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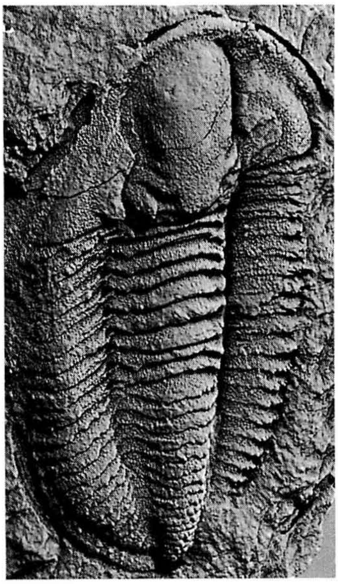

日 本 古 生 物 学 会

Palaeontological Society of Japan

June 30, 1989

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

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875. SILURIAN ORTHOCERATACEAE (MOLLUSCA : CEPHALOPODA) FROM THE YOKOKURAYAMA FORMATION, KUROSEGAWA TERRANE*

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Abstract. Three Silurian orthoconic cephalopods are described from the G3 Member of the Yokokurayama Formation in the Kurosegawa Terrane. These are ; *Kopaninoceras kobayashii*, sp. nov., which marks the first record of this genus in Japan, *Protokionoceras fessicancellatum* Kobayashi, and Geisonoceratid, gen. et sp. indet. Conodonts associated with the cephalopod fauna indicate a late Wenlockian to early Ludlovian age.

Key words. Orthocerataceae, Silurian, Yokokurayama Formation, Kurosegawa Terrane

Introduction

The Middle Silurian to possibly late Devonian Yokokurayama Formation consists essentially of unmetamorphosed strata of tuffaceous, arenaceous and calcareous deposits, which form a huge xenolithic body together with granitic and metamorphic rocks. The linear arrangement of these bodies extending over a more than 500 km distance in an E-W direction forms the basis to be defined collectively as the Kurosegawa Terrane. The Middle to Late Silurian sequence of the Yokokurayama Formation has produced one of the most diverse middle Paleozoic molluscan faunas in Southwest Japan. During our field investigation of the Mt. Yokokura area, four specimens of Silurian cephalopods representing the genera *Kopaninoceras, Protokionoceras* and an indeterminate form assignable to the family Geisonoceratidae were found by one of us (T. Y.). This new collection described herein provides a new insight into the Silurian fauna of the Kurosegawa Terrane. ·

The presence of orthoconic cephalopods in the Mt. Yokokura area has been known since 1965 when Hirata reported the occurrence of *Orthoceras* sp. from the Gomi quarry. Subsequently, Koizumi (1975) reassigned Hirata's specimen to *Kailiceras* (?) sp., but the structure of siphuncle and organic deposits have not been investigated. Furthermore, this specimen is too poorly preserved to determine both its generic and specific assignment. In 1984, Kobayashi published the first detailed description of the Yokokurayama cephalopod fauna including *Michelinoceras alticameratum* Kobayashi, *M. mizobuchii* Kobayashi, *Arionoceras densiseptum*

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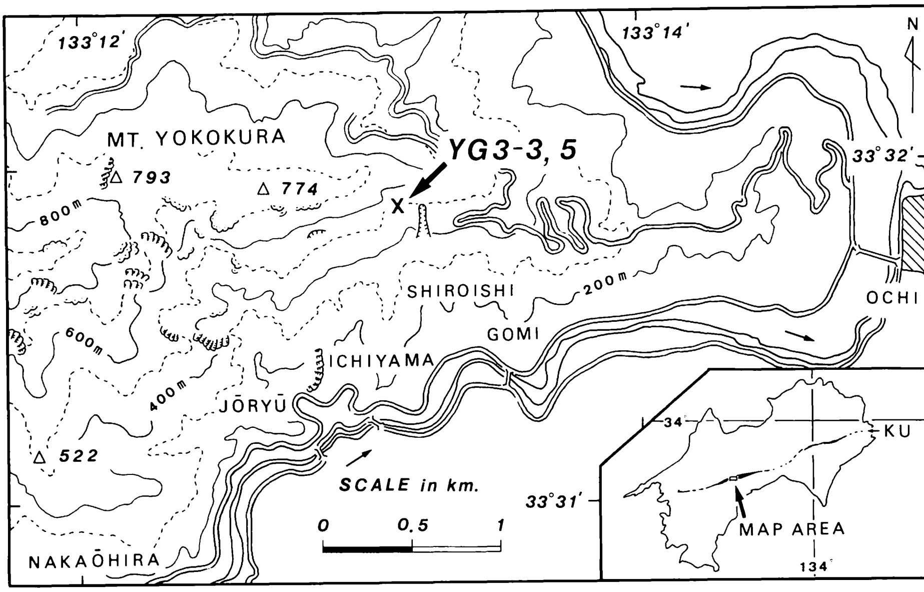


Figure 1. Map showing the fossil locality in the Mt. Yokokura area, Kochi Prefecture. Ku: Kurosegawa Terrane.

