*.

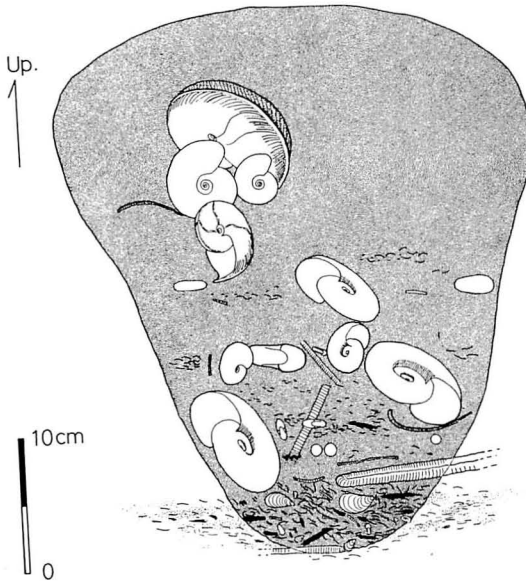


**Figure 4.** Mode of ammonite occurrence and preservation in a lenticular calcareous concretion embedded in weakly bioturbated mudstone at Loc. TP-617, Mf-h member [middle Cenomanian] in the Tappu area. An adult shell of *Desmoceras (Pseudouhligella) japonicum*.

served. Ammonite-bearing calcareous nodules embedded in this *Planolites* mudstone take elliptical shape, and contain several well preserved immature shells of *Tetragonites glabrus* and *Tragodesmocerooides subcostatus*. In usual, their shells lay horizontally, but in some case, they do not show any preferred orientation in

the calcareous nodules. Living chambers of such ammonites are usually collapsed, but their inner whorls are well preserved.

**Occurrence in the middle Turonian to the upper Santonian:** In the upper stratigraphic levels (Ml-o to Uk), mudstone is usually intensely bioturbated, and one calcareous concretion yields usually abundant fossils which are fairly well-preserved and show random orientation in the concretion. Such fossiliferous calcareous concretions thicken vertically and show a spherical or characteristic mushroom shape. Figure 5 is an example of ammonite occurrence in a mushroom-shaped calcareous concretion embedded in intensely bioturbated mudstone at Loc. TP-080 (Ud-e member; lower Santonian; Figure 2). *Tetragonites glabrus* and *Damesites damesi* of various growth stages are scattered in the concretion without any preferred orientation. Most of them are found in a good state of preservation, except for the partial collapse of the living chamber. Air chambers are filled with sparry calcite, but the shell wall, septa



**Figure 5.** Mode of ammonite occurrence in a mushroom-shaped calcareous concretion embedded in intensely bioturbated mudstone at Loc. TP-080, Ud-member [lower Santonian] in the Tappu area. Keeled ammonites: *Damesites damesi*; smooth-shelled ammonites: *Tetragonites glabrus*. Many shell fragments of *Polyptychoceras* sp. and *Inoceramus* (*Sphenoceramus*) *naumanni* and numerous plant remains are concentrated in the lower part of the concretion.

and siphuncular tube have been completely remained. In addition to moderate-sized ammonite shells, numerous immature ammonites, less than 1 cm in diameter occur with their protoconch preserved in the same calcareous concretions, in association with abundant plant remains. The mushroom-shaped calcareous concretions exhibit interesting mode of fossil occurrence. The lower part in these concretions contains numerous small-sized ammonites and *Inoceramus* together with abundant plant remains. On the other hand, the middle to upper part is characterized by sporadic occurrence of larger ammonite shells, and sometimes no megafossils occur in the upper part. Throughout the Cretaceous succession of the Tappu area, the occurrence of fossils are more abundant in calcareous concretions in almost massive or bioturbated horizons than in well-laminated part. The tendency for the stratigraphic change

in the mode of ammonite preservation in the Tappu area seems to recognize in other areas in Hokkaido.

**Discussion:** In the upper Cretaceous of Hokkaido, megafossils occur abundantly in calcareous concretions. Accumulated fossils in nodules are usually well preserved in contrast to the rare and poorly preserved occurrence in surrounding mudstone. There are following two interpretations on such mode of occurrence.

(A): Molluscan shell remains were at first distributed homogeneously in the sediments, and after the formation of calcareous concretions, those in the surrounding rocks had been selectively dissolved away during diagenetic process.

(B): Molluscan shell remains were originally accumulated as patches at places on the sea floor, and calcareous concretions were formed around the accumulations of the shell.

In practice, dissolution of shell is frequently observable in ammonite remains which are extended from calcareous nodule to the surrounding mudstone. Figure 6 shows an example of a shell of *Desmoceras* (*Pseudouhligella*) *japonicum* at Loc. TP-606 (Mf-h member; upper Cenomanian). In this case, the shell is well preserved in the calcareous concretion, whereas, it is completely dissolved away in surrounding mudstone. The mold of dissolved shell is not observable at Loc. TP-605, while it is recognized in some other cases. This mode of occurrence seems to support the interpretation (A).

Different interpretation is obtained from observation of distributional pattern of plant remains in calcareous concretions and surrounding rocks at various stratigraphic levels. At the outcrop, plant remains are not distributed homogeneously but likewise accumulated in the calcareous concretions. There are some calcareous concretions composed mostly of considerable amount of plant remains without megafossils, while plant remains are extremely rare in the surrounding mudstone (e.g. Loc. TP-004: upper Turonian). Plant remains, particularly wood particles, seem to be stable in diagenetic dissolution for very fine carbonaceous flakes are



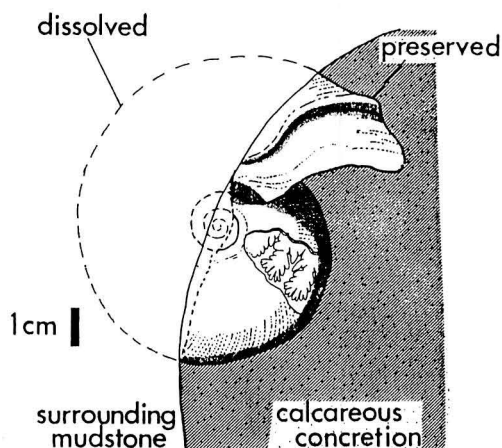


Figure 6. Mode of occurrence of *Desmoceras* (*Pseudouhligella*) *japonicum*, which is extended from calcareous concretion to the surrounding mudstone, at Loc. TP-606, mf-h member [upper Cenomanian] in the Tappu area.

observable in the mudstone. In addition, casts or molds of shell should be preserved in the mudstone if they are dissolved during diagenesis. Such molds or casts are, however, rare in the mudstone except in the circumference of calcareous concretions. It seems natural that the shells and the plant remains were originally accumulated at places on the sea floor, and calcareous concretions were subsequently formed around such accumulations. The accumulated shells out of calcareous concretions might dissolved during post-depositional diagenetic process.

**Co-occurrence of ammonite shells and plant remains:** In both calcareous concretions and surrounding rocks, co-occurrence of ammonites and plant remains seems very interesting. It is not peculiar to the restricted horizons in the Tappu area but is frequently observable in various stratigraphic levels throughout the Cretaceous sequence in Hokkaido. Co-occurrence of ammonites and plant remains in the upper Albian in the Ikushumbetsu area is shown in Figure 7. In this case, about fifteen individuals of *Mortoniceras* (*Deiradoceras*) sp., *Zelandites* sp. and anisoceratid heteromorph are accumulated on a bedding plane of about 40 cm × 40 cm together with large wood trunk. A fragment of aptychus was associated with the assemblage,

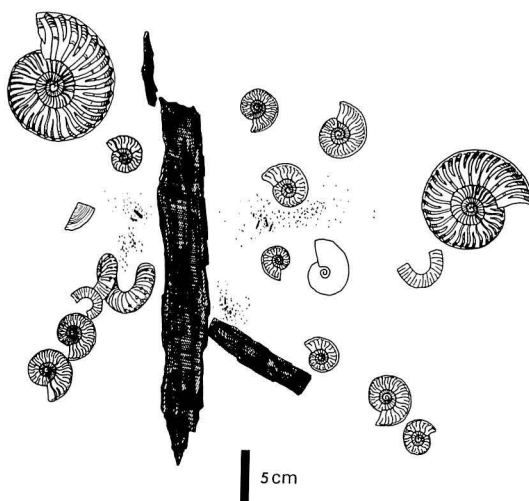


Figure 7. Co-occurrence of ammonites and plant remains in well-laminated mudstone at Loc. IK-1006 [upper Albian] in the Ikushumbetsu area. Shells of *Mortoniceras* (*Deiradoceras*) sp. (ornamented ones), *Zelandites* sp. (smooth-shelled one) and anisoceratid heteromorph are accumulated on a bedding plane of about 40 cm × 40 cm together with large wood trunk.

but no ammonite shells were found with jaw apparatus in situ. They may show allochthonous mode of occurrence, for their living chambers are somewhat damaged by transportation. Similar accumulations, composed of ammonite shells and plant remains, are scattered as patches at places on a bedding plane. Because no calcareous concretions are formed around the locality, preservational bias, originated from partial calcification of sediments, can be neglected in the case. Such mode of occurrence, which is not peculiar to the Yezo Group (e.g. Maeda, 1987: Monobegawa Group [Albian] etc.), may suggest that ammonite shells together with plant remains were transported and accumulated as patches on the sea floor by weak bottom currents.

After death, ammonite shells might have rapidly become waterlogged (Kennedy and Cobban, 1976). Density of waterlogged ammonite shells were much smaller than those of bivalve and gastropod shells, judging from the extremely thin shell tests. Also a part of camera in many shells was probably free from water-

flooding. Possibly, its density may be quite similar to those of waterlogged wood particles (about 1.11 to 1.23 g/cm<sup>3</sup>) or plant remains. If so, it seems quite natural that the waterlogged ammonite shells and plant remains behave hydrodynamically similar way. Their mode of occurrence may suggest that they were similarly transported easily by very weak bottom currents, and that they were finally deposited at the same places on the sea floor.

The shells of ammonite and inoceramid are in usual randomly orientated in the calcareous concretions embedded in intensely bioturbated mudstone of upper stratigraphic levels (Figure 5; Gill and Cobban, 1966). Taking the co-occurrence of benthic body fossils and burrows into consideration, such random orientation of shells in the upper members are possibly attributed to the intense bioturbation by shelled and non-shelled deposit feeders. In all probability, deposit feeders, such as spatangoids, disturb the preferred orientation of ammonite shells on the sea floor or in soft sediments.

#### Preservation of large ammonites

Large ammonites, attaining more than 30 cm in diameter are quite abundant throughout the Yezo Group. Moreover, gigantic ones (exceeding 1 m in diameter) are commonly found at various horizons. They are puzosiids [late Albian to Coniacian], pachydiscids [Santonian to Maastrichtian] and other groups. In comparison with moderate sized ammonites, large ammonites exhibit peculiar mode of occurrence and preservation. They usually occur solitarily and lie horizontally in mudstone. In many specimens, the siphuncular tube is damaged, and inside of the shell, both living chamber and phragmocone, are filled with mud. "Draught-through effect":

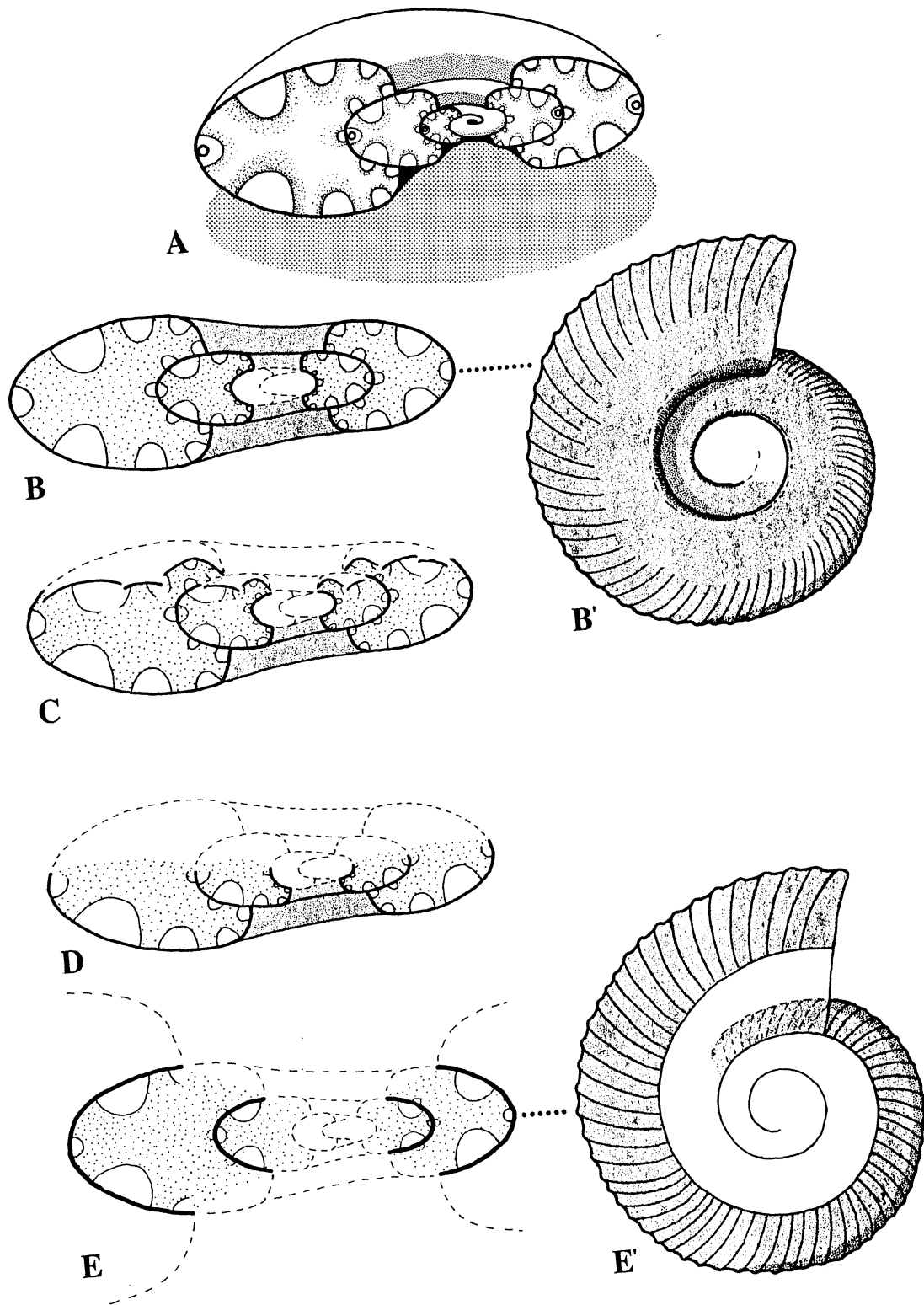
a mechanism of sediment filling into phragmocone chambers, was experimentally revealed by Seilacher (1969). Sediment-infillings are somewhat calcified. Some large shells form single calcareous concretions themselves. They are generally more poorly preserved than the moderate-sized ammonites, even they occur in calcareous concretions. As stated before, moderate-to small-sized ammonites are well-preserved in the intensely bioturbated middle Turonian to Santonian mudstone. In contrast to this, large ammonite shells are more or less damaged throughout the Cretaceous sequence in Hokkaido. This evidence suggests that taphonomic and diagenetic factors seem to be more influential on preservation of large ammonites than on the moderate-sized ammonites.

Figure 8 summarizes typical mode of occurrence of large puzosiid ammonites (phragmocone) in the middle to upper Turonian sequence of the Tappu area. Among the illustrated preservational types, selective dissolution of inner whorls (Figures 8B, 9-2) is most frequently observed in large specimens of puzosiids, pachydiscids and acanthoceratids. Especially, many Santonian *Anapachydiscus* and *Eupachydiscus* shells have suffered dissolution of inner whorls even in the case of less than 15 cm in shell diameter. On the contrary, inner whorls are generally well preserved in gaudryceratids. For example, specimens of *Gaudryceras denseplicatum*, which attains 30 cm or greater in diameter, are sometimes found with well-preserved inner whorls. Gaudryceratid shells may be much resistant against diagenetic dissolution because outer surface of their shells are thickly coated with periostracum film (Birkelund, 1981).

Crush of the upper shell region (Figure 8C) is also fairly common in preservation of large ammonites. In the case of large shells of *Meso-*

→ **Figure 8.** Typical mode of preservation of large puzosiid phragmocones in the middle to upper Turonian sequence of the Tappu area. In many case, several types of preservation are combined in a specimen.

- A: Original shell-morphology.
- B, B': Selective dissolution of inner whorls.
- C: Crush of upper shell region.
- D: "Half-ammonite" preservation.
- E, E': "Ventral-tire" preservation.



*puzosia pacifica*, upper flank: about one third portion of the whorls, has been selectively collapsed and sank into the inner side of the whorls in post-burial diagenetic process. Longitudinal fracture patterns, such as umbilical fracture (Seilacher *et al.*, 1976), are well-observable, but their exact patterns are peculiar to ammonite shell-geometry as stated by Seilacher *et al.* (1976). Both living chamber and septate phragmocone have suffered this kind of post-burial compactional deformation. As to be stated later, dissolution of septa occurred at first, and it might trigger the crush of phragmocone.

Figure 8D is another kind of preservation ("half-ammonite" preservation: Seilacher *et al.*, 1976, p. 349), that the upper half of the horizontally lying shell is dissolved, retaining only the lower side. This mode of preservation is also well-observable in the Yezo Group in various taxa. I will discuss this problem later.

Among the various kinds of preservation shown in Figure 8, Type (E) seems to be the most eccentric (Figures 9-2, 3a, and 3b). The ammonite shell is preserved its venter and outer flanks of the last or last second whorl only, and inner flanks and umbilical margins are dissolved away. Its appearance just looks like a "tire" (it is not clear whether such "ventral-tire" belongs to "tube" type or to "tubeless" type). This "ventral-tire" preservation has not hitherto described, although it is fairly common in large puzosiids, pachydiscids and acanthoceratids in the Cretaceous strata of Hokkaido. The margin of such "ventral-tire" is distinct, and preserved portion of "ventral-tire" is distinct, and preserved portion of "ventral tire" is quite uniform. In the case of *Mesopuzosia pacifica* specimens, for example, ventral 30 to 40% portion of last whorl, which is correspond with shell-involution

of this species, is uniformly preserved. Judging from this, the preserved ventral part might be originally covered with outer whorl of the shell. Only the ventral part, thus not exposed directly to the external environment, might be free from dissolution of shell during diagenesis.

In practice, several types of preservation are combined in a specimen (Figure 9-2).

**Discussion:** I will concentrate my discussion on the preservational history of "half-ammonites" in the Yezo Group. "Half-ammonite" preservation (Figure 8D) has been already recognized by many scholars in the various Mesozoic strata in the world. Roughly speaking, the following three explanations have been presented for the preservational history of "half-ammonite" (Figure 12).

(1) "Cast on sea floor" model: A half-buried ammonite shell had been dissolved away with the sea water during diastem, and the shell-impression was preserved as an external cast on consolidated substrata of the sea floor (Minato, 1953: Triassic Inai Group, Japan).

(2) "Exposed upper-half" model: The lower half of a horizontally lying ammonite shell was buried in mud. The upper half was still exposed above sediment surface, and thereafter exposed part with sea water had suffered pre-burial dissolution in sediment-water interface (Hollmann, 1962: Jurassic Ammonitico Rosso, Italy; Lehmann, 1976; Tanabe *et al.*, 1984: Jurassic Toyora Group, Japan, etc.).

(3) "Post-burial dissolution" model: The upper half of a completely buried ammonite shell had suffered selective shell-dissolution with interstitial water because of the partial sedimentary filling (Seilacher *et al.*, 1976: Jurassic Posidonienschiefer, West Germany, etc.).

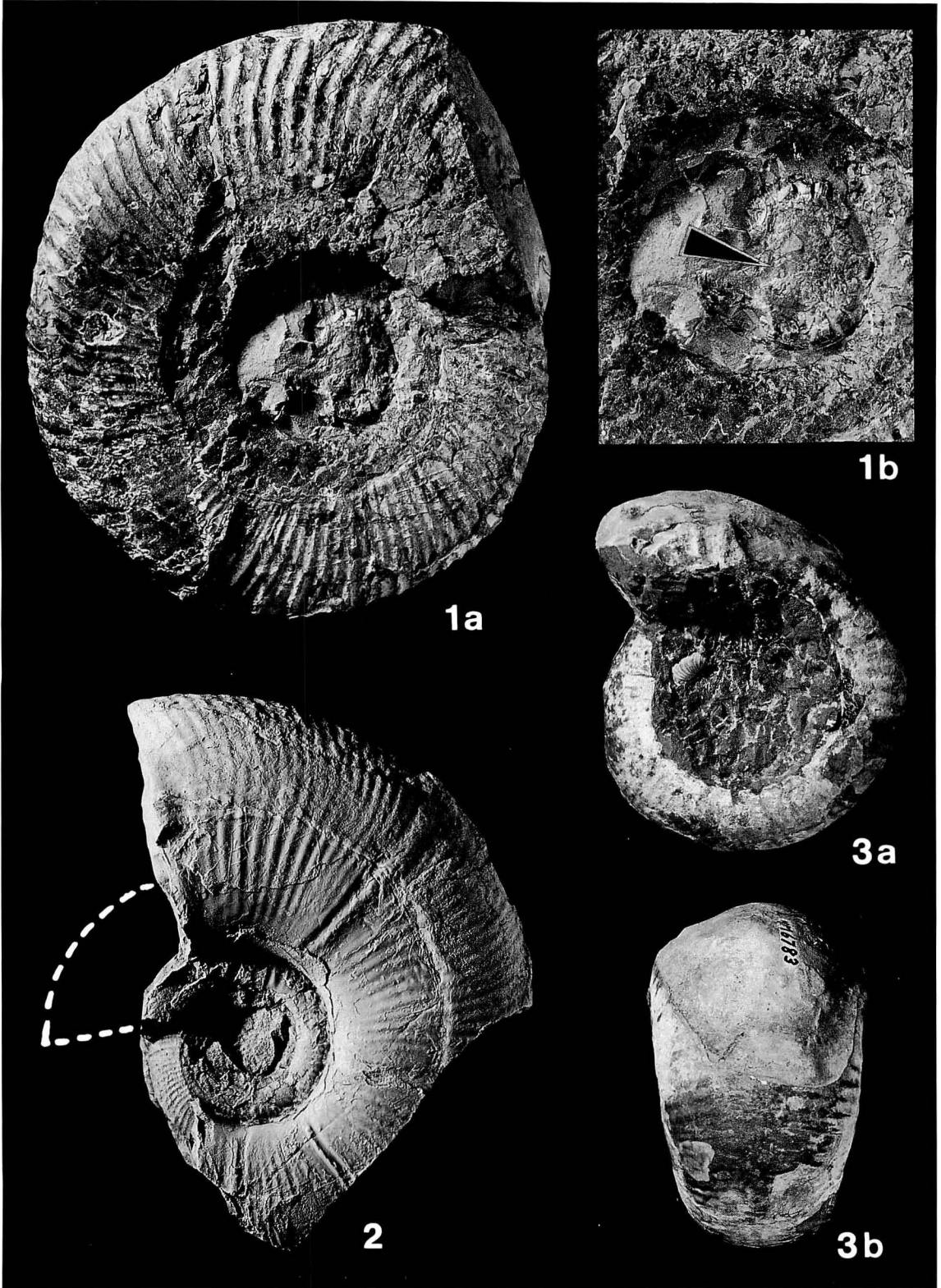
Among them, hypothesis (1) should be re-

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→ **Figure 9.** 1a, b. Large *Canadoceras multicoatum* Matsumoto associated with a spatangoid in the lower umbilical void. UMUT.MM-6862; Campanian; Naibuchi area, Sakhalin. 1a: Lateral view;  $\times 0.28$ . 1b: Close-up of umbilical void of 1a. Well preserved spatangoid shell filled with sparry calcite is indicated by arrow.

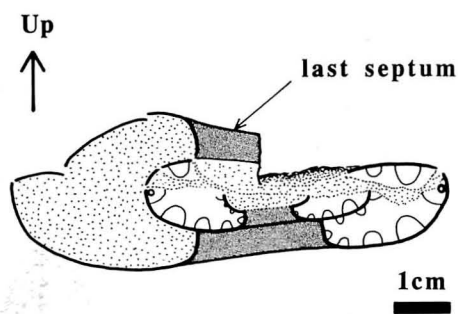
2. *Mesopuzosia pacifica* Matsumoto showing selective dissolution of inner whorls (most inner part) and "ventral-tire" preservation (indicated by arrow). KSG-HM. 1012; Loc. TP-3024, M1-O member [middle Turonian] in the Tappu area;  $\times 0.52$ .

3a, b. *Anapachydiscus sutneri* (Yokoyama) showing "ventral-tire" preservation. UMUT.MM-6783; Santonian; Naibuchi area, Sakhalin;  $\times 0.44$ . 3a: Ventral view. 3b: Lateral view.



jected in the case of “half-ammonites” from the Cretaceous Yezo Group, because calcified shell wall and septa actually remain in the lower half. Hypothesis (2): illustrated in Figures 12A, B, F, seems attractive, for large shells of ammonite might spend much time for their full-burial in the sediments. As a natural consequence, they must have suffered many kinds of diagenetic destruction before their complete burial. But as stated later, there are some problems to explain the practical mode of “half-ammonite” preservation in the Yezo Group by this model.

According to my field and laboratory observations, mode of preservation of many specimens represents an intermediate stage between the types of the upper surface crushing, and “half-ammonite” preservation (Figures 8C, D). In these specimens, outer shell wall and septa in the upper half have suffered not only crushing but also partial dissolution. These features suggest us that the stage of crushing of the upper surface grades into the stage of “half-ammonite” preservation in the process of post-burial diagenesis. It is noticeable that many ammonites exhibit two different states of preservation even in the same specimen: namely, “half-ammonite” phragmocone and crushed living chamber. Typical example of such case is given in Figure 10 (Loc.

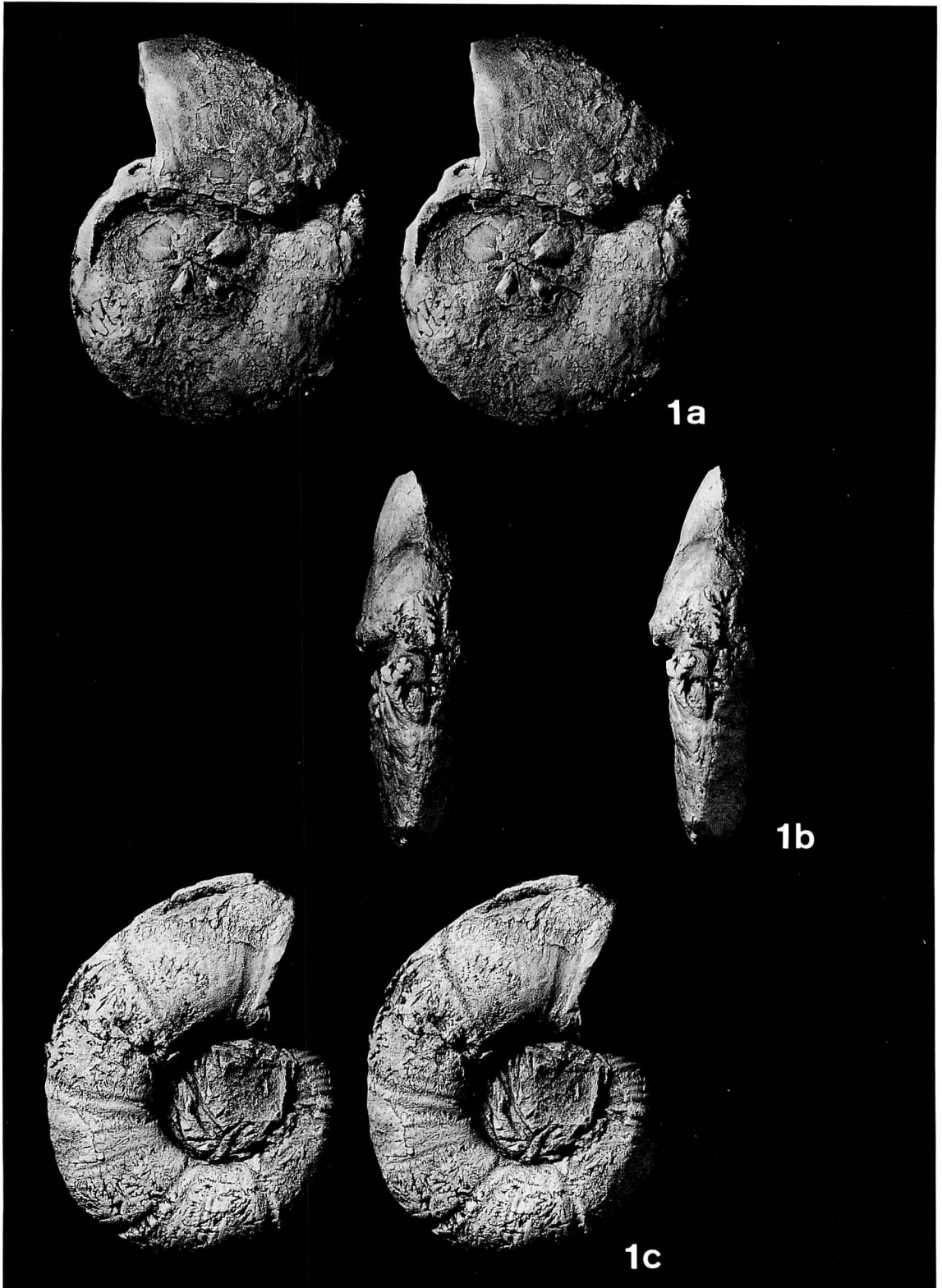


**Figure 10.** A shell of *Mesopuzosia planulatiformis* showing two different states of preservation, which are bounded by the last septum, in a shell. Loc. TP-501, uppermost part of Mj-k member [middle Turonian], Tappu area.

