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The fossil on the cover is *Trilophodon sendaicus* Matsumoto, an extinct elephant, which was described from the Pliocene Tatsunokuchi Formation developed in the vicinity of Sendai, Northeast Honshu, Japan. (IGPS coll. cat no. 87759 (A), length about 18.5 cm)

936. THREE SPECIES OF *KRITHE* (CRUSTACEA : OSTRACODA) FROM SURUGA BAY, CENTRAL JAPAN*

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Abstract. A total of 545 specimens belonging to the genus *Krithe* were obtained from 45 surface sediment samples collected from Suruga Bay, the Pacific side of central Japan. These specimens were classified into three species on the basis of differences in carapace morphology, which can be clearly traced in each species to the young larval stage (A-6). The three species were identified as *K. sawanensis* Hanai, 1959, *K. antisawanensis* Ishizaki, 1966 and *K. surugensis* Zhou and Ikeya n. sp. Each species has a distinct depth range and distributional area in Suruga Bay. *Krithe sawanensis* is distributed throughout the entire bay at depths of 120-1,350 m. In contrast, the distribution of *K. antisawanensis* is restricted to the vicinity of the bay mouth, and *K. surugensis* is limited to the eastern area of the central trough. These two species are distributed at depths between approximately 150-650 m. The difference in distribution pattern and the intraspecific variation of the three species is correlated with environmental parameters such as water depth, water temperature, and dissolved oxygen.

Two populations of *K. sawanensis* having distinct carapace size and vestibule shape were recognized. The populations are separated from each other by an ostracode-barren zone (OBZ) at depths of about 650-810 m.

Key words. *Krithe antisawanensis, Krithe sawanensis, Krithe surugensis*, Ostracoda, Suruga Bay.

Introduction

Recent marine ostracode faunas around the Japanese Islands, including those from such shallow environments as inner bays and continental shelves, have been investigated in detail by several authors (Ishizaki, 1968, 1969, 1971 ; Ikeya and Hanai, 1982 ; Frydl, 1982 ; Bodergat and Ikeya, 1988 ; Tabuki and No-

hara, 1990 ; Ikeya and Itoh, 1991 ; Ikeya *et al.*, 1992). Bathyal faunas, however, have received relatively little attention and only studies conducted in such areas as the South Korean Sea (Choe, 1984 MS), Toyama Bay, Japan Sea (Ishizaki and Irizuki, 1990), and off the Shimane Peninsula, Japan Sea (Ikeya and Suzuki, 1992) have been investigated. On the Pacific side of Japan, only two reports from DSDP sites are known (Hanai *et al.*, 1980 ; Yajima *et al.*, 1985). Therefore, our knowledge of bathyal ostracode taxa, their

ecology and geographic distribution around the Japanese Islands is incomplete.

Several ostracode genera that are generally adapted to the bathyal zone of Japan, including *Krithe, Argilloecia, Bradleya, Pacambocythere, Robertsonites, Cytheropteron*, etc., were found in the samples from Suruga Bay. Of them, *Krithe* is the most abundant in specimens, and thus we were able to conduct detailed ontogenetic studies of the species.

Suruga Bay

Surface sediment samples collected from Suruga Bay provided us with an opportunity to investigate the bathyal ostracodes. The bay is the deepest in Japan and is also unique because it is located at the junction of four tectonic plates. A central trough over 2,000 m deep runs along the long axis of the bay. On the west side of the trough a basin over 900 m deep is present. The bay mouth opens broadly to the south towards the Philippine Sea where a strong warm oceanic current, the Kuroshio Current, flows northeastward. The hydrographic conditions within Suruga Bay are strongly controlled by the variable behavior of the Kuroshio Current. According to Nakamura (1982), the characteristics of the water column near the bay mouth are as follows. The salinity maximum is greater than 34.5 ‰ at depth of between 50–150 m ; the salinity minimum, except for surface water, is lower than 34.3 ‰ at depths of 300–500 m ; and an oxygen minimum zone where the concentration is less than 1.7 ml/l is developed between 700–1,000 m. The depth of the salinity maximum layer changes with seasons. It lies at around a depth of 150 m in winter, roughly 50 m in spring, about 100 m in summer, and approximately 125 m in autumn. This layer reflects the salinity maximum layer (34.9 ‰) of the main Kuroshio Water, and the water temperature is at 14–16°C.

Waters above a depth of 150 m in winter have an almost constant temperature of 14°C because of vertical circulation. The under-

lying salinity minimum layer has a temperature of around 7°C.

Muddy sediments predominate throughout the bay, especially on the continental slope, in the basin, and on the trough bottom.

The genus *Krithe*

Krithe is a blind genus and is most common in infraneritic and bathyal environments throughout the world (Van Morkhoven, 1963). Although it is difficult to identify species of *Krithe* due to the completely smooth surface of the calcareous carapace, the species have recently attracted a great deal of attention for their usefulness in estimating paleodepth and paleotemperature. Van Morkhoven (1972) and Bold (1971, 1981) have correlated carapace size in *Krithe* with water depth. Riha (1989) reviewed the hypothesis of Peypouquet (1977) and correlated the trend of increasing carapace size with an increase in the silicon concentration and the amount of dissolved nutrients in the sea
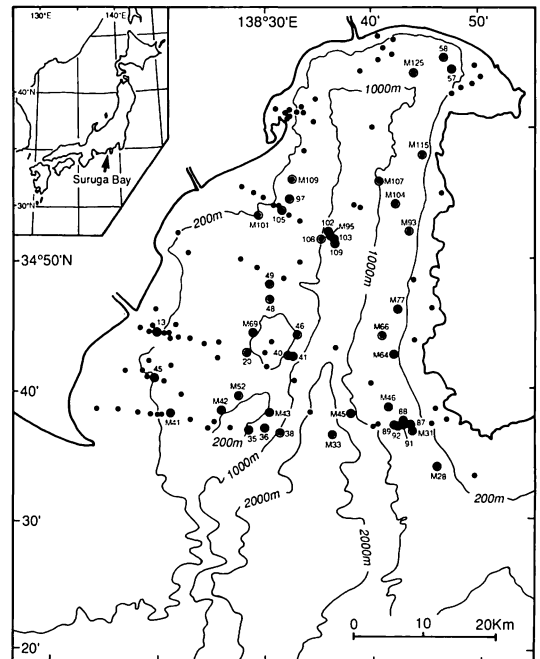

Figure 1. Map of Suruga Bay showing sample localities and bathymetry. Dots circled are *Krithe*-bearing samples.

Table 1. List of *Krithe* bearing samples from Suruga Bay. St. no. = station number, Lat. = latitude, Long. = longitude, M = mud, Sd = sand, gr = gravelly, sdy = sandy, peb = pebbly, f = fine, cly = clayey, sty = silty.

St.no.	Lat.(N)	Long.(E)	Depth (m)	Sediment Type	Total Ostracoda	Total *Krithe*
13	34°44.2′	138°20.1′	150	M	3	1
20	34°42.8′	138°28.0′	295	M	29	19
35	34°36.9′	138°28.4′	230	gr Sd	68	2
36	34°37.0′	138°29.7′	430	sdy M	6	3
38	34°36.4′	138°31.4′	1000	M	1	1
40	34°42.5′	138°32.2′	195	sdy M	24	5
41	34°42.6′	138°32.4′	460	peb M	12	6
45	34°41.0′	138°19.5′	185	sdy M	9	2
46	34°44.1′	138°33.1′	120	peb M	137	1
48	34°47.0′	138°30.3′	435–590	M	53	13
49	34°48.2′	138°30.2′	957–970	M	70	20
57	35°04.5′	138°47.2′	480	M	90	8
58	35°05.4′	138°46.8′	625	M	91	2
87	34°37.1′	138°43.6′	280	sdy M	405	13
88	34°37.1′	138°42.8′	390	M	109	45
89	34°37.1′	138°42.1′	470	M	42	23
91	34°37.1′	138°42.7′	400	M	62	30
92	34°37.0′	138°42.1′	490	M	3	2
97	34°54.8′	138°32.5′	575	M	77	26
102	34°51.7′	138°35.5′	1040	M	19	16
103	34°51.3′	138°36.5′	1350	M	104	92
105	34°53.6′	138°31.6′	400	M	7	1
108	34°51.6′	138°35.4′	1065	M	2	2
109	34°51.5′	138°36.5′	1340	M	1	1
M28	34°33.8′	138°45.9′	335	f Sd	460	9
M31	34°36.2′	138°43.4′	508	sdy Silt	43	12
M33	34°36.5′	138°35.7′	2015	sdy Silt	14	2
M41	34°38.0′	138°21.1′	418	cly Silo	23	14
M42	34°38.5′	138°25.6′	356	cly Silo	34	9
M43	34°38.0′	138°30.0′	180	f Sd	252	1
M45	34°37.8′	138°38.0′	1330	cly Silt	21	18
M46	34°38.4′	138°41.2′	595	cly Silt	49	16
M52	34°39.5′	138°27.2′	380	cly Silt	37	3
M64	34°42.4′	138°42.0′	252	sty Sd	983	7
M66	34°44.1′	138°40.3′	550	sdy Silt	70	15
M69	34°44.2′	138°28.2′	232	cly Silt	4	1
M77	34°46.0′	138°42.2′	370	sty Sd	542	38
M93	34°51.8′	138°43.6′	320	sty Sd	594	29
M95	34°52.2′	138°35.8′	1115	cly Silt	9	6
M101	34°53.6′	138°29.3′	160	sdy Silt	32	3
M104	34°54.0′	138°42.0′	630	cly Silt	45	2
M107	34°55.8′	138°40.3′	1125	sty Clay	44	26
M109	34°55.9′	138°32.3′	400	cly Silt	7	2
M115	34°57.8′	138°44.6′	320	cly Silt	635	74
M125	34°04.1′	138°44.0′	918	cly Silt	75	2

water. Conversely, Pokorný (1980) consid-
ered water temperature to be the primary
factor which determines the absolute dimen-
sions of *Krithe* carapaces.

Peypouquet (1979) identified the vestibule
region in *Krithe* and *Parakrithe* as the site
where haemoglobin regulation occurs in
response to external dissolved oxygen varia-
tion. He hypothesized that the vestibular
size in these two genera is inversely correlated
with dissolved oxygen content of sea water,
which is depth-correlated, and he developed
a method for determining paleodepth by link-
ing vestibular size and shape.

McKenzie *et al.* (1989) made a partial test
of Peypouquet's hypothesis, by examing liv-
ing *Krithe praetexta praetexta*, collected
from about 45 m depth off the west coast of
Sweden. The relationship between ves-
tibular size and O_2 values in early May was
shown to be basically consistent with Peypou-
quet's hypothesis. However, the actual O_2
values in later May and June were rather less
than Peypouquet's prediction. They consid-
ered that the imperfect correlations between
vestibule size and O_2 values might be due to
variations in food supply and other sources of
ostracode shell calcium. This is because
unbalanced calcium distribution in the shell
can also cause an expanded vestibule.

Paleodepth estimates based on carapace or
vestibular size in *Krithe* have been attempted
by many authors (*e.g.*, Donze *et al.*, 1982;
Peypouquet *et al.*, 1982; Benson and
Peypouquet, 1983; McKenzie and Peypou-
quet, 1984; Riha, 1989). De Deckker *et al.*
(1991) found that the Mg/Ca ratio of *Krithe*
valves demonstrates a relationship with ambi-
ent water temperature. This indicates that
analyses on the Mg/Ca ratios of this genus
and other taxa of ostracodes may provide a
very useful tool for reconstruction of bottom
temperature.

The primary purpose of the present study is
to identify the species of *Krithe* living in
Suruga Bay and to describe their mor-
phological and ecological characteristics.

We believe that these data will be important
for understanding intraspecific morpho-
logical variation in this genus and for using
Krithe as a paleoenvironmental indicator.

Material and Methods

The material for this study was derived
from 131 surface sediment samples which
were used for the analysis of the ostracode
fauna from Suruga Bay (Ikeya and Zhou, in
press) (Fig. 1). The 131 samples cover al-
most the entire area of the bay, ranging in
depth from 20 to 2,015 m. From 45 samples
a total of 545 *Krithe* specimens (78 carapaces
and 467 valves) were found. The detailed
station data and *Krithe* occurrence data are
summarized in Table 1.

The samples were treated with solutions of
formalin and Rose Bengal. Only 44 speci-
mens of *Krithe* were found with the soft
chitinous parts preserved. The vestibule
morphology and the distribution pattern for
sensillum pore canals on the carapace surface
of *Krithe* specimens were investigated by
means of an optical microscope. The de-
tailed structures of carapace surface and hinge
were observed by use of a scanning electron
microscope. The identification of species
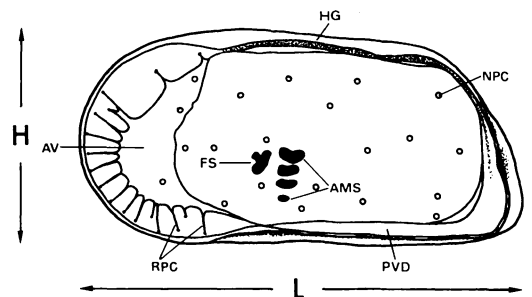was carried out mainly by the general micro-

Figure 2. Internal structure of *Krithe sawanen-
sis* (topotype of male RV). AMS = adductor muscle
scars, FS = frontal scar, AV = anterior vestibule,
PVD = posteroventral duplicature, HG = hinge,
NPC = "normal" pore canal, RPC = "radial" pore
canal, L = length, H = height.

scopic characters of carapace morphology. The shell dimensions were measured using a digital micrometer.

All specimens are deposited in the Institute of Geosciences, Shizuoka University (IGSU). Abbreviations used in this paper include L = length, H = height, T = thickness of valve, V = valve, C = carapace, RV = right valve, LV =

Krithe sawanensis Hanai, 1959
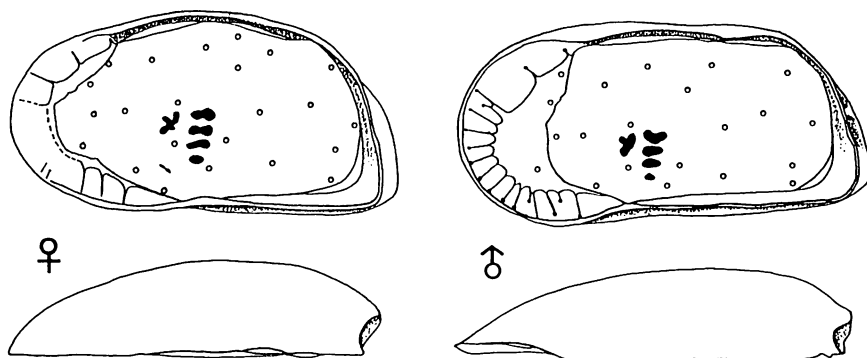
Krithe antisawanensis Ishizaki, 1966
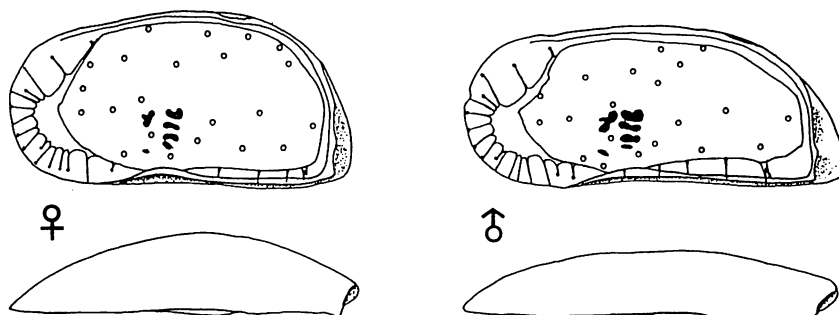
Krithe surugensis n. sp.

0.5mm

Figure 3. Internal and dorsal views of male and female RV of three species in *Krithe* from Suruga Bay. *K. sawanensis* is from station 103, *K. antisawanensis* from station 87 and *K. surugensis* from station M77.

Table 2. Comparison of some distinct characters in three species of *Krithe*.

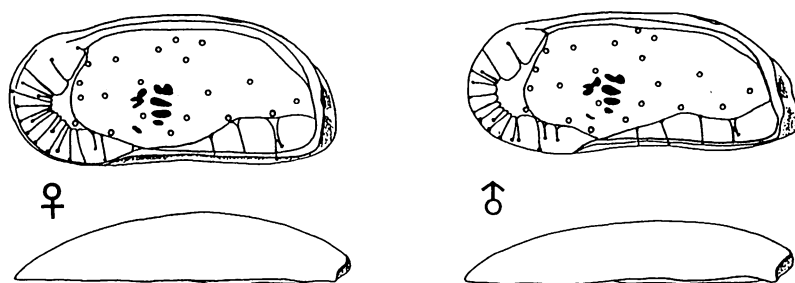|		K. sawanensis (♂ n=12) (♀ n=16)	K. antisawanensis (♂ n=4) (♀ n=10)	K. surugensis (♂ n=9) (♀ n=10)
1)	Size (average L)	♂ 1.00 ♀ 0.96	♂ 0.97 ♀ 0.86	♂ 0.82 ♀ 0.78
2)	Slenderness (average L/H)	♂ 2.09 ♀ 1.87	♂ 2.24 ♀ 1.92	♂ 2.22 ♀ 1.93
3)	Inflation (average T/L)	♂ 0.24 ♀ 0.22	♂ 0.18 ♀ 0.21	♂ 0.18 ♀ 0.22
4)	Hinge overlap	LV < RV	LV > RV	LV > RV
5)	Area of Anterior vestibulum	generally large	small	small
6)	Width of posterior duplicature	narrow, parallel to ventral margin	narrow, parallel to ventral margin	wide and convex
7)	Posteroventral angle (♂)	truncated	tapered	truncated
8)	Curvature of dorsal margin (♀)	somewhat arched	a little arched	nearly straight

left valve, ♂ = male, ♀ = female, A = adult, J = juvenile, n = number of specimens. All measurements are in mm.

Results

Identification of species

Krithe is a genus adapted to bathyal environments and easily distinguished from other bathyal genera by its characteristic carapace features. Figure 2 shows internal features of a right valve of male *Krithe sawanensis*, and a diagram of the measurements and descriptive terms that are used. We have found that all adult specimens of *Krithe* from Suruga Bay possess a common adductor muscle scar pattern, all have between 20–22 "normal" sieve-type pores on the valve, and all have the same general distribution pattern of these pores.

Three distinct species were identified based on differential characters that are shown in Figure 3 and Table 2. The numbers of adult and juvenile specimens of the three species from each station are shown in Table 3. Of the eight characters, hinge overlap and the width of the posteroventral duplicature are the most important in distinguishing the species. *Krithe sawanensis* is easily distin-

guished from the other two by its reversed hingement. *Krithe surugensis* is distinguished from the other two by its wide and arched posteroventral duplicature.

The differences in hinge overlap, slenderness and inflation of carapace can be successively traced to young instars. This fact suggests that, despite the close resemblance of adults, they should be considered as belonging to different biological species.

Two of the three species from Suruga Bay were previously described as *K. sawanensis* Hanai, 1959 from Pliocene Sawane Formation, Sadogashima Island, Japan Sea, and *K. antisawanensis* Ishizaki, 1966 from the Miocene Hatatate Formation, Sendai, on the Pacific coast. The third is described below as a new species, *K. surugensis* n. sp.

Growth charts of the three species are shown in Figure 4a–c. In each species, the adults do not fall on the regression line calculated from dimensions of juveniles, indicating that the animals take a remarkably positive allometric growth in carapace length when passing the last larval stages.

Distribution patterns of *Krithe* species

The geographical distributions of the three species in the bay are clearly different.
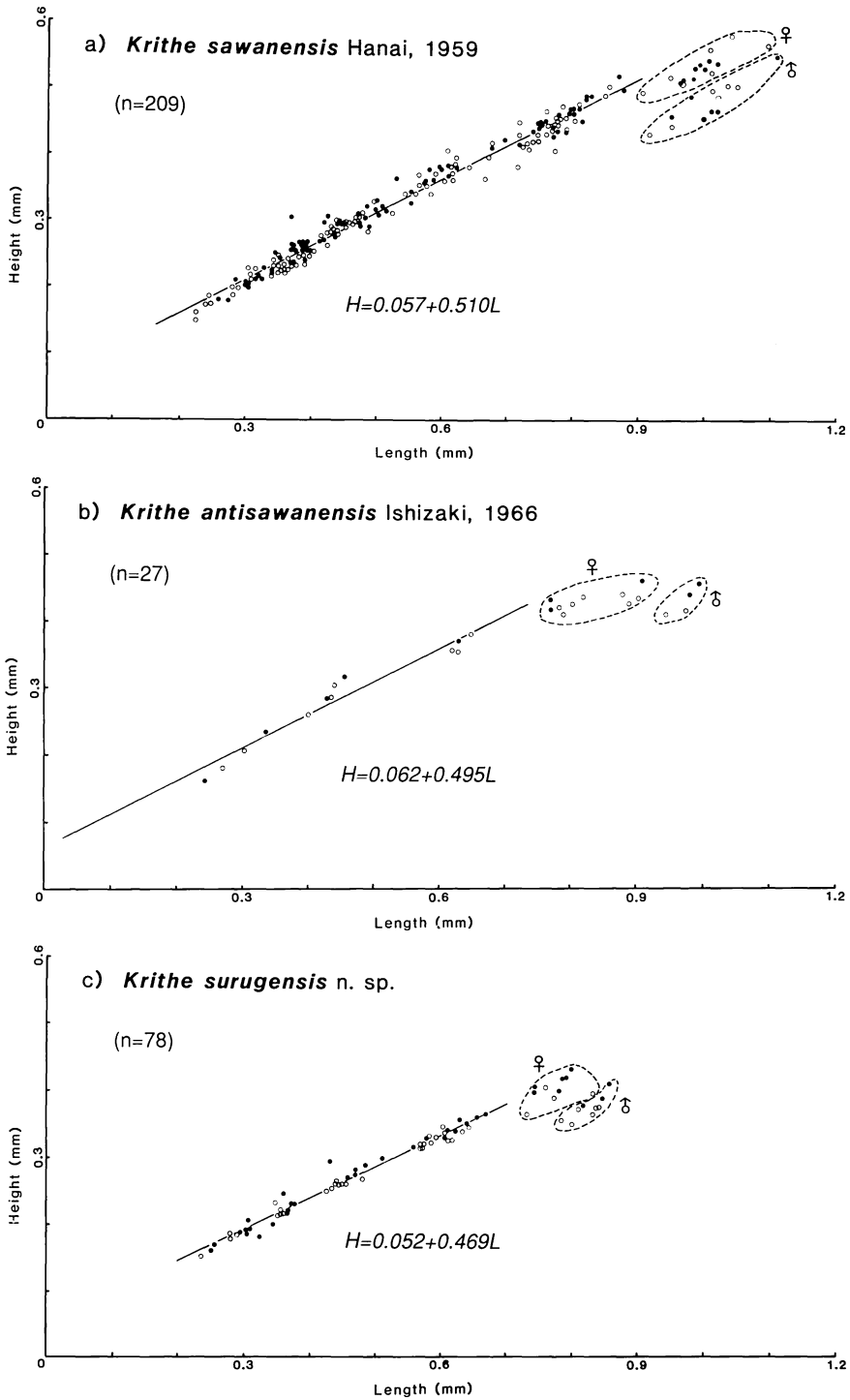
Figure 4. L/H diagram of three *Krithe* species. Dots are LV and circles RV. As for specimens of juveniles, only valves were measured and plotted in this figure. Regression lines are calculated from the dimensions of juveniles.
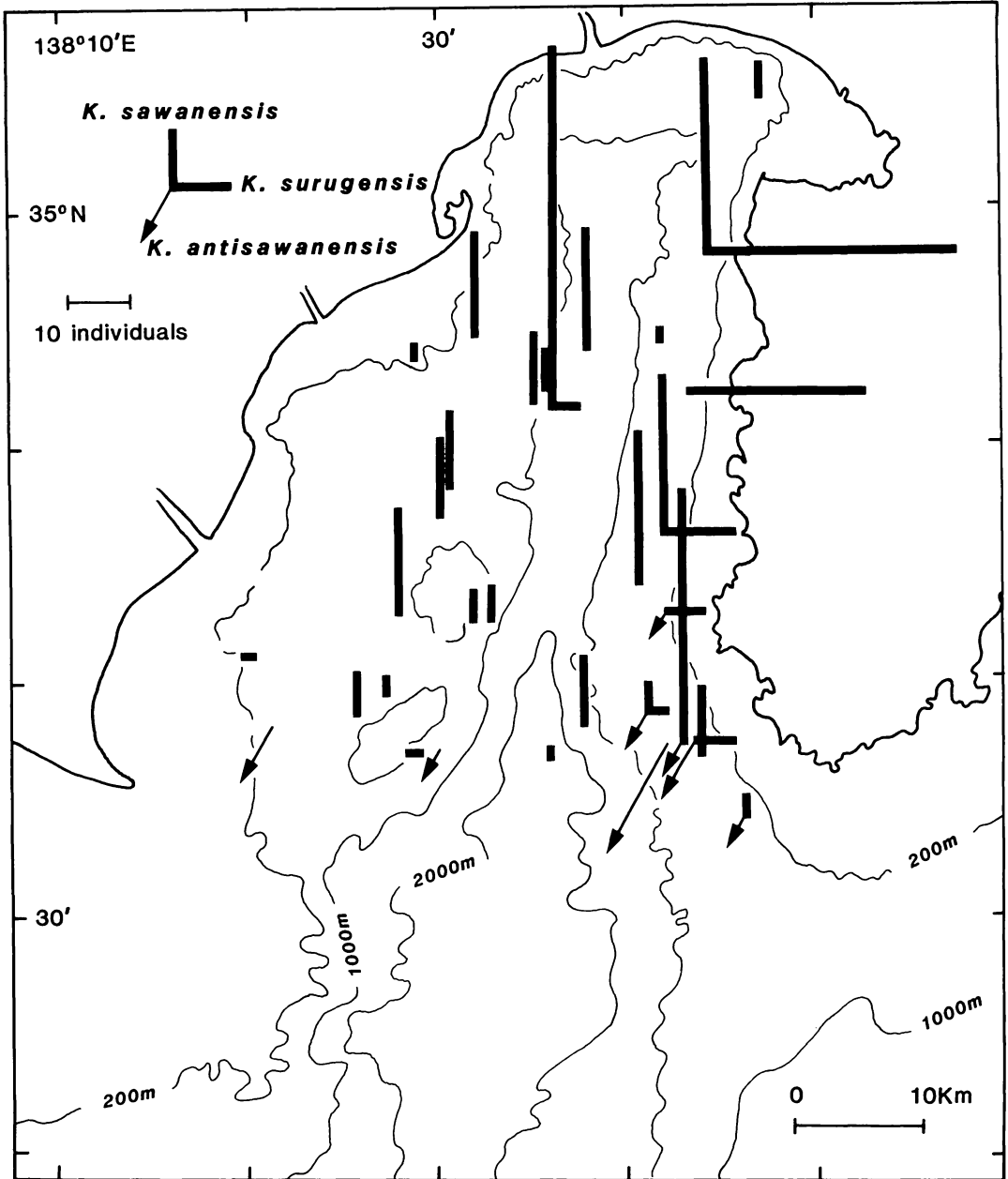
Figure 5. Geographical distribution of three *Krithe* species in Suruga Bay.

Krithe sawanensis is distributed extensively throughout the entire area of the bay. Conversely, *K. antisawanensis* is only found near the bay mouth, and *K. surugensis* is restricted to the east side of the central trough (Fig. 5).