Kobayashi, *Leurocycloceras* (?) sp. indet., *Orthocycloceras gomiense* Kobayashi, *O.* aff. *gomiense* Kobayashi, *Protokionoceras* (?) *fessicancellatum* Kobayashi and two indeterminable cephalopods with a curved conch.

Abbreviations used in the text are as follows: UMUT, University Museum, the University of Tokyo; KGS, Laboratory of Geology, Faculty of Science, Kochi University; and TYC, Toshio Yasui personal collection, Kochi City.

Stratigraphy and fossil occurrence

The cephalopod fauna described herein was collected from two limestone boulders (sample nos. YG3-3, 5) in a calclithite exposed in the upper streams of the Shiroishi-Osawa in the Mt. Yokokura area, Ochi Town, Takaoka County, Kochi Prefecture (Figure 1). The fossil locality is probably the same as that found by Kobayashi (1984). These limestones including the present cephalopods are characterized by the presence of fibrous spar crusts in cavities and *Renalcis* (botryoidal calcareous algae), suggesting deposition in a high energy, reef environment, and lithologically belong to the bioclastic grainstone. As pointed out by Kobayashi and Hamada (1974, 1985), the boulders are probably a derived mass from the wave resistant reef front to the fore-reef talus. The Yokokurayama Formation is more than 1,000 m thick and is divided into the lower and upper, mainly acidic pyroclastic and tuffaceous sedimentary rock members (G1-G2, G4), and the middle, cliff-forming, limestone member (G3) (Hamada, 1959, 1961). According to Yasui (1984), the base of the Yokokurayama Formation abuts on the underlying Yokokurayama granite.

The middle limestone member, from which the cephalopod fossils were collected, is correlated with a middle Wenlockian to early middle Ludlovian interval based on conodonts (Kuwano, 1976, 1980), whereas its trilobite fauna indicates a slightly younger age, *viz.*, late Wenlockian to middle (?) Ludlovian (Kobayashi and Hamada, 1985). We found well-preserved conodonts in sample YG3-5 that is accompanied by *Protokionoceras fessicancellatum* Kobayashi and

Geisonocerid, gen. et sp. indet. The conodont fauna dissolved from a 0.5 kg limestone sample consists of a single element of *Spathognathodus* aff. *sagitta bohemicus* Walliser and two elements of the coniform type (*Walliserodus* sp. and an indeterminate form). *S. sagitta bohemicus* has been recorded from many localities of the world and it is a valuable late Wenlockian to early Ludlovian indicator (*e.g.*, Walliser, 1971). On the other hand, the occurrence of *Kopaninoceras* in the other limestone boulder (YG3-3) suggests the time span ranging from the Middle to Late Silurian age. Although some reworked Ordovician conodonts were reported from the same locality by Kuwano (1983), there are no evidence of any chronological inconsistency between the examined two derived boulders and the surrounding strata.

Systematic paleontology

Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy, 1844
Subfamily Michelinoceratinae Flower, 1945
Genus *Kopaninoceras* Kisselev, 1969

Kopaninoceras Kisselev, 1969, p. 14 (*fide* Barskov and Kisselev, 1970); Barskov and Kisselev, 1970, p. 66-67; Barskov, 1972, p. 39.

Michelinoceras (*Kopaninoceras*); Chen, 1975, p. 281; Chen, Liu and Chen, 1981, p. 18; Kobayashi, 1984, p. 244-245.

Type species: — *Orthoceras jucundum* Barrande, 1870, Upper Silurian, Pridol Horizon, Czechoslovakia.

Diagnosis: — Shell large, orthoconic to slightly cyrtoconic with circular to subcircular cross section. Sutures straight and transverse; shell surface frequently marked by transverse lirae. Siphuncle small and subcentral, with long, suborthochoanitic to orthochoanitic septal necks and cylindrical connecting rings.

Remarks: — Dzik (1984) synonymized the genus *Kopaninoceras* with *Geisonoceras*, giving the diagnosis that "relatively wide siphuncle with a little inflated connecting rings, relatively short living chamber, and elongated embryonic shell". However, *Kopaninoceras* is distinguishable from all other genera in the family Geisonoceratidae, including *Geisonoceras*, on account of its relatively small siphuncle size and long septal necks.

