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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Papyridea harrimani Dall, 1904 (Bivalvia, Cardiidae) as a marker for upper Eocene and lower Oligocene strata of the North Pacific

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Abstract. Statistical analysis indicates that *Papyridea (Fulvia) nipponica* Yokoyama, 1924, *Papyridea matschigarica* Khomenko, 1938, and *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987, are synonyms of *Papyridea harrimani* Dall, 1904, which was originally described from the lower Oligocene Stepovak Formation in Popof Island, Shumagin Islands, southwestern Alaska. *Papyridea harrimani* occurs only in late Eocene and early Oligocene faunas and is useful for correlating strata from northern Honshu to Alaska: Stepovak Formation, southwestern Alaska; Mallenskaya and Ionayskaya Suites, Koryak Upland; Aluginskaya Suite and lower part of the Pakhachinskaya Suite, eastern Kamchatka; Amaninskaya, Utkholokskaya and Vivotekskaya Suites of western Kamchatka; Machigarskaya, Arakayskaya, Gastellovskaya and Akhsnayskaya Suites, Sakhalin; Nuibetsu, Charo and lower Sankebetsu Formations, Hokkaido; Asagai Formation, Honshu. In views of the stratigraphic ranges of *Papyridea harrimani* and other molluscs, strata 3 and 4 of the Pakhachinskaya Suite in eastern Kamchatka may be assigned an age of early Oligocene.

Key words: biostratigraphy, Bivalvia, Cardiidae, Cenozoic, North Pacific, Paleogene, *Papyridea*

Introduction

Marine bivalve molluscs occupy a central position in the Cenozoic stratigraphic framework of the tectonically active North Pacific region from northern Japan to Alaska. Progress in refining this framework has sometimes been inhibited by differing species concepts among Russian, American and Japanese paleontologists. One of the most widespread and biostratigraphically useful bivalve families in this extensive region is the Cardiidae. Kafanov (1997) emphasized the widespread occurrence of a high-latitude North Pacific group of relatively large cardiid species centered around *Papyridea harrimani* Dall, 1904 and *P. matschigarica* Khomenko, 1938. The genus *Profulvia* established by Kafanov (1976) for North Pacific *Papyridea* is considered to be a subgenus of the latter (Kafanov, 1997).

Here we analyze the taxonomic relations between these species and with *Papyridea (Fulvia) nipponica* Yokoyama, 1924, and emphasize the usefulness of this group for broad-scale age control and regional correlations.

Materials and methods

Some of the specimens of *P. matschigarica* examined in this study were collected from the Machigar section in the Schmidt Peninsula, northern Sakhalin, by Y.B. Gladenkov in 1969 and 1979, and by K.B. Barinov in 1996 (Figure 1). The description of the Machigar section we use here is based on a stratigraphic study of the lower part of the Machigarskaya Suite by Y.B. Gladenkov (Barinov and Gladenkov, 1998). We also examined specimens of *Papyridea* in collections of the Central Scientific-Research Geological-Exploration Museum (CNIGRM), St. Petersburg, the All-Russia (formerly All-Union) Petroleum Scientific-Research Geological-Exploration Institute (VNIGRI), St. Petersburg, the Geological (GIN) and Paleontological (PIN) Institutes, Russian Academy of Sciences, Moscow, the University of California Museum of Paleontology, Berkeley, and the California Academy of Sciences, San Francisco, U.S.A.

We have quantitatively defined the main shell characters of *P. matschigarica* by studying numerous topotype specimens, and used statistical analysis to determine the morphological relationships among *P. matschigarica*, *P. mats-*

Sys-tem	Sui-te	Column	Th. (m)	Assemblage	Dominant species	Associated species	
MIOCENE	Lower	TUMSKAYA	170	<i>Macoma-Lucinoma</i>	<i>Macoma simizuensis</i> <i>Lucinoma acutilineata</i>	<i>Chlamys donmilleri</i> * <i>Chl. wajampolkensis</i> * <i>Mytilus ochotensis</i> *	
				OLIGOCENE	TUMSKAYA	320-340	<i>Nuculana Delectopecten</i>
MATCHIGARSKAYA	175	<i>Periploma</i>	<i>Periploma besshoensis</i>				<i>Acila oyamadensis</i> *
		<i>Conchocele</i>	<i>Conchocele smekhovi</i>				<i>Glycymeris nakosoensis</i>
EO.	Up.	MATCHIGARSKAYA	220	<i>Papyridea Ciliatocardium</i>	<i>Papyridea harrimani</i> * <i>Ciliatocardium matchgarensis</i>	<i>Nemocardium iwakiense</i> * <i>Trachycardium kin-simarae</i> * <i>Mya grewingki</i> *	
				35	<i>Corbicula</i>	<i>Corbicula sitakaraensis</i> *, <i>Mytilus littoralis</i> *	
CR.							

Figure 1. Machigar stratigraphic section on the Schmidt Peninsula, northern Sakhalin (type locality of *P. matschigarica*). Legend: *-index species, 1-volcanic rocks, 2-coal, 3-conglomerate, 4-sandstone, 5-siltstone, 6-tuffaceous siltstone, 7-carbonate concretions.

chigarica uspenica, *P. harrimani* and *P. nipponica*. The statistical null hypothesis was reduced to probability analysis of belonging of type-specimens of the above four species to a sampling composed by topotypes of *P. matschigarica*. For that purpose we used the procedure of multidimensional analysis of ejections by sample Mahalanobis distance D^2 (Afifi et al., 1971). The procedure is as follows. Let x_1, \dots, x_k equal a random sampling with distribution $N(\mu, \Sigma)$, and x equal a certain vector of observations with the same distribution. Then

$$D^2 = (x - X)' S^{-1} (x - X)$$

in which X and S are the sampling mean and covariance matrix, respectively. The value of $F = [(k-p)k / (k^2-1)] \cdot D^2$ has an F -distribution with p and $k-p$ degrees of freedom. The checking procedure for the availability of ejections among the observation data utilizes F -statistics in which X and S are calculated from a subset of vectors of the same sample, which has already been checked for ejections. Each of the four variables was preliminarily tested for Gaussian distribution based on χ^2 and Kolmogorov-Smirnov

criteria. All the variables proved to be normally (Gaussian) distributed and required no transformation of the initial data.

The shell characters referred to herein are: L =shell length, H =shell height, B =convexity of one valve (all dimensions in mm), R =number of radial ribs. The dimensions of the holotypes given here differ somewhat from those in the original descriptions, owing to differences in shell orientation during measurement (see Kafanov et al., 1997; Kafanov, 1998).

Results

The nominal species to be described below form a morphologically coherent group consisting of *P. harrimani*, *P. nipponica*, *P. matschigarica* and *P. matschigarica uspenica*. Each is discussed separately.

Papyridea (Profulvia) harrimani Dall, 1904

Figures 2-1, 4-6; 3-1-5

Papyridea harrimani Dall, 1904, p. 114, pl. 10, fig. 5.

Type locality.—Coastal bluffs on the north shore of Popof Island, Shumagin Islands, southwestern Alaska. Stepovak Formation, lower Oligocene.

Depository of the type material.—Holotype, U.S. Natl. Mus. no. 164867.

Comments.—This was originally described as a Miocene species by Dall (1904; see also Schuchert *et al.*, 1905), who thought that the type-locality of *P. harrimani* in Popof Island was correlative with beds in adjacent Unga Island (Figure 4), to which he erroneously assigned a Miocene age. These Unga Island strata were later determined to be largely nonmarine and to contain no molluscs (Marincovich and Wiggins, 1991). Dall's (1904) mollusc collections that are purportedly from these Unga Island strata contain an artificially mixed fauna of Miocene and Oligocene species (MacNeil *et al.*, 1961). Assignment of a Miocene, or possible Miocene age to the Unga Island strata (Dall, 1896, 1904) was repeated by later workers (Schuchert *et al.*, 1905; Burk, 1965; Detterman *et al.*, 1996). The exclusive presence of Oligocene molluscs with *P. harrimani* in the strata of Popof and Unga Islands assigned to the Stepovak Formation has been verified by one of us (Marincovich, 1988, 1989, 1990; Marincovich and McCoy, 1984) during field studies. The early Oligocene age of the Unga Island beds with *P. harrimani* was established by Marincovich and Wiggins (1991) on the basis of dinoflagellates and a potassium-argon age of 31.3 ± 0.3 Ma from biotite in a tuff bed. In the nearby Popof Island, the type-locality of *P. harrimani*, the Stepovak Formation contains the same molluscan fauna as in the Stepovak strata on Unga Island and is undoubtedly of early Oligocene age.

Distribution.—Lower Oligocene, Stepovak Formation at East Head stratigraphic section, Popof Island (type-locality), and West Head stratigraphic section, Unga Island, Shumagin Islands, southwestern Alaska (Dall, 1904; MacNeil in Burk, 1965; Marincovich, 1989). Oligocene Asagai Formation of Honshu. In Japan *P. harrimani* is reported also from the upper Eocene Sakasagawa (=lower Sankebetsu) Formation of the Haboro coal-field, Hokkaido (Noda, 1992a) and from the Paleogene Charo Formation of the Kushiro coal-field, Hokkaido (Honda, 1989). The ages of the Sakasagawa and Charo Formations are controversial. Prof. K. Ogasawara (pers. comm. to A. Kafanov, June 12, 1997) informs us that the Sakasagawa Formation is a tentative name for strata which were previously included in the Sankebetsu Formation. Noda (1992a) reported *P. harrimani* from the Sankebetsu Formation (then of presumed Miocene age), and he divided the Sankebetsu Formation of previous workers into the Sakasagawa Formation and the Sankebetsu Formation. Based on planktonic foraminifers and calcareous nannofossils, the Sakasagawa Formation is now assigned an Eocene age, even though presumed Miocene molluscs (*Anadara* and *Dosinia*) are reported in the upper part of the Sankebetsu Formation (Noda, 1992b). Honda (1989) reported an

Oligocene age for molluscs of the Charo Formation, although planktonic foraminifers (Kaiho, 1984) and calcareous nannofossils (Saito *et al.*, 1984) suggest an Eocene age.

"*Papyridea harrimani*" cited from the middle Miocene Ainonai Formation in Hokkaido (Uozumi *et al.*, 1966, p. 177, pl. 15, figs. 1, 7) cannot be reliably assigned to this species, and more closely resembles *Papyridea (Profulvia) kurodai* Sawada, 1962.

Papyridea (Profulvia) nipponica Yokoyama, 1924*Papyridea (Fulvia) nipponica* Yokoyama, 1924, p. 17, pl. 3, figs. 3, 4.

Type locality.—Tatsuta coal-field, Futaba District, Fukushima Prefecture, Honshu. Asagai Formation, Oligocene.

Depository of the type material.—Lectotype (designated as holotype by Hatai and Nisiyama, 1952, p. 105), CM 22090-University Museum, University of Tokyo, missing. It was refigured by Makiyama (1957, pl. 13, figs. 4, 4a) and by Kafanov (1997, pl. 1, fig. 7).

Distribution.—Known only from Asagai Formation of Fukushima Prefecture, Honshu (Kamada, 1962).

Comments.—This species has been synonymized with *P. harrimani* Dall, 1904 by most Japanese paleontologists (e.g. Oyama *et al.*, 1960), with the exception of Kamada (1962) and Masuda and Noda (1976).

Papyridea (Profulvia) matschigarica Khomenko, 1938

Figures 2-2, 3

Papyridea matschigarica Khomenko, 1938, p. 47, pl. 7, figs. 5-7; pl. 8, fig. 6; pl. 9, fig. 7.

Type locality.—Between Cape Marii and Monchigar Bay, Schmidt Peninsula, Okha Province, Sakhalin. Lower part of Machigarskaya Suite, upper? Eocene-lower Oligocene.

Depository of the type material.—Lectotype (designated by Slodkewitsch, 1938, p. 407), CNIGRM no. 81/5044.

Distribution.—Upper Eocene and lower Oligocene of Far-eastern Russia. Upper Eocene Takaradayskaya Suite and lower part of Machigarskaya Suite of Sakhalin. Lower Oligocene Machigarskaya, Arakayskaya, Akhsnayskaya and Gastellovskaya Suites of Sakhalin; Mallenskaya and Ionayskaya Suites of the Koryak Upland; Amaninskaya Suite of western Kamchatka.

Comments.—According to Slodkewitsch (1938, p. 408), Khomenko (1938, p. 48) noted the wide morphologic variability of this species, along with the similarity of some young individuals to *P. nipponica* and *P. harrimani*, and inferred that "... under the name of *P. nipponica* and *P. harrimani* only young specimens of *P. matschigarica* were described". This inference has yet to be substantiated, although the close relationship between these species is quite evident. *P. harrimani* Dall and *P. nipponica* Yokoyama are easily distinguishable from *P. matschigarica* by their much smaller size, more equilateral contour and smaller number of ribs. Following Slodkewitsch (1938), nearly all Russian authors have considered *P. matschigarica* to be a separate species, even though its shell shape (Figure 5) is similar to that of large *P.*



harrimani. In fact, Makiyama (1934) described Machigarian specimens under the name *P. harrimani*.

Papyridea (Profulvia) matschigarica uspenica Barinov in Gladenkov *et al.*, 1987

Figures 3-6—8

Papyridea matschigarica uspenica Barinov in Gladenkov *et al.*, 1987, p. 39, pl. 13, figs. 9, a, b, 22.

Type locality.—Ugol'naya River, coast of the Gulf of Korf, eastern Kamchatka. Aluginskaya Suite, bed 1, Oligocene.

Depository of the type material.—Holotype, PIN no. 1/1-1.

Distribution.—Oligocene to lower(?) Miocene of Kamchatka. Aluginskaya and Pakhachinskaya Suites of eastern Kamchatka.

Facies-related variability of *Papyridea matschigarica*

Table 1 and Figure 5 both support Khomenko's (1938) conclusion concerning the wide variability of *P. matschigarica* and very close morphological relationships among all considered *Papyridea* species.

The distribution of *P. matschigarica* in the Machigar section of the Schmidt Peninsula, northern Sakhalin (Figure 1) is as follows. *P. matschigarica* first appears virtually at the base of the Machigarskaya Suite in fine grey pebble conglomerates (up to 2 m in diameter) directly overlying a sand- and coal-bearing member (30-32 m thick) that contains remnants of *Mytilus littoralis* Slodkewitsch, *Corbicula sitakaraensis* Suzuki and *Cerithidea quadrimonicosta* Khomenko. At a horizon 45-50 m above the base of the section, *P. matschigarica* occurs in flat-lying strata (up to 85 m thick) of alternating conglomerate (0.5-1 m in diameter), sandstone and claystone (3-5 m thick), and in a superjacent strata (up to 80 m thick) of alternating sandstone (1.5-2 m thick) and claystone (3-14 m thick).

In the part of the Machigar stratigraphic section described above, *P. matschigarica* occurs only in beds of fine pebbly conglomerate and conglomeratic sandstone associated with the following molluscs: *Nemocardium iwakiense* (Makiyama), *Mya* cf. *grewingki* Makiyama, *Thracia schmidtii* Krishtofovich, *Pododesmus schmidtii* Krishtofovich, *Trachycardium kinsimarae* (Makiyama), *Chlamys matchgarensis* Makiyama, *Modiolus matchgarensis* (Makiyama), ? *Megacardita matschigarica* (Khomenko), *Yoldia matschigarica* Krishtofovich, *Y. caudata* Khomenko, *Ciliatocardium asagaiense* (Makiyama), *Laevicardium taracaicum* (Yokoyama), *Liocyma furtiva* (Yokoyama), *Arca sakamizuensis* Hatai and Nisiyama, *Neptunea ezoana* Takeda, and *Turritella importuna* Yokoyama. *In situ* specimens of *P. matschigarica* are mostly molds of single

valves, with some molds of paired valves, and their chaotic orientation indicates post-mortem transport. Specimens in the lowest 75 m of the Machigar section are almost identical in size and shape with the holotype of *P. harrimani* (Figure 5). Higher in the section the same *Papyridea* is abundant in fine pebbly conglomerate and conglomeratic sandstone. However, these specimens are larger in size and more distinctly convex, and they most closely resemble the holotype of *P. matschigarica*. An increase in their average shell size toward the top of the Machigar sequence seems to correlate with a gradual reduction in the proportion of coarse clastics. The type locality of *P. matschigarica* evidently lies in the upper part of the lower member of the Machigarskaya Suite (see Khomenko, 1938). In our opinion, the size and shape differences seen in *Papyridea (Profulvia)* from the upper and lower parts of the Machigar section are related to differences in ecological conditions such as substrate and depth. Conglomerates with a shallow-water molluscan fauna contains "*P. harrimani*," whereas sandstones with deeper-water molluscs contain "*P. matschigarica*" (Figure 5). The number of ribs varies widely and is highly dependent on shell preservation. Most specimens are molds that do not allow for accurate rib counts, because they often lack ribs on their anteriormost and/or posteriormost portions. It should also be noted that in many present-day *Cardiidae* (subfamily *Clinocardiinae*), a difference in the number of ribs to the extent of 10-12 is considered to be in the realm of intraspecific variation, including ontogenetic variation (e.g., Kafanov, 1981, 1998). A statistical analysis of basic shell dimensions for the type specimens of *P. matschigarica*, *P. matschigarica uspenica*, *P. nipponica* and *P. harrimani*, and in topotypes of *P. matschigarica* (Figure 5), clearly shows that they all belong to one general group (Table 2). These data suggest that *P. matschigarica*, *P. matschigarica uspenica* and *P. nipponica* are junior synonyms of *P. harrimani*. It is especially notable that the holotype of *P. harrimani* is more closely related in form to topotypes of *P. matschigarica* than the lectotype of *P. matschigarica* (Table 2).

Discussion

P. harrimani s.l. occurs in upper Eocene to lower Oligocene strata over a wide area of the high-latitude North Pacific, from southwestern Alaska to Hokkaido and northern Honshu. Based on these occurrences, correlations may be made between the following strata: Stepovak Formation, southwestern Alaska; Mallenskaya and Ionayskaya Suites, Koryak Upland; Aluginskaya Suite and lower part of the Pakhachinskaya Suite, eastern Kamchatka; Amaninskaya, Utkholokskaya and Viventekskaya Suites of western Kamchatka; Machigarskaya, Arakayskaya, Gastellovskaya and Akh-

Figure 2. 1a, b. Holotype of *Papyridea harrimani* Dall, 1904. North shore of Popof Island, southwestern Alaska; Stepovak Formation. U.S. Natl. Mus. no. 164867. 2. Lectotype of *Papyridea matschigarica* Khomenko, 1938. Between Marii Cape and Monchigar Bay, Schmidt Peninsula, Okha District, northern Sakhalin; lower part of Machigarskaya Suite. CNIGRM no. 81/5040. 3. Paralectotype of *Papyridea matschigarica* Khomenko, 1938. The same locality as on Fig. 2-2. CNIGRM no. 85/5044. 4. *P. harrimani*. Nairo River, eastern Sakhalin, analog of Machigarskaya Suite. CNIGRM no. 103/6818. 5. *P. harrimani*. The same locality as on Fig. 2-4. CNIGRM no. 104/6818. 6. *P. harrimani*. Schmidt Peninsula, northern Sakhalin, Machigarskaya Suite. PIN no. 90/3962. All figures shown natural size.



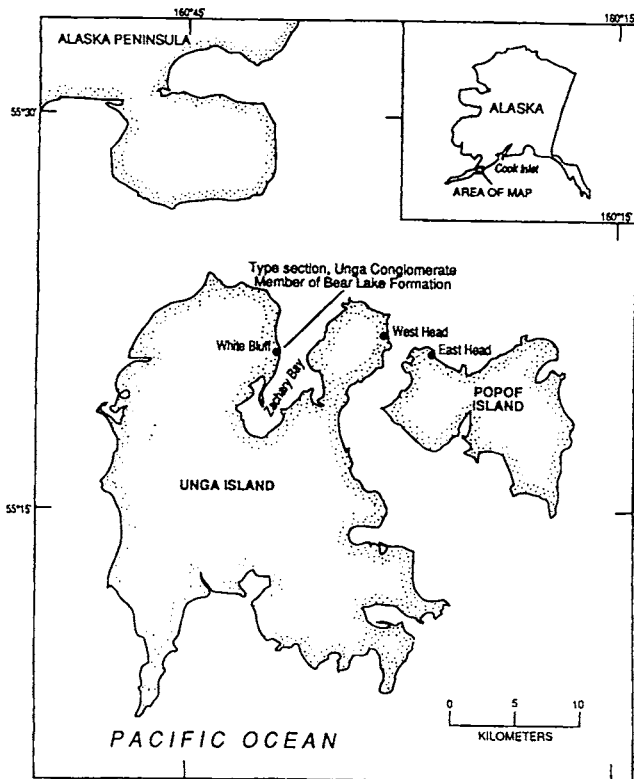


Figure 4. Index map showing the type section of Unga Conglomerate and the type locality (East Head) of *Papyridea harrimani*.

ence of *P. matschigarica uspenica* in beds 3 and 4 of the Pakhachinskaya Suite of the main Gulf of Korf section (Ugol'naya River), and in beds 5 and 6 of an additional section (Bol'shaya Medvezhka River), both of which were assigned to the early and middle Miocene by Gladenkov *et al.* (1987). However, we suggest that the stratigraphic distribution of many common bivalve species in Japan and Sakhalin argues for assigning the middle part of the Pakhachinskaya Suite in eastern Kamchatka (beds 3 and 4 along the Ugol'naya River) to the lower Oligocene. The molluscan fauna of the Pakhachinskaya Suite in this part of the Gulf of Korf section is comparable to the faunas of the Asagai Formation in the Joban coal-field, Honshu, the Utkholokian and Viventekian horizons of western Kamchatka (see also Gladenkov, 1992), and the Machigarian and Kholmskian horizons of South Sakhalin (see Kafanov and Savizky, 1995).

Thus, beds 3 and 4 of the Pakhachinskaya Suite of eastern Kamchatka characteristically contain *Ciliatocardium asagaiense* (Makiyama) and *Thracia kidoensis* Kamada, which Japanese workers (Mizuno, 1964; Honda, 1986) have described as representatives of the Asagai-Poronai fauna (Otuka, 1939). The Asagai-Poronai fauna contains planktonic foraminifers as old as Eocene (Ibaraki, 1986). The consideration of a precise Paleogene age for beds 3 and 4 of the Pakhachinskaya Suite also involves "*Cardium esutoruensis*" mentioned by Gladenkov *et al.* (1987) for bed 4 of the Pakhachinskaya Suite; this species should rather be referred to as *Laevicardium tristiculum* (Yokoyama) (Kafanov and Amano, 1996). The *Laevicardium tristiculum* (= *Cardium esutoruensis*) bearing horizon was established in Sakhalin as a marker of the Arakayskaya Suite and its correlatives by Krishtofovich (1954, 1964) and by Margulis and Savizky (1969). The Asagai Formation in the Joban coal-field of central Honshu contains *Laevicardium tristiculum*. According to Yanagisawa *et al.* (1989), the age of the Shiramizu Group, which includes the Asagai Formation, is early Oligocene according to its diatom flora, molluscs and mammals. In the Uglegorsk Province of southwestern Sakhalin, *L. tristiculum*

snayskaya Suites, Sakhalin; Nuibetsu, Charo and lower Sankebetsu Formations, Hokkaido; Asagai Formation, Honshu. These many occurrences of *P. harrimani* and allow us to judge it as a significant marker for upper Eocene to lower Oligocene strata of the North Pacific.

This conclusion may at first seem to contradict the pres-

Table 1. Measurements (in mm) of type specimens of *Papyridea (Profulvia) harrimani*, *P. (P.) nipponica*, *P. (P.) matschigarica* and *P. (P.) matschigarica uspenica*.

Species (subspecies)	Shell length	Shell height	Convexity of one valve	Number of radial ribs
<i>P. harriman</i>	48.0	40.0	9.5	42
<i>P. nipponica</i>	69.7	51.3	13.0	52
<i>P. matschigarica</i>	95.0	76.4	20.3	55
<i>P. matschigarica uspenica</i>	70.0	59.0	18.0	47

Figure 3. 1. *Papyridea harrimani* Dall, 1904. Schmidt Peninsula, northern Sakhalin, Machigarskaya Suite. PIN no. 90/3962. 2. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 4/7, GIN no. 3618/1. 3. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 5/29, GIN no. 3618/2. 4. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 5/24, GIN no. 3618/3. 5. *P. harrimani*. Machigar section of the Schmidt Peninsula, site 2/15, GIN no. 3618/4. 6. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Ugol'naya River, Gulf of Korf section, eastern Kamchatka, site 10/2-3. Pachachinskaya Suite. GIN no. 3669/3. 7. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Ugol'naya River, Gulf of Korf section, eastern Kamchatka, site 10/2-5. Pachachinskaya Suite. GIN no. 3669/4. 8. Paratype of *Papyridea matschigarica uspenica* Barinov in Gladenkov *et al.*, 1987. Bol'shaya Medvezhka River, Gulf of Korf section, eastern Kamchatka, site 18/7. Pakhachinskaya Suite. GIN no. 3669/7. All figure shown natural size.

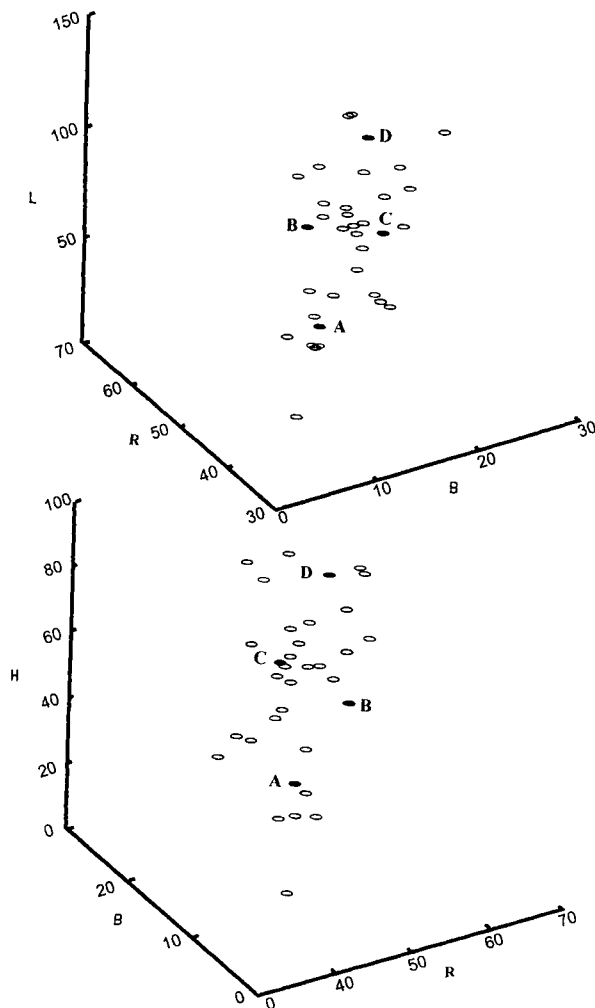


Figure 5. Location of type specimens of *Papyridea harrimani* (A), *P. nipponica* (B), *P. matschigarica uspenica* (C) and *P. matschigarica* (D) in space of characters of *P. matschigarica* topotypes from lower (dotted circles) and upper (white circles) parts of the Machigar section in northern Sakhalin. Abbreviations: L=shell length (in mm); H=shell height (in mm); B=convexity of one valve (in mm); R=number of radial ribs.

Table 2. Probability of assignment of type specimens of *Papyridea matschigarica*, *P. matschigarica uspenica*, *P. nipponica* and *P. harrimani* to sampling of topotypes of *P. matschigarica*. Probabilities P (D^2) of assignment to sampling of each topotype account for the range between 0.998 and 0.131; P (F) between 0.997 and 0.066.

Type specimens	P (D^2)	P (F)
<i>P. harrimani</i>	0.780	0.816
<i>P. matschigarica uspenica</i>	0.749	0.790
<i>P. matschigarica</i>	0.696	0.745
<i>P. nipponica</i>	0.653	0.707

has been found in the upper member of the Arakayskaya Suite. Okamura (1994) assigned a K-Ar age of 38.6 Ma and 30.6 Ma to the lower and middle parts of the Arakayskaya Suite respectively. Thus, in terms of molluscs, strata 3 and 4 of the Pakhachinskaya Suite in eastern Kamchatka may be assigned in age to early Oligocene.

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Upper Paleozoic biostromes in island-arc carbonates of the eastern Klamath terrane, California

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Abstract. The eastern Klamath terrane (eKt) of California, a geographically isolated, island-arc area, was invaded by biostromal communities during three intervals of carbonate deposition in the Carboniferous and Permian. Visean/Serpukhovian biostromes were formed on short-lived carbonate banks by the Tethyan brachiopod *Striatifera* and phylloid algae. Bashkirian biostromes on similar banks were formed by the cosmopolitan microproblematica *Tubiphytes* and *Donezella*. Wolfcampian biostromes occur in a thick carbonate platform and slope section and were formed by *Tubiphytes*, the phylloid alga *Eugonophyllum*, and *Palaeoaplysina*, an enigmatic taxon known mainly from Laurentia. Species diversity of biostrome dwellers increased from the Early Carboniferous to Early Permian, when it reached the level of high-diversity shelf-mud communities. Biostromes in the eKt record the global recovery of Carboniferous-Permian reef biotas during temporal intervals of quiescent volcanism that permitted carbonate deposition.

Key words : biostromes, California, Carboniferous, island-arcs, Permian

Introduction

The Late Paleozoic, noted for its paucity of frame-building metazoans, was an interval of ecologic recovery of reef communities following their collapse in the Late Devonian extinctions (Sheehan, 1985 ; Copper, 1988). Island-arc carbonates of the eastern Klamath terrane, California (Figure 1), offer a picture of this recovery in a setting of geographic isolation, limited availability of favorable environments, and recurring biogeographic invasions from outside areas. Although no Late Paleozoic reefs or mound-like structures are known from the terrane, several reef-forming taxa are locally abundant in tabular limestone beds that represent biostromes. Biostrome formation was dominated by binding, baffling, and production of skeletal grains, and biostromal taxa included a mixture of algae, problematica and brachiopods (Figure 2).

Geologic setting

Devonian through Early Jurassic rocks of the eastern Klamath terrane (eKt) formed in a succession of island-arcs and arc-related basins (Albers and Bain, 1985 ; Renne and Scott, 1988 ; Miller, 1989). Renne and Scott (1988) summarized paleomagnetic data for the eKt, which indicate paleolatitudes equivalent to cratonic North America since at least Permian times. Paleozoic longitudinal position of the eKt with respect to North America has been a matter of debate. Miller (1987), Rubin *et al.* (1990), Miller and Saleeby (1991), Miller *et al.* (1992), and Darby *et al.* (1997) placed the

eKt near the western margin of cratonic North America, based on provenance of detrital zircons and stratigraphic ties with adjacent terranes. In contrast, Stevens *et al.* (1990) and Belasky and Runnegar (1994) concluded that the eKt formed in an oceanic setting thousands of km west of North America, based on Permian faunal composition and biogeographic models. In either scenario, the eKt represents an isolated area of shallow marine environments in the Paleozoic. Like a number of Cordilleran terranes (Soja, 1996), it contains a mixture of cosmopolitan, endemic, Tethyan and North American taxa (Watkins and Wilson, 1989 ; Watkins *et al.*, 1989 ; Potter *et al.*, 1990 ; Stevens *et al.*, 1990 ; Noble and Renne, 1990).

Upper Paleozoic stratigraphy and carbonates

Early to Middle Devonian arc construction in the eKt was followed by extension and development of a large, arc-related basin in which submarine fan sequences of the Upper Devonian to Lower Carboniferous Bragdon Formation were deposited (Watkins, 1986, 1990 ; Miller and Cui, 1987 ; Miller and Saleeby, 1991). Volcaniclastic deltaic sediments with shallow marine limestone lenses appear locally at the top of the Bragdon and in the lower part of the overlying Baird Formation. The brachiopods *Striatifera* and *Titanaria* indicate a Visean or Serpukhovian (Late Mississippian) age for these limestones (Watkins, 1973 ; Gordon and Dutro, 1993). The lenses reach 17 m thick and 1.2 km in length, and consist of bank and slope facies that were deposited over delta lobes (Watkins, 1993a). Deposition of the lime-

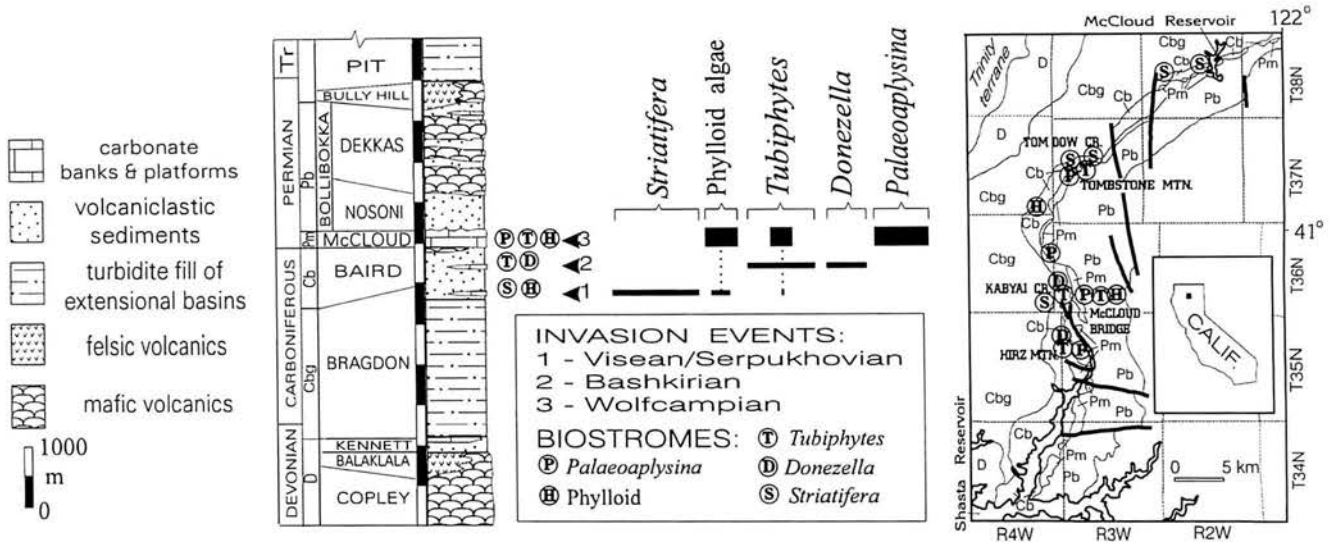


Figure 1. Occurrence of Upper Paleozoic biostromes in the eastern Klamath terrane, California; width of bars for the five taxa indicates their relative importance in biostrome formation. Detailed geologic maps of areas with biostromes are contained in Watkins (1973, 1993a, 1993b).

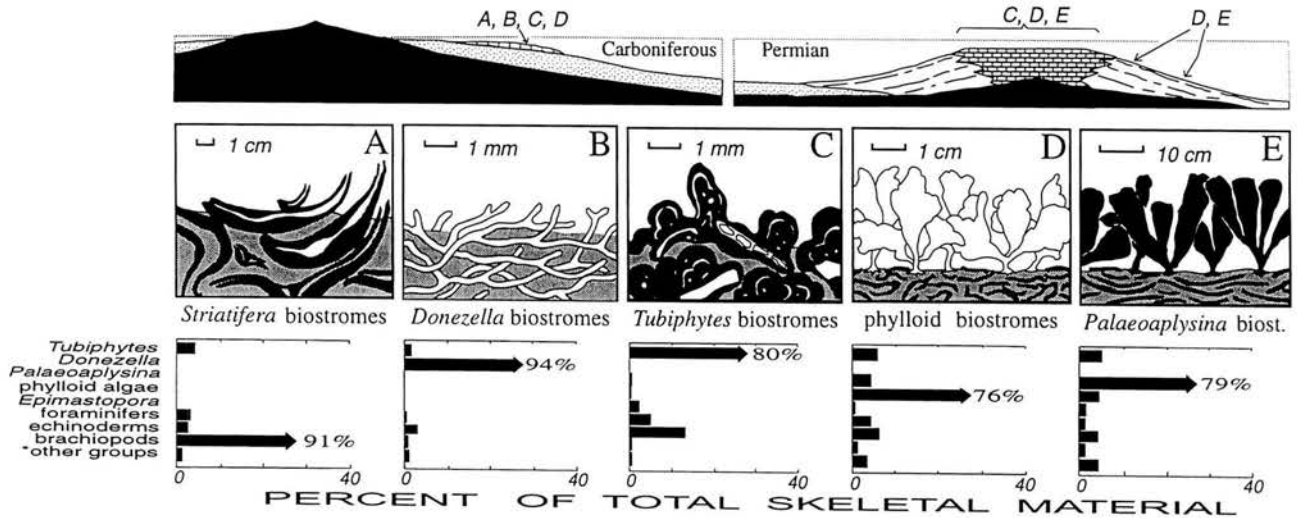


Figure 2. Environmental occurrence, life habit reconstructions, and skeletal composition of biostromes (*other groups include corals, bryozoans, annelids, molluscs, and ostracods).

stone lenses was related either to sea-level rise that cut off volcaniclastic sediment supply, or to switching of active delta lobes. Carbonate deposition on deltas was short-lived and terminated by progradation of volcaniclastic sediments.

Bashkirian (Early Pennsylvanian) limestone lenses in the Baird Formation are dated by the fusulinid *Pseudostaffella* (Skinner and Wilde, 1965). The fusulinid-bearing limestones occur at Kabyai Creek (Watkins, 1973, fig. 4) and Hirz Mountain [the Hirz Mountain Limestone Member of Watkins (1973, fig. 3), who erroneously dated it as "Late Pennsylvanian or Early Permian"]. The lenses include bank and slope-apron facies (Figure 3), and they reach 20 m in thickness and 2 km in breadth. In both areas, the limestone lenses are

overlain by a thick section of volcaniclastic sediments that probably ranges from Bashkirian to latest Carboniferous age.

The Baird is overlain by the Lower Permian McCloud Limestone, which contains basal Wolfcampian to early Leonardian fusulinids (Skinner and Wilde, 1965). The McCloud was deposited during an interval of volcanic quiescence as several carbonate platforms that reached tens of km in breadth (Miller, 1989; Watkins, 1990). Platforms developed over volcanic highs and grew by progradation of slope deposits and aggradation of platform-top deposits, resulting in carbonate sections over 800 m thick (Watkins, 1993b). McCloud deposition was terminated by platform subsidence and drowning in the Leonardian, and volcanism

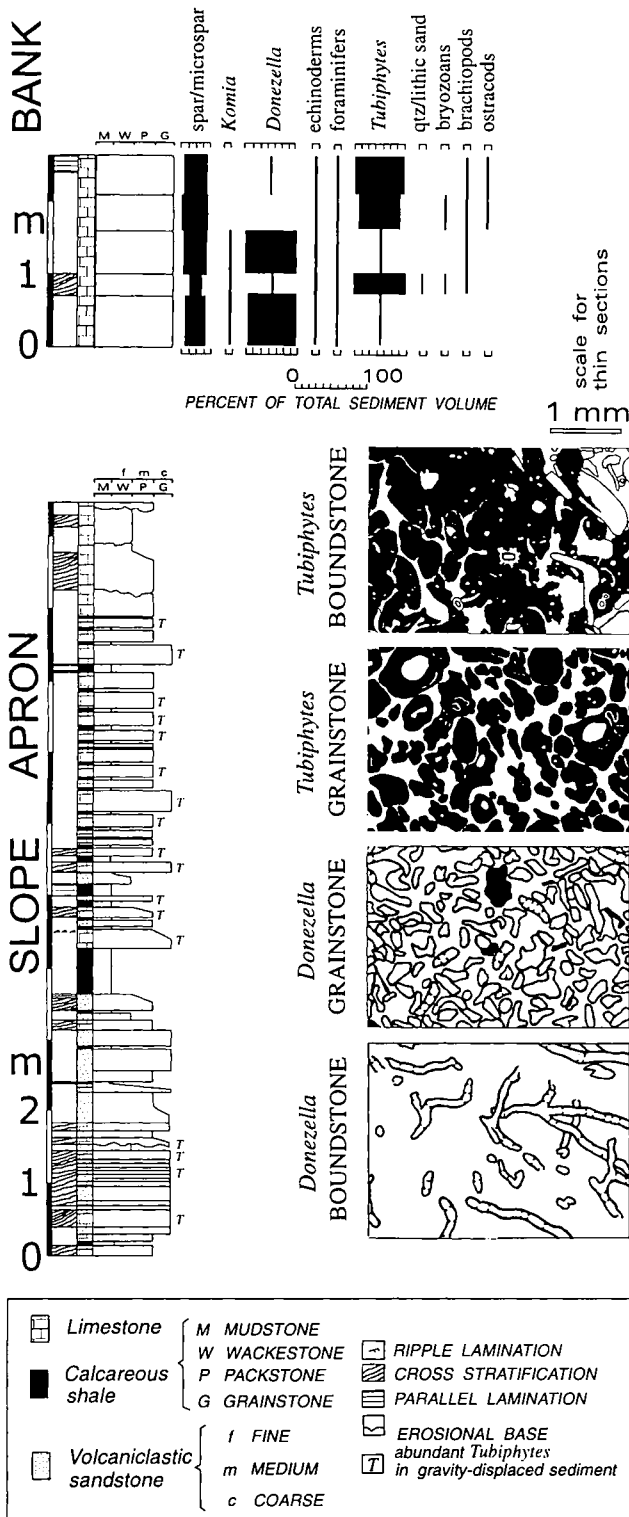


Figure 3. Occurrence of *Donezella* and *Tubiphytes* in bank and slope apron facies of Bashkirian limestone, Baird Formation, Kabyai Creek (NE1/4 NE1/4 sec. 36, T36N R4W). Sketches of thin sections, traced from photos, show typical fabrics and textures.

resumed in the eKt during early Guadalupian time (Renne and Scott, 1988). Small carbonate bank deposits of Guadalupian age occur in the volcanic and volcanoclastic Bollibokka Group, but no biostromes have been reported (Stevens *et al.*, 1987 ; Miller, 1989).