With respect to their depth distributions,

K. sawanensis is distributed over a wide depth range from 120 to 1,350 m, whereas *K. antisawanensis* and *K. surugensis* are restricted to relatively shallow depths, at about 150–650 m (Fig. 6). A few abraded valves of *K. surugensis* obtained from a 1,350 m-deep
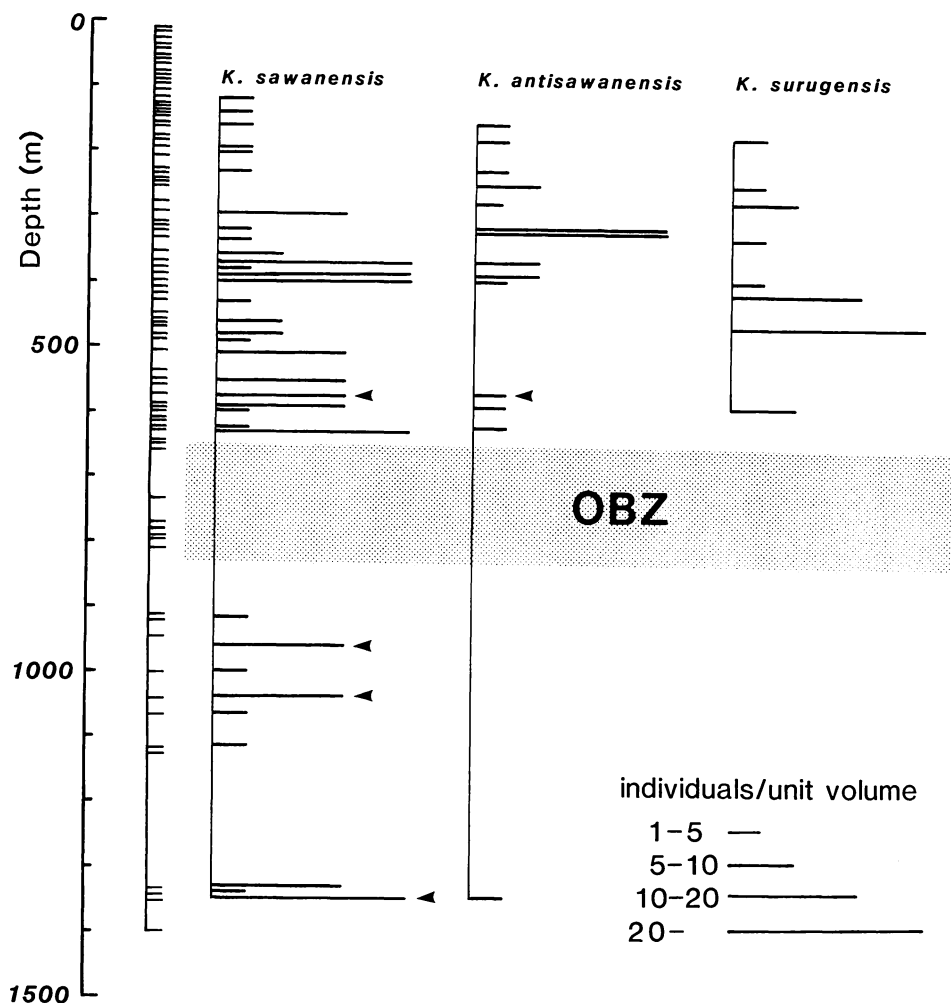
Figure 6. Frequency of three *Krithe* species across depth profile. Arrows indicate depth points from which living *Krithe* specimens were detected. Short bars on the left side are sampling depths. The "unit volume" represents roughly 50 cc wet surface sediment.

sample are regarded as allochthonous specimens because of their isolation from the main occurrence range of this species and their poor preservation. The depth interval of 650-810 m is barren of *Krithe* and other deep water taxa, and is referred to as the ostracode barren zone (OBZ). We found a total of 9 dead ostracode specimens in 3 of the 10 samples collected from that interval. The assemblage is composed of 7 species : *Aurila* sp., *Bradleya japonica* Benson, *Nipponocythere bicarinata* (Brady), *Paracytheridea*

polyspinosa Hu and Cheng, *Propontocypris* sp., *Sclerochilus* sp., and *Xestoleberis* sp. We believe these are all transported from shallow environments.

Intraspecific variation in *Krithe sawanensis*

In adult specimens of *K. sawanensis*, two distinct vestibule types have been recognized. All specimens above the OBZ have an axeshaped vestibulum that shows variability in shape and size. In contrast, all specimens below the OBZ possess a crescent-shaped

Figure 7. Structure of water column near the bay mouth (Lat. 34°34.9′N, Long. 138°35.2′E) (compiled from Nakamura, 1982), and vertical distribution of different vestibule shapes of three *Krithe* species.
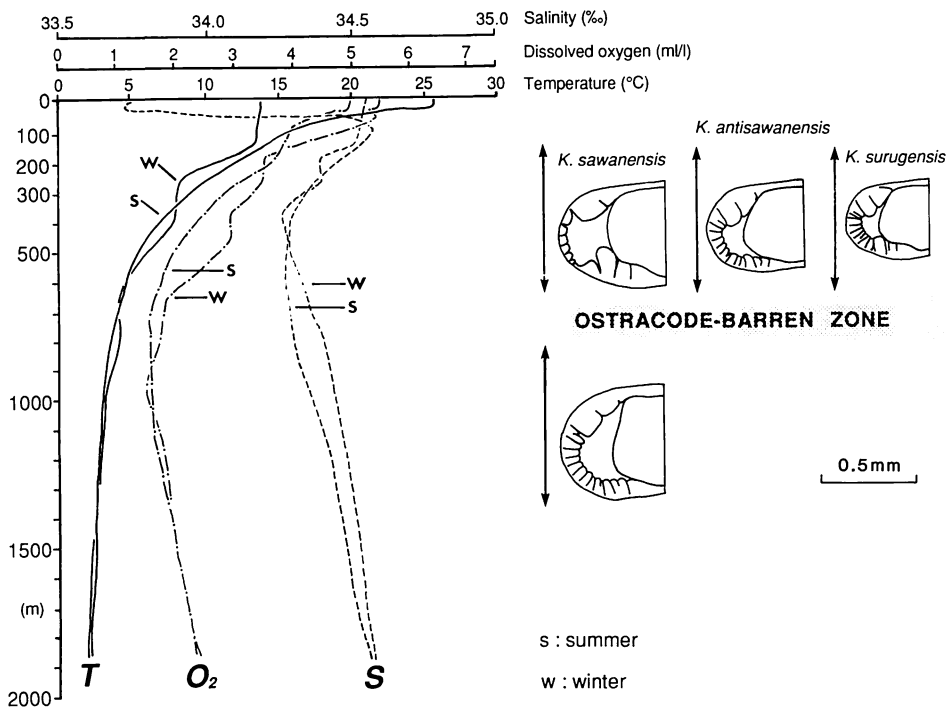
vestibulum that is uniform in morphology (Fig. 7). The areas of the axe-shaped vestibula are smaller than or equal to those of the crescent-shaped ones. Moreover, the volumes of the axe-shaped vestibulum are much smaller. In most cases, the axe-shaped vestibulum is so narrow that it is difficult to permeate it even by alcohol. Bubbles are left in the inner part (see Fig. 10). Consequently, distinct dimorphism is found in the vestibulum of *K. sawanensis* inhabiting different water depths.

Two populations of adult specimens in *K. sawanensis* differ in carapace dimensions (Fig. 8). The total 28 adult valves measured comprise 15 specimens from 8 samples above OBZ and 13 specimens from 3 samples below it. In Figure 8, both male and female specimens from samples above the OBZ display wide size variation, whereas specimens from samples below that zone are characterized by the tightly clustered points.

Discussion

Waters above 200 m in Suruga Bay are under the influence of the Kuroshio Current. Its influence is strongest at the bay mouth, and decreases gradually from the eastern side to the western side through the inner bay. *Krithe sawanensis* is a species tolerant of a variety of environments. For example, it occurs throughout the entire bay and has a wide bathymetric range of from 120 to 1,350 m. The different distribution patterns of *K. antisawanensis* and *K. surugensis* seem to be controlled by the influence of the Kuroshio Current. However, the depth ranges of the two species are 150–650 m, and the lower depth limit is far below the influence of the Kuroshio. The different distribution patterns of these species may reflect differences in oceanic conditions that are still not understood.

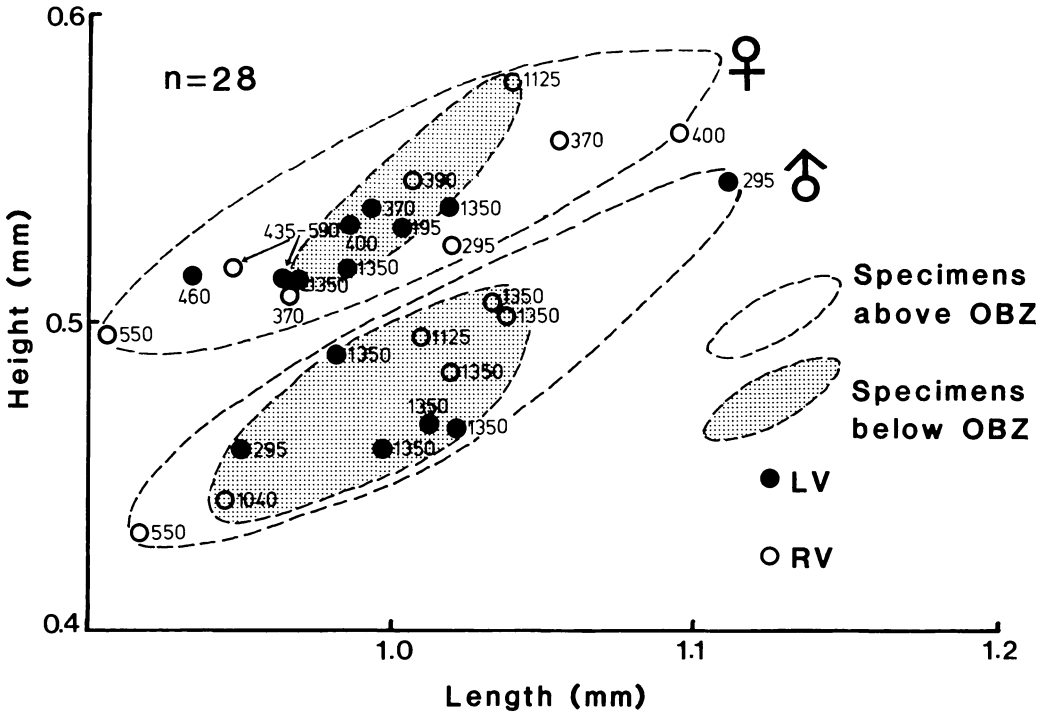On the basis of analysis of the ostracode

Figure 8. L-H scatter diagram of adult *K. sawanensis*. Numbers beside points indicate the sample depths in meters.

fauna from Suruga Bay, Ikeya and Zhou (in press) recognized an assemblage composed of *Krithe* spp. and *Bradleya albatrossia* Benson that has an upper depth limit of between 120 and 150 m. This depth is comparable with the lower limit of the vertical circulation layer during winter, when a clear boundary between the upper and lower water masses forms. This boundary separates the ostracodes into distinct shallow and deep water assemblages in this bay.

Ohta (1983) pointed out that in Suruga Bay a boundary of vertical distribution of the macrobenthos is regulated by the submarine topography of the shelf edge (about 130 m). This boundary is, in fact, comparable with that of the ostracodes found on the eastern side. However, the depth of the shelf edge in Suruga Bay is different in each area, *i.e.*, it is 150-200 m deep on the eastern side, about 100 m on the southwestern side, and about 50-60 m on the northwestern side. Therefore, the

shelf edge in this bay might not be so important a factor in controlling the vertical distribution of ostracodes.

The boundary between shallow and deep water ostracode assemblages is often found between about 150 and 200 m (*e.g.*, Van Morkhoven, 1972; Peypouquet, 1980) in many areas of the world. Van Harten and Droste (1988), on the other hand, reported that the faunal boundary in the Mediterranean is about 250-300 m deep. They suggested that there is a relationship between ostracode assemblages and the photic zone, as originally proposed by Pokorný (1971). In Suruga Bay, we consider that the most significant factor controlling the ostracode faunal boundary is the vertical circulation of oceanic waters in winter.

One of our interests in the present study was to clarify whether or not there is any intraspecific variation in the vestibule morphology of *Krithe*, a feature that seems to be

correlated elsewhere with environmental fac-
tors. In Suruga Bay, individuals with axe-
shaped vestibula occur only above the OBZ;
those with crescent-shaped vestibula occur
only below it. The OBZ corresponds with
the depth of the dissolved oxygen minimum
layer, whose known seasonal fluctuation is
from 700 m (in summer) to 950 m (in winter),
and which in summer is 1.5 ml/l and in
winter 1.8 ml/l. The axe-shaped vestibulum
of *K. sawanensis* above OBZ, like the ves-
tibula of *K. antisawanensis* and *K. surugen-
sis*, is narrow, and the crescent-shaped ves-
tibulum of *K. sawanensisis* below OBZ is
wide. These results therefore support the
hypothesis of Peypouquet (1979) that vesti-
bule size and shape are related to dissolved
oxygen.

In the depth interval from 120 to 650 m,
where one population of *K. sawanensis* lives,
temperature, oxygen and salinity show strong
gradients and appreciable seasonal changes
(see Fig. 7). Conversely, in the depth inter-
val of 918-1,350 m, which is the habitat of the
other population of *K. sawanensis*, the envi-
ronment is nearly homogeneous and shows
little seasonal change. Thus, the large vari-
ance in carapace morphology in the upper
water depths may be related to this environ-
mental variation. This interpretation is
supported by results of the study of *K.
producta* from off Punta Arenas, Chile by
Kaesler and Lohmann (1976).

We stress that the volumes of *K. sawanen-
sis* vestibula below the OBZ are greater than
those of specimens above the OBZ. This
shows the correlation with dissolved oxygen
minima hypothesised by Peypouquet (1977,
1979), but for volume rather than area.

Systematic description

Class Ostracoda Latreille, 1806
Order Podocopida Sars, 1866
Superfamily Cytheracea Baird, 1850
Family Cytherideidae Sars, 1925

Subfamily Krithinae Mandelstam, 1958
Genus *Krithe* Brady, Crosskey
and Robertson, 1874
Krithe sawanensis Hanai, 1959
Figures 8-1, 2, 3

Krithe sawanensis Hanai, 1959, p. 301-303, pl. 18,
figs. 3-7, text-figs. 3, 4; Hanai, 1961, p. 360, text-
fig. 4B, figs. 1a, b, 2a, b; Nohara, 1987, p. 39, 40,
pl. 1, fig. 5; Ishizaki and Irizuki, 1990, p. 59;
Ikeya and Suzuki, 1992, pl. 6, fig. 7.
not *Krithe sawanensis* Hanai: Zhao, 1988, p. 243, pl.
42, figs. 1, 2; Gou *et al.*, 1983, p. 34, pl. 6, figs.
1-13, text-fig. 8.

Type.—Holotype, male LV, UMUT-CA
2908 (L=1.16, H=0.51, T=0.25).

Type locality.—A cliff at Mano Bay,
Sawane-machi, Sado-gun, Niigata Prefecture,
Japan (Lower Pleistocene Sawane Forma-
tion).

Diagnosis.—A species of *Krithe* with in-
flated carapece. Posteroventral duplicature
narrow, parallel to ventral margin; du-
plicature near posterocardinal angle obscure.
Posterior margin meets ventral margin almost
making a right angle. RV overlaps LV.

Remarks.—Of all the *Krithe* species report-
ed from Japan and its adjacent areas, this
species is the largest in carapace size. More-
over, it is quite different from the other
species in having reversed hingement.

In the present study, dimorphism of the
vestibulum has been found in this species.
All adult specimens from depths of 120-650
m have an axe-shaped vestibulum, whereas all
those from depths of 920-1,350 m have a
crescent-shaped one. The two populations
are separated by an ostracode-barren zone
(OBZ) at 650-810 m.

In the L/H scatter diagrams (Fig. 4a), the
regression line for juvenile stages of this
species is similar to that of *K. antisawanensis*,
despite their distinct morphology. Sex was
distinguished by microscopic observation.
All scatter points of male are below those of
female, reflecting the distinct sexual dimor-
phism in this species.

Distribution.—Recent: About 200-1,400 m
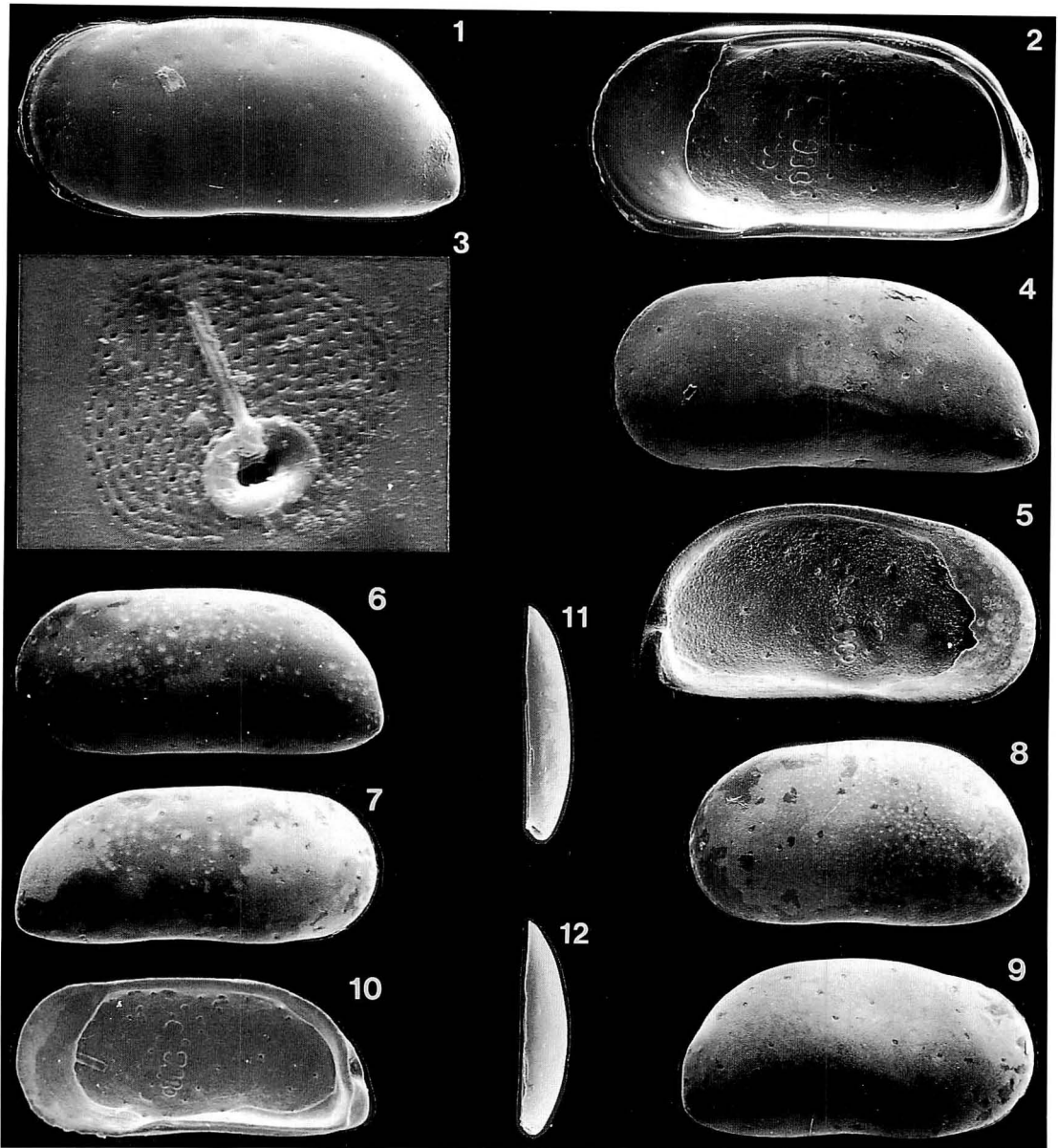
Figure 9. 1-3, *Krithe sawanensis* Hanai, 1959. **1**: External view of male LV (IGSU-948) ; **2**: internal view of male RV (IGSU-O-949) ; **3**: a sensillum pore of male LV (IGSU-O-948). **4, 5,** *Krithe antisawanensis* Ishizaki, 1966. **4**: External view of male LV (IGSU-O- 950) ; **5**: internal view of female LV (IGSU-O-951). **6–12,** *Krithe surugensis* n. sp. **6**: External view of male LV (holotype, IGSU-O-942) ; **7**: external view of male RV of the same individual (paratype, IGSU-O-943) ; **8**: external view of female LV (paratype, IGSU-O-944) ; **9**: external view of female RV (paratype, IGSU-O-945) ; **10**: internal view of male RV (paratype, IGSU-O-946) : **11**: dorsal view of male RV (paratype, IGSU-O-946) : **12**: dorsal view of female RV (paratype, IGSU-O-947). (Magnifications are, **3**: ×3,200 ; **11, 12**: ×40 ; all others : ×60).

Table 3. Occurrence data of three species of *Krithe*. Number of living specimens are in parenthesis.

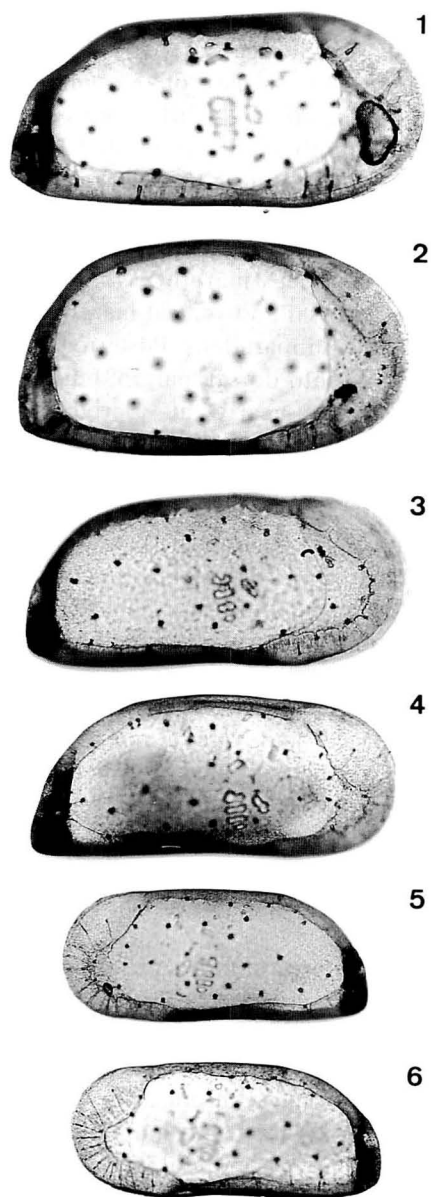| St. no.	K. sawanensis Adult V	K. sawanensis Adult C	K. sawanensis Juvenile V	K. sawanensis Juvenile C	K. antisawanensis Adult V	K. antisawanensis Adult C	K. antisawanensis Juvenile V	K. antisawanensis Juvenile C	K. surugensis Adult V	K. surugensis Adult C	K. surugensis Juvenile V	K. surugensis Juvenile C
13			1									
20	1		14	2								
35									1		1	
36	1		2									
38			1									
40	2		3									
41	2		4									
45											2	
46			1									
48	3		10									
49			6	7(5)								
57			6	1								
58			1								1	
87					8				3		2	
88	1		33	2					3		2	1
89					7		16					
91	4		22	1	1						1	
92			2									
97			13	4(2)					1	1(1)		1(1)
102	1		7	4(2)								
103	6	7(5)	16	26(26)						1(1)		1(1)
105			1									
108				1								
109			1									
M28	2		2		1		4					
M31	3		9									
M33			2									
M41					1		13					
M42			7	1								
M43					1							
M45	4	2	10									
M46			3	2	3	1	3				1	
M52			3									
M64					1				2		4	
M66	4		11									
M69			1									
M77	2	1	21	2					6		3	
M93									2		25	1
M95	1		3	1								
M101			2								1	
M104			2									
M107		2	14	4								
M109	1		1									
M115	4		29						7		32	1
M125			2									

Figure 10. Intraspecific variation of vestibule morphology in *Krithe* species. All photographs are in internal views, magnification ×49. **1**: male LV of *K. sawanensis* with axe-shaped vestibulum; Station 20. **2**: Female LV of *K. sawanensis* with axe-shaped vestibulum; Station M77. **3**: Male LV of *K. sawanensis* with crescent-shaped vestibulum; Station 103. **4**: Male LV of *K. antisawanensis* with crescent-shaped vestibulum; Station M64. **5**: Male RV of *K. surugensis* with crescent-shaped vestibulum; Station M77. **6**: Male RV of *K. surugensis* with very small semi-circular vestibulum; Station M115.

deep, Toyama Bay, Japan Sea (Ishizaki and Irizuki, 1990); 144-1,335 m deep off Shimane, Japan Sea (Ikeya and Suzuki, 1992); below 120 m between Suruga Bay and off Tanega-shima Island, southwest Japan; 140-268 m deep, off northeast Hokkaido, Sea of Okhotsk. Fossil: Lower Pleistocene Sawane Formation, Japan Sea (Hanai, 1959); Plio-Pleistocene Shinzato Formation, Okinawa (Nohara, 1987).

Krithe antisawanensis Ishizaki, 1966

Figures 9-4, 5

Krithe antisawanense [*sic.*] Ishizaki, 1966, p. 137, 138, pl. 18, figs, 17, 24, 25.
Krithe antisawanensis Ishizaki: Hanai *et al.*, 1977, p. 26; Choe, 1984 (MS), p. 124, pl. 6, figs. 15, 16, 17, text-fig. 10-3.
Krithe sawanensis Hanai: Zhao, 1988, p. 243, pl. 42, figs. 1, 2; Gou *et al.*, 1983, p. 34, pl. 6, figs. 1-13, text-fig. 8.

Type.—Holotype, RV, IGPS-87016 (L= 0.97, H=0.50).

Type locality.—An exposure about 1,500 m southeast of Saboyama, Sendai City, northeast Japan (Miocene Hatatate Formation).

Diagnosis.—Carapace laterally compressed. Anterior vestibule narrow, restricted to the lower third of anterior marginal area. Posteroventral duplicature narrow, parallel to ventral margin. Posteroventral angle tapered. LV overlaps RV.

Remarks.—The holotype specimen is a female because it has an arched dorsal margin.

Zhao (1988) reported a *Krithe* species from the East China Sea and recognized it as *K. sawanensis*. In our view, however, the two specimens shown in his illustration are *K. antisawanensis* because they have a tapered posteroventral angle. In addition, a RV in internal view shows a sharp dorsal edge that coincides with the hingement of *K. antisawanensis*, but is the reverse of that of *K. sawanensis*. Gou *et al.* (1983) found a species of *Krithe* and referred it to *K.*

sawanensis. Their species may also be *K. antisawanensis* because the specimen illustrated in the text-figure in internal view has reversed hingement. Moreover, its anterior vestibulum is narrow and restricted to the lower third of the anterior marginal area.

In four examined single valves of this species from Suruga Bay, no variation in vestibule morphology was recognized. This may be due to the small number of specimens examined.

In the L/H scatter diagrams (Fig. 4b), although the regression line for juvenile stages of this species is similar to that of *K. sawanensis*, the carapace size of its adults is different (Fig. 4b).