The genus *Kopaninoceras* has previously been reported from Sardinia, Italy (Serpagli and Gnoli, 1977), Czechoslovakia, Northern Urals and Central Asia (Barskov and Kisselev, 1970; Barskov 1972), Xizang Zizhiqu (Chen, 1975), and southwestern China (Chen, Liu and Chen, 1981). The range of these known specimens is either confined to the Middle to Late Silurian age or questionably has been extended up to the Early Devonian.

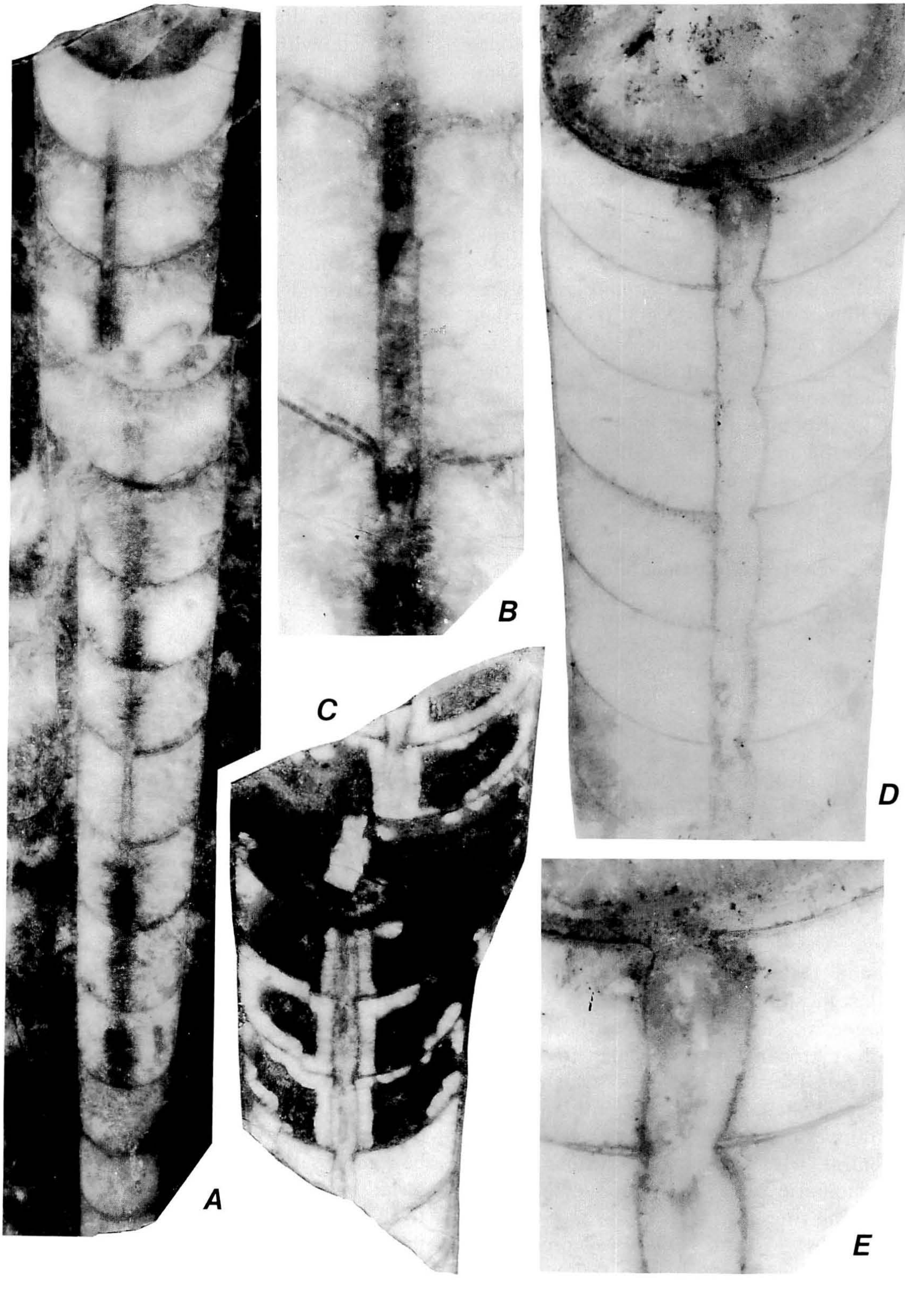
Kopaninoceras kobayashii Niko, Hamada and Yasui, sp. nov.