TP-501; Mj-k member; middle Turonian in the Tappu area), in which two different phases of preservation are sharply bounded by the last septum are observable in a horizontally embedded shell of *Mesopuzosia planulatiformis*. The specimen retains a living chamber filled with mud. The upper side of the living chamber is partly crushed by compaction, but remains shell-material (Type C preservation of Figure 8). On the other hand, the phragmocone shows a quite different mode of preservation from living chamber. Namely, its upper side had been collapsed and flattened. Some collapsed fragments of the upper flank, particularly of inner whorls, had been partly dissolved (intermediate features between Types C and D in Figure 8). Inner whorls of phragmocone actually lack the upper half. Septa, except the last one, had suffered more intense dissolution than the other part of the shell. As calcified shell wall and sutures are preserved in the collapsed upper flank of many specimens, dissolution of septa had occurred prior to that of upper flank (Figures 10, 11). If shell dissolution did occur before complete burial of the shell, upper flank exposed in the sea water should dissolve at first. In addition to this, “exposed upper half” model cannot explain such drastic difference in the mode of preservation between phragmocone and living chamber (Figures 10, 11).

The preservational uniformity of “half-ammonites” puzzles us very much. I have observed at least two hundred “half-ammonite” specimens from the Upper Cretaceous deposits in Hokkaido and Sakhalin. In spite of a wide variety in their locations, horizons, taxonomic positions *etc.*, the mode of “half-ammonite” preservation are quite similar among them. “One third ammonite” or “three-quarter ammonite” preservations are scarcely found. “Two third ammonites” are sometimes observable, but careful examination reveals that they should belong to Type C preservation, *i.e.* for their upper flanks (=upper

→ **Figure 11.** 1a–c. Photostereograph of a specimen of *Mesopuzosia planulatiformis* (Jimbo) showing two different preservational states, which are bounded by the last second septum. KSG-HM. 1011; Loc. TP-501, uppermost part of Mj-k member; middle Turonian; Tappu area;  $\times 0.78$ . 1a: Lateral view (upper side). 1b: Ventral view. 1c: Lateral view (lower side).



“one third”) are merely broken by compaction. “Exposed upper half” model cannot, thus, explain such preservational uniformity observed in “half-ammonites” from the Cretaceous of Hokkaido and Sakhalin. If shell dissolution occurred directly with the sea water before complete burial, the ammonite shells would not need necessarily showing exact “half-ammonite” preservation, but should exhibit various stages of dissolution: for example, “one third ammonites” or “three-quarter ammonites”. Tanabe *et al.* (1984) studied mode of “half-ammonite” preservation embedded in the Liassic laminated black shale of the Toyora Group, southwest Japan. They attributed “keel” of harpoceratids to prevent the upper half of the shell from sinking down into soft sediments, and to stabilize the “half-ammonite” position on sediment-water interface during dissolution of the upper half. Their taphonomic model in the Liassic black shale, however, seems to be inapplicable to the “half-ammonites” from the Cretaceous deposits in Hokkaido. The most “half-ammonites” in the Cretaceous Yezo Group are non-keeled ones as represented by puzosiids and pachydiscids.

In the case of “half-ammonites” from Hokkaido, their phragmocones are similarly preserved from lower flank to the extent of ventral area just exceeding the median line: *i.e.* just above the position of siphuncle or septal neck. Their living chambers are sometimes preserved better than the phragmocones. Their preservational features may suggest us that the mode of “half-ammonite” preservation is not prescribed by their “half-burial” on the sea floor but much decisively by internal structure of phragmocones, which easily raise the partial sedimentary filling. As Seilacher (1969) demonstrated experimentally, sediments can enter phragmocone if siphuncular tube and somewhere of the whorl were damaged. The sediments were predominantly transported into the chambers of the lower phragmocone by “draught-through” current. The current can pile them up even until higher level than median line in inter-septal area, however, the sediments cannot be deposited exceeding the level of septal neck near the septal

area in order to ensure the passway of “draught-through” current. The surface of lower chambers might be sealed with sediments, whereas, those of the upper and septa remained being exposed in the sea water, and even in interstitial water after full-burial of the shell. “Half-ammonite” preservation in the Yezo Group may not be originated from “external” half-burial of the shell on the sea bottom but “internal” half-burial prescribed by the septal neck position which is phylogenetically determined even almost all planispiral ammonites. If so, it seems natural that “half-ammonite” position is quite uniform among many specimens observed. Practical mode of “half-ammonite” preservation in the Yezo Group may suggest that “post-burial dissolution” model (Seilacher *et al.*, 1976: the third hypothesis) is the most convincing explanation.

Figure 12 summarizes presumable taphonomic history of “half-ammonites” in the Yezo Group.

(1) A dead ammonite shell settled horizontally down on the sea floor (Figure 12A).

(2) Before complete burial of the shell, thin-shelled inner whorl dissolved away with the sea water, and siphuncular tube, composed of organic-rich material, was broken. Then, “draught-through” current transported soft sediments into the phragmocone chambers through septal necks, and piled them in the lower part of the chambers (Figure 12C). “Draught-through” current might continue until sediments closed its entrance or pathway, or exit (for example, apertures of living chamber, septal necks in phragmocone, and dissolved inner whorl respectively).

(3) After full-burial of the shell, the living chamber was completely filled with sediments, and the last septum was perfectly sealed with them. On the other hand, phragmocone chambers remained in half-buried state, and the upper half and septa had been still exposed in interstitial water. Then dissolution of fully naked septa, without any kind of sediment sealing, began (Figure 12D), and the dissolution of the upper half might follow this. Dissolution of septa could occur before full-burial of the shell (Figure 12C).



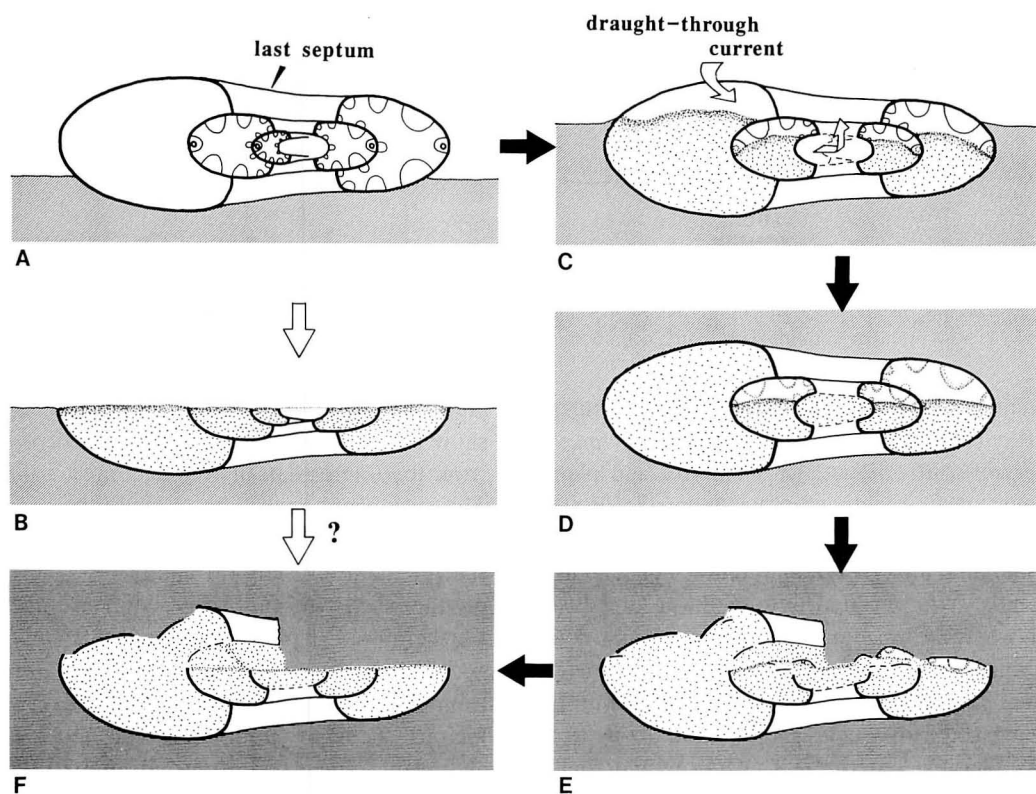


Figure 12. Presumable taphonomic history of "half-ammonite" in the Upper Cretaceous Yezo Group. (Explanation in the text).

(4) The dissolution of septa triggered collapse of the upper half of phragmocone chambers, remained empty, by compaction. On the other hand, the living chamber and the last septum, both of which were sealed with sediment infillings and were almost free from dissolution, might be much resistant against compaction. In this way, two different states of ammonite preservation, which were sharply bounded by the last septum, had been formed (Figure 12E).

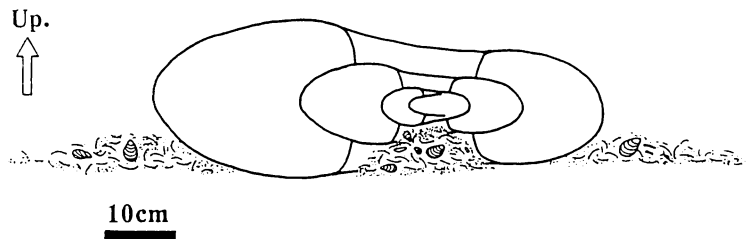
(5) During diagenesis, crushed shell-materials had been dissolved away, and "half-ammonite" preservation, particularly well-observable in the phragmocone, was accomplished (Figure 12F).

There are many factors concerning the preservation of ammonites. The preservational states of ammonites may be controlled by the interaction between the factors for destruction and those for preservation. In addition to the post-

mortem processes mentioned above, shell dissolution could occur since ammonites were still alive, particularly in the case of large ammonites. Further precise observations are needed to answer the problem.

#### Mode of co-occurrence of large ammonites, plant remains and spatangoids

As states above, ammonite shells and plant remains seem to had accumulated as patches at places in the Yezo Group. I could not realize the exact mechanism to form such accumulations on the sea floor, but the following interesting mode of occurrence of large ammonite *Mesopuzosia planulatiformis* from the middle Turonian of the Tappu area (M1-o member) may suggest about it (Figure 13). The specimen, about 70 cm in diameter, was found to form a calcare-



**Figure 13.** Mode of occurrence of large *Mesopuzosia planulatiformis* associated with small shell fragments of *Inoceramus hobetsensis* and numerous plant remains around the shell and in the lower umbilical void. Loc. TP-514, Ml-o member [middle Turonian], Tappu area.

ous concretion itself. A considerable amount of disarticulated immature shells of *Inoceramus hobetsensis* of about 2 to 5 cm size and plant remains occur together in the underside of the ammonite shell. They are accumulated around the marginal area of the ammonite shell, and are the most concentrated in the lower umbilical void where sediments are bioturbated and contain many fecal pellets of 2 to 4 mm in diameter (Figures 13, 14). The shell of *Mesopuzosia* probably triggered off such accumulation acting as a “trap” on the sea floor. The inoceramid shells and plant remains might be transported by bottom current, and accumulated around the shell. Similar occurrence of a large ammonite and plant or small inoceramid shell remains are observable at many stratigraphic horizons in the Cretaceous of Hokkaido. In addition to this, small ammonite shells sometimes occur with the living chamber of a large ammonite. Wright (1935), Casey (1961) and Lehmann (1976) also reported the same type of ammonite occurrence. This type of ammonite occurrence can be also attributed to the same biostratigraphical process (Maeda, in preparation).

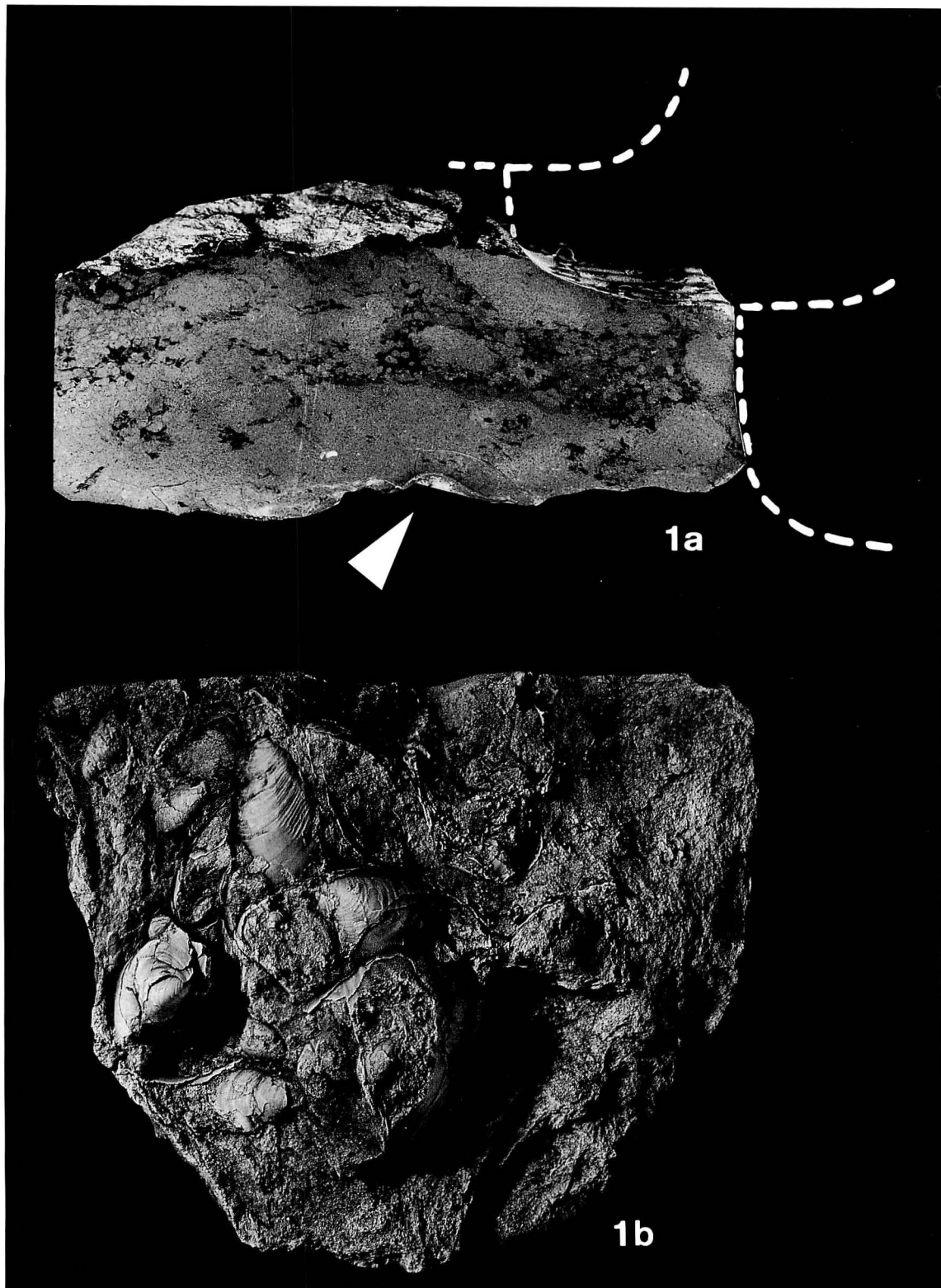
In relation to this type of accumulation, many spatangoid sea urchins show a peculiar mode of occurrence in the lower umbilical voids of the flat lying large ammonite shells. Considerable amounts of shell fragments and plant remains

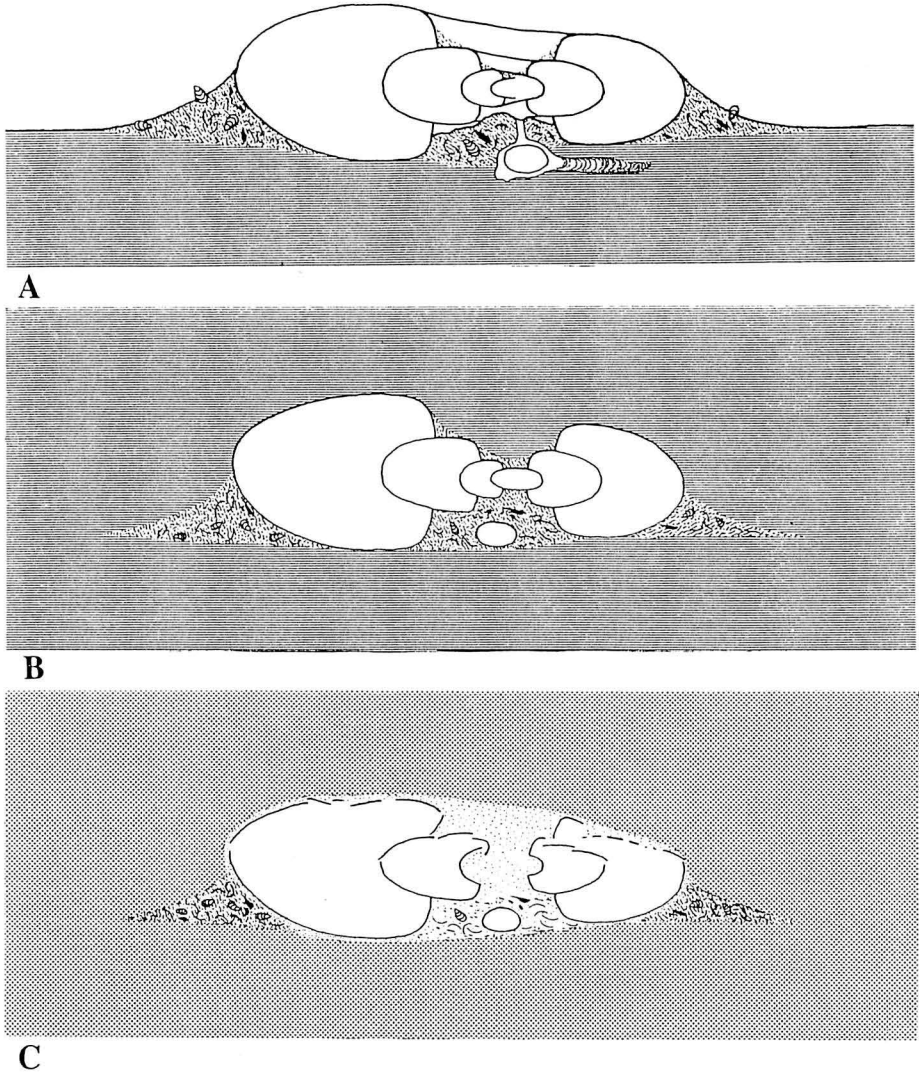
are accumulated in the portion. Figures 9-1a, b show an specimen of *Canadoceras multicostatum* from the Campanian of Naibuchi area, Sakhalin. The spatangoid shell is so perfectly preserved in the lower umbilical void of the ammonite that sparry calcite crystals fill completely the inside of the shell without any sediment infillings. Furthermore, many well-preserved spatangoids occur in the lower part of the spherical or mushroom-shaped calcareous concretions where numerous shells of ammonites and inoceramids, and plant remains are concentrated (e.g., Loc. TP-409, Uf member; lower Santonian). In both cases, the heart urchins are well preserved in the calcareous nodules, and may exhibit indigenous or even in situ mode of occurrence. In modern environments, dead shells of spatangoids are quite easy to break. It is, therefore, strongly postulated that in the above described spatangoids they had fossilized almost in the living place. Indeed, many horizontal burrows made by spatangoids can be observed in a tuff bed just below the sea urchin-bearing calcareous nodule in the lower Santonian sequence in the Tappu area. Similar mode of occurrence of the spatangoids in nodules was also described by Reeside and Cobban (1960) in the Albian of the Western Interior region.

The place where many shell fragments and plant remains accumulated as patches on the sea

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→ **Figure 14.** 1a, b. Accumulation of molluscan shell fragments and plant remains in the lower umbilical void of large *Mesopuzosia planulatiformis*. KSG-HM. 1013; at Loc. TP-514, Ml-o member [middle Turonian] in the Tappu area. 1a: Vertical profile. Many plant remains (dark-colored part) and fecal pellets are observable. 1b: Horizontal view from lower side (indicated by arrow). Disarticulated immature shells of *Inoceramus hobetsensis* are accumulated in their convex-side down. (Figures of natural size)





**Figure 15.** Possible biostratinomical process of large ammonite shell associated with a spatangoid in the lower umbilical void. A: A large ammonite shell triggered off the accumulation of molluscan shell fragments and plant remains in the lower umbilical void and around the shell acting as a "trap" on the sea floor. Deposit feeding spatangoid assembled to the place of such accumulation to feed eutrophic sediments. B: After the spatangoid died in situ, the large ammonite shell was buried completely with soft sediments. C: Several diagenetic processes influenced the preservation of fossils. The large ammonite shell formed single calcareous concretion.

floor seems to be rich in organic matters. I presume that the deposit-feeding spatangoids assembled to the place of accumulation of shells to feed eutrophic sediments: particularly to the lower umbilical void of large ammonite shell, and then died in situ. The above possible bio-

stratinomical process of spatangoid test is diagrammatically shown in Figure 15. It seems interesting that only one spatangoid is generally found in the lower umbilical void of a large ammonite shell, while two or three are sometimes aggregated in a mushroom-shaped calcare-

ous concretion.

**Conclusion**

(1) Numerous ammonites are found in calcareous concretions or surrounding mudstone in the Cretaceous deposits of the Tappu area, Hokkaido. Their detailed modes of occurrence and preservation are quite different by sedimentary features of mudstone and by their size.

(2) Flat, lenticular calcareous concretions are dominant in well-laminated mudstone of the lower to middle Cenomanian. Ammonite fossils in such concretions are, in general, poorly preserved. Collapse and dissolution of ammonite shells suggest that the concretions had consolidated in later stage of diagenesis.

(3) In contrast to this, spherical or mushroom-shaped calcareous concretions, which yield usually many well preserved ammonites including immatures, are abundant in intensely bioturbated mudstone of the middle Turonian to upper Santonian. The concretions embedded in the part might had formed in earlier stage of diagenesis before ammonite shells suffered com-

paction and dissolution. Figure 16 summarizes these features. Not only overburden of the sediments but also organic and inorganic sedimentary conditions of the sea floor at that time; e.g. degree of bioturbation, might have influenced the diagenetic factors.

(4) Ammonite shells and plant remains frequently occur together as patches. Waterlogged ammonite shells and plant remains might hydrodynamically behave similar way, and had been transported by weak bottom currents to the same place.

(5) Large-sized ammonite shells are usually more incompletely preserved in calcareous concretions than those of moderate-sized ones as represented by peculiar mode of preservation such as "half-ammonite" and "ventral tire". Degree of sediment-covering might have influenced to the mode of large-sized ammonite preservation.

(6) Quite uniform "half-ammonite" preservation in the Cretaceous of Hokkaido cannot explained by the half-burial model on the sea floor but "internal half-burial" model of phragmocone by "draught-through" currents. The

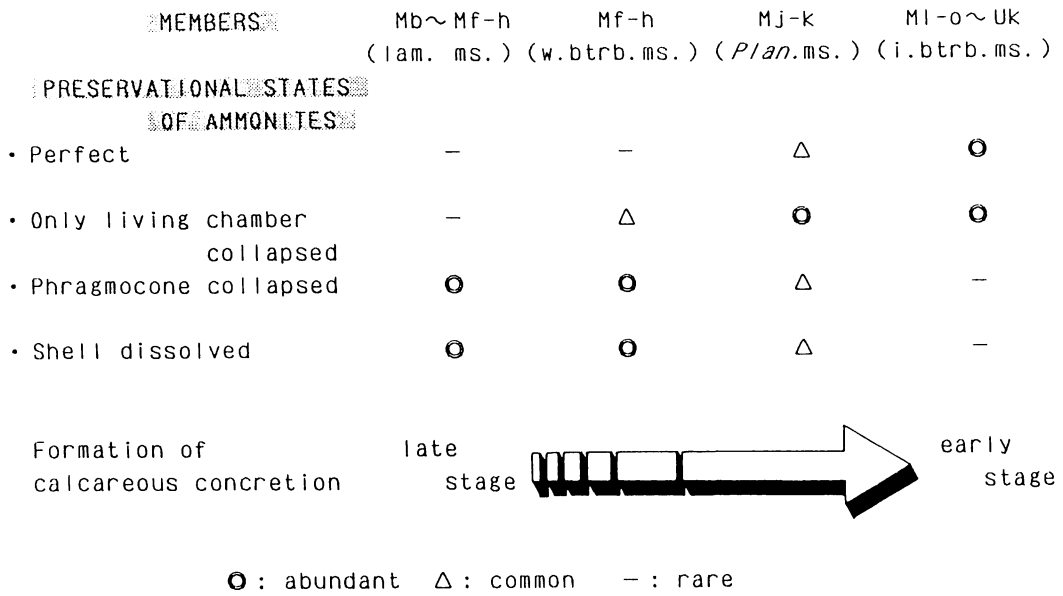


Figure 16. Summary on mode of preservation of moderate-sized ammonites in calcareous concretions.

preservation seems to be prescribed by the septal neck position, which is phylogenetically fixed in almost all planispiral ammonites.

(7) Large ammonite shell probably triggered off the accumulation of shell fragments and plant remains, acting as a "trap" on the sea floor. They had been particularly concentrated in the lower umbilical void of the large ammonite shell. Some spatangoids, preserved regularly in such umbilical void of large ammonite, might assemble to eat organic matter accumulated there.

### Acknowledgments

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北海道北西部達布地域の白亜系蝦夷層群のアンモナイトのタフォノミーについて：北海道からサハリンにかけて分布する上部白亜系から産するアンモナイトのタフォノミーについて、主に達布地域での観察を中心に議論した。平行葉理の発達したセノマニアン階の泥岩では、アンモナイトの殻は石灰質ノジュール中に含まれている場合でも、圧密・溶解を被っている。一方、生物擾乱を強く受けたチューロニアン階中部～サントニアン階上部の泥岩中のノジュールは、圧密・溶解を受けていない保存の良いアンモナイトを豊富に含む。おそらく上位層準のノジュールの方が、下位層準のものよりも続成作用のより早い段階で形成されたと考えられる。大型アンモナイトは、中・小型のものより続成作用の影響を強く受け、“half-ammonite”や“ventral-tire”等の特徴的な保存をしばしば示す。これらの保存は、堆積物が殻内を不均一に埋積するため生じると考えられる。また、アンモナイトの殻は、植物片とよく共存する。これは海水が侵入したアンモナイトの殻の密度が、流木片のそれと近く、両者が水力学的に似かよった挙動を示すためと推測される。これら木片やアンモナイト・イノセラムスの殻破片は、大型アンモナイトのヘソの下に特徴的に掃き寄せられることも多い。植物片や貝の殻破片が集まったこのようなヘソ下部の空間に、堆積物食者のブンブク類ウニが自生的産状で保存されていることがある。 前田晴良

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## 847. BURROWING DEPTH OF INFAUNAL BIVALVES – OBSERVATION OF LIVING SPECIES AND ITS RELATION TO SHELL MORPHOLOGY\*

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**Abstract.** Burrowing depths of 22 infaunal bivalve species living in the Japanese coastal areas were observed. Burrowing depth of each species is variable depending on the shell size, substratum, and other environmental attributes. The most striking is ontogenetic variation: In most species, maximum burrowing depth tends to increase with the increase of shell size.

Difference in burrowing depth among species represents different life habit in bivalves. Particularly, the difference is pronounced, between extremely deep burial (more than 30 cm) of immobile bivalves like *Panopea japonica* A. Adams and shallow burial (less than 15 cm) of most bivalves capable of active movement.

In suspension-feeding siphonate bivalves, the ratio of pallial sinus length to shell length (Pallial Sinus Index) is closely related to the relative maximum burrowing depth. This “sinus-depth relation” may be useful in inferring burrowing depth of extinct species.

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### Introduction

Burrowing habit of bivalves is considered to have developed extensively since Mesozoic (Stanley, 1968), to avoid disturbance by physical agents and to escape from predators. Wide variation of burrowing depth seen among bivalves and other infaunal benthos was regarded as one of the common biological solutions for resource partitioning (Ausich and Bottjer, 1982, 1985), or as different adaptive strategy of each species to physical sedimentary environment.

The difference in burrowing depth among bivalves, on the other hand, may bring about some confusion in paleoecologic interpretation of fossil occurrences. Successive deposition and colonization by bivalves with different burrowing depth apparently resulted in mixing of older shallow burrowers and newer deep burrowers. Some paleontologists have paid a special attention to differences between epi- and in-faunas, and between shallow and deep burrowers in

analyzing post-mortem processes operated during the formation of shell beds (Aigner, 1982; Bloos, 1982; Kidwell and Aigner, 1985).

Previous authors have suggested that the difference in burrowing depth among infaunal bivalves is one of the important factors in inferring the post-mortem processes of the fossil bivalves. Conversely, if burrowing depth of a given fossil bivalve is known, we can reconstruct the realistic post-mortem processes, such as reorientation by living organisms or sediment reworking and subsequent transportation. It is, therefore, important to study relationship between burrowing depth and shell morphology based on observation of burrowing depth of many Recent infaunal bivalves.

Systematic survey on burrowing depth and its relation to shell morphology in the Bivalvia have not been carried out except for the pioneer work by Stanley (1970). He discussed the relationship between life position and shell morphology in many living bivalve species from the Western Atlantic. In his study, emphasis was laid on functional interpretation of the relation between

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life orientation and shell morphology. His data were not sufficient to understand intra- and inter-specific variations in burrowing depth, and not enough to be used as a clue to reconstruct burrowing depth of extinct species.

This study was undertaken to obtain basic data on burrowing depth and its relation to shell morphology in 22 infaunal bivalve species living in the Japanese coastal areas. First, burrowing depth of the bivalves is described with emphasis on intra- and interspecific variation. Second, pallial sinus length will be emphasized as a key morphology for reconstruction of the burrowing depth. Description of life position as well as other life habit and habitat of the species observed are provided in the appendix.

### Acknowledgments

This paper is the first half of the doctoral dissertation submitted to the University of Tokyo. I acknowledge Profs. I. Hayami of the University of Tokyo and K. Chinzei of Kyoto University for their helpful discussions and advice during this study. Thanks are also extended to Prof. Y. Iwasaki of Kumamoto University and Dr. S. Shimoyama of Kyushu University who aided me in the field observation in some tidal flats in Kyushu. Dr. A. Matsukuma of the National Science Museum allowed me to observe and measure specimens of Recent bivalves from the Western Atlantic. Drs. K. Tanabe of the University of Tokyo, H. Kitazato of Shizuoka University, S. Matsui of Utsunomiya University and Prof. T. Okutani of Tokyo University of Fisheries gave me valuable comments on this study. Members of the Misaki Marine Biological Station of the University of Tokyo kindly provided the writer facilities for collection and observation of the bivalves living nearby sea area. Profs. I. Hayami and K. Chinzei, and Dr. K. Tanabe greatly improved the manuscript.