Distribution.—Recent: About 150–600 m deep, Suruga Bay; about 50–200 m deep, South Korean Sea (Choe, 1984 MS); 15–320 m deep, East China Sea (Zhao, 1988); 116–263 m deep off Shimane, Japan Sea (Ikeya and Suzuki, 1992); below 150 m deep between Suruga Bay and Tanegashima Island, off the Pacific coast, southwest Japan. Fossil: Miocene Hatatate Formation, northeast Japan (Ishizaki, 1966); Pliocene deposits in Leizhou Peninsula and Hainan Island, south China (Gou *et al.*, 1983); Pleistocene Chikura Formation, Boso Peninsula; Upper Pleistocene Ninomiya Formation, Kanagawa Prefecture.

Krithe surugensis n. sp.

Figures 9-6—12

Type.—Holotype, male LV and RV of the same specimen (St. M115), IGSU-O-942 (LV: Fig. 9-6; L=0.85, H=0.38, T=0.16. RV: Fig. 9-7; L=0.83, H=0.35, T=0.15). Paratypes, female LV (St. M115), IGSU-O-943 (Fig. 9-8; L=0.76, H=0.42, T=0.16); female RV (St. M115), IGSU-O-944 (Fig. 9-9; L=0.81, H=0.40, T=018); male RV (St. M115), IGSU-O-945 (Fig. 9-10, 11; L=0.82, H=0.35, T=0.15); female RV (St. M77), IGSU-O-946 (Fig. 9-12; L=0.73, H=0.41, T=0.16).

Type locality.—St. M115 (320 m) (34°57.8′ N, 138°44.6′E), Suruga Bay.

Diagnosis.—A species of *Krithe* with a slender and relatively small carapece. Posteroventral duplicature broad and convex; dorsal and ventral margins nearly parallel.

Description.—Carapace slender and moderately small; in lateral view subrectangular. Anterior contact margin symmetrically rounded. Dorsal and ventral margins nearly straight and subparallel. Posterior margin curves gently into dorsal margin, but it meets ventral margin nearly at a right angle. Height about one-third of length. Surface completely smooth, having large and widely spaced normal pore canals. Posterior end possessing two prominent round indentations. Anterior duplicature extremely broad; posterior duplicature broad and convex. Vestibule poorly developed in anterior end, crescent-shaped or subcircular. "Radial" pore canals nearly straight and widely spaced and rare along the ventral margin, about 16 in number. Hinge pseudadont, dorsal hinge of left valve being grooved to receive the edge of the right valve. Adductor scars consist of a ventral row of four posterior scars and one heart-shaped anterior scar.

Sexual dimorphism distinct. Male more elongate and slimmer than female.

Remarks.—This species closely resembles *Krithe hanaii* Ishizaki, 1983 in having a broad posteroventral duplicature. However, the latter has a larger and more inflated carapace, and shows a more arched dorsal margin and an axe-shaped anterior vestibule. Intraspecific variation in vestibule size, although not as distinct as that in *K. sawanensis*, has been found in this species. It generally has a crescent-shaped vestibulum; but in some specimens the vestibulum becomes extremely narrow and its shape is semicircular. This is accompanied by a broadening of the fused zone. No correspondence was found between the vestibule size and environmental parameters.

The L/H regression line of this species has a lower gradient than those of *K. sawanensis* and *K. antisawanensis* (Fig. 4c), reflecting its slender carapace.

Distribution.—Recent: The authors have also found this species below 150 m between Suruga Bay and Hyuga-nada off the Pacific coast, southwest Japan; 730 m deep off Kerama Islands, Okinawa. Fossil: Lower Pleistocene Nekoya Formation, Shizuoka Prefecture, Central Japan; Lower Pleistocene Sunakomata and Hamada Formations, Shimokita Peninsula; Plio-Pleistocene Shinzato Formation, Okinawa.

Acknowledgements

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駿河湾より産出する *Krithe* 属 (甲殻類, 介形虫) の3種: 駿河湾の表層底質試料 (45地点) から, *Krithe* 属の多数の標本が検出された。これらは背甲の形態学的特徴によって, 幼体から成体まで3つのシリーズに分類される。このうちの2つは *K. sawanensis* Hanai, 1959 と *K. antisawanensis* Ishizaki, 1966 に同定され, 残りの1つを *K. surugensis* n. sp. として記載した。

3種は湾内でそれぞれ異なった生息深度と地理的分布を示す。*K. sawanensis* は湾全域の120-1,350 m 深に分布するのに対して, *K. antisawanensis* は湾口域, *K. surugensis* は湾の東半部の共に 150-650 m 深にのみ分布する。3種の分布パターンと海洋環境との関係を論じた。

また, *K. sawanensis* は, 650-810 m 深に存在する貧介形虫帯 (OBZ) によって2つの個体群に分断されている。これらの個体群間にみられる背甲サイズと Vestibulum の形態変異は水温と溶存酸素量に起因すると考えられる。　　　　　　　　　　周　保春・池谷仙之

937. *AMYGDALOPHYLLOIDES* (RUGOSA) FROM THE CARBONIFEROUS OF THE OMI LIMESTONE, CENTRAL JAPAN*

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Abstract. The Omi Limestone Group belonging to the Akiyoshi Terrane yields abundantly rugose coralline fossils of the genus *Amygdalophylloides* from its lower part. The assemblage of *Amygdalophylloides* obtained from the Fukugakuchi area where the lower sequence of the Omi Limestone Group is typically developed, comprises more than 10 forms, from which the following eight species, including five new species and two unidentified species, are herein described and illustrated: *Amygdalophylloides densus*, sp. nov., *A. denticulatus*, sp. nov., *A. uzurensis* (Yamagiwa and Ota), *A. omiensis*, sp. nov., *A. longiseptatus*, sp. nov., *A. parvus*, sp. nov., *A.* sp. A and *A.* sp. B. This coralline assemblage is of Namurian A to Namurian B, Serpukhovian to early early Bashkirian age, except for the occurrence of *Amygdalophylloides* sp. A referred to the late Viséan age.

Introduction

The genus *Amygdalophylloides* is a small geyerophyllid rugose coral having a solid columella with rare additional axial elements, a few or no lonsdaleoid dissepiments and frequent peripheral stereozone. This genus is widely distributed in the Lower Carboniferous to the Lower Permian of the Boreal and Tethyan Provinces, such as Spitzbergen, northern Spain, the Carnic Alps, Yugoslavia, northeastern Egypt, the Moscow Basin, eastern Kazakhstan?, North Vietnam, North and South China and Japan, mostly in the Upper Carboniferous.

Hayasaka (1921, 1922, 1924) listed and described *Axophyllum gracile,* which was later transferred to the genus *Amygdalophylloides* by Kanmera (1961), from the lower part of the "Omi Limestone", Nishikubiki County, Niigata Prefecture, central Japan.

Since then, *Amygdalophylloides* has been reported or described from the Upper Carboniferous rocks of the Yayamadake Limestone (Kanmera, 1961) and the Akiyoshi Limestone (Minato and Kato, 1957, 1975; Hasegawa, 1963; Yamagiwa and Ota, 1963; Haikawa, 1986) in southwest Japan and from the Ichinotani Formation of Fukuji district (Niikawa, 1981) and the north of Tarui (Furutani, 1981) in Gifu Prefecture, central Japan.

Recently, one of the authors (Y.Y.) newly collected a number of specimens of *Amygdalophylloides* from the lower part of the Omi Limestone Group (Hasegawa *et al.,* 1969, 1982) in the Fukugakuchi area (Figure 1). This genus appears suddenly in high frequency in the lowest Upper Carboniferous, providing datum for understanding the boundary problem between the Lower and Upper Carboniferous of Japan.

In this paper, eight species of *Amygdalophylloides* including five new ones are described, and their stratigraphic distribution is
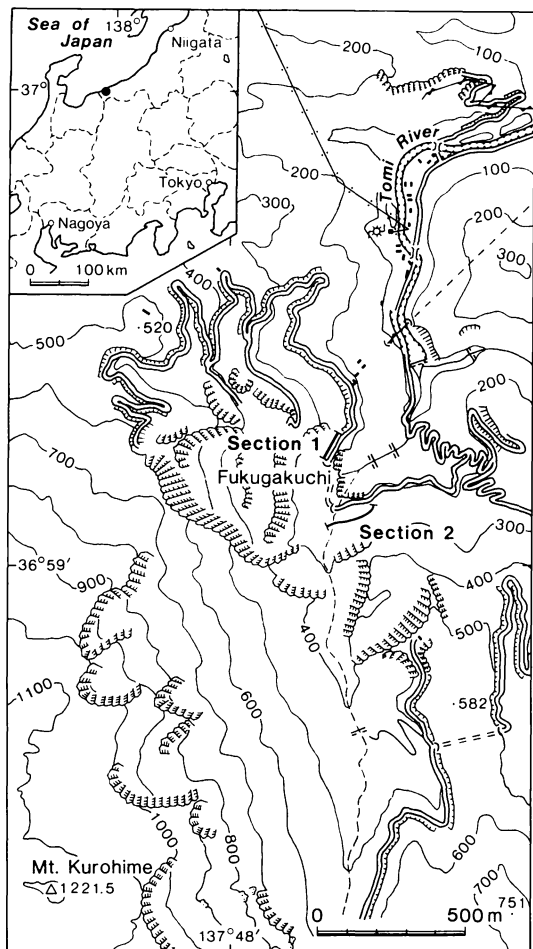
Figure 1. Topographic map of the Fukugaku-chi area showing locations of the section 1 and section 2.

analyzed.

Stratigraphy and fossil occurrence

The so-called Omi Limestone cropping out in the Omi district of Niigata Prefecture, central Japan near the coast of the Japan Sea, is one of the Upper Paleozoic limestone masses aligned isolatedly in the Akiyoshi Terrane (Kanmera and Sano, 1986). It rests conformably on basaltic pyroclastic rocks as do such limestone masses in the Akiyoshi Terrane as the Akiyoshi, Taishaku, Atetsu and Koyama Limestones. This sequence in

the Omi district is called the Omi Limestone Group (Hasegawa *et al.*, 1969, 1982), ranging in age from Early Carboniferous (late Viséan) to late Middle Permian (late Guadalupian).

The lower part of the Omi Limestone Group is typically exposed in the Fukugaku-chi area situated on the northeastern slope of Mt. Kurohime, northern part of the Omi district, in which two sections were measured, namely section 1 and section 2 (Figure 1). The Carboniferous of this area consists of basaltic pyroclastic rocks on the bottom followed by massive limestone without any stratification. The stratigraphic succession measured along the routes shown in Figure 2 is summarized as follows in descending order:
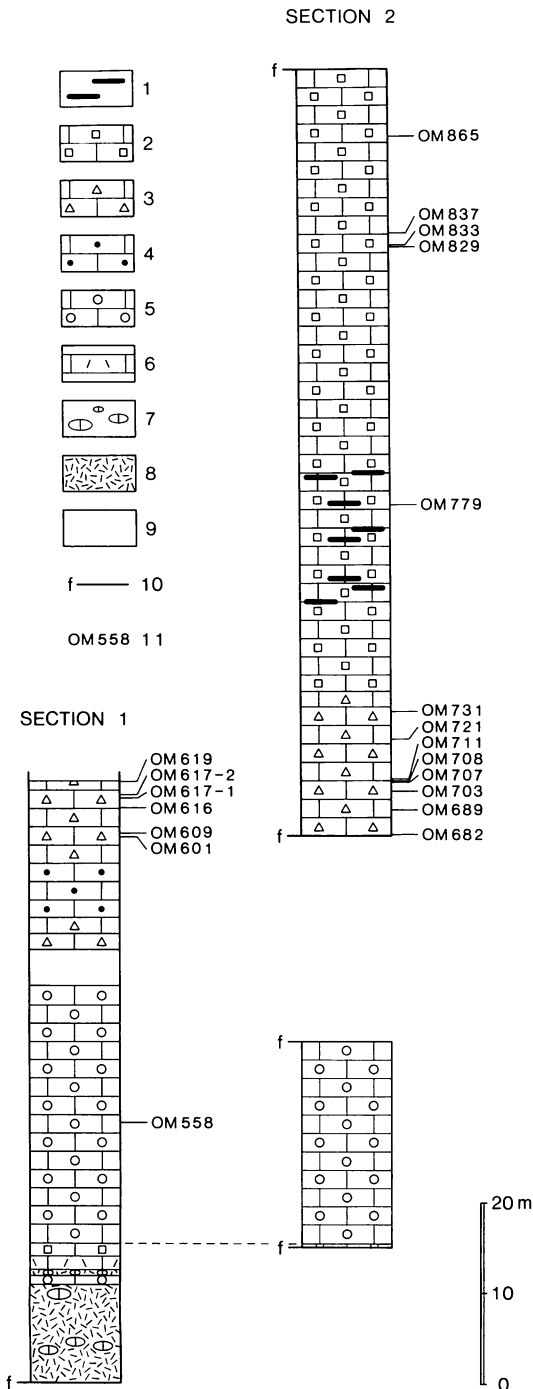
1) light-gray, fine-to medium-grained bio-clastic limestone (packstone) with distorted oolitic grains and intraclasts; more than 67.8 m thick; containing abundant bryozoa and crinoid ossicles. This limestone intercalates with some lenticules of sponge spicular lime-stone in the lower part.

2) gray conglomeratic limestone (lime-stone breccia) and grayish, fine-grained peloidal limestone (wackestone); 25.1 m thick, as far as exposed. The conglomeratic limestone carries various sizes of biolithitic limestone (boundstone) clasts, which are fos-siliferous and contain abundant foraminifers, corals, brachiopods, calcareous algae, and others.

3) gray, fine- to coarse-grained bioclastic limestone (packstone) of 1.4 m thick, rich in bryozoan and crinoidal fragments; being succeeded by light-gray, fine-grained oolitic limestone (grainstone) of 28.3 m thick.

4) greenish or purplish basaltic pyroclas-tic rocks with tuffaceous and bioclastic lime-stone (packstone) clasts of various sizes, inter-calating the oolitic limestone (grainstone) layers near its uppermost part which yielded abundant brachiopods and corals (Yoshida *et al.*, 1987); about 14 m thick.

The specimens of *Amygdalophylloides* were obtained from the oolitic limestone at one

← **Figure 2.** Columnar sections of the lower part of the Omi Limestone Group in the Fukugakuchi area, showing the stratigraphic positions of fossil localities in section 1 and section 2 shown in Figure 1. 1 : lenticular sponge spicular limestone, 2 : bioclastic limestone, 3 : conglomeratic limestone, 4 : peloidal limestone, 5 : oolitic limestone, 6 : bioclastic packstone-rudite with basaltic tuffaceous matrices, 7 : clasts of limestone, 8 : basaltic pyroclastic rocks, 9 : covered interval, 10 : fault, 11 : locality number.

place in section 1 (Loc. OM 558), the conglomeratic limestone at six places in section 1 (Locs. OM 601, 609, 616, 617-1, 617- 2 and 619) and eight in section 2 (Locs, OM 682, 689, 703, 707, 708, 711, 721 and 731) and the bioclastic limestone at five places in section 2 (Locs. OM 779, 829, 833, 837 and 865). A species list of *Amygdalophylloides* from the above mentioned localities and horizons is shown in Table 1.

Biostratigraphical studies of the Omi Limestone Group have been done by Kawada (1954a, b, c), Fujita (1958), Kato *et al.* (1964), Hasegawa *et al.* (1969, 1982) and Watanabe (1973). Hasegawa *et al.* (*op. cit.*) divided the pre-Moscovian formation of the Omi Limestone Group into two zones based on smaller foraminifera and fusulinaceans, namely an *Endothyra* Zone and an *Eostaffella-Millerella* Zone.

Almost all of the coral specimens in the present study fall within the *Eostaffella-Millerella* Zone, except for the sole specimen of *Amygdalophylloides* sp. A. According to Hasegawa *et al.* (1982), the age of the *Eostaffella-Millerella* Zone ranges from the late Viséan to early Bashkirian. However, the occurrences of *Amygdalophylloides* in this Zone may be limited in age as discussed below.

Amygdalophylloides uzurensis was originally described by Yamagiwa and Ota (1963) from the "Uzura" Quarry of the Akiyoshi Limestone, southwest Japan, as one of the important elements of the "Uzura fauna", the age of which has been regarded as early Namurian or late Chesterian by Ota (1971)

Table 1. List of *Amygdalophylloides* from the lower part of the Omi Limestone Group in the Fukugakuchi area (Numerals show the examined specimen-number). The stratigraphic positions of fossil localities are shown in Figure 2.

Locality number (OM-) / Species	Section 1							Section 2												
	558	601	609	616	617-1	617-2	619	682	689	703	707	708	711	721	731	779	829	833	837	865
* *Amygdalophylloides densus*, sp. nov.	42																			
* *A. denticulatus*, sp. nov.	1																			
* *A. uzurensis* (Yamagiwa and Ota)			6				9		1					2	6					
* *A. omiensis*, sp. nov.				10																
* *A. longiseptatus*, sp.nov.											3	1				1				
* *A. parvus*, sp. nov.												1			43					
A. ? gracilis (Hayasaka)								1									3	1	1	
* *A.* sp. A	1																			
* *A.* sp. B												1	15							
A. spp.		3	1	1	4		9	5	4			1				2		2	1	

* Species herein described.

and Matsusue (1986), late early Namurian to early late Namurian by Haikawa (1988) and late Namurian or Morrowan by Igo and Koike (1965) and Igo and Igo (1979).

Meanwhile, the lowest *Amygdalophylloides*-bearing limestone in the *Eostaffella-Millerella* Zone in section 1 (Loc. OM 601) yields the following smaller foraminifera, brachiopod and calcareous sponge (red alga ?): *Endothyra* aff. *E. hortonensis* Rich, *Weiningia* sp. and *Komia* sp. The first form closely resembles *Endothyra hortonensis*, originally described by Rich (1980) from the upper Chesterian of south-central Tennessee. The second form belongs to a genus known from the Lower (?) to Middle Carboniferous of southwest China (Ching and Liao, 1974). The third form is quite similar to representatives of a genus denoting a Pennsylvanian age (Wray, 1977a, b and others).

On the other hand, the fusulinid species, *Pseudostaffella antiqua* (Dutkevich) is first observed at about 3 m above the highest *Amygdalophylloides*-bearing limestone in sec-

tion 2 (Loc. OM 865). This species has been known from the Severokeltmensky Horizon (upper lower Bashkirian, C_1^n e2) of USSR (Semichatova *et al.*, 1979; Groves, 1988, and others) and from Cf 9 (upper Namurian B-Namurian C) of Western Europe (Conil *et al.*, 1980).

According to the viewpoints mentioned above, the present *Amygdalophylloides* assemblage in the *Eostaffella-Millerella* Zone can be estimated to be of Namurian A (Serpukhovian) to Namurian B (early early Bashkirian) age.

The stratigraphic horizon of *Amygdalophylloides* sp. A in section 1 (Loc. OM 558) is equivalent to the upper part of the *Endothyra* Zone of late Viséan age.

Systematic descriptions

All the specimens described and figured in this paper are deposited in the Institute of Geology and Mineralogy, Faculty of Science, Hiroshima University, Higashihiroshima

with prefix IGSH-YY.

Family Geyerophyllidae Minato, 1955
Genus *Amygdalophylloides* Dobrolyubova
and Kabakovich, 1948

Type species (by original designation).
—*Amygdalophyllum ivanovi* Dobrolyubova,
1937, p. 60, pl. 19, figs. 15-20.

Remarks. —The morphological relation-
ship between the genus and the allied genera
are fully discussed by Minato and Kato
(1975) and Rodríguez (1984, 1985).

Amygdalophylloides gracilis (Hayasaka,
1924) is the first species of the genus to have
been described from the Omi Limestone origi-
nally under the generic name of *Axophyllum*.
Amongst our collections a few specimens can
be compared with this species, but these speci-
mens are excluded from the present descrip-
tion because they are so poorly preserved that
their assignment to it is questionable. In
view of the morphologically extremely vari-
able nature of this species, we feel it necessary
to make its specific conception clear.
Hayasaka's (*op. cit.*) original definition of the
species included forms which have a large
corallite, a large number of septa, a compara-
tively well developed stereozone, short minor
septa and a relatively large solid columella.
Later Minato and Kato (1975, p. 21) present-
ed some inked figures of specimens having a
smaller form with a smaller number of septa
(Fig. 3), a thicker stereozone and longer
minor septa (Fig. 2) and a much larger
columella (Fig. 1), compared to the type
specimens. So here we interpret the specific
diagnosis of *A. gracilis* as follows:

Moderately large to large-sized *Amygdalo-
phylloides* having corallite diameter of 12 to
18 mm. Peripheral stereozone 1/7 to 2/5
width of corallite radius. Minor septa 1/5 to
3/5 length of major septa. Columella simple
and solid, 1/7 to 2/7 or more width of coral-
lite diameter. Lonsdaleoid dissepiments
sometimes developed. Tabulae mostly in-
complete, can be complete, commonly steeply
inclined and rather closely spaced.

The following is a key to the nominal
species of *Amygdalophylloides* from the Omi
Limestone.
I.   Stereozone very thick (>2/5 width of
     corallite radius) and minor septa well
     developed (>3/5 length of major septa)
        With small, spindle shaped or smoothy
        elliptical columella........*A. densus*
        With small, denticulate columella hav-
        ing septal lamellae-like projections
        ....*A. denticulatus*
II. Stereozone not very thick (<2/5 width
     of corallite radius)
IIa. Minor septa less well developed (<3/
     5 length of major septa)
     IIa₁. With moderately large to large
           corallite (12-18 mm in diameter),
           and mostly incomplete and
           rather closely spaced tabulae
           ....*A. gracilis*
     IIa₂. With small corallite (7-11 mm in
           diameter), and mostly complete
           and distantly spaced tabulae
           Columella large (1/6-1/4
           width of corallite diameter)
           ....*A. omiensis*
           Columella small (1/8-1/6
           width of corallite diameter)
           ....*A. uzurensis*
IIb. Minor septa well developed (>3/5
     length of major septa)
        With moderately large corallite
        (12-13 mm in diameter) and dis-
        tinct inner wall ..*A. longiseptatus*
        With small corallite (5-7, rarely 9
        mm in diameter) ......*A. parvus*

Geographic and stratigraphic distribution.
—As shown in Figure 3, this genus is dis-
tributed universally in the Boreal and Teth-
yan regions. Its stratigraphic distribution is
Lower Carboniferous (upper Viséan) to
Lower Permian (Artinskian), and its maxi-
mum distribution is in the Upper Carbonifer-
ous, especially in the Moscovian.
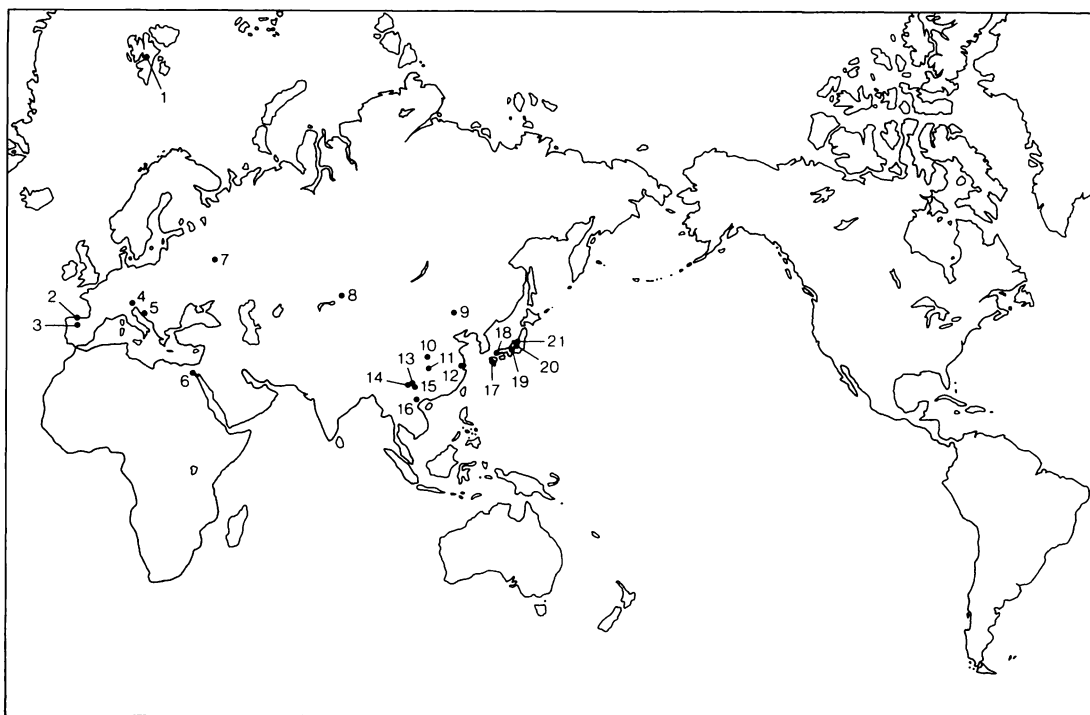
Amygdalophylloides densus Yoshida, sp. nov.

Figure 3. Geographic distribution of *Amygdalophylloides*. 1 : Spitsbergen (Forbes *et al.,* 1958), 2 : Asturias, northern Spain (Rodríguez, 1984), 3 : Palencia, northern Spain (de Groot, 1963), 4 : the Carnic Alps (Heritsch, 1936), 5 : Bosnia, Yugoslavia (Kostic-Podgorska, 1955), 6 : northeastern Egypt (Herbig and Kuss, 1988), 7 : the Moscow Basin (Dobrolyubova, 1937, 1940, 1948 ; Dobrolyubova and Kabakovich, 1948), 8 : eastern Kazakhstan (Bikova, 1974), 9 : Nei Mongol Autonomous Region, North China (Guo, 1983), 10 : Shaanxi Province, South China (Ding and Yu, 1987), 11 : Hubei Province, South China (Xu in Jia *et al.,* 1977), 12 : Jiangsu Province, South China (Yu, 1980), 13 : Guizhou Province, South China (Chi, 1931 ; Ding, 1986 ; Wu and Zhao, 1989), 14 : Yunnan Province, South China (Wang and Zhao, 1989 ; Wu and Zhao, 1989), 15 : Guangxi Province, South China (Xu and Chen in Xu *et al.,* 1986), 16 : North Vietnam, (Fontaine, 1961), 17 : Yayamadake, southwest Japan (Kanmera, 1961), 18 : Akiyoshi, southwest Japan (Minato and Kato, 1957, 1975 ; Hasegawa, 1963 ; Yamagiwa and Ota, 1963 ; Haikawa, 1986), 19 : Tarui, central Japan (Furutani, 1981), 20 : Fukuji, central Japan (Niikawa, 1981), 21 : Omi, central Japan (Hayasaka, 1921, 1922, 1924 ; this paper).

Figures 5-1a—5, 6-1a—7

Derivation of name. —After the feature of corallum having a very thick peripheral stereozone. Latin *densus*—thick, dense.

Material. —Forty-two corallites from Loc. OM 601 in section 1, which is referred to the lower part of the *Eostaffella-Millerella* Zone. Holotype, IGSH-YY 10021, paratypes, IGSH-YY 10022–10062.

From these specimens, 103 transverse and 13 longitudinal thin sections were examined.

Diagnosis. —Comparatively small-sized *Amygdalophylloides* with an extremely broad peripheral stereozone, well developed minor septa and a solid columella, from which a few axial tabellae are differentiated in some cases. Small lonsdaleoid dissepiments sometimes developed.