Figures 2-A, B

Material: — Holotype, UMUT PM 18256; another poorly preserved specimen assigned questionably to this species, TYC 002. Both specimens were obtained from sample YG3-3.

Diagnosis: — *Kopaninoceras* with moderately expanded orthoconic shell, circular cross section, and relatively short camerae for the genus. Siphuncle small and somewhat eccentric.

Description: — The holotype of *Kopaninoceras kobayashii* is a moderately expanded, incomplete phragmocone which is 65 mm in length. The shell is orthoconic with a circular cross section, expanding from 5.3 mm to 11.0 mm with the length of 53 mm. Sutures were not observed but are assumed to be transversal on the basis of observations in serially polished sections. Camerae are relatively short for the genus. Apically, approximately one and one-third camerae occupy a length equal to the apical conch diameter;


A
B
C
D
E

adorally, this ratio increases to two. The curvature of septa is relatively deep. The vertical section at the dorsoventral plane shows a somewhat eccentric siphuncular position. The siphuncle is small, approximately 0.7 mm across at the adoral part, and is slightly constricted at the septal foramen. Septal necks are long (approximately 2 mm at the adoral part) and orthochoanitic (Figure 2-B), joined by thin cylindrical connecting rings. Carbonate within camerae and the siphuncle is inorganic.

Discussion : — Although the surface ornamentation of the holotype is unknown because of the polishing of the specimen through its siphuncle, its generic assignment was made from the shell shape and the presence of relatively long camerae for the subfamily Michelinoceratinae, small siphuncle, and long, orthochoanitic septal necks. This specimen marks the first occurrence of the genus in Japan.

Superficially, the shell morphology of *Kopaninoceras kobayashii* resembles that of *K. ferganense* Barskov (Barskov and Kisselev, 1970, pl. 3, figs. 4a, b, 5 ; Barskov, 1972, pl. 2, fig. 15, pl. 3, fig. 1) from the Upper Silurian rocks in Kirgizskaya S.S.R. However, *K. ferganense* has a larger ratio of the siphuncular diameter to the corresponding shell diameter than that of the present specimen.

Kopaninoceras jucundum (Barrande) (Barskov and Kisselev, 1970, pl. 3, fig. 2 ; Chen, 1975, pl. 4, figs. 3, 4, 7 ; Serpagli and Gnoli, 1977, pl. 1, figs. 1a, b, text-fig. 3) described from the Upper Silurian of Czechoslovakia, northern Urals, Xizang Zizhiqu of China, and Sardinia of Italy has a siphuncular structure similar to that of the present species, but it can be distinguished from *K. kobayashii* by having the longer camerae, a larger ratio of the siphuncular diameter to the corresponding shell diameter, and a less eccentric siphuncular position.

Etymology : — The trivial name honors Dr. T. Kobayashi of the Japan Academy, for his outstanding work on Paleozoic cephalopods.

Family Geisonoceratidae Zhuravleva, 1959
Genus *Protokionoceras* Grabau and Shimer, 1910

Protokionoceras Grabau and Shimer, 1910, p. 58 ; Shimer and Shrock, 1944, p. 541 ; Sweet, 1964, p. K237.

Type species : — *Orthoceras medullare* Hall, 1868, Middle Silurian, Racine Dolomite, Wisconsin.

Diagnosis : — Shell large, moderately expanding orthocones with circular to subcircular cross section. Sutures straight and transverse ; shell surface with cancellate markings produced by intersecting longitudinal and less prominent transverse striae or lirae. Siphuncle subcentral with short and suborthochoanitic septal necks.

Remarks : — The genus *Protokionoceras* was proposed by Grabau and Shimer (1910) with *Orthoceras medullare* Hall as the type species, and is distinguised mainly from the genus *"Orthoceras"* by having cancellate surface ornamentation. The internal structure of the type species has not been figured.

In addition to the Mt. Yokokura area, the genus has been known from North America (*e.g.*, Grabau and Shimer, 1910 ; Foerste, 1928), Norway (Troedsson, 1932 ; Sweet, 1958), and East Australia (Teichert and Glenister, 1952), and it ranges from the Middle Ordovician to the Middle Devonian.

← **Figure 2.** A, B, *Kopaninoceras kobayashii*, sp. nov. **A,** holotype, UMUT PM 18256, vertically and dorsoventrally polished section, ×3. **B,** partial enlargement of the siphuncle of Figure 2-A, ×10. **C,** Geisonoceratid, gen. et sp. indet., TYC 001, vertically polished section, ×3. **D, E,** *Protokionoceras fessicancellatum* Kobayashi. **D,** topotype, UMUT PM 18257, vertical and dorsoventral thin section, venter on left, ×5. **E,** partial enlargement at the adoral end of the siphuncle of Figure **2-D,** ×10.