### Burrowing depth of Recent bivalves

#### Study area and method

Observations of bivalve life position was made

in nature, as far as possible. Some intertidal flats were, then, chosen for observation (Table 1). Physiographic descriptions of the study areas are briefly summarized in the appendix. Life position of intertidal species was observed by digging when the tide is receded. Subtidal and deeper bivalves were dredged at some areas, and were observed in the laboratory in the following manner (Figure 1). They were permitted to burrow in a small vessel filled with native or sometimes exotic sediment. The vessel was placed in a large container filled with running sea water. Life position of these species were observed by digging. A tetrapack, empty tall paper box (7 cm × 7 cm × 19.5 cm in size) was used for observation of deeper burrowers like *Dosinorbis japonicus* (Reeve). The box was filled with sediment, and the bivalves were placed on the sediment surface. After achieving burial, enclosing sediment was removed until the bivalves appeared. The tetrapack is quite convenient in removing the filled sediment, as it is easily cut to open. For observation of *Panopea japonica* A. Adams, an extremely deep burrower, a large bucket was used. As large individuals of *P. japonica* cannot burrow by themselves, they are placed on the bottom of the bucket in inferred life orientation. Then bucket was filled gradually with sediment. *Panopea japonica* expands its siphon to cope with the elevating sediment surface. The bucket continued to be filled with sediment until siphon extension stopped. Maximum burrowing depth of this species was measured in this condition.

#### Intraspecific variation

Among 22 infaunal bivalves observed, sufficient data have been obtained for the following 7 species to understand ontogenetic variation in burrowing depth: (*Ruditapes philippinarum* Adams et Reeve, *Cyclina sinensis* (Gmelin), *Dosinorbis japonicus*, *Macra chinensis* Philippi, *M. veneriformis* Reeve, *Nuttallia olivacea* (Jay) and *Macoma contabulata* (Deshayes). Their burrowing depths were measured as a distance from the sediment surface to the shallowest point on a buried shell, which is the same as

Table 1. List of infaunal bivalve species observed in this study and study area. Numbers in parentheses show study areas in which the observation was made.

	Species name (study area)
Arcidae	<i>Tegillarca granosa</i> (L.) (6)
Glycymerididae	<i>Glycymeris rotunda</i> (Dunker) (3)
Limopsidac	<i>Limopsis tajima</i> Sowerby (4)
	<i>Obolimopa japonica</i> (A. Adams) (3)
	<i>Crenulilimopsis oblonga</i> (A. Adams) (4)
Cardiidae	<i>Nemocardium samarangae</i> (Makiyama) (3)
Veneridae	<i>Circe scripta</i> (L.) (5)
	<i>Meretrix petechialis</i> (Lamarck) (8)
	<i>Gomphina veneriformis melanaegis</i> (Römer) (7)
	<i>Cyclina sinensis</i> (Gmelin) (1, 5)
	<i>Dosinorbis japonicus</i> (Reeve) (2, 3)
Mactridae	<i>Ruditapes philippinarum</i> (Adams et Reeve) (1, 2, 3)
	<i>Mactra veneriformis</i> Reeve (2)
	<i>M. chinensis</i> Philippi (2)
Donacidae	<i>Chion kiusiuensis</i> (Pilsbry) (7)
Asaphidae	<i>Nuttallia olivacea</i> (Jay) (1)
Tellinidae	<i>Macoma contabulata</i> (Deshayes) (1)
	<i>M. incongrua</i> (v. Martens) (5)
Solenidae	<i>Solen strictus</i> Gould (2)
Hiatellidae	<i>Panopea japonica</i> A. Adams (8)
Cuspidariidae	<i>Cuspidaria macrophynchus</i> Smith (3)
Laternulidae	<i>Laternula limicola</i> (Reeve) (1)

#### Study areas

1: intertidal muddy sand flat of Matsukawaura Inlet, Soma City, Fukushima Prefecture. 2: tidal flat and nearby subtidal setting of the Obitsugawa River delta, Kisarazu City, Chiba Prefecture. 3: intertidal zone in Aburatsubo Cove, Miura City, Kanagawa Prefecture. 4: bathyal muddy bottom in the innermost part of Suruga Bay. 5: tidal flat of Tsuyazaki Inlet, Fukuoka Prefecture. 6: intertidal zone of sandy shore in Nata, Fukuoka Prefecture. 7: intertidal mud flat in Shioya, Kumamoto City, Kumamoto Prefecture. 8: observation of specimens purchased in shops.

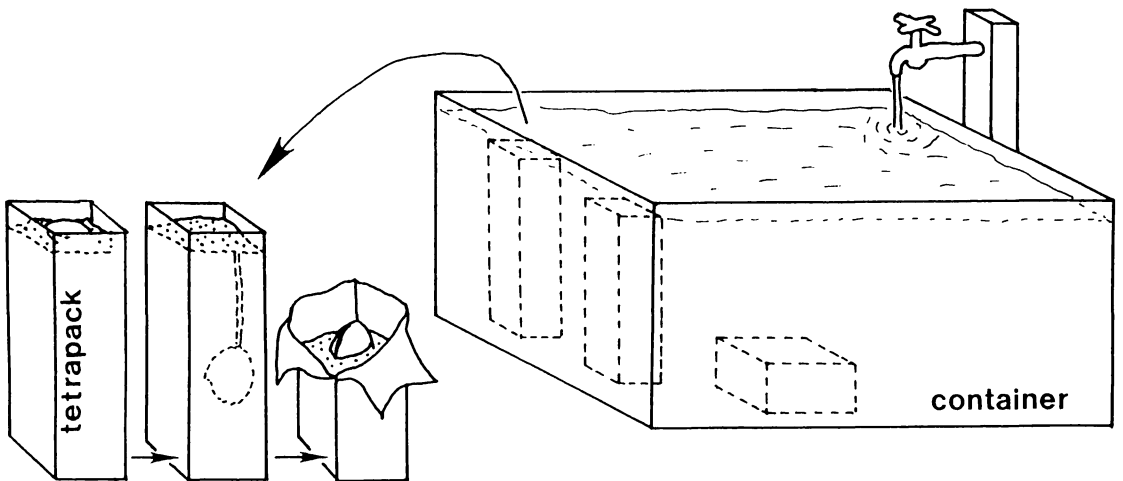


Figure 1. Observation of bivalve life position in the laboratory. For explanation, see text.

Stanley's (1970) definition.

Intraspecific variation in burrowing depth may be classified into three categories: (1) ontogenetic variation, (2) variation due to substratum difference, and (3) variation due to other causes.

*Ontogenetic variation:* This is the most conspicuous among the variations of different categories in burrowing depth of a bivalve species. All of the 7 species examined burrow more deeply as they grow large. Maximum burrowing depth of these species is roughly proportional to shell length. Observation on the intertidal sand flat of the Obitsugawa River delta (study area 2 in Table 1) shows that small individuals of *R. philippinarum* of about 1 cm in shell size, for example, burrow 1.5 cm and intermediate individuals (ca. 2 cm) 3 cm (Figure 2). On the basis of this proportional relationship, maximum burrowing depth (D) in relation to shell length (S) of *R. philippinarum* can be expressed as follows.

$$D = 1.5 S$$

Similarly, those of *C. sinensis* and *N. olivacea* can be expressed as:

$$D = 1.3 S \text{ (} C. \text{ sinensis)}$$

$$D = 3.9 S \text{ (} N. \text{ olivacea)}$$

This proportional relationship between maximum burrowing depth and shell length is quite reasonable, because the extended siphon length, which is comparable to maximum burrowing depth, increases with growth. Difference in maximum burrowing depth among the species examined will be stated in the next section, on the basis of this relationship.

In most species, however, the relationship is well applicable only to relatively small-sized individuals. For example, small-sized individuals of *D. japonicus*, up to 2 cm in shell length, burrow 5 times their shell length, while an individual of 6 cm can burrow only twice the shell length (12 cm).

Such "allometric shallowing" of burrowing depth is commonly recognized in other species, including *R. philippinarum*, *M. veneriformis* and *M. chinensis*. Stanley (1972) reported a more conspicuous example in *Mercenaria mercenaria* (L.): Young individuals (ca. 3–4 cm in

### *Ruditapes philippinarum*

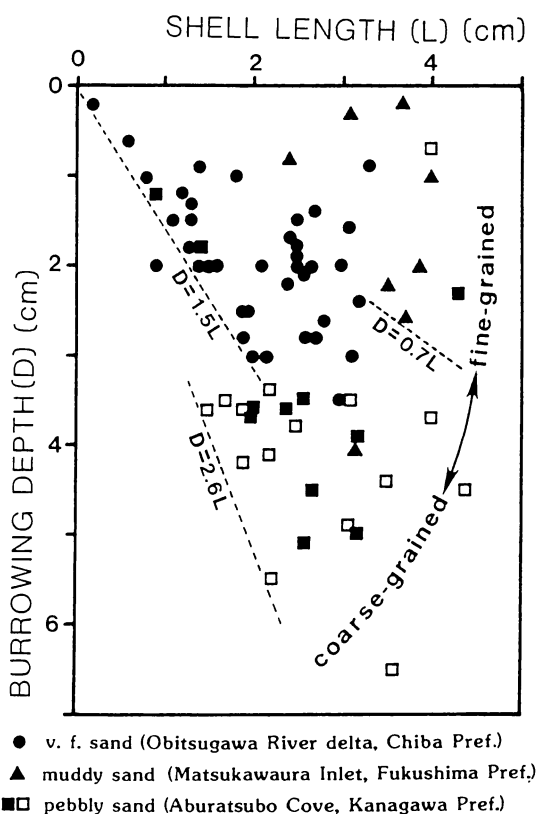


Figure 2. Intraspecific variation in burrowing depth of *Ruditapes philippinarum* in relation to ontogenetic change and substratum difference. Black symbols indicate measurements in nature and open ones in the laboratory tank.

shell length) burrow at 5 cm below the sediment surface, while large (6–7 cm length) ones less than 2 cm in depth. He explained this from the viewpoint of functional morphology: Small individuals are vulnerable to strong current and predators so that they must burrow as deeply and quickly as they can, while larger individuals which are hydrodynamically more stable and less vulnerable to predators need not to burrow so deeply.

*Variation due to substratum difference:* This is one of the important factors controlling the burrowing depth of living bivalves, although it is not well observed in many species. Most notable

example was obtained for *R. philippinarum*. In a very fine sand of the Obitsugawa River tidal flat, living individuals burrow 1.5 times their shell length. In contrast, they burrow shallower (0.7 times) in muddy sand of Matsukawaura tidal flat (study area 1), and deeper (2.6 times) in gravelly sand of Aburatsubo Cove (study area 4). These observations suggest that living animals of this species are apt to inhabit in deeper sediment as the substratum becomes coarser. However, it is not confirmed whether this rule can be applied to other bivalves.

Pratt and Campbell (1956) showed that living individuals of *Mercenaria mercenaria* are found more deeply in clean sand than those in muddy sediments. Stanley (1970, 1972) also provided an example of environmental variation in burrowing depth and life orientation of the same species. According to his observation, animals normally live in compact sand with the long axis of the shell oriented approximately 45 degrees to the vertical, whereas those in muddy substrata tend to live with their long axis nearly vertical.

*Variations due to other causes:* The intra-specific variation due to other causes is sometimes very large: e.g. burrowing depth of *R. philippinarum* of equal shell size (3–4 cm) range from 0.2 to 4.0 cm within one locality in Matsukawaura Inlet (study area 1). It is not apparent whether this variation stems from truly individual variation or from some other unknown causes. In this paper, this type of variation is tentatively included into individual variation.

#### Interspecific variation – Burrowing depth and life habit in *Bivalvia*

As is mentioned earlier, the difference in burrowing depth is compared conveniently by the relative depth – how many times its shell length they can burrow at the maximum. The values range from 0 (most non-siphonate species) to 5.0 (*Dosinorbis japonicus* of less than 2 cm long).

Absolute values of burrowing depth are, however, more meaningful in considering adaptation to physical environment. Figure 3 summarizes

absolute depth distribution of bivalves observed in this study. The graph shows that the depth distribution is not uniform but is concentrated into three ranges: 1) semi-infauna (partly exposed) and shallow burrowers less than 1 cm deep, 2) intermediate burrowers less than 15 cm deep, and 3) deep burrowers less than 30 or 40 cm deep. The most pronounced difference is seen between deep burrowers and other shallower burrowers.

Adult individuals of deep burrowers like *Panopea japonica* and *Mya arenaria*, are permanent burrowers, being unable to reburrow when disintered. Deep burrowing habit guarantees them not to be exposed to severe environmental condition, such as sediment reworking in severe storms for *P. japonica* of Kondo (1987MS) or high temperature for *M. arenaria* of Goshima (1982). On the other hand, most of the shallow burrowing bivalves buried less than 15 cm (mostly less than 10 cm) are active burrowers. They can survive, even if they are exposed on the surface during severe storms, for instance. In short, bivalves inhabiting in shallow water sand bottom are either active shallow burrowers or immobile deep burrowers. These are considered to be two basic adaptive strategies in shallow sandy bottom.

It is interesting to note that the average level of sediment reworking in shallow water sandy bottom is estimated to 15–20 cm, that is, depths between positions of shallow burrowers and deep burrowers (Kondo, 1987 MS). Adaptive divergence of infaunal bivalves in shallow water sand bottom into active shallow burrowers less than 15 cm depth and immobile deep burrowers more than 30 cm depth may be attributed to repeated sediment reworking of about 20 cm depth.

Amount of individual variation within a species also appears to vary among different life habit groups. Burrowing depths of most active burrowers are highly variable. Particularly, large-sized individuals are extremely variable: burrowing depth of *R. philippinarum* of 3–4 cm long ranges from 0.3 to 6.0 cm (Figure 2), for instance. In contrast, burrowing depth of immobile

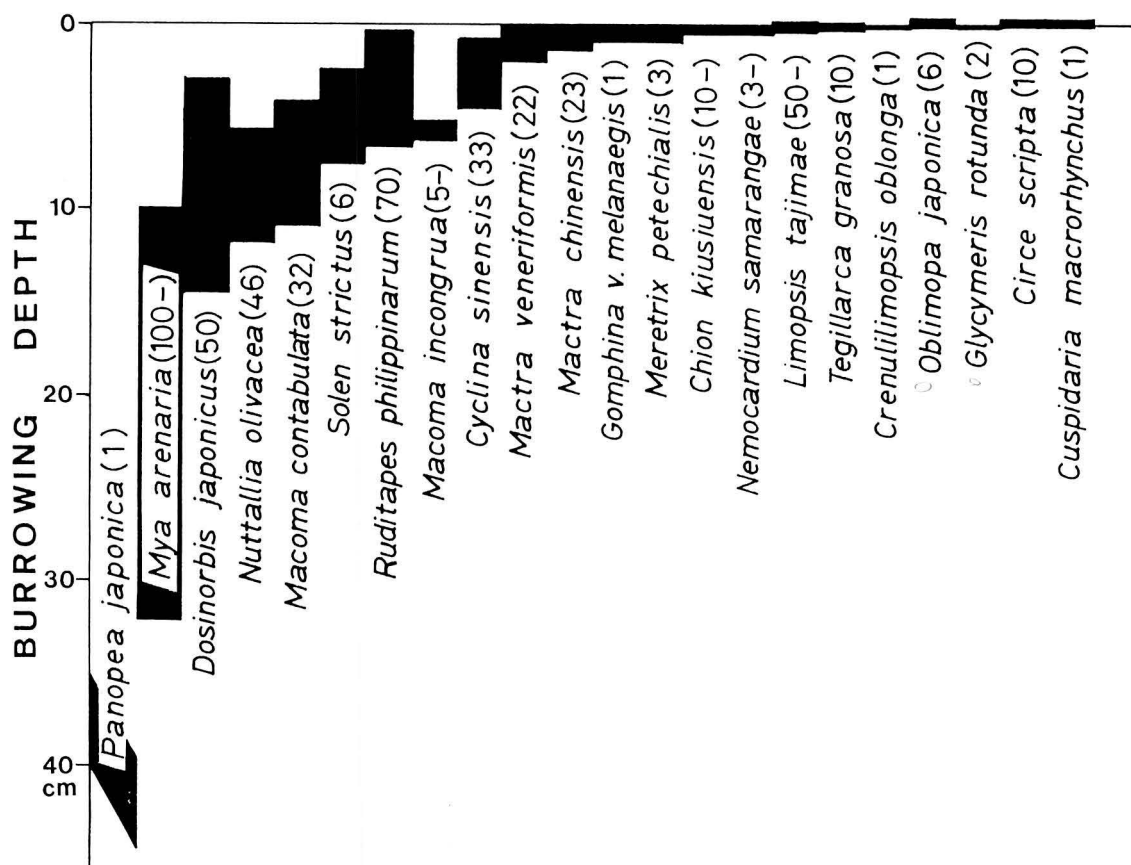


Figure 3. Depth distribution of infaunal bivalves observed in this study. Number of individuals observed is shown in parentheses.

deep burrowers is much less variable, as shown by *Mya arenaria* (fig. 14, Goshima, 1982). They appear to burrow to their maximum depth. This may be explained as follows: deepest burial is necessary for them to avoid reworking, because they can no longer live if they are reworked on the sea floor.

Burrowing depths of siphonate deposit feeders, such as *Macoma contabulata* and *Nuttallia olivacea* seem to fall into somewhere between permanent and active burrowers. They also tend to burrow as deeply as they can.

#### Taphonomic implication of the results

The above results are directly applicable to taphonomic and paleoecologic analysis of Recent

bivalve species yielded from the younger deposits. We have now at hand two kinds of data to reconstruct post-mortem disturbance operated in the different levels of sea bottom. One is shown by observation of differential preservation of life position among various-sized individuals of a single species. Particularly, a measure shown by extremely deep burrowers like *P. japonica* and *M. arenaria* is useful owing to the wide range of burrowing depth and little variation in burrowing depth of the same shell sizes. The other is shown by observation of differential preservation among species of different burrowing depth. Detailed observation of fossiliferous strata using both measures will reveal realistic post-mortem processes (Kondo, 1987 MS).

When we deal with extinct bivalves or living

species of which burrowing depths are unknown, the above measure can no longer be used and we must seek another clue to reconstruct burrowing depth from preservable shell morphology. Next section thus concerns with relationship between burrowing depth and shell morphology in Bivalvia.

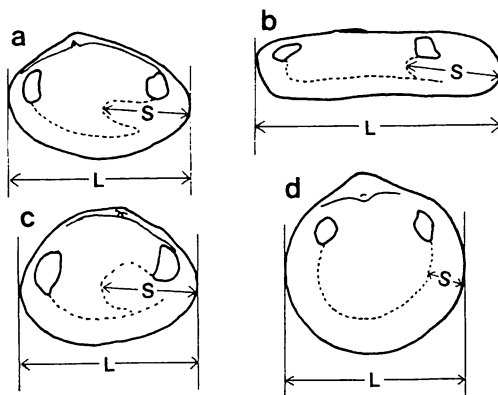
#### Pallial sinus length: an indicator of burrowing depth

On the basis of the extensive ecologic observations of the Western Atlantic bivalves, Stanley (1970) discussed the relation between the burrowing depth and shell morphology. He emphasized the shell thickness and ornamentation as closely related characters with burrowing depth. As shown in his graph (fig. 30, Stanley, 1970), all thick-shelled burrowing bivalves are restricted to shallow burrowers. However, all thin-shelled burrowers are not necessarily deep burrowers. Similarly, all strongly ornamented bivalves are shallow burrowers, while weakly ornamented bivalves are not always deep burrowers (fig. 32, Stanley, 1970). These relationships between the burrowing depth and shell morphology are significant in functional morphological point of view, but they are not applicable to infer the burrowing depth from shell morphology. More directly related character to burrowing depth should be sought.

The burrowing depth of bivalves can be regarded as length of the siphon at its maximum extension in many cases. Pallial sinus seen on the inner surface of siphonate bivalves represents accommodation space of contracted siphon, and has long been regarded as an approximate measure of burrowing depth. In this study, I reevaluate the pallial sinus length as a measure of burrowing depth based on my own data on Japanese species, and also those of Stanley's work (1970).

#### Measurements of pallial sinus length

Measurement of the pallial sinus of siphonate bivalves was made directly with calliper as shown in Figure 4. Pallial sinus length is defined



**Figure 4.** Measurement of pallial sinus length. Measured part is shown for the right valve of representative species. S: pallial sinus length, L: shell length, a: *Ruditapes philippinarum* (active burrowing suspension feeder), b: *Sinonovacula constricta* (probable burrow dweller), c: *Macoma incongrua* (deposit feeder), d: *Fulvia mutica* (active burrowing suspension feeder without pallial sinus).

as a distance from the innermost part of the sinus to posterior shell margin, so as to represent the length of contracted siphon. Some bivalves such as cardiids and some venerids do not show pallial sinus, but they do have siphons. It is not appropriate to adopt pallial sinus length itself to represent contracted siphon length. Pallial Sinus Index (PSI) is thus defined here as ratio of the length from the innermost part of the sinus to the posterior shell margin, to shell length.

Table 2 summarizes measurements of PSI for 38 siphonate bivalves, together with their maximum relative burrowing depth. Intraspecific variation in PSI does not exceed 0.1 in the species examined, except for *Panopea japonica*, *Mercenaria mercenaria* and *Ruditapes philippinarum*. *Panopea japonica* show exceptionally variable PSI. The variation is due partly to ontogenetic decrease, but variation within the individuals of the same shell size is also larger than other species.

Ontogenetic decrease of PSI is seen in other species such as *Dosinorbis japonicus* and *Tresus keenae* (Kuroda et Habe). Only *R. philippinarum* shows ontogenetic increase of PSI.

Table 2. Measurements of Pallial Sinus Index for 38 siphonate bivalves.

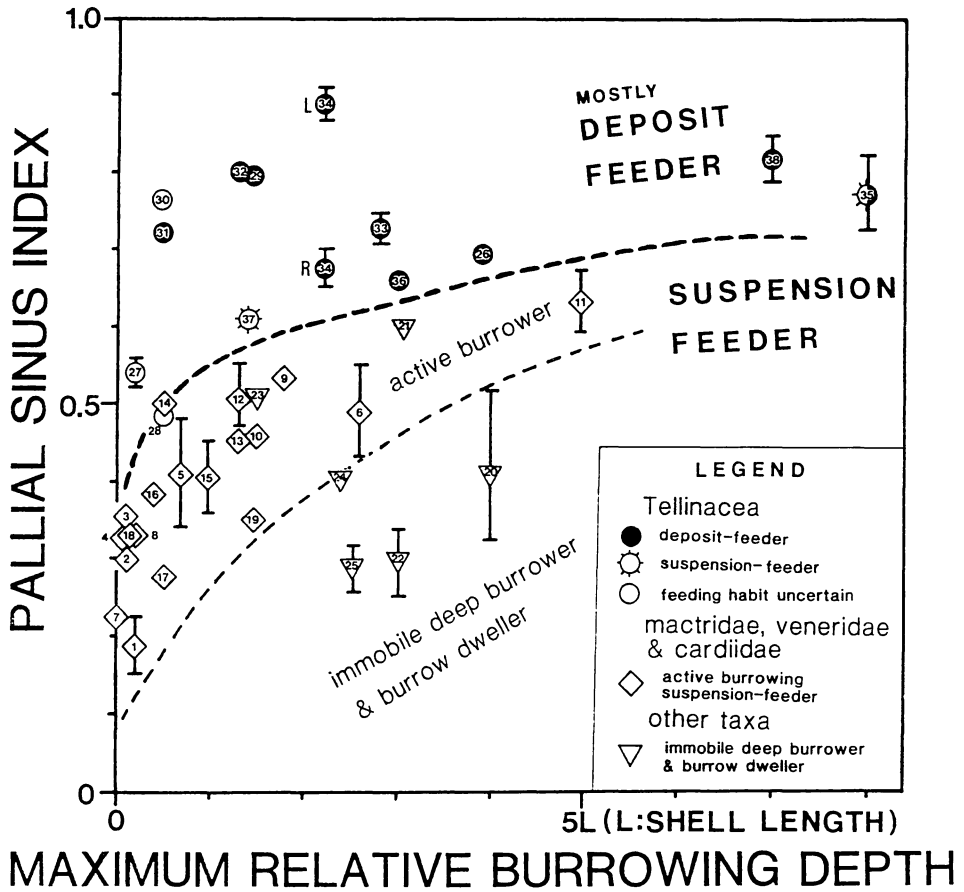
Species Name	Pallial Sinus Index (No. of measurement) (source)	Relative maximum burrowing depth (source)
1. <i>Nemocardium samarangae</i> (Makiyama)	0.149–0.226 (3)	0.2 (a)
2. <i>Chione canacellata</i> (L.)	0.284–0.312 (2)	0–0.1 (b)
3. <i>C. granulata</i> (Gmelin)	0.348–0.358 (1)	0.1 (b)
4. <i>C. paphia</i> (L.)	0.312–0.335 (1)	0–0.1 (b)
5. <i>Mercenaria mercenaria</i> (L.)	0.339–0.478 (8)	0.7 (c)
6. <i>Ruditapes philippinarum</i> (Adams et Reeve)	0.431–0.552 (16)	2.6 (a)
7. <i>Circe scripta</i> (L.)	0.218–0.235 (3)	0 (a)
8. <i>Meretrix petechialis</i> (Lamarck)	0.320–0.337 (4)	0.1 (a)
9. <i>Cyclina sinensis</i> (Gmelin)	0.513–0.553 (4)	1.3, 1.8 (a)
10. <i>Cyclinella tenuis</i> (Récluz)	0.458 (1) (b)	1.5 (b)
11. <i>Dosinorbis japonicus</i> (Reeve)	0.595–0.674 (18)	5.0 (a)
12. <i>Dosinia elegans</i> (Conrad)	0.469–0.552 (5)	1.3 (b)
13. <i>Antigona listeri</i> (Gray)	0.455–0.471 (1)	1.3 (b)
14. <i>Mactra fragilis</i> Gmelin	0.481–0.515 (3)	0.5 (b)
15. <i>M. veneriformis</i> Reeve	0.357–0.451 (7)	1.0 (a)
16. <i>M. chinensis</i> Philippi	0.388–0.391 (7)	0.4 (a)
17. <i>Rangia cuneata</i> Gray	0.283 (1) (f)	0.5 (b)
18. <i>Spisula solidissima</i> (Dillwyn)	0.317–0.347 (2)	0.1 (b)
19. <i>Raeta rostralis</i> (Reeve)	0.326–0.368 (4)	1.5 (a)
20. <i>Panopea japonica</i> A. Adams	0.323–0.520 (16)	4– (a)
21. <i>Mya arenaria</i> (L.)	0.585–0.607 (6)	3.0 (d)
22. <i>Barnea dilatata</i> Yokoyama	0.247–0.341 (3)	3 (a)
23. <i>Laternula limicola</i> (Reeve)	0.519 (1)	1.5 (a)
24. <i>Sinonovacula constricta</i> (Lamarck)	0.382–0.413 (5)	2.4 (c)
25. <i>Solen strictus</i> Gould	0.257–0.317 (6)	2.5 (a)
26. <i>Nuttallia olivacea</i> (Jay)	0.689–0.702 (5)	3.9 (a)
27. <i>Donax variabilis</i> Say	0.518–0.559 (2)	0.2 (b)
28. <i>D. denticulatus</i> L.	0.483 (1)	0.5 (b)
29. <i>Tellina similis</i> Sowerby	0.805–0.835 (2)	1.6–1.7 (b)
30. <i>T. radiata</i> L.	0.754–0.782 (4)	0.4–0.5 (b)
31. <i>T. listeri</i> Röding	0.711–0.728 (1)	0.4–0.5 (b)
32. <i>T. alternata</i> Say	0.788–0.811 (5)	1.3 (b)
33. <i>Macoma contabulata</i> (Deshayes)	0.705–0.749 (5)	2.8 (a)
34. <i>M. incongrua</i> (v. Martens)	0.866–0.909 (6)	2.2–2.3 (a)
35. <i>M. balthica</i> (L.)	0.733–0.823 (6)	8.0 (b)
36. <i>Arcopagia fausta</i> (Pulteney)	0.625–0.673 (2)	3 (b)
37. <i>Semele proficus</i> (Pulteney)	0.600–0.622 (1)	1.4–1.5 (b)
38. <i>Strigilla carnaria</i> (L.)	0.788–0.847 (2)	7 (b)

Sources: a, this study; b, Stanley, 1970; c, Stanley, 1972; d, Goshima, 1982; e, Sugano, 1981; f, Cox, *et al.*, 1969, Fig. E94, 2b.

#### Utility and limitation of Pallial Sinus Index as a measure of maximum burrowing depth of bivalves

Figure 5 shows the relationship between the PSI and the maximum relative burrowing depth. Three life habit groups, namely, deposit feeders,

active burrowers and immobile deep burrowers, apparently occupy the different region on the graph. This strongly suggests different function of their siphons. Maximum burrowing depth in active burrowing siphonate suspension feeder represented by venerids and mactrids increase as PSI becomes large. This “sinus-depth relation”



**Figure 5.** Relation between maximum relative burrowing depth and Pallial Sinus Index. Different life habit groups appear in different region of the graph. In active burrowing suspension-feeders represented by venerids and mactrids, maximum relative burrowing depth increases rapidly as the increase of the Pallial Sinus Index. Numbers in the figure represent species shown in Table 2. Two plots of No. 34 (*Macoma incongrua*) shows different measurements for right and left valves.

seems natural, because larger sinus is needed to accommodate longer siphon.

Lower right region of the graph is occupied by immobile deep burrowers like *Panopea japonica* and *Barnea dilatata*. They have pallial sinus shorter than those expected from their burrowing depth. This is reasonable because the immobile deep burrowers cannot withdraw their siphons and they do not need the accommodation space within the shell. Burrow dwellers (Savazzi, 1986) like *Solen strictus* and *Sinonovacula constricta* also tends to lie lower right region. This may be explained by the fact that the siphon length do not necessarily show the

burrowing depth: They can escape into the deep permanent burrows which are longer than the siphon length.