Description. —Corallum is ceratoid to subcylindrical, and small in size. Although individuals frequently aggregate and in some cases are even flattened on one side by contiguity with other specimens, there is no evidence of branching or budding. Indeed it seems probable that the species is invariably
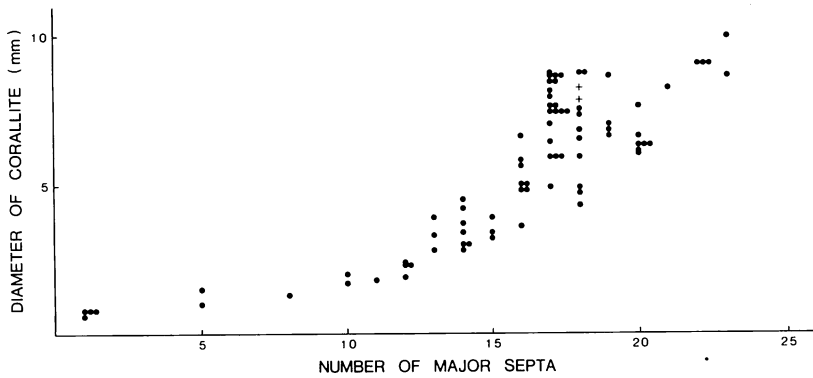
Figure 4. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides densus*, sp. nov.   + : holotype of *A. densus*.

solitary. External characters are unknown.

In transverse section, corallite is round in outline, 10.2 mm in calicular diameter in the largest corallite. Wall is crenulated in outer configuration, suggesting the presence of septal grooves and interseptal ridges. The peripheral stereozone formed by lateral fusion of dilated septa is strongly developed, usually occupying 2/5 to 3/5 (rarely 2/3) of the radius of the mature corallite. Dissepimentarium is completely masked by the development of the stereozone in many specimens. However, in the mature stages of some specimens small peripheral dissepiments are present, which are confined to the stereozone and commonly of only sporadic or partial occurrence ; quite exceptionally in a section of the specimen IGSH-YY 10032 (Figure 6-6a), they show an almost complete vertical. In a few specimens some of these dissepiments become subsequently modified to small lonsdaleoid dissepiments by the retreat of minor septa and sometimes even major septa from the wall (*e.g.* IGSH-YY 10029, Figure 6-3). Such lonsdaleoid vesicles are also observed in the calice of the specimen IGSH-YY 10033 (Figure 6-7), in which a distinct rejuvenation takes place. Tabularium is round in outline, comparatively wide to wide, occupying commonly 2/5 to 3/5 (rarely 1/3) of the diameter of corallite. A few cut edges of tabulae are seen between

major septa. Septa are in two orders, major and minor. They are somewhat pinnately arranged in the early growth stages, but tend to take radial symmetry in the mature stages. Fossula is not observable. Major septa are strongly expanded in the stereozone, gradually attenuated towards the columella, with which only the cardinal septum is normally in contact. The axial ends of major septa are bluntly terminated. Minor septa alternating with the major septa are well developed, attaining 3/5 to 3/4 (rarely 4/5) the length of the latter. They are entirely restricted within the stereozone in general, but uncommonly only just emerge from it. Rarely, septa are interrupted by the development of the lonsdaleoid dissepiments, if present. Septal fine structure is diffuso-trabecular. As many as 23 major septa occur in the 9.9 mm diameter corallite. Relationship between the number of major septa and the diameter of corallite is shown in Figure 4. Axial structure originates from the axial end of the cardinal septum, which usually expands to form a prominent columella in the early growth stage. Generally, in the mature stages the columella becomes independent of the cardinal septum, their conjugation being mere abutting. Thus formed columella is spindle-shaped or smoothly elliptical in outline, and consists of a solid structure with a fairly long median lamella and radiating calcite fibres. How-

ever, in some specimens a few outwardly convex axial tabellae are differentiated from the columella that is continuously connected with the cardinal septum except in the latest mature stage (*e.g.* IGSH-YY 10029, Figure 6-3 ; IGSH-YY 10032, Figures 6-6b—c). Width of the columella is variable, but does not exceed 1/7 the diameter of corallite. A few specimens have an auxiliary columella, which appears in the early growth stages, but disappears in the mature stages (*e.g.* IGSH-YY 10022, left-hand corallites in Figures 5-1a—b). Rejuvenescence occurs frequently and usually it is only indicated by the differentiation of a new wall from calicular wall of the old corallite (Figures 5-2a, 4a). A single specimen IGSH-YY 10033 (Figure 6- 7) represents a more distinct rejuvenation by secreting a new wall around an axial portion of the old calice, which leads to large reduction of the corallite diameter and a complete reconstruction of the morphology.

In longitudinal section, corallite surface is wavy or more commonly irregular due to the frequency of minor rejuvenation. Wall is very thick. Dissepiments are only sporadic, small, weakly elongated, steeply sloping or vertical and in one or rarely two rows, but commonly concealed by the extensive development of stereoplasmic deposits. Tabularium is comparatively wide to wide. Tabulae are mostly complete, but may be locally incomplete. They are subhorizontal or declined axially, and include steeply or gently inclined clinotabulae. Sometimes, they are gently to steeply ascending to the columella. Three to seven tabulae are present in the vertical distance of 2 mm. Only occasionally, vesicular, arched and upwardly convex periaxial tabellae may be developed. In some specimens a few axial tabellae are differentiated from the columella and are steeply tilting or vertical. Columella is narrow to moderately wide, weakly undulated and solid, with the calcite fibres perpendicular to the slightly sinuous median lamella which is vertically continuous. In the early

growth stage of a few specimens columella is split into two parts, one of which is soon degenerate (*e.g.* holotype, Figure 5-1c). Calice is deep and steeply sided, with a prominent columella.

Remarks. —The present new form shows considerable variability in its skeletal elements. Some of the specimens described above differ from the typical form by the presence of peripheral dissepiments and/or lonsdaleoid dissepiments, and a few axial tabellae (*e.g.* IGSH-YY 10029, 10032). Thus they are apt to be treated as representing an independent species. However, these morphological variations occur together at the same locality and even in a single specimen. Therefore they are best regarded as intraspecific variations.

The present form closely resembles *Amygdalophylloides uzurensis* (Yamagiwa and Ota, 1963), but differs from the latter in having a much thicker stereozone and stronger minor septa. It also shows resemblance to the corallites of *Amygdalophylloides gracilis* (Hayasaka, 1924) illustrated by Minato and Kato (1975) as Figs. 2 and 5 on p. 21 in revealing a rather thick stereozone, from which it is distinguished by its smaller corallite with fewer septa and smaller columella, in addition to much thicker stereozone and better development of minor septa.

Amygdalophylloides crassicolumellatus Dobrolyubova and Kabakovich (1948) from the Upper Carboniferous (C_{III}^0 horizon) of the Moscow Basin, is somewhat similar to the present form, but is readily distinguishable by possessing a slightly narrower stereozone, shorter minor septa and a much larger columella with some open holes in it.

On the other hand, the specimens with lonsdaleoid dissepiments are reminiscent of *Darwasophyllum* sp. aff. *D. irregulare* forma *compacta* Pyzhjanov, described and figured by Rowett and Kato (1968, p. 37, pl. 10, figs. 1-6), which was obtained from the Moscovian of the Akiyoshi Limestone, southwest Japan. The latter is, however, said to be a

1a

1c

1b

1d

2a

2b

3a

3b

4a

4b

5
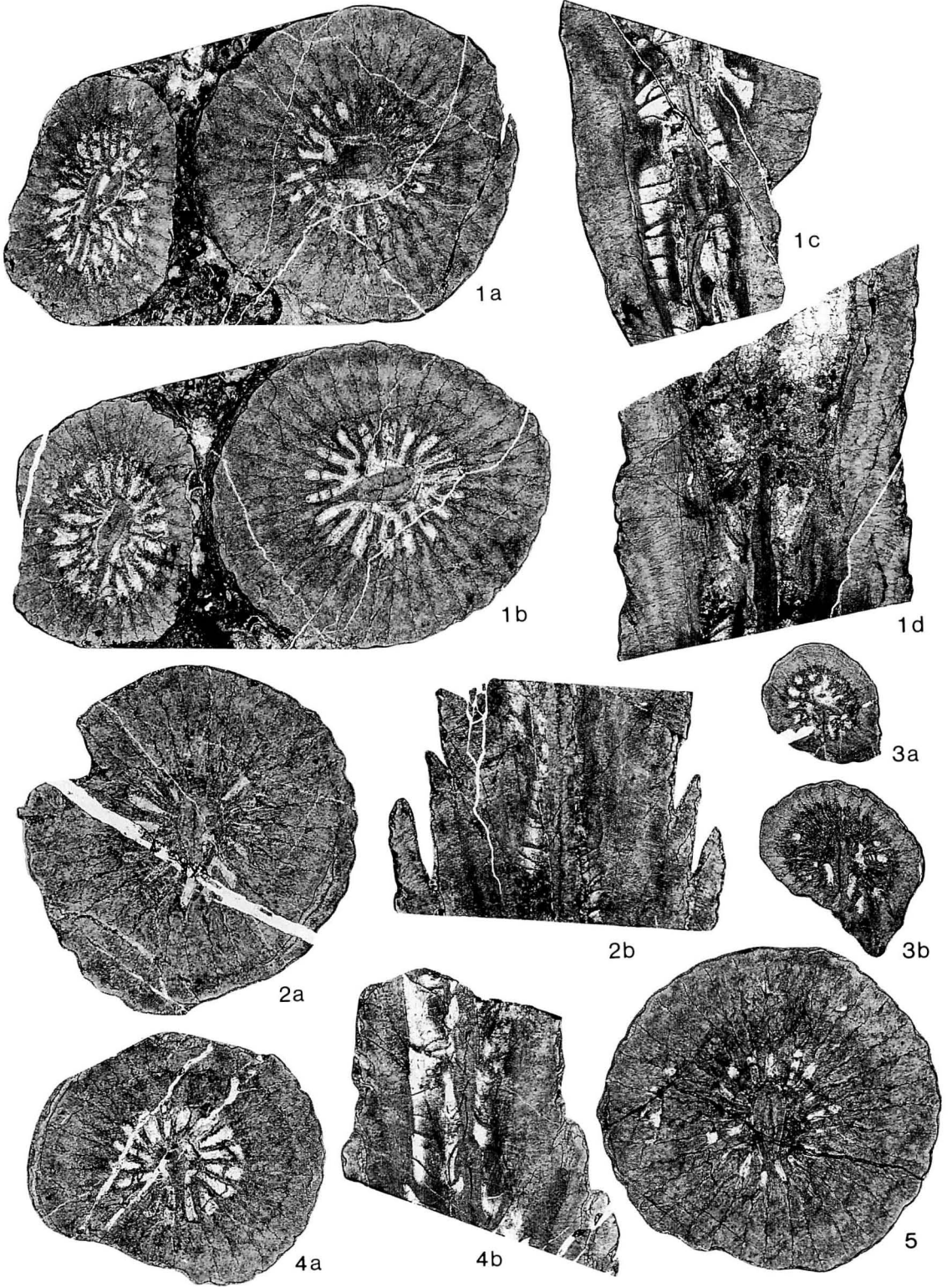
loosely fasciculate form, and is provided with a few irregular and curved septal lamellae. Furthermore, it bears a narrower stereozone, shorter minor septa and a slightly thicker columella compared to the present form.

Amygdalophylloides denticulatus
Yoshida, sp. nov.
Figures 8-1a—f

Derivation of name. —Based on the feature of corallum with denticulate columella.

Material. —A single corallite from Loc. OM 601 in section 1, which is referable to the lower part of the *Eostaffella-Millerella* Zone. Holotype, IGSH-YY 10063.

Five transverse and one longitudinal sections have been cut from this material.

Diagnosis. —Comparatively small sized *Amygdalophylloides* having a particularly thick peripheral stereozone, well developed minor septa and a solid, denticulate columella with septal lamellae-like projections which are circumscribed by a few axial tabellae.

Description. —Corallum is solitary, ceratoid and small in size. Surface characters are unknown.

In transverse section, corallite is round in outline, attains 8.2 mm in the largest diameter. Wall has an external crenulation, showing the presence of septal grooves and interseptal ridges. The peripheral stereozone made up by lateral contiguity of dilated septa is strongly developed, occupying the width of about 1/2 the half diameter of corallite. Dissepimentarium is entirely masked by the development of the stereozone except in one section of the mature stage (Figure 8-1e), in which a few, small peripheral dissepiments are to be seen. Tabularium is round in outline, wide, occupies approximately 1/2 of

the corallite's diameter. A few cut edges of tabulae are seen between major septa. Septa are radially arranged in two orders, major and minor, in alternation. Fossula is not discernible. Major septa strongly expand in the stereozone, gradually tapering towards axis, with bluntly ended axial terminations. They come close to the axial structure, but almost never connect with it, except that the cardinal septum always touches the periphery of the columella. Minor septa are well developed, 3/5 to 3/4 the length of the major, but do not project beyond the stereozone. Fine structure of septa is diffuso-trabecular. Major septa are 19 in number in the corallite with 8.2 mm diameter. Relationship between the number of major septa and the diameter of corallite is shown in Figure 7. Axial structure is irregular in outline, occupies 1/5 to 1/4 of the diameter of corallite. It is composed of a thick, solid columella having a denticulated outline with a few, short septal lamellae-like protuberances which are circumscribed by a single row of thickened, outwardly convex axial tabellae. A fairly long median lamella and radially disposed calcite fibres are to be seen in the columella. The columella is attached to the cardinal septum, but the median lamellae of these structural elements do not join each other. Width of the columella is less than 1/8 of the diameter of corallite. A small elliptical auxiliary columella is present only in the early growth stage. The corallite reveals a distinct rejuvenation by secreting a new wall around an axial portion of the old calice, which causes large reduction of the corallite diameter and a repetition of younger morphology (Figure 8-1f). Also minor rejuvenescence occurs, which is only indicated by the differentiation of a new wall from

← **Figure 5.** 1-5: *Amygdalophylloides densus,* sp. nov. 1a-d, successive transverse (1a-b) and longitudinal (1c-d) sections (1a-b, right-hand corallites and 1c-d, holotype, IGSH-YY 10021 ; 1a-b, left-hand corallites, paratype, IGSH-YY 10022) ; 2a-b, transverse (2a) and longitudinal (2b) sections (paratype, IGSH-YY 10023) ; 3a-b, successive transverse sections (paratype, IGSH-YY 10024) ; 4a-b, transverse (4a) and longitudinal (4b) sections (paratype, IGSH-YY 10025) ; 5, transverse section (paratype, IGSH-YY 10026). All figures ×6.
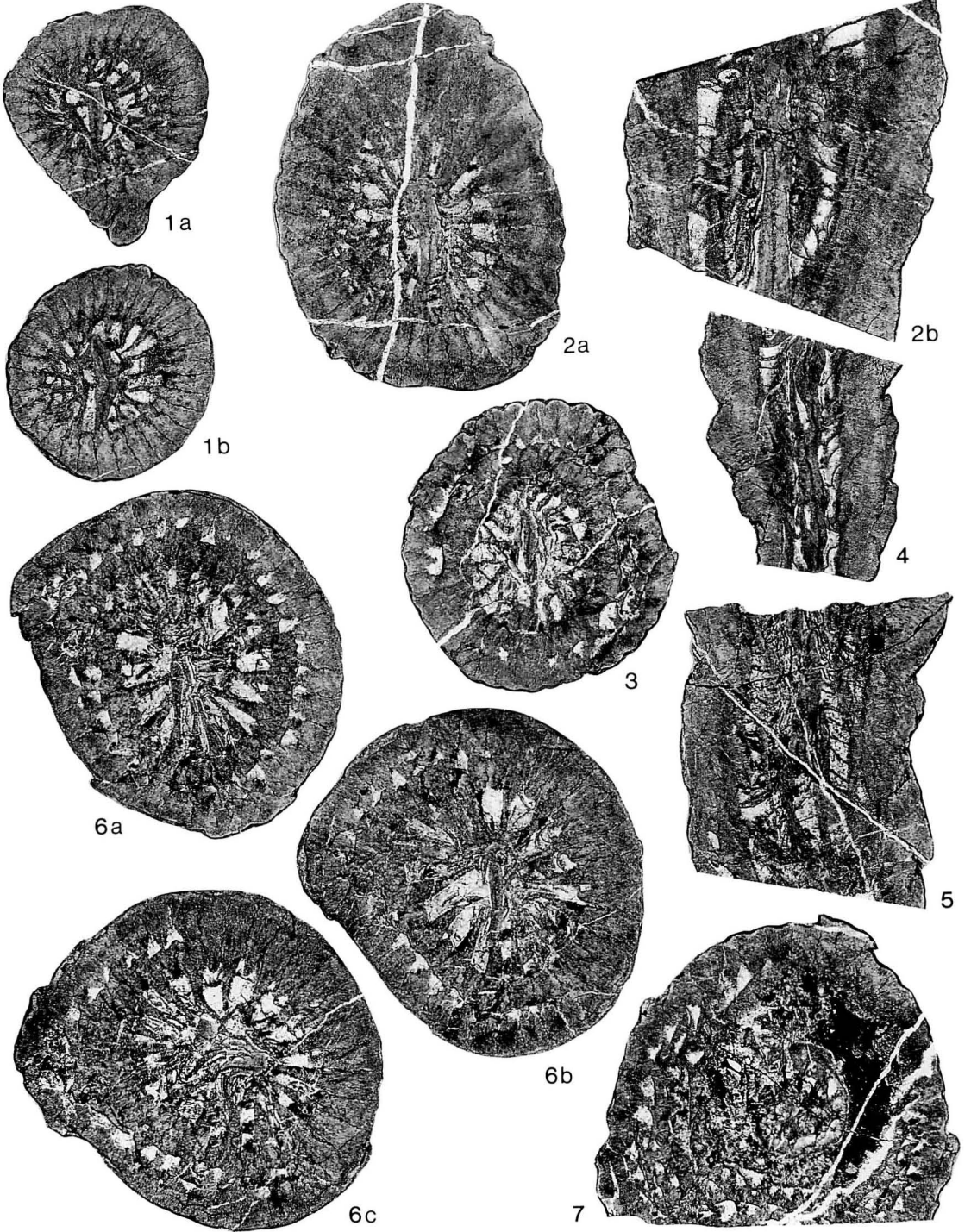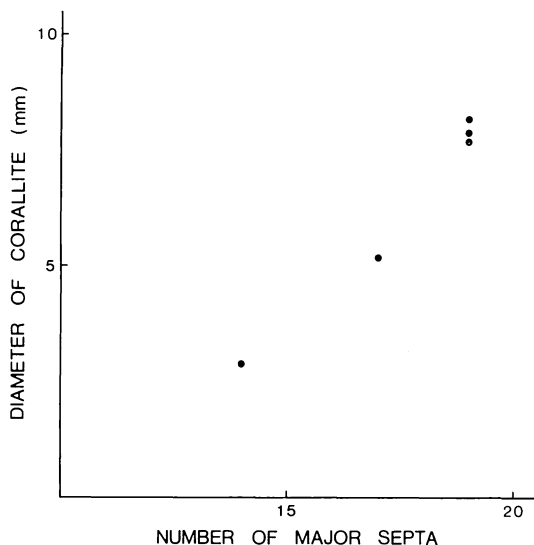
Figure 7. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides denticulatus*, sp. nov.

calicular wall of the old corallite (Figures 8-1e—f).

In longitudinal section, corallite surface is not smooth owing to the presence of repeated minor rejuvenescences. Wall is very thick. No dissepiments are observable in an available longitudinal section. Tabularium is wide. Tabulae are subhorizontal or declined axially, and include gently inclined clinotabulae. They are mostly complete, although they can be locally incomplete, and rather coarsely spaced, counting 3 to 7 in the vertical distance of 2 mm. Large, elongate, vertical, vesicular structures (cystose clinotabulae) are to be seen in the outer marginal part of tabularium in the mature stage. Axial tabellae are sparsely disposed, steeply sloping or vertical, and thickly coated with stereoplasmic deposits. Columella is rather wide, more or less sinuous and solid,

consisting of the calcite fibres perpendicular to the feebly undulated and vertically continuous median lamella. There exists an auxiliary columella in the early growth stage, but it is soon degenerate.

Remarks. —The present form is represented by only one specimen in our collections, but is considered sufficiently distinctive to warrant erection of a new species. Closest similarities are shown to *Amygdalophylloides densus*, sp. nov. described above. This species has, however, a spindle-shaped or smoothly elliptical columella, from which sometimes a few axial tabellae may be differentiated, whereas the columella of the present form reveals denticulated outline with septal lamellae-like projections that are circumscribed by one row of axial tabellae.

Amygdalophylloides uzurensis (Yamagiwa and Ota, 1963) somewhat resembles the present form, but is clearly distinguished in possessing a narrower stereozone and shorter minor septa, together with a simpler axial structure.

Amygdalophylloides uzurensis
(Yamagiwa and Ota, 1963)
Figures 10-1—7b

Lophophyllidium uzurense Yamagiwa and Ota, 1963, p. 91, pl. 1, fig. 6; pl. 2, figs. 1-5.
Amygdalophylloides uzurense; Minato and Kato, 1975, p. 7.

Material. —Twenty-four corallites: IGSH-YY 10064-10069 from Loc. OM 609 and IGSH-YY 10070-10078 from Loc. OM 619 in section 1, and IGSH-YY 10079 from Loc. OM 703, IGSH-YY 10080-10081 from Loc. OM 721 and IGSH-YY 10082- 10087 from Loc. OM 779 in section 2; all these localities are equivalent to the lower half of the *Eostaffella-Millerella* Zone.

← **Figure 6.** 1-7: *Amygdalophylloides densus*, sp. nov. 1a-b. successive transverse sections (paratype, IGSH-YY 10027); 2a-b, oblique transverse (2a) and longitudinal (2b) sections (paratype, IGSH-YY 10028); 3, transverse section (paratype, IGSH-YY 10029); 4, longitudinal section (paratype, IGSH-YY 10030); 5, longitudinal section (paratype, IGSH-YY 10031); 6a-c, serial transverse sections (paratype, IGSH-YY 10032); 7, transverse section (paratype, IGSH-YY 10033). All figures ×6.
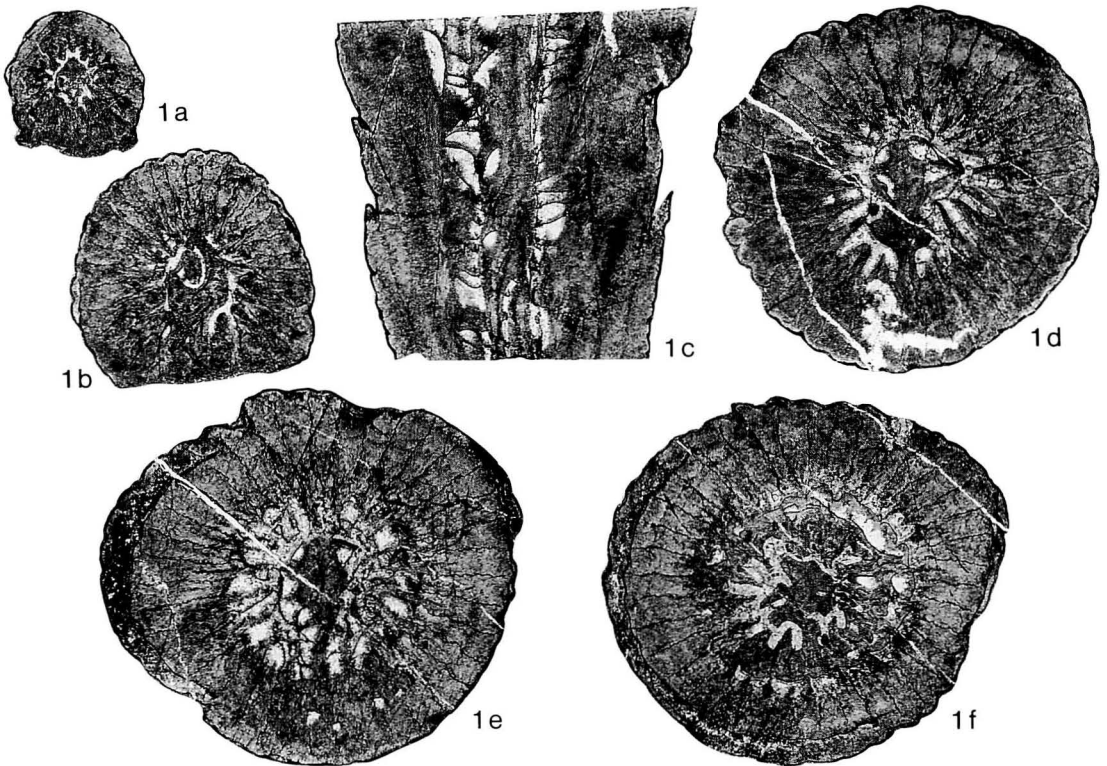
Figure 8.   1 : *Amygdalophylloides denticulatus,* sp. nov. **1a–f**, serial transverse (**1a–b, 1d–f**) and longitudinal (**1c**) sections (holotype, IGSH-YY 10063).   All figures ×6.

From these, 37 transverse and 7 longitudinal thin sections have been prepared.

Description. —Corallum is solitary with a ceratoid form and small in size.   Frequently, a few corallites belonging to different individuals are nearly placed and in one case even appressed, so as to give a false impression of a compound corallum (Figure 10–7a).   Surface characters are unobservable.

In transverse section, corallite is round in outline, measures 7.2 mm in diameter in the largest corallite.   External surface of wall is crenulated to reveal the presence of septal grooves and interseptal ridges.   A pronounced stereozone is formed by lateral fusion of peripherally thickened septa, varies in its width from 1/4 to 2/5 of the radius of corallite in the mature stages.   Dissepimentarium is completely filled by the development of the stereozone in some specimens.
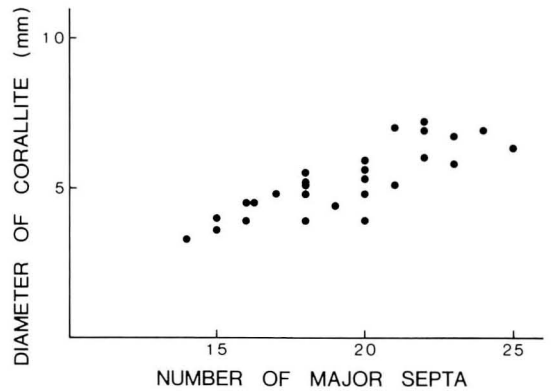
Figure 9.   Relationship between number of major septa and diameter of corallite in *Amygdalophylloides uzurensis* (Yamagiwa and Ota).