Protokionoceras fessicancellatum Kobayashi

Figures 2-D, E ; 3-A—D

1983 *Protokionoceras* (?) sp. nov.: Kobayashi, p. 293.
1984 *Protokionoceras* (?) *fessicancellatum* Kobayashi, p. 249, 250, pl. 4, figs.3a, b.
1988 *Protocycloceras* (?) *fessicancellatum* Kobayashi, p.1.

Material : — Holotype, KGS 3587 : The specimen from the Yokokurayama Formation was originally designated as the holotype by Kobayashi (1984). A specimen UMUT PM 18257 from sample YG3-5 is herein designated as the topotype.

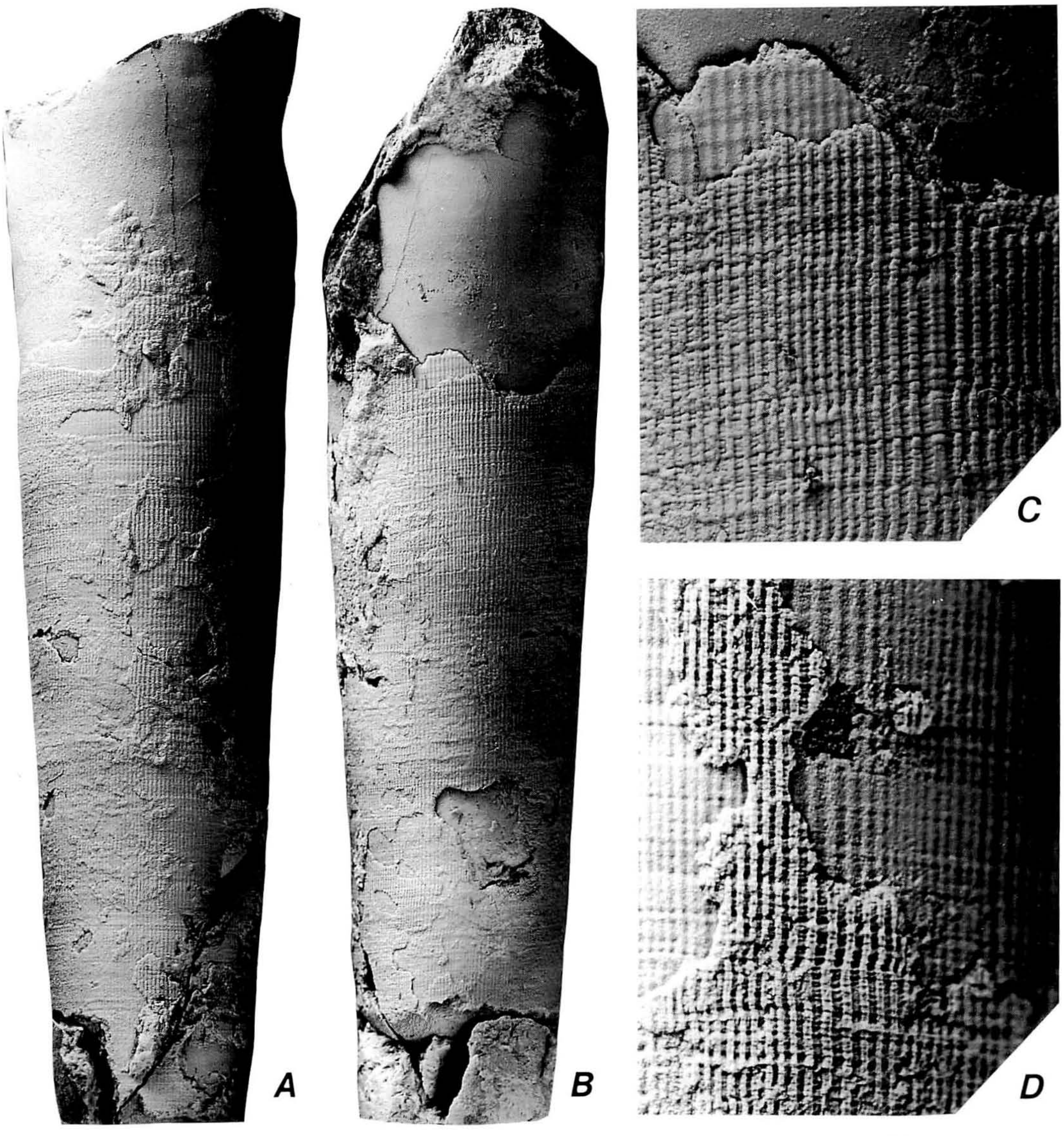


Figure 3. *Protokionoceras fessicancellatum* Kobayashi, topotype, UMUT PM 18257. **A,** dorsal view, ×3. **B,** lateral view, venter on left, ×3. **C,** partial enlargement of the shell surface, ×10. **D,** partial enlargement of the denuded part of the shell showing latticework, ×10.