Siphonate deposit feeders represented by Tellinidae appear in the upper region of the graph. This means that they have deeper pallial sinus than suspension-feeders of the same burrowing depth do. This is also reasonable because their siphons are feeding organs projecting well on the sediment surface to feed on surface deposits (Young, 1949; Holme, 1961; Stanley, 1970).

In summary, PSI of only active burrowing suspension feeders can be used as a key morphology. The empirical relationship shown in



Figure 5 may allow prediction of maximum relative burrowing depth of living bivalves of which burrowing depth is unknown. If we assume that the relationship was applicable in the geologic past, it can also be used in extinct bivalves.

As is obvious in Figure 5, it is almost impossible to infer maximum burrowing depth of deposit feeding bivalves from the PSI. Immobile deep burrower and burrow dweller are also difficult to infer the burrowing depth. In summary, PSI is practically useful in siphonate suspension feeding bivalves represented by venerids. We cannot, of course, reconstruct the burrowing depth of non-siphonate bivalves such as lucinaceans. Shell thickness and shell ornamentation are not very useful index, either. At the present knowledge, there is no useful character in shell morphology to infer the burrowing depth of these bivalves.

Another line of approaches concerns with outcrop observation. For example, in the case that fossil bivalves are buried *in situ* in the sediment, in which any exotic materials such as thin fine tuff or scoria bed is intercalated, we may directly know the probable burrowing depth of the bivalve by recognizing the distance of the lowest presence of the tuff or scoria. Burrowing depth of fossil *Panopea japonica* is at least 50 cm (Figure 6), as estimated in this manner in the Late Pleistocene Shimosa Group, Chiba Prefecture, Japan. This method appears to be most reliable, although its application is rather restricted. It is also important to test its validity of "sinus-depth relation" by such field observations.

### Conclusions

(1) In most infaunal bivalves, maximum burrowing depth increases as they grow in a proportional manner. It is then convenient to express maximum burrowing depth of each species as a relative value – the ratio of maximum burrowing depth to the shell length. The above proportional relationship is, however, unclear in larger individuals. Relative burrowing depth of larger

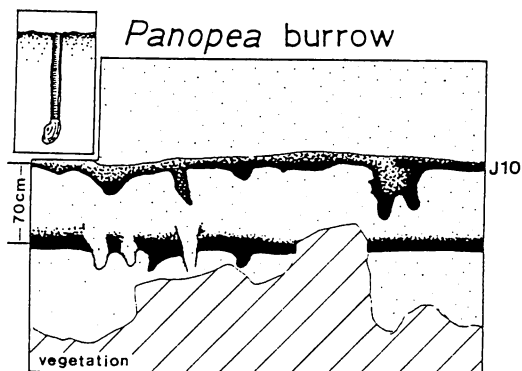


Figure 6. Possible *Panopea* burrow observed in the Late Pleistocene Jizodo Formation, at Okura, Ichihara City, Chiba Prefecture, Central Japan. Fine scoria sand numbered as J10 (Tokuhashi and Endo, 1984) and black mud are intercalated in the poorly-bedded bioturbated very fine sand. Large burrows observed were formed before and after the deposition of the intercalation. No fossils were found in the burrow. However, *Panopea japonica* valves were found in a burrow *in situ* similar to these in size and shape in another outcrop.

individuals of many species are generally shallower than those of smaller ones.

(2) Interspecific difference in burrowing depth among infaunal bivalves reflects well different life habit of each species. Difference between shallow active burrowers and immobile deep burrowers is especially large. In shallow subtidal sandy bottom, burrowing depths of most bivalves capable of active movement are less than 15 cm. Greater burrowing depth (more than 30 cm) is attained only by immobile burrowers like *Panopea japonica*. This may be significant in considering adaptive strategy and evolution of infaunal bivalves: In shallow subtidal sandy bottom, average levels of sediment reworking is 15~20 cm, and repeated sediment reworking resulted in divergence into active, shallow burrowers and immobile deep burrowers.

(3) Ratio of pallial sinus length to shell length (Pallial Sinus Index: PSI), is useful in inferring the maximum relative burrowing depth of active burrowing, suspension-feeding siphonate bivalves including extinct species. Reconstruction of burrowing depth is, however, difficult owing to the "allometric shallowing" of bur-

rowing depth. We cannot infer burrowing depth of deposit-feeding siphonate bivalves from the PSI. Field observation of *in-situ* bivalve fossil remains may be more reliable to infer the actual burrowing depth.

## Appendix

### Description of life position of some common Japanese infaunal bivalves

#### Notes on physiography and molluscan communities of the study areas

##### (1) Matsukawaura Inlet, Some City, Fukushima Prefecture

Matsukawaura is a small inlet of about 4 km in N-S trend, situated on the Pacific side of northern Honshu. It is shallow in water depth, closed with a sand bar running south to north, and connected to the Pacific through 120 m wide opening at its northeastern end. A sand flat in the northern part of the inlet has been famous for clamming. Systematic survey of the molluscan fauna within the inlet was made by Kotaka *et al.* (1955). My observation was carried out at an intertidal muddy sand flat in the northwest of the inlet, near a small sand spit projecting toward the center of the inlet. At the locality occurs a dense population of bivalves, such as *Ruditapes philippinarum*, *Cyclina sinensis*, *Nuttallia olivacea*, *Macoma contabulata* and *Later-nula limicola* (Reeve). Banks of *Crassostrea gigas* (Thunberg) also occur patchily on the nearby soft muddy bottom (fig. 7-2, Chinzei, 1982).

##### (2) Obitsugawa River delta, Kisarazu City, Chiba Prefecture

An arcuate delta of the Obitsugawa River is developed on the eastern coast of Tokyo Bay. An intertidal sand flat of 2 km wide spreads on the seaward of the delta coast, fringing the arcuate coastline. The geomorphic and other environmental settings of this tidal flat were described by Kosugi (1986). *Macraa veneriformis* and locally *Umbonium moniliferum* (Lamarck) are abundant on the middle tidal flat where *Zostera nana* is densely distributed. Extremely abundant individuals of *Ruditapes philippinarum*

are due to an artificial scattering for a commercial purpose. A lower tidal flat is inhabited by *Dosinorbis japonicus* and *Solen strictus*. Subtidal zone is characterized by a dense population of *Macraa chinensis* with association of *Fulvia mutica* (Reeve) and *Clinocardium buellowi* (Rolle).

##### (3) Aburatsubo area, Miura City, Kanagawa Prefecture

Aburatsubo is a small inlet with a width of 100–200 m and a length about 500 m. Near the mouth of the inlet lies Misaki Marine Biological Station of the University of Tokyo. An intertidal gravelly sand flat near the station is inhabited by *Ruditapes philippinarum*, *Dosinorbis japonicus* and more rarely *Saxidomus purpuratus* (Sowerby) and *Heteromacoma irus* (Hanley). The flat is covered by mats of *Musculus senhausia* (Benson). Only dead shells of *Mya arenaria* were found in life position in the gravelly sand. Small-sized and thin-shelled species as *Raeta rostralis* (Reeve) and *Theora lubrica* Gould are living in the subtidal mud of the inlet.

*Oblimopa japonica* A. Adams, *Glycymeris rotunda* Dunker, *Venus foveolata* Sowerby, *Nemocardium samarangae* (Makiyama), and *Cuspidaria macrorhynchus* Smith are common in sandy mud of about 100 m deep, 2 km northwest off Aburatsubo in Sagami Bay (Horikoshi, 1957). They were dredged by R/V Rinkai-Marui of the Misaki Marine Biological Station and observed in the laboratory.

##### (4) Off Osezaki, Suruga Bay, Shizuoka Prefecture

A large population of *Limopsis tajimae* Sowerby is distributed in the northeastern part of Suruga Bay, off Osezaki (Horikoshi and Tanaka, 1980; Horikoshi *et al.*, 1983; Kondo, 1986). Sampling station is 200–300 m in deep, and the bottom substrate consists of soft mud. A molluscan fauna at this station is characterized by high species diversity; major constituents are *Limopsis tajimae*, *Yoldia similis* Kuroda et Habe, *Acila divaricata* Adams et Reeve, *Crenulimopsis oblonga* A. Adams, *Modiolus margaritaceus* (Nomura et Hatai), *Machaeroplax myssona* (Dall), and *Antalis rhabdotum* (Pilsbry). A box

core sampler was used to observe life position of *Limopsis tajimae* in KT-86-1 cruise of R/V Tansei-Marui of the University of Tokyo.

(5) Tsuyazaki area, Fukuoka City, Fukuoka Prefecture

A small inlet, named Irie, is situated in the northwest of Tsuyazaki. The inlet, about 2 km in maximum length, extends from north to south, and opens to the Genkainada Sea through a narrow channel. The environmental settings of this tidal flat was described by Shimoyama (1984). Dominant bivalves at an intertidal muddy sand flat in the inner part of the inlet, are *Solen strictus*, *Macoma incongrua* (v. Martens), *Cyclina sinensis* and *Ruditapes philippinarum*.

Distribution of *Circe scripta* (L.) are restricted to intertidal pebbly sand of the inlet mouth.

(6) Nata, Fukuoka Prefecture

A long sand bar is developed in the north of Fukuoka City, by which Hakata Bay is separated from the Genkainada Sea. Nata beach is situated on the north side of the sand bar facing Genkainada Sea. A single individual of *Gomphina veneriformis melanaegis* Römer and numerous *Chion kiusiensis* (Pilsbry) were collected in the intertidal sandy beach.

(7) Shioya, Kumamoto Prefecture

Shioya is located in the southeastern part of Ariake Bay. *Tegillarca granosa* L. is commonly found on an intertidal mud flat (Iwasaki, 1983), associated with *Cyclina sinensis* and *Arcopagia diaphana* (Deshayes).

*Tegillarca granosa* is rather rare in June, 1986, though it was found abundantly until several years ago (Y. Iwasaki, personal communication). This may be caused by environmental changes due to artificial deposition of a large amount of exotic sand in the offshore area of this mud flat.

#### Description of life position and other ecological attributes

##### *Tegillarca granosa* (L.)

About ten individuals were observed on the intertidal mud flat at Shioya, Kumamoto City, Kumamoto Prefecture.

Like other infaunal arcids (Stanley, 1970), this species lives with its posterior flat surface being horizontal, just above the sediment surface. The commissure plane may incline on both sides, though the deviation from the vertical is small. The posterior flat surface, exposing when alive, is commonly encrusted by barnacles.

##### *Glycymeris rotunda* (Dunker)

Four individuals were collected from the sandy mud of about 100 m deep, off Aburatsubo. In the eastern part of Sagami Bay, this species occur commonly in muddy substrata, but is rare in shelly coarse sand bottom. The preference of muddy substrata seems to deviate from the general preference of rigorous environment of this genus (Thomas, 1975).

Four individuals were laid on the native sediment in the laboratory tank overnight. The smallest individual attained vertical, posterior-up life orientation, with the posterior margin just beneath the sediment surface. Middle-sized one burrowed completely within the sediment at 5–10 mm below the sediment surface, with the commissure plane oblique. Remaining two large individuals did not burrow during the observation. This result is not adequate to draw a definite conclusion on life position of this species, but it does not differ very much from the life habit described by Stanley (1970) for a congeneric species, *Glycymeris pectinata* (Gmelin).

##### *Limopsis tajimae* Sowerby

This species is common in mud bottom of upper bathyal zone in the Western Pacific under influence of Kuroshio warm current. It occurs very abundantly in the northeastern part of Suruga Bay, off Osezaki, 200–300 m deep (Station B, Horikoshi and Tanaka, 1980). Life habit of this species was observed by means of a box core sampler at the station in February, 1986. The substratum sampled together with abundant living specimens is soapy, fine-grained mud.

This species has a horizontal life position; lying on one valve, indifferently right or left,

just beneath the sediment surface. The commissure plane is roughly horizontal, though there are some individuals showing variable orientation. This life position is similar to that of an Atlantic species, *Limopsis aurita* (Brocchi) reported by Oliver and Allen (1980) and Oliver (1981). Some individuals were observed to burrow a few centimeter from the surface. The horizontal life position is well reflected to the distribution of epibionts attached on the shells, such as small mytilid *Modiolus margaritaceus*; wide range of distribution on either side of the shells shows horizontal, very shallow or exposed life position.

*Oblimopa japonica* (A. Adams)

More than ten individuals were dredged from muddy sand bottom of about 100 m deep, off Aburatsubo. Six individuals were laid, with their right valve down, on their native sediment in the tank, and were left overnight. They crawled on the sediment surface, leaving sinuous traces. All of them were oriented vertical to slightly oblique to the sediment surface, with at least half of their shells being exposed. This orientation corresponds to 'erect probing orientation' (Stanley, 1970) of most burrowing bivalves: orientation with the ligament axis roughly horizontal. Most of the individuals examined secreted byssus of 1 to 2 cm long, attaching to coarse sand grains. This life position differs greatly from that of *Limopsis tajimae* of the same family.

*Crenulilimopsis oblonga* (A. Adams)

A large number of individuals were collected with beam trawl from mud of 200–300 m deep at the northeastern part of Suruga Bay, off Osezaki. Several individuals were permitted to burrow in their native sediment. Only one individual attained life position, which was vertical, posterior-up orientation, with the posterior margin above the sediment surface. The rocking movement was very slow, once in every 30 to 60 seconds.

*Nemocardium samarangae* (Makiyama)

Several individuals were collected from muddy sand of about 100 m deep, off Aburatsubo. Life position of this species was observed within their native sediment in the laboratory. Burrowing behavior and life position observed were consistent with those of cardiids described by Stanley (1970). Living animals quickly burrow and reach the life position in several rocking movements. Slightly forward rotation from the erect probing orientation is needed to attain life position. The siphon is short and an individual of 3 cm long burrowed only 0.5 cm.

*Circe scripta* (L.)

About ten individuals were collected from the gravelly sand in the intertidal zone near the mouth of Tsuyazaki inlet, Fukuoka Prefecture. The substratum is partly grass-covered pebbly sand. Living animals were found completely exposed, on one valve in nature. In the laboratory tank, six individuals were permitted to burrow in exotic fine sand with their right valve down overnight. They attained an oblique orientation, with their anterior half buried in the sediment. The upward valves are either right or left.

The posterior area of every specimen observed was attached with calcareous algae, and this suggests normal life position of this species is oblique, with their anterior half in the sediment as observed in the laboratory. In the Veneracea this species may be one of the rare examples which show non-vertical life orientation.

*Meretrix petechialis* (Lamarck)

This species is distributed in the coastal areas of Korea and China (Okutani and Habe, 1975). Several individuals were purchased at a fish market in Aburatsubo. In the laboratory, they were released on very fine sand, which is similar to their probable native sediment. Living animals show a vertical life orientation, with their long axis nearly vertical to the sediment surface. An individual of 6 cm long could burrow at a depth of about 1 cm.

*Gomphina veneriformis nelanaegis* (Römer)

A single individual was collected from intertidal zone of sandy beach of the Genkainada sea, Nata, Fukuoka Prefecture. Life position was observed in their native clean sand in the laboratory: The commissure plane is vertical, with the long axis nearly vertical. Burrowing depth is several millimeters. The posterior portion is attached by green algae, showing nearly exposed condition in life.

*Cyclina sinensis* (Gmelin)

Life position of this species was observed at two localities; the intertidal muddy sand flat of Matsukawaura Inlet, and the intertidal sandy mud flat of Tsuyazaki Inlet. At both localities, this species shows a vertical, posterior-up orientation. Maximum burrowing depth of living animals tends to increase as they grow. The maximum relative burrowing depth is 1.3 in Matsukawaura (Figure 7), whereas it is 1.8 in Tsuyazaki.

*Dosinorbis japonicus* (Reeve)

Life position of this species was observed in nature on the intertidal sand flat of the Obitsu-gawa River delta. Laboratory observation was also made for individuals from the intertidal gravelly sand of Aburatsubo Cove.

Living animals show a vertical, mostly posterior-up and occasionally beak-up orientation. Maximum burrowing depth increases as they grow. In small individuals burrowing depth is about 5 times as deep as their shell length (Figure 7). Young individuals of this species have the maximum value of the relative burrowing depth among the bivalve species examined in this study. Large individuals, however, do not burrow so

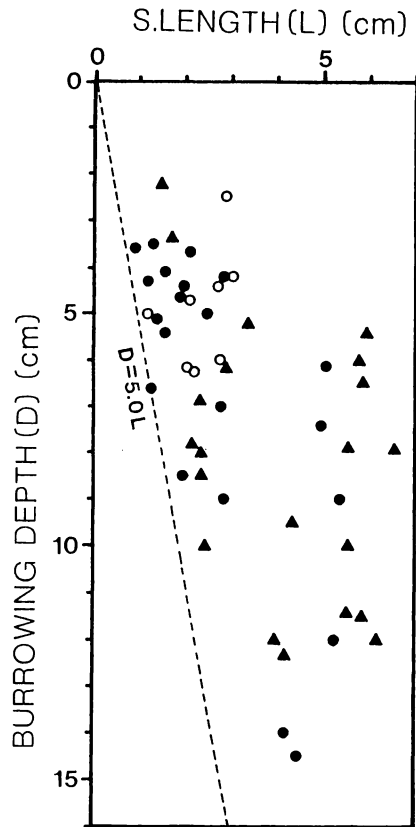
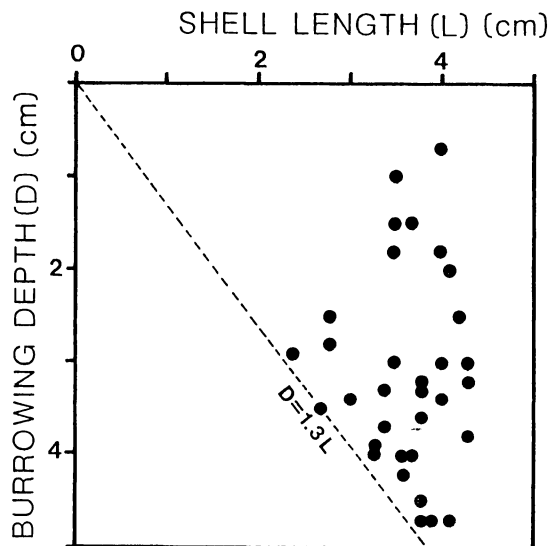
*Dosinorbis japonicus**Cyclina sinensis*

Figure 7. Ontogenetic variation in burrowing depth of *Dosinorbis japonicus* observed in Aburatsubo area ( $\bullet$ ,  $\circ$ ) and the Obitsu-gawa River delta ( $\blacktriangle$ ), and of *Cyclina sinensis* in Matsukawaura Inlet. Black symbols indicate measurement in nature and open ones in the laboratory tank.

deeply in relation to their shell length than young ones. The maximum burrowing depth in the specimens examined is 15 cm.

*Ruditapes philippinarum* (Adams et Reeve)

This species is one of the most common edible bivalves in Japan. A large number of individuals were observed at three localities: intertidal muddy sand flat of Matsukawaura Inlet, intertidal sand flat of the Obitsugawa River delta, and intertidal gravelly sand of Aburatsubo Cove. The substrata in the study area are variable from muddy sand to gravelly sand.

This species shows a vertical, posterior-up orientation, with its long axis slightly oblique from the vertical at every locality. Relative maximum burrowing depth is variable according to the substratum type: ranging from 2.6 times its shell length (gravelly sand of Aburatsubo Cove) to 0.7 (muddy sand of Matsukawaura) as shown in Figure 2.

Young individuals smaller than 2 cm long employ byssus to attach a small pebble or a sand grain.

I happened to observe orientation during escape from burial with sediment. In this situation, all the individuals show anterior-up vertical orientation. This orientation is the same as the "inverted erect probing orientation" of Krantz (1974), and suggests that this species pulls themselves with foot upward during escape from

burial.

*Mactra veneriformis* Reeve

Life position of this species was observed on the intertidal sand flat of the Obitsugawa River delta. This species shows an erect probing orientation with the posterior flattened surface nearly horizontal to the sediment surface. Life orientation is with the long axis nearly vertical. The maximum relative burrowing depth is 1.0 (Figure 8).

*Mactra chinensis* Philippi

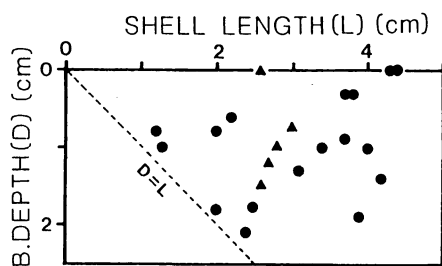
Small individuals of this species were observed in nature on the intertidal sand flats of Ena Bay, near Aburatsubo. Large individuals were dredged in great abundance from sandy mud of about 10 m deep, off Obitsugawa River delta.

Erect probing orientation is with the posterior flattened surface horizontal. When this species attains life position, the long axis of the shell is directed nearly vertical. The maximum relative burrowing depth is 0.4 (Figure 8).

*Chion kiusiuensis* (Pilsbry)

A number of individuals were collected from the sandy intertidal zone of Nata beach. Observed life orientation is vertical, with the posterior flat margin horizontal at just beneath the sediment surface. Judging from the extended

*Mactra veneriformis*



*Mactra chinensis*

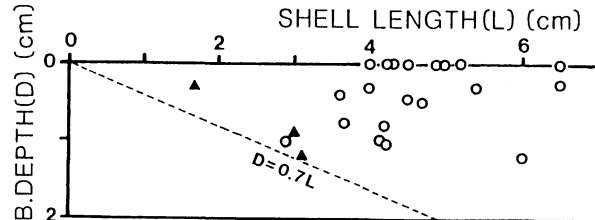


Figure 8. Ontogenetic variation in burrowing depth of *Mactra veneriformis* and *M. chinensis* observed in the Obitsugawa River delta (●○) and Ena Bay (▲). Black symbols indicate measurement in nature and open ones in the laboratory tank.

siphon length of about half of the shell size, animals can probably burrow at the same depth.

*Nuttallia olivacea* (Jay)

A large number of individuals were observed in the intertidal muddy sand flat of Matsukawaura Inlet. The life orientation observed is a vertical, posterior-up, with the posterior flat margin approximately horizontal. The maximum relative burrowing depth is 3.9 (Figure 9). The siphon of this species is slender and long, being similar to that of deposit-feeding tellinids. I did not, however, observe deposit-feeding activities of this species.

*Macoma contabulata* (Deshayes)

A large number of individuals were observed on the intertidal muddy sand flat of Matsukawaura Inlet. The life orientation observed is vertical, posterior-up, with the long axis roughly vertical. This vertical orientation is rather unusual in tellinids, most of which employ right-

valve-up, horizontal orientation (Holme, 1961; Stanley, 1970). However, the nearly equivalve condition of this species seems to suggest a vertical life orientation, as in *Macoma balthica* (L.) described by Stanley (1970). The maximum relative burrowing depth is 2.8 (Figure 9).

This species was observed to deposit feed, using the vermiform siphon.

*Macoma incongrua* (v. Martens)

Only dead specimens of this species were observed, although it was formerly abundant on the intertidal sandy mud bottom of Tsuyazaki Inlet. They still preserve their probable normal life position within the sediment. The "life orientation" observed is roughly horizontal with their right valve upward. Burrowing depth is almost constant, and the maximum relative depth ranges from 2.2 to 2.3.

*Solen strictus* Gould

Several individuals were observed on the intertidal sand flat of the Obitsugawa River delta. This species is abundant in the lower part of the sand flat, commonly associated with *Dosinorbis japonicus*. Living animals are found in burrows which is very thinly lined with silt. Owing to the lining, the inner wall of the burrow is smooth. The burrows are usually oriented 0 to 30 degrees from the vertical. When observed, most of the individuals were found in the lowermost part of the burrows, although they are supposed to be able to go up and down in the burrows. Maximum length of the burrows are 3.5 times the shell length. Maximum relative burrowing depth is, therefore, 2.5.

*Panopea japonica* A. Adams

The specimens observed were purchased at a fish market in Aburatsubo. In an attempt to know the extended siphon length, the specimen was buried within the sediment, keeping an assumed life orientation. The maximum extension of the siphon within the sediment is regarded as the burrowing depth of this species.

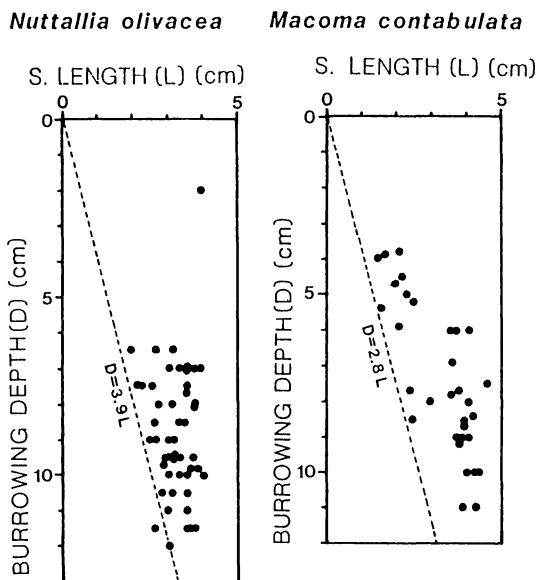


Figure 9. Ontogenetic variation in burrowing depth of *Nuttallia olivacea* and *Macoma contabulata* observed in nature on the intertidal flat of Matsukawaura Inlet.

In this way, probable maximum burrowing depth was measured about 4 times the shell length. The average adult individuals thus burrow as deep as 40–50 cm.

#### *Cuspidaria macrorhynchus* Smith

A few individuals were dredged from the sandy mud of about 100 m deep, off Aburatsubo. Living animals show a vertical posterior-up life orientation, with the long axis nearly vertical. The posterior projected part of the shell is exposed above the sediment surface.

#### *Laternula limicola* (Reeve)

Several individuals were observed on the intertidal muddy sand flat of Matsukawaura Inlet. Living animals keep a vertical posterior-up life orientation, with the long axis 15 degrees inclined from the vertical. The maximum relative burrowing depth is 1.5.

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Matsukawaura 松川浦, Obitsugawa River 小櫃川, Kisarazu 木更津, Aburatsubo 油壺, Miura 三浦, Sagami 相模, Osezaki 大瀬崎, Suruga Bay 駿河湾, Tsuyazaki 津屋崎, Nata 奈多, Hakata Bay 博多湾, Genkainada Sea 玄海灘, Shioya 塩屋, Ariake Bay 有明海, Ena Bay 江奈湾。

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内生二枚貝の潜入深度——現生種の観察および殻形態との関係：日本各地の干潟などで22種の内生二枚貝の底質への潜入深度を計測した。

二枚貝の潜入深度は、同一種であっても、体サイズ、底質、その他の条件によって変化するので、ある種の潜入深度を簡単に表現することはできない。しかし、潜入深度の最大値に注目すると、それは体サイズの成長にはほぼ比例して増大することが分かった。したがって、最大潜入深度の体サイズに対する比を用いてその種の潜入能力を表現しておくことと便利である（例えば、アサリは2.6、カガミガイは5.0）。

潜入深度が種ごとに違うのはそれぞれの生活様式の違いをよく反映しているためである。特に著しいのは、アサリやバカガイのように、浅く潜りながら（概して15cmより浅い）、洗い出されても再び潜る能力を備えた種類と、ナミガイのように極めて深く潜るかわりに（30–40cmより深い）洗い出されたあと再び潜る能力を放棄した種類との違いであって、これらは頻繁に海底面上に洗い出される危険の高い浅海の、特に砂底において内生二枚貝が取り得るふたつの生活様式である。

化石種の潜入深度を復元するためには、套線湾入の深さ（ただし、水管を持ち活発に潜る濾過食者に限られる）が、最も有効であることが分かった。しかし、このような殻形態に基づく復元には限界があり、自生的産状の化石の露頭観察などの直接的な証拠に基づいた復元もあわせて行うことが望ましい。

近藤康正

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## 848. CRETACEOUS *CAESTOCORBULA* (BIVALVIA) FROM JAPAN\*

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**Abstract.** Six species of the genus *Caestocorbula* Vincent, including three new species, *C. antiqua*, sp. nov., *C. monobensis*, sp. nov. and *C. ohtai*, sp. nov., are described from ten localities of the Cretaceous in Japan.

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### Introduction

Hayami (*in* Hayami and Oji, 1980) has newly introduced two species, *C. shikamai* Hayami and *C. minima* Hayami, in *Caestocorbula* from the Choshi district, Chiba Prefecture. Subsequently Tashiro and Otsuka (1982) established *C. obsoleta* Tashiro et Otsuka from the Upper Himenoura Subgroup in Amakusa-shimojima Island, Kyushu. In addition, Kozai (1986) mentioned that "*Pulsidis higoensis* (Matsumoto)" is probably referable to *Caestocorbula* because of its hinge structure and features of right valve.

In the present article six species including three new species are described on the basis of newly collected materials from ten localities distributed in Kyushu, Shikoku and Kanto (Figure 1). The previously described species from Choshi and Amakusa are also re-examined by additional specimens being well preserved and detail observations.

The specimens described in this paper are mostly kept in the Geological Collections of Faculty of Science, Kochi University (KSG), Kochi and partly in the University Museum, the University of Tokyo (UMUT), Tokyo.

### Fossil localities

Loc. 1. (= Hy.5032 in Hayami, 1966) Fine-

grained sandstone in the upper part of the Tatsukawa Formation at a roadside exposure, about 800 m south of Hiroyasu, Katsuura-cho, Katsuura-gun, Tokushima Prefecture. Neocomian (Figure 1-a).

Loc. 2. Medium to fine-grained sandstone in the lower member of the Hibihara Formation, at an exposure near a path, about 500 m north of Doiban, Monobe-mura, Kami-gun, Kochi Prefecture. Lower Aptian (Figure 1-C).

Loc. 3. Medium-grained sandstone in the lower member of the Hibihara Formation, at an exposure near a path, about 1 km northwest of Kaminaro, Monobe-mura, Kami-gun, Kochi Prefecture. Probably Lower Aptian (Figure 1-C).

Loc. 4. Medium-grained sandstone in the lower member of the Hibihara Formation, at a roadside exposure, about 1 km northwest of Kaminaro, Monobe-mura, Kami-gun, Kochi Prefecture. Probably Lower Aptian (Figure 1-C).