Methods

Data on biostromes were collected as part of a sedimentologic study of Upper Paleozoic carbonates in the eKt (Watkins, 1993a, 1993b). This study involved outcrop mapping and bed-by-bed logging of five depositional lenses of Viséan/Serpukhovian limestones (80 m of total section), three depositional lenses of Bashkirian limestones (142 m of total section), and one Wolfcampian slope and platform complex (901 m of total section).

In the course of this work, 81 samples were made from 60 biostromes, and 39 samples were made from beds of gravity-displaced biostromal sediment. All samples were prepared as thin sections. Compositional data were obtained as counts of 100 to 200 points per thin section, and data were pooled for samples from the same biostrome type to yield the histograms in Figure 2. Samples with larger biostrome formers were also studied as polished slabs. Twelve samples were etched in HCl to obtain silicified fossils used for measurement of species diversity.

Comparative paleoecology of biostrome and shelf-mud faunas, discussed later, uses the guild concept. Reef and biostrome guilds recognized by Fagerstrom (1987) include constructors, bafflers, binders, destroyers, and dwellers. This report follows Watkins (1993c) in subdividing the dweller guild on the basis of class-level taxonomy and functional morphology.

Biostromal deposits

Biostromes formed by *Striatifera*, phylloid algae and *Palaeoaplysina* are readily apparent in the field, but their lateral extent is difficult to determine because of brush cover. *Striatifera* biostromes have been traced for lateral distances of 45 m, and *Palaeoaplysina* and phylloid biostromes have been traced for distances of 130 m. Biostromal beds dominated by *Donezella* and *Tubiphytes*, which appear as medium-grained, relatively featureless limestone in the field, were identified by thin sections. These beds have been traced only across small roadcuts and ledges.

***Striatifera* biostromes**

Striatifera is a linoproductid brachiopod that attached to conspecific shells with its spines, forming biostromes similar to modern mussel beds (Muir-Wood and Cooper, 1960). An undescribed species of *Striatifera*, similar to *S. striata* Fischer de Waldheim, occurs as a biostrome former in Viséan/Serpukhovian limestones of the Bragdon and Baird formations.

The biostromal beds range from 40 to 110 cm thick and contain a loose framework of in-place *Striatifera*. Articulated individuals rest upon one another in a convex-downward

orientation (Figure 4A) and are attached by cementing spines. Growth asymmetry caused by crowding is common, and shells range from juveniles a few mm in size to adults 18 cm in length. These beds contain 28 to 58% *Striatifera* and 33 to 59% micrite and microspar matrix. Small encrustations of *Tubiphytes* are present on *Striatifera* (Figure 5A) and form <1 to 14% of sediment volume. Other skeletal taxa are mainly matrix-supported and scattered between the large productoids; they form <1 to 10% of sediment volume and

include crinozoans, foraminifers, small brachiopods, gastropods, corals, echinoids, and bivalves (Watkins, 1973).

Beds with in-place productoids are interbedded with erosively based packstones that contain sorted, horizontally stratified *Striatifera* valves and fragments (Figure 4B). These two lithologies, which form horizons up to 3 m thick (Figure 4C), were deposited in a moderate to high energy, bank-edge setting (Watkins, 1993a).

Donezella biostromes

Boundstone, packstone, and grainstone beds with abundant *Donezella lutugini* Maslov occur in Bashkirian limestones of the Baird Formation (Figure 3). Mamet (1991) placed *Donezella* and similar genera in the algal group Palaeosiphonocladales, but they have also been interpreted as sponges (Termier *et al.*, 1977) and possible foraminifers (Riding, 1977). Mamet *et al.* (1987) interpreted the tubules of *Donezella* as branching thalli that stood upright above the bottom and functioned as sediment baffles. However, a sediment-binding habit for donezellids is also possible (Davies and Nassichuck, 1988).

Massive beds from 35 to 120 cm thick contain 25 to 30% *Donezella* as an open-branching network of septate tubules 0.08 to 0.27 mm in diameter. The tubule network is partly contained in micrite (13–55% of sediment volume) and partly encloses spaces to 3.5 mm in size that consist of sparite (5 to 30%) and pelloidal grainstone (14–25%). Fragments of echinoderms, bryozoans, foraminifers, and monaxial spicules occur in the micrite matrix, and areas of *Tubiphytes* up to 1.3 mm in size encrust *Donezella* tubules. These beds are interpreted as boundstone. Their texture and fabric are very similar to beresellid-donezellid boundstone in Bashkirian to early Moscovian reefs in the Canadian Arctic (Davies and Nassichuk, 1988).

Massive to cross-stratified beds of grainstone and packstone are 30 to 105 cm thick and contain 60 to 70% broken *Donezella* tubules (Figure 5C), 18 to 34% sparite or micrite matrix, and 1 to 8% other bioclasts, including *Komia*, *Tubiphytes*, echinoderms, foraminifers, bryozoans, brachiopods, and ostracods. Tubule fragments are 3 mm or less in length, and in some beds they show a parallel alignment of long axes. Other bioclasts, which reach 10 mm in size, are dispersed and often abraded. These beds represent sediment derived from *Donezella* boundstone, and they formed in moderate to high energy, bank and bank-edge settings.

Tubiphytes biostromes

Tubiphytes is an encruster that has been interpreted as a cyanobacterium, alga, foraminifer, sponge, or metazoan of uncertain affinity (Riding and Guo, 1992). It consists of an outer envelope of dark, fine-grained calcite and internal tubules. Senowbari-Daryan and Flügel (1993) recognized only the envelope as *Tubiphytes* and considered the internal tubules as separate, overgrown organisms. Grainstones dominated by *Tubiphytes obscurus* Maslov occur in Bashkirian limestones of the Baird Formation and Wolfcampian zones A, B and G of the McCloud Limestone (Figures 3, 6).

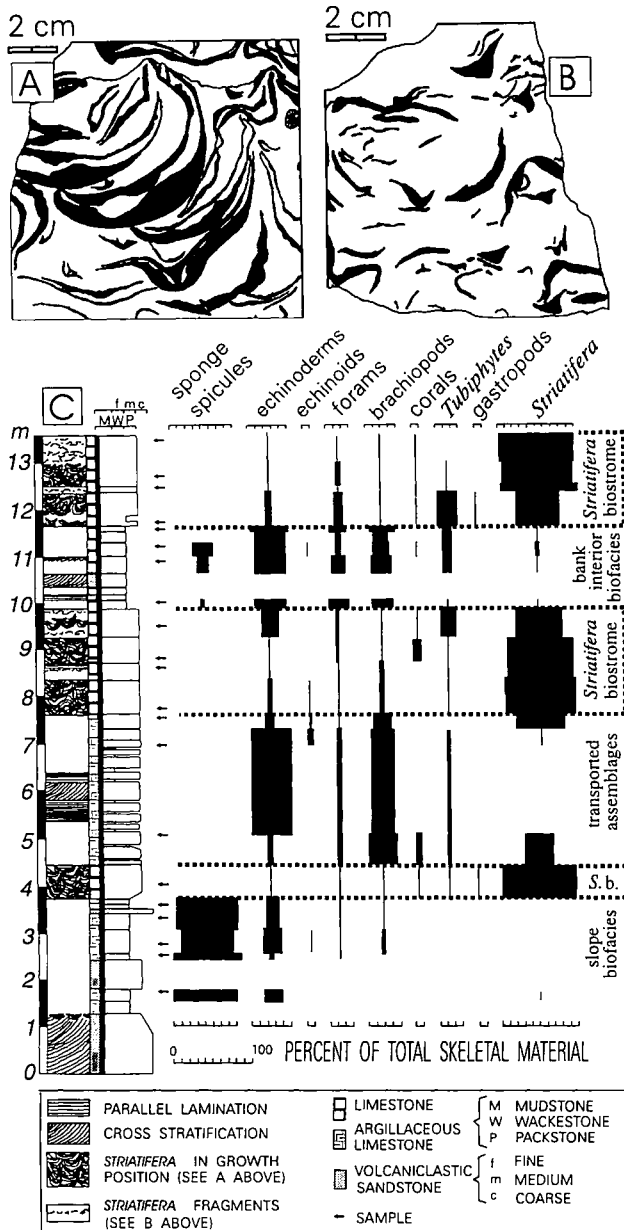


Figure 4. A. *Striatifera* in growth position. B. Rede-deposited *Striatifera* valves and fragments. C. Occurrence of *Striatifera* biostromes in limestone of the Baird Formation at Tom Dow Creek; see Watkins (1993a) for photos and location of this section.

In the bank facies of Bashkirian limestones, *Tubiphytes* grainstone forms massive to cross-stratified beds 30 to 140 cm thick. In the slope facies of these limestones, *Tubiphytes* grainstone and packstone form 10- to 30-cm-thick beds that include normal grading and small-scale cross-lamination (Figure 3). Wolfcampian *Tubiphytes* grainstone forms isolated, massive beds 0.4 to 5 m thick within platform successions of thick-bedded crinoid packstone, fusulinid packstone, and skeletal packstone (Figure 6). In Wolfcampian slope deposits at McCloud Bridge (fusulinid zone A of Skinner and Wilde, 1965), *Tubiphytes* grainstone is interbedded with limestone conglomerate and forms 10- to 60-cm-thick beds that include small-scale cross-lamination, horizontal lamination, and normal grading. At Tombstone Mountain, pebbles to small boulders of *Tubiphytes* grainstone are abundant in limestone conglomerates of fusulinid zone G.

The grainstones contain 43 to 80% *Tubiphytes* (Figure 5E) and 11 to 38% sparite to microspar matrix. *Tubiphytes* grains range from 0.3 to 1.5 mm, with a maximum size of 5 mm. Abrasion and rounding are common, particularly among smaller *Tubiphytes* grains that contain no other bioclasts. Larger *Tubiphytes* grains contain nuclei of small skeletal fragments or envelop and bind together several bioclasts. Other bioclasts, which include echinoderms, foraminifers, corals, bryozoans, brachiopods, and ostracods, reach 10 mm in size and form 1 to 19% of sediment volume. Permian beds also include the dasycladacean *Epimastopora* and indeterminate phylloid algae.

The grainstone beds indicate abundant *Tubiphytes* growth in shallow, high-energy settings where the volume of binders exceeded that of encrusted skeletal grains. Although small areas of *Tubiphytes* boundstone occur within skeletal packstone, no *Tubiphytes* bed with a complete boundstone fabric has been observed. This may indicate that *Tubiphytes* crusts were more or less continuously reworked as they formed. Kershaw (1994), in a classification of biostrome types, noted that not all biostromes consist of *in situ* skeletons. In Kershaw's classification, the *Tubiphytes* grainstone beds can be considered as "parabiostromes," which consist largely of reworked biostrome-formers, with 20% or less *in situ* material. Much of this sediment was also redeposited on slope aprons bordering bank and platform margins.

Phylloid biostromes

Phylloid algae are a morphological group of leaf-like genera that may include both red and green algae (Riding and Guo, 1991). In Late Paleozoic reefs and biostromes, their functional role included sediment baffling and voluminous production of skeletal particles (Toomey and Babcock, 1983).

Phylloid packstone occurs as two 20-cm-thick beds in a single Viséan/Serpukhovian limestone lens in the Baird Formation (Watkins, 1993a). Baird phylloids (Figure 5B) are recrystallized and generically indeterminate. In the Wolfcampian McCloud Limestone, phylloid packstone forms massive beds 0.3 to 4.5 m thick in platform successions (Figure 6). In McCloud slope deposits, gravity-displaced

phylloid packstone occurs as clasts in limestone conglomerate and thin beds with erosional bases and normal grading. Slope deposits also include less common, massive beds to 80 cm thick that represent in-place biostromes. McCloud phylloids include *Eugonophyllum* sp., but specimens in most samples are too recrystallized for identification.

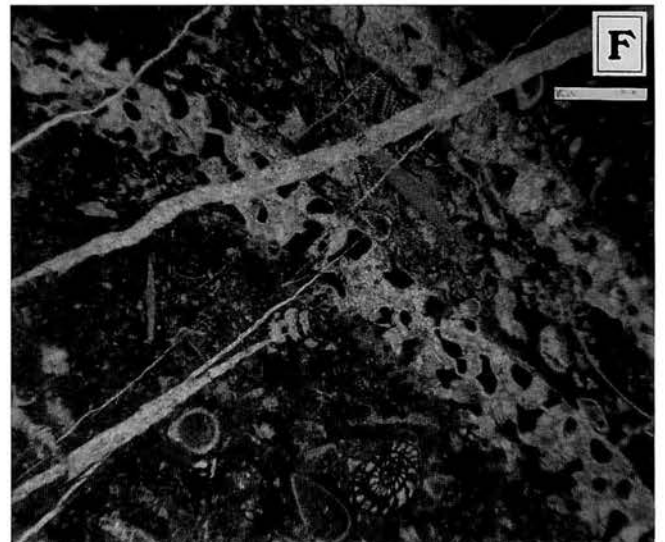
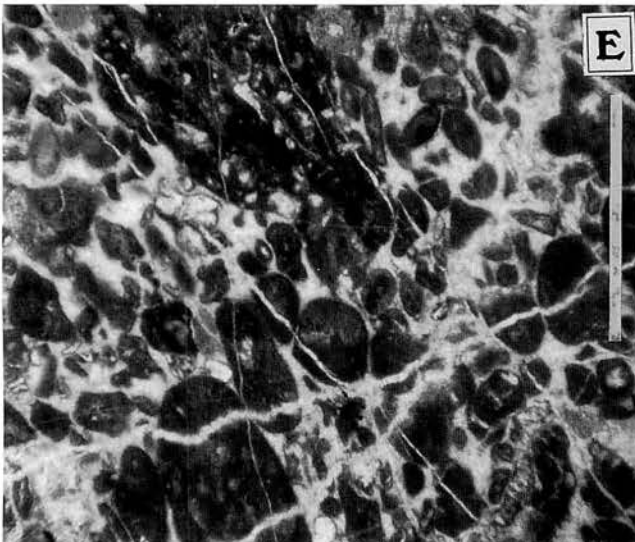
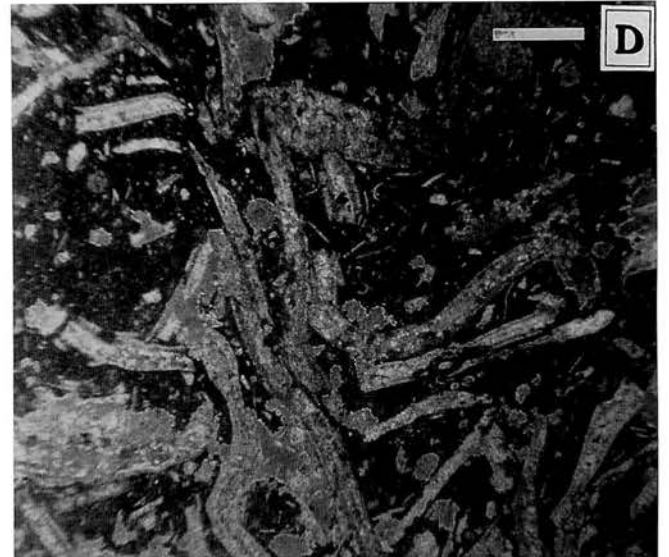
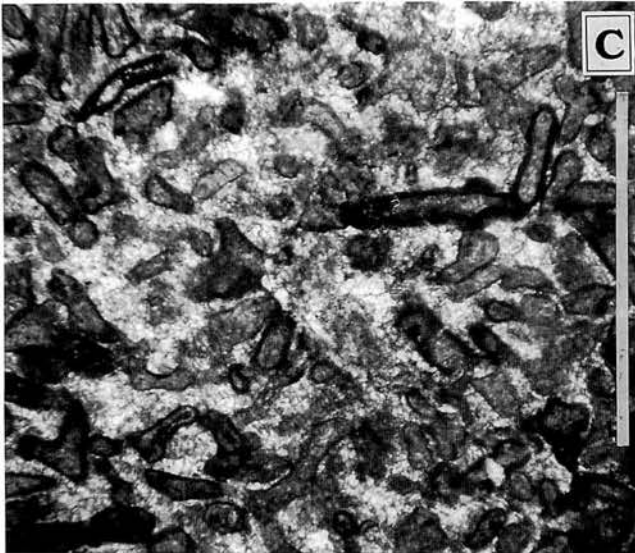
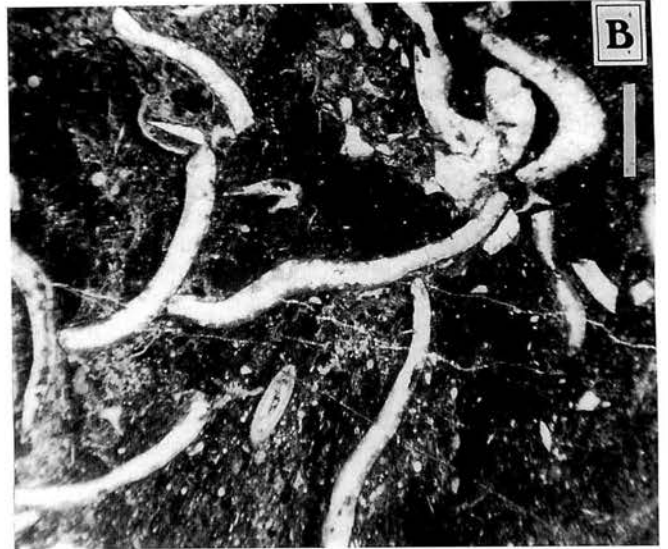
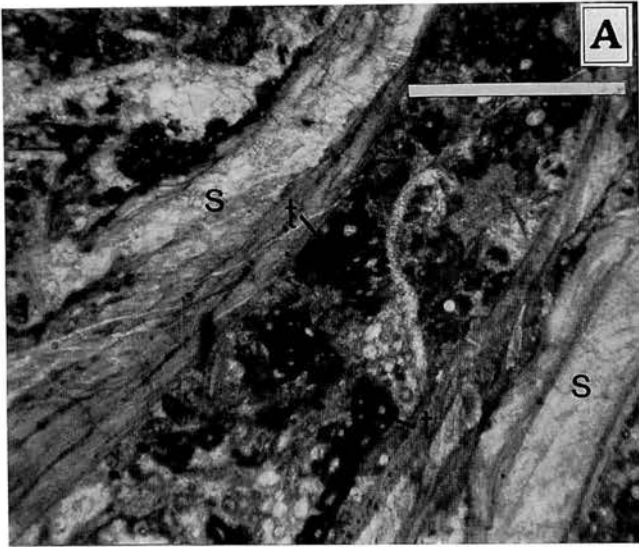
Packstones in the McCloud Limestone include 24 to 43% phylloids (Figure 5D) and 42 to 66% micrite and microspar matrix. Phylloid plates are 2 to 18 mm long, variably oriented, and closely to loosely packed. Edges of plates often appear broken but are unabraded. *Tubiphytes* forms <1 to 9% of sediment volume and occurs as loose grains and encrustations up to 4 mm long on phylloid plates. Spirorbids, fenestellid holdfasts, other bryozoans, and tetraxiid foraminifers also encrust phylloids. Other bioclasts form 6 to 14% of sediment volume and are scattered, mostly matrix-supported, and mainly less than 5 mm in size. They include *Palaeoaplysina*, *Epimastopora*, bryozoans, foraminifers, echinoderms, gastropods, brachiopods, ostracods, and corals.

Palaeoaplysina biostromes

The enigmatic genus *Palaeoaplysina*, which consists of thin calcareous plates with an internal canal system and cellular structure, has features in common with hydrozoans, sponges, and algae (Davies and Nassichuk, 1973). *Palaeoaplysina* is an important reef and biostrome former, but its mode of life is uncertain (Beauchamp *et al.*, 1988). Breuninger (1976) inferred a binding habit for the plates, but Davies and Nassichuk (1973) and Watkins and Wilson (1989) presented evidence for an erect, frond-like growth habit.

Palaeoaplysina laminaeformis Krotov is locally common in the Wolfcampian McCloud Limestone (Figure 6). In the platform facies of the McCloud, massive beds of *Palaeoaplysina* wackestone to packstone are 0.7 to 2.2 m thick. These beds occur both as isolated units within successions of skeletal wackestones, packstones, and grainstones, and they are also interbedded with phylloid packstones as composite biostromal horizons over 4 m thick (Watkins and Wilson, 1989). McCloud slope deposits with limestone conglomerates also include common *Palaeoaplysina* beds (Watkins, 1993b). Massive *Palaeoaplysina* wackestone to packstone beds from 0.5 to 3 m thick are identical to those in the platform facies, and they are interpreted as in place biostromes of slope aprons. Less common, redeposited beds of *Palaeoaplysina* packstone are 10 to 30 cm thick and have loaded bases and ripple-laminated tops.

Beds of intergrading wackestone to packstone consist of 23 to 49% *Palaeoaplysina* (Figure 5F) and 38 to 69% micrite and microspar matrix. Plates of *Palaeoaplysina* reach 20 cm long, are mainly oriented parallel to bedding, and range from loosely to closely packed. Encrustors on *Palaeoaplysina* include *Tubiphytes*, which forms <1 to 4% of sediment volume, as well as spirorbids and bryozoans. Other bioclasts, which form 3 to 11% of sediment volume, include phylloid algae, *Epimastopora*, echinoderms, foraminifers, corals, bryozoans, brachiopods, gastropods, bivalves, and ostracods.



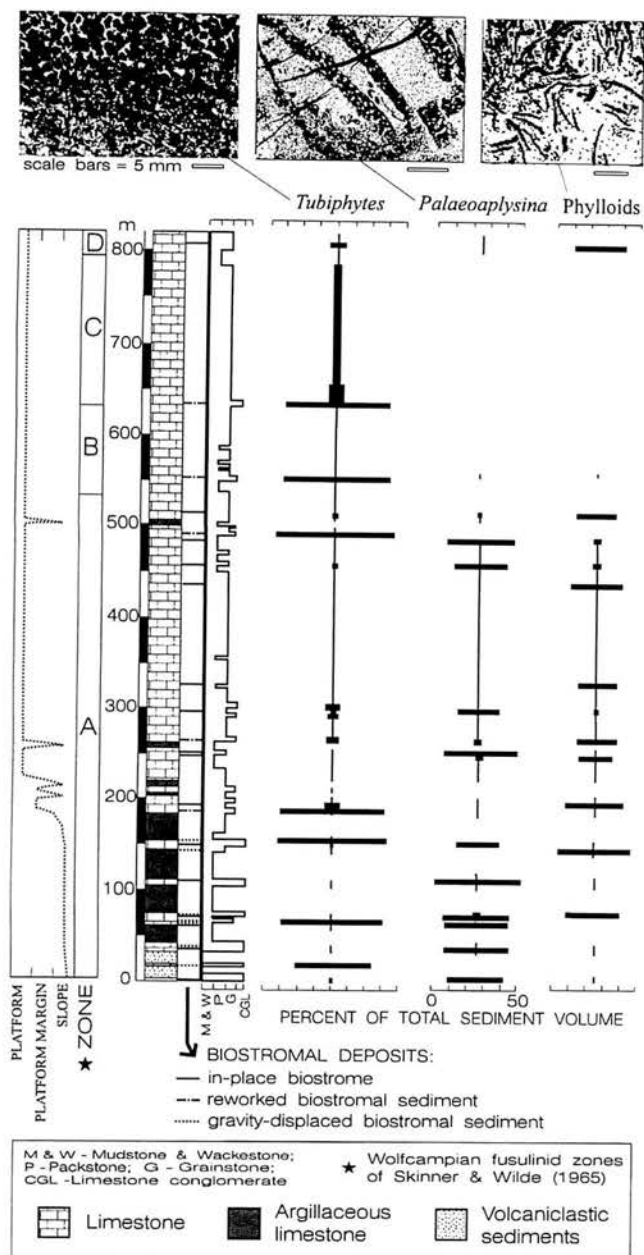


Figure 6. Biostrome occurrence in the Lower Permian McCloud Limestone at McCloud Bridge; see Watkins (1993b) for location, details of nonbiostromal lithologies, and bed-by-bed logs of parts of the section.

Biogeographic and sedimentary relations of biostrome formers

Three intervals of Late Paleozoic carbonate deposition in the eastern Klamath terrane were accompanied by bio-

strom formation. Biostromal taxa appear at or near the base of each carbonate horizon and range throughout their entire thicknesses; they have not been recorded through intervening clastic deposits. This suggests three separate invasions of the terrane by biostromal communities.

Biostromes were poorly developed during the Visean/Serpukhovian interval of carbonate deposition. The brachiopod *Striatifera* formed beds with a loose framework structure in several limestone lenses. However, *Striatifera* beds are not present in all lenses of this age (Watkins, 1993a), and their level of binding and sediment production was much less than those of other biostromes. *Striatifera* probably arrived in the eKt from the east, as it is a Tethyan genus that occurs in North Africa, Western Europe, Russia, Kazakhstan, China, and Japan (Muir-Wood and Cooper, 1960; Gordon and Dutro, 1993). Phylloid algae, which dominate two beds in one limestone lens, had only a limited role in sediment production, and their occurrence in the Baird Formation predates their Late Carboniferous rise as important producers of carbonate sediment (Chuvashov and Riding, 1984). The binder *Tubiphytes* is a minor constituent of the Visean/Serpukhovian biostromes, where its occurrence also predates its attainment of global abundance.

Bashkirian limestones of the eKt record the return of *Tubiphytes* and the appearance of *Donezella* as important biostrome formers. *Tubiphytes* grainstone forms up to 50% of the thickness of bank sections, and redeposited beds of *Tubiphytes* form up to 40% of sections deposited as slope aprons. The Bashkirian occurrence of *Tubiphytes* grainstones in the eKt corresponds to its rise in abundance during the Late Carboniferous, when it attained a cosmopolitan distribution as both a major and accessory reef and biostrome former (Chuvashov and Riding, 1984; Mamet, 1991; Senowbari-Daryan and Flugel, 1993). *Donezella* beds also form up to 50% of Bashkirian bank sections in the eKt. The Bashkirian/Moscovian was the temporal acme of *Donezella* as a sediment producer, and it forms reefs and biostromes of this age in North Africa, Eurasia, and North America (Mamet, 1991). Although phylloid algae were important and widely distributed reef and biostrome formers during the Late Carboniferous (Chuvashov and Riding, 1984; Mamet, 1991), they have not been observed in Bashkirian limestones of the Baird Formation.

Biostromes played a minor role in the construction of Wolfcampian carbonate platforms in the eKt. Beds dominated by *Tubiphytes*, phylloid algae and *Palaeoaplysina* form less than 10% of the thickness of platform sections. Lack of importance of biostromes and absence of reefs on McCloud platforms may be due to very high rates of subsidence and absence of well-defined platform margins (Watkins, 1993b). *Tubiphytes* and phylloids had a cosmopolitan distribution as important reef and biostrome formers in the Early Permian (Chuvashov and Riding, 1984; Riding and Guo, 1991; Senowbari-Daryan and Flugel, 1993). *Palaeo-*

Figure 5. A. Detail of *Striatifera* bed showing small encrustations of *Tubiphytes* (t) on *Striatifera* valves (s), Baird Formation, Tom Dow Creek. B. Phylloid packstone, Baird Formation, North Fork. C. *Donezella* grainstone, Baird Formation, Kabyai Creek. D. Phylloid packstone, McCloud Limestone, McCloud Bridge. E. *Tubiphytes* grainstone, McCloud Limestone, Tombstone Mountain. F. *Palaeoaplysina* packstone, McCloud Limestone, McCloud Bridge. All scale bars are 2 mm.

aplysina first appears in the Middle Pennsylvanian of Utah, and by the Wolfcampian it is present as a major reef and biostrome former in a belt around the northern margin of Laurentia, including occurrences in Idaho, British Columbia, the Canadian Arctic, Svalbard, and the Urals (Ritter and Morris, 1997). *Palaeoaplysina* is also known from the Akiyoshi terrane of Japan (Machiyama, 1991).

Early Permian *Palaeoaplysina* buildups appear to have had a relatively wide environmental range, occurring in the Canadian Arctic from inner shelf to upper slope settings (Beauchamp *et al.*, 1988). This relation is also evident in the McCloud Limestone, where *Palaeoaplysina* biostromes are present in both platform and slope deposits. McCloud slope deposits consist of alternations of thin-bedded argillaceous limestones and horizons with limestone conglomerates (Figure 6). *Palaeoaplysina* biostromes form 15 to 45% of the thickness of conglomeratic horizons. Occurrence of *Palaeoaplysina* biostromes on tops of conglomerates, as well as on volcanoclastic breccia at the very base of the McCloud Limestone (Watkins, 1993b, fig. 4), suggest a role as a pioneer community among carbonate sediment producers.

Comparison of biostromes and shelf-mud biofacies

Paleoecological aspects of the biostromes can be best understood by comparison with contemporaneous shelf-mud biofacies of the eKt (Figure 7). The shelf biofacies occur in bioturbated, clastic and carbonate muds of Viséan/Serpukhovian to early Guadalupian age (Coogan, 1960; Watkins, 1973; Yancey and Hanger, 1985). Echinoderms (mainly crinoids) form 50-70% of skeletal material in these biofacies, followed by brachiopods (4-36%), bryozoans (3-13%), foraminifers (1-11%), and molluscs, corals, and minor groups (<1-10%). Four bivalve guilds, three bryozoan guilds, two

brachiopod guilds, and a gastropod "superguild" include most of their macrofaunal species. Species data for echinoderms, which occur as disarticulated ossicles, are not available.

In contrast, all five types of biostromes are dominated by a single binding, baffling, or framebuilding species that forms over 70% of skeletal material (Figure 2). Although several such species may cooccur within a biostrome, only one predominates. For example, *Tubiphytes*, phylloids, and *Palaeoaplysina* commonly occur together in Lower Permian beds, but in each case one of these taxa is clearly dominant (Figure 6). Dweller guilds generally form 20% or less of skeletal material in beds, and their composition is similar in all five types of biostromes. Crinozoans and foraminifers are the most common dweller taxa (Figure 2), and small amounts of skeletal material (usually 2% or less each, except for *Striatifera* biostromes) are represented by brachiopods, bryozoans, molluscs, corals, annelids, and ostracods.

Bulk collections of silicified specimens from *Striatifera* and phylloid biostromes permit a more detailed consideration of dweller taxa (foraminifers, ostracods, and echinoderms have not been studied and are not included in this discussion or in plots of species diversity in Figures 7 and 8). The most diverse groups among dweller taxa are brachiopods and gastropods, followed in decreasing order by bryozoans, bivalves, corals, rostroconchs, and annelids. The composition and species diversity of dweller taxa in the biostromes is nearly identical to that in carbonate shelf-mud biofacies of Bashkirian and Wolfcampian age (Figure 7). In the Wolfcampian, the same species occur in shelf-mud biofacies, phylloid biostromes, and *Palaeoaplysina* biostromes (Watkins and Wilson, 1989). These relations suggest that most dweller taxa in the biostromes were not specialized for these habitats, but were immigrants from level-bottom, carbonate

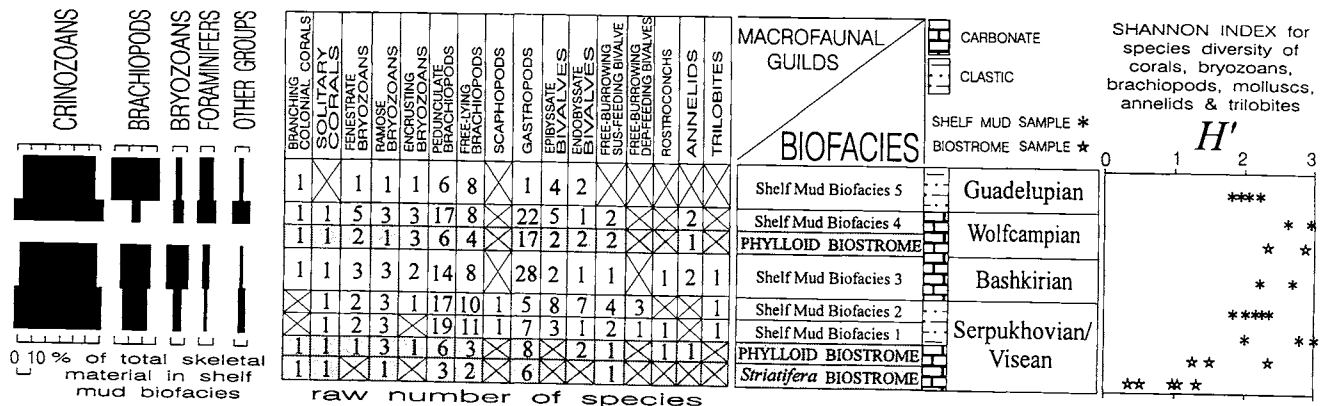


Figure 7. Faunal comparison of Upper Paleozoic biostromes and shelf-mud biofacies of the eastern Klamath terrane. Biofacies are arranged vertically by four intervals of time, but this plot is not a stratigraphic section. For the Serpukhovian/Visean, relative stratigraphic position of phylloid and *Striatifera* biostromes is not known, and both overlap in stratigraphic range with shelf-mud biofacies. For the Wolfcampian, plotting of the phylloid biostrome below the shelf-mud biofacies is arbitrary, as these biotas are interbedded. Shelf-mud biofacies and number of specimens in samples (*n*) are as follows: 1-*Dorsoscyphus* association, Bragdon Formation, *n* = 442; 2-*Rugosochonetes* association, Baird Formation, *n* = 1203; 3-*Lissomarginifera* association, Hirz Mountain Limestone Member of Baird Formation, *n* = 1734; 4-*Crurithyris* (= *Cruricella*) association, McCloud Limestone, *n* = 1663; 5-*Anidanthus-Spiriferella* faunule, *n* = 435. Sample sizes for biostromes are as follows: Wolfcampian phylloid, *n* = 472; Serpukhovian/Visean phylloid, *n* = 2496; *Striatifera*, *n* = 1261.

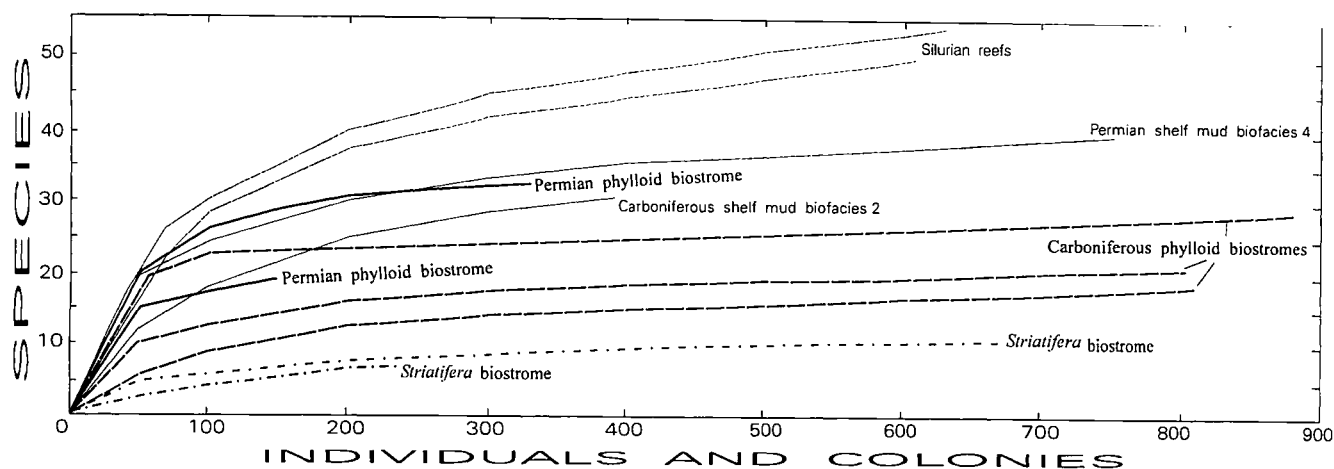


Figure 8. Rarefaction curves for Upper Paleozoic biostromes and shelf-mud biofacies of the eastern Klamath terrane. Also shown for comparison are two samples from Silurian reefs (Watkins, 1996). Data are for corals, bryozoans, brachiopods, molluscs, annelids and trilobites.

mud environments.

Trends in species diversity

Following the Late Devonian extinctions, the global number of marine families increased rapidly, reaching a stable level near the end of the Early Carboniferous that was maintained for the rest of the Paleozoic (Sepkoski, 1992). This pattern of Late Paleozoic stasis is also shown by species diversity of Visean/Serpukhovian to early Guadalupian shelf-mud biofacies of the eKt, as measured by H' and rarefaction (Figures 7, 8). Reef biotas were much slower to recover from the Late Devonian extinctions, and complex reef communities were not reestablished until the Middle Permian (Sheehan, 1985; Copper, 1988). This slow recovery is also suggested by species diversity data from Upper Paleozoic biostromes in the eKt. Average species-diversity in eKt Carboniferous biostromes is less than that of shelf-mud biofacies. Species diversity in phylloid biostromes increased by the Early Permian, when they attained a diversity equivalent to that of carbonate shelf-mud biofacies (Figures 7, 8). Even so, diversity of the Early Permian biostromes did not reach the levels of reefs that existed before the Late Devonian extinctions, as shown by rarefaction curves for Silurian reefs (Figure 8).

Conclusions

Three intervals of Late Paleozoic volcanic quiescence and carbonate deposition in the eastern Klamath terrane were accompanied by development of biostromal communities. Except for loosely cemented productoid brachiopods, framebuilders are absent, and bafflers and binders of algal or problematic affinity are the dominant biostrome formers. Stratigraphic ranges and peaks in abundance of eKt biostromal taxa are like their occurrences elsewhere. Biostrome formers include a mixture of cosmopolitan, Tethyan and Laurentian affinities. An increase in species diversity from

Early Carboniferous to Early Permian biostromes in the eKt probably reflects global recovery of reef biotas following the Late Devonian extinctions.

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The turrilitid ammonoid *Mariella* from Hokkaido — Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin — LXXXVI)

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Abstract. The following five taxa of the genus *Mariella* of the Turrilitidae from the Upper Albian and Lower Cenomanian of Hokkaido are described: (1) *M. (Mariella) bergeri* (Brongniart, 1822), (2) *M. (M.) aff. bergeri* (Brongniart), (3) *M. (M.) miliaris* (Pictet and Campiche, 1861), (4) *M. (M.) cf. carrancoi* (Böse, 1923) and (5) *M. (M.) gallienii* (Boule, Lemoine and Thévenin, 1907). The present study gives new or revised information as to the taxonomy and stratigraphic occurrences of these species.

Key words : Late Albian-early Cenomanian, *Mariella (Mariella) bergeri*, *M. (M.) carrancoi*, *M. (M.) gallienii*, *M. (M.) miliaris*

Introduction

In Part 1 Matsumoto *et al.* (1999) described three well defined species of *Mariella* from the Lower Cenomanian of the Soeushinai area (northwestern Hokkaido). In Part 2 we continue to describe some more species (five taxa) from the Upper Albian and Lower Cenomanian of Hokkaido. The material is mostly from the Soeushinai area, except for a supplementary specimen from the Shuparo [=Shuyubari] area of the Yubari Mountains (central Hokkaido).

With respect to the location and stratigraphic assignment of the material from the Soeushinai area, readers may refer to the route maps in the two papers by Nishida *et al.* (1996, figs. 3-5 ; 1997, fig. 11) and for more information to the locality guide and maps given by Matsumoto and Nishida (1999, figs. 6, 7) as an Appendix to Part 1. The locality in the Shuparo area will be identified more specifically in the description of the species concerned.

The following symbols are used for the repositories of the specimens described in this paper.

GK : Type room, Department of Earth and Planetary Sciences, Kyushu University, Fukuoka

GS : Geological Collections, Faculty of Culture and Education, Saga University, Saga

Palaeontological descriptions

(Continued from Part 1)

Mariella (Mariella) bergeri (Brongniart, 1822)

Figure 1

Turrilites bergeri Brongniart, 1822, p. 395, pl. 7, fig. 3.

Mariella bergeri (Brongniart). Spath, 1937, p. 510, pl. 57, fig. 28 ; text-fig. 178 ; Drushchits, 1960, p. 266, pl. 12, figs. 2, 3 ; Seyed-Emami, 1982, p. 419, pl. 7, figs. 11, 12.