However, in other specimens a few small peripheral dissepiments are present, and some of them become subsequently modified to lonsdaleoid dissepiments by the withdrawal
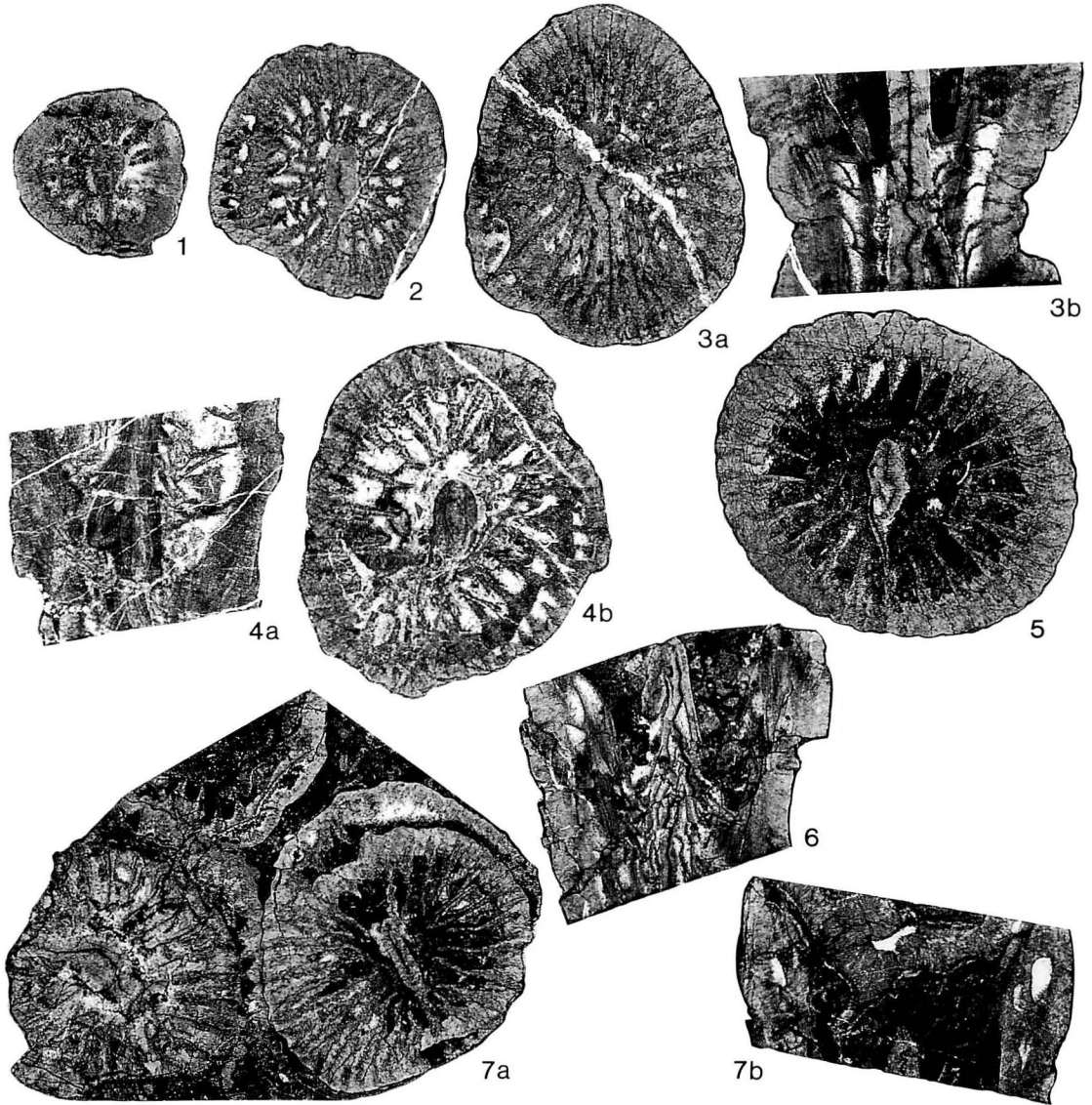
Figure 10. 1-7 : *Amygdalophylloides uzurensis* (Yamagiwa and Ota). **1**, transverse section (IGSH-YY 10064) ; **2**, transverse section (IGSH-YY 10070) ; **3a-b**, transverse (**3a**) and longitudinal (**3b**) sections (IGSH-YY 10065) ; **4a-b**, longitudinal (**4a**) and transverse (**4b**) sections (IGSH-YY 10082) ; **5**, transverse section (IGSH-YY 10066) ; **6**, longitudinal section (IGSH-YY 10067) ; **7a-b**, transverse (**7a**) and longitudinal (**7b**) sections (**7a**, left-hand corallite, **7b**, IGSH-YY 10071 ; **7b**, right-hand corallite, IGSH-YY 10072). All figures ×6.

of minor septa and rarely even major septa from the wall. Tabularium is round in outline, wide, occupying 3/5 to 3/4 of the diameter of corallite. There are a few cut edges of tabulae visible between major septa. Septa are of two orders, major and minor. Arrange-ment of septa is somewhat pinnate in the early growth stages, but tends to be radial in the mature stages. No fossula is discernible. Major septa show strong dilation in the stere-ozone and sometimes also in the tabularium. They fall short of the columella except the

cardinal septum. Inner ends of major septa are bluntly terminated. Minor septa alternate with the major septa, 2/5 to 3/5 (rarely 2/3) as long as the latter. They are normally embedded in the stereozone, but may just penetrate the tabularium. Only occasionally, minor septa are interrupted by the development of the lonsdaleoid dissepiments, if the latter is present. Septa are diffuso-trabecular in their fine structure. As many as 25 major septa are counted in a corallite of 6.3 mm in diameter. Relationship between the number of major septa and the diameter of corallite is shown in Figure 9. Axial structure consists of a solid columella which is a slightly thickened extension of the cardinal septum beginning in the early growth stage. In the mature stages the columella has elliptical and smooth outer configuration, with a fairly long median lamella and radially arranged calcite fibres. The columella is in contact with the cardinal septum, but the median lamellae of these two structural elements are usually disconnected. In a few specimens the columella is only partly replaced by axial tabellae which are outwardly convex (*e.g.* IGSH-YY 10066, Figure 10-5). Width of the columella is usually 1/8 to 1/6 of the diameter of corallite. Rare specimens have auxiliary columella (*e.g.* IGSH-YY 10065, Figure 10-3a). Rejuvenation may occur, but not frequently, and it is represented by the differentiation of a new wall from calicular wall of the old corallite (*e.g.* IGSH-YY 10072, right-hand corallite in Figure 10-7a).

In longitudinal section, wall is thick, and feebly undulated or in rare cases irregular by the presence of minor rejuvenescences. Dissepiments are only sporadic, small, a little elongated, steeply sloping and in one or two rows, but commonly suppressed by the stereoplasmic deposits. Tabularium is wide. Tabulae are mostly complete, but sometimes locally incomplete. They are subhorizontal, slightly sagging or descending towards the columella, and include gently or steeply tilting clinotabulae. In a vertical distance of 2

mm, 2 to 6, commonly 3 to 5 tabulae are counted. Only rarely axial tabellae are differentiated from the columella and are steeply inclined or vertical ; quite exceptionally, in the specimen IGSH-YY 10067 (Figure 10-6), one or two vertically continuous rows of axial tabellae are developed. Columella is comparatively wide, slightly sinuous and solid, made up of the calcite fibres perpendicular to the vertically continuous median lamella that is a little flexuous. Calice is deep with steep sides and has a prominent columella.

Remarks. —The present form shows no significant differences from the type material of *Amygdalophylloides uzurensis*, which was collected by Yamagiwa and Ota (1963) from the lower Upper Carboniferous of the Akiyoshi Limestone, southwest Japan. *A. uzurensis* was originally assigned to the genus *Lophophyllidium* (Yamagiwa and Ota, 1963, p. 91). However, Minato and Kato (1975, p. 7) transferred this species to the genus *Amygdalophylloides* on the grounds of its possession of lonsdaleoid dissepiments and clinotabulae. Indeed, study of the present Omi specimens clearly reveals that the columella originates from the axial end of the cardinal septum, instead of the counter one as in *Lophophyllidium*

A. uzurensis shows closest similarities to *Amygdalophylloides omiensis*, sp. nov. described below, from which it differs in having a less swollen columella.

Amygdalophylloides gracilis (Hayasaka, 1924) resembles *A. uzurensis*, but the smaller size of corallite and more complete and more widely spaced tabulae of the latter serve to distinguish the two from one another.

Amygdalophylloides omiensis
Yoshida, sp. nov.

Figures 12-1a—2b

Derivation of name. —After the Omi Limestone in Niigata Prefecture, Japan.
Material. —Ten corallites from Loc. OM

616 in section 1, which is assignable to the lower part of the *Eostaffella-Millerella* Zone. Holotype, IGSH-YY 10088, paratypes, IGSH-YY 10089–10097.
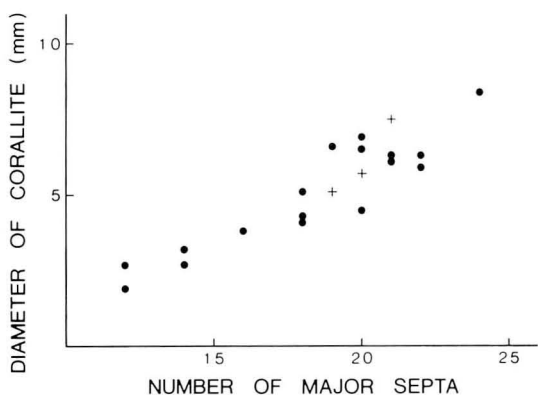

Figure 11. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides omiensis,* sp. nov. + : holotype of *A. omiensis.*

Twenty-six transverse and four longitudinal thin sections are available for study.

Diagnosis. —Comparatively small-sized *Amygdalophylloides* with a thick peripheral stereozone and a solid columella which is relatively large for the size of corallite. Small lonsdaleoid dissepiments rarely developed.

Description. —Corallum is solitary, ceratoid and small in size. Sometimes, two corallites belonging to different individuals are observed to be closely situated and grow parallel to each other, so as to give a false impression of being colonial (Figures 12– 1b, 1d). Surface characters unknown.

In transverse section, corallite is round in outline, the largest being 9.2 mm in calicular diameter. Wall is crenulated on its external surface, suggesting the presence of septal grooves and interseptal ridges. A prominent stereozone is produced by lateral coalition of
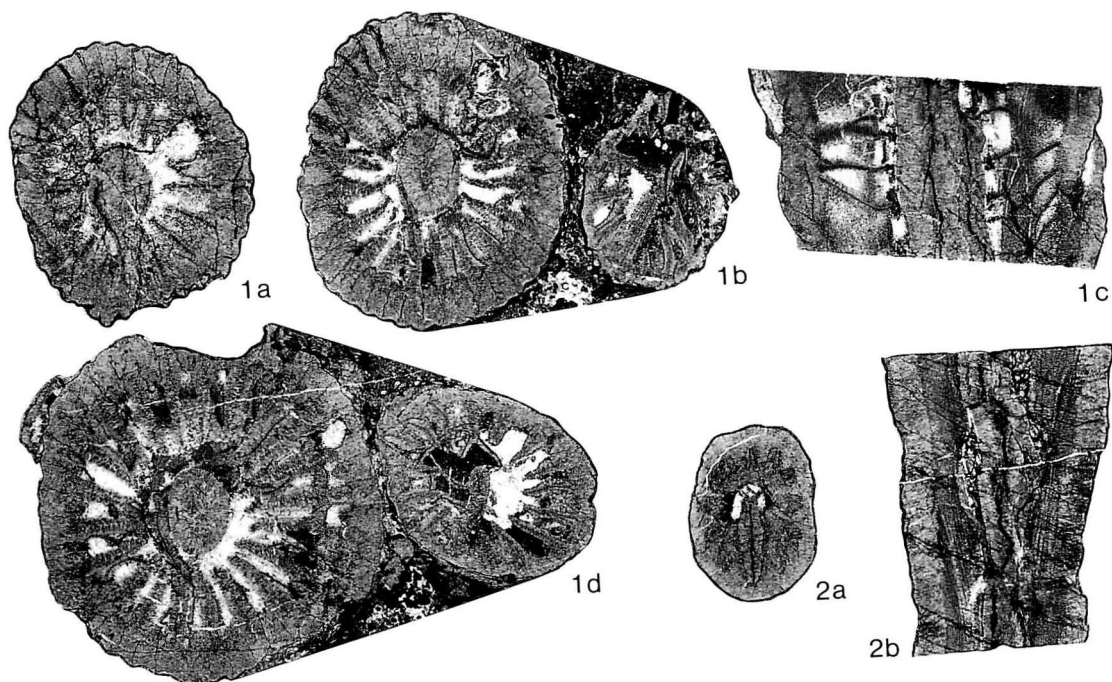
Figure 12. 1–2 : *Amygdalophylloides omiensis,* sp. nov. **1a–d,** serial transverse (**1a–b, 1d**) and longitudinal (**1c**) sections (**1a, 1b, 1d,** left-hand corallites, **1c,** holotype, IGSH-YY 10088 ; **1b, 1d,** right-hand corallites, paratype, IGSH-YY 10089) ; **2a–b,** transverse (**2a**) and longitudinal (**2b**) sections (paratype, IGSH-YY 10090). All figures ×6.

peripherally dilated septa, ranging in its width from 1/4 to 1/3 of the radius of corallite. Dissepimentarium is entirely masked by the development of the stereozone except in one section of the holotype specimen (left-hand corallite in Figure 12-1d), in which a few small lonsdaleoid dissepiments interrupting the continuation of minor septa are to be seen. Tabularium is round in outline, wide, occupying 2/3 to 3/4 of the diameter of corallite. There are a few cut edges of tabulae observable between major septa. Septa are in two alternating orders, major and minor. They are somewhat pinnately disposed in the early growth stages, but tend to show a radial arrangement in the mature stages. Fossula is not observed. Major septa taper gradually towards axis from the stereozone, with bluntly terminated axial ends. They are not connected with the columella, except for the cardinal septum. Minor septa are ordinarily confined to the stereozone, commonly 2/5 to 1/2 as long as the major. Septa have diffuso-trabecular fine structure. As many as 24 major septa are present in a corallite with the diameter of 8.4 mm. Relationship between the number of major septa and the diameter of corallite is shown in Figure 11. Axial structure is a solid columella that first appears as a slight axial swelling of the distal part of the cardinal septum. In the mature stages the columella is smoothly elliptical in outline and fairly large with regard to the diameter of corallite, comprising a relatively long median lamella and radiating calcite fibres. The columella is in touch with the cardinal septum except in the calice, but the median lamellae of these two structures are usually separated. Width of the columella is 1/6 to 1/4 (usually 1/5) of the corallite's diameter.

In longitudinal section, wall is thick, and weakly undulated or rarely irregular because of the presence of minor rejuvenescences. Dissepiments are only sporadical, small, flattened, vertical and in a single row, but generally concealed by the stereoplasmic deposits. Tabularium is wide. Tabulae are mostly complete, but may be locally incomplete. They are subhorizontal or descending to the columella, and include gently or steeply inclined clinotabulae. Two to four tabulae are contained in a vertical distance of 2 mm. Columella is wide, a little sinuous and solid, composed of the calcite fibres perpendicular to the median lamella which is slightly flexuous and vertically continuous. Calice is deep and steep-sided, having a prominent columella.

Remarks. —The present new form morphologically stands in between *Amygdalophylloides uzurensis* (Yamagiwa and Ota, 1963) and *A. gracilis* (Hayasaka, 1924). It differs from *A. uzurensis* in having a more swollen columella, and from *A. gracilis* in providing a smaller form and more incomplete tabulae which are more widely spaced.

Amygdalophylloides stenotabulatus Wang and Zhao (1989) from the Upper Carboniferous Weining Formation of Huize, Yunnan, South China, may bear some resemblance to the present form, but is easily distinguished from the latter by having a narrower stereozone, shorter minor septa, better developed dissepiments, no clinotabulae and a much larger columella from which septal lamellae are differentiated.

Amygdalophylloides longiseptatus Yoshida, sp. nov.

Figures 14-1a—4b

Derivation of name. —After the feature of corallum having long minor septa.

Material. —Five corallites: holotype, IGSH-YY 10098 and 2 paratypes, IGSH-YY 10099, 10100 from Loc. OM 707, 1 paratype, IGSH-YY 10101 from Loc. OM 708 and 1 paratype, IGSH-YY 10102 from Loc. OM 829 in section 2; these horizons are referrable to the *Eostaffella-Millerella* Zone.

Nine oblique transverse and three longitudinal thin sections were obtained from the specimens stated above.

Diagnosis. —Moderately large-sized *Amygdalophylloides* with long minor septa, a narrow tabularium and a solid columella, from which a few irregular axial tabellae may be differentiated in some cases. Small lonsdaleoid dissepiments sometimes developed. Intrathecal dilation is frequent, making the inner wall prominent.

Description. —Corallum is solitary, ceratoid and moderately large in size for the genus. No external characters are known.

Corallite observed in obliquely cut transverse section is elliptical in outline, attaining 12.5 mm in short diameter in the largest corallite. Internally it consists of wall, dissepimentarium, tabularium and axial structure. Wall is thick, comparatively smooth or marked only by faint septal grooves and interseptal ridges in outer configuration. Dissepimentarium is narrow, usually occupying 1/5 to less than 1/3 of the radius of corallite in the mature stages, and sometimes so reduced as to be replaced by the thick peripheral stereozone formed by lateral fusion of dilated septa in the early growth stage (Figure 14-3). It is composed mainly of 1 to 4 rows of irregularly arranged interseptal dissepiments which are straight, oblique or inwardly convex. Frequently, small lonsdaleoid dissepiments are developed ; they are indicated by the discontinuation of minor septa and only rarely even major septa. Intrathecal dilation on the septa and the internal surface of the dissepimentarium is often very distinct and inner wall is clear in that instance. Tabularium is narrow, well differentiated from the dissepimentarium, occupying 2/5 to 1/2 of the diameter of corallite. Cut edges of tabulae are seen between septa. Septa are radially arranged in two orders, major and minor. No fossula is observable. Septa are almost straight in the tabularium, and are often greatly thickened by intrathecal dilation. They may be however slightly sinuous and occasionally discontinuous in the dissepimentarium. Major septa are long, extending close to the axial structure, but only the
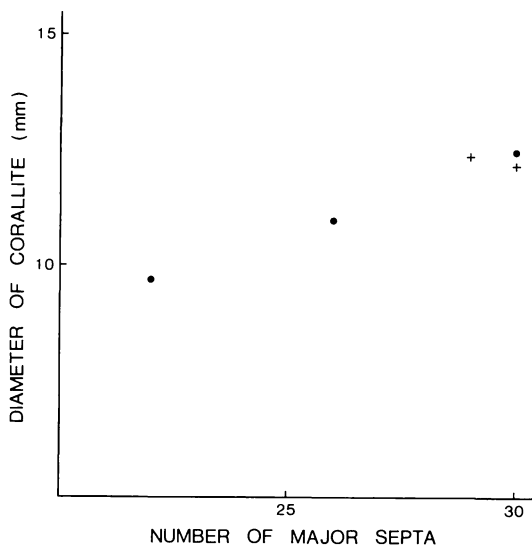
Figure 13. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides longiseptatus,* sp. nov. + : holotype of *A. longiseptatus.*

cardinal septum joins its periphery. Minor septa are almost as thick as the major ones with which they alternate. They are also long, attaining 2/3 to even 7/8 the length of the major, and are prolonged into the tabularium or terminated within the inner wall. Axially both septa end bluntly. Fine structure of septa is of the diffuso-trabecular type. The number of major septa is as many as 30 in a corallite with a short diameter of 12.5 mm. Relationship between the number of major septa and the diameter of corallite is shown in Figure 13. Axial structure is represented by a fairly large, smoothly elliptical solid columella which comprises a rather long median lamella and radially distributed calcite fibres. Sometimes, a few irregular axial tabellae can be differentiated from the periphery of the columella. The columella touches the cardinal septum, but the median lamellae of these two structures are not united. Width of the columella is approximately 1/5 of the diameter of corallite.

In longitudinal section, trizonal arrangement of skeletal elements is clear. Wall is thick and weakly undulated. Dissepimentar-
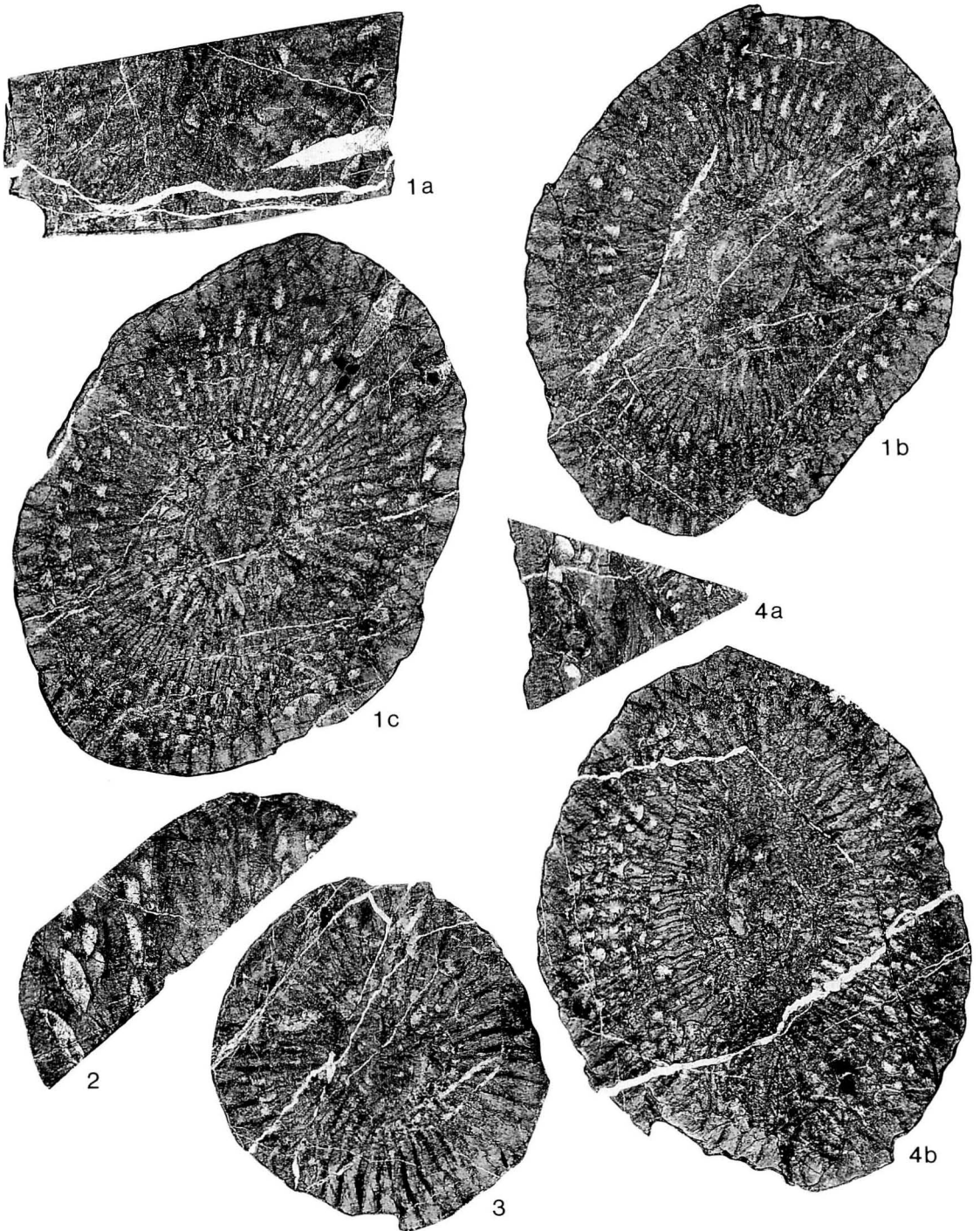
Figure 14. **1-4:** *Amygdalophylloides longiseptatus,* sp. nov. **1a-c,** longitudinal (**1a**) and successive oblique transverse (**1b-c**) sections (holotype, IGSH-YY 10098) ; **2,** longitudinal section (paratype, IGSH-YY 10099) ; **3,** transverse section (paratype, IGSH-YY 10100) ; **4a-b,** longitudinal (**4a**) and oblique transverse (**4b**) sections (paratype, IGSH-YY 10101). All figures ×5.
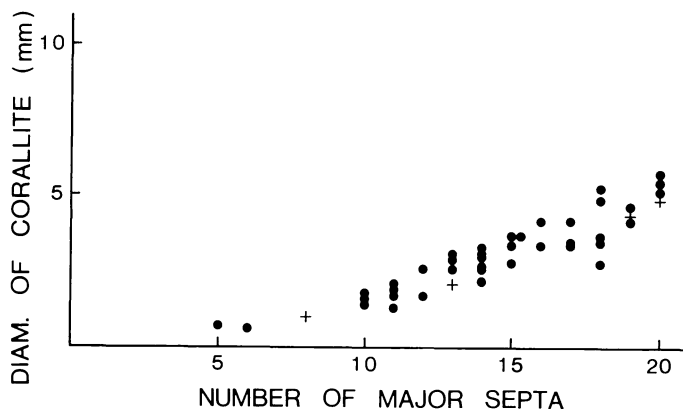
Figure 15. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides parvus*, sp. nov. + : holotype of *A. parvus*.

ium is narrow, with 1 to 2 rows of small, steeply tilting globose dissepiments. Strong intrathecal dilation occurs on the internal surface of the dissepimentarium. Tabularium is narrow, well differentiated from the dissepimentarium, made up of subhorizontal transverse tabulae and steeply sloping clinotabulae. All the tabulae are rather distantly spaced. Columella is wide, a little sinuous and solid, consists of the calcite fibres oriented perpendicularly towards the slightly flexuous and vertically continuous median lamella. A few axial tabellae may appear in the columella.

Remarks. —With its long minor septa, the present form is unlikely to be confused with any other known species of *Amygdalophylloides*. The type species, *Amygdalophylloides ivanovi* (Dobrolyubova, 1937), may have some similarities, especially in corallite size, number of septa and the general character of axial structure. The present form is distinguished, however, by its stronger dilation of septa, much longer minor septa and a narrower tabularium.

Amygdalophylloides parvus Yoshida, sp. nov.

Figures 16-1a—7

Derivation of name. —After small dimensions. Latin *parvus*—small.

Material. —Forty-four corallites : holotype, IGSH-YY 10103 and 42 paratypes, IGSH-YY 10104-10145 from Loc. OM 731 and 1 paratype, IGSH-YY 10146 from Loc. OM 708 in section 2 ; these localities are referred to the lower part of the *Eostaffella-Millerella* Zone.

From these specimens, 97 transverse and 3 longitudinal thin sections were made for the systematic study.

Diagnosis. —Small-sized *Amygdalophylloides* with a thick peripheral stereozone, fairly long minor septa and a solid columella. Small lonsdaleoid dissepiments only rarely developed.

Description. —Corallum is solitary with a ceratoid to subcylindrical form and small in size. No surface characters are known.