Loc. 5. (= Loc. 7 in Tashiro and Otsuka, 1980, 1982) Medium-grained sandstone in the uppermost formation of the Upper Himenoura Subgroup, at an exposure near a path, about 350 m north of Masuno, Ushibuka City, Kumamoto Prefecture. Maastrichtian (Figure 1-B).

Loc. 6. (≠ Loc. 20 in Tamura, 1976, 1979) Fine-grained sandstone in the lower formation of Mifune Group, at a roadside exposure, about 150 m north of Masunoo, Mifune-cho, Kamimasuki-gun, Kumamoto Prefecture. Cenomanian (Figure 1-D-1).

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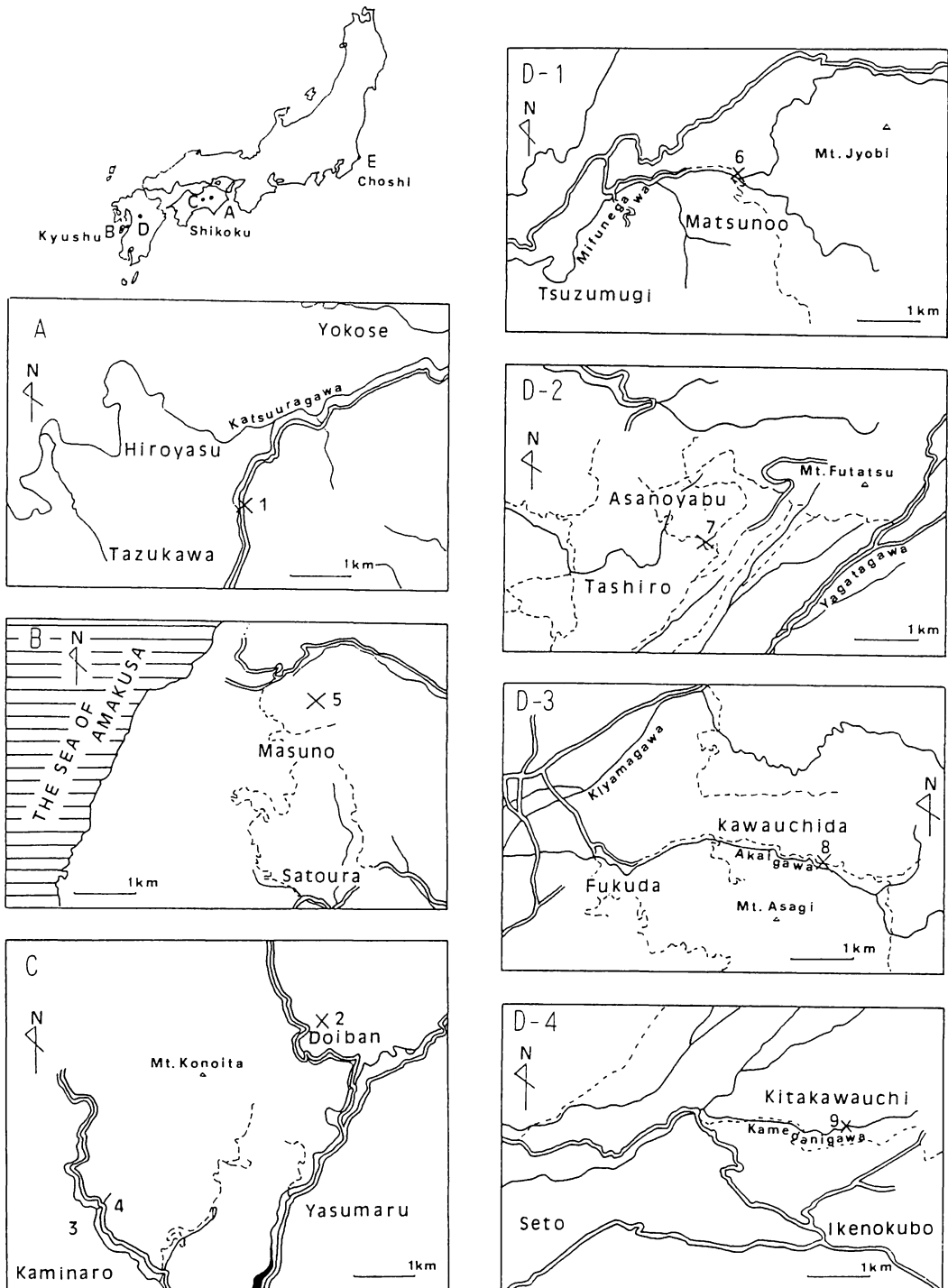


Figure 1. Map showing fossil localities.

A=Katsura area, Tokushima Prefecture. B=Amakusa-Shimajima area, Kumamoto Prefecture. C=Monobe area, Kochi Prefecture. D=Mifune area, Kumamoto Prefecture. E=Choshi district (see Hayami and Oji, 1980). X=Fossil locality.

Loc. 7 ( $\cong$  Loc. 5 in Tamura, 1976, 1979) Fine-grained sandstone in the lower formation of Mifune Group, at a roadside exposure, about 1 km southeast of Asanoyabu, Mifune-cho, Kamimasuki-gun, Kumamoto Prefecture (Figure 1-D-2).

Loc. 8. ( $\cong$  Loc. 11 in ditto) Fine-grained sandstone in the lower formation of Mifune Group, at a roadside outcrop, about 1.5 km east of Kawauchida, Mifune-cho, Kamimasuki-gun, Kumamoto Prefecture. Cenomanian (Figure 1-D-3).

Loc. 9. ( $\cong$  Loc. 4 in ditto) Fine-grained sandstone in the lower formation of Mifune Group, exposed on a river side, about 500 m east of Kitakawauchi, Yabe-cho, Kamimasuki-gun, Kumamoto Prefecture. Cenomanian (Figure 1-D-4).

Loc. 10. (= Loc. 2 in Hayami and Oji, 1980) Choshi District. See Hayami and Oji, 1980, p. 421, Text-fig. 1.

### Systematic description

Family Corbulidae Lamarck, 1818

Subfamily Caestocorbulinae Vokes, 1945

Genus *Caestocorbula* Vincent, 1910

*Type species*:—*Corbula henckeliusiana* Nyst

*Remarks*:—Vokes (1945) established Caestocorbulinae, and included the genera *Caestocorbula* and *Parmicorbula* in it. *Parmicorbula* differs from *Caestocorbula* in having a shallow, inconspicuous groove on the siphonal plate. Later *Parmicorbula* is regarded as a subgenus of *Caestocorbula* by Keen (in Cox *et al.*, 1969).

*Caestocorbula* (s.l.) *antiqua*, sp. nov.

Figures 4-21–28

*Material*:—Holotype, KSG-K074, internal mould of right valve; Paratypes; KSG-K077, KSG-K080, KSG-K081 and KSG-K085, internal moulds of left valves; KSG-K082, external mould of left valve; KSG-K083, external mould of right valve; all the specimens are collected from loc. 1.

*Diagnosis*:—Small-sized species of *Caesto-*

*corbula* characterized by elongated area and flattened interior area.

*Description*:—Shell small, inequivalve, inequilateral, moderately inflated, longer than high; right valve larger than left; test moderately thick; anterior dorsal margin short, slightly curved; posterior dorsal margin long, nearly straight or broadly arched; ventral margin gently arched; umbo slightly prosogyrate, situated at about one-third of shell-length in right valve but about mid-length in left; area rostrated; surface covered with fine concentric ribs, which are regularly spaced, round-topped; interior of right valve grooved with margin of left valve; interior of area flattened; hinge plate narrow; pallial line indistinctly impressed, not sinuated; adductor muscle scars clearly impressed, subelliptical; posterior one larger than anterior; cardinal tooth of right valve projected, heavy, rounded; resillial pit excavated, rounded, located at anterior of cardinal tooth; cardinal socket large, chondrophore slightly prominent.

*Measurements* (in mm):—

Specimens	L	H	B	U	S	H/L	U/L	S/L
KSG-K074, R.in.m.	8.0	4.1	—	2.7	2.2	0.51	0.34	0.28
KSG-K075, L.in.m.	5.8	3.5	—	2.9	—	0.61	0.50	—
KSG-K076, L.in.m.	5.6	3.1	—	2.6	—	0.55	0.46	—
KSG-K077, R.in.m.	7.3+	3.5	—	2.1	—	—	—	—
KSG-K080, R.in.m.	7.5+	3.6	—	3.5	—	—	—	—
KSG-K081, R.in.m.	7.0+	3.2	—	2.1	—	—	—	—
KSG-K082, L.ex.m.	6.8	4.2	1.5	3.5	—	0.61	0.51	—
KSG-K083, R.ex.m.	6.9	4.3	2.0	2.5	—	0.62	0.36	—
KSG-K085, R.in.m.	6.9	3.5	—	2.7	1.8	0.51	0.39	0.26

L.=left valve, R.=right valve, in.m.=internal mould, ex.m.=external mould, L=length, H=height, B=breadth, U=distance from beak to anterior end, S=discrepancy between right valve and left valve.

*Remarks*:—About 40 specimens were collected from loc. 1 in the Tatsukawa Formation. This species occurs together with brackish-water molluscs as; *Costocyrena otsukai* (Yabe et Nagao), *Hayamina naumanni* (Newmayer) and *Protocardia ibukii* Nakazawa et Murata. Caestocorbulid species have been hitherto only reported from marine deposits. Therefore this is the first report of the occurrence from non-marine deposits. Although the siphonal plate is not actually ascertained, the present species

shows a similar hinge structure to that of the known species of *Caestocorbula*.

The surface ornamentation in almost all the specimens is weathered, but several specimens, e.g. KSG-K082 and KSG-K084, show concentric ribs clearly near the ventral margin. Concentric ribs are numbered about 9 in 1 mm. Ratios of S/L are 0.28 (KSG-K074) and 0.26 (KSG-K085). These values indirectly support the idea that this species has siphonal plate. Because the siphonal plate is not determined whether this species is referred to the subgenus *Caestocorbula* (*Caestocorbula*) or *C. (Parmicorbula)*.

*Comparison*:—This new species is similar to *Caestocorbula minima* Hayami, 1980, from the Choshi district, Chiba Prefecture, in having the subpyriform outline, but has a more elongated area in the left valve than that of the latter. It is also similar to *Caestocorbula (Parmicorbula) neaeroides* (Blanckenhorn, 1890) (*in Vokes*, 1945) from Aptian in the Lebanon Mountains, Republic of Lebanon, in having fine concentric ribs on the surface, but the latter has a more elongated area than the former.

*Occurrence*:—Occasionally found at loc. 1. Neocomian.

*Caestocorbula (?Parmicorbula) minima* Hayami

Figures 4-21–23

1980. *Caestocorbula minima* Hayami, *in* Hayami and Oji, p. 437–438, pl. 53, figs. 15, 16.

*Material*:—Holotype, left valve (UMUT MM 9764); Paratypes, left (UMUT MM 9766), right (UMUT MM 9765). These specimens were collected from the Kimigahama Formation in the Choshi district, Chiba Prefecture by Hayami and Oji.

*Remarks*:—This species was established by Hayami (1980) based on 3 conjoined valves and a left valve from the Choshi Group, Chiba Prefecture. The surface ornamentation is well preserved in them, but hinge and other internal characters are unknown. The siphonal plate is possibly present in them, judging from the discrepancy of both valves. This species has a distinct pos-

terior carina in the left valve, but no posterior carina in the right.

This species is similar to *Caestocorbula (Parmicorbula) striatula* (Sowerby, 1827) (*in Vokes*, 1946) from the Lower Greensand in England and *Caestocorbula (Parmicorbula) aequilineata* (Vokes, 1946) from the Aptian in the Lebanon Mountains, in fine concentric ribs and elongated area, but latter has distinct posterior carina in both valves. However, the Japanese species have no posterior carina in the right.

*Occurrence*:—Very rare, at loc. 10. Barremian.

*Caestocorbula (?Parmicorbula) shikamai* Hayami

Figures 4-1–9

1980. *Caestocorbula shikamai* Hayami, *in* Hayami and Oji, p. 436–437, pl. 53, figs. 8–12.

1986. *Caestocorbula* sp. cf. *C. shikamai* Hayami; Tashiro and Matsuda, p. 385, pl. 1, fig. 31.

*Material*:—Holotype, right valve (UMUT MM 9735) illustrated by Hayami (1980, pl. 53, fig. 10) was collected from the Ashikajima Formation at Ashikajima, Choshi district, Chiba Prefecture. Additionally, 11 specimens are collected from the Hibihara Formation in Kochi Prefecture (locs. 2, 3) for the following description.

*Diagnosis*:—Medium-sized species of *Caestocorbula* characterized by strongly inflated valves and less rostrated area.

*Description*:—Shell medium-sized, strongly inflated, subtrigonal, a little longer than high; test thick, heavy; right valve shortly rostrated, larger than left; anterior-dorsal margin weakly concave; ventral margin broadly arched, slightly sinuated near area; postero-dorsal margin nearly straight; umbo located at about mid length, slightly prosogyrate; surface ornamented with concentric ribs, which are round-topped, regularly spaced, denser in posterior half than in anterior; internal margin of right valve distinctly grooved as a receptional scar of margin of left valve; inner areal part flat; cardinal tooth of right valve large; resilial pit large and deep; adductor scars well marked in suboval; posterior adductor scar larger than anterior one; chondrophore sub-trigonal.

*Measurements* (in mm):—

Specimens	L	H	B	U	S	H/L	U/L	S/L
KSG-K110, R.in.m.	5.9	4.1	—	3.3	0.5	0.65	0.56	0.08
KSG-K111, L.in.m.	5.6	3.7	—	3.3	—	0.66	0.59	—
KSG-K112, L.ex.m.	8.1	5.8	2.8	5.0	—	0.72	0.62	—
KSG-K113, L.in.m.	7.5	5.9	—	4.8	—	0.89	0.64	—
KSG-K114, L.in.m.	6.9	4.4	—	3.5	—	0.65	0.51	—
KSG-K115, R.in.m.	7.9	5.3	—	3.6	0.7	0.67	0.46	0.09
KSG-K116, L.in.m.	6.7	5.1	—	4.0	—	0.76	0.59	—
KSG-K118, L.in.m.	7.4	5.6	—	4.1	—	0.71	0.55	—

*Remarks*:—This species was described by Hayami (*in* Hayami and Oji, 1980) based on 11 specimens from Choshi Group, Chiba Prefecture. As these specimens are preserved well, the external and internal features are well recognized. The specimens from Choshi were at first treated as *Pulsidis higoensis* (Matsumoto) by Shikama and Suzuki (1972), but Hayami (*in* Hayami and Oji, 1980) established *Caestocorbula shikamai* for them.

The specimens from the lower part of the Hibihara Formation are smaller than the type specimen, but are safely identified with *C. shikamai* in their diagnostic features, such as strongly inflated and less rostrated valve. The value of 0.08 or 0.09 in S/L is the smallest one among the species of this genus from Japan.

This species was also described from the Sakawa area, Kochi Prefecture by Tashiro and Matsuda, 1986.

*Occurrence*:—Occasionally found at loc. 10. Rare at loc. 2 and common at loc. 3. Aptian.

*Caestocorbula* (?*Parmicorbula*) *monobensis*,  
sp. nov.

Figures 3-1–11

1986. *Caestocorbula minima* Hayami; Tashiro and Matsuda, p. 384–385, pl. 77, figs. 27–30.

*Material*:—Holotype, KSG-K063, internal mould of right valve; 11 paratypes, KSG-K064 – KSG-K067 and KSG-K062, internal moulds of right valves; KSG-K068, KSG-K072 and KSG-K073, external moulds of right valves; KSG-K069 and KSG-K070, internal moulds of left valves; KSG-K071, external mould of left valve. These specimens were collected from loc. 4.

*Diagnosis*:—Medium-sized species of *Caestocorbula* characterized by absence of carina in the left valve and the disk hollowed on the posterior part.

*Description*:—Shell inequilateral, moderately inflated, longer than high; right valve larger, more inflated and more rostrated than left one; test comparatively thick; anterior dorsal margin nearly straight or gently concave; ventral margin broadly arched; posterior dorsal margin sharply curved in rear of umbo, longer than anterior dorsal margin; anterior margin nearly semi-circular; ventral margin gently arched; umbo of right valve small prosogyrate, moderately prominent, situated at about mid-length of the shell; umbo of left valve somewhat prominent, situated at some distance in front of the mid-length; surface covered with regular fine concentric ribs, which are round-topped, regularly spaced, and denser on the umbonal part of disk than on the ventral part; disk hollowed on posterior part; internal margin of right valve grooved as a receptional scar of margin of left valve; supporting buttress presented; internal area faintly or shallowly grooved; hinge plate narrow, long grooved on lateral part; pallial line indistinctly impressed; posterior adductor scar elliptical, moderately impressed, larger than anterior one; cardinal tooth of right valve triangular, heavy, round-topped; resilial pit triangular, deeply excavated; cardinal socket large, deeply excavated; chondrophore triangular, and thin.

*Measurements* (in mm):—

Specimens	L	H	B	U	S	H/L	U/L	S/L
KSG-K063, R.in.m.	11.4	7.5	—	6.1	1.4	0.66	0.54	0.11
KSG-K062, R.in.m.	13.1+	8.1	—	8.1	1.5	—	—	—
KSG-K064, R.in.m.	13.2	10.1	—	7.0	1.5	0.77	0.53	0.12
KSG-K065, R.in.m.	10.0	7.5	—	4.0	1.2	0.75	0.40	0.10
KSG-K066, R.in.m.	12.0	8.5	—	5.3	1.5	0.71	0.44	0.12
KSG-K067, R.in.m.	10.5	7.4	—	—	1.5	0.70	—	0.14
KSG-K068, R.ex.m.	11.7	6.6+	2.8	6.1	—	—	0.52	—
KSG-K069, L.in.m.	12.2	7.8	—	7.0	—	0.64	0.57	—
KSG-K070, L.in.m.	11.4	6.0+	—	6.4	—	—	0.57	—
KSG-K071, R.ex.m.	12.8	8.5	2.7	8.1	—	0.66	0.63	—
KSG-K072, R.ex.m.	12.5+	8.1	3.3	6.0	—	—	—	—
KSG-K073, R.ex.m.	11.2	8.0	2.8	6.4	—	0.71	0.51	—

*Observation*:—About 30 specimens were collected from the lower part of the Hibihara For-

mation. Almost all of them show smooth surface, but this is certainly due to predepositional abrasion. A few specimens (*i.e.* KSG-K072 and KSG-K037) have clear concentric ribs. Right valves are much more numerous than the left ones. The ratio H/L is 0.71 on an average in the right valve and 0.64 in the left valve. Ratio of U/L is 0.51 on an average in the right valve and 0.57 in the left. An average of U/L is 0.12. This consequence is related to existence of siphonal plate. The siphonal plate has not been recognized yet, but it may have been existent in this species, because the interior of right valve is grooved for the reception of the left valve margin.

*Comparison*:—This species is similar to some species of *C. (Parmicorbula)* in the surface ornamentation, but it is difficult to decide whether it belongs to *C. (Caestocorbula)* or *C. (Parmicorbula)*. This new species is somewhat similar to *Caestocorbula shikamai* Hayami in the inflated valve, but is distinguished from the latter by its more rostrated area. In this respect, it is similar to *Caestocorbula minima* Hayami, but it differs from the latter in more elongated area. As to the external characters, the present species is similar to *Caestocorbula (Parmicorbula) sinnosa* (Stephenson, 1941), from the Woodbine Formation of Texas and *Caestocorbula (Parmicorbula) neaeroides* (Blanckenhorn, 1890) (*in Vokes*, 1945), from the Aptian of the Lebanon Mountains, Republic of Lebanon, but this species is distinguished from the latter by more prominent umbo, more rostrated area in the left valve and smaller ratio of siphonal plate in the whole length of shell: 12 per cent of length in this species, as compared with 20 per cent in the latter two. It is fairly similar to *Caestocorbula antiqua*, sp. nov. in the outline and elongated area, but the right valve is more rostrated in the latter than in the former.

*Occurrence*:—Rare at loc. 2 and common at loc. 4. Probably lower Aptian.

*Caestocorbula* (s. l.) *ohtai*, sp. nov.

Figures 3-12-20

1964. *Pulsidis higoensis* (Matsumoto); Ota, p. 153-

155, pl. 21, figs. 13-17.

1975. *Pulsidis higoensis* (Matsumoto); Hayami, p. 145-146.

1977. *Pulsidis higoensis* (Matsumoto); Tamura, p. 141, pl. 10, figs. 1-6.

*Material*:—Holotype, KSG-K050, internal mould of right valve from loc. 6; 11 paratypes; KSG-K059 - KSG-K061 from loc. 8 and KSG-K051 from loc. 6, internal moulds of right valves; KSG-K052 from loc. 8 and KSG-K057 from loc. 7, external moulds of right valves; KSG-K055, KSG-K056, KSG-K058 from loc. 8 and KSG-K053 from loc. 7, internal moulds of left valves; KSG-K054, external mould of left valve from loc. 8.

*Diagnosis*:—Small-sized species of *Caestocorbula* characterized by the well rostrated right valve and the long sized inner areal part.

*Description*:—Shell small, moderately inflated, inequilateral, subtriangular in outline, fairly longer than high, with right valve larger than left; area well rostrated from umbo to postero-dorsal margin; test comparatively thick; antero-dorsal margin short and arched; postero-dorsal margin slightly curved and excavated; anterior margin convex; ventral margin broadly arched, more or less concave at about two-thirds from anterior extremity; umbo moderately prominent, slightly prosogyrate, situated at about one-third of shell length in right valve and nearly at middle in left; carina blunt, extended from umbo to posterior ventral corner; area narrow, long concave; internal mould sulcate from umbo to posterior ventral margin; shell surface ornamented with regularly spaced concentric ribs, wider than their interspaces, round-topped, and gradually crowded from anterior part to posterior; interior of right valve grooved for reception of margin of left valve; inner areal part long raised in median part towards posterior extremity; supporting buttress projected behind anterior adductor scar; hinge plate rather wide and stout; pallial line distinctly impressed, straight except for lower part of posterior adductor scar; adductor scars fairly large, subelliptical, posterior one larger than anterior; cardinal tooth of right valve triangular, round-topped, separated from dorsal margin side by a

shallow groove; resilial pit large, triangular, situated behind the cardinal tooth, deeply excavated, larger than cardinal tooth; chondrophore small and scarcely prominent.

*Measurements* (in mm):—

Specimens	L	H	B	U	S	H/L	U/L	S/L
KSG-K050, R.in.m.	9.1	4.9	—	3.0	2.5	0.54	0.33	0.27
KSG-K051, R.in.m.	9.9	5.7	—	3.5	2.5	0.58	0.35	0.25
KSG-K052, R.ex.m.	8.5	4.6	1.8	2.7	—	0.54	0.32	—
KSG-K053, L.in.m.	7.1	4.8	—	4.1	—	0.68	0.58	—
KSG-K054, L.ex.m.	7.5	5.3	1.7	4.1	—	0.71	0.55	—
KSG-K055, L.in.m.	7.1	4.4	—	4.4	—	0.62	0.62	—
KSG-K056, L.in.m.	7.5	3.6	—	4.6	—	0.48	0.61	—
KSG-K057, R.ex.m.	8.7+	5.0	—	3.7	—	0.57	0.43	—
KSG-K058, L.in.m.	5.2	3.0	—	3.3	—	0.58	0.63	—
KSG-K059, R.in.m.	8.7+	3.3+	—	—	—	—	—	—
KSG-K060, R.in.m.	8.5+	4.7	—	2.6	—	0.55	0.31	—
KSG-K061, R.in.m.	7.5+	5.0	—	—	—	0.67	—	—

*Remarks*:—About 50 specimens were collected from the Goshonoura and Mifune Groups in Kumamoto Prefecture. The specimens which have hitherto been called “*Pulsidis higoensis* (Matsumoto)” are referred to this species.

Matsumoto (1938) described *Aloides higoensis* based on three specimens from the Goshonoura Group in Kumamoto Prefecture. Later, Ota (1964) established the genus *Pulsidis* and included *Aloides higoensis* in this genus, designating UMUT MM7755 (Matsumoto, 1938, pl. 2, fig. 8) as its lectotype, but the hinge structure of this lectotype was not observed. Its surface is sculptured, with regular concentric ribs, which are a little more crowded in the posterior part. In this respect the lectotype evidently differs from Ota's other specimens. Moreover the outline is nearly isosceles triangle in the former, but subpyriform in the latter. On the other hand, other two specimens of Matsumoto (1938, text-figs. 9a and 9b), i.e. UMUT MM 7841 and MM 7844, are similar to “*Nipponicorbula mifunensis* Ota” or “*Pulsidis okadai* Ota” in the concave disk on the middle part and subtriangular cardinal socket. To sum up, it is concluded that *Aloides higoensis* Matsumoto, 1938 differs from “*Pulsidis higoensis*” in the sense of Ota (1964).

On the basis of above observations I propose herein a new name for a species represented by the Ota's specimens. The specimens treated by Ota (1964) are deficient in the area of right

valve. If this part is observed carefully, the inner areal part of the right valve is elongated and raised in the median part. That of left valve is not raised, and the right valve is fairly elongated than the left. Average of S/L is 0.26. These facts support the idea that this species had siphonal plate which, however, is not preserved.

Tamura (1979) reported that this species was collected with *Pterotrignonia* (*Ptilotrignonia*) *mashikensis* (Tamura et Tashiro) and *Inoceramus concentricus costatus* Nagao et Matsumoto (the latter now emended as *Birostrina tamurai* Matsumoto et Noda, 1986). According to Tashiro and Matsuda (1983), *P. (P.) mashikensis* occurred in the environments of brackish water or shallow sea water. Consequently this species must have favoured the environment of more higher salinity than that of *C. antiqua*, sp. nov.

*Comparison*:—This new species is similar to *Caestocorbula semina* Vokes, 1946, from the Aptian of the Lebanon Mountains, in the broad ribs, but differs from the latter in the rostrate area and the median ridge on the inner areal part of the right valve. It is similar to *Caestocorbula antiqua*, sp. nov. in its elongate area, but evidently differs in having the ridge on the inner area of the right valve.

*Occurrence*:—Common at locs. 6, 7, 8, 9. Cenomanian.

*Caestocorbula* (?*Parmicorbula*) *obsoleta*  
Tashiro et Otsuka

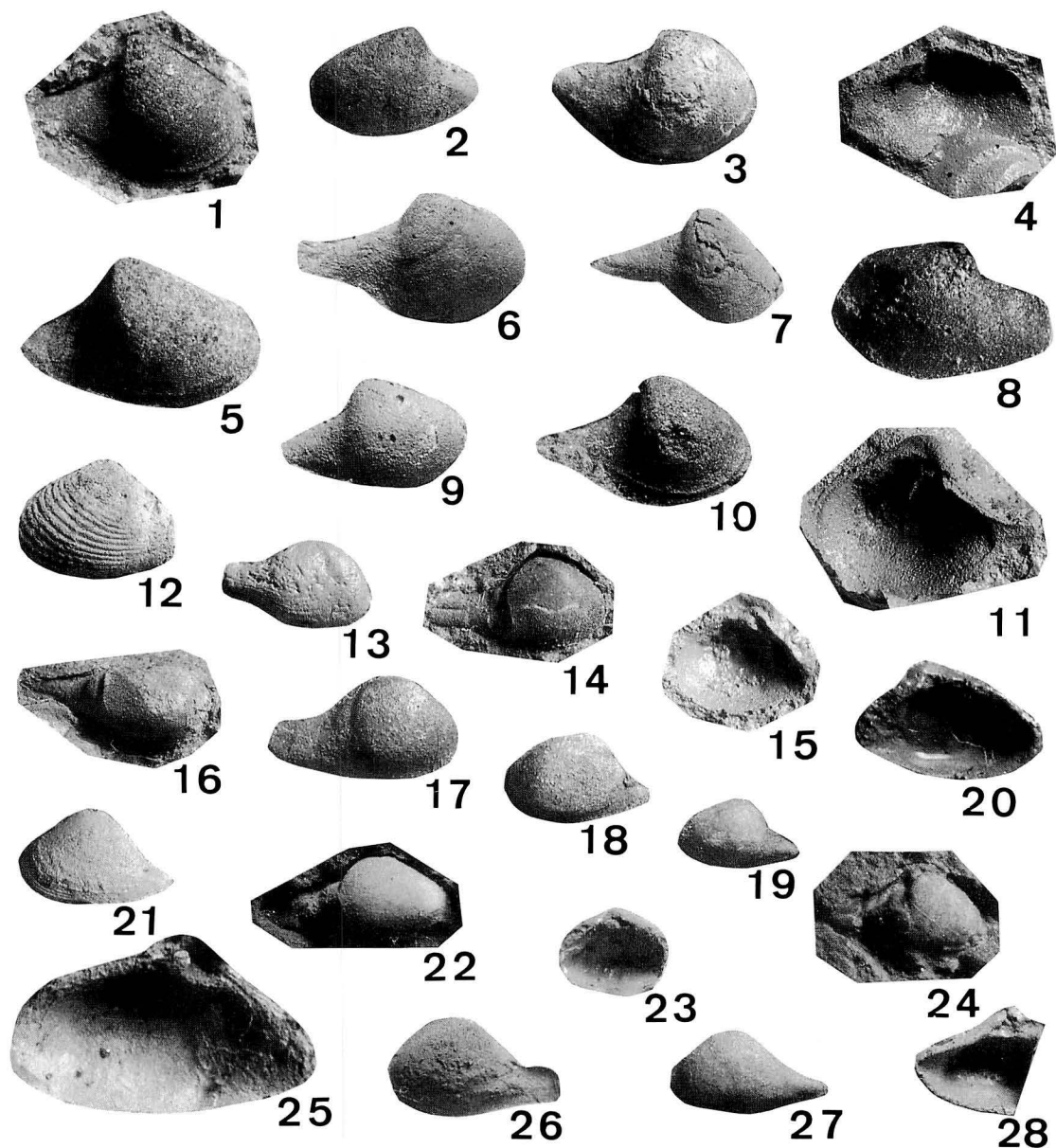
Figures 4-15–18, 20–22

1982. *Caestocorbula* (*Parmicorbula*) *obsoleta* Tashiro et Otsuka, p. 18–19, pl. 5, figs. 15–18, 20–22.