Mariella (Mariella) bergeri (Brongniart). Chiriac, 1960, p. 6, pl. 1, figs. 10, 11 ; Klinger and Kennedy, 1978, p. 28, text-fig. 6E (only) ; Atabekian, 1985, p. 27, pl. 2, figs. 4, 5 ; pl. 3, figs. 1-11 ; pl. 4, figs. 1-7 ; Kennedy, 1996, *in* Gale *et al.*, p. 583, figs. 16o, 28a, b, i, j, l, o, p ; 29h, i, m.

Paraturrilites (Bergericeras) bergeri (Brongniart). Wiedmann and Dieni, 1968, p. 80, pl. 7, fig. 5 ; pl. 9, figs. 2, 5.

Turrilites (Bergericeras) bergeri bergeri (Brongniart). Scholz, 1979, p. 40, pl. 8, figs. 12, 14, 15, 17.

Holotype.—The original of *Turrilites bergeri* Brongniart, 1822, pl. 7, fig. 3 (by monotypy).

Material.—GS. G183 (Figure 1-1, 2) collected by Y.K. on 25 September 1995 at loc. R803 and GS. G184 (Figure 1-3) collected by Y.K. and others on 15 August 1996 at loc. R813, both in situ from the upper part of the Member My2, (mudstone with frequently intercalated laminae and beds of sandstone), well exposed on the floor of the Sounnai River (for its location see fig. 6 in Part 1) ; GK. H8512, a small specimen collected by Jun Aizawa and T.M. on 14 August 1998 at loc. R8005 (close to R803) from a lenticular layer of sandstone in the Member My2.

Description.—Each of the three specimens is a fragmentary whorl of half ammonoid preservation. They can be regarded as representing whorls of roughly successive growth stages. The small, unillustrated GK. H8512 preserves shelly matter, showing small tubercles in four rows at

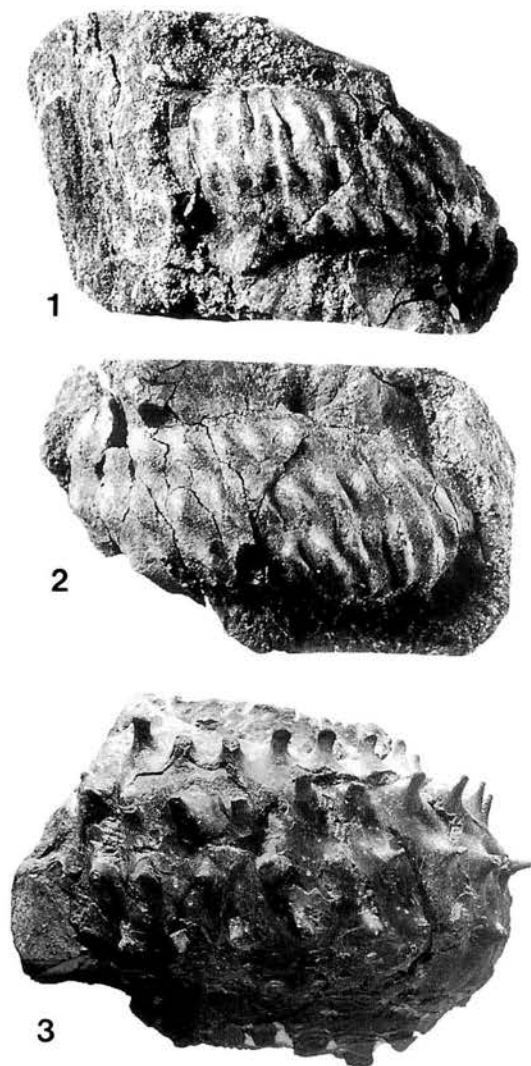


Figure 1. *Mariella (Mariella) bergeri* (Brongniart). 1. GS. G183, slightly oblique, lateral view showing the sedimentary structure of the host rock in the left part, $\times 1$. 2. GS. G183, upside-down lateral view, showing the whole part of the preserved flank, $\times 1.2$. 3. GS. G184, upside-down lateral view, $\times 1$. (Photos by N. Egashira without whitening.)

subequal intervals. The tubercles are connected by weak ribs.

GS. G183, about 22 mm in height, is somewhat deformed. It shows three rows of transversely elongated tubercles at equal intervals on the flank. The tubercles are aligned obliquely on weak ribs. Eleven tubercles are counted on the exposed part of the flank, showing ornamentation of moderate density. There is an extra tubercle in the upper row, but it is finer and its upwardly extended rib is faint (see the upper left part of Figure 1-1 or the lower right part of Figure 1-2). As the specimen is an abraded internal mould, the tubercles are not pointed. The tubercles of the fourth row are not exposed on the flank.

GS. G184 is comparatively large, 32 mm in whorl height

and 65 mm in diameter. It is in a nodule and slightly deformed. Shell material is preserved for the most part. The exposed whorl face is subrounded, with a broadly convex main flank and a well rounded upper shoulder. The tubercles are in four rows. They are uniformly spinose and conical at their base. The three rows on the main flank are equidistant; the fourth row is closer to the third at the base. The heads of the spines are, however, nearly equidistant, since the first spine extends obliquely upward, the second laterally, the third slightly downward and the fourth vertically downward (see Figure 1-3, in which the whorl is set upside down). The tubercles are connected transversely by low ribs in somewhat oblique orientation and those of the first row extend upward to the ribs. Some of the ribs appear to be doubled between the tubercles of adjacent rows.

Comparison.—The small specimen (GK. H8512) is comparable with a young specimen illustrated by Atabekian (1985, pl. 3, fig. 1). The second specimen (GS. G183) is comparable with a middle-aged whorl of a figured example (e.g., Atabekian, 1985, pl. 4, fig. 6). The third specimen (GS. G184) is roughly as large as the preserved last whorl of such examples as figured by Scholz (1979, pl. 8, figs. 12, 14, 15), but the uniform spinosity of its ornamentation seems to be peculiar. It should be noted, however, that on a portion of this specimen where the shell layer is stripped off, there are no spines and the tubercles are expressed as transversely elongated elevations like those of GS. G183.

Judging from the above observations, the described specimens can be identified with *M. (M.) bergeri*, although they are incomplete.

Occurrence.—As for material. The upper part of the Member My2 is regarded as the uppermost Albian (Nishida *et al.*, 1996, p. 93; Matsumoto and Nishida, 1999, p. 116).

Discussion.—Klinger and Kennedy (1978, p. 28, pl. 7, figs. C, D; text-fig. 7A) have recorded *M. (M.) cf. bergeri* from the "Lower Cenomanian I" of Zululand (South Africa). It shows a lower apical angle and its lower three rows of tubercles are according to those authors equidistant. It is possibly an example of *M. (M.) dorsetensis* (Spath) from South Africa, whereas "*M. (M.) dorsetensis*" of Klinger and Kennedy (1978, p. 31, pl. 7, fig. F; text-figs. 3A, 8A) is certainly *M. (M.) lewesiensis* (Spath).

Mariella (Mariella) acanthotuberculata Klinger and Kennedy (1978, p. 30, pl. 7, figs. C, D; text-fig. 7A), from the "Lower Cenomanian II" of Zululand, has spinose tubercles in four rows on every whorl, but its ribs and tubercles are relatively coarser and less numerous than those of our specimen (GS. G184). Moreover, it shows a higher apical angle (50° – 60°) and it is different in whorl shape from any example of *M. (M.) bergeri*, for its whorls show a quadrate section and a much lower ratio of height to diameter. Incidentally, the described specimens of *M. (M.) acanthotuberculata* are tiny but beautifully preserved. Here again the spinosity is finely shown when the shell is well preserved.

Mariella (Mariella) aff. bergeri (Brongniart, 1822)

Figures 2; 3-1

Material.—A single specimen, GS. G185 (Figure 2), collected by Y.K. on 29 June 1992 from one of the boulders (p4) at loc. R520 of the East Suribachi-zawa (for the location see Matsumoto and Nishida, 1999, fig. 6). It was probably derived from the basal part of the Member My3. *Graysonites adkinsi* Young was obtained from another boulder at R520.

Description.—Shell is of moderate size, about 140 mm in tower height (total whorl height, including the inferred missing portion) and 55 mm in diameter of the last septate whorl. The rate of size increase between successive whorls is moderate, maintaining a value of 1.37. The apical angle is estimated at 42° . The ratio between whorl height and diameter in the septate stage is constant at 0.43 (see Table 1).

The exposed part of the whorl face is rounded in gross view. In more detail, a nearly flat but narrow space is recognized in the uppermost part of the whorl face. This slopes down gradually to the convex main flank, which then

slopes down inward toward the lower whorl seam. The whorl junction is thus deep and well marked. The siphuncle runs along the midline of the uppermost flat belt.

Despite the regular shell shape in the septate stage, the last part (*i.e.*, the body chamber) of this specimen is much distorted and curved upward. This aberrant shape is similar to that in certain species of *Eubostrychoceras* Matsumoto, 1967. However, whether it is an original character or a product of secondary deformation cannot be decided from this single specimen.

There are three rows of tubercles on the exposed whorl face. The first row is somewhat above the middle of the flank, the second row is well below the midline and closer to the third row, which in turn runs slightly above or nearly along the lower whorl seam. These three rows tend to shift downward with growth. The tubercles of the fourth row are not observable from the outside. They probably lie on the unexposed lower whorl face. The tubercles increase in number with growth, from 24 in the preserved young whorl to 34 in the last septate whorl. Those of the two rows on the main flank are moderately coarse and strengthen with growth. The tubercles in the first row extend upward to

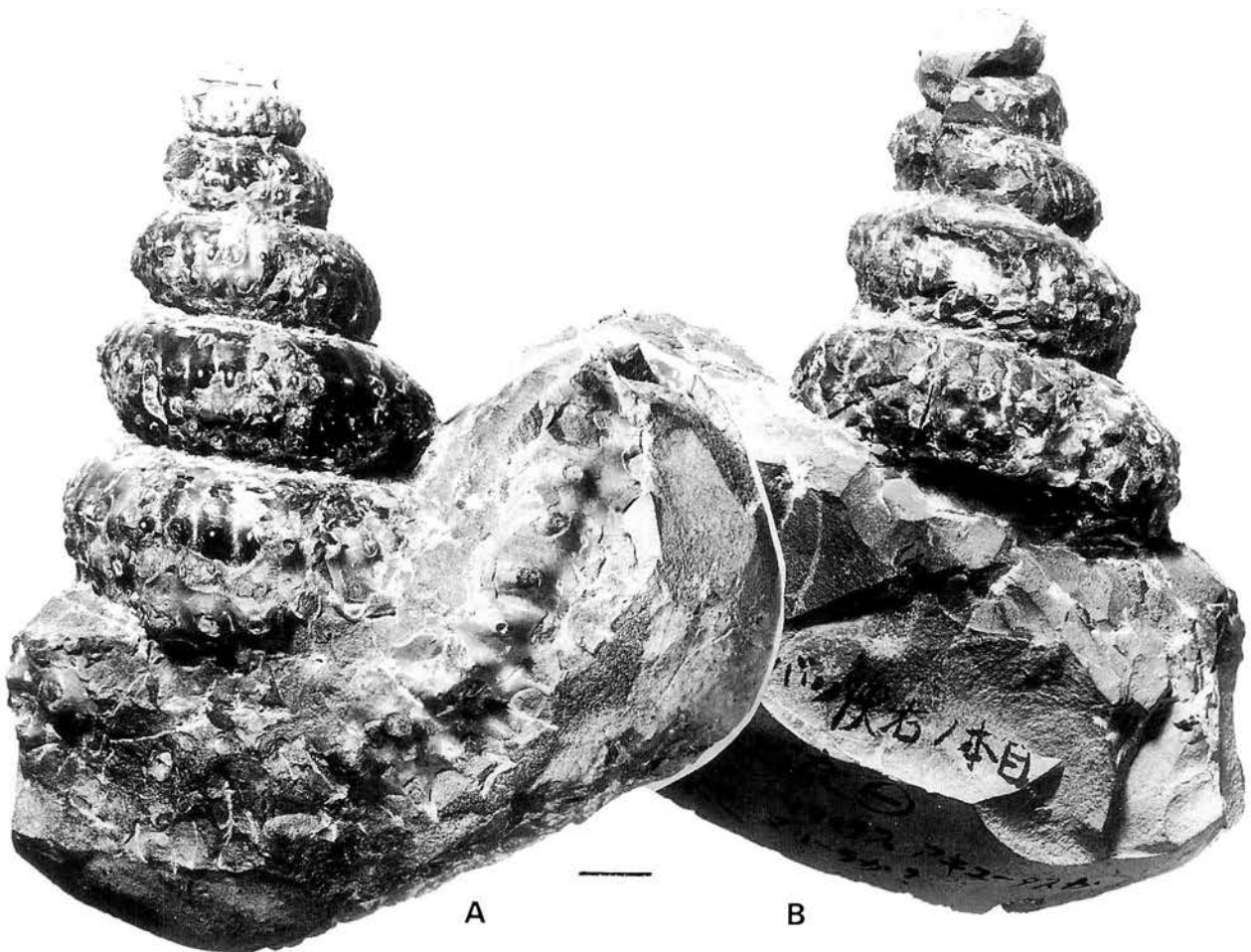


Figure 2. *Mariella (Mariella) aff. bergeri* (Brongniart). GS. G185, two lateral views, in which A is turned 180° to B, $\times 1$. (Photos by N. Egashira without whitening.)

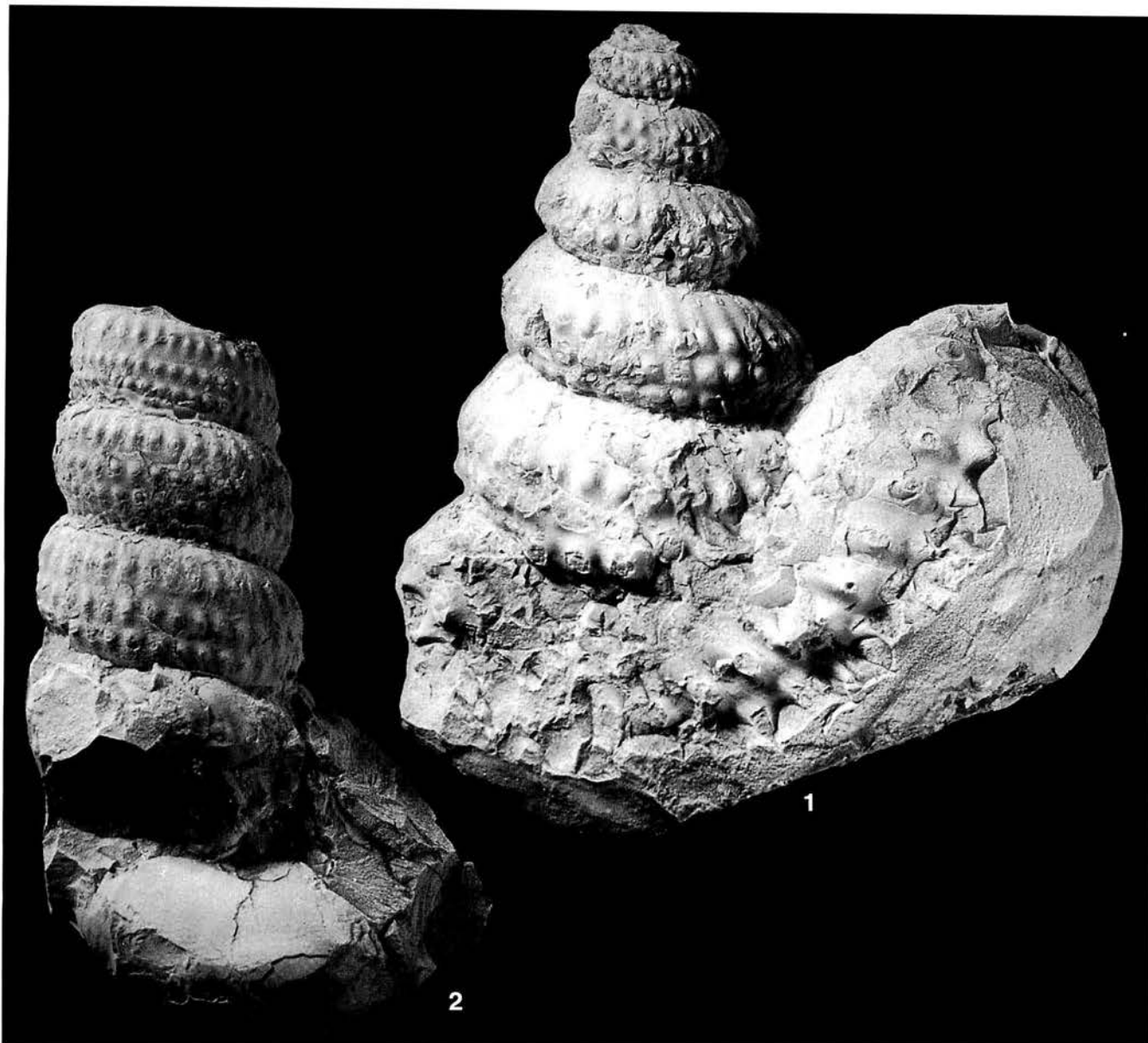


Figure 3. 1. *Mariella (Mariella) aff. bergeri* (Brongniart). GS. G185, lateral view, $\times 1.1$. 2. *Mariella (Mariella) miliaris* (Pictet and Campiche). GS. G186, lateral view, $\times 1.1$. (Photos by N. Egashira with whitening.)

form distinct ribs which fade away onto the uppermost flat belt. The tubercles of the second row are conical and become slightly larger than those of the first row with growth. On the body chamber the tubercles of these two rows strengthen and become spinose. The spines of the tubercles in the second row are much elongated and sharply pointed terminally.

The suture is observable here and there, although it is not traced completely.

Measurements.—See Table 1.

Comparison.—In gross view the septate part of this specimen is similar to some specimens of *Mariella (Mariella) bergeri* (see list of synonymy in the preceding species). The apical

Table 1. Measurements of *Mariella (Mariella) aff. bergeri* (Brongniart). Measured specimen: GS. G185 (Figure 2).

Whorl (Order)*	1st	2nd	3rd	4th	5th
Diameter (in mm)	16.5	25.5	35.0	48.0	65.0
Height (in mm)	7.5	11.0	15.0	20.0	28.0
Height/Diameter	.45	.43	.43	.42	.43
Tubercles per whorl	24	26	28	30	33

* The 1st, 2nd, 3rd etc, on the line "Whorl" indicate the descending order of the whorl (=in an adapertural direction) within the preserved part of the specimen.

angle of the former is certainly larger than the average of the latter, but it can be placed at the extreme end of the wide range of variation in the latter. The existence of a flat belt in the uppermost part of the exposed whorl face seems to be particular to this specimen, although the belt is narrow.

The increase in the number of tubercles or ribs per whorl with growth from 24 in youth to 34 in the last septate stage may be characteristic of this taxon. This rib density is between that of *M. (M.) bergeri* and of *M. (M.) miliaris* (*vide infra*), but the ribs and tubercles are not so fine as those of *M. (M.) miliaris*, becoming rather coarser with growth. The strong tubercles on the flank in the adult whorl have prominent spines. This is another diagnostic feature of this specimen. If the ascending feature of the last part of the body chamber were an original character, it could be regarded as another diagnostic feature, but this should be confirmed by additional material.

To sum up, this specimen probably represents an early Cenomanian new species which was derived from typical *M. (M.) bergeri* of late Albian age. As only a single specimen from a boulder nodule is available, it would be better to call it provisionally *Mariella (M.) aff. bergeri* (Brongniart).

Occurrence.—As for material.

Discussion.—*Turrillites spinosus* Kossmat (1895, p. 142, pl. 20, fig. 3) [= *Turrillites brazoensis* of Stoliczka, 1866, p. 189, pl. 88, fig. 3, (*non* Roemer, 1852)], from the lower Utatur Group of South India, has four rows of spinose tubercles. The original specimen is a large fragmentary whorl (probably body chamber) on which ribs are often bifurcated at the tubercle and some riblets are irregularly added. Certainly it has no affinity with the present taxon. It might be a *Pseud-helicoceras*, as Breistroffer (1947, p. 44) suggested.

***Mariella (Mariella) miliaris* (Pictet and Campiche, 1861)**

Figures 3-2; 4-1, 2

Turrillites bergeri Brongniart var. *miliaris* Pictet and Campiche, 1861, p. 136; 1862, pl. 58, fig. 5.

Mariella miliaris (Pictet and Campiche). Spath, 1937, p. 514, pl. 57, figs. 25, 26, text-fig. 179.

Mariella (Mariella) miliaris (Pictet and Campiche). Chiriac, 1960, p. 456, pl. 1, figs. 14-16; pl. 2, figs. 17-20; Renz, 1968, p. 88, pl. 18, fig. 10; text-figs. 31m, 32h; Förster, 1975, p. 189, pl. 7, figs. 6; Klinger and Kennedy, 1978, p. 29, pl. 3, fig. J, text-fig. 3E; Atabekian, 1985, p. 29, pl. 5, figs. 5-12, pl. 6, figs. 1-3; Wright and Kennedy, 1996, p. 333, pl. 100, fig. 28.

Turrillites (Bergericeras) bergeri bergeri Brongniart. Scholz, 1979, p. 40 (pars), pl. 9, fig. 1 only.

Holotype.—The original of Pictet and Campiche, 1861, p. 136; 1862, pl. 58, fig. 5 (reillustrated by Renz, 1968, pl. 18, fig. 10) (by monotypy).

Material.—GS. G186 (Figures 3-2 and 4-1), obtained by Y.K. on 16 August 1982 from a transported nodule at loc. R575 of the Suribachi-zawa, probably derived from the Member My3. GS. G187 (half ammonoid preservation) found by Y.K. on 31 July 1997 in a transported nodule at loc. R967 (for the location see Nishida *et al.*, 1997, fig. 11) on the upper course of the River Kotanbetsu within the outcropping area of the Member My5. GS. G188 (Figure 4-2) (half ammonoid preser-

vation) obtained by Y.K. on 18 October 1993 from a nodule in the second northern branch rivulet of the Kita-no-sawa, a tributary of the River Shuparo in the Yubari Mountains. It is inferred to have been derived from one of the Members Mc to Me of Kawabe *et al.* (1996, p. 449, fig. 4-3). These members correspond to units 11c and 11d of Matsumoto (1942) and are referred to the lower part of the Cenomanian.

Description.—The three specimens are moderately large. They preserve several whorls. GS. G186 consists of four slightly distorted whorls with a low ratio of increase in diameter. Hence, the apical angle appears to be acute, although whorls of earlier growth stages are not preserved. In the two other specimens of middle to late growth stages, the ratio of increase in diameter is slightly larger than the above and the estimated apical angle would be about 25°, provided that their original total whorl height (=tower height) was about 200 mm.

The exposed whorl face is semielliptical, although the main part of the flank is less convex in GS. G186 in comparison with the two others. The contact between whorls is moderate, showing an impressed junction.

Tubercles in four rows are moderately crowded and numerous, 36 per whorl in GS. G186 and 17 or 18 to half a whorl in GS. G188. They are disposed regularly; those of the first row are placed some way above midflank and extend upward to the ribs which reach the upper whorl seam with decreasing intensity. The conical tubercles of the second row lie below midflank. The tubercles of the third row are somewhat smaller than the above and appear to be granular. The tubercles of the fourth row lie in the inter-whorl junction. They may be somewhat clavate. The tubercles of the three rows on the flank are disposed on an adapturally displaced line, i.e., an approximate extension of the upper rib. The interval of the three rows on the flank slightly decreases downward. The fourth tubercle lies close to the third and the rib is bent at the lower whorl seam, running on the lower whorl surface with a gentle curvature toward the umbilicus.

The suture is only partly exposed and hardly traced wholly.

Measurements.—See Table 2.

Comparison.—The holotype of this species is a piece of a whorl as shown by a photographic illustration of Renz (1968, pl. 18, fig. 10). It was distinguished as a variety from typical "*Turrillites bergeri*" by finer and denser ornament. Although *M. miliaris* was raised to the status of an independent species by Spath (1937, p. 514), the available material was not ample. More material was added by subsequent authors, especially by Chiriac (1960) from Eastern Europe and by Atabekian (1985) from Western Asia. Thus, it has become clear with time that this species shows a considerable extent of variation in morphological characters.

The number of tubercles (or ribs) in each row is around 36 in our specimens. This is within the range of variation from 33 to 40 in the material of Atabekian (1985, p. 29). The apical angle is recorded as 42° in a British specimen (Wright and Kennedy, 1996, p. 333), whereas it is 35°, 30° and even 25° in some specimens from Western Asia (Atabekian, 1985, p. 29). In this respect the described specimens from Hokkaido can be regarded as examples with a comparatively

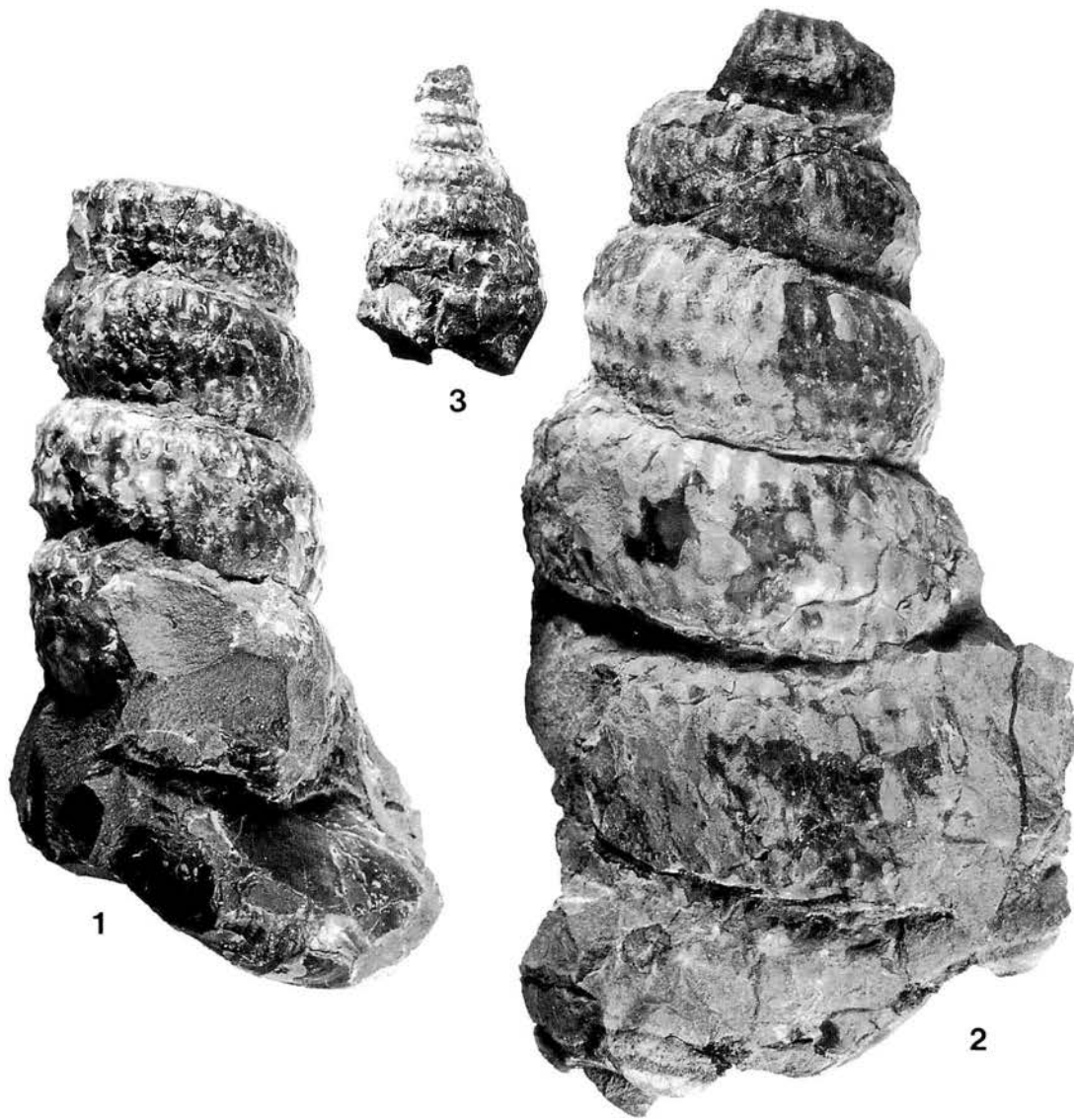


Figure 4. 1, 2. *Mariella (Mariella) miliaris* (Pictet and Campiche). 1. GS. G186, lateral view (90° anticlockwise turned from the view of Figure 3-2), $\times 1$. 2. GS. G188, lateral view, $\times 1$. 3. *Mariella (Mariella)* cf. *carrancoi* (Böse). GK. H8507, lateral view, $\times 1.5$. (Photos by N. Egashira without whitening.)

smaller apical angle within the range of this species.

Hitherto described specimens of this species from various regions of the world are rather small. Most of them are not adult. In fact, the two specimens figured by Atabekian (1985, pl. 5, fig. 5; pl. 6, fig. 1) appear to exemplify whorls of younger stages which can be succeeded developmentally by specimens such as ours which are of middle to late growth stages.

The largest of the whorls measured by Atabekian (1985, p. 29) is 50 mm in diameter, but in GS. G188 (Figure 4-2) from Hokkaido the diameter of the whorl preceding the last is 62 mm. The last whorl (i.e., body chamber) of this shell is deformed, but it has an eroded remnant of the rostrum and, thus, represents an adult shell.

Occurrence.—As for material.

Discussion.—The relationship between *M. (M.) bergeri* and *M. (M.) miliaris* has been discussed by previous authors. Morphologically and also stratigraphically they are intimate. They cannot be distinguished by the difference in apical angle, since the extent of variation in the angle is great in both species.

The proportion of the height (H) to diameter (D) of a whorl is fairly constant in our specimens, 0.46 to 0.48 (see Table 2). This is the same as that of the holotype, in which $D=37.5$, $H=18.0$, $H/D=0.48$ on the basis of Renz' (1968, pl. 18, fig. 10) illustration. A similar value can be estimated for the whorls of many, if not all, of the illustrations of less deformed specimens of *M. (M.) bergeri* (e.g., Renz, 1968, pl. 18, figs. 3, 4 ;

Table 2. Measurements of *Mariella (Mariella) miliaris* (Pictet and Campiche).

Whorl (Order)*	1st	2nd	3rd	4th
Measured specimen : GS. G186 (Figure 4-1)				
Diameter (in mm)	31.0	35.2	39.2	44.0
Height (in mm)	14.2	16.8	18.7	—
Height/Diameter	.46	.48	.48	—
Tubercles per whorl	36	36	36	35
Measured specimen : GS. G188 (Figure 4-2)				
Diameter (in mm)	42.0	52.6	~60.0	—
Height (in mm)	19.5	25.2	28.0	31.5
Height/Diameter	.46	.48	.47	—
Tubercles/half whorl	17	18	~17	—

* : as for Table 1. ~ : approximate

Atabekian, 1985, pl. 2, figs. 4, 5 ; pl. 3, fig. 9). This is another feature that shows the resemblance between the two species.

A sole distinction between the two species is in the ornamentation, namely finer, denser and more numerous ribs and tubercles in *M. (M.) miliaris* in comparison with *M. (M.) bergeri*. In both species, however, there is a considerable variation even in this. The number of tubercles to a whorl is recorded to extend from 33 to 54 in *M. (M.) miliaris* against 25 to 30 in *M. (M.) bergeri*. Thus, the extent of variation in the number of tubercles appears to be continuous between the two taxa. A statistical examination would give a clear solution of the problem.

Stratigraphically *M. (M.) miliaris* has been recorded from the Upper Albian *dispar* Zone in many cases, but in England it is reported also from the Lower Cenomanian (Wright and Kennedy, 1996, p. 333). Our present material suggests, if not clearly indicates, the occurrence in the lower part of the Cenomanian in Hokkaido.

***Mariella (Mariella)* cf. *carrancoi* (Böse, 1923)**

Figure 4-3

Compared.—

Turrillites carrancoi Böse. 1923, p. 147, pl. 10, figs. 25-31.

Turrillites multipunctatus Böse, 1923, p. 154, pl. 10, figs. 48-58.

Mariella (Mariella) carrancoi (Böse). Clark, 1965, p. 44, pl. 13, figs. 1-4, 7, 10.

Lectotype.—IGM. 1076-C, figured by Clark, 1965, pl. 13, fig. 3 (designated by Clark, 1965, p. 44).

Material.—GK. H8507 (Figure 3-3) and GK. H8508-H8511 from a transported nodule collected by Nishida and others on 20 August 1988 at loc. R449 of the upper reaches of the Suribachi-zawa (for the location see Matsumoto and Nishida, 1999, fig. 6). The nodule is inferred to have been derived from the Member My3 from its location and lithology, although the sandstones and mudstones in thin-bedded alternation like those of the Member My2 crop out narrowly between R456 and R460.

Description.—The specimens are more or less incomplete ; six whorls are preserved in GK.H8507, three in H8508, two in H8509, slightly over one in H8510 and only one in H8511.

They are small ; the largest one, H8507, is about 30 mm in tower height and 17 mm in diameter of the last whorl. The apical angle is 43° in H8507 and H8508 but maybe somewhat more acute in H8509. The whorl is subquadrate in section with a trapezoidal flank. The ratio of height to diameter in each whorl is very low, about 0.33 to 0.35 in H8507 and H8508, but it varies to some extent with growth and also between individuals (e.g., 0.42 in H8509). Whorls are tightly coiled and their junction is deep.

The main part of the flank is ornamented by two rows of relatively coarse tubercles, with an apparent spiral groove between them. This feature is more pronounced on young whorls where these tubercles show nodular protuberances and are apparently crowded. The tubercles of the third row are disposed along the lower whorl seam. Those of the fourth row are on the lower whorl face and concealed by the succeeding whorl, unless the basal surface is exposed. The number of tubercles per whorl is 24 to 27. Ribs are scarcely discernible on the younger whorls, but on later whorls the tubercles of the first row extend shortly upward in riblike fashion, the tubercles of the second row are somewhat transversely elongated as if connected with the tubercles of the third row, which in turn give rise to radial ribs on the lower face. The tubercles of the fourth row are tiny and each rests on a rib. This feature is observable partly in GK. H8508 and impressed on the upper surface of GK. H8509.

Suture (E/L saddle and L) is partly discernible on the flank of the middle-aged whorl in GK. H8507.

Comparison.—The above-described specimens are rather peculiar to Japan, but they are well comparable with *M. (M.) carrancoi* (Böse), from the "Vraconian" of Zacatecas, Mexico, redefined by Clark (1965, p. 44, pl. 13, figs. 1-4, 7, 10). Although the absence of ribs is taken as a character of this species by Clark and also by Klinger and Kennedy (1978, p. 31), this is applied to the flank ornament of rather earlier growth stages. At least the riblike extension is observable even in the illustration of the lectotype (Clark, 1965, pl. 13, fig. 3) and more elongated ribs are discernible on the whorl of later growth stages in other specimens (e.g., Clark, 1965, pl. 13, figs. 1, 7 and 10). Even in our specimens the mode of lighting, especially its orientation, gives dissimilar appearances to this character. Some of the figures by Böse (1923, pl. 10, figs. 25-31, 48-58) show variation in the ornament between individuals and also with growth. The low ratio between whorl height and diameter is another diagnostic character of this species. The lectotype, measured on the illustration (Clark, 1965, pl. 13, fig. 3), gives 0.31, 0.32, 0.40 and 0.42 in accordance with growth. Our specimens fall in the same ratio range.

To sum up, a set of specimens from loc. R449 can be almost certainly identified with *Mariella (Mariella) carrancoi* (Böse, 1923). However, the five specimens have some deficiencies in preservation. It would be better to call them tentatively *M. (M.)* cf. *carrancoi*, until material of better preservation is obtained from rocks of a definite stratigraphic level.

Occurrence.—As for material. It should be noted that the present material is inferred to have been derived from the Member My3 of early Cenomanian age, whereas *M. (M.) carrancoi* has been reported to occur in the upper part of the

Albian of Zacatecas, Mexico. The species may range across the Albian–Cenomanian boundary. This should be examined in future.

Mariella (Mariella) gallienii (Boule, Lemoine and Thévenin, 1907)

Figure 5

Turrilites puzosianus d'Orbigny var. *gallienii* Boule, Lemoine and Thévenin, 1907, p. 40, pl. 7, figs. 4, 4a, 4b, 5, 5a.

Turrilites gallienii Boule, Lemoine and Thévenin. Collignon, 1931, p. 89, pl. 9, figs. 15, 16.

Paraturrilites gallienii (Boule, Lemoine and Thévenin). Collignon, 1964, p. 12, pl. 320, figs. 1379, 1380.

Mariella (Mariella) gallienii (Boule, Lemoine and Thévenin) *evoluta* Klinger and Kennedy, 1978, p. 29, pl. 3, figs. C, H, I; pl. 6, figs. B, D, O; pl. 7, figs. A, B; text-figs. 1E; 4E–G.

Mariella (Mariella) gallienii gallienii (Boule, Lemoine and Thévenin). Wright and Kennedy, 1996, p. 333, pl. 98, figs. 2, 3, 25, 27; text-fig. 134, D, E, L.

Lectotype.—The original of Boule, Lemoine and Thévenin, 1907, pl. 7, figs. 4, 4a, 4b, from the Cenomanian of Diégo Suarez, northeastern Madagascar (designated by Wright and Kennedy, 1996, p. 333).

Material.—GS. G189 (Figure 5-1), GS. G190 (Figure 5-2, 3), GS. G191 (Figure 5-4), GS. G192 (half ammonoid preservation) and GS. G193 (fragmentary), collected by Y.K. and N. Egashira on 21 June 1996 from a nodule contained in the mudstone of the Member My3 at loc. R906 of the Hotei-

zawa, Soeushinai area (for the location see fig. 7 in Part 1).

Description.—GS. G189 consists of two tightly coiled whorls, although the earliest part is unpreserved. Its whorl is subrounded in cross section, with a broadly convex main part of the flank which passes across the abruptly rounded shoulder to the narrow upper face and likewise downward to the gently convex lower surface. The estimated apical angle is high (60°). The ornament of this specimen consists of numerous, densely disposed, weakly oblique ribs on which small tubercles are set in four rows at subequal intervals. The ribs start at the upper whorl seam and run across the upper shoulder to the main part of the flank and further across the lower shoulder to the basal surface. The ribs are thus continuous, but they slightly weaken at the interspaces of the three tubercles, resulting in two shallow spiral depressions on the flank (Figure 5-1a, b). The tiny fourth tubercles are discernible on the basal surface where ribs run to the umbilical margin with a gentle curvature (Figure 5-1c).

The three specimens, GS. G190–G192, show a tall turreted shape, consisting of several (4 to 6) whorls. They seem to show an apparently low apical angle, but the actual apex is not known, because several whorls of the youngest stage are not well shown. The whorls are rather loosely coiled in the main to later growth stages and the last one (body chamber) is detached in GS. G191 (Figure 5-4), although this feature might be secondary. It should be noted that the whorls in earlier stages seem to be fairly tightly coiled (Figure 5-2, 3, 4). In the young stage of these specimens the whorl shape is fairly similar to that of the above small specimens

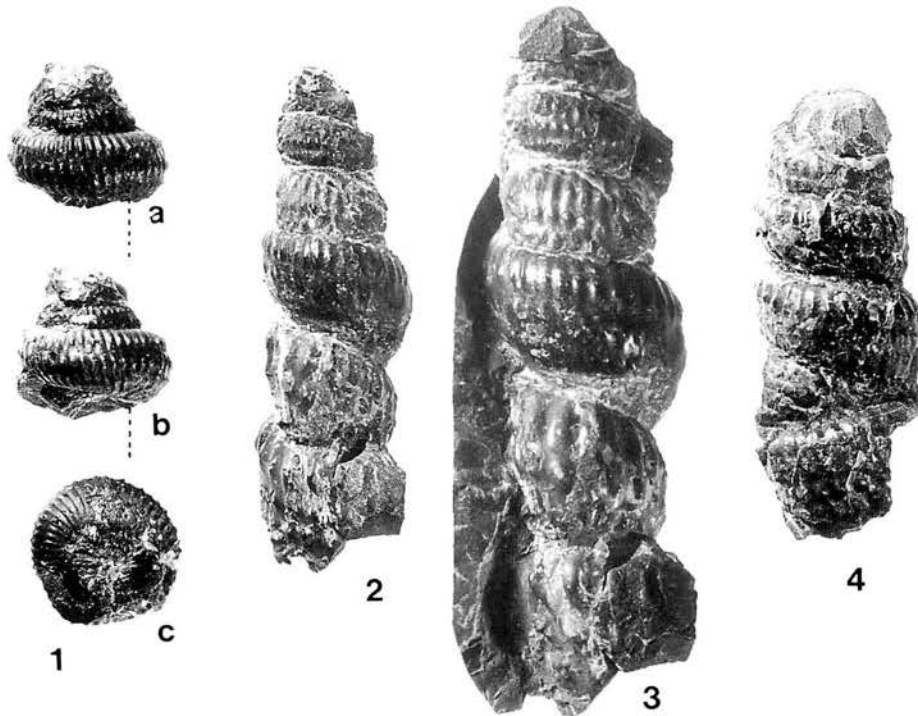


Figure 5. *Mariella (Mariella) gallienii* (Boule, Lemoin and Thévenin). 1. GS. G189, two lateral (a, b) and basal (c) views, × 4/3. 2. GS. G190, lateral view, ×1. 3. GS. G190, lateral view before it is detached from the host rock, ×1.4. 4. GS. G191, lateral view, × 4/3. (Photos by N. Egashira without whitening.)