In transverse section, corallite is round to subround in outline. The largest corallite has a calicular diameter of 9.0 mm, but this is exceptional as the next largest one is only 6.5 mm in diameter of calice. External crenulation of wall indicates the presence of septal grooves and interseptal ridges. The peripheral stereozone composed of dilated marginal ends of septa is thick, its width being usually 1/4 to 1/3 (rarely 1/5) of the corallite radius. Dissepimentarium is completely masked by the development of the stereozone in many specimens. However, in rare specimens a
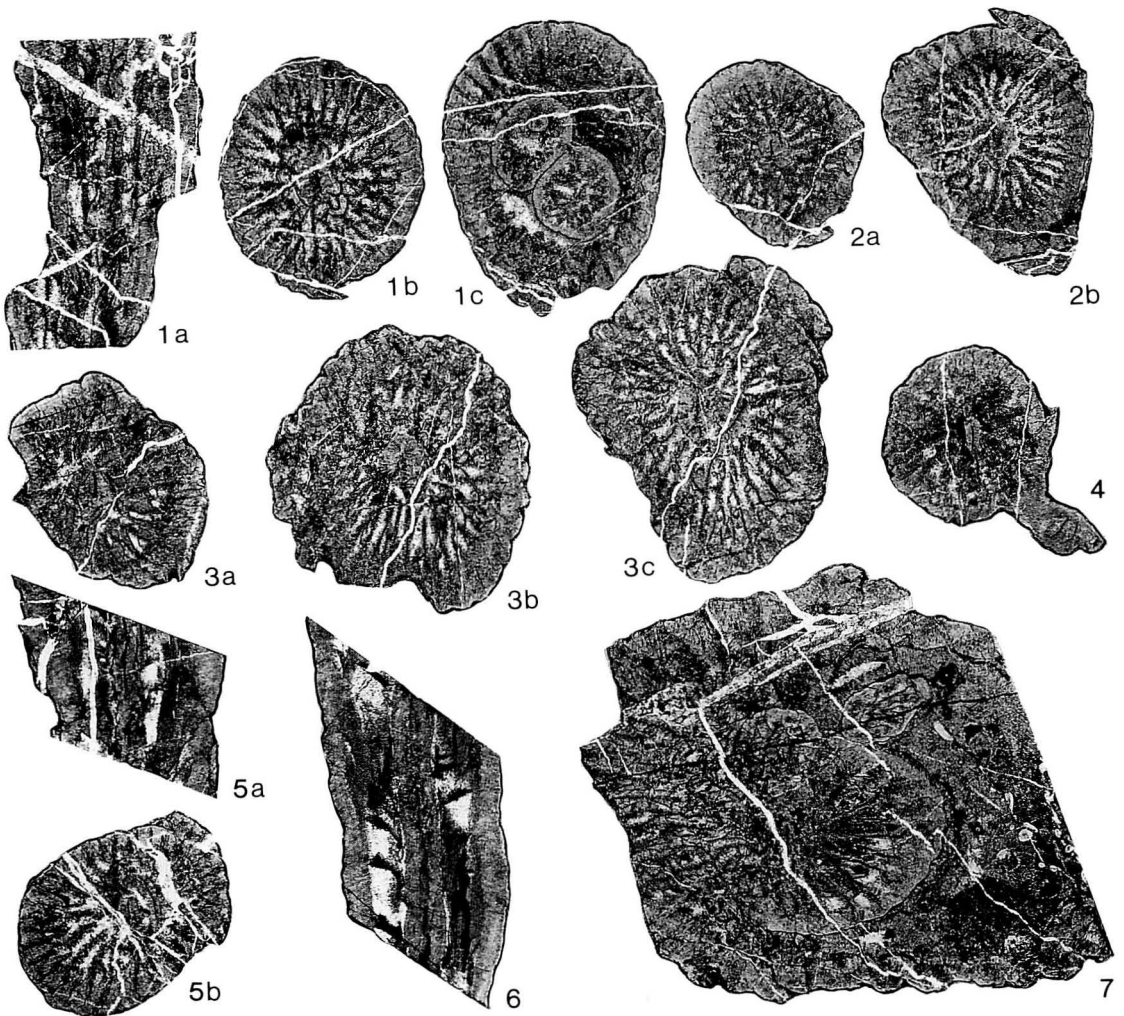
Figure 16. 1-7 : *Amygdalophylloides parvus,* sp. nov. **1a-c**, longitudinal (**1a**) and successive transverse (**1b-c**) sections (holotype, IGSH-YY 10103) ; **2a-b**, successive transverse sections (paratype, IGSH-YY 10104) ; **3a-c**, serial transverse sections (paratype, IGSH-YY 10105) ; **4**, transverse section (paratype, IGSH-YY 10106) ; **5a-b**, longitudinal (**5a**) and transverse (**5b**) sections (paratype, IGSH-YY 10107) ; **6**, longitudinal section (paratype, IGSH-YY 10108) ; **7**, transverse section (paratype, IGSH-YY 10109). All figures ×6.

few, small interseptal dissepiments are observable. Quite exceptionally, small lonsdaleoid dissepiments are partly developed in the calice. Tabularium is round in outline, wide, occupying normally 2/3 to 3/4 of the diameter of corallite. A few cut edges of tabulae are visible between septa. Septa are of two orders, major and minor. Septal arrangement is somewhat pinnate in the early growth stages, but shows a tendency to be radial in the mature stages. No fossula is observed. Major septa are very thick at their bases, but gradually attenuating towards the columella, with which only the cardinal septum is connected. They have bluntly terminated axial ends. Minor septa alternating with major ones are rather long compared with the size of the corallite, commonly protruded into the tabularium. Length of the minor septa is 3/5 to even 4/5 of the
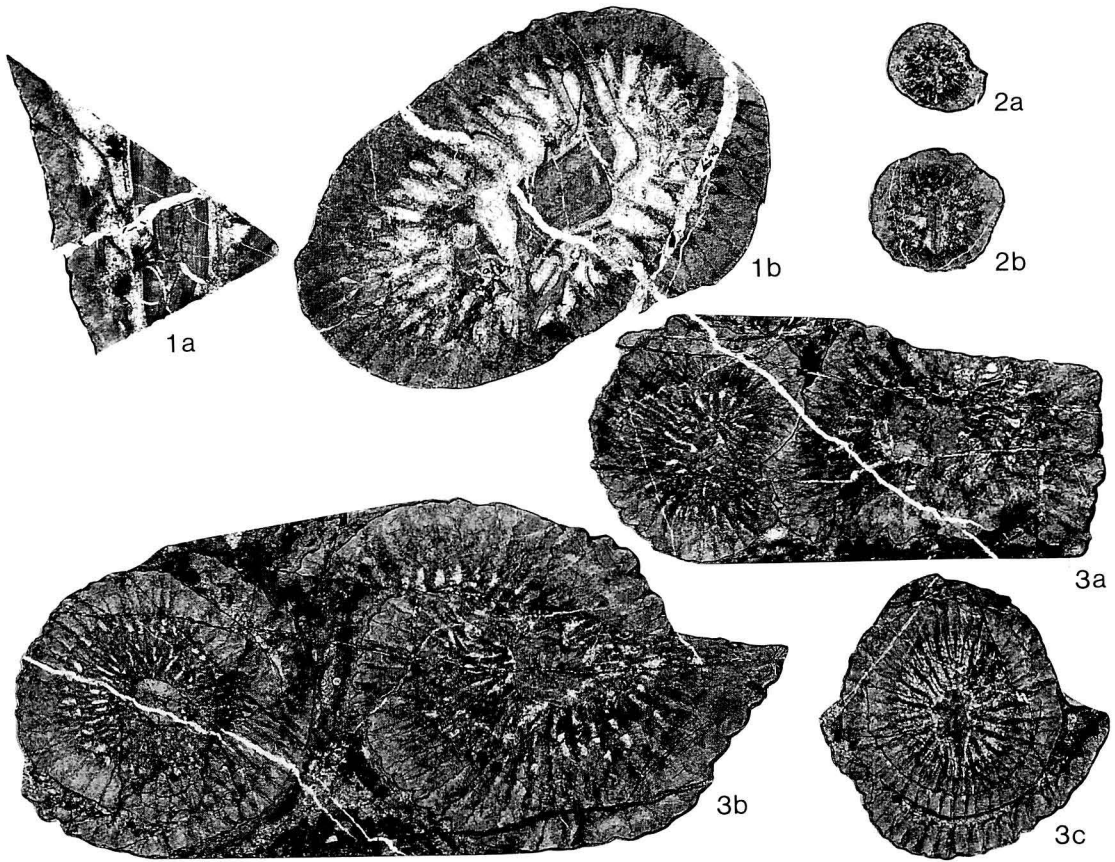
Figure 17. 1: *Amygdalophylloides* sp. A. **1a–b**, longitudinal (**1a**) and oblique transverse (**1b**) sections (IGSH-YY 10147). **2–3:** *Amygdalophylloides* sp. B. **2a–b**, successive transverse sections (IGSH-YY 10149) ; **3a–c**, successive transverse sections (**3a–b**, left-hand corallites, **3c**, IGSH-YY 10150 ; **3a–b**, right-hand corallites, IGSH-YY 10151). All figures ×6.

major septa in the mature stages. Septa are diffuso-trabecular in fine structure. The number of major septa is as many as 20 in a corallite of 5.8 mm in diameter. Relationship between the number of major septa and the diameter of corallite is shown in Figure 15. Axial structure is composed of a solid columella which is formed by a slight expansion of the axial end of the cardinal septum at first. In the mature stages the columella is fusiform or smoothly elliptical in outline, consisting of a fairly long median lamella and radially disposed calcite fibres. The columella is in contact with the cardinal septum, but the median lamellae of these

structural elements do not join each other. Width of the columella is usually 1/6 to 1/5 (rarely 1/7) of the diameter of corallite. Simple budding is discernible in the holotype (Figure 16–1c) and the paratype specimen IGSH-YY 10109 (Figure 16–7), in which two small offsets arise in the axial area in the mother corallite. Also in the paratype, IGSH-YY 10106 (Figure 16–4), one small offset springs out from the sidewall of the mother corallite. A few specimens show evidence of rejuvenescence.

In longitudinal section, wall is thick and feebly undulated. Dissepiments are only sporadical, small, flattened and vertical and

in one row, but commonly suppressed by the stereoplasmic deposits. Tabularium is wide, made up of complete or incomplete tabulae which are mostly inclined axially and include steeply or gently sloping clinotabulae. Two to four tabulae are situated within a vertical distance of 2 mm. Columella is comparatively wide to wide, slightly sinuous and solid, with the calcite fibres perpendicular to the median lamella which is weakly undulating and vertically continuous.

Remarks. —The small corallite size clearly separates the present new form from the other Japanese representatives of *Amygdalophylloides*.

Amygdalophylloides rareseptatus Dobrolyubova and Kabakovich (1948) from the Upper Carboniferous (C_{III}^0 horizon) of the Moscow Basin, has similar dimensions to the present form, but is easily distinguished from the latter by having a narrower stereozone, better developed dissepiments and shorter minor septa.

Putting aside small size of corallite, the present form somewhat resembles *A. gracilis* (Hayasaka, 1924), but differs from that species in possessing longer minor septa for the size of corallite, and more complete tabulae which are more distantly spaced.

Amygdalophylloides sp. A

Figures 17-1a—b

Material. —Single fragmental corallite from Loc. OM 558 in the section 1, which belongs to the upper part of the *Endothyra* Zone. IGSH-YY 10147.

Two obliquely cut transverse and longitudinal thin sections were made from this specimen.

Description. —Corallum is solitary, small in size. Externals are not available.

Oblique transverse section of a corallite in mature stage is elliptical in outline, and 6.5 mm in minimum diameter. External surface of corallite is crenulated, as far as preserved.

Stereowall is thick, formed by peripheral dilation of septa. No dissepiments are observable. Tabularium is wide, where cut edges of tabulae are seen between septa. Septa are in two orders, major and minor. They are somewhat pinnately arranged, but fossula is indistinct. Major septa are 27 in number, very thick at their bases, gradually taper towards axis, with bluntly ended axial terminations. They do not reach the columella except for the counter and cardinal septa ; the counter septum joins the columella laterally, while the cardinal one meets it directly. Minor septa are 1/2 to 3/5 the length of the major septa with which they alternate, and most of them project only slightly into the tabularium. Fine structure of septa is diffuso-trabecular. Axial structure is a fairly large, spindle-shaped, solid columella that is formed by a extremely strong expansion of the axial end of the cardinal septum.

In longitudinal section, wall is thick. Dissepiments are unobservable. Tabularium is wide, with gently or steeply inclined, complete clinotabulae which are fairly distantly spaced. Columella is wide, smooth and solid, comprising the calcite fibres oriented perpendicularly to the feebly undulating median lamella, which is vertically continuous.

Remarks. —The present unidentified form closely resembles *Amygdalophylloides omiensis*, sp. nov. described above, but is distinguished by possessing a much longer counter septum attached to the columella and slightly longer minor septa, most of which just penetrate the tabularium, and a columella that is continuously connected with the cardinal septum even in the mature stage. It also resembles *Amygdalophylloides gracilis* (Hayasaka, 1924). The two forms can be distinguished by the latter having a larger form and more closely spaced tabulae which are mostly incomplete, besides a counter septum separated from the columella. The present form may represent a new species, but
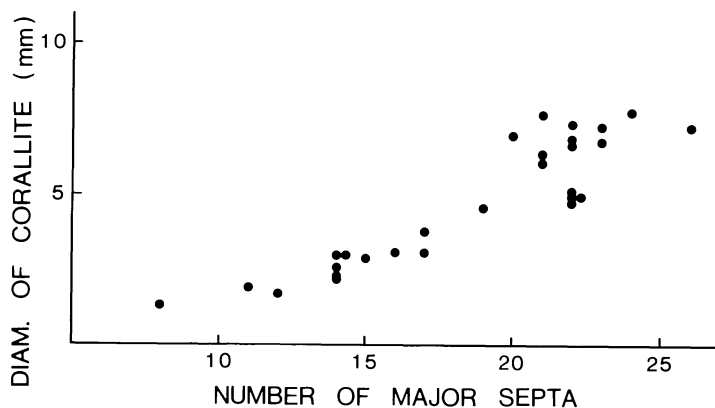
Figure 18. Relationship between number of major septa and diameter of corallite in *Amygdalophylloides* sp. B.

the final decision is deferred pending discovery of more well preserved specimens.

Amygdalophylloides sp. B

Figures 17-2a—3c

Material. —Sixteen fragmental corallites: IGSH-YY 10148 from Loc. OM 708 and IGSH-YY 10149–10163 from Loc. OM 711 in section 2, which are equivalent to the lower part of the *Eostaffella-Millerella* Zone.

From these, 50 transverse thin sections have been examined.

Description. —Corallum is solitary, small in size ; individuals are commonly aggregated and are often in contact with each other (Figure 17-3a), but there is no indication of branching or budding. Surface characters are unobservable.

In transverse section corallite is round in outline, the largest having a diameter of 7.8 mm. Wall is crenulated externally with septal grooves and interseptal ridges. The peripheral stereozone produced by lateral fusion of expanded septa is strongly developed, ranging in width from 1/4 to 3/5 (generally 1/3 to 1/2) of the radius of corallite in the mature stages. Dissepimentarium is entirely filled by the development of the stereozone except in a few specimens, in which sparse, small interseptal dissepiments are vis-

ible. Tabularium is wide, occupies normally 1/2 to 2/3 (rarely 2/5) of the diameter of corallite. A few cut edges of tabulae are discernible between septa. Septa are in two orders, major and minor. They are more or less pinnately arranged in the early growth stages, but become radial in the mature stages. Fossula is not observed. Major septa are strongly dilated in the stereozone, gradually tapering axially. They fall short of or touch the columella. Minor septa are fairly long and almost as thick as the major with which they alternate. They may be confined to the stereozone, but more commonly intrude into the tabularium. Length of the minor septa is usually 3/5 to 3/4 (rarely 4/5) of the major. The axial ends of both septa are bluntly terminated. Septal fine structure is diffuso-trabecular. As many as 26 major septa are counted in the 7.3 mm diameter corallite. Relationship between the number of major septa and the corallite diameter is shown in Figure 18. Axial structure consists of a solid columella which is a slight axial swelling of the distal part of the cardinal septum at first. In the mature stages a median lamella and radially situated calcite fibres form an elliptical or spindle-shaped columella, which in some instances may have a denticulated outline with a few short septal lamellae-like projections. The columella is attached to

the cardinal septum except near the calice, but the median lamellae of these structural elements do not unite with each other. Width of the columella is usually 1/7 to 1/5 of the corallite diameter. There may be an auxiliary columella in the early growth stage (*e.g.* IGSH-YY 10150, left-hand corallite in Figure 17-3a). A few specimens show rejuvenescence, which is indicated by the differentiation of a new wall from the old calicular wall (*e.g.* IGSH-YY 10150, left-hand corallite in Figure 17-3b, Figure 17-3c). No longitudinal section is available.

Remarks. —Although the material certainly represents a new species, longitudinal sections were not obtainable, so that it is not a suitable basis for a new taxon. Closest similarities can be seen to both *Amygdalophylloides denticulatus* and *A. densus*, sp. nov. described above. These forms have, however, minor septa which are generally embedded in the stereozone, whereas most of the minor septa only just project into the tabularium in the present form. Furthermore, they are provided with a smaller columella compared to the present form ; the columella is circumscribed by a few axial tabellae in *A. denticulatus* and it bears no septal lamellae-like projections in *A. densus*.

Amygdalophylloides gracilis (Hayasaka, 1924) is distinguished from the present form in having a larger form, shorter minor septa and more numerous cut edges of tabulae in transverse section.

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青海石灰岩の石炭系より産する *Amygdalophylloides* (四射サンゴ類): 新潟県青海石灰岩層群下部層からは豊富なサンゴ化石を産出する。ここでは黒姫山北東斜面に位置する福来ケ口地域より採集した *Amygdalophylloides* のうち, 次の 5 新種を含む 8 種を記載する: *Amygdalophylloides densus*, sp. nov., *A. denticulatus*, sp. nov., *A. uzurensis* (Yamagiwa and Ota), *A. omiensis*, sp. nov., *A. longiseptatus*, sp. nov., *A. parvus,* sp. nov., *A.* sp. A, *A.* sp. B。このサンゴ化石群の時代は *A.* sp. A が後期ビゼー世であるのを除いてはナムール世 A からナムール世 B (セルプコフ世から前期バシキール世初期) であると考えられる。

吉田　靖・沖村雄二

938. AMMONITES OF THE GENUS *ACOMPSOCERAS* AND SOME OTHER ACANTHOCERATID SPECIES FROM THE IKUSHUNBETSU VALLEY, CENTRAL HOKKAIDO

(STUDIES OF THE CRETACEOUS AMMONITES FROM HOKKAIDO—LXXIII)

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Abstract. We have recently investigated the hitherto unexplored outcrops of Lower Cenomanian sandy rocks not far from the type section of the Mikasa Formation along the River Ikushunbetsu of central Hokkaido. Although bivalves predominate there, at least ten ammonite species are identified. In this paper the following four species are described, since they have not yet been recorded in Hokkaido : *Acompsoceras renevieri* (Sharpe), *Utaturiceras vicinale* (Stoliczka), *Mantelliceras* aff. *japonicum* Matsumoto, Muramoto & Takahashi and *Mantelliceras saxbii* (Sharpe). Also a biostratigraphic correlation with the type section is attempted with a suggestion that the *Acompsoceras*-bearing bed may represent, though locally and with lateral change of facies, the next higher level than the Zone of *Mantelliceras japonicum* in the type section of the lower Cenomanian in the Ikushunbetsu Valley.

Introduction

One of us (T.T.) recently noticed hitherto unexplored outcrops of fossiliferous sandy rocks which could be referred to the lower part of the Mikasa Formation. This seemed important in that the obtained material might supplement the knowledge of Cenomanian ammonite zones which were established primarily along the main course of the River Ikushunbetsu [=Ikushumbets]. Subsequently, we visited the outcrops frequently for further hunting. Although bivalves predom-

inate there, we have identified at least ten species of ammonoids, of which an *Acompsoceras* and three other acanthoceratids mark the first occurrence in Hokkaido. We describe them in this paper and give brief remarks on their biostratigraphic implications.

Notes on stratigraphy

The outcrops mentioned above are located 1,250 m northeast in plan and 300 m higher in altitude from the bridge called the Katsura-Ohashi, i.e., loc. Ik 1054, on the Ikushunbetsu River (see Matsumoto, compiler, 1991, fig. 3).
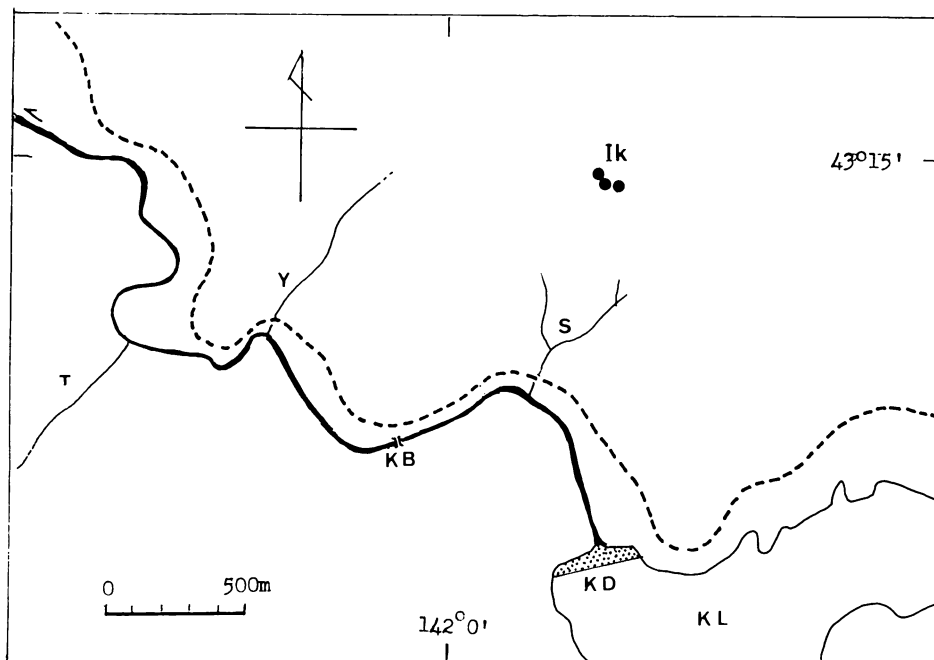
Figure 1. Map of the Ikushunbetsu Valley (part), showing the locations of the described ammonites by three small solid circles around Ik from NW to SE: Ik 7001, 7002 and 7003. KB: bridge called Katsura-Ohashi KD: Katsura-zawa dam. KL: Katsura-zawa Lake, S: Suido-no-sawa, T: Torii-zawa, Y: Yu-no-sawa.

They are on the slope of a mountain and were cuttings along a forestry road which was active several years ago but is now abandoned and covered with bush (Figure 1).

The following succession of strata is observable there in ascending order:

A (loc. Ik 7001): A unit of dark grey silty fine-grained sandstones or sandy siltstones, at least 30 m in thickness, of which upper part (10 m) is well exposed. *Desmoceras kossmati* Matsumoto, *Mantelliceras saxbii* (Sharpe) and *Sciponoceras* cf. *baculoides* (Mantell) are yielded from some nodules. Unit A is underlain by layers of milky white to gray, compact tuff and tuffaceous sandstone.

B (loc. Ik 7002): Fine- to medium-grained sandstones, bedded or laminated and filled with molluscan shells in some layers. Turritellas are often aligned in roughly parallel orientation. Ammonites are rather few, fragmentary and scattered. *Desmoceras* sp., *Mantelliceras* cf. *japonicum, Turrilites cos-*

tatus Lamarck, etc. may be found. At least 7 m thick.

C (loc. Ik 7003): Medium- to coarse-grained sandstones, containing abundantly *Cucullaea ezoensis* Yabe and Nagao and *Pterotrigonia* (*Ptilotrigonia*) *mifunensis* (Tamura and Tashiro). *Inoceramus tenuis* Mantell and *Inoceramus* cf. *virgatus* Schlüter are collected rarely. Ammonites yielded sporadically are as follows: *Hypophylloceras* (*Neophylloceras*) *seresitense* (Pervinquière), *Desmoceras* (*Pseudouhligella*) *japonicum* Yabe, *D.* (*P.*) *ezoanum* Matsumoto, *Mantelliceras* aff. *japonicum, Utaturiceras vicinale, Acompsoceras renevieri, Prionocycloides* cf. *proratus* (Coquand), *Zelandites europae* Wright and Kennedy and *Turrilites costatus*.

Overlying strata are not exposed here on account of displacement by a wrench fault.

Let us attempt to correlate the above sequence with that of the type section along the main course of the River Ikushunbetsu

(See Matsumoto *et al.*, 1991 or Matsumoto, comp., 1991 for the type section). The tuffaceous rocks below unit A are certainly a key marker at about the Albian-Cenomanian boundary or immediately below the lowest fossiliferous bed of the lower Cenomanian.

Unit A is correlated with the Zone of *Desmoceras kossmati* in the basal member (IIa) of the Mikasa Formation in the type section. Unit B is certainly an extension of the Zone of *Mantelliceras japonicum*, i.e. lower part of Member IIb in the type section, with lateral change of facies to a near-shore environment, where shells were often transported by washing processes and the sediments are thinner.

Now Unit C can be regarded as an extension of the ammonite-poor sandstone with trigoniids and other bivalves in the middle part of Member IIb in the type section. Noteworthy is the fact that *Acompsoceras renevieri*, *Utaturiceras vicinale* and *Mantelliceras* aff. *japonicum* (instead of undoubted *M. japonicum*), which have not been recorded in Hokkaido, are found in this Unit C. *A. renevieri*, however, may have a longer range, if its occurrence in Europe (see Wright and Kennedy, 1987) is taken into consideration.

It should be further noted that in Hokkaido *Turrilites costatus* appears at a lower level than in Europe, occurring in the Zone of *M. japonicum* together with *Hypoturrilites*
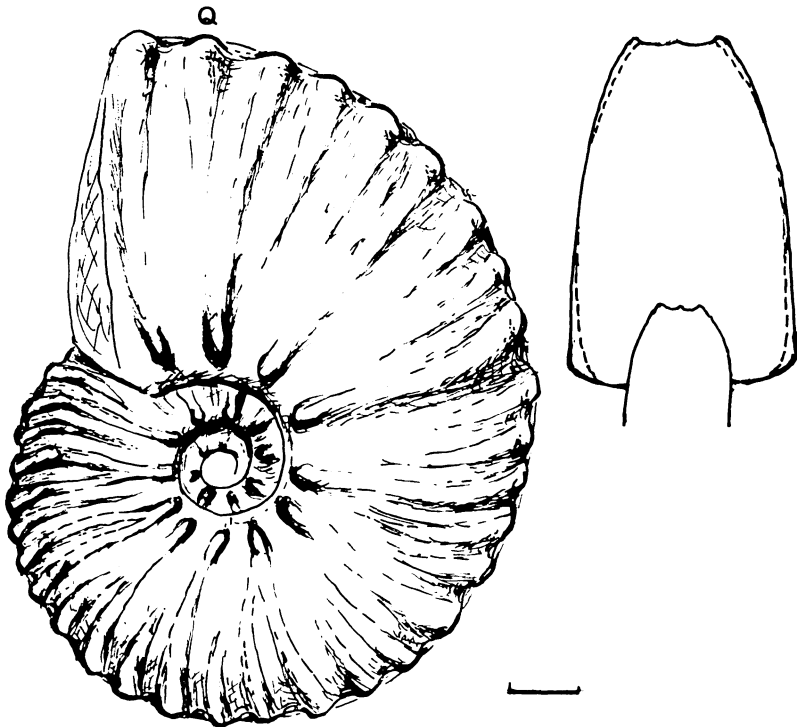
Figure 2. *Acompsoceras renevieri* (Sharpe).
Diagrammatic sketch of TTC. 020415-1. Right lateral view and whorl section at Q. Scale bar = 10 mm.
T.M. delin.