Description : — The present topotype of *Protokionoceras fessicancellatum* is a longiconic orthocone approximately 49 mm in length, the oral 22 mm of which is represented by the body chamber. The cross section of the shell is circular, expanding from 8.5 mm to 13.0 mm in diameter over the length of the fragment. The shell surface is marked by numerous longitudinal lirae with flattened crests ; the lirae are separated by interspaces of similar width and beaded by closely spaced nodes which are crossed by slightly oblique transverse lirae. The width of longitudinal lirae shows some variation, and they rarely adhere to adjacent lirae (Figure 3-C). A fine lattice of lirae is recognizable at the denuded part of the shell (Figure 3-D). On the exfoliated portion of the shell, there is a wrinkled layer on the internal mold. Sutures are straight and directly transverse. Camerae are relatively short. Apically, approximately two and one-half camerae occupy the length equal to the apical conch diameter ; adorally, this ratio increases to approximately three and one-half. The siphuncle is medium-sized, circular in cross section and slightly removed to the dorsal side at the oral part. Septal necks are short and suborthochoanitic ; the last septal neck, however has a cyrtochoanitic appearance at the dorsal side (Figure 2-E). Connecting rings are homogeneous and somewhat thickening in the vicinity of the septal foramen. Siphuncular segments are constricted at the septal foramen ; there is a dorsal expansion of the rings into the camerae. The maximum diameter of the segments, located near the tip of septal necks in each segment, increases from 1.3 mm in the most apical camera to 1.7 mm in the most adorad camera. Cameral deposits are mural. Calcite within the siphuncle is difficult to interpret due to recrystallization and solution.

Discussion : — The present specimen is conspecific with the type specimen that was once described by Kobayashi (1984) as *Protokionoceras* (?) *fessicancellatum*. The original description of this species was based on a single ill-preserved specimen, which was characterized by "slightly curved and more or less breviconic in adapical part" and the surface ornamentation of "fine lattice of lirae". No internal structure of the holotype was figured. Although the "breviconic" appearance located only in the adapical part would indicate an inordinate shell shape in the Orthocerida, the diagnosis is probably due to the secondary deformation of the shell. Its ornamentation is virtually identical to the lattice pattern in the denuded part of the shell of the present specimen. It can be concluded, both from the external and internal structure of the topotype, that the systematic position of the present species lies in the genus *Protokionoceras* (Geisonoceratidae), and the specific concept should be amended to represent those characteritics of the topotype. Recently, Kobayashi (1988) tentatively referred this species to *Protothycloceras*. However, this Early Ordovician genus possesses prominent annulations which are not visible on the shell surface of *Protokionoceras fessicancellatum*.

Protokionoceras fessicancellatum resembles *P. medullare* (Hall) (Grabau and Shimer, 1910, fig. 1262 ; Foerste, 1928, pl. 69, fig. 1, pl. 70, fig. 2 ; Shimer and Shrock, 1944, pl. 221, fig. 1 ; Sweet, 1964, fig. 169, 7) which occurs in the Racine Dolomite (Middle Silurian) of Illinois and Wisconsin. However, the present species is distinguishable from the latter in having a more slender shell, finer longitudinal lirae and slightly oblique transverse lirae.

Kionoceras styliforme Chen and Liu (Chen, Liu and Chen, 1981, pl. 8, figs. 1, 6-8, 12, 15) from the Xiushan Formation (middle Wenlockian) in Sichuan Province possesses an interal structure similar to the examined specimen except for the siphunclar position and the shape of its connecting rings. The Chinese form lacks some diagnostic charactesistics of the genus *Kionoceras*, and thus its taxonomic position is in need of reexaminations.

Geisonoceratid, gen. et sp. indet.

Figure 2-C

Descriptive remarks : — This figured specimen (TYC 001) from sample YG3-5 is an imperfect fragment (approximately 33 mm in length) of the orthoconic phragmocone, which has a circular cross section, approximately 12 mm in diameter near the apical end. Sutures were not observed but are assumed to be transversal on the basis of observations in serially polished sections. Camerae are relatively short ; three camerae occupy the length equal to the apical conch diameter. The siphuncle is subcentral with short and suborthochoanitic septal necks which are joined by cylindrical connecting rings. These rings are slightly constricted at the septal foramen.