(GS. G189), but in later stages the whorl becomes increasingly higher, with a weakly convex to nearly flat main flank and a rather oblong section. The ornamentation of these specimens is fundamentally similar to that of the first specimen (GS. G189), but the rib density (or the number of ribs per whorl) varies with growth and between individuals. The variation in the rib density and also in shell shape may be expressed by the columns Ribs and H/D in Table 3. Thus, the ribbing becomes less dense with growth. In GS. G190 the ornament is especially coarse on the loosely coiled last whorl (Figure 5-3).

Septal sutures are observable where the shell layer is taken away, as on the third whorl from the bottom in GS. G190.

Measurements.—See Table 3.

Comparison.—GS. G189 (Figure 5-1) is fairly similar to the lectotype (see above) of this species. Although the ribs are denser in the latter, the difference is by no means great (see Table 3). Our specimen is morphologically intermediate between the lectotype and paralectotype (Boule *et al.*, 1907, pl. 7, figs. 4 and 5) from Madagascar.

The two whorls of the middle growth stage in GS. G190 and GS. G191 resemble those of MNHP R1073 from Madagascar described by Collignon (1931, pl. 9, fig. 16) and reillustrated by Wright and Kennedy (1996, text-fig. 134 L). Another specimen from the lectotype locality in Madagascar, illustrated by Collignon (1964, pl. 320, fig. 1379) and reillustrated by Wright and Kennedy (1996, text-fig. 134E) exemplifies a distinct change of relative whorl diameter at a certain young stage. This may support the presumed shape of the missing or poorly preserved young part of the three specimens (GS. G190-192) mentioned above.

Occurrence.—As for material. Outside Hokkaido, this species has been recorded in the Lower Cenomanian of Madagascar, South Africa and England (see references in the synonymy).

Discussion.—This species was established as a variety of

Table 3. Measurements of *Mariella (Mariella) gallienii* (Boule, Lemoine and Thévenin).

Specimen Whorl*	Diameter	Height	H./D.	Ribs
GS. G189 (1st)	10.2	3.4	.33	—
GS. G189 (2nd)	14.5	6.5	.45	46
GS. G190 (2nd)	13.5	6.8	.50	~36
GS. G190 (4th)	20.4	13.3	.65	42
GS. G191 (1st)	17.0	6.4	.38	~32
GS. G191 (2nd)	21.0	10.0	.48	34
GS. G191 (3rd)	23.0	13.5	.59	37
Lectotype	16.0	7.5	.47	50
GK specimen	19.0	10.5	.55	34

* The order in the column "Whorl" as for Table 1. Ribs: number of ribs per whorl; ~approximate number of ribs estimated from the measurable number in case of half whorl preservation. Lectotype is measured on the illustration in Boule *et al.*, 1907, pl. 7, fig. 4a, b. GK specimen means an example from the Lower Cenomanian I at Skoenberg, Zululand, South Africa, kindly donated by W. J. Kennedy.

Ostlingoceras puzosianus. This assignment has been revised by subsequent authors, as indicated in the synonymy list.

Klinger and Kennedy (1978, p. 29, pl. 3, figs. C, H, I; pl. 6, figs. B, D, O; pl. 7, figs. A, B; text-figs. 1E, 4E-G) established a subspecies *M. (M.) gallienii evoluta*, "which is characterized by loose coiling in which successive whorls are only slightly impressed." Although we have not looked at the actual specimen, the holotype of subspecies *evoluta* (*op. cit.*, pl. 6, fig. C) does not seem to be so loosely coiled as the middle-to-late-stage of GS. G190 and G191. In our material the mode of coiling (loose or tight coiling) varies with growth and also between individuals. Moreover, the tightly coiled small specimen and larger ones with loosely coiled later whorls are contained in the same nodule. The Hokkaido material shows good conformity with that from Madagascar, which lay close to Zululand in mid-Cretaceous time. Some of the specimens from England (e.g., Wright and Kennedy, 1996, pl. 98, fig. 25) seems to show a rather loose coiling. A specimen from Zululand, donated to GK by Kennedy, is intermediate in the mode of coiling and rib density. For these reasons we are inclined to regard the subspecific separation as unnecessary and unnatural.

Concluding remarks

The genus *Mariella* of the Turrilitidae ranges from the Upper Albian to the Lower Cenomanian and includes a fair number of species. In these two successive papers altogether eight species of the subgenus *Mariella (Mariella)* from Hokkaido (northern Japan) have been described.

In Part 1 *M. (M.) dorsetensis* (Spath), *M. (M.) oehlerti* (Pervinquieré) and *M. (M.) pacifica* Matsumoto, Inoma and Kawashita have been recorded to occur fairly commonly or very abundantly (the second species) in the Lower Cenomanian of the Soeushinai area (northwestern Hokkaido). *M. (M.) dorsetensis* and *M. (M.) oehlerti* are distributed worldwide in the Lower Cenomanian. They can be regarded as cosmopolitan elements of the fauna and are useful for interregional correlation. *M. (M.) pacifica*, which was established in Part 1, is so far endemic, but its wider distribution would be expected in view of its similarity to *M. (M.) torquatus* Wright and Kennedy and *M. (M.) numida* (Pervinquieré) and its having some affinity with late Albian *M. (M.) camachoensis* (Böse).

The five species described in Part 2 are based on a rather small number of specimens, but they are interesting in creating some problems either in taxonomy or in stratigraphic occurrence. *M. (M.) bergeri* was obtained from the upper part of the Member My2 in the Soeushinai area, that is a correlative of the uppermost Albian. One of the specimens shows finely preserved spines. The second species tentatively called *M. (M.) aff. bergeri* is probably new for its particular characters. It came from the lower part of the Member My3, i.e., the basal Cenomanian. The third is identified with *M. (M.) miliaris* redefined by Atabekian (1985). It is based on three specimens which are inferred to have been derived from the Lower Cenomanian. The fourth is referred to *M. (M.) cf. carrancoi* (Böse). *M. (M.) carrancoi* is originally from the Upper Albian of Mexico, but our material

probably came from the Lower Cenomanian. The fifth is *M. (M.) gallienii* from the Lower Cenomanian. The subspecific separation of *M. (M.) gallienii gallienii* and *M. (M.) gallienii evoluta* may be unnecessary, for the reasons stated.

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Planktonic foraminifera and biochronology of the Cenomanian–Turonian (Cretaceous) sequence in the Oyubari area, Hokkaido, Japan

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Abstract. A Cenomanian and Turonian (Late Cretaceous) sequence along the Shirakin River, Oyubari area, central Hokkaido, Japan contains seven datum planes of planktonic foraminifera that can be used to establish international correlations. These datum planes are marked by the first appearance of *Praeglobotruncana gibba*, *Rotalipora greenhornensis*, *Rotalipora deecke*, *Marginotruncana schneegansi* and *Marginotruncana pseudolinneiana*, and the last appearance of *Rotalipora deecke* and *Rotalipora cushmani*. These datum planes can be correlated with international Cretaceous planktonic foraminiferal zones in the interval KS17–KS22. Seventeen planktonic foraminiferal species are described including five new species: *Hedbergella kyphoma*, *Praeglobotruncana compressa*, *Praeglobotruncana inermis*, *Praeglobotruncana shirakinensis*, and *Dicarinella takayanagii*.

Key words: biostratigraphy, Cenomanian, Cretaceous, datum plane, planktonic foraminifera, Turonian, Yezo Group

Introduction

The Cretaceous Yezo Group in Hokkaido, Japan yields abundant ammonites and inoceramids that have been used to create a number of regional biostratigraphic zones. However, most of these molluscan fossils cannot be used for high resolution biochronology and international correlation (e. g. Matsumoto, 1942, 1943; Hirano *et al.*, 1977, 1981; Hirano, 1982). On the other hand, there have been few biostratigraphic studies of calcareous microfossils in the Yezo Group. A planktonic foraminiferal biostratigraphy of the Yezo Group was first established by Takayanagi in 1960. Subsequently, Takayanagi and Iwamoto (1962) and Takayanagi and Okamura (1977) have reported planktonic foraminiferal occurrences from the group. Maiya and Takayanagi (1977) and Maiya (1985) summarized a Japanese planktonic foraminiferal zonation. However, these zonations have not been adequate for detailed interregional correlation of local Japanese Cretaceous sequences. In this decade, Motoyama *et al.* (1991), Hasegawa and Saito (1993), Hasegawa (1997) and Takashima *et al.* (1997) reported Cretaceous planktonic foraminiferal biostratigraphy from the Oyubari area of central Hokkaido and their reported taxa suggest that age-diagnostic species are available for international correlation. Nishida *et al.* (1993) presented additional data on the

biostratigraphic correlation of the Oyubari sequence based on micro- and megafossils. Hasegawa (1995) further clarified the precise stratigraphic position of the last appearances of *Rotalipora greenhornensis* and *Rotalipora cushmani* and of the first appearance of *Marginotruncana schneegansi* near the Cenomanian/Turonian (C/T) boundary. Recently, Hasegawa (1997) used a comprehensive biostratigraphy of planktonic foraminifera to demonstrate interregional synchronicity of carbon isotopic events during Cenomanian–Turonian age. However, with the exception of Kaiho's (1992) work on Campanian species, no descriptive work on planktonic foraminiferal species of the Yezo Group has been presented in recent years.

This study describes seven planktonic foraminiferal datum planes recognized in the Cenomanian–Turonian sequence exposed along the Shirakin River in the Oyubari area and attempts biostratigraphic correlation with the international zonation established by Sliter (1989). Planktonic foraminiferal species, including twelve age-indicative species and five new species, are described.

Materials and methods

Samples used in this study were collected from the Yezo Group mainly along the Shirakin (=Hakkinzawa) River,

Oyubari area, central Hokkaido, Japan (Figures 1, 2). The Yezo Group is interpreted as a forearc basin facies (Okada, 1979, 1983). In the Oyubari area, the Cenomanian-Turonian sequence of the group is represented by the Hikagenosawa and Takinosawa Formations as defined by Motoyama *et al.* (1991). Approximately 300 samples were collected and processed. Near the C/T boundary, sampling was at approximately 2.5 m intervals. Faunal analyses are based on 49 planktonic foraminifera-bearing samples consisting largely of siltstone in the Cenomanian-Turonian section. Samples weighing approximately 240 g were disaggregated using sodium sulfate, naphtha solution (Maiya and Inoue, 1973), and sodium tetraphenylborate plus sodium chloride (Hanken, 1979), washed through a 63 μm screen and dried. All specimens larger than 180 μm were identified. Additionally, larger samples (500–800 g) were analyzed in the boundary sequence from 7 m below to 40 m above the C/T boundary. All specimens described herein are deposited in the Department of Geoenvironmental Science, Faculty of Science, Tohoku University.

Biostratigraphy

The planktonic foraminiferal assemblages are listed in Table 1. A detailed biostratigraphy near the C/T boundary has been established along the Shirakin River, based on continuous occurrences of planktonic foraminifera (Hasegawa, 1995; Hasegawa, 1997). Common occurrence of internationally recognized species, especially those within the genera *Rotalipora* and *Marginotruncana* allow correlation with datum planes as summarized by Caron (1985) and Sliter (1989).

The stratigraphic distribution of planktonic foraminifers in the Oyubari section is shown in Figures 3 and 4. In addition, two late Cenomanian samples collected from the Kashimamigimata River (Figure 2) are included in the data presented in Figure 3. Although the Hikagenosawa Formation (Figure 3) includes a low-diversity assemblage, several species have biostratigraphic utility, including *Rotalipora gandolfii* (Luterbacher and Premoli-Silva) from the lower to middle, and *Præglobotruncana gibba* Klaus, *Rotalipora greenhornensis* (Morrow) and *Rotalipora deeckeii* (Franke) from the uppermost part of the formation. On the other hand, the lower part of the Takinosawa Formation is characterized by highly diversified assemblages including such international zonal species as *Rotalipora cushmani* (Morrow) and *Helvetoglobotruncana helvetica* (Bolli) as well as the age-indicative species *R. greenhornensis*, *R. deeckeii* and *Marginotruncana schneegansi* (Sigal). In the middle to upper part of the Takinosawa Formation and in the overlying Shirogane Formation, the planktonic foraminiferal diversity declines again, with only two biochronologically important species, *Marginotruncana pseudolinneiana* Pessagno and *Marginotruncana coronata* (Bolli), having correlational significance.

Datum planes

Based on the stratigraphic distribution of the species that belong to the genera *Rotalipora* and *Marginotruncana* and other important age-diagnostic species (e.g., *Helvetoglobotruncana helvetica* and *Præglobotruncana* spp.), seven bioevent horizons (i.e., FAD, first appearance datum; LAD, last appearance datum) were recognized in the Shirakin River section as reliable datum planes. These are discus-

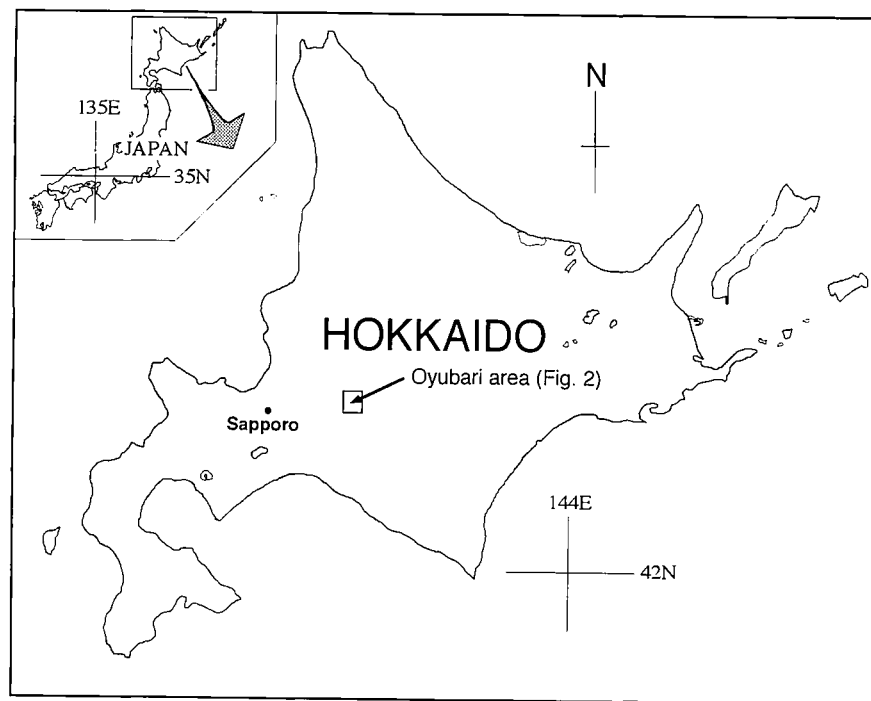


Figure 1. Index map showing the locality of the Oyubari area.

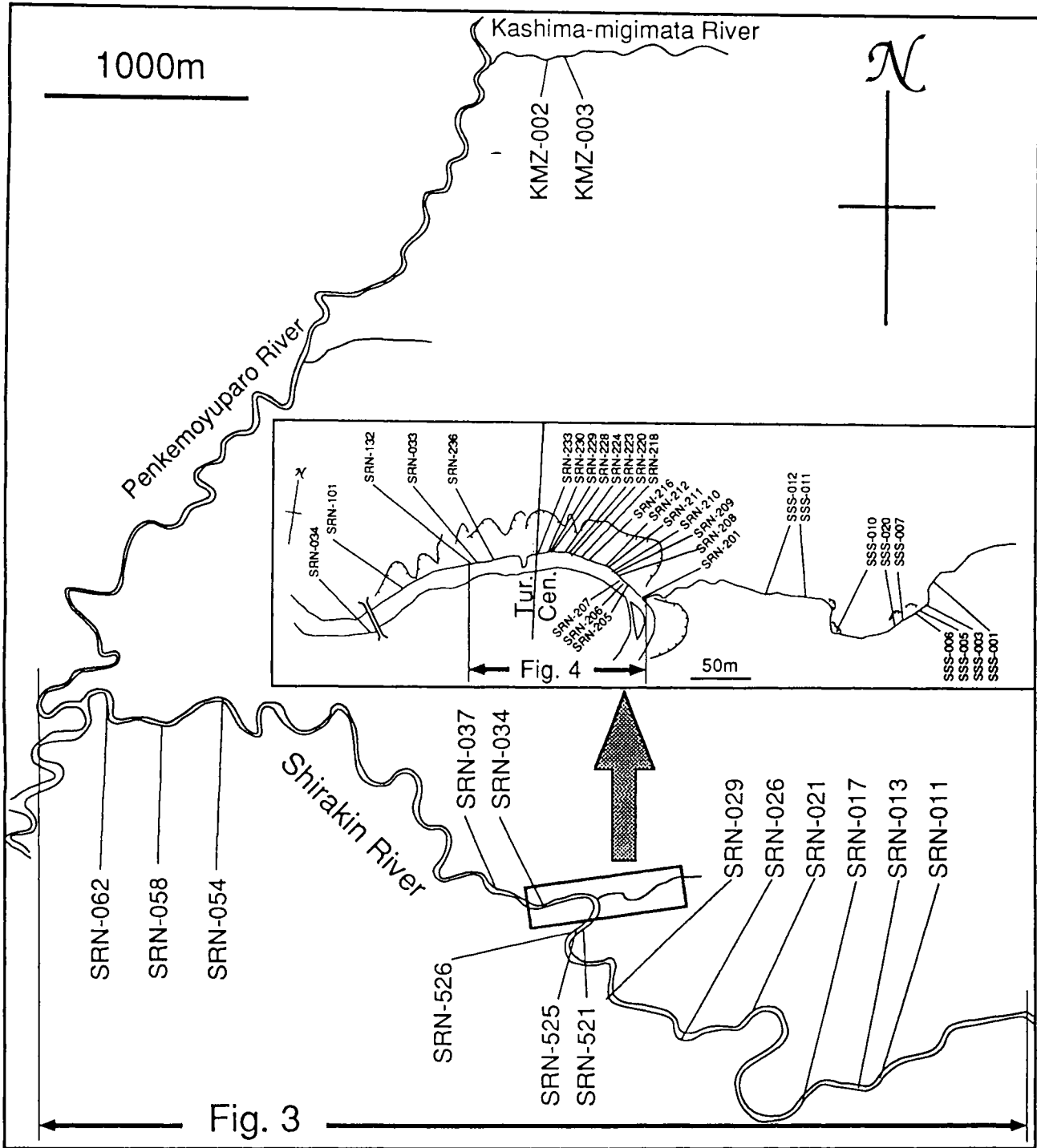


Figure 2. Map showing sampling localities in the Oyubari area.

sed separately below.

A: FAD of *Praeglobotruncana gibba*

This datum is early Cenomanian. FAD of *P. gibba* in the middle part of the Hikagenosawa Formation is observed about 180 m below the FAD of *R. greenhornensis*. Accord-

ing to Caron (1985), the FAD of *P. gibba* is located just below the FAD of *R. greenhornensis*, which is consistent with its first occurrence in the Oyubari section. *Rotalipora brotzeni* first occurred above this datum, but its occurrence is too rare to establish a reliable datum level. The planktonic foraminiferal assemblage below this datum is mainly composed

Table 1. Stratigraphic occurrences of planktonic foraminifera in the Oyubari area. Symbols denote the number 2" or "1/4" written under the total number mean that 1/2 or 1/4 fraction of residues of 240 g rock samples were rences shown with parentheses indicate the inclusion of specimens of which specific name can only be given with

Species	sample No.	SRN	SRN	SRN	SRN	SRN	SRN	KMZ	SRN	SSS	SSS	KMZ	SSS	SSS	SSS	SSS	SSS	SSS	SRN	SRN	SRN	SRN	
		011	013	017	021	022	025	003	026	001	003	002	005	006	007	020	010	011	012	029	201	205	206
<i>Globigerinelloides</i>	<i>ultramica</i>							R				F	R										
G.	<i>cf. bentonensis</i>																						
G.	<i>cf. eaglefordensis</i>																						
G.	spp.																						
<i>Hedbergella</i>	<i>delrioensis</i>		C	R	F				R	A	VA	F	C	VA	R	R	R	F	(A)				
H.	<i>planispira</i>		F	R	R			F			VA		R						R	C			
H.	<i>kyphoma</i> sp. nov.							F															
H.	spp.									R													
<i>Rotalipora</i>	<i>cf. appenninica</i>									R													
R.	<i>gandolfii</i>				R			R								R							
R.	<i>brotzeni</i>				R			R				R											
R.	<i>greenhornensis</i>				F		R	C			R	F	F									R	
R.	<i>deeckeii</i>							R				F											
R.	<i>cushmani</i>												F	R								R	
R.	spp.				R							R											
<i>Praeglobotruncana</i>	<i>delrioensis</i>	R		A	VA	R			A	R	A		C	C	F		C	A	C		R	R	
P.	<i>stephani</i>			C	VA	R	R		A	VA	C	F	VA	F	F	R	A	VA	C	A	R	A	F
P.	<i>gibba</i>			F	A				A	A	C	A	F	F	F	R	A	C	F	R	A	C	
P.	<i>anumalensis</i>					R				VA	VA	R	VA	VA				VA	A	F		A	C
P.	<i>shirakinensis</i> sp. nov.				A					C												C	
P.	<i>inermis</i> sp. nov.							R	A	C		F	F	R			C	R				A	
P.	<i>compressa</i> sp. nov.													R		F	F		R	R	C		
P.	spp.								A	C		C	R			A	F		R	A			
<i>Whiteinella</i>	<i>cf. archaеоcretacea</i>								A	R			F	R		R						R	
W.	<i>aprica</i>				R			R									C	(F)					
W.	<i>baltica</i>									A		F	A					C					
W.	<i>brittonensis</i>								F	A							R	(R)					
W.	<i>inornata</i>																						
W.	spp.								C				F		R	C	A					C	
<i>Dicarinella</i>	<i>imbricata</i>							R	F					R								F	
D.	<i>canaliculata</i>								A														
D.	<i>takayanagii</i> sp. nov.								A			(R)											
D.	<i>hagni</i>																		(R)				
D.	<i>roddai</i>																						
D.	<i>japonica</i>																						
D.	spp.								R					R									
<i>Helvetoglobotruncana</i>	<i>helvetica</i>														R								
<i>Marginotruncana</i>	<i>marginata</i>																						
M.	<i>schneeigansii</i>																						
M.	<i>pseudolinneiana</i>																						
M.	<i>cf. coronata</i>																						
Indeterminable specimens		1	4	1		1	0	0	9	34	11	1	30	24	10	1	3	23	11	2	0	17	0
Total number		2	14	28	335	7	2	20	56	132	103	22	164	154	25	9	29	100	109	15	9	110	19
									(1/2)	(1/2)			(1/2)										

of long-ranging species such as *Hedbergella delrioensis* (Carsey), *Hedbergella planispira* (Tappan), *Globigerinelloides ultramica* (Subbotina), *Praeglobotruncana delrioensis* (Plummer) and *Praeglobotruncana stephani* (Gandolfi).

B: FAD of *Rotalipora greenhornensis*

This datum is early-middle Cenomanian. The FAD of *Rotalipora greenhornensis* occurs in the upper part of the Hikagenosawa Formation. According to Caron (1985) and Sliter (1989), *R. greenhornensis* and *R. cushmani* have the same FAD. However, *Rotalipora cushmani* first occurs above the FAD of *R. greenhornensis* in the Oyubari section. The first occurrence of *R. cushmani* in the Oyubari section is observed above the LAD of *Rotalipora deeckeii* and even above the first-occurrence horizon of the genus *Dicarinella*. This delayed first occurrence of *R. cushmani* is interpreted as a migration event of this species in this area. The strati-

graphic relationship of the FAD of *R. greenhornensis* with other bioevents is concordant with that shown by Caron (1985) and Sliter (1989). The planktonic foraminiferal assemblage between the FAD of *P. gibba* and the FAD of *R. greenhornensis* is similar to that occurring below the FAD of *P. gibba*.

C: FAD of *Rotalipora deeckeii*

This datum is late Cenomanian. *Rotalipora deeckeii* is a short-ranging age-diagnostic species of late Cenomanian age. According to Sliter (1989) and Robaszynski and Caron (1979), the total range of *R. deeckeii* characterizes the upper part of the *Rotalipora cushmani* Zone (the range of *Rotalipora deeckeii* is not shown in the range distribution chart of Caron, 1985). Stratigraphically, the FAD of *R. deeckeii* lies near the top of the Hikagenosawa Formation. The occurrences of *Whiteinella* spp. and *Dicarinella* spp. within the total range of

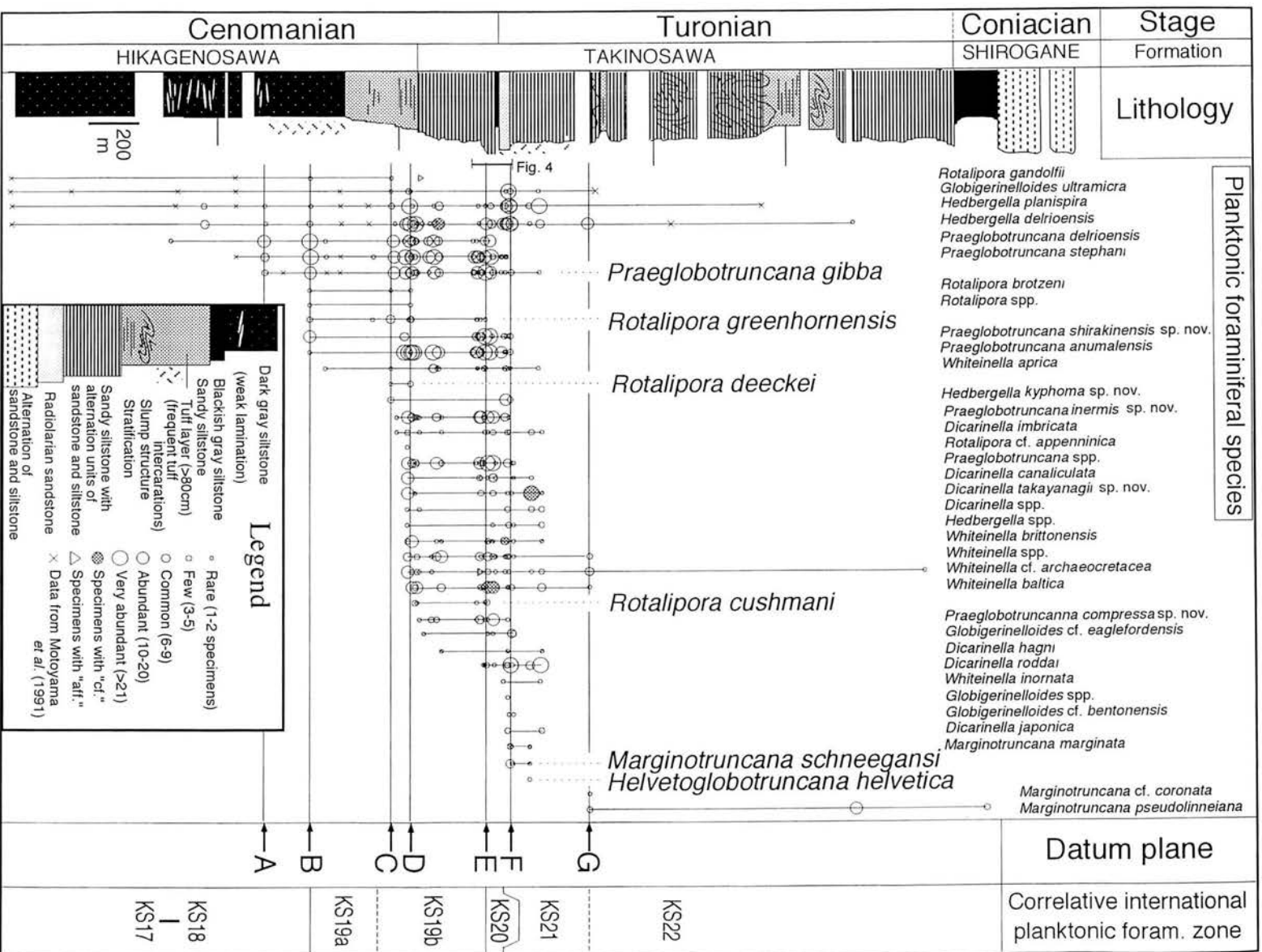
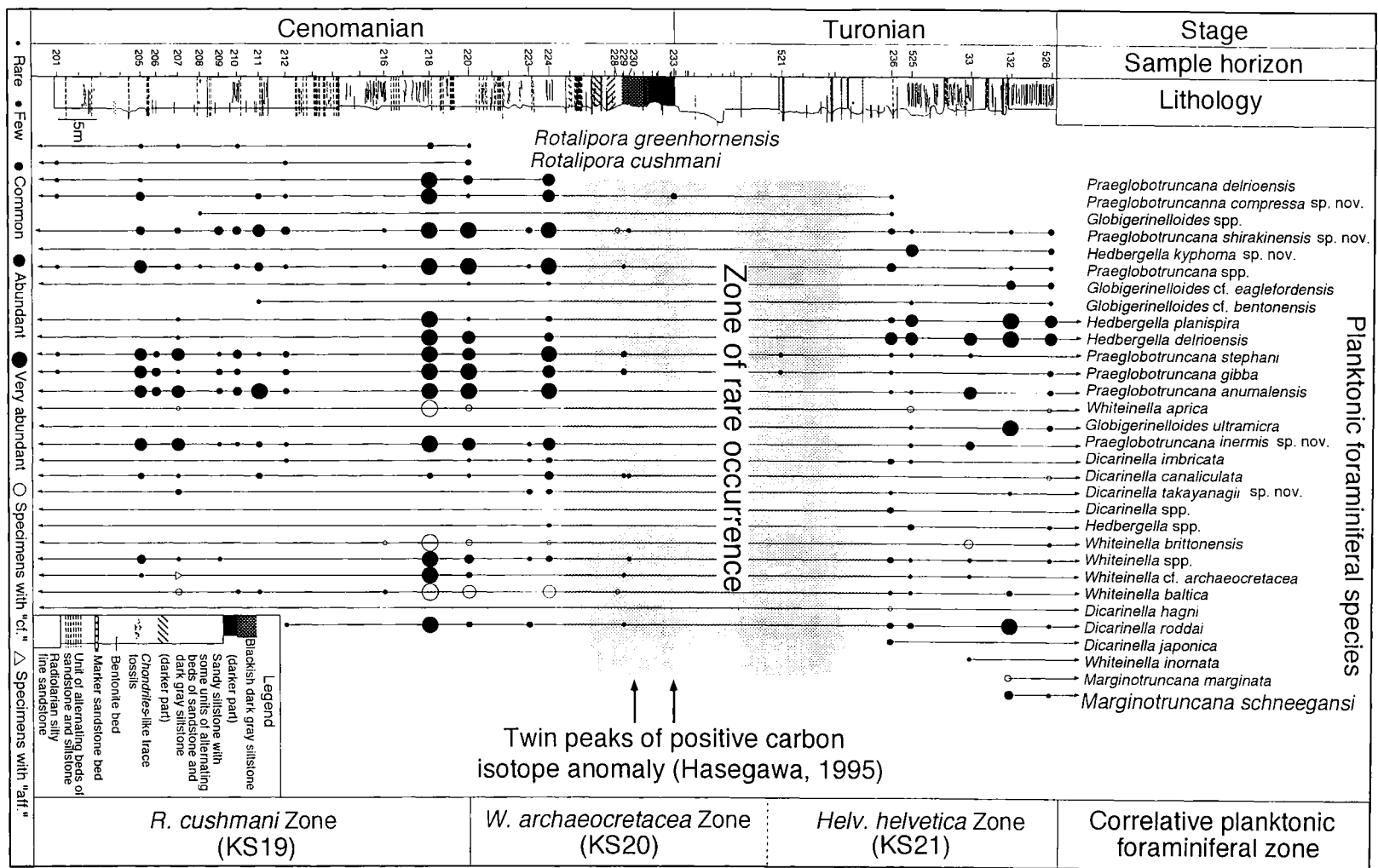


Figure 3. Stratigraphic distribution of planktonic foraminiferal species along the Shirakin River and the tributary of Penkemyuuparo River in the Oyubari area (reproduced from Hasegawa, 1997, with permission from Elsevier Science). Seven reliable datum planes are recognized in the section (see text for notation of datum planes). Symbols denote the number of specimens included in each 240 g rock sample.



Planktonic foraminifera from Hokkaido

Figure 4. Stratigraphic distribution of planktonic foraminiferal species just across the Cenomanian/Turonian boundary along the Shirakin River (Hasegawa, 1995 : Reproduction permitted by the Geological Society of Japan). Horizons of twin peaks of positive $\delta^{13}C$ anomaly and stratigraphic range of rare planktonic foraminiferal occurrences are also indicated. Symbols denote the number of specimens included in each 240 g rock sample. Very abundant : >21 specimens, Abundant : 10~20, Common : 6~9, Few : 3~5, Rare : 1 or 2.

occurrences. Jarvis *et al.* (1988) and Hart and Leary (1989) also noted nearly synchronous last occurrences of these two species in Southeast England. Therefore, the LAD of *R. cushmani* observed in Hokkaido is regarded as a reliable datum plane for interregional correlation. The planktonic foraminiferal assemblage between the LAD of *R. deecke* and LAD of *R. cushmani* shows the highest diversity in the Oyubari area. The most abundant species of the assemblage are *Praeglobotruncana* spp. with common *Whiteinella* spp. and less *Rotalipora* spp. and *Dicarinella* spp.

In the northern Oyubari area, Takashima *et al.* (1997) attempted to recognize KS zones (Sliter, 1989). Rare occurrences of *Rotalipora* species did not allow them to correlate their upper Cenomanian sequences to KS zones directly with zone-indicative species. Such rare occurrences of *Rotalipora* may partly depend on the marine paleoenvironment of the northern Oyubari area being a shallower one than in the southern area, where the samples of this study were collected.

F: FAD of *Marginotruncana schneegansi*

This datum is early Turonian. The FAD of *Marginotruncana schneegansi* occurs just above the "Radiolarian sandstone" (Hasegawa and Saito, 1993; Hasegawa, 1995) developed in the lower-middle part of the Takinosawa Formation. *Helvetoglobotruncana helvetica*, which is a commonly used datum species for the recognition of early Turonian age occurred above the FAD of *M. schneegansi*. According to Caron (1985) and Sliter (1989), the concurrent range of these two species is quite restricted. Therefore, the FAD of *M. schneegansi* is interpreted to be a reliable datum plane in Hokkaido. The planktonic foraminiferal assemblage between the LAD of *R. cushmani* and the FAD of *M. schneegansi* is also a high-diversity assemblage except in the middle part of the interval (Figure 4). Between SRN-224 and SRN-236, planktonic foraminifers are rare and the diversity is low despite a high density of large samples (500–800 g). This low-diversity event has also been recognized in other areas of the world (e.g. Hart and Leary, 1989). An oceanic event termed "Oceanic Anoxic Event (OAE)" (Schlanger and Jenkyns, 1970) or "Cenomanian Turonian Boundary Event (CTBE)" (Thurrow and Kuhnt, 1986) may be responsible for this worldwide synchronous phenomenon.

G: FAD of *Marginotruncana pseudolinneiana*

This datum is middle Turonian. The FAD of *Marginotruncana pseudolinneiana* is located in the middle of the Takinosawa Formation and this species is a common one in the

middle Turonian and Coniacian interval. The stratigraphic distributions of other international species across this datum in the Oyubari section are consistent with occurrences known from other parts of the world (e.g. Robaszynski and Caron, 1979; Caron, 1985; Sliter, 1989). Therefore, the FAD of *M. pseudolinneiana* is considered to be a reliable datum plane. The stratigraphic interval between the FAD of *M. schneegansi* and the FAD of *M. pseudolinneiana* yields a moderately diversified assemblage. However, the upper part of this interval and sequence above the FAD of *M. pseudolinneiana* yield less abundant and lowly diverse assemblages.

Recognition of zonal boundary

Stratigraphic units equivalent to the international planktonic foraminiferal zones are recognized in the Oyubari section (Figures 3 and 4) by correlating these datum planes with those shown by Sliter (1989) and Caron (1985). The upper limit of each zone is drawn as follows:

KS18: at the FAD of *R. greenhornensis*;

KS19a: estimated to lie just below the FAD of *R. deecke* and above the FAD of *R. greenhornensis*;

KS19b: at the LAD of *R. cushmani*;

KS20: estimated to lie just below the FAD of *Pseudaspidoceras flexuosum* (an ammonoid) below the FAD of *M. schneegansi* (see Hasegawa, 1995 for further discussion). At the north of the studied area, Takashima *et al.* (1997) recognized the zonal marker species, *Helvetoglobotruncana helvetica*;

KS21: estimated to occur near the FAD of *M. pseudolinneiana*.

Systematic paleontology

Superfamily Rotaliporacea Sigal, 1958

Family Hedbergellidae Loeblich and Tappan, 1961

Subfamily Hedbergellinae Loeblich and Tappan, 1961

Genus *Hedbergella* Bronnimann and Brown, 1958

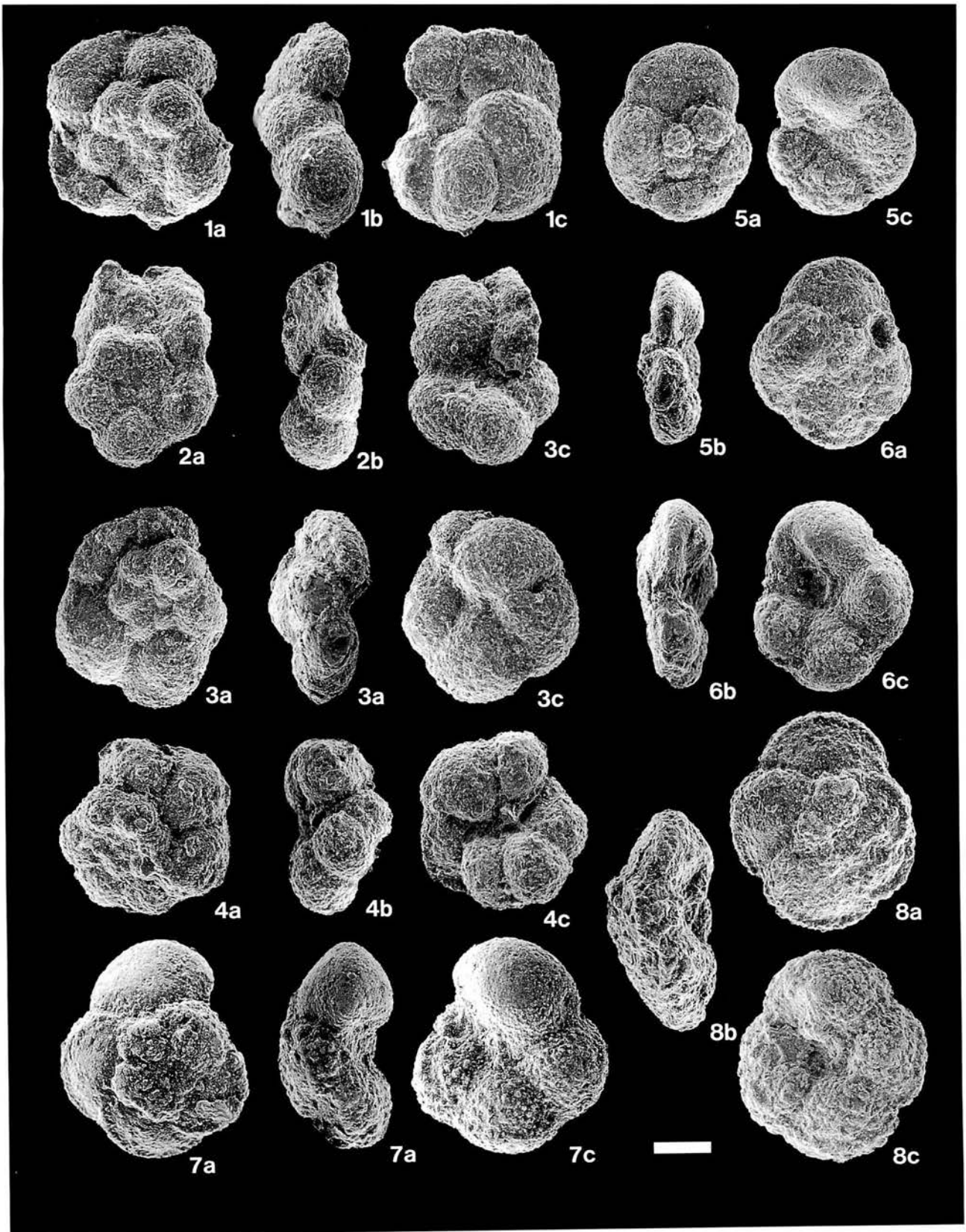
Hedbergella kyphoma sp. nov.