→ **Figure 3.** *Acompsoceras renevieri* (Sharpe).
TTC. 020415-1, phragmocone in 4 views (a–d), ×1. Photos by M. Noda.

a

b

c

d
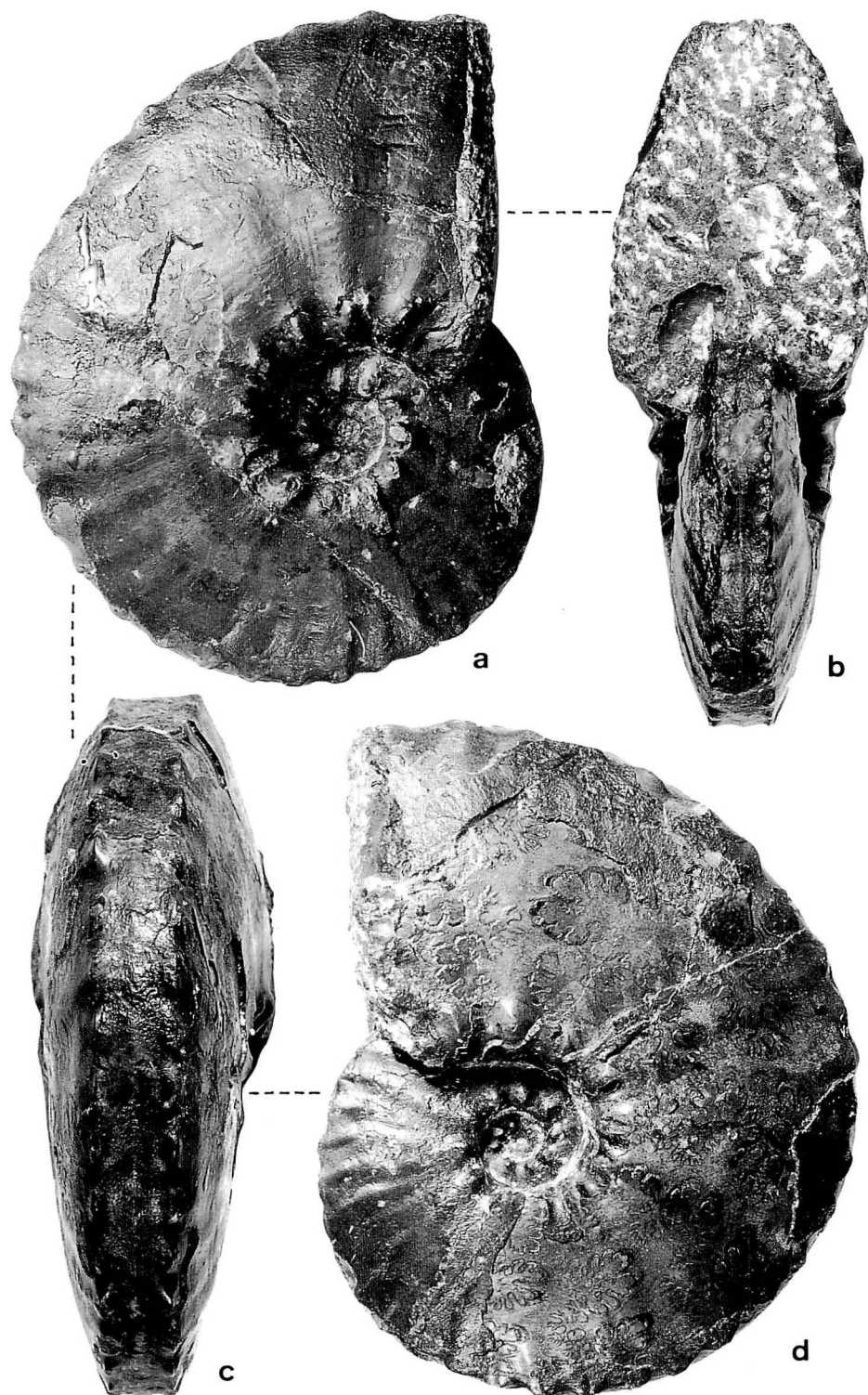
gravesianus (d'Orbigny) and *Neostlingoceras carcitanense* (Matheron), and is found also in Unit C. (Turrilitid ammonoids from Japan should be monographed on another occasion.) The true stratigraphic range and vertical distribution of *Utaturiceras vicinale* should be worked out further, as our examples are solitary juveniles.

Systematic descriptions

The morphological terms in the following descriptions are the same as those explained by Matsumoto (1988, p. 4), who generally follows those in the *Treatise* (Arkell *et al.*, 1957), with a slight alteration. Abbreviations used in the measurements include D = diameter of shell, U = width of umbilicus, H = whorl-height, B = whorl-breadth, h = whorl-height at half whorl earlier than H, Inv. = degree of involution, LT = lectotype, c = costal, ic = intercostal, LS = last septum.

The described and figured specimens are numbered under the heading of TTC (Takemi Takahashi's Collection) and will be kept in the Museum of Mikasa City. Their plaster casts are kept in the Type Room of the Department of Earth and Planetary Sciences, Kyushu University 33, Fukuoka.

Family Acanthoceratidae
de Grossouvre, 1894
Genus *Acompsoceras* Hyatt, 1903

Type species.—*Ammonites bochumensis* Schlüter, 1871 by original designation, which is a synonym of *Ammonites renevieri* Sharpe, 1857.

Remarks.—See Wright and Kennedy, 1987, p. 139–140 for the diagnosis and comments.

Distribution.—Rather rare but widespread in Europe, North Africa, the Middle East, Madagascar, east and west Africa, Texas (U.S.A.). This is the first record in Japan.

Acompsoceras renevieri (Sharpe, 1857)

Figures 2–4

Ammonites renevieri Sharpe, 1857, p. 44, pl. 20, fig. 2.
Ammonites bochumensis Schlüter, 1871, p. 1, pl.1, figs. 1–4; pl. 2, fig. 1.
Ammonites essendiensis Schlüter, 1871, p. 3, pl. 1, figs. 5–7; pl. 2, fig. 2.
Acompsoceras renevieri (Sharpe); Wright and Kennedy, 1987, pl. 140, pl. 43, fig. 2; text-figs. 34G, 35D-f, 36A-F, 37–40 (with full synonymy).

Material.—Two specimens collected by T. Takahashi from loc. Ik 7003: TTC. 020415-1 (Figures 2, 3), a well-preserved phragmocone, and TTC. 030512-1 (Figure 4), a fragmentary body-chamber.

Description.—The phragmocone is nearly 100 mm in diameter, consisting of fairly involute whorls with a high ratio of expansion (H/h = 1.6). Its umbilicus is fairly narrow, about 20 percent of shell-diameter, surrounded by nearly vertical wall and abruptly bent edge. The preserved last whorl is higher than broad, keeping B/H at about 2/3. It is subtrapezoid in cross-section, showing gently convex and outward converging flanks, sharp outer ventrolateral shoulder on either side of nearly flat but rather narrow venter, with a weak but nearly continuous train of siphonal clavi.

The phragmocone is ornamented with numerous ribs of unequal length on the flank, fairly strong tubercles at the umbilical edge and sharp-headed clavi at the outer ventrolateral shoulder. On the outer flank of the younger part, there is a row of very weak nodes, which may be called the inner ventrolateral.

The ornamentation of this wholly septate specimen is regular. Between the two primary ribs, which arise from the umbilical tubercle, normally two, though occasionally one, secondary ribs are intercalated. The ventrolateral clavi are thus nearly three times as numerous as the umbilical tubercles; actually 34 of the former versus 12 of the latter in an entire volution. On the early part of the preserved outer whorl the ribs are narrow and the secondaries sometimes look as if branched from the primary at the bullate umbilical

Figure 4. *Acompsoceras renevieri* (Sharpe).
TTC. 030512-1, incomplete body-chamber in left lateral (a) and ventral (b) views.   Scale bar = 10 mm.
Photos by M. Noda.

tubercles. The ribs gradually broaden and lower as the whorl grows; the secondaries shorten, but the sharp ventrolateral clavi persist. On the earlier part the ribs are gently flexuous, with some forward inclination on the outer flank. Later some ribs are nearly rectiradiate.

Colour patterns are discernible where the test is preserved, with light-coloured spiral bands on the middle of the flank and a less distinct display along the row of inner ventrolateral weak nodes.

The suture is that of *Acompsoceras*, showing the phylloid terminals of the folioles. The stems of the lobes L and U2 and subdividing lobules are fairly narrow in this specimen.

The fragmentary body-chamber, with test partly preserved, of about 150° in spiral angle lacks the part around the umbilicus but shows the venter, middle to outer part of the left flank and the outer portion of the right flank. The preserved parts of the flanks converge outward. The venter, which is demarcated by angular to subangular outer ventrolateral shoulders, is relatively narrow, adapically 15 mm and adorally 18 mm in breadth. The ventrolateral clavi are well developed on the earlier 50° and much weaken later. Also the spiral elevation is traced on some part of the mid-venter.

On the flank there are very faint rib-like elevations, periodic shallow groove along some of them, weak lirae or striae, all of which are gently flexuous, with a broad convexity on the middle part and a gentle projection in approaching the ventrolateral shoulder. Weak striae or lirae and also shallow grooves may run across the venter vertically.

Dimensions.—Measurements in mm of the wholly septate TTC. 020415-1 in comparison with the lectotype (below) are as follows:

	D	U	H	B	B/H	H/h	Inv.
TTC	96.5 (1)	19.5 (.20)	49.5 (.51)	32.5 (.34)	0.66	1.6	0.59
LT*	115.0 (1)	26.5 (.23)	54.0 (.47)	34.5 (.30)	0.64	—	0.57

* cited from Wright & Kennedy (1987), except for H/h and Inv. by T.M

Comparison.—The two specimens from Ikushunbetsu described above are generally similar to the types and other well known examples of *Acomposoceras renevieri* (Sharpe, 1857). This species has been recently redefined by Wright and Kennedy (1987), who regarded *Ammonites bochumensis* Schlüter, 1871 and *Ammonites essendiensis* Schlüter, 1871 as synonyms of *A. renevieri*. We agree with them in this point, since one of us (T.M.) once examined Schlüter's specimens from northwestern Germany as well as Sharpe's and other specimens from southern England.

The wholly septate specimen from Ikushunbetsu particularly resembles in shell form the illustrated paralectotype of *A. bochumensis* Schlüter (1871, pl. 1, figs. 3-4) and another example from Nigeria figured by Reyment (1957, pl. 8, fig. 3, under *Acomposoceras subwaterloti* Venzo), both identical with *Ac. renevieri* as Wright and Kennedy pointed out. Our specimen, however, shows some difference in ornamentation, viz. its ribs are gently flexuous at least in younger part and more numerous, with normally two secondaries on each interval of the primaries, whereas in the latter two specimens and also the lectotype of *A. renevieri* (see Wright and Kennedy, 1987, pl. 43, fig. 2) the ribs are nearly rectiradiate and less numerous with one by one alternation of the primary and secondary ribs.

The material from western Europe as well as that from Japan may be insufficient to inspect precisely the extent of variation. The paralectotype of *Amm. essendiensis*, refigured by Wright and Kennedy (1987, text-fig. 13 D-F), with its still inner whorl (Schlüter 1871, pl. 1, fig. 7), shows gently flexuous ribs with some ventrolateral projection. Its ribs are very fine but appear to be numerous. The number of its umbilical bullae and that of ventrolateral clavi are respectively quite similar to that in our specimen (see Figure 2). This suggests strongly that the difference in ornamentation noted above between our specimen and representative ones of *A. renevieri* is

very probably within the extent of variation.

Incidentally, the above mentioned Schlüter's specimen, which is still septate, has so fine and faint ornament that it looks somewhat similar to our second specimen of bodychamber.

To sum up, the two specimens from Ikushunbetsu are regarded as examples of *Acompsoceras renevieri* (Sharpe, 1857) from Japan.

Genus *Utaturiceras* Wright, 1957

Type species.—*Ammonites vicinalis* Stoliczka, 1864 by original designation.

Remarks.—See Matsumoto *et al.*, 1966, p. 306–307 for the diagnosis and affinities of this genus.
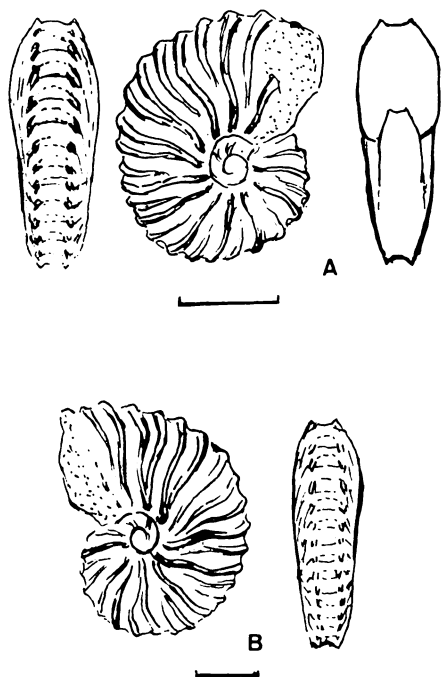
Figure 5. *Utaturiceras vicinale* (Stoliczka). Diagrammatic sketches of two juveniles, A : TTC. 020415-2 (with scale bar = 10 mm) and B : TTC. 020415-3 (with scale bar = 5 mm).   T.M. delin.

Utaturiceras vicinale
(Stoliczka, 1864)

Figure 5A, B ; Figure 7C, D

Ammonites vicinalis Stoliczka, 1864, p. 84, pl. 44, figs. 1, 4, 5, 7, 8.
Utaturiceras vicinale (Stoliczka) ; Matsumoto *et al.*, 1966, p. 297, pl. 32, fig. 1 ; pl. 33, figs. 1–3 ; textfigs. 1–4.

Material.—Two small specimens collected by T. Takahashi from loc. Ik 7003 : TTC. 020415-2 (Fig. 5A ; Fig. 7C) and TTC. 020415-3 (Fig. 5B ; Fig. 7D).

Description.—The above two specimens are involute, with a narrow umbilicus, which is less than 20 percent of diameter, and have a compressed whorl, with a narrow venter demarcated by trains of outer ventrolateral tubercles, sloping facets on outer portion of flanks, and nearly flat and parallel main parts of flanks, which can incline more or less distinctly toward the umbilical edge in youth.

The ornament is characterized by fairly crowded, more or less flexuous ribs some of which arise in pairs from feeble umbilical bullae and others which are intercalated. The inner ventrolateral tubercles are weak and can show merely as accents where ribs are bent forward toward more distinct outer ventrolateral tubercles.

The ribs are asymmetric in cross-section with adorally gentle and adapically steep slopes. This may give apparently low and broad ribs or rather sharp ones, depending on lighting orientation or angle of view. Likewise the venter varies in appearance. Generally the ribs cross the venter between the outer ventrolateral clavi, but they are lower than the flank ribs. When the sharply clavate tubercles are exaggerated by certain lighting, the venter looks almost smooth. The ribs on the venter are lowered and broadened, with adorally forward curve on the extension of a clear projection on the ventrolateral facet, but they run straight across the venter on their adapical side. The adoral outline of the ribs on the venter sometimes form an obtuse chev-

ron.

Sutures are discernible on the early part of the preserved outer whorl of the larger specimen at H = 6 mm or so. Their pattern is essentially similar to the one illustrated by Kossmat (1895, pl. 25, fig. 2) but less intricate because of immaturity.

Dimensions.—Our two specimens and a paralectotype (GSI. 187) are measured (in mm) as follows:

Specimen	D	U	H	B	B/H	Ribs (180°)
Fig. 5A	25.0	4.5 (.18)	12.3 (.49)	9.4 (.38)	0.76	5/16
Fig. 5B	18.0	2.6 (.16)	9.7 (.54)	6.5 (.36)	0.68	9/18
GSI. 187	31.8	6.5 (.20)	15.2 (.48)	11.0 (.35)	0.72	8/17

Ribs (180°): Number of long or primary ribs/that of all the ribs in a half whorl.

Comparison and discussion.—One of our two specimens (Fig. 5A) closely resembles a paralectotype (GSI. 187) of *Utaturiceras vicinale* (Stoliczka) (1864, pl. 44. fig. 5), which one of us studied at the Geological Survey of India (GSI), Calcutta (see also Matsumoto *et al.*, 1966, pl. 33, fig. 2; text-fig. 3). In the lectotype (Stoliczka, 1864, pl. 44, fig. 8; Matsumoto *et al.*, 1966, pl. 32, fig. 1), which represents a late growth stage, but preserves only a portion of the body chamber, many of the ribs are less flexuous and the umbilical bullae tend to weaken or become obsolete. In its observable earlier part and also in GSI. 189 of moderate size (Stoliczka, 1864, pl. 44, fig. 7; Matsumoto *et al.*, 1966, pl. 33, fig. 3) the flanks are subparallel, some ribs are fairly flexuous and often paired ribs arise from the umbilical bullae. The smaller specimens mentioned above are thus reasonably regarded as juveniles of *Utaturiceras vicinale*.

Incidentally the venter of the body-chamber in the lectotype is crossed by the ribs which form on their adoral side obtuse chevrons along with obliquely disposed outer ventrolateral tubercles.

The character mentioned above and also that of the immature specimens give us some doubt about the generic distinction between

Utaturiceras Wright, 1956 and *Mrhiliceras* Kennedy and Wright, 1985. This question, however, will remain unsettled until we examine the type species of the latter, i.e. *Mammites lapparenti* Pervinquière, 1907, which is now defined very broadly to include inflated forms with rectiradiate coarse ribs and compressed ones with flexuous fine ribs (Kennedy and Wright, 1985).

Occurrence.—Our immature specimens were yielded from a calcareous nodule in the same bed which contained *Acompsoceras renevieri*. Fragmentary pieces of *Turrilites costatus* were obtained from the same nodule. The bed is allocated to the upper horizon of the lower Cenomanian in our section.

The localities of *Ammonites vicinalis* were recorded as north and west of Odium, Utatoor [Ootatoor] Group of South India (Stoliczka, 1864, p. 85), but their precise stratigraphic position has yet to be worked out.

Genus *Mantelliceras* Hyatt, 1903

Type species.—*Ammonites mantelli* J. Sowerby, 1814 by original designation (Hyatt, 1903, p. 111).

Remarks.—See Wright and Kennedy, 1984, p. 97–99 for the diagnosis, affinities and distribution.

Mantelliceras aff. *japonicum* Matsumoto, Muramoto and Takahashi

Figure 6; Figure 7A, B

Compare.—

Mantelliceras japonicum Matsumoto, Muramoto and Takahashi, 1969, p. 253, pl. 25, figs. 1–2; pl. 26, figs. 1–3; pl. 27, figs. 1–2; text-figs. 1–2.

Material.—TTC. 030512-2 (Fig. 6; Fig. 7A) obtained by T. Takahashi from loc. Ik 7003. TTC. 030512-3 (Fig. 7B), a fragment, may be another example.

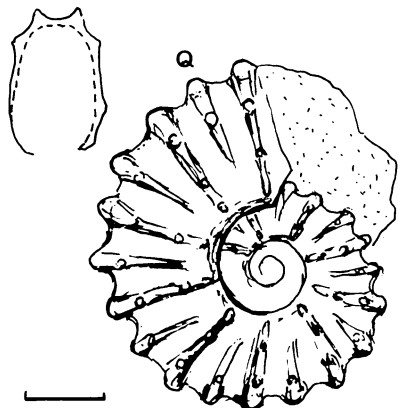*Dimensions.*—This specimen is rather small and measures as follows:

Figure 6. *Mantelliceras* aff. *japonicum* Matsumoto, Muramoto & Takahashi. Diagrammatic sketch of TTC. 030512-2. Left lateral view and whorl section at Q. Scale bar = 10 mm. T.M. delin.

	D	U	H	B	B/H	Ribs (180°)
(c)	43.0 (1)	12.6 (.29)	18.2 (.42)	13.5 (.31)	0.74	6/11
(ic)	40.0 (1)	12.0 (.30)	16.2 (.40)	12.3 (.31)	0.76	6/11

Descriptive remarks.—The whorl is compressed, with B/H smaller than that of any measured specimen of *M. japonicum*, and suboval in intercostal section, with flanks gradually inclined to the umbilical wall without forming an abruptly bent umbilical edge.

Although the shell is partly broken, the observable main whorl is ornamented with alternately long and short, fairly strong ribs, all of which are provided with inner ventrolateral nodes of moderate intensity and prominent outer ventrolateral clavate tubercles. The tubercles on the long ribs are doubled around the umbilicus, those on the inner flank being somewhat stronger than those at the umbilical end. The above characters of the ornamentation are essentially similar to those of *M. japonicum*, in which sometimes a long rib on one side extends to a short one on the other side (see Matsumoto *et al.*, 1969, text-fig. 1). The same feature is exhibited in the specimen from loc. Ik 7003

(Fig. 6).

There are, however, unnegligible differences in ornamentation between this specimen and young shells of *M. japonicum* of corresponding size. The ribs of the former are narrow, more sharp-headed and separated by wider interspaces than those of the latter. The ribs are somewhat prorsiradiate in the former, whereas they are rather rectiradiate in the latter. As to the double tubercles on the long ribs those at the umbilical end tend to weaken and disappear in the latter but persist distinctly in the former, although how the ornamentation would change on the presumably lost still later part of the former is not known.

As only a single incomplete specimen is available, whether the above differences in shell form and ornamentation deserve specific or subspecific distinction or otherwise is hardly decided. It is hence tentatively called *Mantelliceras* aff. *japonicum*.

Occurrence.—Rare in the bed with *Acompsoceras renevieri* at loc. Ik 7003, which is regarded as the next higher horizon than the extension of the bed with *Mantelliceras japonicum* in the main section along the River Ikushunbetsu.

Mantelliceras saxbii (Sharpe, 1857)

Figure 7E

Ammonites saxbii Sharpe, 1857, p. 45, pl. 20, fig. 3.
Mantelliceras saxbii (Sharpe); Wright and Kennedy, 1984, p. 121; pl. 23, fig. 4; pl. 32, figs. 1–3; pl. 33, figs. 1–4; pl. 34, figs. 1–4; pl. 35, figs. 1–5; pl. 36, figs. 2, 3; pl. 39, fig. 1; text-figs. 25B-D, I; 26B; 28L-P (with full synonymy).

Material.—A single well preserved specimen, TTC. 030502-1 (Fig. 7E), collected by T. Takahashi and T. Matsumoto from loc. Ik 7001.

Dimensions.—The specimen measures:
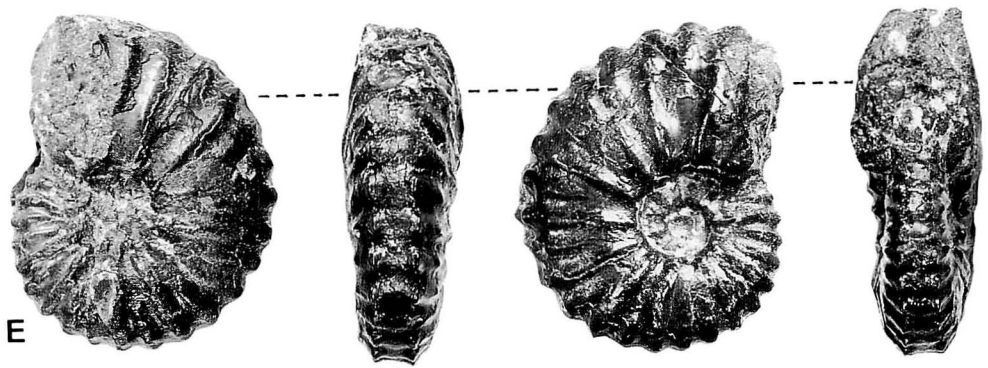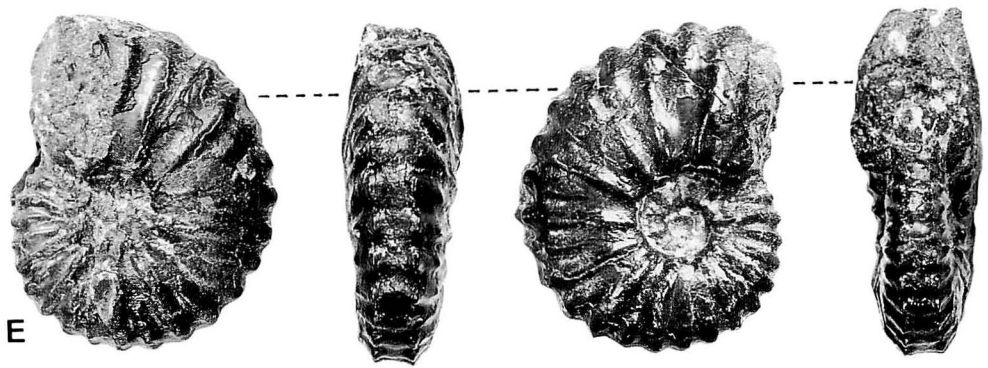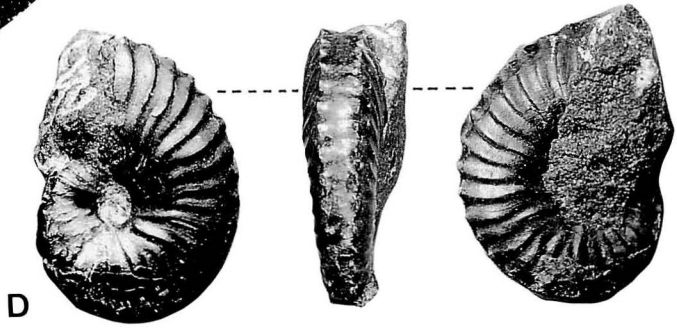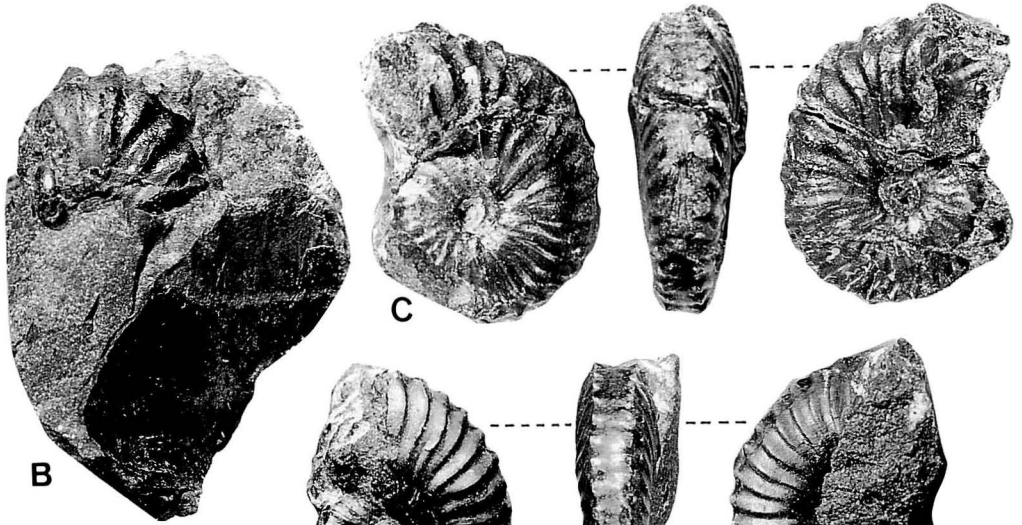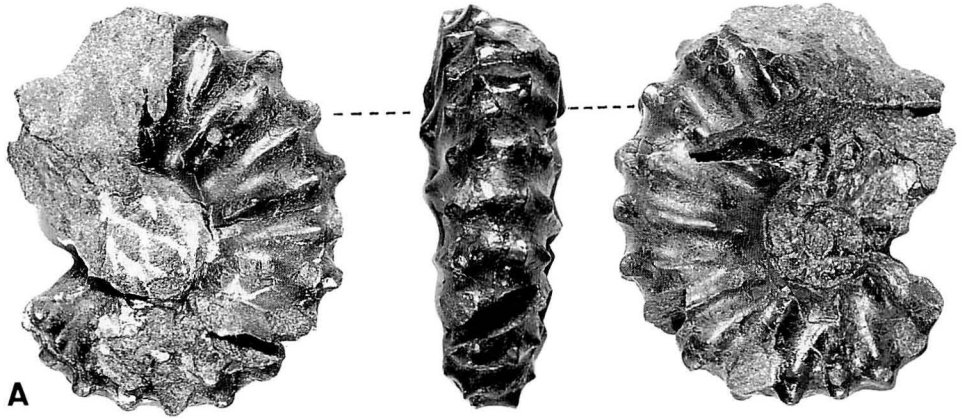
	D	U	H	B	B/H	Ribs (180°)
At L (c)	34.0	8.7 (.26)	15.6 (.46)	12.4 (.36)	0.79	7/14
Behind Ls (ic)	32.0	8.2 (.26)	15.2 (.47)	11.5 (.37)	0.76	7/14

It preserves the beginning of the body-chamber at its adoral end.

Descriptive remarks.—This specimen shows a moderately involute form, with fairly narrow umbilicus. Its whorl is higher than broad and subtrapezoid in costal section, with slightly convex flanks.