*Material*:—The holotype is an external mould of right valve (KSG 3053) which was collected from the upper part of the Upper Himenoura Subgroup at Masuno, Ushibuka City, Kumamoto Prefecture (loc. 5) from where 14 specimens (KSG-K119 – KSG-K132) are also collected for the present description.

*Diagnosis*:—Medium-sized species of *Caestocorbula* characterized by lack of the carina in the left valve and less discrepancy between the right and left valves.

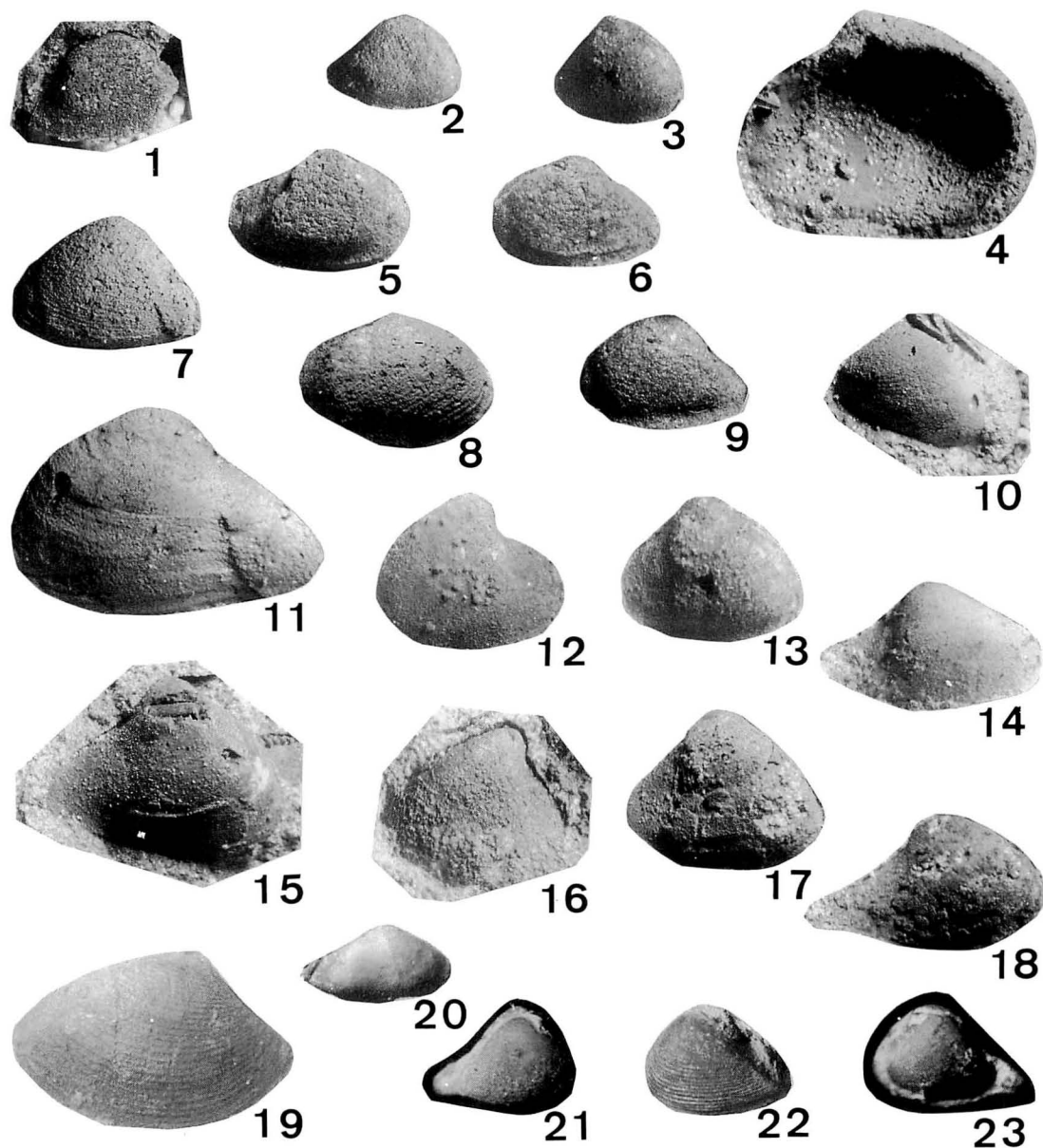




**Figure 3.** 1–11. *Caestocorbula* (?*Parmicorbula*) *monobensis*, sp. nov., internal moulds (1, KSG-K063,  $\times 2.5$ ; 3, KSG-K066,  $\times 2.5$ ; 5, KSG-K062,  $\times 2.5$ ; 8, KSG-K069,  $\times 2.5$ ; 10, KSG-K065,  $\times 3$ ). Gum cast of external moulds (2, KSG-K071,  $\times 2$ ; 6, KSG-K-72,  $\times 2.5$ ; 7, KSG-K068,  $\times 2.5$ ; 9, KSG-K073,  $\times 2.5$ ). Gum cast of internal moulds (4, KSG-K070,  $\times 2.5$ ; 11, KSG-K064,  $\times 2.5$ ).

12–20. *Caestocorbula* (s.l.) *ohtai*, sp. nov., gum cast of external moulds (12, KSG-K054,  $\times 3$ ; 13, KSG-K052,  $\times 2.5$ ). Gum cast of internal moulds (15, KSG-K060,  $\times 2.5$ ; 20, KSG-K058,  $\times 5$ ). Internal moulds (14, KSG-K050,  $\times 3$ ; 16, KSG-K059,  $\times 3$ ; 17, KSG-K051,  $\times 3$ ; 18, KSG-K055,  $\times 3$ ; 19, KSG-K053,  $\times 2$ ).

21–28. *Caestocorbula* (s.l.) *antiqua*, sp. nov., gum cast of external moulds (21, KSG-K084,  $\times 3.5$ ; 26, KSG-K082,  $\times 3.5$ ). Gum cast of internal moulds (23, KSG-K079; 25, KSG-K085,  $\times 6$ ; 28, KSG-K078,  $\times 4$ ). Internal moulds (22, KSG-K074,  $\times 3.5$ ; 24, KSG-K077,  $\times 3$ ; 27, KSG-K075,  $\times 3.5$ ).



**Figure 4.** 1–9. *Caestocorbula* (?*Parmicorbula*) *shikamai* Hayami, internal moulds (1, KSG-K114, X3; 2, KSG-K110, X3; 3, KSG-K120, X3; 5, KSG-K115, X3; 6, KSG-K116, X3.5; 9, KSG-K113, X3). Gum cast of internal mould (4, KSG-K118, X5.5). Gum cast of external moulds (7, KSG-K112, X3.5; 8, KSG-K117, X3.5).

10–18. *Caestocorbula* (?*Parmicorbula*) *obsoleta* Tashiro et Otsuka, gum cast of external moulds (10, KSG-K128, X3; 11, KSG-K123, X5). Internal moulds (12, KSG-K127, X3.5; 13, KSG-K124, X4; 14, ISG-K126, X4; 15, KSG-K129, X3.5; 16, KSG-K122, X4; 17, KSG-K125, X3; 18, KSG-K119, X4.5).

19, 20. *Aloides higoensis* Mstsumoto, left valve (19, MM 7755, X3). Internal mould (20, MM 7755, X3).

21–23. *Caestocorbula* (?*Parmicorbula*) *minima* Hayami, right valve (21, MM 9764, X3). Left valves (22, MM 9764, X3; 23, MM 9765, X3).

*Description*:—Shell medium-sized, moderately inflated, subtrigonal, a little longer than high; right valve a little larger than left; test thick; antero-dorsal margin broadly arched; postero-dorsal margin weakly concave near the umbo; ventral margin broadly arched; posterior margin vertically truncated; umbo situated at about mid-length of the valve, very prominent and slightly prosogyrate or orthogyrous; surface ornamented with concentric ribs; inner areal part flat; cardinal tooth of right valve triangular, strongly projected, but rounded at top; resillial pit large and deep, situated behind the cardinal tooth.

*Measurements* (in mm):—

Specimens	L	H	B	U	S	H/L	U/L	S/L
KSG-K119, R.in.m.	7.5	4.9	—	3.9	0.8	0.65	0.52	0.11
KSG-K120, R.in.m.	8.3	5.5	—	3.6	0.7	0.66	0.43	0.08
KSG-K121, L.ex.m.	6.9	5.1	2.0	3.7	—	0.74	0.54	—
KSG-K122, L.in.m.	7.3	6.0	—	3.5	—	0.82	0.48	—
KSG-K123, L.ex.m.	9.2	6.9	1.5	4.6	—	0.75	0.50	—
KSG-K124, R.in.m.	6.2	4.9	—	3.5	—	0.79	0.56	—
KSG-K125, R.in.m.	10.2+	8.2	—	4.5	—	0.80	0.44	—
KSG-K126, R.in.m.	7.1	3.3+	—	3.7	—	0.46+	0.52	—
KSG-K127, L.in.m.	7.0	5.5	—	3.8	—	0.79	0.54	—
KSG-K129, R.in.m.	10.9	8.3	—	5.2	0.6	0.76	0.48	0.04

*Remarks*:—Numerous specimens were collected from the type-locality. Almost all of them look smooth on the surface, owing to pre-depositional abrasions, but a few specimens (*i.e.* KSG-K123 and KSG-K128) have distinct concentric ribs which are counted about 4 in the distance of 1 mm along the height in the central part of adult specimen. Ratio S/L is about 0.08 which is the smallest among species of the genus *Caestocorbula*. In this respect this species is similar to *Caestocorbula shikamai* Hayami, but the latter has more strongly inflated valve and shorter area. It is similar to *Parmicorbula vokesi* Stephenson, 1953, from the Woodbine Formation of Texas, in elongated area, but is distinguished from the latter by its more longly rostrated left valve.

*Occurrence*:—Abundant at loc. 5. Maastrichtian.

#### Further remarks

In this paper six species of the genus *Caestocorbula* are described.

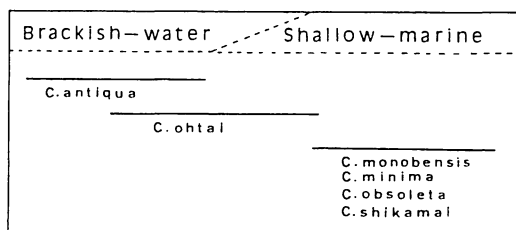


Figure 2. Environments of *Caestocorbula* in Japan.

1. The specimens belonging to the genus *Caestocorbula* in Japan occur in the brackish-water deposits and shallow-marine deposits. From the environmental point of view, the six species may be divided into two or three categories as shown in Figure 2.

2. The shallow-marine species have shell forms similar to those of *Parmicorbula*, but the species which lived in the brackish-water have shell forms which differ from *Parmicorbula*. However, it is difficult to determine the subgenus of either *Parmicorbula* or *Caestocorbula*, because the siphonal plate is often unpreserved.

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日本の白亜系産 *Caestocorbula* 属について：これまで記載されてきたものも含めて、本邦白亜系の10地点から産した *Caestocorbula* 属の化石を再検討し、それらを6種に分類し、各種の特徴を明らかにした。6種の中には、3新種、*C. antiqua*, sp. nov., *C. monobensis*, sp. nov., *C. ohtai*, sp. nov., が含まれる。

香西 武

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849. MIDDLE CARBONIFEROUS ORTHOCERATACEAE AND  
PSEUDORTHOCERATACEAE (MOLLUSCA: CEPHALOPODA)  
FROM THE AKIYOSHI LIMESTONE, YAMAGUCHI PREFECTURE  
(MOLLUSCAN PALEONTOLOGY OF THE AKIYOSHI LIMESTONE GROUP-VIII)\*

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**Abstract.** The Akiyoshi Limestone Group (Early Carboniferous to Middle Permian) in Yamaguchi Prefecture contains a diverse fossil molluscan fauna, including cephalopods. In this paper, we describe for the first time 6 species of orthocerid cephalopods from the Isa area where lies in the southwestern margin of the Akiyoshi Limestone Plateau (*s.l.*). Stratigraphic levels and lithofacies of the cephalopods locality are divided into two types *i.e.*, 1) Bioclastic grainstone, rich in crinoid fragments, of the *Pseudostaffella antiqua* zone (Bashkirian) including *Brachycycloceras* sp. indet. and 2) Coquinite of the *Fusulinella biconica* zone (Moscovian), limestone of which yields *Brachycycloceras akiyoshiensis*, sp. nov., *Geisonoceras sejunctus*, sp. nov., *Geisonocerina cribrella*, sp. nov., *Striacoceras* (?) sp. indet. and *Reticycloceras* (?) sp. indet.

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### Introduction

Since Ozawa's classical paper in 1925 on fusulinids, there are many paleontological works on rich and varied Akiyoshi flora and fauna that include algae, foraminifers, conodonts, echinoderms, brachiopods, bryozoans, corals, arthropods and molluscus. Among them, description of cephalopods fauna in the Akiyoshi Limestone Group and from the slump blocks of limestone in terrigenous sediments in the surrounding area began with Nishida (1971) and was followed by later paleontological and biostratigraphical studies

(Nishida and Kyuma, 1982, 1984, 1985, 1986; Nishida *et al.*, 1985; Kyuma and Nishida 1987). Those series of papers have resulted in the identification of 45 ammonoid species, including 5 new genera and 21 new species, however, so far as other cephalopod taxa on a large quantity *i.e.* Nautiloidea and Bactritoidea are concerned, little work has previously been accomplished. The purpose of this report is to describe 6 species of Nautiloidea including Brachycycloceratidae, Geisonoceratidae and Pseudorthoceratidae, representatives of which were collected by T.N. and Y. K. in cooperation with many students of Saga University from two localities (Loc. IM 01; IM 60) in the Isa area of southwestern margin of the

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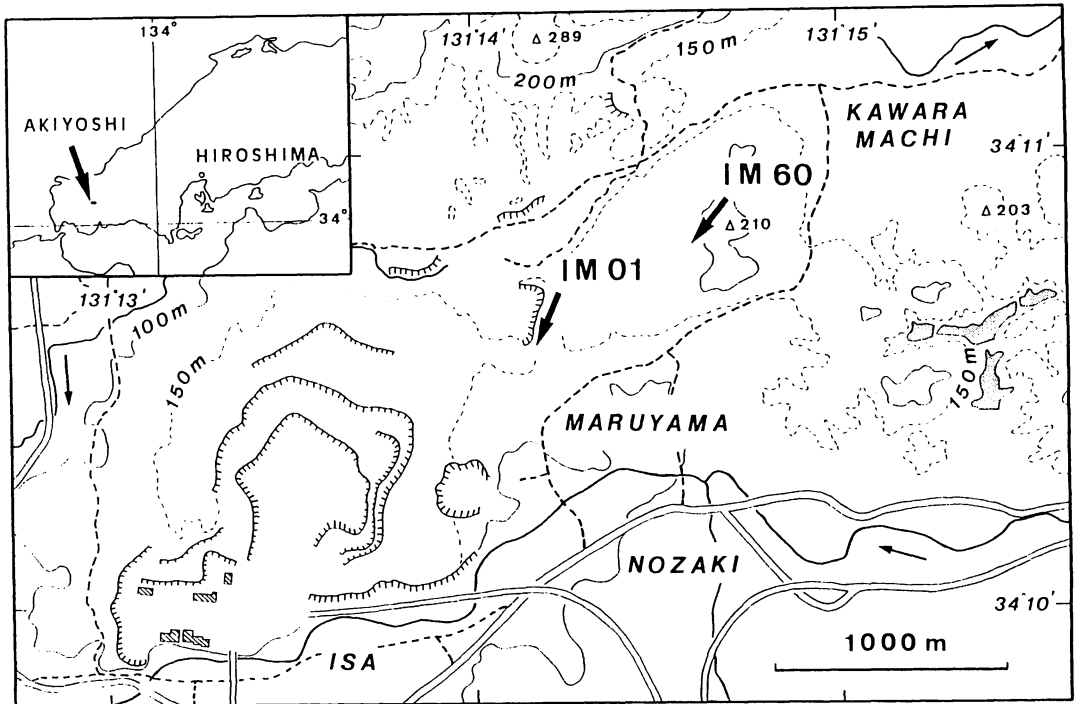


Figure 1. Location map of the Isa area, southwestern margin of the Akiyoshi Limestone Plateau (*s.l.*).

Akiyoshi Limestone Plateau (*s.l.*), Mine City, Yamaguchi Prefecture (Figure 1).

The Akiyoshi Limestone is a large body (about 8 × 16 km across) of reef complex that was deposited on the top of a seamount through the late Tournaisian (Early Carboniferous) to late Guadalupian (Middle Permian) age. It forms a tectonic collage together with siliceous deposits (Beppu Group) synchronous with the limestone body, and terrigenous clastic sediments (Tsunemori Group; Ota Group) of probably Middle to Late Permian, whose emplacement was ascribed to the subduction of pre-Late Triassic age (Kanmera, 1983; Kanmera and Nishi, 1983; Uchiyama *et al.*, 1986). The lithofacies and biostratigraphy of the Akiyoshi Limestone have been described in detail (Ozawa, 1923; Toriyama, 1954, 1958; Okimura, 1963; Eto, 1967; Ota, 1968; 1977; Nagai, 1978; Matsusue, 1986). Thus, only a brief outline will be given here. Ota (1968) described 16 limestone-types on the basis of a reef-lagoon dual concept and suggested that the

Akiyoshi Limestone might represent a carbonate depositional environment of organic reef complex with a core of hermatypic corals, bryozoans and algae, and analogous to the modern oceanic fringing reef to atoll. Biostratigraphically, the Akiyoshi Limestone is divided into 21 zones based on the combination of fusulinaceans and smaller foraminifera (*Endostaffella*) as a supplementary element in the pre-middle Viséan part.

Besides one specimen (*Brachycycloceras* sp. indet.) the cephalopods occur in coquinoid limestone in Loc. IM 60 which consists mainly of ammonoid shell with thick fibrous spar crusts in cavities ("Grossoolith") of early diagenetic origin in reefy environment and is associated closely with bafflestone and bindstone of true reef facies of Ota's definition. In this rock, specimens of Orthocerida are relatively rare in comparison with ammonoids, and 9 individuals are recognized so far, including *Brachycycloceras akiyoshiensis*, sp. nov., *Geisonoceras sejunctus*, sp. nov., *Geisonocarina cribrella*, sp. nov., *Striacoceras* (?) sp.

indet. and *Reticycloceras* (?) sp. indet. Fusulinids from this interval represent the *Fusulinella biconica* zone (Moscovian). On the other hand, *Brachycycloceras* sp. indet. collected from Loc. IM 01 of bioclastic grainstone, rich in crinoid fragments, of the *Pseudostaffella antiqua* zone (Bashkirian).

Materials used in this paper are registered and deposited in the Akiyoshi-dai Museum of Natural History (ASM).

*Acknowledgments.*—We are deeply grateful to Drs. T. Kobayashi of the Japan Academy and T. Hamada of The University of Tokyo for their beneficial discussion and critical reading of the manuscript. Many students, including Mr. Hirofumi Kuga, of Saga University were of great help in collecting and adjusting samples for this study.

### Systematic paleontology

Superfamily Orthocerataceae M'Coy, 1844

Family Brachycycloceratidae Furnish,  
Glenister and Hansman, 1964

Genus *Brachycycloceras* Miller,  
Dunbar and Condra, 1933

*Brachycycloceras* Miller, Dunbar and Condra, 1933, p. 105–107; Demanet, 1941, p. 102; Flower, 1943, p. 124; Shimer and Shrock, 1944, p. 539; Schmidt, 1956, p. 47; Balashov and Zhuravleva, 1962, p. 84–85; Furnish, Glenister and Hansman, 1962, p. 1345–1347; Furnish and Glenister, 1964, p. K232; Gordon, 1964, p. 107–108; Shimansky, 1968, p. 67.

*Type species:*—*Brachycycloceras normale* Miller, Dunbar and Condra, 1933.

*Diagnosis:*—*Brachycycloceras* consisting of orthoconic to gently cyrtococonic deciduous conch with annulations and truncated mature conch. Cross section circular to subcircular or quadrate. Mature part breviconic, strongly inflated and weakly sculptured. Camerae relatively short. Septa form shallow lobe at venter and dorsum, and corresponding saddle on each flank. Siphuncle subcentral to subventral and small; septal necks short and suborthochoanitic. Siphuncular segments slightly expanded in camerae.

*Remarks:*—The generic description given above is essentially the same as that of Furnish, Glenister and Hansman (1962), which is accepted without any emendation. The genus *Brachycycloceras* has been reported previously from the western Europe (Belgium; Germany), U.S.S.R. (Moscow Basin; Urals; Kirgizskaya S.S.R.) and North America. The known specimens are confined to occur in the late Early to Late Carboniferous.

*Brachycycloceras akiyoshiensis* Niko,  
Nishida and Kyuma, sp. nov.

Figures 2-1, 2

*Material:*—Holotype, ASM 51301 from Loc. IM 60 (*Fusulinella biconica* zone).

*Diagnosis:*—Relatively large, slightly cyrtococonic *Brachycycloceras* with subcircular cross section. Ornamented with weakly sinuous annulations and fine lirae.

*Description:*—The holotype, only known specimen of *Brachycycloceras akiyoshiensis*, is a deciduous portion, about 36 mm long. The conch is slightly cyrtococonic with subcircular cross section, expanding from about 10 mm to 17 × 18 mm over a length of the fragmented specimen. Prominently rounded and slightly sinuous annulations occur both on shell surface and the internal mould of shell. Annulations are nearly transverse to the conch axis; oral, five to six annuli occupy a length equal to the adoral shell diameter. Interspaces of adjacent crest are marked by a series of fine lirae, which are parallel to annulations.

*Discussion:*—The initial stages and mature portion of this species are not known; besides, no internal structures are preserved. However, the slightly cyrtococonic and relatively large shell are the most distinctive features separating *Brachycycloceras akiyoshiensis* from most of other species of the genus.

*Brachycycloceras normale* Miller, Dunbar and Condra (Miller *et al.*, 1933, pl. 3, figs. 3–5; Furnish *et al.*, 1962, pl. 179, figs. 2–4, pl. 180, figs. 7, 8, 10, 11) described from the Desmoinesian to Virgilian of the Midcontinent Region,

North America seems to be referable to *B. akiyoshiensis*, although the former has more rapidly expanding orthoconic shell and smaller shell diameter in corresponding stages. This species somewhat resembles *B. washingtonense* Gordon (Gordon, 1964, pl. 5, figs. 4, 5, pl. 16, figs. 4, 5, text-fig. 10) which was described from the Fayetteville shale (Upper Mississippian) of Arkansas, but differs in its more prominent annulation and smaller shell size.

*Brachycycloceras* sp. indet.

Figures 2-5, 6

*Material*:—ASM 51302 from Loc. IM 01 (*Pseudostaffella antiqua* zone).

*Descriptive remarks*:—The examined specimen is a decollated longicone, about 33 mm in length, broken at the both ends. The conch is orthoconic circular in cross section, which expanding from 5.0 mm to 12.2 mm over a length of the fragmented specimen. Surface is marked by a series of narrowly rounded annulations, which are slightly oblique to the long axis of the conch. Septa are shallow, forming almost straight and transverse sutures. Siphuncular structure of this specimen is not known.

This specimen is tentatively assigned to the genus *Brachycycloceras* on the basis of its shell shape and characteristic surface ornamentation.

*Brachycycloceras subquadratum* Shimansky (Shimansky, 1968, pl. 3, figs. 4, 5) from the Viséan and Namurian rocks of southern Urals and Kirgizskaya S.S.R. somewhat resembles this specimen. But subquadrate cross section, characteristic to *B. subquadratum*, is not observed in the present material.

Family Geisonoceratidae Zhuravleva, 1959

Genus *Geisonoceras* Hyatt, 1884

*Geisonoceras* Hyatt, 1884 (Flower, 1939); Flower, 1939, p. 163–164; Shimer and Shrock, 1944, p. 537; Balashov and Zhuravleva, 1962, p. 85; Sweet, 1964, p. K236–K237.

*Type species*:—*Orthoceras rivale* Barrande, 1866.

*Diagnosis*:—Slender orthocone to gently cyrtocone with circular to subcircular cross section. Sutures straight, transverse or slightly oblique, and surface marked by transverse bands. Siphuncle orthochoanitic to suborthochoanitic and central to subcentral. Cameral and endosiphuncular deposits well developed.

*Discussion*:—The genus *Geisonoceras* was established by Hyatt based on *Orthoceras rivale* Barrande in 1884. Flower (1964) regarded Barrande's *Orthoceras rivale* as "a good *Michelinoceras*" and indicated that the boundary of *Geisonoceras* and *Michelinoceras* is not clear. We regard the genus *Geisonoceras* as a distinct taxon based on not having a small and empty siphuncle, relatively long and thin necks, and smooth shell surface characteristic to *Michelinoceras*. However, there is a possibility that the species which have been attributed to *Geisonoceras* would be an artificial grouping. The specimens studied here are fragmentary and having ill preserved internal structures, making taxonomic interpretation difficult. Thus, the present identification is tentative.

*Geisonoceras* has previously been known from North America, Eurasia and Asia of the Middle Ordovician to Late Devonian.

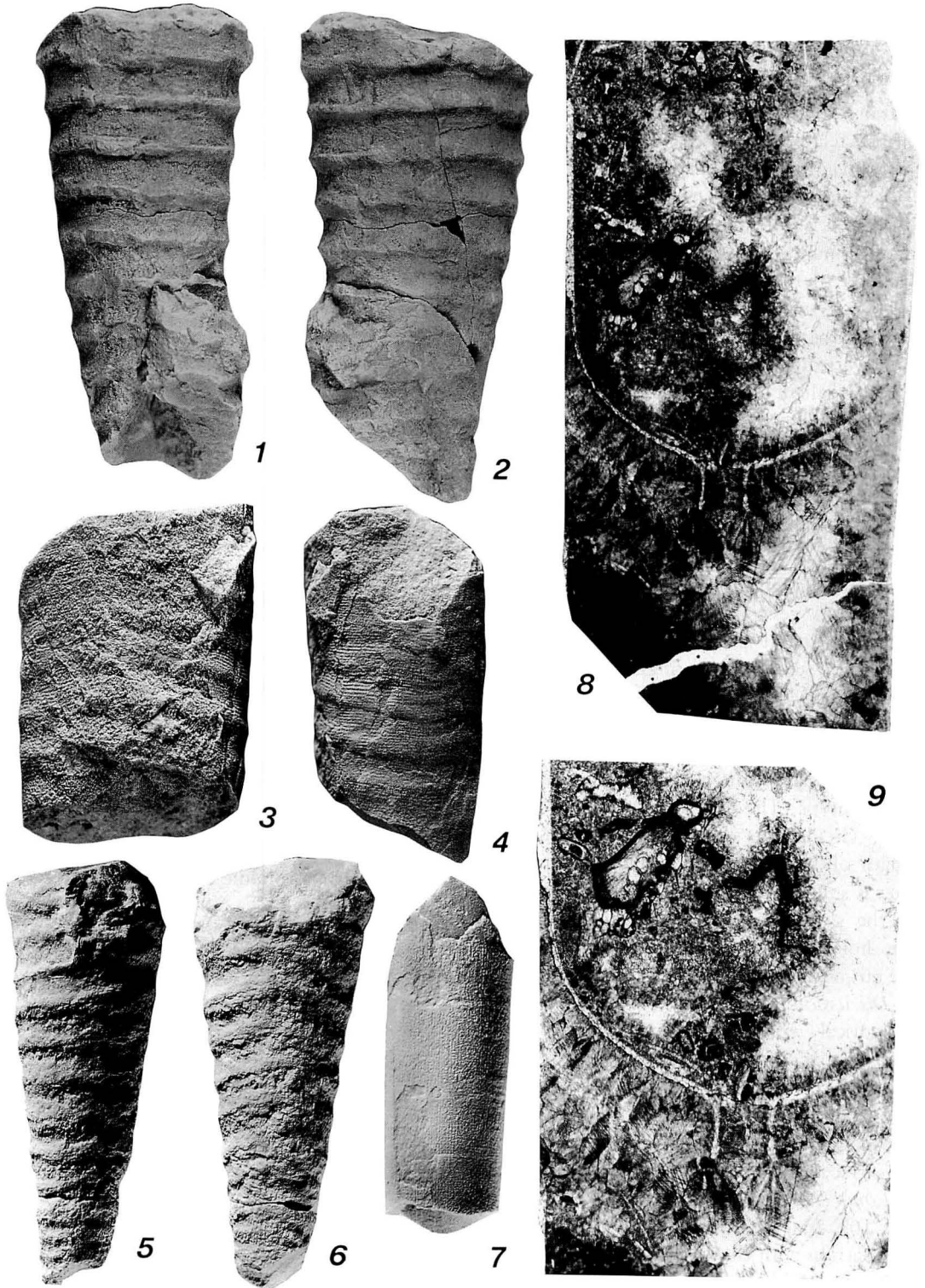
*Geisonoceras sejunctus* Niko, Nishida and Kyuma, sp. nov.

Figures 3-1–6

*Material*:—Holotype, ASM 51303 (Figures 3-1–3, 5, 6); paratype, ASM 51304 (Figure 3-4).

→ **Figure 2.** 1, 2. *Brachycycloceras akiyoshiensis* Niko, Nishida and Kyuma, sp. nov. Holotype, ASM 51301: 1, lateral view, venter on left, X2; 2, dorsal view, X2. 3, 4. *Reticycloceras* (?) sp. indet. Figured specimen, ASM 51309: 3, ventral (?) view, X3; 4, lateral view, venter (?) on left, X3. 5, 6. *Brachycycloceras* sp. indet. Figured specimen, ASM 51302: 5, lateral view, venter on right, X2; 6, ventral view, X2. 7–8. *Striacoceras* (?) sp. indet. Figured specimens, ASM 51300: 7, lateral view, X4; 8, vertical thin section, X10.5; 9, partial enlargement at septal foramen of Figure 2-8, X13.5.





The specimens studied are from Loc. IM 60 (*Fusulinella biconica* zone).

*Diagnosis*:—*Geisonoceras* with slender orthocone, straight sutures and shell surface marked by transverse, narrow imbricate bands. Siphuncle central, relatively small; septal necks short and orthochoanitic; connecting rings cylindrical.