The fragmentary nature and lack of data on its surface ornamentation preclude the generic and specific assignment of the present specimen.

Acknowledgments

The authors wish to thank Dr. T. Kobayashi of the Japan Academy for his valuable suggestions, and also Dr. H. Igo of the University of Tsukuba for identification of conodonts and critically reviewing the manuscript. The first author in greatly indebted to Dr. T. Nishida of Saga University for his encouraging discussions and to Dr. I. S. Barskov of Moscow State University, U.S.S.R. for providing the literature used in this study. We acknowledge the Japan Academy for partial financial support toward this research.

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Gomi 五味, Kochi 高知, Kurosegawa 黒瀬川, Ochi 越知, Shiroishi-Osawa 白石大沢, Sichuan* 四川, Takaoka 高岡, Xiushan* 秀山, Xizang Zizhiqu* 西蔵自治区, Yokokura-yama (＝Mt,Yokokura) 横倉山.

(*Chinese name)

黒瀬川帯，横倉山層からのシルル紀頭足類 Orthocerataceae：高知県高岡郡越知町横倉山地域の黒瀬川帯，横倉山層（G3 部層）から筆者らの一人安井が採集した 4 個のシルル紀頭足類化石を基に，国内では従来産出記録がなかった属，*Kopaninoceras* の一新種，*K. kobayashii* を含む，*Protokionoceras fessicancellatum* Kobayashi, Geisonoceratid, gen. et sp. indet. の 3 種を識別記載した。随伴するコノドント化石は，ウエンロック世後期からラドロウ世前期を示す。

児子修司・浜田隆士・安井敏夫

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876. *NUMMULITES* AND *ASSILINA* FROM TANSEN AREA, PALPA DISTRICT, THE NEPAL LESSER HIMALAYAS*

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Abstract. Middle Eocene (Lutetian) *Nummulites beaumonti* d'Archiac and Haime and *Assilina papillata* Nuttall are described from the Bhainskati Formation (Kirthar Series), Tansen Group in the Tansen area, Palpa district, the Nepal Lesser Himalayas. This is the first description of both species from Nepal. The specimens include only the megalospheric form and their internal morphology is discussed. Two species are useful in establishing a local and interregional correlation of marine Eocene strata. The paleoecology of the Nepal nummulitid bed is briefly described.

Key words. *Nummulites, Assilina*, Eocene, Nepal, Himalaya

Introduction

Much information concerning the geology and paleontology of the Nepal Lesser Himalayas has been accumulated in the last nineteen years (Hagen, 1969; Frank and Fuchs, 1970; Hashimoto *et al.*, 1973; Sharma, 1977; Sakai, 1982, 1983, 1985; Kimura *et al.*, 1985). Recently, the junior author, one of Japan Overseas Cooperation Volunteers has undertaken the geological survey around the Tansen-Palpa region, the Nepal Lesser Himalayas from 1980 to 1983. In the course of the survey, he could collect shaly limestone materials from the Bhainskati Formation (Kirthar Series), Tansen Group, and submitted them to the senior author for a paleontological study. The present paper contains an account of *Nummulites beaumonti* d'Archiac and Haime and *Assilina papillata* Nuttall with a general discussion on species described from the middle Kirthar (Lutetian) of Kutch, northwestern India and the Middle Kirthar (Lutetian) of the Karachi district, Pakistan, respectively.

The hypotypes of *Nummulites* and *Assilina* and slides described herein have been deposited in the collections of Department of Geology, Faculty of Education, Saitama University. The specimens collected from the same locality are deposited in the Geological Museum of Department of Geology, Trichandra Campus, Tribhuvan University.

Fossil locality and notes on the geology

Nummulites beaumonti d'Archiac and Haime and *Assilina papillata* Nuttall are found from a new locality in the western part of Tansen, in a *Nummulites*-bearing shaly