Ribs are of moderate intensity and density, normally alternately long and short, gently flexuous and prorsiradiate, with some projection on the ventrolateral part; nearly straight ribs occur occasionally. All the ribs have weak inner and moderately strong clavate outer ventrolateral tubercles and run across the venter, lowering and broadening. Longer ribs have bullate tubercles at the umbilical edge and faint but often perceptible small nodes on the inner flank or slightly below the mid-flank, where ribs are weakly flexed.

Based on the above characters this specimen is certainly identified with *Mantelliceras saxbii* (Sharpe), recently redefined by Wright & Kennedy (1984). It is in particular similar to the young to middle-aged part of an illustrated specimen (*op. cit.*, pl. 35, fig. 4) from the Lower Chalk of southern England. It may represent a phragmocone of a microconch but could be a juvenile macroconch.

Occurrence.—This specimen occurred rarely in the Basal Member (Sandy siltstone) of the Mikasa Formation at loc. Ik 7001, low in the lower Cenomanian.

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← **Figure 7.** A, B: *Mantelliceras* aff. *japonicum* Matsumoto, Muramoto & Takahashi, TTC. 030512-2 (A) and TTC. 030512-3 (B), both × 1.2. C, D: *Utaturiceras vicinale* (Stoliczka), juveniles, TTC. 020415-2 (C), ×1.5 and TTC. 020415-3 (D), ×2. E: *Mantelliceras saxbii* (Sharpe), TTC. 030502, ×1.2.

Photos by M. Noda.

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Fukuoka 福岡, Hanazono-cho 花園町, Hokkaido 北海道, Ikushunbetsu [=Ikushumbets] 幾春別, Katsura-Ohashi 桂大橋, Katsura-zawa 桂沢, Mikasa 三笠, Oita 大分, Suido-no-sawa 水道の沢, Torii-zawa 鳥居沢, Tsukuba つくば, Yayoi 弥生, Yu-no-sawa 湯の沢.

北海道幾春別川流域産の *Acompsoceras* その他のアカントケラス科菊石類：この地域の三笠層模式断面のある本流から遠くない谷の斜面に，従来未検討だった露頭（連続する3地点）があり，そこの砂質シルト岩～砂岩から，北海道としては初めての菊石類 (1) *Acompsoceras renevieri* (Sharpe), (2) *Utaturiceras vicinale* (Stokiczka), (3) *Mantelliceras* aff. *japonicum* Matsumoto, Muramoto and Takahashi（典型的なものより幅が狭い），(4) *Mantelliceras saxbii* (Sharpe) を得たので記載した。露頭は下から A, B, C の3層序区分を代表するが，すべて下部セノマニアンである。A は *Desmoceras kossmati* 帯で (4) を産した。B は *M. japonicum* 帯に相当するが，貝殻層を幾枚か含む沿岸浅海相で，菊石類は断片が散在する。C は本流沿いの三角貝砂岩の延長に当るが，(1)-(3) のほか若干の菊石が得られた。局部的ではあるが，*M. japonicum* 帯の上位の亜帯を代表する。

<div align="right">松本達郎・高橋武美</div>

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939. A RECORD OF *PSEUDOPHYLLITES INDRA* (LYTOCERATINA, TETRAGONITIDAE) FROM THE UPPER CRETACEOUS OF HOKKAIDO AND SAKHALIN*

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Abstract. A tetragonitid ammonite, *Pseudophyllites indra* (Forbes) is described based on material from the Orannai Formation in the Soya area of northern Hokkaido and from the Krasnoyarka Formation in the Naiba area of south Sakhalin. *P. indra*, occurring in the *Schlueterella kawadai* Subzone of the *Metaplacenticeras subtilistriatum* Zone, which corresponds to the upper Campanian, has a nearly circular initial chamber in median section, a subellipsoid caecum with weakly constricted base and a ventrally located siphuncle. In various areas of the North Pacific region, the present species first appeared almost synchronously in the upper Campanian. From Santonian to early Campanian times, *P. indra* was distributed in the Indian region. This evidence shows that this species extended its geographical distribution from the Indian region to the North Pacific region in late Campanian time.

Key words. *Pseudophyllites*, upper Campanian, Soya, Naiba, ontogeny, paleobiogeography.

Introduction

The genus *Pseudophyllites* Kossmat, 1895 of the family Tetragonitidae is considered to be one of the offshoots from *Tetragonites* (Kennedy and Klinger, 1977). Species of *Pseudophyllites* are known to occur from the Santonian to Maastrichtian worldwide (Collignon, 1956). In Hokkaido several fragmentary specimens of *Pseudophyllites* were described as *P. indra* (Forbes, 1846) and *P.* cf. *teres* (Van Hoepen, 1920) by Matsumoto and Miyauchi (1984) from the upper Campanian of the Soya area, but further work based on more sufficient material is required to discuss the taxonomy, biostratigraphy and paleobiogeography of this genus.

Recently, I have discovered many well preserved specimens referable to *P. indra*

from the upper Campanian of the Soya area of Hokkaido and from the Naiba (=Naibuti) area of Sakhalin, as described below.

Paleontological description

Order Ammonoidea Zittel, 1884
Suborder Lytoceratina Hyatt, 1889
Superfamily Tetragonitaceae Hyatt, 1900
Family Tetragonitidae Hyatt, 1900
Genus *Pseudophyllites* Kossmat, 1895

Type species.—Ammonites indra Forbes, 1846 by original designation.

*Diagnosis.—*Very involute tetragonitids with a high whorl expansion rate and a small umbilicus. Early whorls rounded in cross section, later whorls becoming elliptical, with a convex venter, somewhat flattened flanks and a steeply sloping umbilical wall. Shell surface ornamented by fine striae, inflected

foward and passing radially across venter. Constriction absent. Suture very finely divided with asymmetrically trifid or asymmetrically bifid major saddles having subphylloid terminations.

Pseudophyllites indra (Forbes, 1846)

Figures 1-4

Ammonites indra Forbes, 1846, p. 105, pl. 11, fig. 7; Stoliczka, 1865, p. 112, pl. 58, fig. 2; Whiteaves, 1879, p. 105, pl. 13, fig. 2.
Pseudophyllites indra (Forbes); Kossmat, 1895, p. 137, pl. 16, figs. 6–9, pl. 17, figs. 6–7, pl. 18, fig. 3; Whiteaves, 1903, p. 331; Woods, 1906, p. 334, pl. 41, fig. 6; Spath, 1922, p. 119; Collignon, 1938, p. 24, text-fig. E; Usher, 1952, p. 57, pl. 3, figs. 2–13; pl. 31, figs. 15–17; Collignon, 1956, p. 90; Matsumoto, 1959, p. 134, Jones, 1963, p. 25, pl. 7, figs. 6–7, pl. 8, pl. 29, figs. 7–12, text-fig. 10; Collignon, 1969, p. 12, pl. 516, fig. 2032; Kennedy and Klinger, 1977, p. 182, text-figs. 19–22; Matsumoto and Miyauchi, 1984, p. 54, pl. 21, fig. 5; Henderson and McNamara 1985, p. 50, pl. 2, figs. 7, 8, pl. 3, figs. 4, 5, text-fig. 5a, d.
Tetragonites glabrus (Jimbo); Shigeta, 1989, p. 334, text-fig. 12(3).

Type.—The holotype is the specimen originally figured by Forbes (1846, pl. 11, fig. 7), BMNH C51068, from the Valudayur Group near Pondicherry, southern India.

Material.—In addition to the specimen (MNH. 231) described by Matsumoto and Miyauchi (1984, pl. 21, fig. 5) from the Soya Harbor, 14 specimens collected from the upper part of the Orannai Formation in the Soya area of northern Hokkaido and three specimens from the middle part of the Krasnoyarka Formation in the Naiba area of south Sakhalin are used in the following description: UMUT MM18991–18997 from fishery harbor of Soya (upper Campanian); UMUT MM18998 from fishery harbor of Kiyohama-I (upper Campanian); UMUT MM18999–19002 from new fishery harbor of Kiyohama-II (upper Campamian); UMUT MM19003 and MM19004 from old fishery harbor of Kiyohama-II (upper Campanian); UMUT MM19005 from locality NB3031 (=

N100 of Matsumoto's locality, upper Campanian); UMUT MM19006 and MM19007 from the middle course of the Krasnoyarka River (NB3023P) (upper Campanian). All the specimens from the Soya area and two specimens from the Naiba area were obtained from floated calcareous nodules. For details of their localities and ages see Matsumoto and Miyauchi (1984) and Matsumoto (1942).

All the specimens utilized herein are deposited at the University Museum, University of Tokyo (UMUT). The specimen (MNH. 231) described by Matsumoto and Miyauchi (1984) is now kept at UMUT (UMUT MM19008) by courtesy of Mr. T. Miyauchi.

Dimensions.—

	Shell diameter (D) (mm)	Breadth of umbilicus (U) (mm)	Whorl height (H) (mm)	Whorl breadth (B) (mm)	U/D	B/H
MNH. 231 (MM19008)	110.0	18.0	61.0	50.0	0.16	0.82
MM18991	185.0	30.0	100.0	75.0	0.16	0.75
MM18998	40.6	9.0	19.7	19.8	0.22	1.01
MM18999	33.0	7.5	14.7	15.7	0.23	1.07
MM18994	28.4	6.3	14.3	14.5	0.22	1.01
MM18995	23.8	5.7	11.7	12.0	0.23	1.03
MM19003	21.3	5.2	9.8	10.0	0.24	1.02
MM19001	17.2	4.4	8.1	8.5	0.25	1.05

Description.—
Early internal shell structure (Figure 1)
The initial chamber is nearly circular in median section. The caecum is subelliptical in lateral view with a weakly constricted base, and its adapical end connects with the initial chamber wall by a short, adorally concave prosiphon. The siphuncle occupies a central position near the proseptum and then immediately shifts toward the venter within the second chamber. Thereafter it keeps a ventral position. Initial chamber size, ammonitella size and its spiral length in the specimen UMUT MM18996 in median section are 712 μm, 1,550 μm, and 336° respectively.
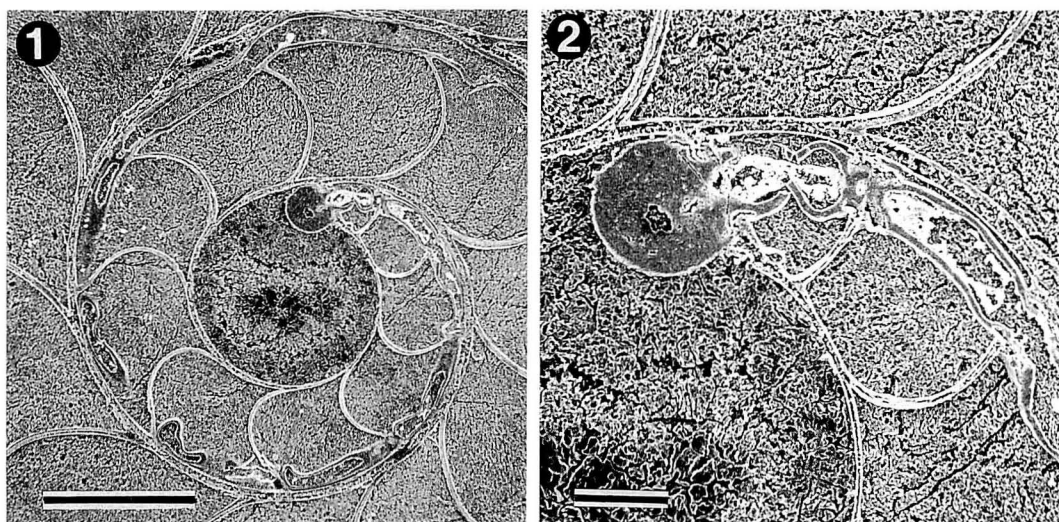
Figure 1. Scanning electron micrographs of the early internal shell structure of *Pseudophyllites indra* (Forbes) in median section. Scale bar in 1, 500 μm. Scale bar in 2, 100 μm. UMUT MM18996, the upper Campanian, fishery harbor of Soya.
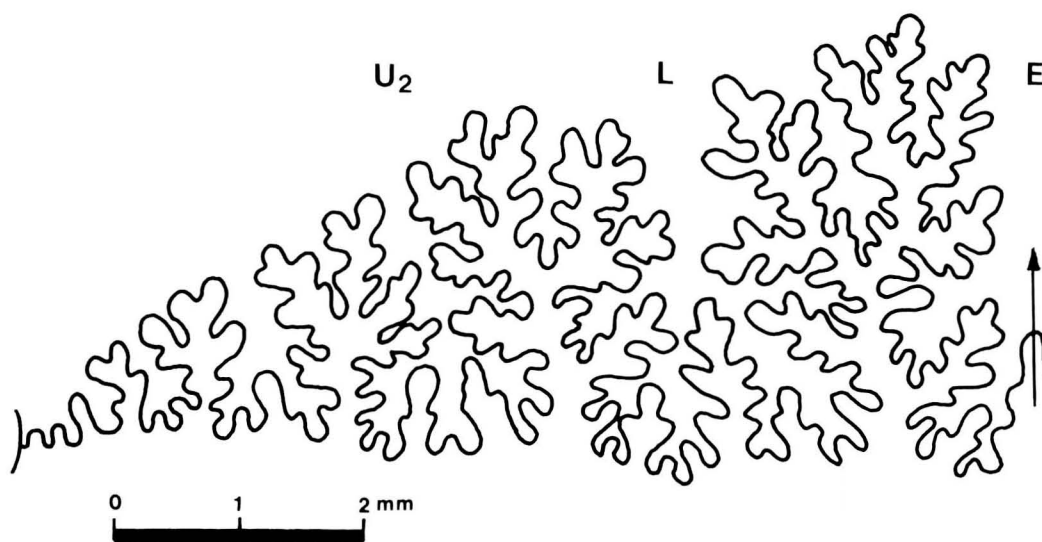

Figure 2. External suture at a whorl height of 6.2 mm of *Pseudophyllites indra* (Forbes). UMUT MM18994, the upper Campanian, fishery harbor of Soya.

Early to middle whorls (10–60 mm in diameter) (Figures 2 and 3)

The shell is very involute, rapidly expanding, with a depressed whorl section. The umbilicus is narrow and deep, with an abruptly rounded shoulder. The shell surface is ornamented by fine striae which arise across the umbilical seam, sweep slightly backwards across the umbilical wall, flex backwards over the shoulder, and pass across the flanks in a prorsiradiate direction. The striae sweep backwards across the ventrolater-

1a   1b   2a   2b   3a   3b

4a   4b   5

6a   6b
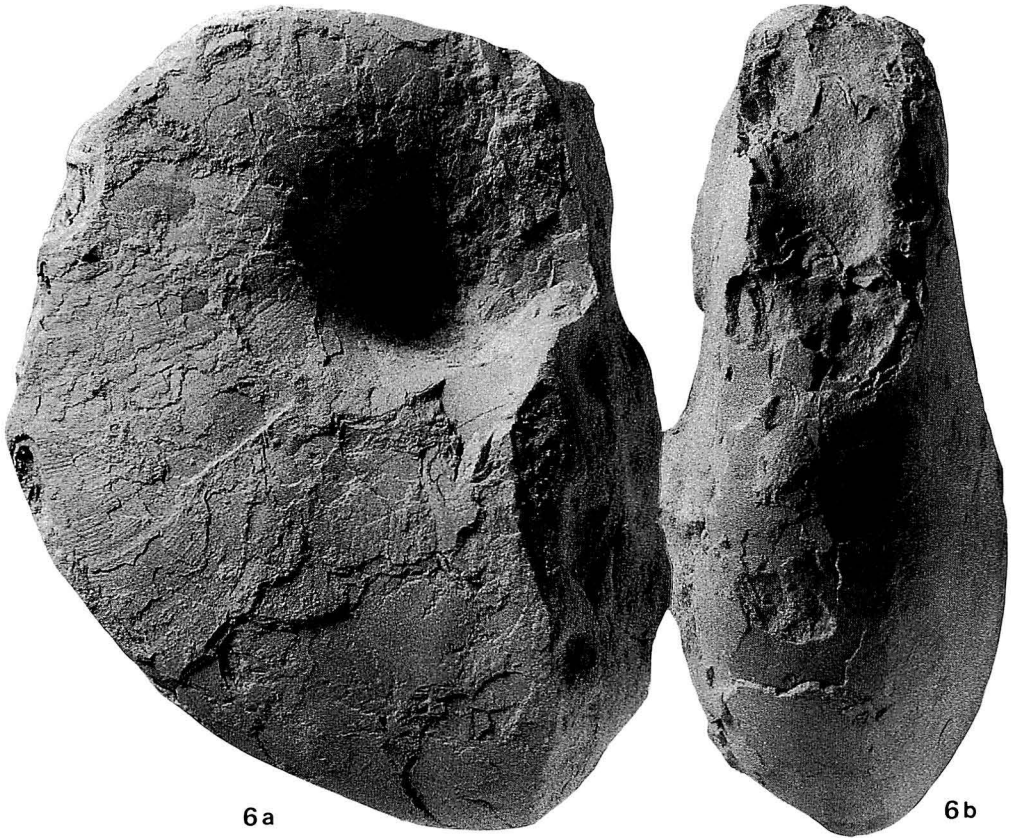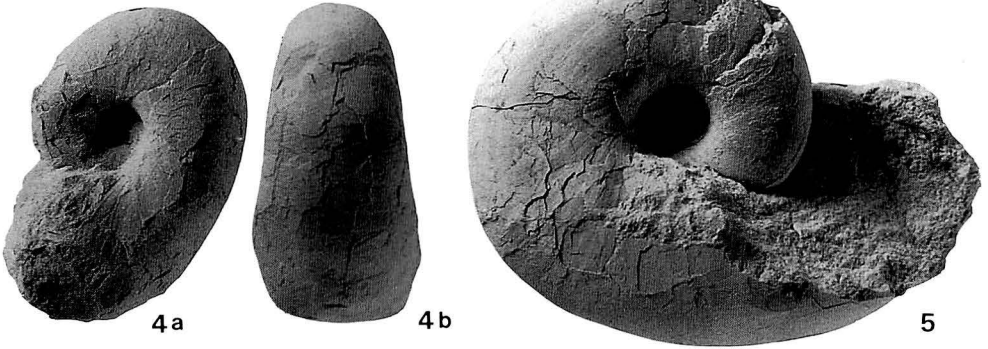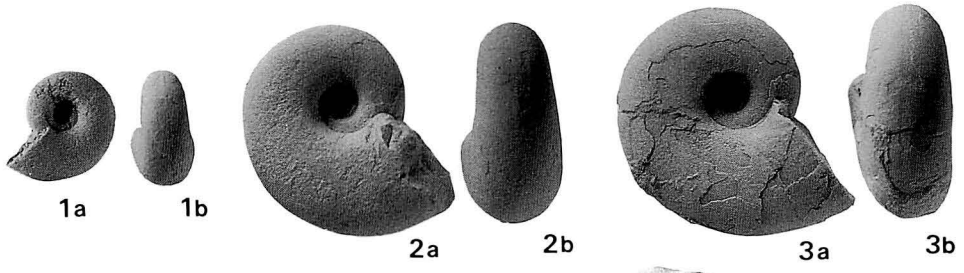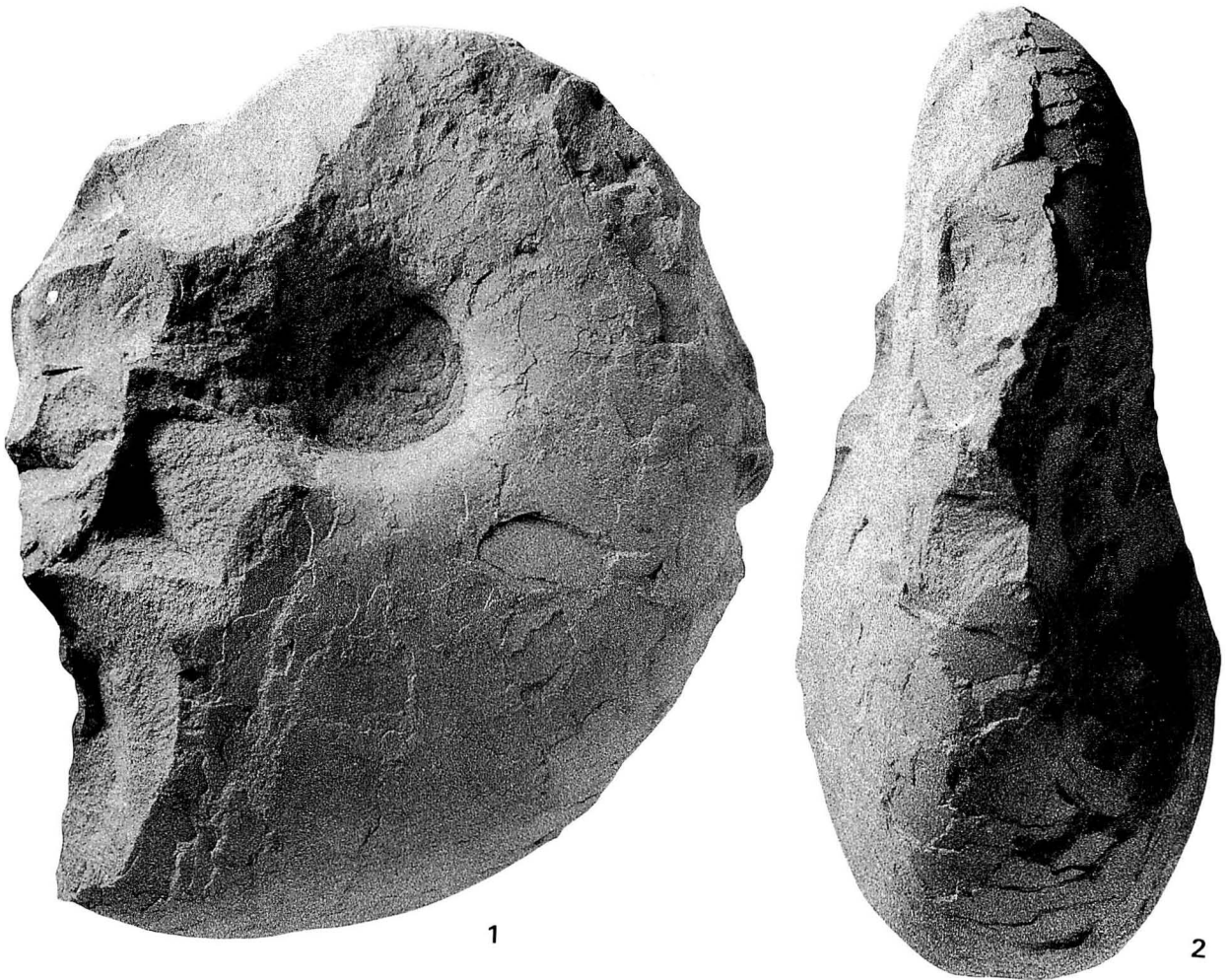
Figure 4. *Pseudophyllites indra* (Forbes), ×0.7. UMUT MM18991, the upper Campanian, fishery harbor of Soya. 1 : lateral view, 2 : ventral view.

al shoulder and cross the venter with a broad, faint, concave ventral sinus.

The suture (Figure 2) is highly subdivided, with a large irregularly trifid first lateral saddle (E/L), a smaller bifid second lateral saddle (L/U₂), a deeply incised bifid lateral lobe (L), and a suspensive lobe with a large bifid first auxiliary saddle.

Later whorls (over 60 mm in diameter) (Figure 4)

The largest specimen in the present material, 185 mm in diameter, lacks a majority (5/6) of the body chamber. The shell is very involute, with compressed whorls and a high

← **Figure 3.** *Pseudophyllites indra* (Forbes), ×1.0. 1a-b. UMUT MM19001, the upper Campanian, new fishery harbor of Kiyohama-II. 2a-b. UMUT MM18994, the upper Campanian, fishery harbor of Soya. 3a-b. UMUT MM18995, the upper Campanian, fishery harbor of Soya. 4a-b. UMUT MM19007, the upper Campanian, the middle course of the Krasnoyarka River, Naiba area. 5. UMUT MM19005, the upper Campanian, NB3031 (N100), Naiba area. 6a-b. UMUT MM19008 (MNH. 231), the upper Campanian, fishery harbor of Soya.

whorl expansion rate. The umbilicus is small and deep, with a sloping wall and abruptly rounded shoulder. It is ornamented by fine and dense striae which show a gently backward curve on the ventrolateral part.

The suture is poorly visible, but consists of numerous deeply incised elements, with subphylloid terminals of folioles.

Comparison.—In the juvenile stage *P. indra* most closely resembles *Tetragonites glabrus,* a Turonian to lower Campanian species known from Hokkaido, Sakhalin, Alaska, California and South Africa in having a subellipsoid caecum with weakly constricted base, ventrally located siphuncle, a high whorl expansion rate and a small umbilicus, but is distinguished from *T. glabrus* in having a rounded umbilical shoulder and weakly adorally concave sinuous aperture on venter. The specimens illustrated as *T. glabrus* by Shigeta (1989, UMUT MM18636-16, 29, 35, 37, 47, 51, 58) from the upper Campanian of the Soya area are regarded as a juvenile specimen of *P. indra.*

Occurrence.—*P. indra* is a cosmopolitan species known from the upper Santonian to lower Maastrichtian in South Africa, southern India and western Australia, and from the upper Campanian to lower Maastrichtian in southern Alaska and Vancouver Island. In Hokkaido and Sakhalin, this species occurs in the *Schlueterella kawadai* Subzone of the *Metaplacenticeras subtilistriatum* Zone, which is equivalent to the upper Campanian.

Stratigraphical significance of the occurrence

P. indra occurs in the *Metaplacenticeras pacificum* Zone and the *Pachydiscus suciaensis* Zone in British Columbia (Usher, 1952), in the *M. pacificum* Zone in California (Matsumoto, 1960), in the *Pachydiscus kamishakensis* Zone in Alaska (Jones, 1963), and the *M. subtilistriatum* Zone in Hokkaido and Sakhalin (Matsumoto, 1984; this study).

According to the zonal correlation of megafossils in the Northern Pacific region, this species is restricted to an interval from the upper Campanian to the lowest Maastrichtian (Muller and Jeletzky, 1970; Ward, 1978; Matsumoto, 1984). The upper limit of the occurrence of this species in Hokkaido and Sakhalin has not yet been sufficiently elucidated because in many areas megafossils are rather rare in the uppermost Campanian to the lowest Maastrichtian. However, the first appearance of this species in Hokkaido and Sakhalin is nearly synchronous with that in the Pacific coast of North America.

From Santonian to early Campanian times, *P. indra* was distributed in the Indian region (South Africa, Madagascar, and southern India) (Kossmat, 1895; Kennedy and Klinger, 1977). This evidence shows that this species extended its geographical distribution from the Indian region to the North Pacific region in late Campanian time.

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Hokkaido 北海道, Kiyohama 清浜, Naibuti 内淵, Soya 宗谷.

北海道及びサハリンの上部白亜系産テトラゴニテス科アンモナイト *Pseudophyllites indra* について：北海道・宗谷地域のオランナイ層及びサハリン・ナイバ地域のクラスノヤルカ層より産出した *Pseudophyllites indra* について，初期殻体内部構造および殻形の個体発生を記載した。標本はカンパニアン階上部の *Metaplacenticeras subtilistriatum* 帯の *Schlueterella kawadai* 亜帯からのみ産出したが，両地域での本種の産出時期は他の北太平洋地域での初産出時期とほぼ一致する。本種はサントニアン後期からカンパニアン前期には南アフリカや南インドに分布していたことから，カンパニアン後期に北平洋地域へ分布域を拡大したものと考えられる。　　　　　　　　　　重田康成

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