*Description*:—Holotype, ASM 51303; The holotype is a portion of an orthoconic phragmocone, 25 mm long, with a circular cross section. Diameter of the conch 8.5 mm near the apical end. Shell surface marked by a series of transverse and narrow imbricate bands. Bands are flat, slightly irregular in width, and sometimes forming weak salient (Figure 3-2); their lower margins abruptly delineated. Sutures are straight and transverse. Curvature of septa is relatively deep. This specimen revealed two and one-half camerae in the thin section. An apical camera occupies a length to the adoral conch diameter, adorally, camera has a half length of the adoral conch diameter. Siphuncle is central and relatively small for the genus, 1.10 mm across. Septal necks are short, stout and straight, joined by thin cylindrical connecting rings. Both siphuncle and camera are apparently devoid of organic deposits.

Paratype, ASM 51304; This represents a portion of phragmocone in more earlier stages than the holotype. The conch orthoconic of 47 mm long, circular in section which expands in a length of 39 mm from 6.0 mm to 8.5 mm. Surface is somewhat weathered, and ornamentation of the specimen is almost identical to that of the holotype. Sutures and internal structures are not observed.

*Discussion*:—The relatively long camerae and cylindrical connecting ring of *Geisonoceras sejunctus* is, in some respects, atypical of *Geisonoceras* which possesses two to two and one-half camerae par adoral conch diameter and expanded connecting ring. In addition, the band of surface ornamentation of the type species of *Geisonoceras rivale* (Barrande) (Sweet, 1964, fig. 169, 6) possesses many times the width in comparison with that of the examined specimen. The only Middle Devonian species of *Geisono-*

*ceras teichertii* Flower (Flower, 1939, pl. 7, fig. 8, pl. 9, fig. 19) appears similar to the internal structure of *G. sejunctus*. The Middle Devonian form, collected from the Onondaga Limestone in New York, is distinguished from *Geisonoceras sejunctus* in having larger siphuncular size and shorter septal necks.

#### Genus *Geisonocerina* Foerste, 1935

1935 *Geisonocerina* Foerste, p. 22; Shimer and Shrock, 1944, p. 539; Flower, 1945, p. 682; Schmidt, 1956, p. 50.

1964, ? *Geisonocerina*, Sweet, p. K237.

1968, *Geisonocerina*, Shimansky, p. 69–70.

*Type species*:—*Orthoceras wauwatosense* Whitfield, 1882.

*Diagnosis*:—*Geisonocerina* is applied to longiconic orthocones with a circular cross section. Surface ornamented by fine transverse lirae, and sometimes occurs weak longitudinal lirae. Sutures straight, transverse or slightly oblique. Camerae relatively long. Septal necks short, orthochoanitic to suborthochoanitic, joined by cylindrical connecting rings.

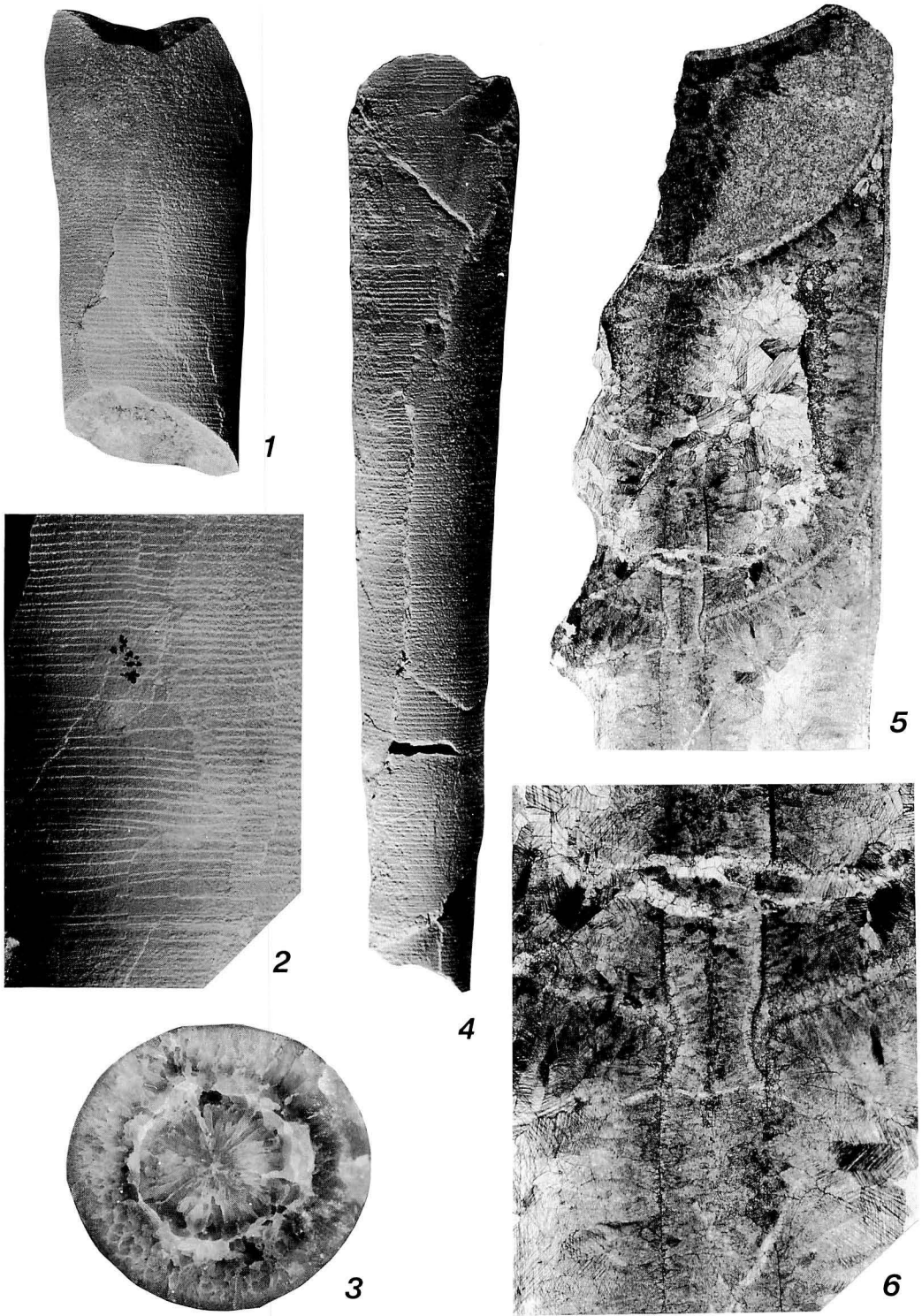
*Remarks*:—This genus was proposed by Foerste in 1935 for taxa with *Geisonoceras*-like orthoconic cephalopods but distinguished in having the close raised transverse lirae instead of bands. The internal structure of the type species has not been figured. The genus *Geisonocerina* has been reported previously from Upper Ordovician to Middle Carboniferous.

#### *Geisonocerina cribrella* Niko, Nishida and Kyuma, sp. nov.

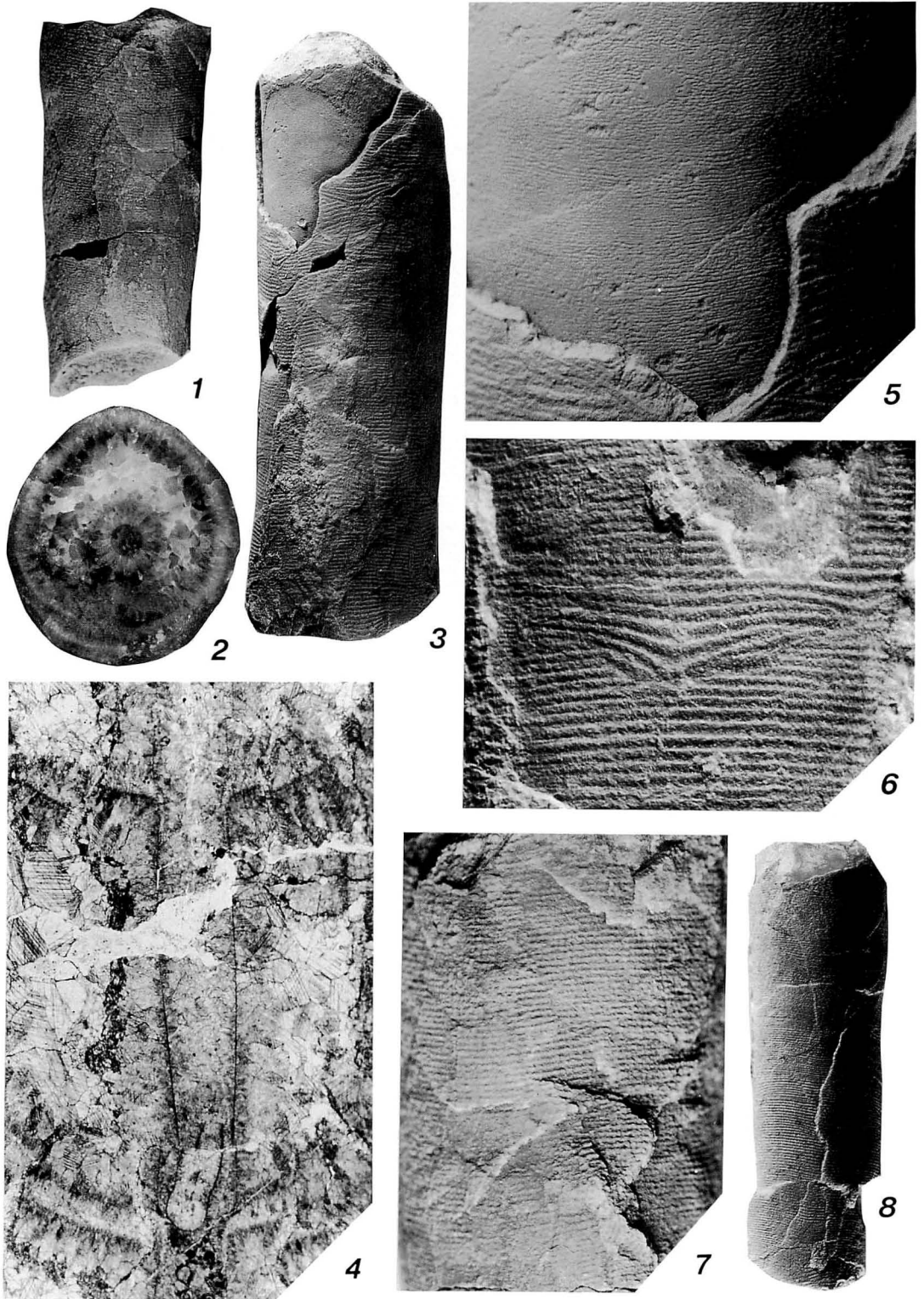
Figures 4-1–8

*Material*:—Holotype, ASM 51305 (Figures 4-1, 2, 4, 7); paratypes, ASM 51306 (Figures 4-3, 5, 6), ASM 51307 (Figure 4-8); unfigured specimen ASM 51308. The studied specimens were obtained from Loc. IM 60 (*Fusulinella biconica* zone).

*Diagnosis*:—*Geisonocerina* with slender orthocone and shell surface marked by slightly undulated transverse lirae and weak longitudinal



**Figure 3.** 1–6. *Geisonoceras sejunctus* Niko, Nishida and Kyuma, sp. nov. Holotype, ASM 51303: 1, lateral view, X2; 2, partial enlargement of shell surface showing narrow imbricate bands and weak salients, X6; 3, polished cross section near the apical end, X5; 5, vertical thin section, X6; 6, partial enlargement at septal foramen of Figure 3-5, X13.5. Paratype, ASM 51304: 4, lateral view, X3.



**Figure 4.** 1–8. *Geisonocerina cribrella* Niko, Nishida and Kyuma, sp. nov. Holotype, ASM 51305: 1, lateral view, X3, 2, polished cross section near the apical end, X5; 4, vertical thin section, X12; 7, partial enlargement of shell surface, X6.5. Paratype, ASM 51306: 3, lateral view, X2; 5, partial enlargement of exfoliated part of shell showing ornamentation of “wrinkled layer”, X6.6; 6, partial enlargement of shell surface at overlapped part of ornamentation, X6. Paratype, ASM 51307: 8, lateral view, X3.

lirae. Siphuncle central; septal necks relatively long and orthochoanitic; connecting rings slightly expanded in camerae.

*Description*:—Holotype, ASM 51305: The holotype consists of a phragmocone of longiconic orthocone, 21 mm long. Cross section of the shell is oval probably because of the secondary deformation. Surfaces marked by a series of slightly undulated transverse lirae and weak longitudinal lirae. Sutures are not observed, but they are assumed to be transverse to the long axis of the conch. Camerae are relatively long; one to one and one-half camerae occupy a length equal to the adoral conch diameter. Siphuncle is central, circular in cross section and with a diameter of 0.9 mm at the septal foramen. Septal necks are thin, relatively long and orthochoanitic. Siphuncle segments are slightly expanded in camerae. No cameral and siphonal deposits are evident.

Paratype, ASM 51306: The specimen is a fragment of the body chamber, somewhat crushed, and about 46 mm long. Surface is ornamented by a series of slightly sinuous transverse lirae sometimes forming salients (Figure 4-6). Longitudinal lirae are very weak, besides partly disappeared. On exfoliated part of the shell, "wrinkled layer" appears to be developed on internal mould (Figure 4-5).

Paratype, ASM 51307: This is a portion of the orthoconic phragmocone, 24 mm long. Conch circular in cross section, and its diameter near the apical end is 6.7 mm. Well preserved surface ornamentation is seen on this specimen. Surface of the specimen bears a series of transverse lirae which are slightly sinuated and form weak salients. Fine longitudinal lirae also occur on the shell surface. These longitudinal lirae are developed only at interspaces of the transvers lirae. No internal structures are observed.

*Discussion*:—The present species somewhat resembles *Geisonoceras homeocincta* Shimansky (Shimansky, 1968, pl. 3, figs. 7, 8) which occurs in the early Namurian rocks of southern Urals. However, the presence of longitudinal lirae and weak salients of transverse lirae make *G. cribrella* the most easily recognizable features of

this new species of *Geisonoceras*.

Somewhat similar surface ornamentation with the examined specimens appears in some Carboniferous species of *Dolorthoceras* and *Sueroceras*. However, these specimens are assigned to *Geisonoceras*, rather than the above-mentioned two genera, because of their less constricted siphuncle at the septal foramen.

#### Genus *Striacoceras* Flower, 1936

##### *Striacoceras* (?) sp. indet.

Figures 2-7-9

*Material*:—ASM 51300 from Loc. IM 60 (*Fusulinella biconica* zone).

*Descriptive remarks*:—The examined specimen is a portion of the slender orthoconic phragmocone, 14 mm long. Cross section of the shell is circular, and with apical diameter of 4.4 mm. Surface is ornamented with cancellate markings which are produced by intersecting longitudinal and transverse lirae. Sutures are slightly oblique to the long axis of the conch. About one camera occupies a length equal to the apical conch diameter. Curvature of septa is deep. Siphuncle is central and relatively large for the corresponding shell diameter. Septal neck is long and orthochoanitic, joined by thin cylindrical rings. Both siphuncle and camerae are apparently devoid of organic deposits.

In tentatively assigning this specimen to *Striacoceras*, rather than *Protokionoceras*, because of its slender shell. And the lack of strongly prominent longitudinal ribs and its relatively large siphuncle are the most distinctive features separating *Striacoceras* (?) sp. indet. from the species of the subfamily Kionoceratinae.

#### Superfamily Pseudorthocerataceae

Flower and Caster, 1935

#### Family Pseudorthoceratidae

Flower and Caster, 1935

#### Genus *Reticycloceras* Gordon, 1960

##### *Reticycloceras* (?) sp. indet.

Figures 2-3, 4

*Material*:—ASM 51309 from Loc. IM 60 (*Fusulinella biconica* zone).

*Descriptive remarks*:—Only a fragmentary specimen is available for this study. This figured specimen is an annulated orthocone, about 18 mm long. Cross section of the shell is depressed, expanding from 10.5 × 8.5 mm to 11.8 × 10.5 mm over a length of the fragment. Annuli are weak, rounded and slightly oblique to the long axis of the conch. In addition, surface is marked by a numerous transverse lirae, and edges of lirae are minutely and somewhat irregularly crenulated. No internal structures are preserved in the specimen examined.

This specimen is questionably assigned to *Reticycloceras* because of the similarity of its surface ornamentation to that of the *R. croneisi* Gordon (Gordon 1960, pl. 27, figs. 9–11; 1964, pl. 6, figs. 9–14, 25–28, 32).

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秋吉石灰岩からの石炭紀中期頭足類 Orthocerataceae, Pseudorthocerataceae: 秋吉石灰岩層群からは頭足類を含む多様な軟体動物化石群を産出する。本論では、秋吉台の南西縁に位置する伊佐地域より産出した6種のオルソセラス超科の頭足類を、秋吉地域では初めて記載する。頭足類化石の産出層準および岩相は、(1) *Brachycycloceras* sp. indet. を産出する *Pseudostaffella antiqua* 帯 (Bashkirian) の海百合片に富む bioclastic grainstone, (2) *Brachycycloceras akiyoshiensis*, sp. nov., *Geisonoceras sejunctus*, sp. nov., *Geisonocerina cribrella*, sp. nov., *Striacoceras* (?) sp. indet., *Reticycloceras* (?) sp. indet. を産出する *Fusulinella biconica* 帯 (Moscovian) の coquinite に二分される。

児子修司・西田民雄・久間裕子

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850. EARLY SHELL MORPHOLOGY OF *KARSTENICERAS*  
(ANCYLOCERATID) FROM THE LOWER CRETACEOUS CHOSHI GROUP,  
JAPAN AND ITS SIGNIFICANCE TO THE PHYLOGENY  
OF CRETACEOUS HETEROMORPH AMMONITES\*

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**Abstract.** *Karsteniceras obatai*, sp. nov., (Ancyloceratinae) from the Barremian Kimigahama Formation of the Choshi area, Kwanto district is described. The classification and phylogeny of heteromorph ammonites at supra-superfamily level is discussed on the basis of the internal shell features of the early ontogeny in this species. *K. obatai* is allied to *Karsteniceras asiaticum* (Yabe et Shimizu) in shell form; both possessing a ventral groove on the middle stage of each chamber, but the new species is distinguished by the stoutly ventro-lateral tubercles on the ribbing at mid-whorl and by the numerous lirae on the later whorl. These two species are considered to have derived from a common ancestral species. Some internal structural features of the nepionic stage of the shell of *K. obatai* are observable. One of the features, the siphuncular position, is interpreted as providing an important evidence for the classification and phylogeny of heteromorph ammonites at ordinal level, and that the existing classification of these ammonites is polyphyletic.

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### Introduction

The early ontogenetic stages of ammonoids have been studied from the view-point of major taxonomy and phylogeny, especially at ordinal level, by several paleontologists (e.g. Drushtchits and Doguzhayeva, 1974, 1981; Drushtchits *et al.*, 1977a, b; Mikhailova, 1974, 1982; Tanabe *et al.*, 1979; Birkelund, 1981; Ohtsuka, 1986). Accordingly, it would appear that the evidence provided by the internal structural features of early shell growth are useful when there are differing opinions concerning the classification and phylogeny of heteromorph ammonites based on the septal suture line. These studies, however, were concerned mainly with the development of planispiral ammonites and less so with the heteromorphs. The chief reason may be that the

internal structural features of early shell ontogeny of the planispiral ammonites are more easily observed, because the adult shell partly encloses its early shell growth. On the other hand, the early whorls of heteromorph ammonites are not always partly enclosed in its adult shell and the record of early shell growth is often separated from the adult part of shell or lost.

I have been fortunate enough to find internal structural features of the early shell growth in an ancyloceratid ammonite collected by H. Tsuda, from the Lower Cretaceous Choshi Group. From this observation, I have reached the following conclusions: i) these ancyloceratid specimens belong to the genus *Karsteniceras*, ii) ammonites may be divided into two groups on the basis of the position of nepionic siphuncle.

This paper gives a detailed description, including internal structural features of these specimens which are referred to a new species of the genus *Karsteniceras*. The paper also discusses the classification and phylogeny of heteromorph ammo-

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nites at supra-superfamily level on the basis of observed internal shell structure and previously reported data by other workers.

At Choshi, the east end of the Kwanto district, the Cretaceous outcrops occur over a small area along the coastline facing the Pacific Ocean. According to Obata and Matsukawa (1982), the succession can be subdivided lithologically into five units, named the Ashikajima, Kimigahama, Inubouzaki, Toriakeura and Nagasakihana Formations in ascending order. The species to be described in this paper was obtained from calcareous concretions in the mudstone of the middle part of the Kimigahama Formation, where it is associated with *Crioceratites (Emericeras) emerici* Léveillé, *Olcostephanus (Neostieria) cadocerooides* (Karakasch), *Barremites (B.) difficilis* (d'Orbigny), *Holcodiscus* sp. and other species. Thus, the ammonite fauna of the Kimigahama Formation shows a close affinity to that from the Tethyan realm, e.g. the stratotype of the Lower Barremian in France (Busnardo, 1965) and the Barremian of the Sably Mine in the Crimea, Russia (Karakasch, 1907). Accordingly, the Kimigahama Formation can be assigned to the Lower Barremian.

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## Depository

The specimens with the prefix NSM are preserved in the Department of Paleontology, National Science Museum, Tokyo.

## Systematic description

Order Ammonoidea Zittel, 1884

Suborder Ancyloceratina Wiedmann, 1960

Superfamily Ancylocerataceae Meek, 1876

Family Ancyloceratidae Meek, 1876

Subfamily Ancyloceratinae Meek, 1876

Two opinions, by Casey (1960) and Wiedmann (1973), have been presented concerning the classification of the superfamily Ancyloceratinae. Casey (1960, p. 19) stated that the Ancyloceratinae (s.s.) consists of the ponderous heteromorphs of the Aptian genera, i.e. *Ancyloceras*, *Tropaeum*, *Australiceras*, *Epancyloceras*, *Ammonitoceras* and *Lithancyclus*. Wiedmann (1973) mentioned that Ancyloceratinae includes Valanginian to Barremian micromorphs which are called leptoceratids, i.e. *Eocrioceratites*, *Menuthiocrioceras*, *Karsteniceras* and *Hamulinites*. Certainly, the evolutionary trend demonstrated by progression from ancyloceratid to crioceratid coiling about ponderous heteromorphs of the Aptian Lower Greensand (Casey, 1960) is different from that of leptoceratids which does not show the tendency toward coiling. So, the leptoceratids are probably attached to other subfamily with the exception of Ancyloceratinae, if Ancyloceratinae is defined as that including only those ponderous heteromorphs of the Aptian genera. It is suggested that these leptoceratids are grouped within the Subfamily Leptoceratoideinae (Thieuloy, 1966), because one of the Barremian leptoceratids described as *Leptoceratoides* by Thieuloy (1966) or by Vašiček (1972) is distinguished from other leptoceratids in having constrictions in the adult stage. The constriction is, indeed, one of the criteria for classification at superfamily level as exemplified by Desmocerataceae. Leptoceratoidinae

(Thieuloy, 1966), however, was synonymous with the Ancyloceratinae by Wiedmann (1973). Accordingly, reexamination of the criteria for classification at subfamily level concerning leptoceratids is necessary. As this is not an appropriate place to discuss the criteria for classification at superfamily level concerning leptoceratids, I tentatively follow the lumping scheme of Wiedmann (1973).

Genus *Karsteniceras* Royo y Gomez, 1945

*Type species:* *Ancyloceras beyrichii* Karsten, 1858.

*Generic characters:* Whorls of small-size with thin shell and septal walls, coiled crioceraticone or cyrtocone with open spire followed by a slightly curved shaft and hook. The initial one-half to two whorls are closely coiled, followed by loose coiling in a single plane. The adult shell shows nearly flat sides ornamented by strong simple ribs which are interrupted along the siphonal line terminating either in ventro-lateral tubercles or the rib may be merely slightly effaced, possessing no ventro-lateral tubercles, in the middle growth stage. The final portion of the body chamber is covered with numerous lirae. The suture is ELUI, with slightly indented trifid lobes.

*Discussion:* This genus was separated by Royo y Gomez (1945) from the genus *Ancyloceras*, on the basis of having crioceraticone shells with non-tuberculate ribs, and a *Worthoceras*-like saddle in the suture-line. Some specimens which can be assigned to *Karsteniceras*, collected from the Barremian Kimigahama Formation in Japan, have both of these characters, crioceraticone coiling and non-tuberculate ribs. In these specimens, however, the characters are merely observable at only the part of ontogeny described below as the latter part of the third phase of shell growth. Tuberculate ribs are recognizable on these specimens from the Kimigahama Formation at another ontogenetic phase. From the above characters, it may be inferred that *Karsteniceras* has a variable morphology throughout its ontogeny, a view held also by Dr. J. Wiedmann (personal

communication, November 1985). The ontogenetic description, however, is probably not satisfied within the description of the genus *Karsteniceras* by Royo y Gome (1945).

The leptoceratid heteromorph ammonites, which have been described either as *Leptoceras* or leptoceras-like ammonites, form two groups, one ranging from the Berriasian to Valanginian and the other being restricted to the Barremian. These two groups are interpreted as separate subfamilies on the basis of their stratigraphic interruption at Hauterivian, although they both show resemblances to each other (e.g. Thieuloy, 1966; Wiedmann, 1973). According to Wiedmann (1973), the former group, which ranged from the Berriasian to Valanginian, consists of the genus *Leptoceras* only and is attached to the subfamily Protancyloceratinae encompassing such genera as *Protancyloceras*, *Cochlocrioceras*, *Vinalesites* and *Leptoceras*. The latter group occurring in the Valanginian to Barremian is grouped in the Ancyloceratinae including *Eocrioceratites*, *Menuthiocrioceras*, *Karsteniceras* and *Hamulinites*.

The classification of leptoceratids based on ontogenetic characters is judged as follows: *Karsteniceras* (generic characters are described as above) is closely allied to *Leptoceras* (Thieuloy, 1966, p. 287) from the Berriasian of Switzerland and southern France in its cyrtocone or criocone shell which shows, initially, normal coiling followed by a smooth shaft and later cyrtocone coiling ornamented by ribbing. These two genera can be distinguished, however, from each other by the presence in *Karsteniceras* of a ventral groove and distinct ventro-lateral tubercles in the middle growth stage and numerous lirae in the late growth stage.

The Barremian leptoceratids included in Ancyloceratinae have been reduced in number to two genera by Wiedmann (1973) based on the coiling form. These are *Karsteniceras* Royo y Gomez, 1945 (= *Veleziceras* Wright, 1957 *pro Orbignyceras* Royo y Gomez, 1945; = *Leptoceratoides* Thieuloy, 1966), which is crioceraticone, and *Hamulinites* Paquier, 1900 (= *Eoleptoceras*, *Wrightites* and *Tzankoviceras* Manolov,

1962) which is an ancyloceraticone. It is possible, however, that the characters of surface ornamentation are useful in the classification at generic level. For example, *Karsteniceras* as described above from Japanese material is capable of being separated from *Karsteniceras*, as defined by Royo y Gomez (1945), because the generic characters described by him are already present in the young stage. This feature of the Japanese material may merit a new name in consequence. *Leptoceratoides* (Thieuloy, 1966), such as the species described by Vašiček as *Leptoceratoides pumilus* (Uhlig) (1972, p. 54, pl. 4, fig. 5) and *L. subtilis* (Uhlig) (1972, p. 54, pl. 7, fig. 4, text-fig. 16), is distinguished from *Karsteniceras* (Royo y Gomez, 1945) in having constrictions in the adult stage.

*Karsteniceras* differs from the Barremian genus *Eoleptoceras* described by Manolov (1962, p. 532–533) from northern Bulgaria, which was included in the genus *Hamulinites* by Wiedmann (1973), in its style of coiling and ornamentation. The coiling in the former is crioceraticone or cyrtocone, but in the latter it is ancyloceraticone. In *Eoleptoceras*, the ribs pass over the venter without interruption at all growth stages. This feature is only seen in *Karsteniceras* in the later growth stage. The ventral groove and stout ventro-lateral tubercles on the middle stage of growth in *Karsteniceras* are not developed in *Eoleptoceras*.

*Leptoceras*, *Eoleptoceras* and *Karsteniceras* are comparable in the configuration of the coiling in their initial one-half to two whorls and in their slightly curved smooth shafts, and in their possession, suturally, of trifid lobes. These features are interpreted as indicating the phylogenetic affinity of these genera and that they have a common ancestor as suggested by Wiedmann (1973).

The Barremian leptoceratids present diverse coiling, ribbing and tuberculation. For instance, *Karsteniceras* is characterized by crioceraticone, interrupted ribbing with ventro-lateral tubercles and link-like ribbing across the venter without tubercles in the middle growth stage. On the other hand, *Eoleptoceras* is char-

acterized by ancyloceraticone coiling and link-like ribbing across the venter without tubercles. These same features in both of the above genera are observable in the Berriasian protancyloceratids as well as the Barremian leptoceratids. *Himantoceras* for example is distinguished by its crioceraticone coiling, link-like ribbing across the venter without tubercles and constrictions with tubercles, whereas *Leptoceras* is characterized by cyrtocone or criocone coiling, link-like ribbing across the venter without tubercles. Characteristic features of *Protancyloceras* are cyrtocone and interrupted ribbing across the venter, whereas *Vinalesites* is typified by ancyloceraticone coiling and link-like ribbing across the venter. The development of these similar morphological characteristics in both the earlier and later groups of leptoceratids suggests that these two groups adapted to their surroundings by using the same morphological strategy.