Figures 5-1-4

Diagnosis.—A low trochospiral species of *Hedbergella* with last four chambers umbilically shifted, compressed, and spirally elongate. Umbilicus narrow, sutures of last four chambers slightly curved.

Description.—Test of medium size, initially very low tro-

Figure 5. 1-4. *Hedbergella kyphoma* sp. nov. 1. Holotype, IGPS No. 102504, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 2. Paratype, IGPS No. 102505, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 3. Paratype, IGPS No. 102506, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 4. Paratype, IGPS No. 102507, sample loc. no. SRN-525A, lower part of the Takinosawa Formation, lower Turonian. 5, 6. *Praeglobotruncana compressa* sp. nov. 5. Holotype, IGPS No. 102707, sample loc. no. SRN-207, lower part of the Takinosawa Formation, upper Cenomanian. 6. Paratype, IGPS No. 102708, sample loc. no. SRN-207, lower part of the Takinosawa Formation, upper Cenomanian. 7. Intermediate form between *Praeglobotruncana inermis* sp. nov. and *Praeglobotruncana shirakinensis* sp. nov., IGPS No. 102508, sample loc. no. SRN-210, lower part of the Takinosawa Formation, upper Cenomanian. 8. *Praeglobotruncana shirakinensis* sp. nov., holotype, IGPS No. 102523, sample loc. no. SRN-210, lower part of the Takinosawa Formation, upper Cenomanian. Scale bar = 100 μ m



chospiral, later becoming medium trochospiral, equatorial periphery lobulate; chambers initially globular, later slightly compressed and spirally elongated, 11 to 14 in all arranged into 2.5 to 3 whorls, enlarging gradually in size as added except for last 3 or 4 which enlarge irregularly, 6 or 7 in last whorl, last 3 or 4 characteristically elongated, compressed and shifted toward umbilicus, last chamber variable in size and shape; sutures initially radial and depressed on dorsal side except for last 3 or 4 chambers in which they are curved, slightly curved and depressed on ventral side; coiling axis initially stable, later rapidly tilted for last 3 or 4 chambers, as a result, initial umbilicus occasionally being covered by last 3 or 4 chambers; umbilicus shallow, very narrow, less than 1/5 of maximum diameter of test; primary aperture bordered by a narrow lip, interiomarginal, umbilical-extraumbilical, extending to periphery; wall calcareous, surface poorly ornamented.

Remarks.—This species resembles *Hedbergella planispira* (Tappan) in its initially very low trochospiral shape and the number of chambers in the last whorl, but differs from the latter species in having a narrower umbilicus and umbilically shifted and compressed last 3 or 4 chambers.

Etymology.—From *kyphoma*, a Greek noun referring to the humpbacked nature of the pattern of chamber growth in this species.

Material.—Holotype IGPS No. 102504, paratypes IGPS No. 102505–102507.

Dimensions.—Maximum diameter of holotype 0.36 mm, maximum thickness 0.20 mm.

Type locality and horizon.—The holotype and paratypes are all from sample SRN-525A (43°2.50'N, 142°9.72'E), lower part of the Takinosawa Formation, lower Turonian.

Subfamily Rotundininae Bellier and Salaj, 1977

Genus *Praeglobotruncana* Bermudez, 1952

***Praeglobotruncana compressa* sp. nov.**

Figures 5-5, 6

Diagnosis.—A low trochospiral species of *Praeglobotruncana* with compressed and wedge-shaped chambers in last whorl.

Description.—Test of medium to small size, very low trochospiral, equatorial periphery slightly lobulate; chambers wedge-shaped on dorsal side, triangular and slightly inflated on ventral side, about 10 chambers in all, enlarging rapidly in size as added, about 4.5 chambers in last whorl, with a peripheral band formed of aligned pustules; final chamber occasionally obliquely shifted toward umbilical direction; chambers in last whorl diagnostically elongated toward spiral direction; sutures on dorsal side gently curved, depressed, ventrally radial or slightly curved and depressed; umbilicus shallow, medium in size, about 1/3–1/4 of maximum diameter of test, umbilical flaps extending into an umbilicus from each chamber; primary aperture bordered by a narrow lip, interiomarginal, umbilical-extraumbilical; wall calcareous, earlier chambers pustulated.

Remarks.—This species is distinguished from *Praeg-*

lobotruncana compressiformis (originally described as *Praeglobotruncana hessi compressiformis* by Pessagno, 1962) and other species of *Praeglobotruncana* in possessing wedge-shaped chambers having depressed sutures in the last whorl on the dorsal side, spirally elongated chambers in the last whorl, and in its generally compressed shape.

Etymology.—From Latin, *compressa* referring to the compressed feature of chambers compared with other species of *Praeglobotruncana*.

Material.—Holotype IGPS No. 102707, paratype IGPS No. 102708.

Dimensions.—Maximum diameter of holotype 0.30 mm, maximum thickness 0.10 mm.

Type locality and horizon.—The holotype and paratype specimens are both from sample SRN-207 (43°2.60'N, 142°9.78'E), lower part of the Takinosawa Formation, upper Cenomanian.

***Praeglobotruncana gibba* Klaus, 1960**

Figure 6-5

Praeglobotruncana stephani (Gandolfi) var. *gibba* Klaus, 1960, p. 304–305, holotype designated in Reichel, 1950, pl. 16, fig. 6, pl. 17, fig. 6.

Praeglobotruncana stephani (Gandolfi). Loeblich and Tappan, 1961, p. 280–284, pl. 6, figs. 4a, b, 5a–c, 6, 7a–c.

Praeglobotruncana gibba Klaus. Robaszynski and Caron, 1979, p. 33–38, pl. 44, figs. 1a–c, 2a–c, pl. 45, figs. 1a–c, 2a–c; Caron, 1985, p. 65, pl. 30–5a–c, 6a–c.

Remarks.—This species is easily distinguished from *Praeglobotruncana stephani* by its high trochospire and from *Praeglobotruncana inermis* n. sp. by its distinct raised suture with a beaded keel on the dorsal side. This species is abundant in the upper part of the *R. cushmani* Zone.

Material.—Hypotype IGPS No. 102503.

Locality and horizon.—The figured specimen is from sample SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian.

***Praeglobotruncana inermis* sp. nov.**

Figures 6-1–4

Diagnosis.—A high trochospiral species of *Praeglobotruncana* with slight peripheral pustule lines, distinct lip near umbilicus and 4 smooth-walled chambers in last whorl.

Description.—Test of medium to large size, medium to high trochospiral, equatorial periphery lobulate; chambers petaloidal in shape on dorsal side, trapezoidal to subglobular, inflated on dorsal side, about 12 in all arranged into 2 to 2.5 whorls, enlarging gradually in size as added, characteristically 4 chambers in final whorl, with a weak peripheral band formed of an aligned concentration of pustules which tends to be shifted toward spiral side; final chamber shifted toward umbilical direction; sutures on dorsal side radial and depressed except for that of first chamber in last whorl which occasionally is raised, ventrally radial and depressed; umbilicus shallow, medium to narrow in size, less than 1/4 of maximum diameter of test; primary aperture bordered by a

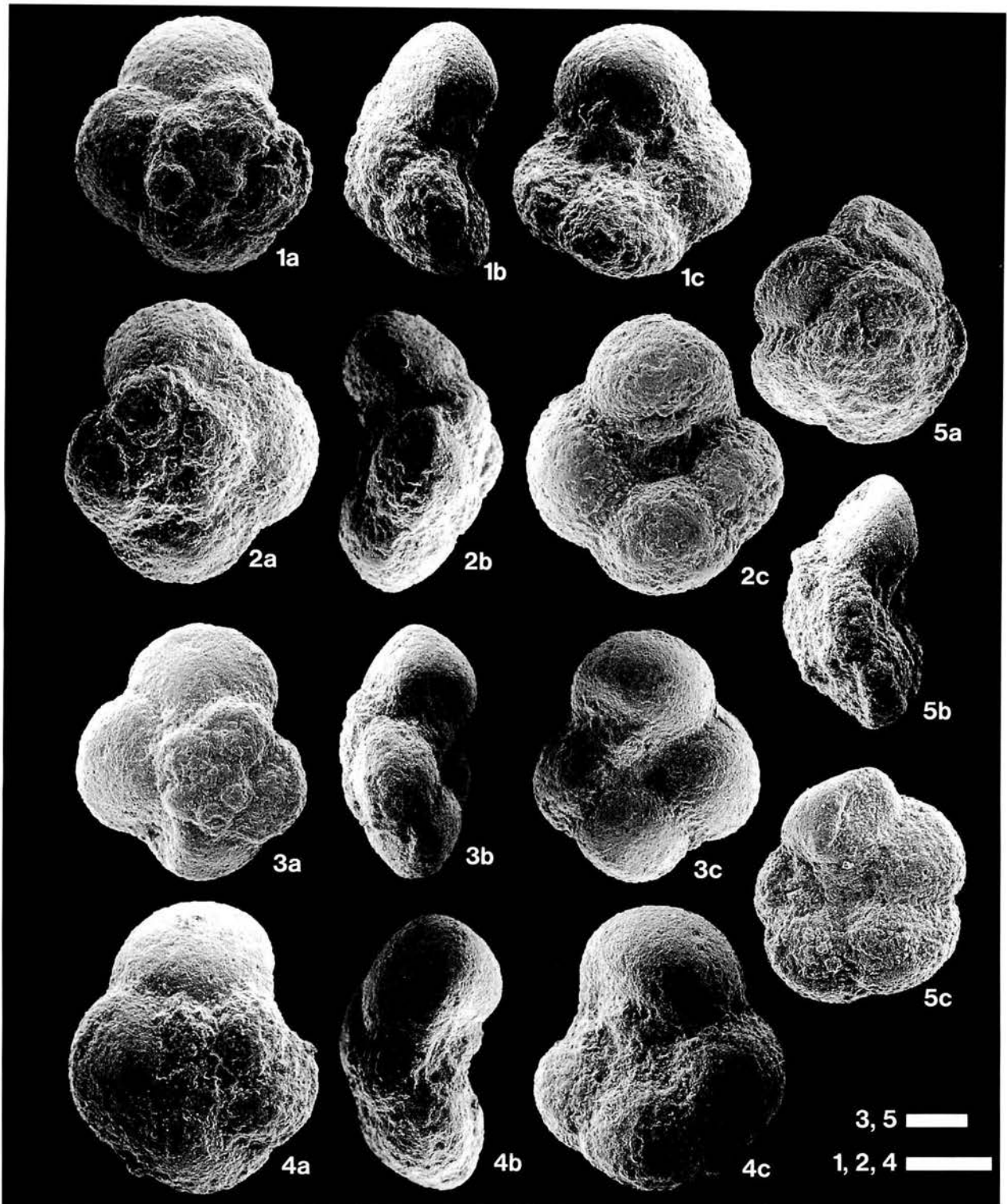


Figure 6. 1–4. *Praeglobotruncana inermis* sp. nov. 1. Paratype, IGPS No. 102703, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. Holotype, IGPS No. 102704, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 3. Paratype, IGPS No. 102705, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 4. Paratype, IGPS No. 102706, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 5. *Praeglobotruncana gibba* Klaus, IGPS No. 102503, sample loc. no. SSS-020, lower part of the Takinosawa Formation, upper Cenomanian. Scale bars = 100 μm .

distinct lip that expands markedly near umbilicus, interiomarginal, umbilical-extraumbilical; wall calcareous, surface smooth, earlier chambers weakly pustulated.

Remarks.—This species closely resembles *Praeglobotruncana anumalensis* (Sigal), but differs in lacking the conspicuous pustules on earlier chambers, in having diagnostically 4 chambers in the last whorl, more lobulated periphery and more inflated chambers.

Etymology.—From Latin, *inermis* referring to the smooth-walled chambers of this species compared with other species of *Praeglobotruncana*.

Material.—Holotype IGPS No. 102704; paratypes IGPS No. 102703, 102705, 102706.

Dimensions.—Maximum diameter of holotype 0.34 mm, maximum thickness 0.21 mm.

Type locality and horizon.—The holotype and paratypes are all from sample SRN-220 (43°2.60'N, 142°9.72'E), lower part of the Takinosawa Formation, uppermost Cenomanian.

***Praeglobotruncana shirakinensis* sp. nov.**

Figure 5-8

Praeglobotruncana sp. Leckie, 1985, p. 139-149, pl. 3, figs 9-15.

Diagnosis.—A medium trochospiral species of *Praeglobotruncana* with about 5 moderately compressed and slightly lobulated chambers of last whorl.

Description.—Test of medium size, medium trochospiral, equatorial periphery slightly lobulate; chambers initially inflated and globigerine-like, later ones becoming petaloidal on dorsal side, trapezoidal in shape on ventral side, about 10 to 12 chambers in all arranged into about 2.5 whorls, enlarging gradually in size as added, about 5 slightly compressed chambers in final whorl, with a peripheral band formed of an aligned concentration of pustules paralleling periphery; sutures on dorsal side curved, raised and beaded, ventrally radial or slightly curved, depressed; umbilicus shallow and narrow, its width about 1/4 of maximum diameter of test; primary aperture bordered by a wide distinct lip, interiomarginal, umbilical-extraumbilical, extending nearly halfway to periphery; wall calcareous, with marked accumulation of pustules on early chambers.

Remarks.—This species resembles *Praeglobotruncana stephani*, but differs in the following characters: spirally slightly elongated and ventrally more inflated chambers of the last whorl; fewer chambers (normally 4 to 5) having almost similar size in the last whorl; less lobulated periphery; and thinner spiral sutures. An intermediate form between *P. inermis* and *P. shirakinensis* is also figured (Figure 5.7).

Etymology.—With reference to the type locality (the Shirakin River) where the holotype specimen occurred.

Material.—Holotype IGPS No. 102523.

Dimensions.—Maximum diameter of holotype 0.38 mm, maximum thickness 0.20 mm.

Type locality and horizon.—The holotype specimen is from sample SRN-210 (43°2.60'N, 142°9.77'E), lower part of the Takinosawa Formation, upper Cenomanian.

Subfamily Helvetoglobotruncaninae Lamolda, 1976

Genus ***Helvetoglobotruncana*** Reiss, 1957

Helvetoglobotruncana helvetica (Bolli, 1945)

Figure 9-1

Globotruncana helvetica Bolli, 1945, p. 226, pl. 9, fig. 6.

Praeglobotruncana helvetica (Bolli). Robaszynski and Caron, 1979, p. 39-42, pl. 46, figs. 1a-c, 2a-c.

Helvetoglobotruncana helvetica (Bolli). Wonders, 1980, p. 117, pl. 3, fig. 2a-c; Caron, 1985, p. 60, figs. 30-7, 8a-c; Loeblich and Tappan, 1988, p. 463-464, pl. 498, figs. 4-7.

Remarks.—Poorly preserved specimens of this species were obtained from only one horizon. Nevertheless, the figured specimen is identified as *H. helvetica* on the basis of its asymmetrical planoconvex lateral view, thick single keel that is shifted toward the spiral side, and staircase-like imbricate structures on the spiral side. This species is very rare in the area of study; however, it is quite important for interregional correlation.

Material.—Hypotype IGPS No. 102517.

Locality and horizon.—The figured specimen is from sample SRN-101, middle part of the Takinosawa Formation, middle Turonian.

Subfamily incertae sedis

Genus ***Dicarinella*** Porthault, 1970

Dicarinella hagni (Scheibnerova, 1962)

Figure 7-5

Praeglobotruncana hagni Scheibnerova, 1962, p. 219, figs. 6a-c.

Praeglobotruncana sp. cf. *P. hagni* Scheibnerova. Butt, 1966, p. 174, figs. 2a-c (not 1a-c, 3a-4c).

Globotruncana kupperi Thalmann. Marianos and Zingula, 1966, p. 340-341, pl. 39, figs. 6a-c.

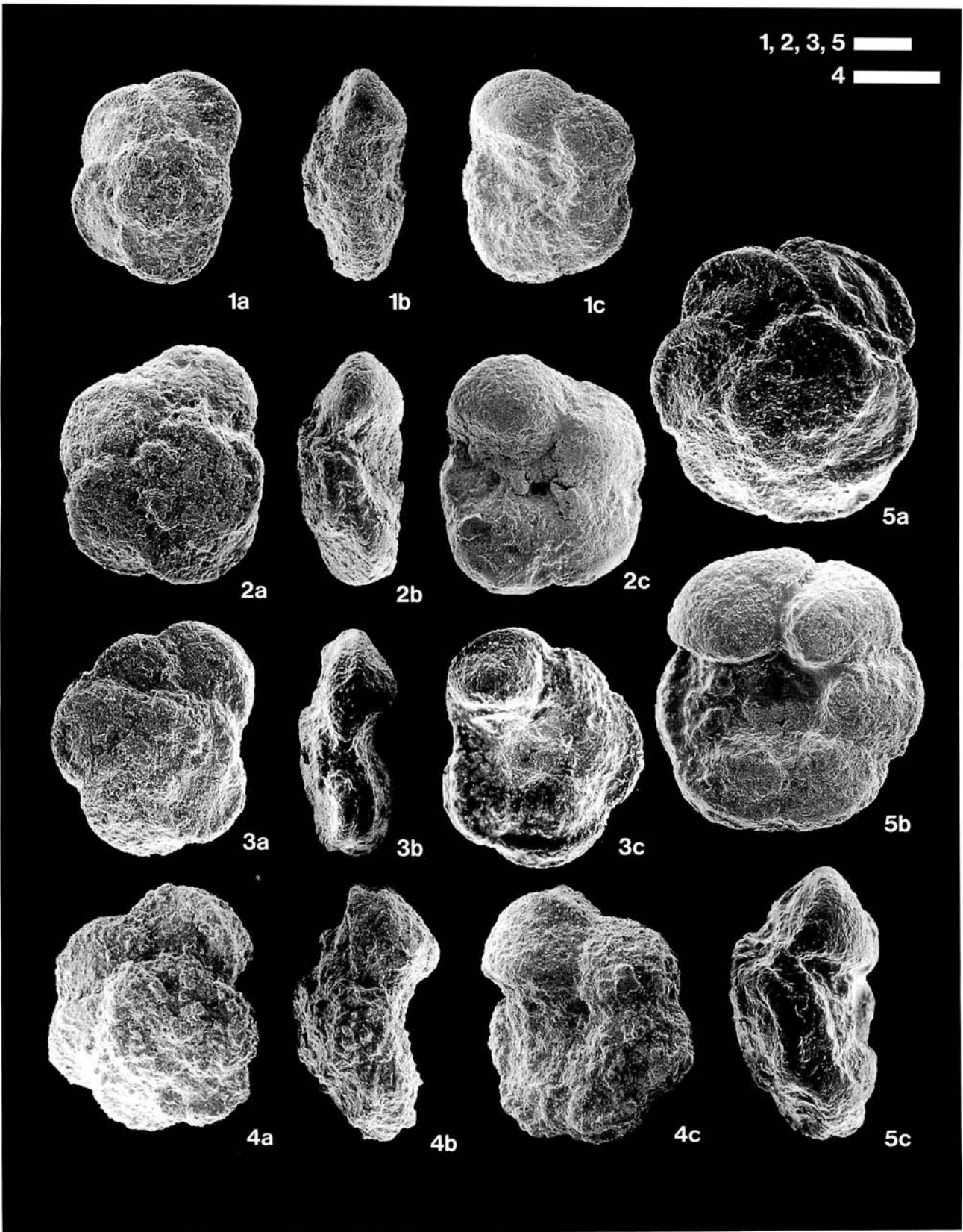
Dicarinella hagni (Scheibnerova). Robaszynski and Caron, 1979, p. 79-86, pl. 56, figs. 1a-c, 2a-c, pl. 57, figs. 1a-c, 2a-d; Caron, 1985, p. 45, figs. 18-2a-c, 3a-c.

Remarks.—This species differs from *Dicarinella roddai* in having chambers which increase their size more gradually and in having a greater number of chambers in the last whorl.

Material.—Hypotype IGPS No. 102509.

Locality and horizon.—The figured specimen is from sample SRN-034, middle part of the Takinosawa Formation,

Figure 7. 1-3. *Dicarinella roddai* (Marianos and Zingula). 1. IGPS No. 102520, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. IGPS No. 102511, sample loc. no. SRN-132, lower-middle part of the Takinosawa Formation, lower Turonian. 3. IGPS No. 102512, sample loc. no. SRN-034, middle part of the Takinosawa Formation, middle Turonian. 4. *Dicarinella imbricata* (Mornod), IGPS No. 102510, sample loc. no. SRN-034, middle part of the Takinosawa Formation, middle Turonian. 5. *Dicarinella hagni* (Scheibnerova), IGPS No. 102509, sample loc. no. SRN-034, middle part of the Takinosawa Formation, middle Turonian. Scale bars=100 μ m.



middle Turonian.

Dicarinella imbricata (Mornod, 1950)

Figure 7-4

Globotruncana (Globotruncana) imbricata Mornod, 1950, p. 589-590, figs. 5 (III a-d).

Dicarinella imbricata (Mornod). Robaszynski and Caron, 1979, p. 87-92, pl. 58, figs. 1a-c, 2a-d, pl. 59, figs. 1a-c, 2a-c; Caron, 1985, p. 45, figs. 18-4a-c, 5a-c.

Remarks.—This species is easily distinguished from other species by its diagnostic stair-like imbrication of chambers on the dorsal side.

Material.—Hypotype IGPS No. 102510.

Locality and horizon.—The figured specimen is from sample SRN-034, middle part of the Takinosawa Formation, middle Turonian.

Dicarinella roddai (Marianos and Zingula, 1966)

Figures 7-1-3

Globotruncana roddai Marianos and Zingula, 1966, p. 340, pl. 39, 5a-c.

non *Præglobotruncana roddai* (Marianos and Zingula). Douglas, 1969, p. 171-172, pl. 2, 2a-c.

Description.—Test medium to large in size, initially a low to medium-height trochospire, equatorial periphery slightly lobulate; chambers dorsally semicircular, ventrally trapezoidal in shape, somewhat inflated on ventral side, about 9 to 11 chambers in all arranged into 2 to 2.5 whorls, enlarging gradually in size as added, last 4 chambers almost similar in size, 5 slightly imbricated chambers in final whorl, with distinct double peripheral keels; sutures on dorsal side curved, raised with a keel which continues to one of double peripheral keels, ventrally radial, depressed, occasionally slightly raised; umbilicus shallow, its width about 1/4 of maximum diameter of test; primary aperture bordered by distinct, narrow- to medium-width lip, interiomarginal, umbilical-extraumbilical extending nearly to periphery; wall calcareous, weakly pustulated on earlier chambers.

Discussion.—This species resembles *Dicarinella hagni* but is distinguished by having less inflated chambers on ventral side, fewer and slightly imbricated chambers. Although Takayanagi (1965) described this species as *Globotruncana marginata*, Jirová's neotype figures of *G. marginata*, (Jirová, 1956, p. 253, figs. 1a-c) and one of the figured specimens of Reuss's syntypes which was later selected as the lectotype by Bolli *et al.* (1957) (Jirová's neotype has priority) are apparently different from Takayanagi's (1965, figs. 3a-c, 4a-c)

figures in having more chambers in the last whorl which are more globular and inflated, more gradually increasing in size as added, equatorial periphery more lobulate, narrower spaced keels, and a wider umbilicus. Marianos and Zingula (1966) stated that *D. roddai* (originally described as *Globotruncana roddai*) was a good marker for the lower Turonian in the type locality of this species, however, the stratigraphic distribution of this species in the area of study is restricted to the uppermost Cenomanian to lower part of the middle Turonian (Figure 3). In this stratigraphic range, this species occurs commonly. Therefore, it may be a useful supplemental species to locate the interval of the Cenomanian/Turonian boundary in Japan.

Material.—Hypotype IGPS No. 102520, 102511, 102512.

Locality and horizon.—The specimen IGPS No. 102520 is from SRN-220, lower part of the Takinosawa Formation, upper Cenomanian. IGPS No. 102511 is from sample SRN-132, lower-middle part of the Takinosawa Formation, middle Turonian. IGPS No. 102512 is from sample SRN-034, middle part of the Takinosawa Formation, middle Turonian.

Dicarinella takayanagii sp. nov.

Figures 8-1-4

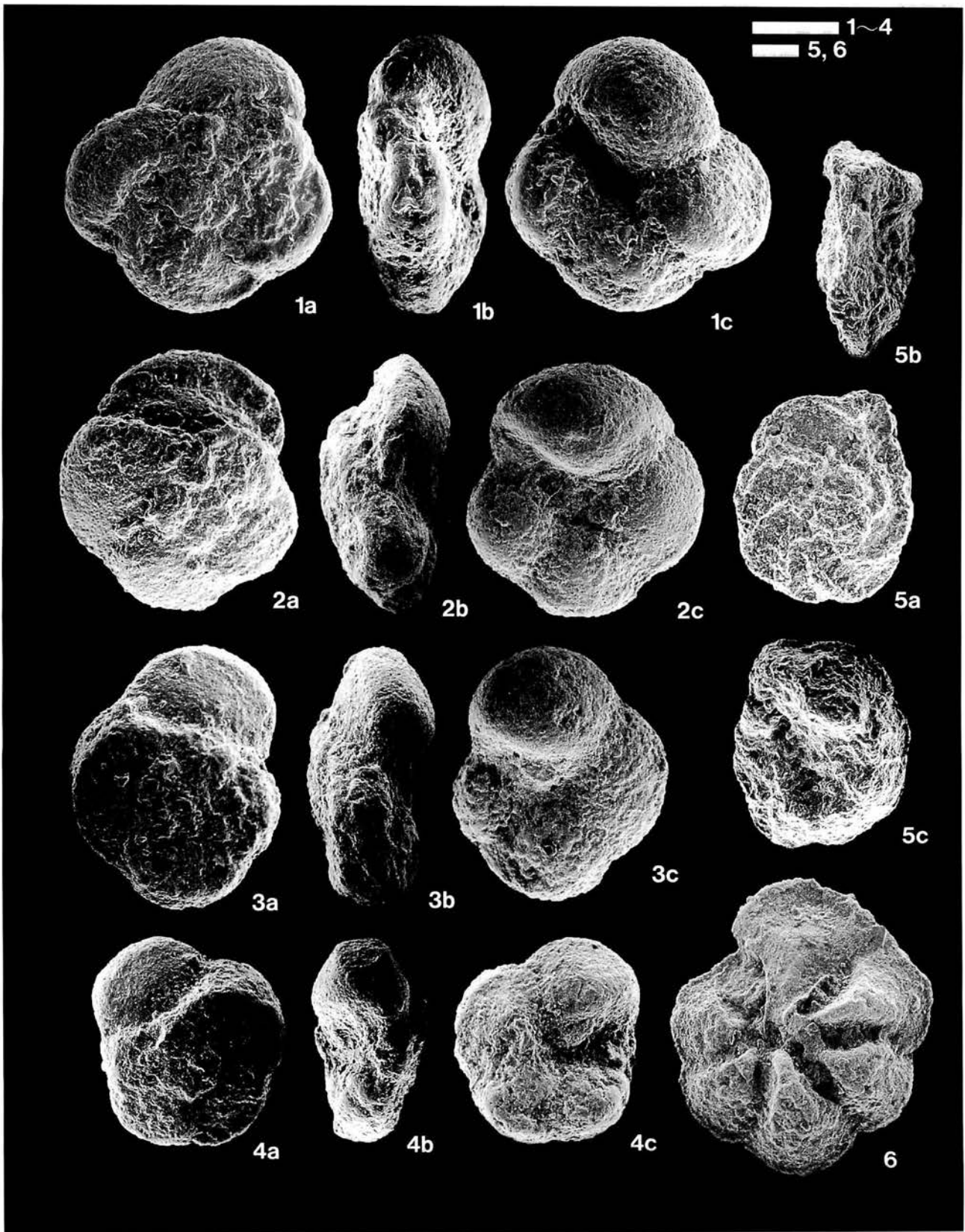
Diagnosis.—A low trochospiral species of *Dicarinella* with wedge-shaped chambers in last whorl and small umbilicus.

Description.—Test of medium to large size, low trochospiral, equatorial periphery lobulate; chambers initially globigerine-like, later ones becoming wedge-shaped and flat on dorsal side, triangular and inflated in shape on ventral side, about 10 chambers in all, enlarging rapidly in size as added, about 4.5 chambers in last whorl, with widely separated weak double peripheral keels, one of which is shifted toward spiral side; final chamber obliquely shifted toward umbilical direction, as a result, keels being discontinuous to final chamber; final chamber diagnostically elongated in spiral direction, occasionally lacking peripheral keels; sutures on dorsal side gently curved, raised with keels that are continuous to one of peripheral keels, sutures on ventral side radial and depressed; umbilicus shallow and narrow, its width about 1/4 of maximum diameter of test; primary aperture bordered by a distinct lip, interiomarginal, umbilical-extraumbilical; wall calcareous, earlier chambers weakly pustulated.

Remarks.—This species is distinguished from other species of *Dicarinella* in possessing wedge-shaped chambers in the last whorl on the dorsal side, spirally elongated final chamber and a narrower umbilicus.

Etymology.—In honor of Prof. Emeritus Y. Takayanagi in recognition of his contribution to the study of Cretaceous

Figure 8. 1-4. *Dicarinella takayanagii* sp. nov. 1. Paratype, IGPS No. 102513, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 2. Paratype, IGPS No. 102514, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 3. Holotype, IGPS No. 102515, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 4. Paratype, IGPS No. 102516, sample loc. no. SRN-223, lower part of the Takinosawa Formation, uppermost Cenomanian. 5. *Rotalipora deeckei* (Franke), IGPS No. 102519, sample loc. no. KMZ-002, the uppermost part of the Hikagenosawa Formation, upper Cenomanian. 6. *Rotalipora cushmani* (Morrow), IGPS No. 102472, sample loc. no. SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). Scale bars = 100 μ m.



foraminifera in Japan.

Material.—Holotype IGPS No. 102515; paratypes IGPS No. 102513, 102514, 102516.

Dimensions.—Maximum diameter of holotype 0.29 mm, maximum thickness 0.17 mm.

Type locality and horizon.—The holotype and all paratypes are from sample SRN-223 (43°2.60'N, 142°9.73'E), lower part of the Takinosawa Formation, uppermost Cenomanian.

Family Rotaliporidae Sigal, 1958
Subfamily Rotaliporinae Sigal, 1958
Genus *Rotalipora* Brotzen, 1942

Rotalipora cushmani (Morrow, 1934)

Figures 8-6; 9-4

Globorotalia cushmani Morrow, 1934, p. 199, pl. 31, fig. 4a-b.

Rotalipora cushmani (Morrow). Loeblich and Tappan, 1961, p. 297-298, pl. 8, figs. 1-8, 10 (not fig. 9); Pessagno, 1967, p. 292-293, pl. 51, figs. 6-9; Robaszynski and Caron, 1979, p. 69-74, pl. 7, figs. 1a-c, pl. 8, figs. 1a-c, 2a-c; Wonders, 1980, p. 125-126, pl. 3, fig. 3a-c; Caron, p. 69, figs. 31-8-11.

Remarks.—This species is distinguished from other species of *Rotalipora* by having a lobulated periphery, semi-circular chambers ornamented by pustules in the last whorl, pronounced supplementary apertures with developed lips. The last occurrence of this species corresponds to that of the genus *Rotalipora* in this study. This species is a very important index in Japan for interregional correlation.

Material.—Hypotypes IGPS No. 102471, 102472.

Locality and horizon.—Two figured specimens are from SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian.

Rotalipora deecke (Franke, 1925)

Figure 8-5

Rotalia deecke Franke, 1925, p. 88, 90, pl. 8, figs. 7a-c (This inaccessible literature is indirectly accessible from "Ellis and Messina, 1940 et seq., Catalogue of Foraminifera").

Rotalipora deecke (Franke). Robaszynski and Caron, 1979, p. 75-80, pl. 9, figs. 1a-2c, pl. 10, 1a-2c.

Remarks.—This species is very similar to *Rotalipora reicheli*, but differs in having periumbilical ridges extended from raised sutures on the ventral side and narrower umbilicus.

Material.—Hypotype IGPS No. 102519.

Locality and horizon.—The figured specimen is from KMZ-002, uppermost part of the Hikagenosawa Formation, upper

Cenomanian.

Rotalipora sp. aff. *R. gandolfii* Luterbacher and Premoli-Silva, 1962

Figure 9-3

Remarks.—This species resembles *Rotalipora gandolfii*, but differs in having the hemispherical last two chambers. This morphological feature is rather reminiscent of *Rotalipora cushmani*.

Material.—Hypotype IGPS No. 102524.

Locality and horizon.—The specimen IGPS No. 102524 is from SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian.

Rotalipora greenhornensis (Morrow, 1934)

Figure 9-5

Globorotalia greenhornensis Morrow, 1934, p. 199, pl. 31, figs. 1a-c.

Rotalipora greenhornensis (Morrow). Loeblich and Tappan, 1961, p. 299-301, pl. 7, figs. 5-10; Pessagno, 1967, p. 295-297, pl. 50, fig. 3, pl. 51, figs. 15-17, 19-21 (not figs. 13, 14, 18); Pessagno, 1967, p. 289-292, pl. 50, figs. 4-6; Robaszynski and Caron, 1979, p. 85-90, pl. 12, figs. 1a-c, 2a-c, pl. 13, figs. 1a-c, 2a-c; Caron, 1985, p. 69, text-figs. 32-1, 2.

Remarks.—This species is easily distinguished from other species of *Rotalipora* by having greater number of chambers in the last whorl and crescent-shaped chambers which are often concave on the dorsal side. The last occurrence of this species is at the same stratigraphic horizon as that of *Rotalipora cushmani* in the area of study.

Material.—Hypotype IGPS No. 102473.

Locality and horizon.—The figured specimen is from SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian.

Subfamily Globotruncaninae Brotzen, 1942
Genus *Marginotruncana* Hofker, 1956

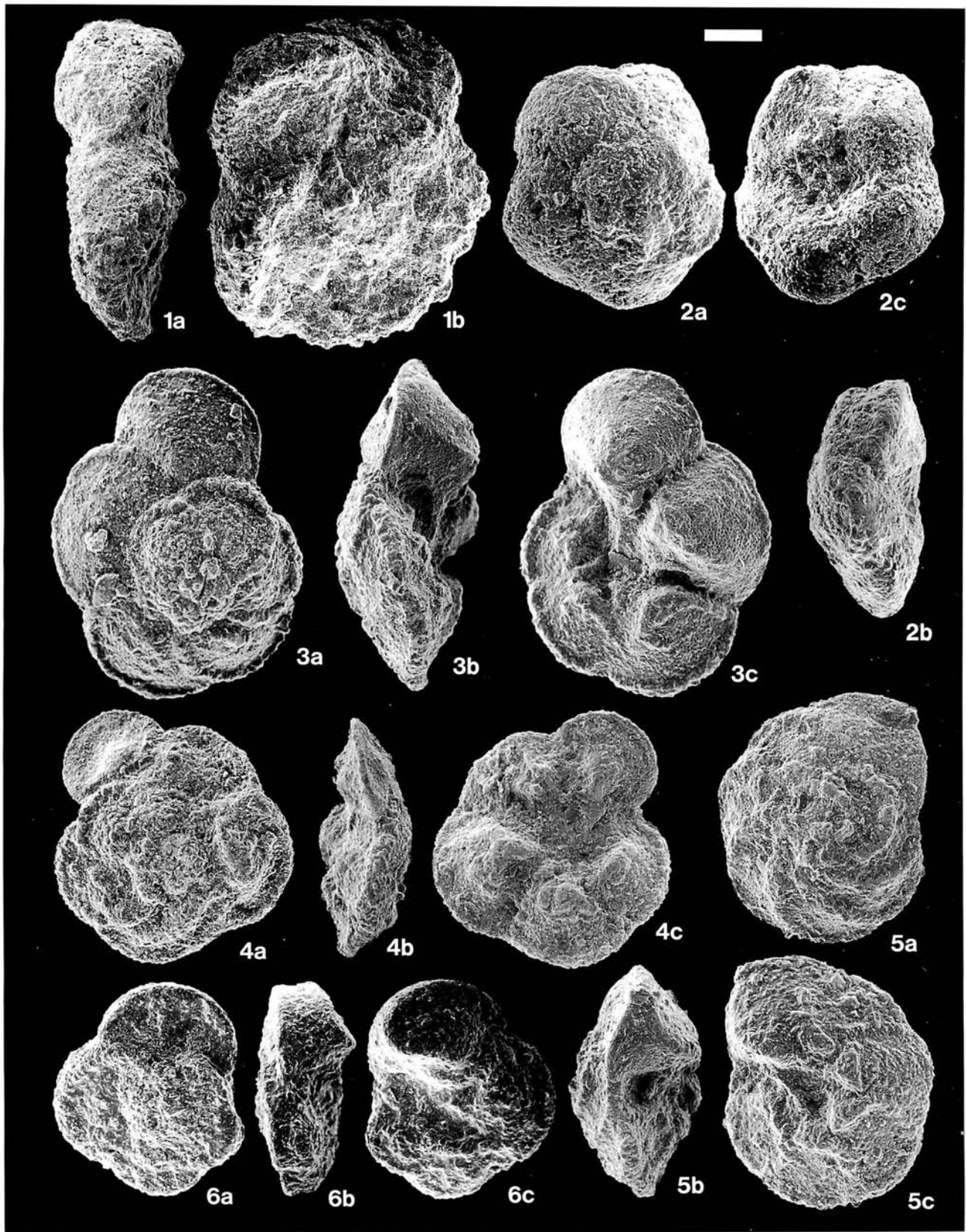
Marginotruncana pseudolinneiana Pessagno, 1967

Figure 9-6

Marginotruncana pseudolinneiana Pessagno, 1967, p. 310, pl. 65, figs. 24-27; Robaszynski and Caron, 1979, p. 123-128, pl. 67, 1a-2d, pl. 68, 1a-2c; Caron, 1985, p. 61, text-figs. 26-7, 8.

Remarks.—This species is easily distinguished from other

Figure 9. 1. *Helvetoglobotruncana helvetica* (Bolli), IGPS No. 102517, sample loc. no. SRN-101, middle part of the Takinosawa Formation, middle Turonian. 2. *Marginotruncana schneeegansi* (Sigal), IGPS No. 102521, sample loc. no. SRN-132, lower-middle part of the Takinosawa Formation, lower Turonian. 3. *Rotalipora* sp. aff. *R. gandolfii* Luterbacher and Premoli-Silva, IGPS No. 102524, sample loc. no. SSS-020, lowermost part of the Takinosawa Formation, upper Cenomanian. 4. *Rotalipora cushmani* (Morrow), IGPS No. 102471, sample loc. no. SRN-220 (last occurrence horizon of *R. cushmani*), lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). 5. *Rotalipora greenhornensis* (Morrow), IGPS No. 102473, sample loc. no. SRN-220, lower part of the Takinosawa Formation, uppermost Cenomanian. Same specimen as that shown in Hasegawa and Saito (1993). 6. *Marginotruncana pseudolinneiana* Pessagno, IGPS No. 102522, sample loc. no. SRN-062, lower part of the Shirogane Formation, upper Turonian. Scale bar = 100 μ m.



species by its diagnostically rectangular shape in lateral view. This species characterizes the middle Turonian to Coniacian interval in Japan.

Material.—Hypotype IGPS. No. 102522.

Locality and horizon.—The figured specimen is from SRN-062, lower part of the Shirogane Formation, upper Turonian.

***Marginotruncana schneegansi* (Sigal, 1952)**

Figure 9-2

Globotruncana schneegansi Sigal, 1952, p. 33, text-fig. 34.

Marginotruncana schneegansi (Sigal). Robaszynski and Caron, 1979, p. 135-140, pl. 70, fig. 1a-2e, Pl. 71, 1a-2d; Caron, 1985, p. 61, text-figs. 27, 3-6.

Remarks.—The first occurrence of this species characterizes the lower Turonian in Japan.

Material.—Hypotype IGPS No. 102521.

Locality and horizon.—The figured specimen is from SRN-132, lower-middle part of the Takinosawa Formation, lower Turonian.

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Tidal growth patterns and growth curves of the Miocene potamidid gastropod *Vicarya yokoyamai*

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Abstract. Continuous growth sequences are recorded in vertical (= median longitudinal) sections of the columella of the fossil potamidid gastropod *Vicarya yokoyamai* Takeyama, from subtropical Miocene faunas of Japan. Shells from the Mizunami, Uchiura, Bihoku, and Masuda groups show semidiurnal tidal growth patterns. This suggests that *V. yokoyamai* lived in the intertidal zone. Growth curves were reconstructed on the basis of numbers of tidal growth lines. These growth curves were found to be very similar with one another, and indicated that shell-height increased from 1.5 cm to 8 cm in two years.

Key words : columella, growth rate, intertidal, micro-growth increment, micro-growth line, tide

Introduction

Invertebrate hard parts such as molluscan shells and coral skeletons grow incrementally, forming alternating sequences of micro-growth lines and micro-growth increments that constitute their micro-growth patterns. Micro-growth patterns reflect physiological and environmental changes that occurred during their formation. Reconstruction of these changes from micro-growth patterns observed in the hard parts of a variety of organisms has been attempted in many studies (e.g. Wells, 1963; Berry and Barker, 1968; House and Farrow, 1968; Pannella and MacClintock, 1968; Pannella *et al.*, 1968; Dolman, 1975; Scrutton, 1978; Lutz and Rhoads, 1980 among others).

Intertidal organisms such as bivalves, gastropods, and barnacles record the effects of changing tides, as exposure and immersion are commonly reflected in their micro-growth patterns (Evans, 1972; Bourget and Crisp, 1975; Crisp and Richardson, 1975; Richardson *et al.*, 1979, 1980a, 1980b, 1981; Richardson *et al.*, 1980c; Ekarante and Crisp, 1982; Ohno and Takenouchi, 1984; Ohno, 1984, 1985, 1989; Richardson, 1987, 1988a, 1988b; Tojo and Ohno, 1999). Using these records, ancient tidal periods and tidal patterns have been reconstructed from fossil bivalves (Ohno, 1984, 1989; Tojo *et al.*, 1999). Tidal growth patterns are also a suitable index for the time scale of growth, so they can be used to reconstruct the growth rates of hard parts (Richardson, 1987; Tojo and Ohno, 1999). Previous studies of growth rates are based in many cases on annual rings that were recognized by comparative analysis of growth lines and oxygen isotopes of the shells (Jones *et al.*, 1978; Jones, 1980; Thompson *et al.*, 1980; Jones, 1981), but many gastropods have no obvious yearly rings. Thus we attempt the reconstruction of growth

curves from tidal growth patterns.

Few studies of micro-growth patterns in gastropod shells have been undertaken, because coiling of the gastropod shell obstructs the collection of continuous growth sequences spanning the whorls. However, Tojo and Ohno (1999) have proposed an easy method to obtain a continuous micro-growth pattern from one whorl to the next in the Recent potamidid gastropod *Terebralia palustris* (Linnaeus), using sections of the columella. This method made it easy to access records of gastropod growth. Tojo and Ohno (1999) observed tidal growth patterns in shells of *T. palustris*. They inferred that one micro-growth line corresponds to a 12.4 hour interval of low tides and reconstructed the growth curve of an individual *T. palustris* shell. This growth curve was consistent with one that had been reconstructed from a population analysis. Analysis of micro-growth patterns by this method permits the reconstruction of changing growth rates even from a single fossil specimen or species known only from small populations.

The fossil potamidid gastropod *Vicarya* has been regarded as a characteristic element of warm-water faunas from Eocene to Miocene in age. Tojo and Sakakura (1998) reported tidal growth patterns in shells of *Vicarya yokoyamai* from the Mizunami Group. However, little is known of the growth of *Vicarya* because it is an extinct genus.

The method of Tojo and Ohno (1999) can be applied to shells of *V. yokoyamai*. We observed tidal growth patterns in shells of *V. yokoyamai* from four localities (Figure 1) and reconstructed their growth curves.

Material

In this study, we used fragments of *V. yokoyamai* from

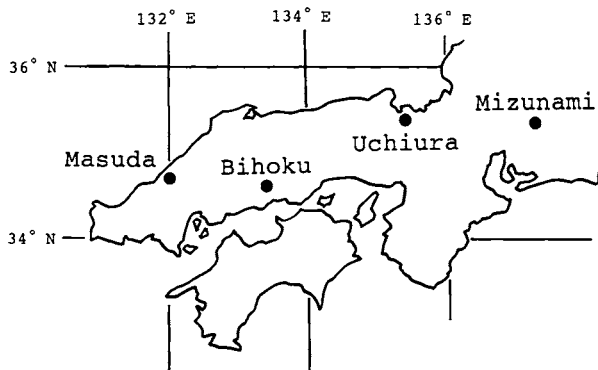


Figure 1. Locality map for *Vicarya yokoyamai* specimens utilized in this study.

subtropical tidal or shallow marine facies of Miocene age in Japan. To reconstruct the growth curve of *V. yokoyamai* (Figure 2A), we used a total of six specimens, three from the Mizunami Group in Gifu Prefecture, and one each from the Uchiura Group in Kyoto Prefecture, the Bihoku Group in Okayama Prefecture, and the Masuda Group in Shimane Prefecture (Figure 1). In the following discussion, specimens are referred to by the group name, and the three specimens from the Mizunami Group are called Mizunami A, B and C. Two species names that had been established, *V. yokoyamai* and *Vicarya japonica*, were synonymized by Kanno (1986).

Preparation for columella method

In order to prepare vertical (=median longitudinal) and horizontal (=cross) sections of the gastropod shell, samples were cut and ground with a graded series of carborundum and polished with diamond paste. A binocular microscope and a scanning electron microscope (SEM) were used for observation of shell micro-growth patterns (Figure 2B). For observation with the SEM, polished samples were etched with 0.5 mol/l HCl and then coated with gold.

Results

Micro-growth pattern

Micro-growth pattern consists of two components of growth layers, micro-growth lines and micro-growth increments. Micro-growth lines are the layers which are relatively resistant to etching. Thus, they are observed as lineridges under SEM. Micro-growth increments are the layers between micro-growth lines. Micro-growth lines show various thicknesses, but are generally thinner than micro-growth increments.

Micro-growth lines of *V. yokoyamai* appear as relatively light layers under the binocular microscope (Figures 2B, D).

Formation of columella

Before observing the columella sections, we examined the outer shape of the columella to understand its formation (Figure 2C). The basal part of the columella has a trough-like structure along its coiling axis. One flank of the trough continues to the outer lip; the other covers the bottom of the preexisting whorl (Figure 2C). During growth of the shell, the trough extends downwards (abapically) in the direction of coiling, the apical end being filled with new shell material. The formation of new growth layers over this surface results in the formation of the columella.

Growth layers at the bottom of the trough contribute to growth of the central part of the columella, and those on the preexisting outer surface of the neck contribute to growth of the columella rim and a part of a whorl. This layer becomes part of the "ceiling" of the new shell whorl. The new shell is laid down directly upon that formed in the previous whorl. This surface of contact appears as a line in shell sections that is referred to as the "borderline" (Figures 2B, D; Tojo and Ohno, 1999).

Appearance of the growth layers in sections

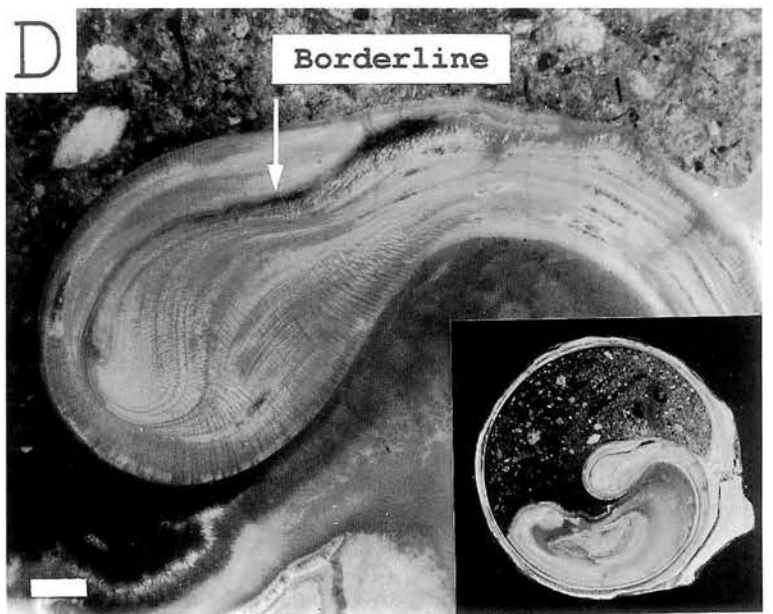
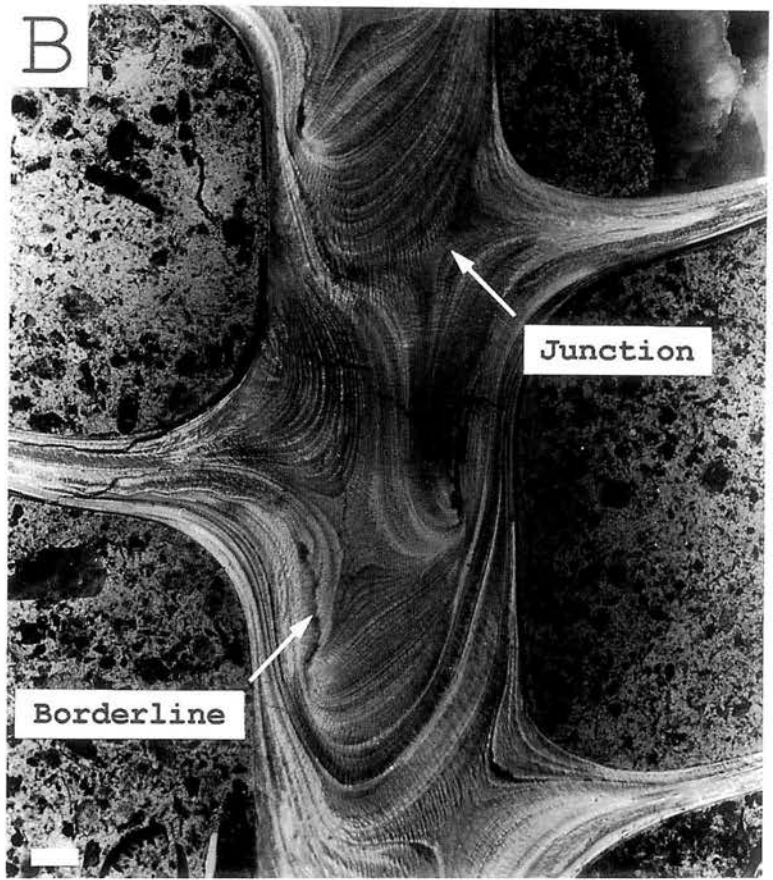
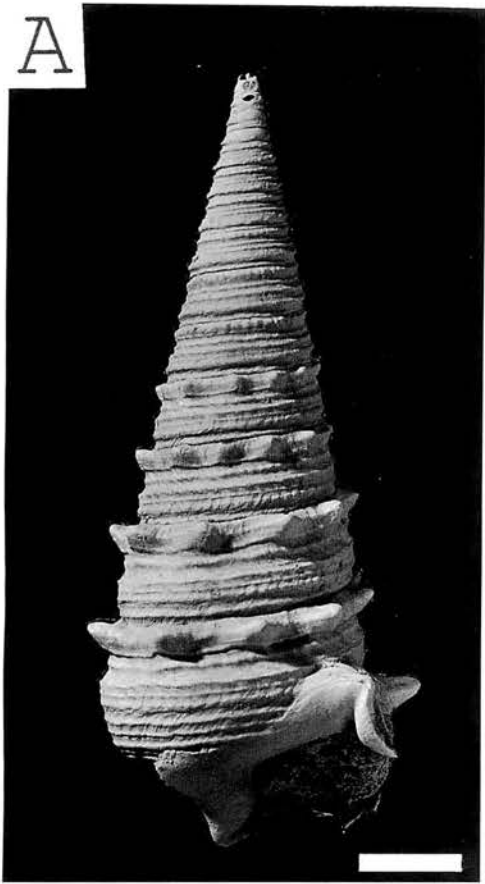
In vertical (=median longitudinal) section, each whorl shows a pair of more or less hyperbolic patterns, alternately on the right and left sides of the coiling axis (Figures 2B, 3). One is the trace of the trough facing the observer, and the other is that of the trough opposing the observer. The center of this hyperbolic pattern is called the "junction" (Figure 2B; Tojo and Ohno, 1999). The shell of the columella between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Borderlines are also observed in vertical sections (Figure 2B).

Continuous growth sequence on the vertical shell section

Correlation of the growth layers was accomplished by tracing them on vertical (=median longitudinal) and horizontal (=cross) sections. First a vertical section was made and the growth layers on it were documented (Figure 2B). Then the two halves of the shell were glued together with adhesive. The "repaired shell" was then cut horizontally. The cut surface was polished and its growth layers were documented (Figure 2D). Then the surface was ground away until shell corresponding to 90° of coiling had been removed. Polishing and documentation of horizontal sections at 90° intervals was repeated for more than one full whorl of the shell (Figure 3).

The columella occupies the center of the cross section,

Figure 2. A. A shell of *Vicarya yokoyamai* Takeyama, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1cm long. B. A vertical section of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. Along the coiling axis, micro-growth lines and intervening micro-growth increments are observed. The scale bar is 1mm long. C. The basal part of columella of *Vicarya yokoyamai*, Middle Miocene, Mizunami Group, Gifu Pref. The trough running along the columella and the new shell layer covering the previous whorl surface can be seen. The scale bar is 1cm long. D. A horizontal section of *Vicarya yokoyamai* with the columella at the center, Middle Miocene, Mizunami Group, Gifu Pref. The scale bar is 1mm long. (Photomicrographs of sections taken with binocular microscope.)



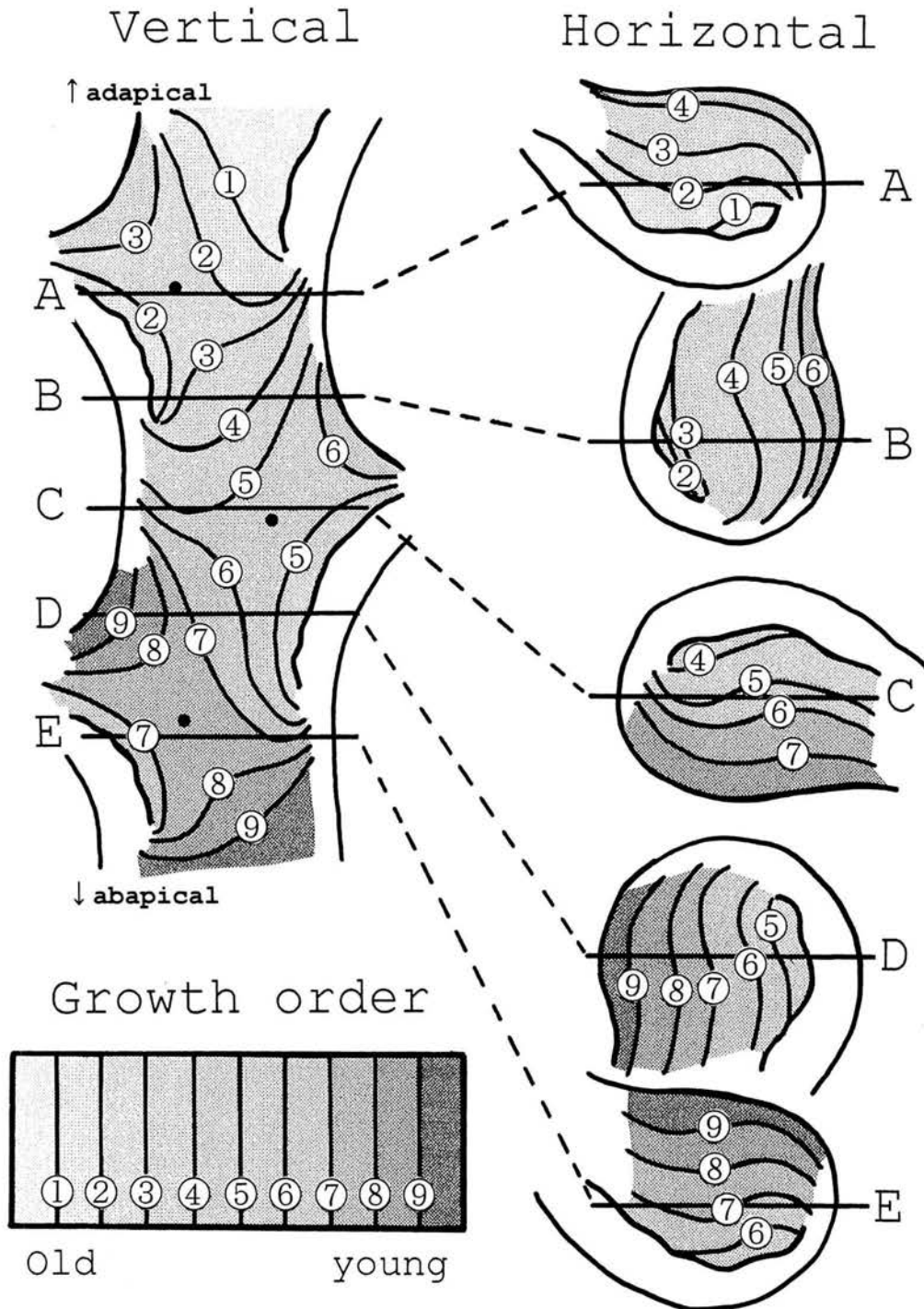


Figure 3. Correlation of growth layers on vertical (=median longitudinal) sections and horizontal (=cross) sections. Growth layers are numbered in temporal order from 1 to 9. Lines A to E show the correspondence of vertical and horizontal sections. On vertical section dots show junctions.

with a portion of the whorl extending away from it as if it were a vortex (Figure 2D). One side of the link between the columella and the vortex forms a concave surface and the other side is convex. The concave surface is underlain by

an accumulation of numerous U-shaped layers. In successive horizontal sections, viewed abapically, the vortex rotates clockwise. New growth layers are added to the surface of the concave side, move to the convex side abapically, and

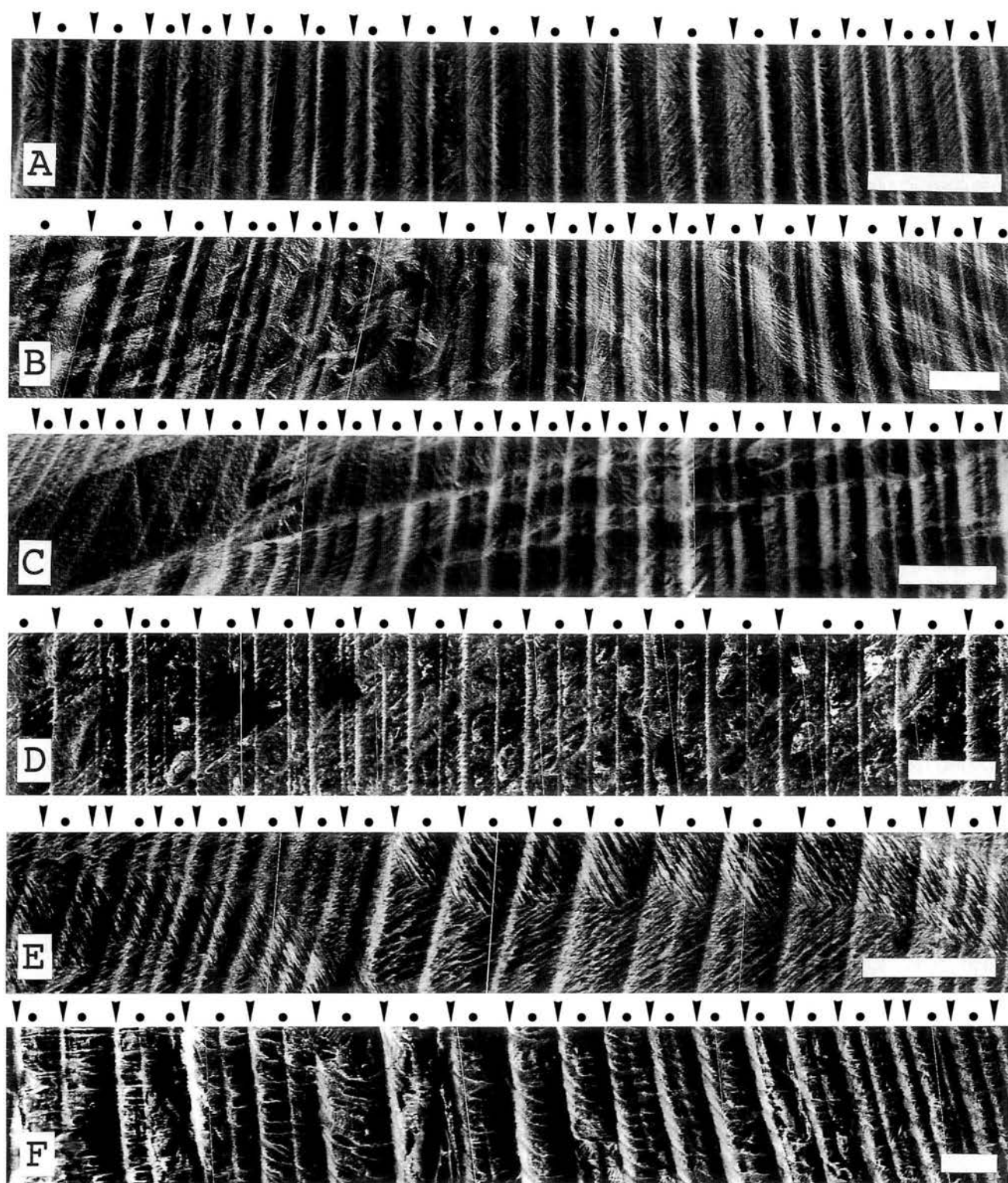


Figure 4. Tidal growth patterns recorded in the columella sections of *Vicarya yokoyamai*. **A.** Mizunami A specimen. **B.** Mizunami B specimen. **C.** Mizunami C specimen. **D.** Uchiura specimen. **E.** Bihoku specimen. **F.** Masuda specimen. Continuous semidiurnal tidal growth patterns are indicated by the alternation of thicker (arrowhead) and thinner (dot) micro-growth lines. The order of micro-growth line thickness changes. All scale bars represent 100 μm . (Photomicrographs taken with SEM.)

finally vanish.

Through observation of successive horizontal sections at 90° intervals the growth layers could be examined and numbered. In Figure 3 (right) the stack of numerous U-shaped growth layers is shown diagrammatically. Only lines with characteristic features, which could easily be correlated in vertical and horizontal sections, were numbered; the oldest conspicuous growth layer was numbered 1 and the newest numbered 9. All the corresponding growth layers could be seen on the vertical section for this growth interval, corresponding to more than one shell whorl (Figure 3 left). Since the mode of growth of the *V. yokoyamai* shell does not change during its ontogeny, all visible growth layers can be recognized and counted on the median longitudinal section of the shell.

Tidal growth patterns

Vicarya yokoyamai shells from the four localities show two sorts of accretionary patterns of micro-growth lines on the columella (Figure 4). One is the alternation of thicker (indicated by arrowheads in Figure 4) and thinner (dots in Figure 4) micro-growth lines. The other is an inversion of the arrangement of thicker and thinner micro-growth lines at approximately every 28.5 growth lines. The same micro-growth patterns of *V. yokoyamai* were reported in specimens from the Mizunami Group by Tojo and Sakakura (1998). These are characteristic features of tidal growth patterns (Dolman, 1975; Richardson *et al.*, 1979, 1980a, 1981; Richardson, 1988b; Ohno, 1989).

Identical alternations and inversions are reported from intertidal bivalves (Richardson *et al.*, 1979, 1981; Ohno, 1984, 1989; Richardson, 1988b) and gastropods (Ohno and Takenouchi, 1984; Tojo and Ohno, 1999). In bivalve shells from semidiurnal, mesotidal regimes, the alternation of thicker and thinner micro-growth lines is caused by differences in temperature between daytime and nighttime exposures to the air (Richardson *et al.*, 1980a; Richardson 1988b; Ohno, 1989). Inversions in the order of thicker and thinner micro-growth lines result from the different periodicities of approximately semidiurnal tides and of the 24 hour cycle of day and night. The zone where the inversion occurs is called the "switch zone" (Ohno, 1989). This mechanism may be responsible for the alternations and inversions observed in the succession of micro-growth lines of *V. yokoyamai* (Figure 4) from the Middle Miocene. This result is compatible with the tidal growth patterns of fossil bivalves from the Mizunami Group recognized by Ohno (1989). The preservation of this micro-growth pattern in all specimens suggests that *V. yokoyamai* lived in the intertidal zone.

The relationship between the number of tidal emersions and micro-growth lines in intertidal bivalves and gastropods has been confirmed by several experiments (Richardson *et al.*, 1979, 1980a, 1980b; Richardson *et al.*, 1980c; Ekarante and Crisp, 1982; Ohno, 1983, 1985, 1989; Richardson, 1987, 1988a, 1988b). Hence, it is reasonable to infer that one micro-growth line in the shell of *V. yokoyamai* is formed in each tidal cycle.

Reconstruction of growth curves

A continuous growth record can be obtained from the vertical section of a columella (Figures 2, 3). If shell growth was semidiurnal in *V. yokoyamai*, it should be possible to reconstruct growth curves using these observations.

Height of shell

To reconstruct the growth curve of *V. yokoyamai*, we had to estimate the original height of the shell. However, all specimens had lost some part of the apical portion of the shell. We extrapolated to determine the original height from the angle defined by the whorls of the surviving shell (Figure 5).

Growth curves of Mizunami specimens

We counted the number of micro-growth lines and measured the shell height at which each junction between whorls of the Mizunami specimens was formed (hereafter called junction height: Figure 5). The shell between successive junctions on the same side of the coiling axis corresponds to the growth record of one shell whorl. Therefore, the number of micro-growth lines between successive junctions, multiplied by 12.4 hours, represents the

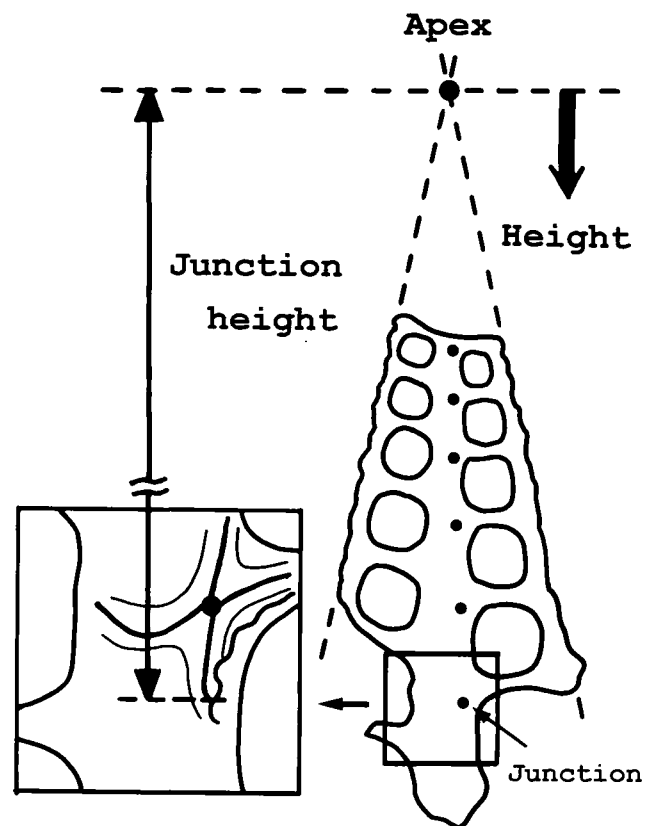


Figure 5. Shell height is the vertical distance between the tip of the columella and the reconstructed position of the apex, extrapolated from the outer surface of surviving shell whorls. Junction height is the shell height at which each junction was formed.

time required for growth of the shell whorl. Given the junction heights, we were able to reconstruct the growth curve.

First, the data for Mizunami C were plotted on a graph (Figure 6A). Then, data for Mizunami A and B were plotted as if their first junction heights lined up with that of Mizunami C (Figure 6A). The points plotted are based on the total number of clear micro-growth lines plus half the number of

unclear micro-growth lines. Error bars represent the accumulated number of unclear micro-growth lines. This graph shows that the growth curves of Mizunami specimens are similar. The growth rate gradually decreased with growth.

Growth curves of other specimens

We counted the numbers of micro-growth lines and

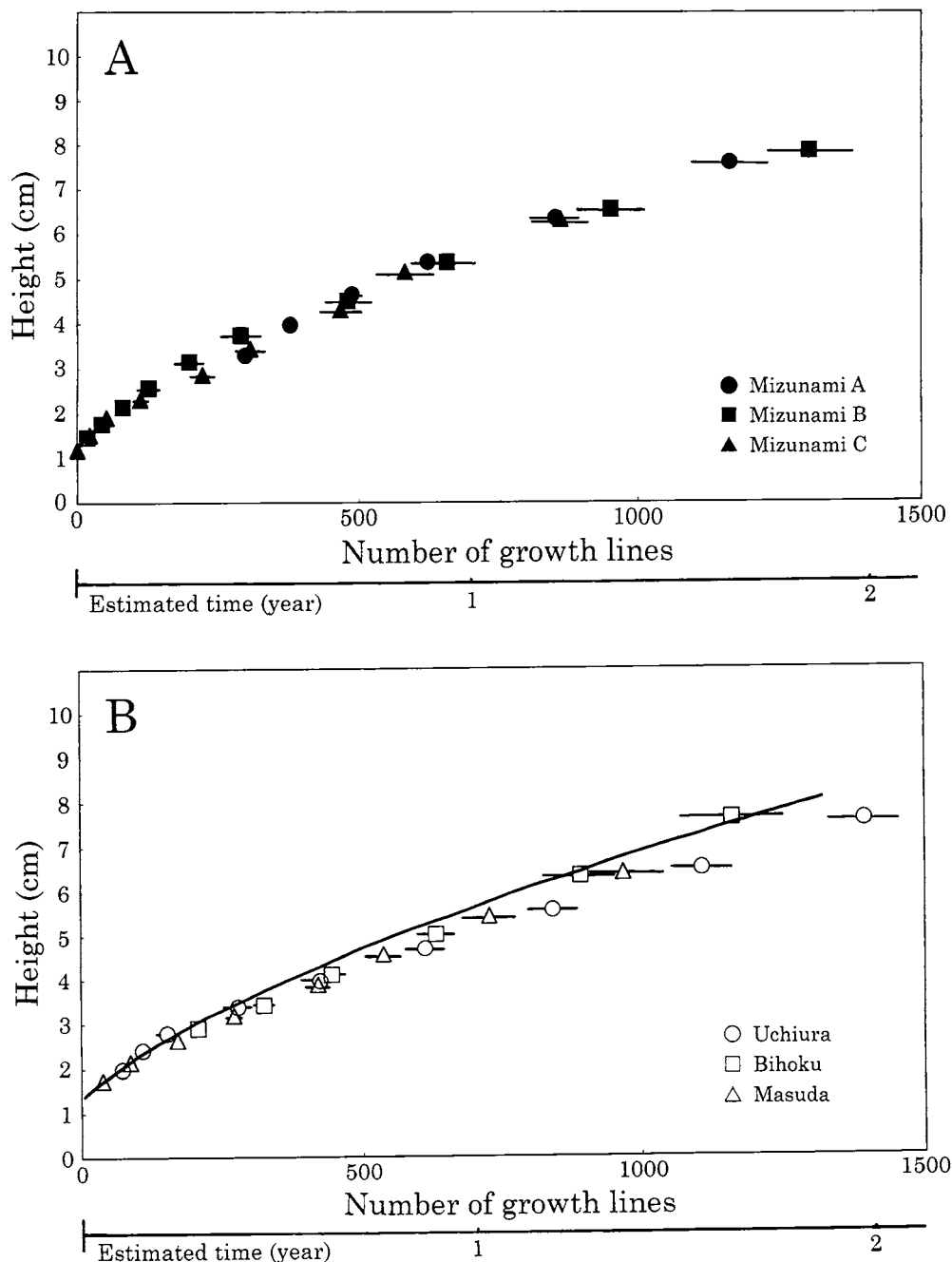


Figure 6. A. Reconstructed growth curves of *Vicarya yokoyamai* from the Mizunami specimens. B. Reconstructed growth curves of *Vicarya yokoyamai* from various areas. The solid line is the approximate growth curve of the Mizunami specimens.

measured the junction heights of other specimens, plotting similar growth curves (Figure 6B). In the figure, the solid line is the curve of best fit to the Mizunami specimen data. Data from other specimens were plotted so that their first junction heights lie on the Mizunami curve (Figure 6B). This graph shows that the growth curves of the Uchiura, Bihoku, and Masuda specimens are similar to those of shells from Mizunami.

Discussion

Previous studies have suggested that *Vicarya* lived in the intertidal zone of a subtropical mangrove swamp (Oyama, 1950; Chinzei, 1978; Itoigawa and Tsuda, 1986). This inference is corroborated by the pattern of tidal growth documented here. The alternation of thicker and thinner micro-growth lines is reported only from intertidal organisms. The observation of such alternations in all specimens suggests that *V. yokoyamai* lived in an intertidal zone where it was emersed twice a day.

Distinct major growth breaks, such as winter or spawning breaks, were not observed in this study. This is consistent with the subtropical habitat of *V. yokoyamai*, which lived during the warm Neogene climatic optimum (Chinzei, 1978; Chinzei, 1986; Ozawa *et al.*, 1995). Hence, there was no necessity for a winter break in growth.

We reconstructed the growth curves of six specimens from continuous growth records and the assumption that one micro-growth line formed in a tidal interval. Reconstructed growth curves approximate a logistic form. The logistic pattern of declining growth rate is typical of most invertebrates, indeed of most animals. This suggests the reconstruction is correct. The shells grew from 1.5 cm to 8 cm in height over two years. The adult shell of *Vicarya* has a prominent, thick outer lip. The growth curves suggest that these animals reached maturity and formed the prominent outer lip at the age of two years.

Jones (1981) showed that the standardized growth rate of *Spisula solidissima* changes drastically in conjunction with monthly average mean sea surface temperatures. The change of growth rate is largely explained by the presence of the winter break. In contrast to this cool-water species, the reconstructed growth curves of the *Vicarya* specimens show no or weak seasonal fluctuations. This suggests that *V. yokoyamai* grew in a stable subtropical environment without any climatic deterioration. This inference should be tested by studies of the growth of cooccurring fossils.

The number of specimens studied here is small, due to weathering and recrystallization of most specimens. However, the good agreement of the growth curves in shells from different formations and localities suggests that the columella-method and tidal growth analysis can be used to infer high-resolution population dynamics of fossil gastropod assemblages of various ages.

Conclusion

The columella method yields evidence of continuous growth sequences in shells of the fossil potamidid gastropod

V. yokoyamai. The tidal growth patterns of *V. yokoyamai* shells suggest that this gastropod lived in the intertidal zone, under the influence of semidiurnal tides. The reconstructed growth curves of specimens from the Mizunami, Uchiura, Bihoku, and Masuda groups show that their shells grew at similar rates, from 1.5 cm to 8 cm in height in two years.

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Ordovician cephalopods from the Maggol Formation of Korea

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Abstract. A cephalopod fauna consisting of 11 species belonging to 7 genera is described from the Lower Ordovician Maggol Formation near Taebaeg City in South Korea. The fauna includes two new species, *Ormoceras weoni* and *Michelinoceras cancellatum*, and *Wutinoceras*, a primitive genus of the family Actinoceratidae first reported from South Korea. *Ormoceras cricki* from the Middle Ordovician Duwibong Formation occurs in the uppermost horizon of the Maggol Formation, and thus may be regarded as a forerunner of the ormocerids in Korea.

The Maggolian cephalopod fauna comprising *Wutinoceras robustum*, *Kogenoceras nanpiaoense*, and *Manchuroceras* spp. shows closest affinities with those from the Setul Limestone of the Langkawi Islands, Malaysia and from the Beianzhuang Formation of Hwangho Basin, North China. This fauna is, therefore, assigned in age to the late Ibexian to early Whiterockian in the American Early Ordovician scale.

Key words : cephalopod fauna, lower Whiterockian, Maggol Formation, Ormoceratidae, upper Ibexian, Korea

Introduction

Kobayashi (1927) first described seven cephalopod species from the Ordovician of South Korea, including *Kotoceras grabau* from the Middle Ordovician Maggol Formation. In a subsequent monograph (Kobayashi, 1934), the stratigraphic occurrences of these species were reassigned to the overlying Middle Ordovician Jigunsan Formation.

Cephalopod fossils seldom occur in the Maggol Formation. They are commonly found as partial phragmocones whose internal structures are difficult to recognize because of recrystallization. Despite such generally unfavorable fossil preservation, more than fifty well preserved cephalopod specimens have been recently collected from the Maggol Formation of Sanaegol, Taebaeg City, Kangweondo, Korea (Figure 1).

This paper describes the cephalopod fauna of the formation based mainly on newly collected material in addition to Kobayashi's (1927) type and figured specimens. Comparison with contemporary faunas from other regions is also given in this paper, with discussion of the biostratigraphic and paleobiogeographic implications of the Maggol fauna.

All specimens described herein are housed in the Department of Earth Science, Teachers College, Kyungpook National University (prefix KPE), Taegu, Korea.

Geological setting

The Maggol Formation was originally named by Kobayashi (1927) for a limestone formation "the Great Limestone Group"

exposed near the village "Maggol", at the Sangdong Scheelite Mine, Sangdong, Yeongweol. The formation extends from east to west in the southern limb region of the Baegunsan Syncline where the Duwibong type Joseon Supergroup is widely distributed. The formation ranges from 250 m to 400 m in thickness.

The Maggol Formation conformably overlies the Dumugol Formation and is overlain by the Jigunsan Formation. Almost complete sequence of the formation is exposed along the Sanaegol Section, 7 km southwest of Hwangjidong in Taebaeg City (Figure 1). In this section, the lower part of the formation is barren of macrofossils. Cephalopod fossils were found in two stratigraphic units, the middle-upper and uppermost parts of the formation (Figure 2).

Lithologic components of the formation consist of bioturbated limestone, well bedded limestone and bioclastic limestone with frequent intercalations of dolomite and dolomitic limestone. Flat pebble conglomerates are included in the lower part of the formation, but they were not observed in the section examined. The boundary between the underlying Maggol and overlying Jigunsan Formations was observed at a small waterfall, about 1.5 km upstream along the valley from Sanaegol village. The lithic facies at this place shows an abrupt change from bioclastic grainstone consisting mostly of oölitic particles to calcareous black shale. Based on the general composition and sedimentary structures such as desiccation cracks, ripple marks, bird's-eye structures, and bioturbation, Paik (1985, 1987, 1988) suggested tidal flats as the depositional environments of the Maggol Formation. Cephalopod fossils were collected mainly from the bioclastic

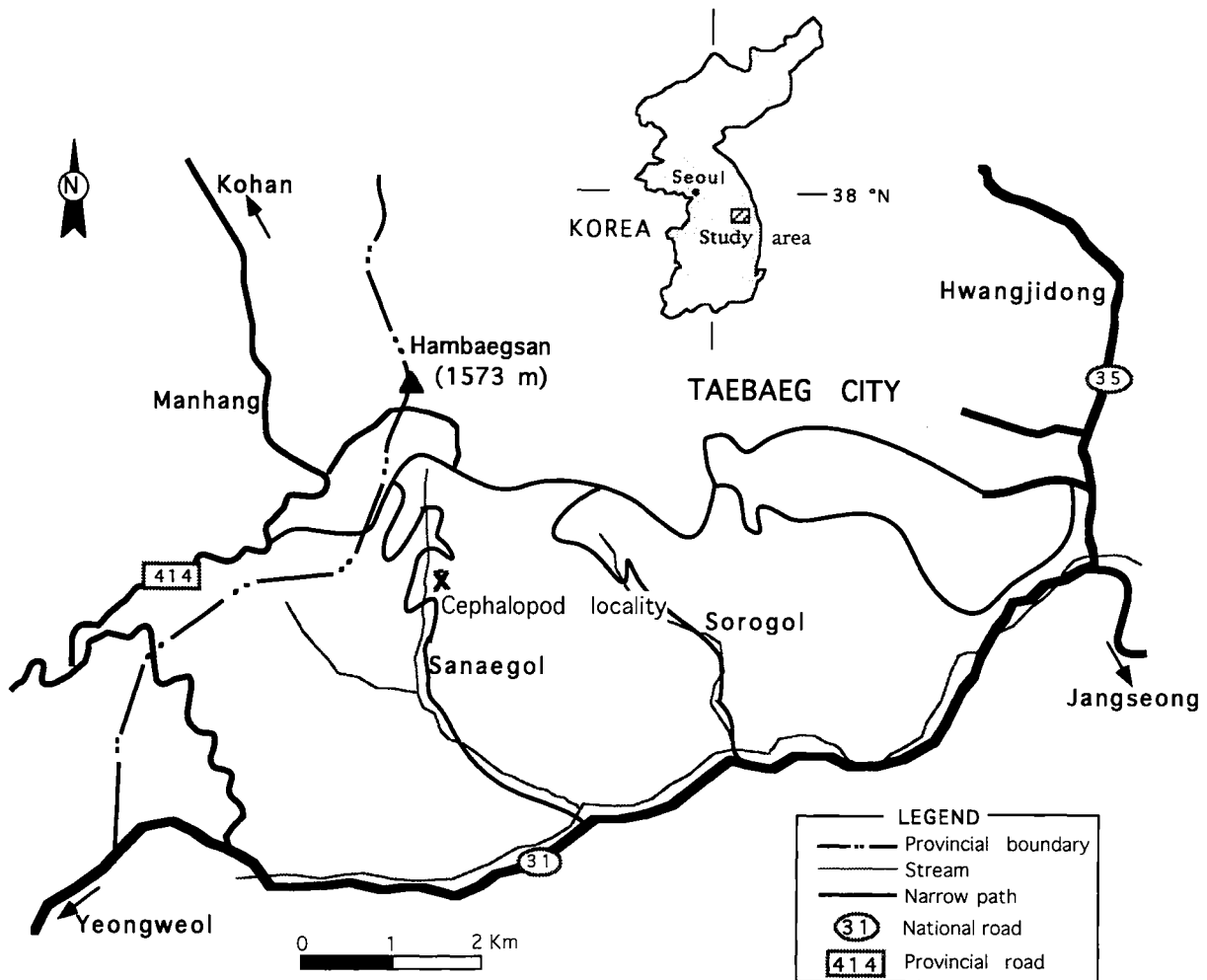


Figure 1. Index map of fossil locality on the western area of Taebaeg City, Kangweondo.

and bioturbated limestones in the two stratigraphic levels mentioned above, being especially abundant in the uppermost horizon of this formation.