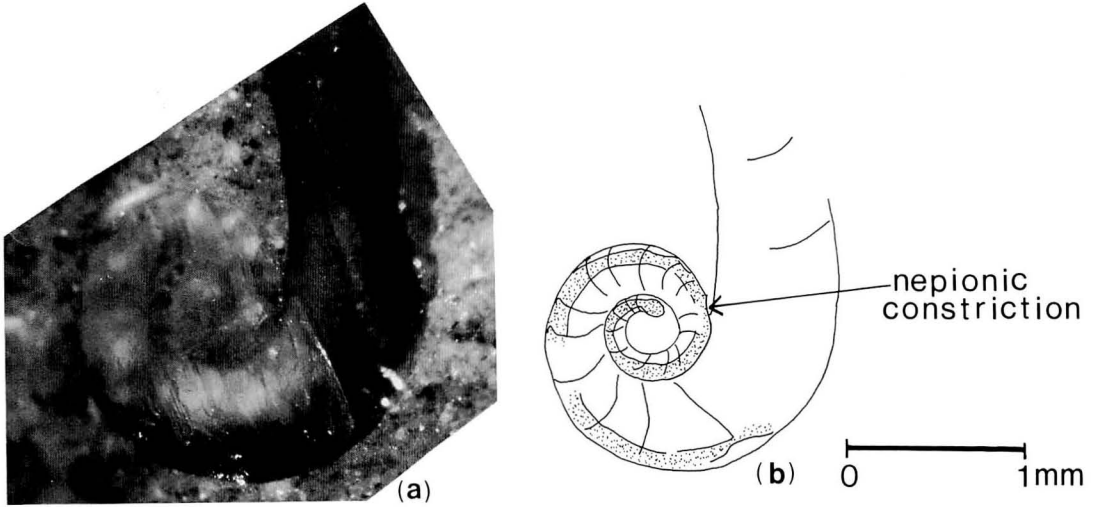
*Karsteniceras obatai*, sp. nov.

Figures 1, 2, 3-1–4, 4

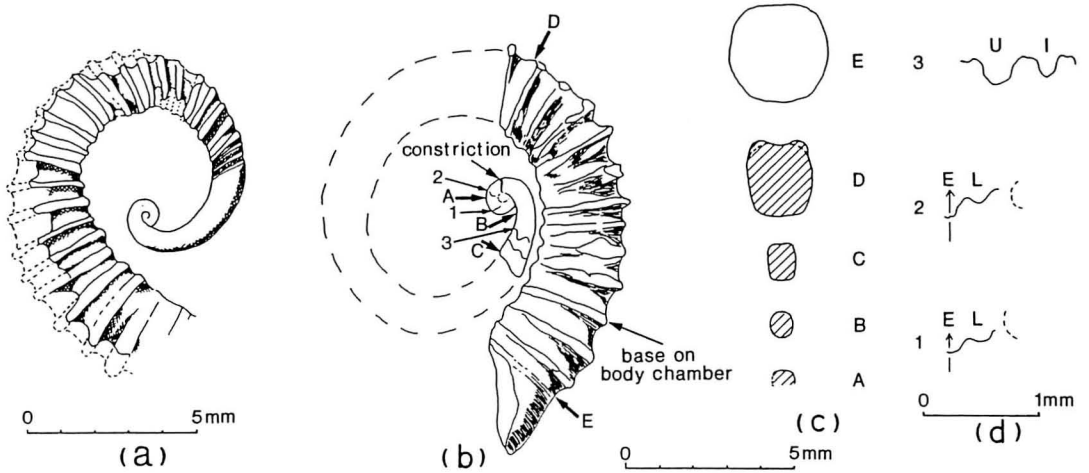
1926. *Ancyloceras* ? sp. Yabe and Shimizu, p. 17, pl. 15, figs. 12, 13.

*Material*: NSM-PM 9589, holotype; and NSM-PM 9590, paratype; both collected by H. Tsuda. These specimens were collected from loc. 7309. Other paratypes were collected as follows: NSM-PM 9591 collected by H. Tsuda, from loc. 7403; NSM-PM 9592, and NSM-PM 9593 collected by T. Asada from loc. 7433. All material was collected from the middle part of the Kimigahama Formation at Isejigaura, Choshi City, Chiba Prefecture. For descriptions of the localities yielding these specimens, see Obata *et al.* (1975) and Obata and Matsukawa (1982).

*Specific diagnosis*: Shell of small size, coiling cyrtocone being about 14 mm in maximum diameter of loose spire. Ornament of young shell is smooth, middle portion is ornamented by ribbing and the later portion is covered with numerous lirae. The ribs are rectiradiate, regularly arranged, elevated, slender, and somewhat sharpened at the top. The interspaces of ribs are



**Figure 1.** The early stage of *Karsteniceras obatai* Matsukawa. (a) The early part of NSM-PM 9590. (b) Drawing of a median section of the same specimen to show the position of the siphuncle and septa.



**Figure 2.** *Karsteniceras obatai* Matsukawa. Diagrammatic sketch of NSM-PM 9590 (a) and 9589 (b, c, d), showing the mode of coiling and ornamentation (a, b), whorl section (c) and suture (d) in its early ontogeny.

twice or thrice as broad as the ribs themselves.

*Ontogenetic description:* See Table 1.

(i) *the first phase (protoconch and three quarters of the first whorl).* This phase is divided into protoconch and nepionic stages. The protoconch is roughly ellipsoidal in shape, being laterally expanded by the succeeding first whorl. It is 0.32 mm (e.g. NSM-PM 9590) in maximum

diameter. A clear nepionic constriction occupies  $323^\circ$  (e.g. NSM-PM 9590) of the total rotation angle from the axis of coiling. The nepionic size is 0.61 mm (e.g. NSM-PM 9590). Initially, the siphuncle is located at the central part of the nepionic whorl but then shifts its position to the ventral side rapidly as the shell grows. The septa are adorally convex and almost regularly

spaced from each other. The characters of this phase can not be shown clearly in an electron microscope photograph because the two specimens showing this initial stage are too badly fractured. Figure 1(a) is a photograph taken under the microscope of the initial whorls of NSM-PM 9590 with an accompanying explanatory drawing in reconstruction.

(ii) *the second phase (the proximal part of the first whorl and most of the second whorl)*. This phase is normally coiled. The diameter of shell is about 1.7 mm (e.g. NSM-PM 9590), and the shell is narrowly umbilicate at the early 3.5 phi stage. The umbilicus is shallow with an inclined wall. The whorl section is initially roughly elliptical, much broader than high in a form ratio of 1.8 (e.g. NSM-PM 9589), but changes to a circular shape during the growth of the second whorl. The surface is smooth without any ornamentation. The siphuncle is wholly ventral in this stage. The septa are about 12 in number, adorally convex and regularly spaced. The suture line at this stage shows a shallowly bipartite external lobe and lateral lobe.

(iii) *the third phase (the proximal part of the second whorl to the end of the third whorl)*. This phase is characterized by a loose cyrtocone coil form together with the abrupt appearance of strong ribbing at an early stage. The diameter of whorl is above ca. 2.00 mm. The whorl section shifts from a circular shape to an oblong shape with ventral groove, during the growth of the early to middle stages in this third whorl. The ventral groove disappears, however, at the proximal end of the third whorl. In the earliest stage of this phase, the surface is still smooth without any ornamentation. In the middle stage, stout sharp ribs with ventro-lateral tubercles appear, which are interrupted on the venter. This rib pattern modifies towards the proximal end producing ribs which cross the venter without tubercles. The number of ribs increases to about 13 or 16. The sutural pattern can be expressed by the formula ELUI, and is characterized by a tripartite U-shaped umbilical lobe and an asymmetrically bipartite lateral saddle.

(iv) *the fourth phase (the fourth whorl)*. A

loose coil form with smooth surface, showing a polygonal cross section, is characteristic of this phase. The whorl becomes of equal height and breadth with a ratio of 1:1. The surface is covered with numerous lirae.

*Comparison*: This new species is allied, in its coiling characteristics, to *Karsteniceras asiaticum* (Yabe et Shimizu) which was originally described from the Sanchu Terrane by Yabe and Shimizu (1926, p. 73, pl. 15, fig. 21) as *Leptoceras asiaticum* and which was revised subsequently by Wiedmann (1973), but is distinguished mainly by differences in the ornamentation. In the former species, the ribs are rectiradial, somewhat sharpened at the top, and interrupted on the venter. In *K. asiaticum*, the ribs are rursiradial, nearly flat on the outer whorl and without ventral interruption. The ventro-lateral tubercles in the former species are stouter than those in the latter. These two species are considered here to be derived from a single common ancestor. *Karsteniceras beyrichii* (Karsten), the type species of the genus, from the Barremian of Colombia (Royo y Gomez, 1945, p. 460–461; pl. 71, fig. 1) seems to resemble *K. obatai* in having crioceratid coiling and a ventral groove. But *K. beyrichii* is distinguished from the latter by possessing link-like ribbing across the venter and narrow interspaces between ribs without ventro-lateral tubercles. *K. beyrichii* is also similar to *Leptoceratoides pumilum* (Uhlig) (Vašiček, 1972, p. 54, pl. 4, fig. 5) from Silesia (Poland) in showing crioceratid coiling and a smooth initial whorl. *L. pumilum*, however, shows shallow constrictions which are absent in *Karsteniceras*. Furthermore, the ribs are rectiradial in the former, whereas proursiradial in the latter. Yet, if the classification of Barremian leptoceratids is based on Wiedmann (1973), *Leptoceratoides* would be synonymous with *Karsteniceras*.

*Occurrence*: Loc. 7309, a calcareous concretion contained in the mudstone bed at Isejigaura. In addition to the new species, *Crioceratites (Emericiceras) emerici* Léveillé and *Lissonia* spp. occur in the same concretion.

Loc. 7403, a calcareous concretion included

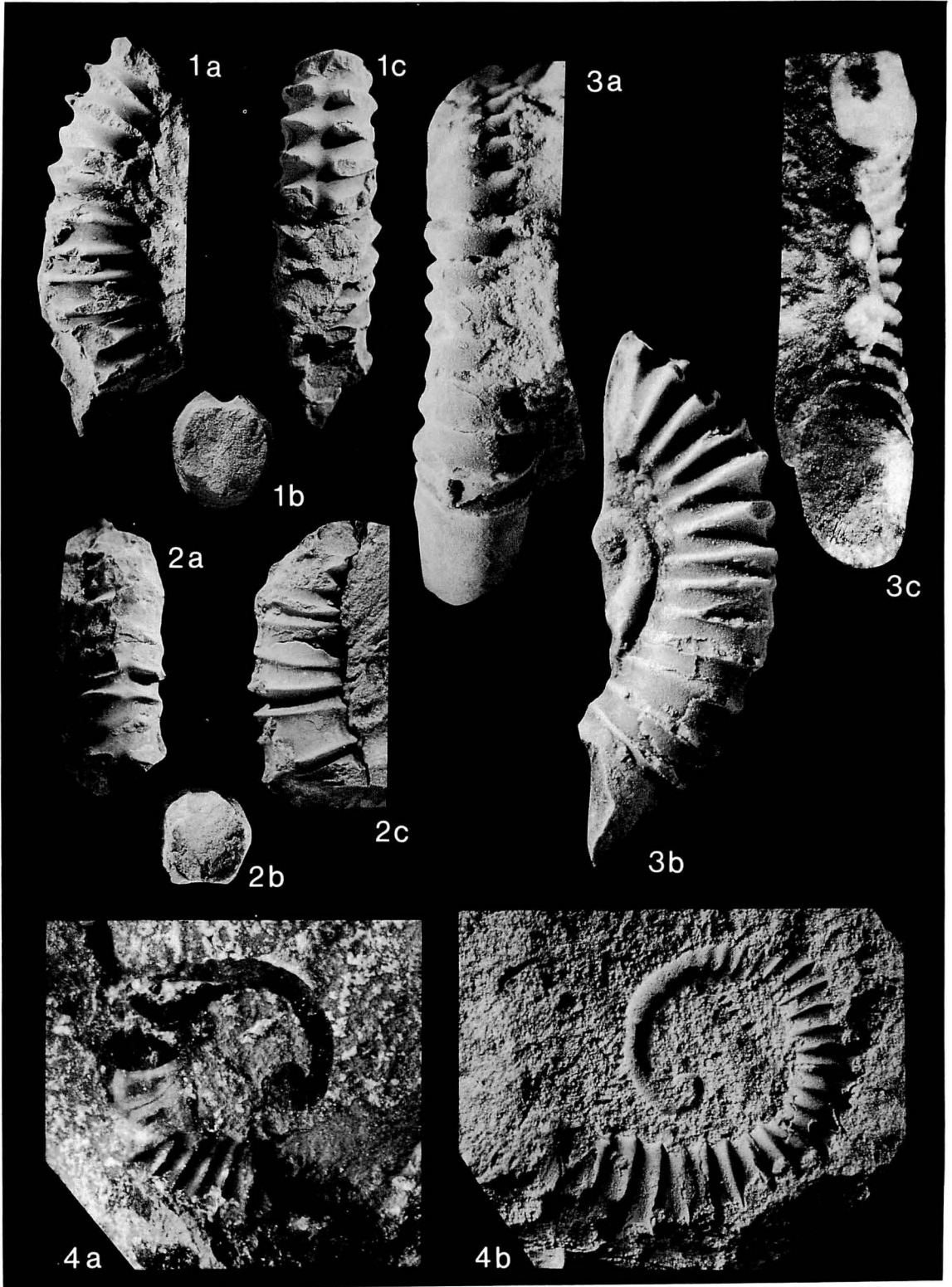


Table 1. Ontogenetic development in *Karsteniceras obatai* based on NSM-PM 9590.

Coiling form	Whorl	Diameter (mm)	S = $\frac{B}{H}$	Existence of ventro-lateral tubercles	Number of ribs	Shape of whorl section	Suture	Position of siphuncle	Ontogenetic phase		
									1st		
Abnormally	4th			absent	0			ventral	4th		
	6π				13±						
	3rd	5.40		present	16						
	Normally	4π	2.26						central	2nd	
		3π	1.16		absent	0					
		2π	0.68								
		1π	0.54								
		proto-conch	0.32								
				nepionic constriction							

← **Figure 3.** *Karsteniceras obatai*, sp. nov. from the middle part of the Kimigahama Formation, Lower Barremian. 1. NSM-PM 9591, paratype from loc. 7403 (H. Tsuda coll.). Lateral (a), front (b) and ventral (c) views, x3.0. 2. NSM-PM 9593, paratype from loc. 7433 (H. Tsuda coll.). Ventral (a), front (b) and lateral (c) views, x3.0. 3. NSM-PM 9589, holotype from loc. 7309 (H. Tsuda coll.). Ventral (a), lateral (b) and front (c) views, x6.0. 4. NSM-PM 9590, paratype from loc. 7309 (H. Tsuda coll.). Lateral (a, b), x6.0.

in the mudstone at Isejigaura. In addition to this species, *Hypophylloceras* sp., *Eotetragonites* sp., *Crioceratites* (*Emericiceras*) *emerici* Léveillé, *Acrioceras?* sp., *Olcostephanus* (*Neoastieria*) *cadoceroides* (Karakasch), *Lissonia* sp., *Neocomites?* sp., *Barremites* (*Barremites*) *difficilis* (d'Orbigny), *Barremites* (*Raspailiceras*) *cassida* (Raspail), *Barremites* (*Barremites*) sp., *Holcodiscus* sp. also occur at the same horizon in this locality. These calcareous concretions also include many fragmented plant fossils.

Loc. 7309 is 350 metres south of Loc. 7403.

The above localities are all in Choshi City, Chiba Prefecture. They are in the middle part of the Kimigahama Formation; Lower Barremian.

### Discussion

One of the major factors used in the classification of ammonites at the family and superfamily levels is the configuration of the septal suture line. Opinions concerning the subdivisions of the family groups of the Cretaceous ammonites, however, have been diverse. For instance, it is clear from Kullmann and Wiedmann (1970), Wright (1981) and Mikhailova (1982) that there is a disagreement concerning the taxonomic rank and position based on the septal sutural configuration and its ontogenetic development. Especially, this is so in the case of the heteromorph ammonites. Their phylogeny is interpreted to be monophyletic by Kullmann and Wiedmann (1970) and Wright (1981), but to be polyphyletic by Mikhailova (1982). The monophyletic phylogeny of the heteromorphs is derived from the fact that the Ancyloceratina, as a suborder, shows a consistent ELUI formula in their sutural pattern throughout their growth stage. On the other hand, the concept of a polyphyletic phylogeny is based on the view that the heteromorph ammonites are made up of two types, one having bifid and the other trifid lateral and umbilical lobes. The former is shown by the Turrilitaceae and Scaphitaceae, which therefore have something in common with Lytoceratida. The latter is shown in the Ancylocerataceae, which therefore has something in

common with Ammonitida. These two contrasting opinions on the phylogeny are considered here to be incapable of reconciliation because each stand point is fundamentally dissimilar.

The internal structural features of early shell growth is useful for the subdivision at order level in the planispiral ammonites (e.g. Tanabe *et al.*, 1979). In the case of the heteromorph ammonites, examples showing the internal shell structural features of early shell growth are not always reported in publications, because the record of the early shell growth is not always preserved intact with the adult shell, and may be broken-off and separated. Table 2 gives the tabulation of the internal shell structural features of early shell growth including protoconch size, spiral length of ammonitella and position of siphuncle based on the description by Branco (1879–1880), Smith (1901), Drushtchits *et al.* (1977b), Birkelund (1981), Drushtchits and Doguzhayeva (1981), Doguzhayeva and Mikhailova (1982) and this study. In Table 2, those genera which were discussed by these authors are assigned to respective superfamilies by adopting the opinion of Wright (1981). The protoconch size shows the following maximum diameter: *Ptychoceras* and *Karsteniceras* is about 0.3 mm, *Hypoturrilites*, *Deshayesites* and *Luppovia* are some 0.4 and 0.5 mm. The spiral length of the ammonitella is as follows: *Discoscaphites* and *Luppovia* are about 300°, *Ptychoceras* is some 310°, and *Karsteniceras* and *Baculites* are approximately 320° and 340°, respectively. The siphuncle in these genera occupies a ventral or central position: It is ventral in *Discoscaphites*, *Deshayesites*, *Ammonitoceras*, *Leptoceras* and *Karsteniceras*, whereas it is central in *Luppovia*. In *Baculites* and *Ptychoceras*, the position of siphuncle is central throughout the major part of the nepionic stage, but shifts to a ventral position at the end of this stage. From these observations, admittedly the data are rather poor, the present author concludes that the protoconch size may be small in *Ptychoceras*, middle size in *Karsteniceras*, and large in *Hypoturrilites*, *Deshayesites* and *Luppovia*. The spiral length of the ammo-



Table 2. Table showing the diagnostic characters in the early growth-stages of previously described genera and *Karsteniceras*.

Superfamily	Genus	Suture	Abnormally coiled stage	Normally coiled stage	Internal Protoconch size (mm)	Internal characters of nepionic stage Spiral length of ammonitella	Position of siphuncle
Turrilitaceae	1 <i>Baculites</i>	E L U I (bifid lateral lobe)	straight shaft	$2\pi - 2.5\pi$	unknown	345°	center → venter
	2 <i>Ptychoceras</i>	E L U I (E,L and U are bifid)	straight two parallel shaft	$2\pi$	0.28-0.29	311°	center → venter
	3 <i>Hypoturrilites</i>	E L U I	helical coiling	unknown	0.45	unknown	unknown
Scaphitaceae	4 <i>Discoscaphites</i>	ELUI → ELP <sub>1</sub> P <sub>2</sub> P <sub>3</sub> UV <sub>d</sub> I	normally flatside with coiled hook	$4\pi$	unknown	299°	venter
Deshayesitaceae	5 <i>Deshayesites</i>	ELU <sub>2</sub> ?I → ELU <sub>2</sub> ?U <sub>3</sub> ?U <sub>1</sub> ?I	all stage tightly planispiral	all stage	0.39-0.40	unknown	venter
Ancylocerataceae	6 <i>Ammonitoceras</i>	E L U I (L,U and I are trifid)	loosely coiling in a planispiral	$2\pi$	unknown	unknown	venter
	7 <i>Luppovia</i>	E L U I (trifid)	loosely coiling in a planispiral	$2\pi$	ca. 0.5	300°	center
	8 <i>Leptoceras</i>	E L U I (trifid)	loosely coiling in a planispiral	$3.5\pi - 4\pi$	unknown	unknown	venter
	9 <i>Karsteniceras</i>	E L U I (trifid)	loosely coiling in a planispiral	$3.5\pi - 4\pi$	0.32	323°	venter

1: Smith(1901), 2,5,6: Drushtchits et al.(1977), 4: Birkelund(1981), 5: Drushtchits & Doguzhayeva(1981),

7: Doguzhayeva & Mikhailova(1981), 8: Branco(1879-1880), 9: This study

Superfamily: adapted from Wright(1981)

nitella is small in *Discoscaphites* and *Luppovia*, median in *Ptychoceras*, and large in *Karsteniceras* and *Baculites*. At the least, one can assert that the siphuncle occupies the ventral position in the Deshayesitaceae, Scaphitaceae and Ancylocerataceae with the exception of *Luppovia*, and the central position in the Turrilitaceae and *Luppovia*. The relationship in these ammonites between the siphuncular position and planispiral coiling tends to confirm the following conclusions. Some ammonites with a ventrally positioned siphuncle, except for *Ammonitoceras*, have more tightly coiled whorl possessing of one and three quarters to two coiling, whereas the group having a centrally positioned siphuncle unites its whorl at about a coiling. Whatever happens to be the case, the position of siphuncle is considered here to show support for the Wright (1981) subdivision of the superfamily based on the suture, except in the case of the genus *Luppovia*. This view is different from Mikhailova (1982). *Luppovia* possessing a central siphuncle may be taken as a group which attempted to improve its siphuncle position in the manner as that observed among the primitive cephalopods which varied their siphuncle at a venter, central or dorsal position. To our regret, any standard criteria for subdivision of the superfamily is considered to be not detected from these data.

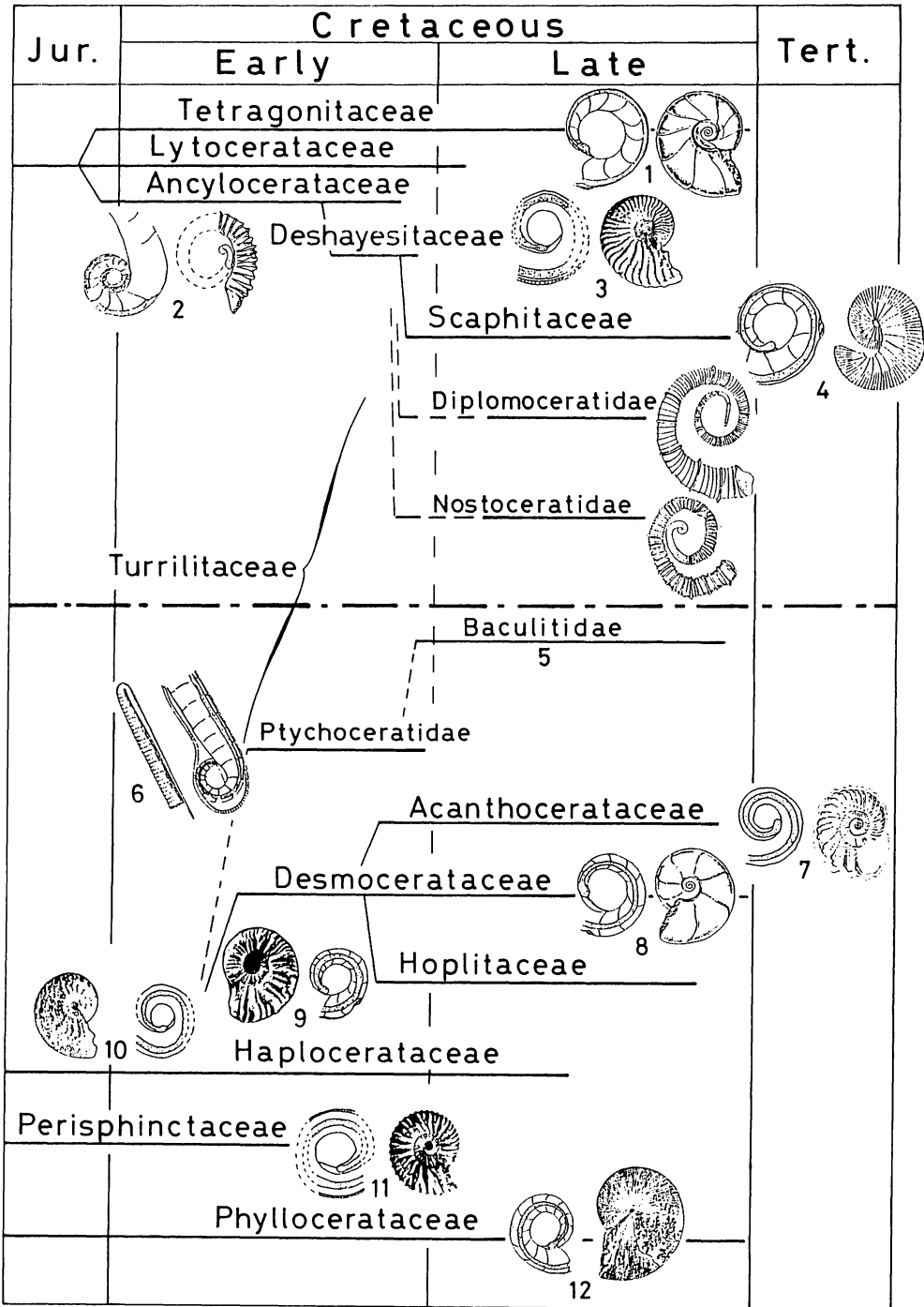
In the planispiral coiled ammonites, the position of the siphuncle is observed in numerous species, and can be seen to be different at some superfamily and suborder levels. For example, the Phylloceratina, consisting of Phyllocerataceae and Ammonitina, of Acanthocerataceae, Desmo- cerataceae, Hoplitaceae, Haplocerataceae and Perisphinctaceae, possess a centrally positioned siphuncle in the nepionic stage, and both the Lytoceratina of Tetragonitaceae and Lyt- ocerataceae has a ventrally positioned one (Obata and Matsukawa, 1979; Tanabe *et al.*, 1979, 1981; Drushtchits and Doguzhayeva, 1981). Thus, the position of siphuncle is variable in both the heteromorph and planispiral ammonites. Ammonites may be divided into two groups on the position of nepionic siphuncle. The first group

with an initial siphuncle placed in a central position consists of the Phyllocerataceae, Acantho- cerataceae, Desmo- cerataceae, Hoplitaceae, Peri- sphinctaceae and Turrilitaceae (part). The second group with an initial siphuncle in the ventral position consists of the Tetragonitaceae, Lytocerataceae, Deshayesitaceae, Scaphitaceae, Ancylocerataceae (part) and Turrilitaceae (part). The initial siphuncular positions are considered here to be useful, therefore, in the determina- tion of phylogeny in heteromorph ammonites. From the view point of the siphuncle position, it is possible to conclude that the heteromorph ammonites are derived from two main stocks. Ancylocerataceae, Deshayesitaceae, Scaphitaceae and turrilitaceans composed of Diplomoceratidae and Nostoceratidae are derived either from Tetragonitaceae or Lytocerataceae, while tur- rilitaceans composed of Baculitidae and Ptycho- ceratidae originated either from Haplocerataceae or Perisphinctaceae (Figure 4). Furthermore, on the basis of tiny protoconch size represented in the Ptychoceratidae and some other families in Ammonitina, such as Desmo- ceratidae, which are the smallest in the heteromorph or planispiral ammonites respectively, it may be warrantable to suggest that they originated from a common stock.

### Concluding remarks

The ancyloceratid ammonites from the Choshi Group described here represent a new species of *Karsteniceras* of early Barremian age in Japan. This species, named *Karsteniceras obatai* Matsukawa, sp. nov., is allied to *Karsteniceras asiaticum* (Yabe et Shimizu) also of early Barremian in age, from the Sanchu Terrane in Japan, in its coiling and the whorl section with ventral groove on the middle stage shell. It differs from *K. asiaticum*, however, in possessing stout ventro-lateral tubercles on the ribs.

Some features of the internal shell structure in the nepionic stage in the new species are observable. One of the notable characters is that the siphuncle occupies the ventral position from the early growth stage.



1,4,7,8,12: Tanabe et al.(1979) 2: This study 9: Obata & Matsukawa(1979)  
 3,10,11: Drushtchits & Doguzhayeva(1981) 6: Drushtchits et al.(1977) 5: Smith(1901)  
 Family tree: adapted from Wright(1981)

Figure 4. Phylogenetic relationships of Cretaceous ammonites on the basis of siphuncle position.

The siphuncle position of heteromorph ammonites in the early growth stage is recognized to be of two types, ventral or central in position. These features are compared with those in the planispiral ammonites: in the *Lytoceratina* the siphuncle occupies the ventral position, but in both the *Ammonitina* and *Phylloceratina*, it takes the central position in extreme youth. Accordingly, the heteromorph ammonites having the siphuncle in the ventral position are considered to be allied to the *Lytoceratina*, whereas those having the siphuncle in central position are considered to have an origin in the *Ammonitina* and/or *Phylloceratina*, as one possibility. These interpretations suggest that the current assumed phylogeny of the heteromorph ammonites is polyphyletic.

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下部白亜系銑子層群産 *Karsteniceras* 属 (アンキロセラス類アンモナイト) の初期殻の形態および、その白亜紀異常巻アンモナイトの系統にとっての意義：銑子地域のバレミアン君ヶ浜層から産出したアンキロセラス科に属する異常巻アンモナイト1種を識別して *Karsteniceras obatai* と命名、新種として記載した。そして、その成長初期の殻の内部構造と既に報告されている異常巻アンモナイトのそれともあわせて、超科より高次の段階の分類と系統を議論した。

この新種は、*Karsteniceras asiaticum* (Yabe et Shimizu) に類似する。しかし、その成長中期の段階の殻で、腹部の肩の位置にある肋に頑丈な疣をもつこと、成長後期で、数多くの繊細な条線をもつことで区別される。両種は、同一の祖先から派生したものと考えられる。

準模式標本の一つで成長初期殻の内部構造が観察される。そのうち連室細管の位置に注目すると、異常巻アンモナイトでも、それが腹部側にあるものと中央に位置するものと二つのタイプに区分できる。これは、正常巻アンモナイトがその二つのタイプからなるのと同様に、異常巻アンモナイトが多系統であるとする一つの論拠を示していると考えられる。 松川正樹

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## Errata

No. 146, 830. YAJIMA, Michiko: Pleistocene Ostracoda from the Atsumi Peninsula, central Japan

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64	right		between 16 and 17 lines the following synonymy is inserted.		

*Coquimba poga* Hu, 1986, p. 122, 124, pl. 3, figs. 13, 16–18, 21, 22, text-fig. 4a.

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