Faunal characteristics and correlation

Based on a relatively limited number of cephalopod specimens, Kobayashi (1966) designated three fossil horizons in the middle and upper parts of the Maggol Formation; *Manchuroceras*, *Polydesmia*, and *Sigmorthoceras* horizons in ascending order (Table 1), and correlated them with upper Canadian, and lower and middle Chazyan (Whiterockian in the present usage) in North America, respectively. Kobayashi (1977) studied Takuhiro Shiraki's collection and described four endoceroid species belonging to *Manchuroceras* from the Maggol Formation, without documentation of their exact localities and stratigraphic positions. Since siphuncular remains of *Manchuroceras* were not found in the overlying Jigunsan and Duwibong Formations, Kobayashi (1966) assigned the horizon of the *Manchuroceras* fauna to the middle part of the Maggol Formation.

Table 1. Lithostratigraphic and biostratigraphic division of Ordovician Duwibong type sequence of Joseon Supergroup in Korea (Compiled from Kobayashi, 1966; Kim *et al.*, 1991).

Formation	Macrofossil zone
Duwibong	Actinoceroids
Jigunsan	Orthoceroids
Maggol	<i>Sigmorthoceras</i> <i>Polydesmia</i> <i>Manchuroceras</i> <i>Clarkella</i>
Dumugol	<i>Kayseraspis</i> <i>Protopliomerops</i> <i>Asaphellus</i>
Dongjeom	<i>Pseudokainella</i>

In this study, 53 cephalopod specimens from seven horizons in the Maggol Formation were collected and analyzed (Figure 2). The following 11 species belonging to 7 genera

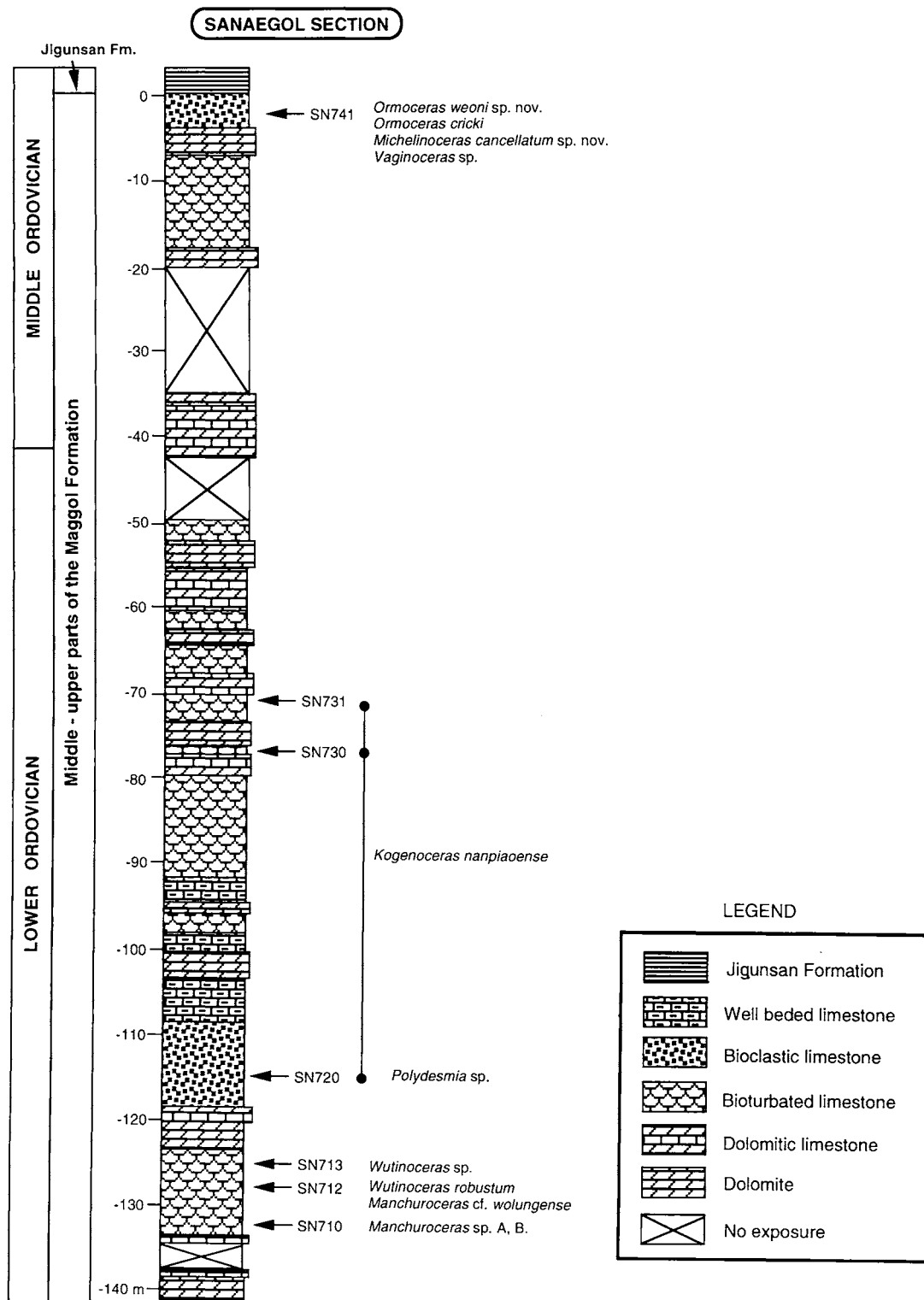


Figure 2. Geologic column of the middle to upper parts of the Maggol Formation at Sanaegol section, showing the cephalopod-bearing horizons. SN stands for the locality name, "Sanaegol".

were recognized: *Ormoceras weoni* sp. nov., *Ormoceras cricki* Kobayashi, 1934, *Michelinoceras cancellatum* sp. nov., *Vaginoceras* sp., *Kogenoceras nanpiaoense* (Kobayashi and Matsumoto, 1942), *Polydesmia* sp. cf. *P. canaliculata* Lorenz, 1906, *Wutinoceras robustum* (Kobayashi and Matsumoto, 1942), *Wutinoceras* sp., *Manchuroceras* sp. cf. *M. wolungense* (Kobayashi, 1931), *Manchuroceras* sp. A, and *Manchuroceras* sp. B.

Of these species, the two *Wutinoceras* species are the first report of the genus in Korea. *Wutinoceras* is widespread in the lower-middle Whiterockian strata of North America (Flower, 1957, 1968, 1976), Australia (Teichert and Glenister, 1953; Flower, 1968; Stait, 1984; Stait and Burrett, 1984), North China (Endo, 1930; Kobayashi and Matsumoto, 1942; Chang, 1965; Zhu and Li, 1996) and Malaysia (Stait and Burrett, 1982). Teichert (1935) and Flower (1968) regarded *Polydesmia* as the oldest and most primitive of the actinoceroids, relying on their thick connecting ring and dendritic

radial canal system. In the Ordovician of China, however, *Polydesmia* does not occur prior to *Wutinoceras* (Chen, 1976; Chen *et al.*, 1980). Therefore, *Wutinoceras* may be the ancestor of the Actinoceratidae, as suggested by Flower (1976).

The three species of *Manchuroceras* from the Maggol Formation listed above are always represented by partial siphuncles and were found in the middle part of the Maggol Formation (Figure 2). The two horizons (SN710 and 712 in Figure 2) yielding these fossils may be equivalent to the *Manchuroceras* horizon of Kobayashi (1966). The genus name *Manchuroceras* was first proposed by Ozaki (1927) without describing its type species, and was subsequently emended and redescribed in detail by Kobayashi (1935). This genus characterizes the Wolungian stage in North China. A total of 28 species assigned to *Manchuroceras* are described from the Ordovician of various regions (Table 2), among which 20 species are known from China, 4 species

Table 2. List of *Manchuroceras* species hitherto described.

Species	Occurrence	Reference
<i>Manchuroceras</i> nom. nud. Ozaki	Wolungian (Lower Ordovician) limestone of Manchoukou, Manchuria	Ozaki (1927)
<i>Manchuroceras wolungense</i> (Kobayashi)	Wolungian (L. Ordovician) limestone of Manchoukou, Manchuria	Kobayashi (1935), Obata (1939)
<i>M. endoi</i> Kobayashi	Lower Ordovician Santao Formation, Liaotoug, Manchuria	Kobayashi (1935) cf. Endo (1932)
<i>M. ozakii</i> Obata	Daling limestone, Manchuria; Liangjiashan Formation of Hupeh, China	Obata (1939)
<i>M. compressa</i> (Kobayashi)	Wolung limestone of Wolung, Manchuria; Liangjiashan Formation of Hupeh, China	Obata (1939)
<i>M. platyventrum</i> (Grabau)	Daling limestone, Manchuria; Liangjiashan Formation of Hupeh, China	Obata (1939)
<i>M. ishidae</i> Obata	Liangjiashan Formation of Hupeh, China	Obata (1939)
<i>M. yenchouchengense</i> Obata	Daling limestone, Manchuria	Obata (1939)
<i>M. kobayashii</i> Obata	Liangjiashan Formation of Hupeh; Maggol Formation of Yongyeon-chon, Taebaeg, S. Korea	Obata (1939), Kobayashi (1977)
<i>M. katsunumai</i> Obata	Liangjiashan Formation of Hupeh, China	Obata (1939)
<i>M. steanei</i> Teichert	L. Ordovician, Adamsfield, Tasmania	Teichert (1947)
<i>M. excavatum</i> Teichert	L. Ordovician, Adamsfield, Tasmania	Teichert (1947)
<i>M. asiasticum</i> Balashov	Early Middle Ordovician Krivolutsky Formation, Siberia Platform	Balashov (1962)
<i>M. sp.</i>	L. Ordovician Lower Jiacun Group of Nyalam, Xiuang, China	Chen (1975)
<i>M. qingshuiheense</i> Chen	L. Ordovician Liangchiashan Fm., Qingshuihe, Inner Mongolia	Chen (1976)
<i>M. tochuanshanense</i> Chang	Lower Ordovician, upper part of Tochuanshan limestone, Chinghai, N.W. China	Chang (1965)
<i>M. lemonei</i> Hook & Flower	Florida Mountains Formation, El Paso, Texas	Hook & Flower (1977)
<i>M. cf. platyventrum</i> (Grabau)	Maggol Formation of Gaesan-chon, Taebaeg City, Kangweondo, S. Korea	Kobayashi (1977)
<i>M. tenuise</i> Kobayashi	Maggol Formation of Guemdae-chon, Sangjangmyeon, Samcheok-gun, Kangweondo, Korea	Kobayashi (1977)
<i>M. hanense</i> Kobayashi	Maggol Formation of Godoo-am, Guraeri, Samgdong, Yeongweol, Kangweondo, S. Koera	Kobayashi (1977)
<i>M. ? sp.</i>	Maggol Formation of Godoo-am, Guraeri, Samgdong, Yeongweol, Kangweondo, S. Koera	Kobayashi (1977)
<i>M. limatum</i> Xu.	L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China	Xu (1981)
<i>M. densum</i> Xu	L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China	Xu (1981)
<i>M. pachymuratum</i> Xu	L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China	Xu (1981)
<i>M. yangteense</i> Xu	L. Ordovician Honghuayuan Formation of Yichang, Hupeh, Central China	Xu (1981)
<i>M. yazipingense</i> Zou	L. Ordovician Liagchishan Formation of Shanxi, North China	Zou (1981)
<i>M. minitum</i> Zou	L. Ordovician Liagchishan Formation of Shanxi, North China	Zou (1981)
<i>M. pianguanense</i> Zou	L. Ordovician Liagchishan Formation of Shanxi, North China	Zou (1981)
<i>M. platyventrum</i> (Grabau)	L. Ordovician Liagchishan Formation of Hebei, North China	Lai <i>et al.</i> (1982)
<i>M. nakamense</i> Stait & Burrett	Upper Ibexian Thungsong Formation of Ron Phibum, Southern Thailand	Stait & Burrett (1984)

from South Korea, 2 species from Tasmania, 1 species from the Siberian Platform, and 1 species from Texas, U.S.A. Most of them, excluding the Russian one, are known to occur in the Lower Ordovician (upper Ibexian). The *Manchuroceras* horizon of the Maggol Formation in Korea is correlated with the Liangchiashan Formation, Hwangho Region and with the Hunghuayuan Formation, Yangtze Region (Chen *et al.*, 1980). The cephalopod fauna including *Manchuroceras nakamense* from the Lower Setul Limestone of Malaysia shows some affinities with that from the Maggol Formation. The OT8 zone of the Karmberg Limestone, Tasmania, proposed by Banks and Burrett (1980) may also be correlated with the Maggol Formation.

The specialized actinoceroid *Polydesmia*, which is characterized by a vertically lamellate structure of the siphuncular filling and high obliquity of the radial canal, is only known from East Asia, including North Korea, Inner Mongolia, South Manchuria and Shandong in China. Kobayashi (1966) designated the *Polydesmia* horizon in the upper part of the Maggol Formation, based on a single specimen of this genus. Unfortunately, he did not illustrate this specimen and it is probably lost. Furthermore, all of the type specimens of the four *Polydesmia* species described by Kobayashi (1940) from China and North Korea are lost. According to Chen *et al.* (1980), *Polydesmia* is typically found in the Lower Ordovician Beianzhuang Formation of Hubei and Shandong in North China, which is conformably underlain by the *Manchuroceras*-bearing Liangchiashan Formation. The occurrence of *Polydesmia* cf. *canaliculata* in the upper part of the Maggol Formation supports the validity of the *Polydesmia* horizon established by Kobayashi (1966). This genus co-occurs with two other genera, *Wutinoceras* and *Manchuroceras* in Korea and China. Since the upper part of the Korean Maggol Formation yields *Polydesmia*, its age is assigned to the early Whiterockian in the North American scale.

Wutinoceras robustum (Kobayashi and Matsumoto, 1942) occurs in the middle part of the Maggol Formation, together with some *Manchuroceras* specimens (Figure 2). The higher horizons (locs. SN730 and 731 in Figure 2) yield the annulated orthoconic cephalopod *Kogenoceras nanpiaoense* (Kobayashi and Matsumoto, 1942). These two species have previously been recorded from strata of uncertain age within the Ordovician in Nanpiao Coalmine, Nanpiao County, Liaoning Province, and were assigned to the Toufangian in South Manchuria by Kobayashi and Matsumoto (1942). Stait and Burrett (1982) described *W. robustum* from the Lower Setul Limestone of Whiterockian age in the Langkawi Islands, Malaysia. Subsequently, Stait *et al.* (1987) described *Kogenoceras nanpiaoense* from a slightly higher horizon than the *W. robustum*-bearing strata in the same area and assigned it a Whiterockian age. These lines of evidence suggest that the cephalopod fauna of the Maggol Formation has strong affinities to the Southeast Asian and North Chinese faunas of equivalent age.

Four species belonging to 3 genera were identified among many small-sized cephalopod specimens recovered from the horizon just below the boundary of the Maggol and Jigunsan Formations (loc. SN741 in Figure 1). Of these species, *Ormoceras weoni* sp. nov and *O. cricki* occur most abundant-

ly, making up more than 90 per cent of the cephalopod assemblage. The latter species is common in the Duwibong Formation, the uppermost Ordovician formation in Korea (Kobayashi, 1934), indicating that this species has a long range from the Maggol Formation to the Duwibong Formation. This species possibly represents the oldest type of the ormocerids in the upper Jigunsan and Duwibong Formations.

Systematic paleontology

The terminology and measurements of various shell morphological characters used in this paper are shown in Figure 3.

Subclass Endoceratoidea Teichert, 1933

Order Endocerida Teichert, 1933

Family Manchuroceratidae Kobayashi, 1935

Genus *Manchuroceras* Ozaki, 1927 emend. Kobayashi, 1935

Type species: *Piloceras wolungense* Kobayashi, 1931

Manchuroceras sp. cf. *M. wolungense* (Kobayashi, 1931)

Figures 4-1a, b; 7-5a, b

Material.—Isolated partial siphuncle, KPE20073 from loc. SN712.

Description.—Partial siphuncle with apical end, 71.2 mm in length; its dorsal side somewhat weathered and apical portion distorted by local joint and calcite vein; apex bluntly pointed; dorsoventral and lateral diameters nearly equal at a distance of 49.7 mm from apex, i.e., circular in cross section, 30.5 mm in diameter; inner side of siphuncle lined with crystalline calcite, recrystallized endosiphosheaths, this lining thinnest on dorsal side, becoming thicker laterally, ventral side of siphuncle strengthened by additional deposits, forming endosiphowedge, 12.4 mm thick at a distance of 49.7 mm from apex; endosiphococone rapidly expanding, its apical angle approximately 45 degrees, its apex continuing into endosiphotube, in which endosiphuncular segments are detected.

Remarks.—This species appears to be closely allied to *Manchuroceras wolungense* (Kobayashi) from the Wolung Limestone of South Manchuria (Kobayashi, 1931 p. 170, pl. 17, figs. 2, 3a, b, 6; pl. 18, figs. 2a, b; pl. 19, fig. 1) in having a circular cross section of the siphuncle and well developed endosiphowedge. Specific identification requires additional better preserved specimens.

Occurrence.—Known from the middle part of the Maggol Formation of Sanaegol, Taebaeg City, Kangweondo, South Korea.

Manchuroceras sp. A

Figures 4-2a, b; 7-1a—c

Material.—Isolated partial siphuncle, KPE20256 from loc. SN710.

Description.—Internal mould of siphuncle, 77.7 mm long; straight, with its diameter expanding twice as rapidly laterally

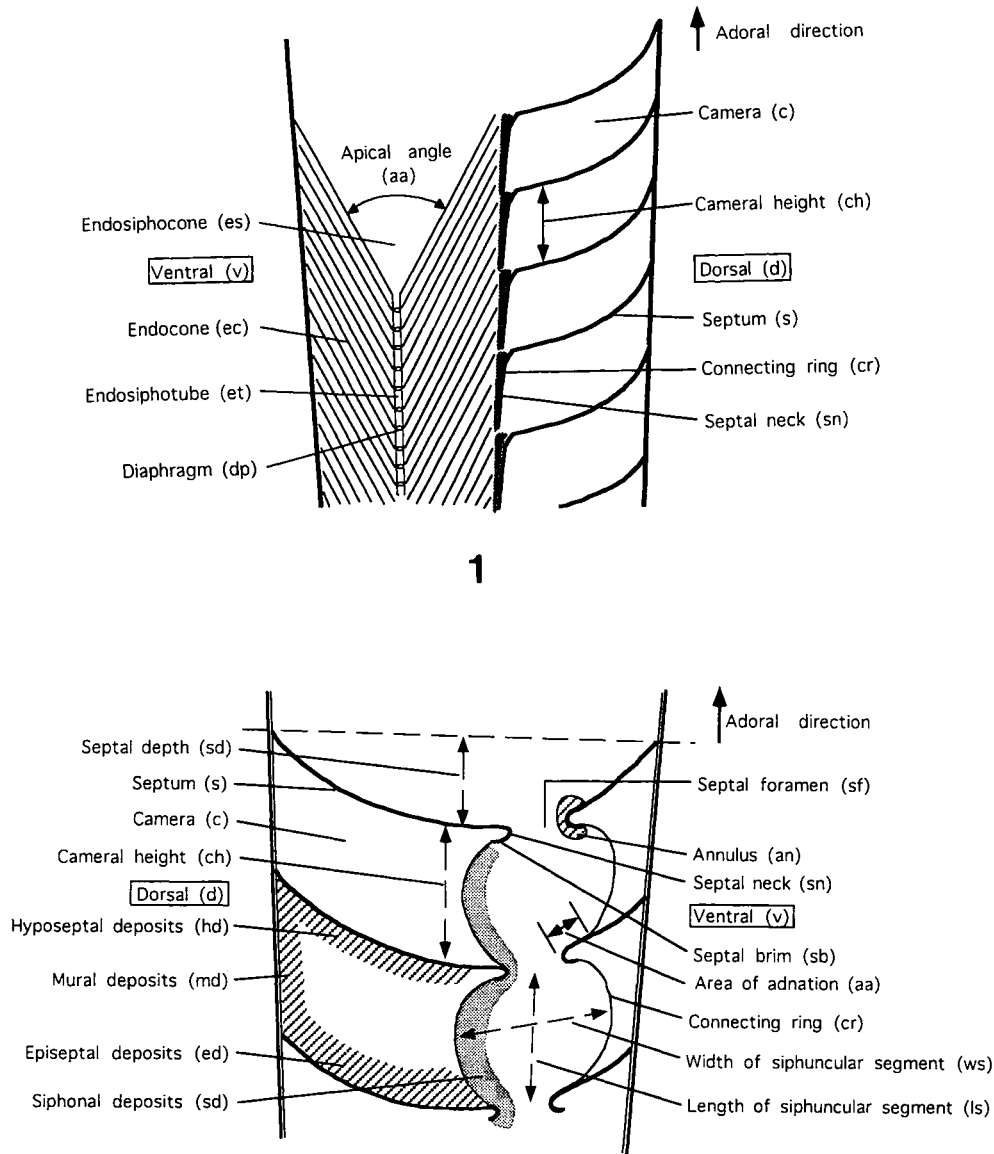


Figure 3. Terminology and measurements of internal shell structures of idealized endoceroid (1) and actinoceroid (2) cephalopods used in this paper. Abbreviations of various shell characters are written in parentheses. Compiled and modified from Teichert *et al.* (1964), Aronoff (1979), and Zhu and Li (1996).

as dorsoventrally; its cross section circular in juvenile stage, but becomes elliptically depressed with growth, ratio of dorsoventral to lateral diameters of siphuncle at adoral end being 3:4; endosiphuncular deposits nearly uniform in thickness, not forming endosiphowedge, endocones recrystallized; endosiphococone slender, deep, rapidly expanding with apical angle of 25 degrees, its apex acutely pointed and situated at endosiphuncular center, continuing into endosiphotube which pierces apex; outside of siphuncle appears to be smooth.

Remarks.—This species is allied to *Manchuroceras tenuise Kobayashi* from Guemdae-chon, Taebaeg City, Kangweondo (Kobayashi, 1977) in the small apical angle of the endosi-

phococone and ovate cross section, but is distinguished by evenly thickened endosiphuncular linings. *Manchuroceras yenchouchengense* Obata from the Daling Limestone of Liaoning, South Manchuria (Obata, 1939, p.103, pl. 7, figs. 4, 6; pl. 8, fig. 2; pl. 10, fig. 6) may be related to this species in the elliptical cross section, but its blunt endosiphococone and greater dorsoventral diameter serve to distinguish this species from *M. yenchouchengense*. This comparison indicates that the present species belongs to *Manchuroceras*, but well preserved additional specimens are needed for species-level assignment.

Occurrence.—Known only from the middle part of the Maggol Formation in Sanaegol.

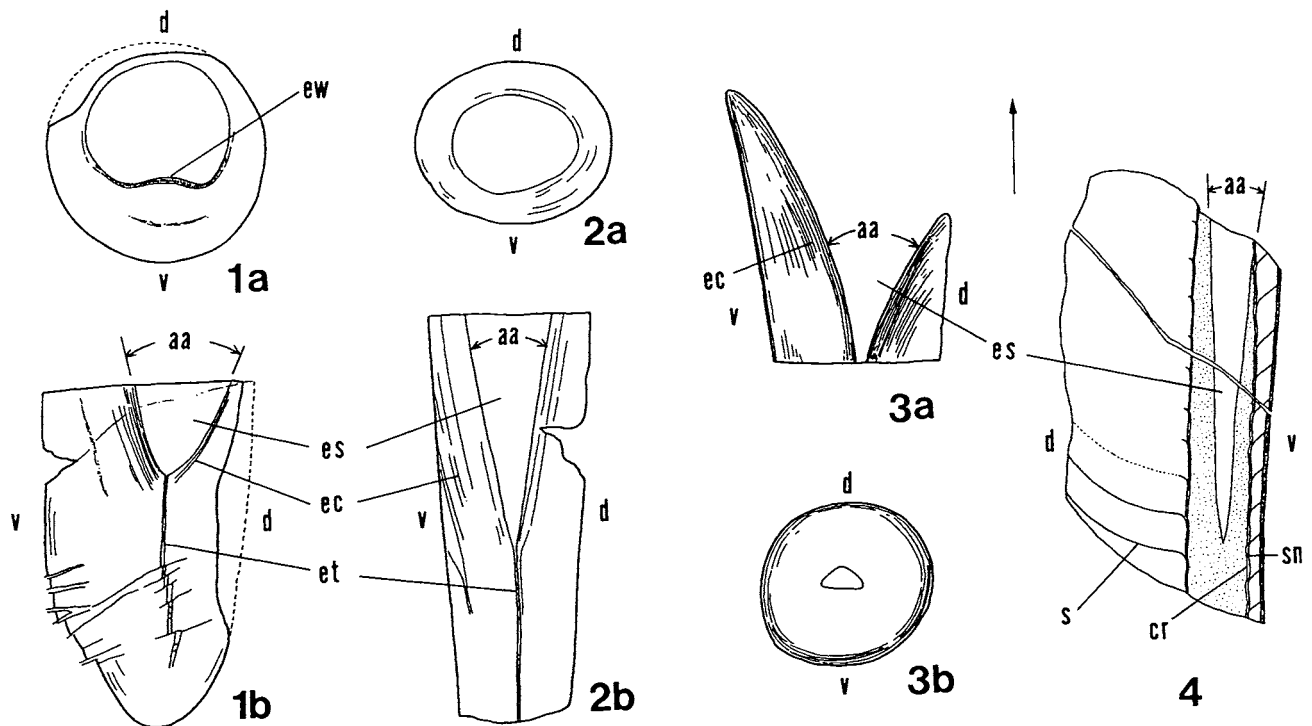


Figure 4. Diagrammatic drawings of endoceroid cephalopods described herein. **1a, b.** *Manchuroceras* sp. cf. *M. wolungense* (KPE20073), $\times 0.9$, 1a: cross section at the adoral end, 1b: longitudinal section. **2a, b.** *Manchuroceras* sp. A (KPE20256), $\times 1$, 2a: cross section at the adoral end, 2b: longitudinal section, **3a, b.** *Manchuroceras* sp. B (KPE20065), $\times 0.9$, 3a: longitudinal section, 3b: cross section at the adapical end, **4.** *Vaginoceras* sp. (KPE20230), $\times 1.4$. The arrow indicates the adoral direction for 1b, 2b, 3a, and 4. For abbreviations see Figure 3, except for ew: endosiphonwedge.

Manchuroceras sp. B

Figures 4-3a, b; 7-4a, b

Manchuroceras sp. indet. Kobayashi, 1977, p. 24, pl. 3, figs. 3a, b.

Material.—Partial siphuncle, KPE20065 from loc. SN710.

Description.—Imperfect siphuncle; slowly expanding, with apical angle 13 degrees; adapical end circular in cross section but endosiphococone triangular, its tip somewhat rounded, more flattened ventrally than dorsally, its basal length and height 5 mm and 2.5 mm, respectively; apical angle of endosiphococone about 65 degrees, but abruptly decreasing toward adapical end at broadly curving point of endosiphonling, attaining 15 degrees; endocone asymmetrical, rapidly extending anteriorly and more thickened on ventral side than on dorsal side, numerous lamelliform endococones well developed; no cameral portion detected.

Remarks.—This species is allied to *Manchuroceras tenuise* Kobayashi from Guemdae-chon, Sangjangmyeon, Samcheok, Kangweondo, Korea (Kobayashi, 1977, p. 23, pl. 4, figs. 2a, b) in its triangular endosiphococone in cross section, but differs by its centrally located and more slowly expanding endosiphococone. This species is distinguished from *Manchuroceras* sp. A described above, in the much more rapidly expanding endosiphococone.

Meanwhile, the apical angle of the endosiphococone and

thickness of endocone in this species are similar to those in the specimen of *Manchuroceras*? sp. indet. described by Kobayashi (1977) from Godoo-am, Guraeri, Sangdong, Yeongweol. However, incomplete preservation of the present specimen precludes exact specific assignment.

Occurrence.—Known only from the middle part of the Maggol Formation in Sanaegol.

Family Endoceratidae Hyatt, 1883

Genus *Vaginoceras* Hyatt, 1883

Type species: *Endoceras multitubulatum* Hall, 1847

Vaginoceras sp.

Figures 4-4; 7-2a, b

Material.—Partial phragmocone, KPE20230 from loc. SN741.

Description.—Partial phragmocone, 36 mm in length, medium-sized orthocone containing endosiphococone; conch wall 0.6 mm thick on ventral side; slowly expanding; somewhat laterally compressed, ratio of dorsoventral to lateral diameter about 1.4:1; siphuncle submarginal in position, 1.5 mm distant from ventral margin, nearly circular in cross section, broad, its diameter a little less than one-third of dorsoventral conch diameter; septa on dorsal portion mostly obliterated during fossilization, but two preserved septa at

basal part having septal depth one and a half times the cameral height, while septa on ventral side are comparatively well preserved, attached to ventral wall at an angle of 45 degrees; septal necks holochoanitic, extending just to preceding ones; connecting rings about three times thicker than septal neck, embracing inside of septal necks; cameral height 2.5 mm, six camerae distributed in a length corresponding to dorsoventral conch diameter at adoral end; no cameral deposits observed; siphonal deposits well developed, dorsally more extended in longitudinal section, long and slender endosiphococone bounded by last endocone having wedge-shaped section and its apical angle about 15 degrees; shell surface smooth.

Remarks.—The presence of a thick connecting ring and acute endosiphococone indicates that this species belongs to *Vaginoceras*. Unfortunately, incomplete preservation of the specimen examined precludes species-level assignment.

In the long endosiphococone and ectosiphuncular morphology, this species can be allied to *Vaginoceras endocylindricum* Yü from the beds just below the red limestone near Tawushu, north of the western end of Peiyangshan, Chungyanghsien (Yü, 1930, p. 33, pl. 2, figs. 5a–c; pl. 3, figs. 2a–d, 3a, b), but the former is distinguished from the latter by more closely spaced septa and more compressed conch.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Order Orthoceratida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus *Michelinoceras* Foerste, 1932

Type species: *Orthoceras michelini* Barrande, 1866

***Michelinoceras cancellatum* sp. nov.**

Figures 5-1; 7-7, 8a–c

Type material.—Holotype, KPE20254 and paratype, KPE20255 both from loc. SN741.

Diagnosis.—Longiconic orthocone with circular cross section; siphuncle central; septal spacing wide; camerae with well developed mural-episeptal deposits; surface ornamented with transverse lines and very fine longitudinal lirae, forming cancellate markings.

Description.—Holotype, KPE20254 (Figures 5-1 and 7-8a–c) represented by a partial phragmocone of juvenile conch; very slender, longiconic orthocone, 21.4 mm in length, consisting of 8 camerae; circular in cross section; very slowly expanding at a rate of 1 mm in 15 mm; siphuncle central in position, tubular, parallel to shell wall, narrow, about 1 mm in diameter, corresponding to one-sixth of conch diameter; septa gently concave adorally; its depth one-third of cameral height, septal necks short, orthochoanitic; connecting rings thin; septa broadly spaced, averaging 2 mm distant between them, 2.5 camerae occurring in a length equal to conch diameter of 6.1 mm; camerae with L-shaped mural-episeptal deposits, remaining space filled with ooid particles and inorganic matrix; siphuncle filled with some

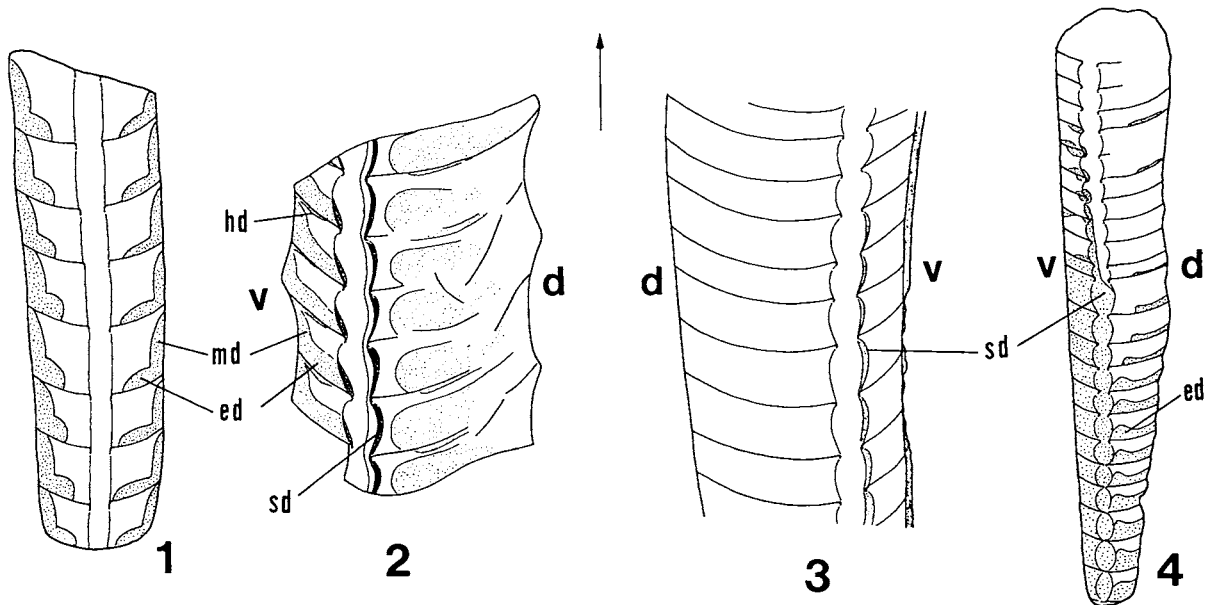


Figure 5. Diagrammatic drawings of median dorsoventral section of orthocerid (1-2) and actinocerid (3-4) cephalopods described herein. 1. *Michelinoceras cancellatum* sp. nov. (holotype; KPE20254), $\times 1.5$. 2. *Kogenoceras nanpiaoense* (KPE20208), $\times 2$. 3. *Ormoceras weoni* sp. nov. (holotype; KPE20260), $\times 2$. 4. *Ormoceras cricki* (KPE20232), $\times 2.5$. For abbreviations see Figure 3.

oids and matrix; surface ornamented with transverse growth lines and longitudinal lirae, forming cancellate network, spaces between growth lines and between lirae 0.16 mm and 0.07 mm respectively

Paratype, KPE20255 (Figure 7-7), a partial phragmocone consisting of 9 camerae, 33.2 mm long; probably belongs to adolescent stage in view of higher camera and broader conch than those of holotype; siphuncle central, cylindrical, narrow; septal distance increasing from 3 mm to 3.5 mm during the stage observed; camera with mural-episeptal deposits.

Remarks.—In the surface ornament pattern, this species resembles *Michelinoceras reticulatum* (Kobayashi) from the Jigunsan Formation of Homyeong (Kobayashi, 1934, p. 406, pl. 16, figs. 3-5). In the former species, however, are weaker and thinner longitudinal lirae than transverse growth lines, whereas in the latter species transverse lines are more crowded than longitudinal ones. In addition, the siphuncle in the present species is central in position, not submarginal as in *M. reticulatum*.

This species is similar to *Michelinoceras shangliense* Qi from the Middle Ordovician Datianba Formation of Anhui, China (Qi, 1980, p. 251, pl. 4, fig. 1) in the expansion rate of conch and septal spacing, but the former is distinguished from the latter by its peculiar latticed ornamentation and central siphuncle. This species is also allied to *Michelinoceras paraelongatum* Chang from the Middle Or-

dovician of Gansu, North China (Chang, 1962, p. 517, pl. 1, figs. 5a-c) in its small-sized conch with circular cross section, but the former has more narrowly spaced septa and broader siphuncle than the latter. In its surface markings, *Michelinoceras guichiense* Ying from the Middle Ordovician Datianba Formation of Guichi, Anhui, China (Ying, 1989, p. 630, pl. 3, figs. 5, 6) exhibits an affinity to the present species, but longitudinal lirae occurring in the present species are absent in *M. guichiense*.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Superfamily Pseudorthocerataceae Flower and Caster, 1935
Family Stereoplasmoderataceae Kobayashi, 1934

Genus **Kogenoceras** Shimizu and Obata, 1936

Type species: *Tofangoceras huroniforme* Kobayashi, 1927

Kogenoceras nanopiaense
(Kobayashi and Matsumoto, 1942)

Figures 5-2; 7-3, 6, 9a, b

Tofangoceras nanopiaensis Kobayashi and Matsumoto, 1942, p. 313, pl. 31, figs. 10-12; Chao *et al.*, 1965, p. 96, pl. 22, fig. 11.

Kogenoceras nanopiaense (Kobayashi and Matsumoto). Chen *et al.*, 1980, p. 177, pl. 3, fig. 18; Text-fig. 10; Lai *et al.*, 1982, pl. 6, figs. 12, 13; Stait, Wyatt and Burrett, 1987, p. 385, figs. 6-2-4.

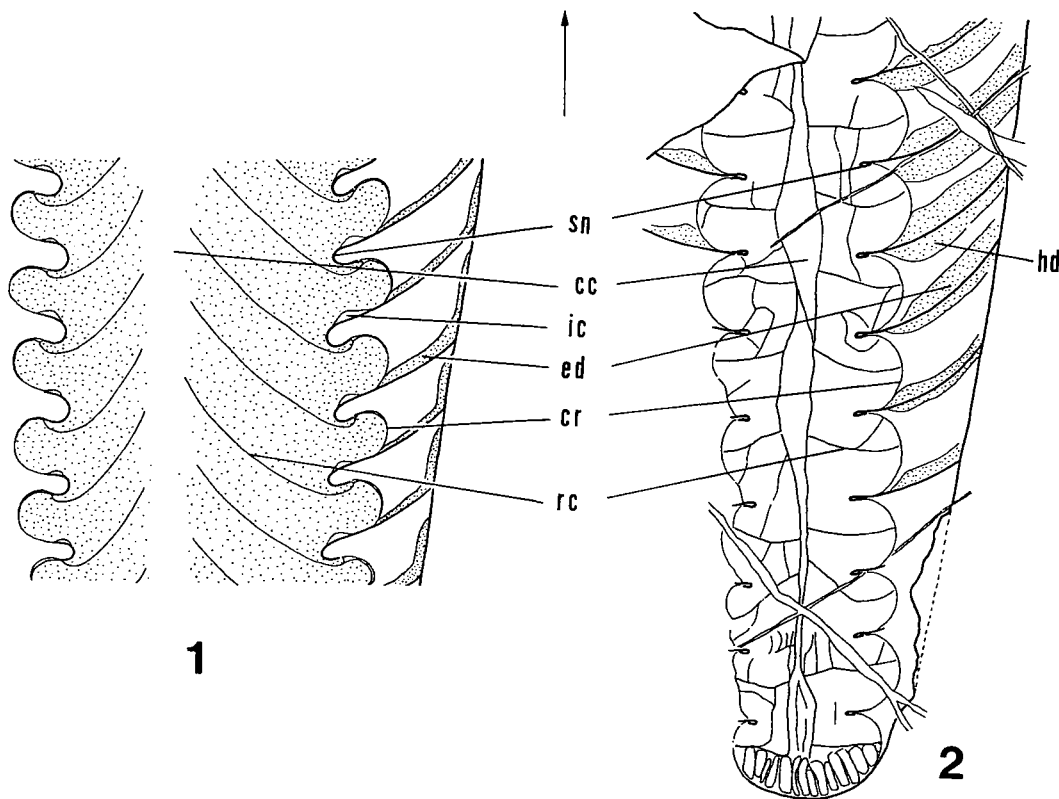


Figure 6. Diagrammatic drawings of actinoceroid cephalopods described herein. 1. *Polydesmia* sp. cf. *P. canaliculata* (KPE20323), $\times 1$. 2. *Wutinoceras robustum* (KPE20206), $\times 1$. For abbreviations see Figure 3, except for ic: interseptal cavity, cc: central canal, rc: radial canal.

Material.—Six partial phragmocones from the upper part of the Maggol Formation at localities, SN720 (KPE20282, 20283 and 20327), SN730 (KPE20209), and SN731 (KPE20208 and 20210).

Diagnosis.—Annulated cyrtochoanitic orthocone; camerae with episeptal and hyposeptal deposits; siphuncle with dorsally intermittent and ventrally connected parietal deposits.

Description.—Medium-sized annulated longiconic orthocone with eccentric siphuncle.

KPE20208 (Figures 5-2, 7-9a, b), a fragmentary phragmocone with 6 siphuncular segments, 21 mm long, very slowly enlarging, circular in cross section; siphuncle eccentric, midway between center and venter, narrow, occupying a little more than one-sixth of dorsoventral conch diameter; siphuncular segments *Huronina*-like in shape, greatly expanding in upper third, 2.8 mm in length and 2.3 mm in maximum diameter, contracting to 1.2 mm at septal foramen; septa gently concave adorally, partly crushed on dorsal side, septal depth equal to half or more of the cameral height; septal neck cyrtochoanitic, short, 0.3 mm in length; cameral height low, about 2.8 mm at upper part, 5 camerae in a length corresponding to the dorsoventral conch diameter on the crest of annuli; connecting rings thin, not adnate to the septa; camera filled with both episeptal and hyposeptal deposits; siphuncle deposits with parietal deposits consisting of longitudinal thin lamellae, dorsally occurring successively whereas ventrally intermittent; surface ornamented with strong annulations at intervals of 7.3 mm wide, corresponding to 2.5 camerae, its height from the base of the interspace about 0.8 mm.

KPE20209 (Figure 7-3), 49 mm in length, its adapical portion not preserved; conch nearly circular in cross section; siphuncle close to venter, narrow, its width one-eighth of dorsoventral conch diameter; siphuncular segments somewhat expanded between septal foramina at a point about one fourth from its anterior end, ratio of width to length 0.8; septa crowded, septal depth attaining one and a half times cameral height; camerae with both epi- and hyposeptal deposits, but siphuncular deposits not distinctly detected; surface ornamented with broadly rounded annulations at intervals of 6 mm.

Remarks.—Kobayashi and Matsumoto (1942) proposed *Tofangocerina nanpiaoensis* from the Tofangian, Nanpiao Coalmine, based on the type specimen, UMUT PM1903 which are characterized by well-developed endosiphuncular deposits and submarginal siphuncle with the *Huronina*-like siphuncular segments. However, Chen *et al.* (1980) and Stait *et al.* (1987) attributed the generic position of this species to *Kogenoceras* of Shimizu and Obata (1936) because of the characteristic features of *Kogenoceras* such as cyrtochoanitic annulated orthoceracone, circular cross section, and narrow eccentric siphuncle, with *Huronina*-like segments. The enlarged photo of the siphuncle of *K. nanpiaoense* from the Lower Ordovician Lower Setul Limestone of the Langkawi Islands, Malaysia (Stait *et al.*, 1987, p. 386, fig. 6-4) shows cyrtochoanitic septal necks, though these authors mistakenly described the septal neck type as orthochoanitic.

This species is similar to *Kogenoceras huroniforme*

(Kobayashi) from the Duwibong Formation of Hwarari, Kangweondo, Korea (Kobayashi, 1934, p. 435, pl. 27, figs. 9-11, 14) in the *Huronina*-like siphuncular segments and eccentric siphuncle, but is easily distinguished by the presence of the parietal deposits along the siphuncular wall.

Occurrence.—In addition to the present material, specimens assigned to this species are known from the Lower Ordovician of Nanpiao Coalmine, Nanpiao County, Liaoning Province, South Manchuria (Kobayashi and Matsumoto, 1942; Lai *et al.*, 1982), Beianzhuang Formation of Shandong, North China (Chen *et al.*, 1980) and the Lower Setul Limestone on the east coast of Pulau Langgun, Langkawi Islands, Malaysia (Stait *et al.*, 1987).

Order Actinocerida Teichert, 1933

Family Ormoceratidae Saemann, 1853

Genus *Ormoceras* Stokes, 1840

Type species: *Ormoceras bayfieldi* Stokes, 1840

Ormoceras cricki Kobayashi, 1934

Figures 5-4; 8-1-8

Ormoceras cricki Kobayashi, 1934, p. 444, pl. 23, fig. 7; pl. 25, fig. 7.

Ormoceras sp. B., Chang, 1959, p. 266, pl. 5, fig. 5.

Material.—15 specimens, KPE20231-20245 from loc. SN741, among which 14 are partial phragmocones and one (KPE20231) is a well-preserved, almost complete adult conch.

Diagnosis.—Conch cross section elliptical in juvenile stage, but becomes subcircular in adult stage; eccentric siphuncle with globular segments; camera with episeptal deposits forming a pointed ridge just in front of connecting ring; hyposeptal deposits absent; siphuncle filled with parietal deposits along the inside of connecting ring.

Description.—Small to medium-sized cyrtochoanitic longiconic orthoceracone; smooth shell, no sculpture discernible; conch cross section strongly depressed, elliptical in juvenile stage, but becoming subcircular with growth, adult body chamber nearly circular in cross section; its diameter moderately expanding at a rate of 1 mm per 8 mm in lateral and dorsoventral lengths; siphuncle eccentric, close to venter, located at about 2/3 of conch diameter from dorsal margin, narrow, its diameter a third of dorsoventral conch diameter in juvenile stage, but becoming smaller, being one-fifth of the corresponding diameter in the adolescent shell because of nearly uniform expansion rate of siphuncle; siphuncular segments globular, as long as broad; septa gently concave adorally, septal depth as wide as a half of cameral height; septal necks cyrtochoanitic, abruptly recurved, adnate for a short distance to adapical part of connecting ring, but just meeting the adoral end of connecting ring; septal brim very short; suture directly transverse, but slightly sloping from dorsal to ventral side; camerae low, increasing from 1.1 mm to 1.5 mm during ontogeny, four camerae occurring in a length equal to dorsoventral conch diameter of 6.5 mm in KPE20232 (Figures 5-4 and 8-2b); camera with well-developed mural-episeptal deposits, in which mural deposits

vestigial dorsally but more concentrated ventrally.

The degree of development of cameral deposits changes during ontogeny (see Figure 5-4); In juvenile stage, dorsal episeptal deposits becoming thicker toward nummuli, forming a pointed ridge just in front of connecting ring and abruptly thinning out to a saucer-like shape, the apex of pointed ridge rather acute and gradually shifting to the shell wall adorally whereas it is difficult to recognize on the ventral side due to secondary recrystallization. In adolescent stage, episeptal deposits shortened dorsally, not swollen and mural-episeptal deposits still thicker ventrally. In adult stage cameral deposits seldom present.

Siphuncle filled with biogenic deposits in both juvenile and adolescent stages. The deposits more heavily developed ventrally than dorsally in adult stage, subsequently appearing to be annulosiphonate deposits ventrally.

Remarks.—This species resembles *Ormoceras woodwardsi* Kobayashi from the Jigunsan Formation of Homyeong, Jeongseon (Kobayashi, 1934, p. 445, pl. 31, fig. 5) in the globular siphuncular segments and submarginal siphuncle, but is distinguished by the absence of episeptal deposits. It is similar to *Ormoceras harioi* (Kobayashi) from the Tofango Limestone of Tofango, South Manchuria (Kobayashi, 1927, p. 196, pl. 22, fig. 12; pl. 21, fig. 9) in having episeptal deposits, but differs from the latter in the broader siphuncle in proportion to conch diameter and the more rapidly expanding conch.

In the saucer-like shape of episeptal deposits, *Parormoceras nanum* (Grabau) from the Tofango Limestone of South Manchuria (Kobayashi, 1927, p. 195, pl. 20, fig. 11; pl. 21, fig. 8; pl. 22, fig. 5) is closely related to this species, but the former is distinguished from this latter by the presence of such characters as *Huronia*-like siphuncular segments, more rapidly expanding conch and more closely spaced septa.

Occurrence.—In addition to the uppermost horizon of the Maggol Formation of Sanaegol described herein, this taxon is known from the Duwibong Formation of Hwajeolchi, Jungdong-myeon, Yeongweol area, and of Homyeong, Dongmyeon, Jeongseon area and Gaesandong, Taebaeg City, Kangweondo (Kobayashi, 1934).

Ormoceras weoni sp. nov.

Figures 5-3; 8-9-12; 9-1-3

Types.—Holotype, KPE20260, an incomplete phragmocone with an adjacent part of body chamber; 7 paratypes, KPE20261-20267, all from loc. SN741.

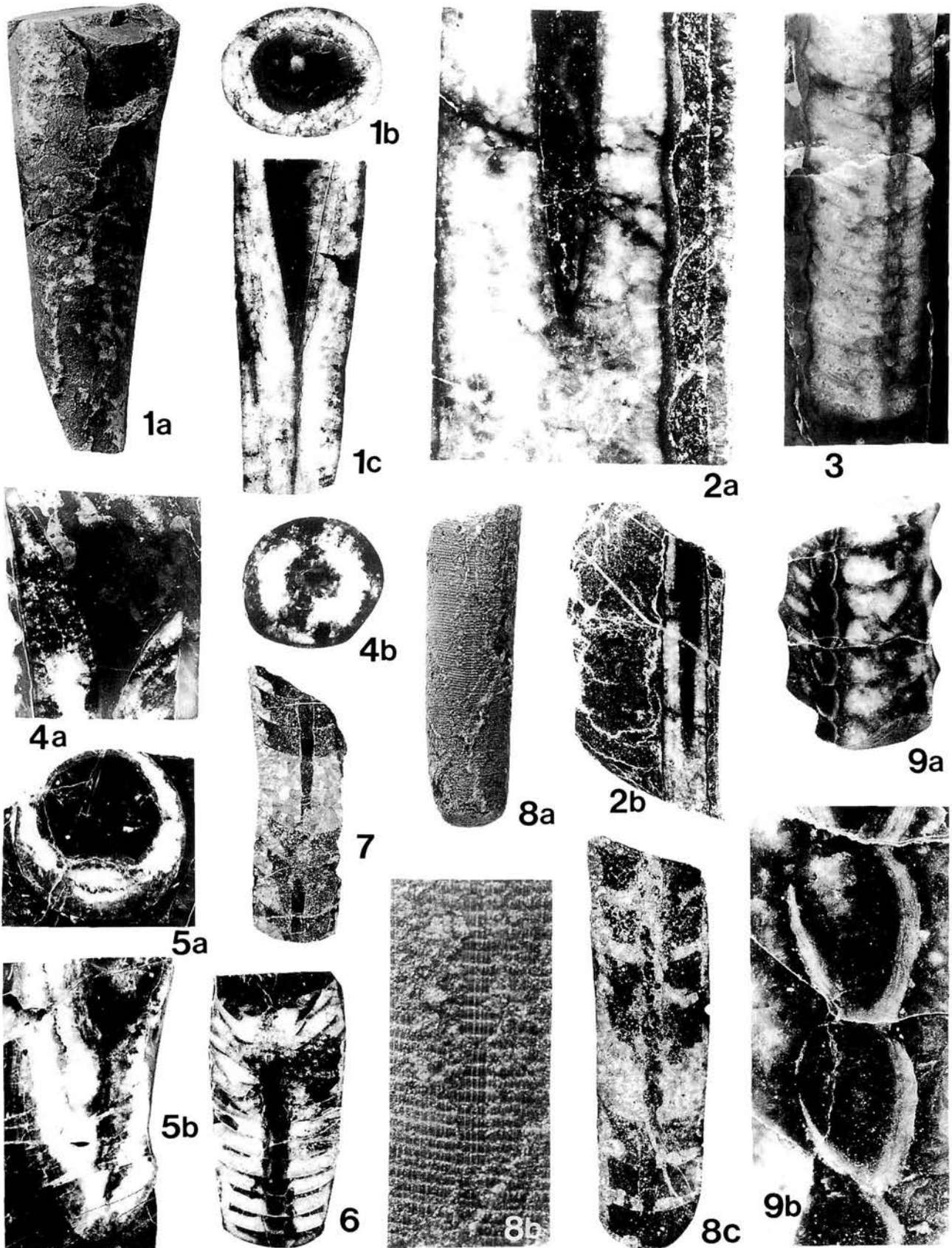
Material.—In addition to the above type specimens, seven specimens (KPE20268-20274) belong to this species. Of these, six (KPE20268-20273) were collected from the type locality, while one (KPE20330) came from the equivalent horizon of the Maggol Formation at Sesong.

Etymology.—The specific name is dedicated to Dal-Gi Weon, who collected many Paleozoic fossils from Kangweondo region and kindly provided some specimens to the author.

Diagnosis.—Longiconic or slightly curved orthocone; conch subcircular, ovately elliptical in cross section; body chamber long; siphuncle submarginal; siphuncular segments somewhat expanded; no cameral deposits detected.

Description.—Medium-sized longiconic or slightly curved orthocone; conch diameter moderately expanding at a rate of 1 mm per 6.5 mm in conch height of the holotype (Figures 8-9a-d); body chamber long; ovately elliptical in cross section, ratio between dorsoventral and lateral diameters at the apical end 4:5 in one of the paratypes (KPE20262; Figure 9-1b); siphuncle submarginal, narrow, occupying about one-eighth of dorsoventral conch diameter; siphuncular segments nummuloidal, more or less expanded, 1.5 mm long and 1.1 mm in maximum diameter in the upper third of the height within camerae, contracting to 0.6 mm at the septal foramen in the holotype; septa gently concave adorally, septal depth ranging from one to one and a half of cameral height, septal necks cyrtochoanitic, very short, just meeting the adoral end of connecting ring; septal spacing narrow, 7 to 8 camerae within the corresponding length of dorsoventral conch diameter; suture directly transverse in two steinkern specimens, KPE20264 (Figure 8-12) and KPE20265 (Figure 8-11); no cameral deposits detected; siphuncle filled with inorganic matrix, but in the holotype and one of the paratypes (KPE20262; Figure 5-1d), endosiphuncular deposits line siphonal surface of venter; surface smooth.

Figure 7. 1a-c. *Manchuroceras* sp. A. partial siphuncle, KPE20256 from SN710, $\times 1$, 1a: ventral view, 1b: cross section at the adoral portion, venter down, 1c: longitudinal section, venter on left, showing endocones and endosiphuncle. **2a, b.** *Vaginoceras* sp. partial phragmocone, KPE20230 from SN741, 2a: detail of siphuncle and ventral camerae, showing very slender endosiphuncle, $\times 5$, 2b: longitudinal section, venter on right, $\times 1.5$. **3, 6, 9a, b.** *Kogenoceras nanpiaense* (Kobayashi and Matsumoto, 1942). 3. Partial phragmocone, KPE20209 from SN730, longitudinal section, venter on right, $\times 1.5$, 6: Partial phragmocone, KPE20282 from SN720, longitudinal section in lateral direction, $\times 1$, 9a, b: Partial phragmocone, KPE20208 from SN731, 9a: longitudinal section, venter on left, $\times 2$, 9b: enlarged view of siphuncular structure, showing parietal deposits and moderately expanded siphuncular segments, $\times 7$. **4a, b.** *Manchuroceras* sp. B. partial siphuncle, KPE20065 from SN710, $\times 1$, 4a: longitudinal section, venter on left, showing more prolonged ventral endocone adorally, 4b: cross section at the adapical end, venter down, showing triangular endosiphuncle with flattened ventral side. **5a, b.** *Manchuroceras* sp. cf. *M. wolungense* (Kobayashi, 1931), partial siphuncle, KPE20073 from SN712, $\times 1$, 5a: cross section at the adoral end, venter down, showing circular outline and endosiphuncle, 5b: longitudinal section, venter on left, showing the blunt apical end and endosiphontube. **7, 8a-c.** *Michelinoceras cancellatum* sp. nov. 7. Partial phragmocone, paratype, KPE20255 from SN741, longitudinal section, acetate peel, $\times 1.5$, 8a-c. Partial phragmocone, holotype, KPE20254 from SN741, 8a: side view, $\times 2.5$, 8b: details of surface ornamentation, showing cancellate ornaments, $\times 12$, 8c: longitudinal section, acetate peel, showing well developed mural-episeptal deposits, $\times 3.5$.



Remarks.—This present species closely resembles *Ormoceras yokoyamai* (Kobayashi) from the Jigunsan Formation of Maggol and Homyeong (Kobayashi, 1934, p. 439, pl. 27, figs. 1-6; pl. 28, fig. 2) in the narrow, submarginal siphuncle with somewhat expanded segments, but differs from the latter by the presence of endosiphuncular linings and the lack of ventral flattening in cross section.

Ormoceras cricki Kobayashi from the Duwibong Formation of Homyeong and Gaesanchoon (Kobayashi, 1934, p. 444, pl. 23, fig. 7; pl. 25, fig. 7) and from the uppermost bed of the Maggol Formation at Sanaegol (see Figures 8-1-8 in this paper) is allied to this present species in having closely spaced septa and ectosiphuncular morphology. The former, however, can be distinguished from the latter by the presence of episeptal deposits, more depressed conch, and much smaller siphuncular diameter in relation to conch diameter.

Occurrence.—Known only from the uppermost part of the Maggol Formation in Sanaegol.

Family Polydesmiidae Kobayashi, 1940

Genus *Polydesmia* Lorenz, 1906

Type species: *Polydesmia canaliculata* Lorenz, 1906

Polydesmia sp. cf. *P. canaliculata* Lorenz, 1906

Figures 6-1; 9-4a, b

Material.—Fragmentary phragmocone, KPE20323 from loc. SN720.

Description.—Longiconic orthocone, 97 mm long, naturally weathered to the level of siphuncle; outline of cross section unknown; siphuncle large, slightly eccentric, conch diameter slowly expanding at a rate of 1 mm per 8 mm in conch height at the adapical portion; siphuncular segments very wide and comparatively low; septal necks cyrtocoanitic, evenly curved and long, equalling about one-third of cameral height, represented by a septal loop which corresponds to two-thirds of a circle; septal brims broad, moderately separated from septum; connecting rings thick, expanded largely into camerae, its posterior part forming a triangular elevation toward adoral side (ic in Figure 6-1), which was called "interseptal cavity" by Kobayashi (1940, p. 36); posterior area of adnation very broad; septa moderately concave adorally, septal depth equivalent to one and a half times or less of cameral height; camerae low, 3.2 mm high; endosiphun-

cular canal system of dendritic type, central canal narrow, off-center, radial canal steeply oblique, extending adapically through about 2 siphuncular segments before entering perispatium, its terminating point located at the tip of septal brim; annuli projected toward antero-inner side, horn-shaped in longitudinal section, internal lamellate structure obscure owing to recrystallization; camerae with mural-episeptal deposits.

Remarks.—This species is most closely allied to *Polydesmia canaliculata* Lorenz from south of Chiang-chiawan, Liaoyang-hsien, Manchoukuo, North China (Kobayashi, 1940, p. 34, pl. 3, figs. 1-3 and pl. 4, figs. 17-19) in having the strongly oblique radial canal and triangular interseptal cavity, but incomplete preservation of the present specimen without conch outline and siphuncular position precludes exact species-level assignment.

Occurrence.—Known only from the upper part of the Maggol Formation of Sanaegol.

Family Wutinoceratidae Shimizu and Obata, 1936 emend. Flower, 1968

Genus *Wutinoceras* Shimizu and Obata, 1936 emend. Flower, 1957

Type species: *Nybyoceras foerstei* Endo, 1930

Wutinoceras robustum (Kobayashi and Matsumoto, 1942)

Figures 6-2; 10-1, 2

Jeholoceras robustum Kobayashi and Matsumoto, 1942, p. 315, pl. 30, figs. 1-5; pl. 31, fig. 6.

Armenoceras robustum (Kobayashi and Matsumoto). Chao *et al.*, 1965, p. 70, pl. 17, figs. 7-9.

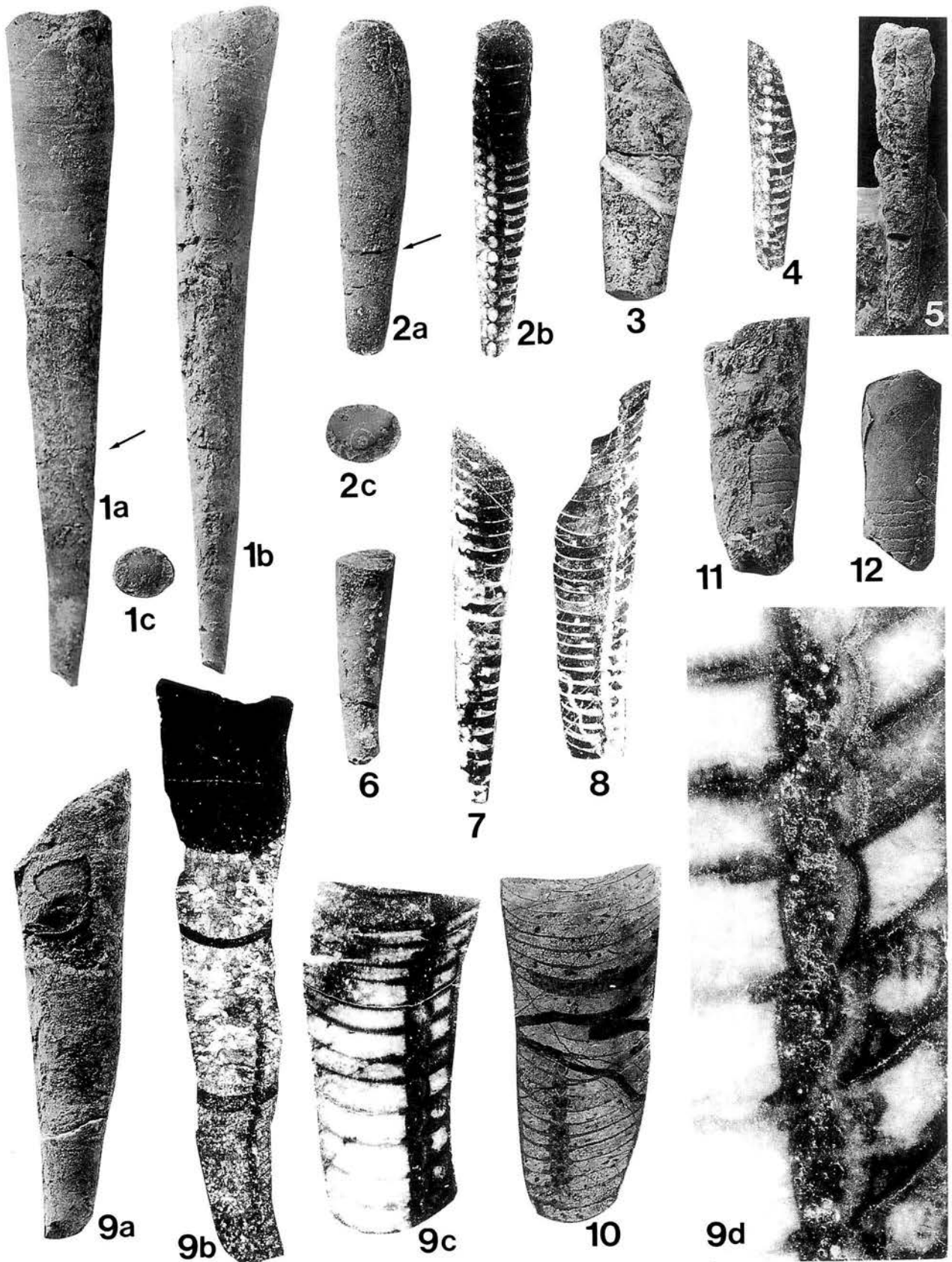
Armenoceras cf. *robustum* (Kobayashi and Matsumoto). Chen, 1983, p. 122, pl. 2, figs. 5, 6.

Wutinoceras robustum (Kobayashi and Matsumoto). Stait and Burrett, 1982, p. 194, figs. 2A-L

Material.—Two phragmocones, KPE20206, 20207 from the middle part of the Maggol Formation of Sanaegol at loc. SN712.

Diagnosis.—Siphuncle eccentric, close to venter, broad; siphuncular segments nummuloidal, highly expanded; thickened connecting ring; septal brims longer than necks, varying from recumbent to slightly hooked, nearly touching the septa only at their tip; reticulate canal system; episeptal and hyposeptal deposits present.

Figure 8. 1-8. *Ormoceras cricki* Kobayashi, 1934. All collected from SN741. 1a-c. Nearly complete conch without apical portion, KPE20231, $\times 1.5$, 1a: ventral view, 1b: lateral view, venter on right, 1c: septal view at position indicated by arrow given in 1a. 2a-c. Partial phragmocone, KPE20232, $\times 1.5$, 2a: ventral view, 2b: longitudinal section, venter on left, showing well developed episeptal deposits, 2c: septal view at position indicated by arrow given in 2a. 3. Partial phragmocone, KPE20237, ventral view, $\times 2$. 4. Partial phragmocone, KPE20235, longitudinal section, venter on left, $\times 1.5$. 5. Partial phragmocone, KPE20233, ventral view, $\times 1.5$. 6. Partial phragmocone, KPE20245, dorsal view, $\times 1.5$. 7. Partial phragmocone, KPE20234, longitudinal section in slightly askew dorsoventral direction, $\times 1.5$. 8. Partial phragmocone, KPE20244, dorsoventral section, venter on right, $\times 1.5$. 9-12. *Ormoceras weoni* sp. nov. All collected from SN741. 9a-d. Adoral phragmocone and contiguous partial body chamber, holotype, KPE20260, 9a: dorsal view, $\times 1$, 9b: longitudinal section, venter on right, acetate peel, $\times 1.5$, 9c: enlarged view of apical portion, $\times 3$, 9d: details of siphuncle and septa, $\times 12$. 10. Partial phragmocone, paratype, KPE20261, longitudinal section, venter on left, acetate peel, $\times 1.5$. 11. Partial phragmocone, paratype, KPE20265, showing transverse septal sutures, $\times 1.5$. 12. Partial phragmocone and contiguous body chamber, paratype, KPE20264, shell exfoliated, showing transverse septal sutures, $\times 1.5$.



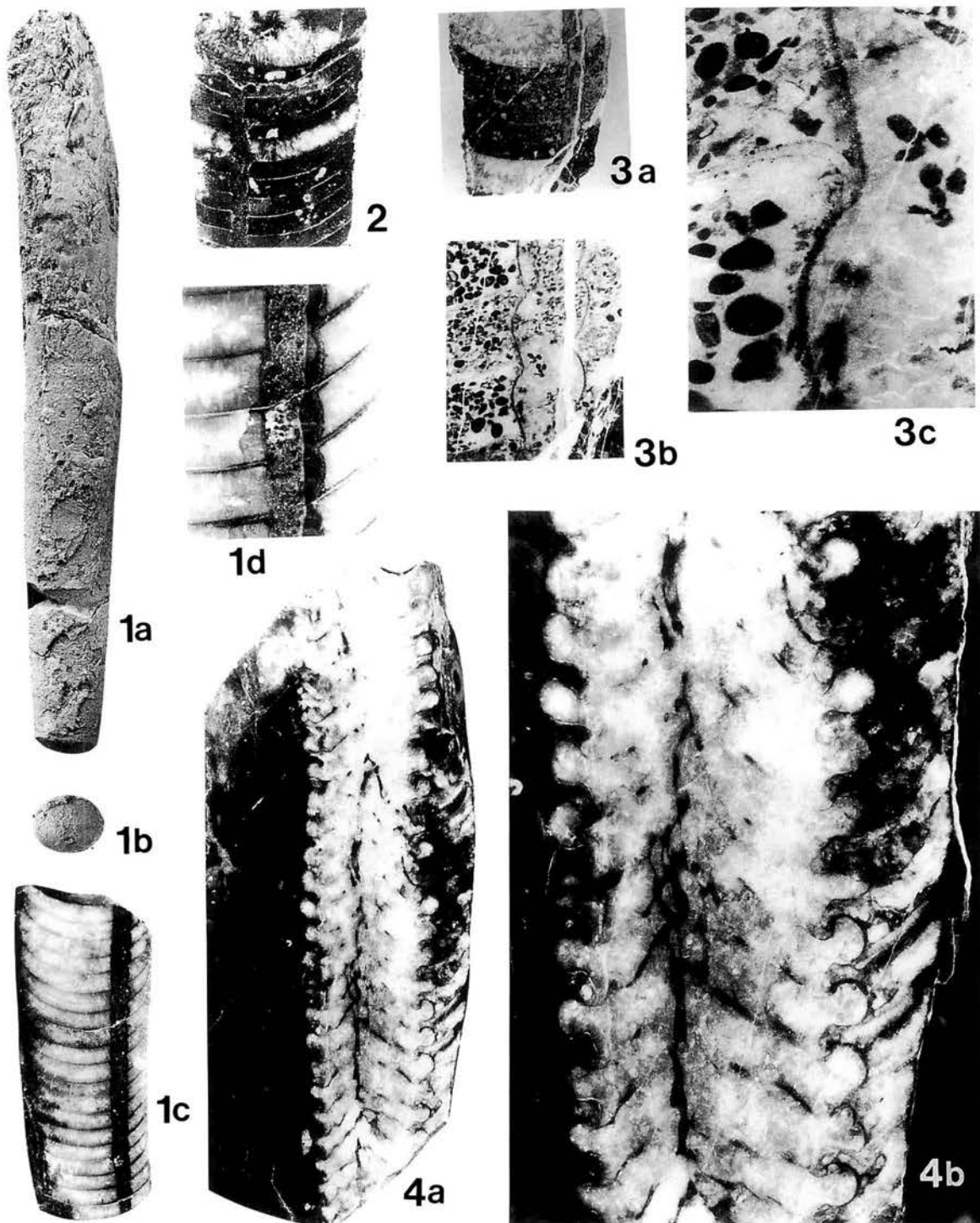


Figure 9. 1-3. *Ormoceras weoni* sp. nov. All collected from SN741. 1a-d. Adoral phragmocone and contiguous body chamber, paratype, KPE20262, 1a: ventral view, body chamber somewhat distorted, $\times 1$, 1b: septal view of apical end, showing position of the siphuncle, $\times 1$, 1c: dorsoventral section, venter on right, $\times 2$, 1d: details of siphuncular structure, showing endosiphuncular linings on ventral side, $\times 7$. 2. Partial phragmocone, paratype, KPE20267, dorsoventral section, venter on left, $\times 2.2$. 3a-c. Partial phragmocone, paratype, KPE20263, 3a: dorsoventral section, venter on right, $\times 2$, 3b: detail of siphuncle, $\times 7$, 3c: enlarged view of cytochoanitic septal neck, $\times 30$. 4a, b. *Polydesmia* sp. cf. *P. canaliculata* Lorenz, 1906. partial phragmocone, KPE20321, loc. SN720, 4a: longitudinal section, $\times 1$, 4b: enlarged view of siphuncular structure, showing triangular interseptal cavities on the adoral side of septa and steeply inclined radial canals, $\times 5$.

Description.—Large-sized longiconic orthocones with well defined reticulate canal system.

KPE20206 (Figures 6-2 and 10-1a, b), a partial phragmocone with apical end, 115 mm long consisting of 10 siphuncular segments including initial chamber; presumably subcircular in cross section; cameral portion of apical part mostly lost during taphonomic process; siphuncle eccentric, its width broad, occupying nearly a half of conch diameter; siphuncular segments nummuloidal, highly expanded, having a length of 11.2 mm and a width of 27.5 mm at the point of maximum expansion, constricted to 13.7 mm at septal foramen; septa moderately curved, septal depth corresponding to a little less than one and a half times cameral height; septal necks cyrtchoanitic, recurved but free; septal brims longer than necks, varying from recumbent to slightly hooked, nearly touching the septa only at their tip; cameral height rather high, averaging 10.2 mm; connecting ring relatively thick, apically adnate for a long distance, 3.8 mm to adoral surface of septum, just meeting the septal brims adorally; siphuncular deposits of annulosiphonate type, canal system forming reticulate structure, narrow radial canals branched off from irregularly arranged central canal entering to the midpoint of perispatium; episeptal and hyposeptal deposits well developed; shell surface unknown.

KPE20207 (Figures 10-2a, b), represented by a partial phragmocone with one side crushed; a gastropod belonging to *Pagodispira* (?) detected in a camera in cross section (indicated by arrow, see Figure 10-2b); conch somewhat flattened and siphuncle slightly elliptical in cross section; siphuncle eccentric, close to venter; siphuncular segments uniform in dimension, 8.5 mm long and 23.3 mm in maximum diameter within camerae, pinched to 13.1 mm at the septal necks; posterior area of adnation moderately broad, 3.2 mm; central canal sigmoidally curved in longitudinal direction, its width ranging from 1.6 mm to 3.5 mm while radial canal is narrow, 0.4 mm or less, radially distributed bunches of annulosiphonate deposits in cross section of adoral end.

Remarks.—The present species is similar to *Wutinoceras foerstei* (Endo) from the Lower Ordovician Wuting Formation of South Manchuria (Endo, 1930, p. 208, pl. 60, figs. 1A-C) in ectosiphuncular structure and reticulate canal system, but the latter differs from the former in having a more ventrally positioned siphuncle and less cameral deposits. This species may be allied to *Wutinoceras logani* Flower from the Table Head Formation of Newfoundland (Flower, 1968, p. 8, pl. 10, figs. 1-3; pl. 11, figs. 1-7) in the large-sized conch and strongly flattened siphuncular segments, but the former is distinguished from the latter in having more thickened cameral deposits and less recumbent septal brims.

This species is also similar to *Wutinoceras remotum* Chen from the Lower Ordovician, lower part of Jiacun Group of Nielamu County, China (Chen, 1975, p. 274, pl. 1, figs. 7, 8) in the mode of endosiphuncular and cameral deposits, but the latter differs from the former in the longer septal necks and much narrower siphuncular segments.

Occurrence.—In addition to the present materials, this species is known from the Toufangian strata in the vicinity of Nanpiano Coalmine, Nanpiano County, Liaoning Province, South Manchuria (Kobayashi and Matsumoto, 1942) and the Lower Ordovician Lower Setul Limestone on Pulau Langgun of the Langkawi Islands, Malaysia (Stait and Burrett, 1982).

Wutinoceras sp.

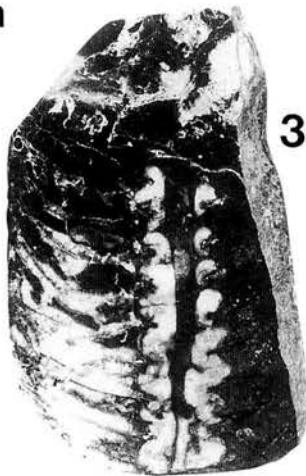
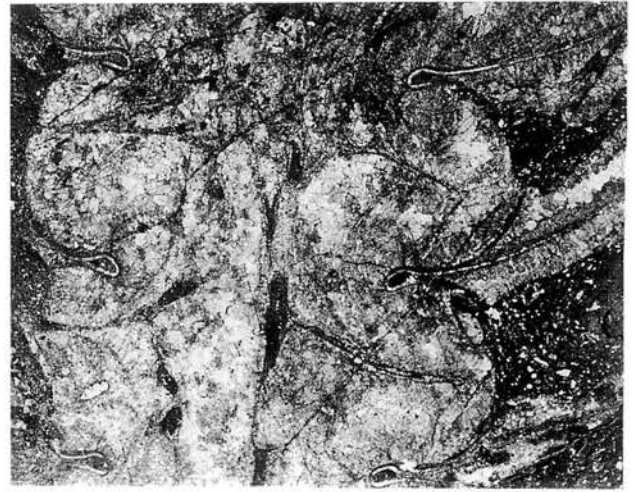
Figures 10-3a—d

? *Wutinoceras* sp. Zhu and Li, 1996, pl. 1, fig. 11.

Material.—Partial phragmocone, KPE20202 from loc. SN713.

Description.—Medium-sized orthocone, preserved phragmocone 60 mm long, its expansion rate not measured owing to secondary deformation, conch subcircular in cross section; siphuncle central, large, 11.5 mm in maximum diameter, occupying about one-third of conch diameter; siphuncular segments strongly nummuloidal, 4.2 mm in length and 11.5 mm in maximum diameter at mid-portion within camerae, contracting to 6.6 mm at septal foramen; septa moderately concave adorally, septal depth one and a half times cameral height, septal necks cyrtchoanitic, strongly recurved, septal brims far longer than necks, its end adnate to the adapical surface of septum, especially in juvenile stage, but not adnate in later stage; connecting ring adnate for a relatively long distance to adoral surface of septum dorsally, but free ventrally, just meeting the tip of septal brim; suture slightly sloping from venter to dorsum, but transverse when viewed from dorsal side; camera about 4.3 mm high, 8 camerae preserved in a partial conch 37 mm in length; annulosiphonate deposits well developed (Figures 10-3c, d), annuli embracing the inner margin of septa at septal necks, gradually decreasing adorally in bulk, its shape asymmetrical in longitudinal section, more concentrated to the adoral side, adjacent annuli in contact with each other, remaining spaces forming radial canal, which branches off from much broader central canal, in some cases, radial canal divided into two branches and entering in perispatium; camerae filled with episeptal and hyposeptal deposits only on ventral side, also deposits in ventral camera forming pseudoseptum at mid-portion of camera joining to radial canal.

Figure 10. 1, 2. *Wutinoceras robustum* (Kobayashi and Matsumoto, 1942). 1a, b. Partial phragmocone, KPE20206 from SN712, 1a: longitudinal polished section of an originally weathered specimen, $\times 1$, 1b: details of septal necks and reticular canal system, acetate peel, $\times 2.4$. 2a, b. Partial phragmocone, KPE20207 from SN712, $\times 1$, 2a: longitudinal section, venter on left, 2b: cross section at the adapical end, venter down. Arrow indicates a gastropod, *Pagodispira* (?) sp. 3a-d. *Wutinoceras* sp. partial phragmocone, KPE20202 from SN713, 3a: lateral view, venter on right, $\times 1$, 3b: septal view of the apical end, venter down, showing position of the siphuncle, $\times 1$, 3c: longitudinal section, venter on left, showing the annulosiphonate deposits, $\times 1$, 3d: details of siphuncular structure, acetate peel, showing free septal necks, but tip of septal brims adnate to the adapical surface of the septum, and well-developed annulosiphonate deposits, $\times 5$. Abbreviations in Figure 3d: an; annulus, cc; central canal, rc; radial canal.



Remarks.—This species resembles *Wutinoceras giganteum* Flower from the early Middle Ordovician Table Head Limestone of Newfoundland (Flower, 1976, pl. 2, fig. 4; pl. 3, fig. 12; pl. 4, figs. 1, 2; pl. 5, fig. 6) in the nearly central position of the siphuncle, but is distinguished by its more crowded camera, obliquely inclined septal suture and the presence of the well-developed canal system. In the flattened siphuncular segments and recumbent septal necks, this present species is somewhat similar to *Wutinoceras logani* Flower from the Table Head Limestone, Newfoundland (Flower, 1968, p. 8, pl. 10, figs. 1–3; pl. 11, figs. 1–7), but differs by its more undulating central endosiphuncle and thicker mural-episeptal deposits.

Wutinoceras lui Chang from the Inner Mongolia (Chang, 1959, pl. 2, fig. 3; pl. 3, fig. 5) is also allied to this species, but the former differs from the latter in its eccentric siphuncle and less flattened siphuncular segments. Furthermore, the present species is allied to *Wutinoceras shihuigouense* Chang from the upper part of the Lower Ordovician Tochuanshan Limestone, Shihuigou, Chinghai (Chang, 1965, p. 352, pl. 1, fig. 4) in the subcentral position of the siphuncle and the constant relation of the septa and segments, but in *W. shihuigouense*, the septa are more steeply inclined and the connecting ring is rather uneven. *Wutinoceras* sp. from the Lower Ordovician Xiamajiagou Formation of Southern Jilin, China (Zhu and Li, 1996, pl. 1, fig. 11) may be compared to the present species in its free septal necks and somewhat broader area of adnation.

Occurrence.—Known only from the middle part of the Maggol Formation of Sanaegol.

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Erratum

In the article by Amano, Lutaenko and Matsubara (*Paleontological Research*, Vol. 3, No. 2), a sentence below should be included in the figure caption of Figure 4 on page 98.

6a, b : *Macoma (Rexithaerus) hokkaidoensis* Amano and Lutaenko, sp. nov., JUE no. 15654 (Paratype), Oshamanbe (Recent).

行事予定

- ◎ 2000 年年会・総会は、2000 年 1 月 28 日 (金)~1 月 30 日 (日) に「早稲田大学」で開催されます。一般講演の申し込み締め切りは 1999 年 12 月 3 日です。1 月 28 日にシンポジウム「白亜紀の炭素循環と生物多様性の変動：世話人・平野弘道・坂井 卓・松川正樹・中森 亨・西 弘嗣・利光誠一・斎木健一・長谷川卓」が行われます。
- ◎ 第 149 回例会 (開催予定時期：2000 年の 6 月末頃) には、「群馬県立自然史博物館」から開催申し込みがありました。
- ◎ 1999 年総会で、2001 年からの年会・総会と例会の開催時期の変更が決定されました。年会・総会は 6 月下旬から 7 月の初め頃 (現在の例会の開催時期)、例会は 1 月下旬から 2 月の初め頃 (現在の年会・総会の開催時期) 開催されます。開催を計画されている機関がありましたら、行事係までお申し込み下さい。

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