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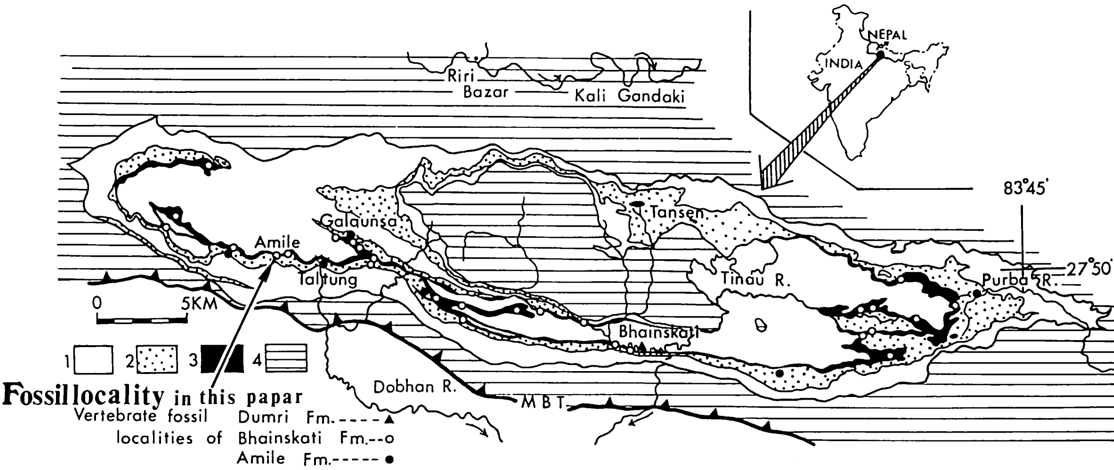


Figure 1. Map showing the fossil locality of Nepal *Nummulites* and *Assilina*, and sketch-map of the geology of the studied area. 1, Sisne, Taltung and Dumri Formations; 2, Amile Formation; 3, Bhainskati Formation; 4, Kali Gandaki Supergroup; MBT, Main Boundary Thrust.

limestone bed whose exposure extends from the upper stream of the Badahare-Amile River to Taltung in the Tansen area, located midway between Pokhara and Butwal. The estimated position of this locality lies at Lat. 27° 50′N, Long. 83°20′E. (Figure 1).

The Tansen area is situated in the Nepal Lesser Himalayas, which is bounded by the Main Boundary Thrust from the sub-Himalayan Siwalik belt comprising Neogene post-orogenic sediments in the south, and it is physiographically divided into the Mahabharat Range and the Midland Range. Those structually complex, unfossiliferous and poor outcrop conditions of the Lesser Himalayas have hitherto impeded progress of geological studies.

The Lesser Himalayan rocks in the Tansen area are grouped into two major stratigraphic units, the Tansen Group and the Kali Gandaki Supergroup, by the junior author (1982, 1983, 1985). The Tansen Group consists of the Gondwana and post-Gondwana rocks of clastic sediments ranging in age from late Carboniferous to Tertiary. This group is separated from the underlying Kali Gandaki Supergroup ranging in age from late Precambrian to early Paleozoic by a distinct unconformity. The Tansen Group is subdivided into the Lower Gondwana Sisne Formation (1020 m thick), Upper Gondwana Taltung Formation (250 m), Amile Formation (230 to 300 m), Bhainskati Formation (160 to 200 m) and Dumri Formation (100 to 725 m) in ascending order, based mainly on paleontological and lithostratigraphic evidence (Figure. 2). The *Nummulites*-bearing shaly limestone bed treated in the present study is included in the Bhainskati Formation, which is especially unique and important formation in the Lesser Himalaya because of the presence of fossiliferous beds yielding *Nummulites beaumonti* d'Archiac and Haime, *Assilina papillata* Nuttall, *Asteracantus* sp., land mammals, Teleostei, Chelonia and Trionichidae (Sakai, 1983). Furthermore, the Bhainskati Formation is sandwiched between the Cretaceous to probable Palaeocene Amile Formation consisting of thick massive quartzose sandstones and the Oligocene to possible early Miocene Dumri Formation comprising a series of fluvial sandstones intercalated with shale.

Paleoecology of the nummulitic shaly limestone or limy shale bands of the Bhainskati Formation of the studied area

As seen in the stratigraphic succession of the studied area (Figure 2), the Bhainskati Formation overlies the Amile conformably and is composed of a black shale which intercalates both molluscan fossil beds and nummulitic shaly limestone or limy shale bands in the lower part. In the upper part, the Bhainskati consists of a red-purplish and green mottled shale, molluscan fossil beds and oolitic hematite, and is disconformably overlain by the thick fluvial sandstones of the Dumri Formation. In the lower part of the Bhainskati, the interbedded limestone or limy shale bands indicate shallow warm marine conditions with the precipitation of carbonate rocks. This interpretation is conformable to a paleolatitude estimate of $10° \pm 6°$ S for the uppermost part of the Bhainskati Formation, based on the paleomagnetic study (Yoshida and Sakai, 1984).

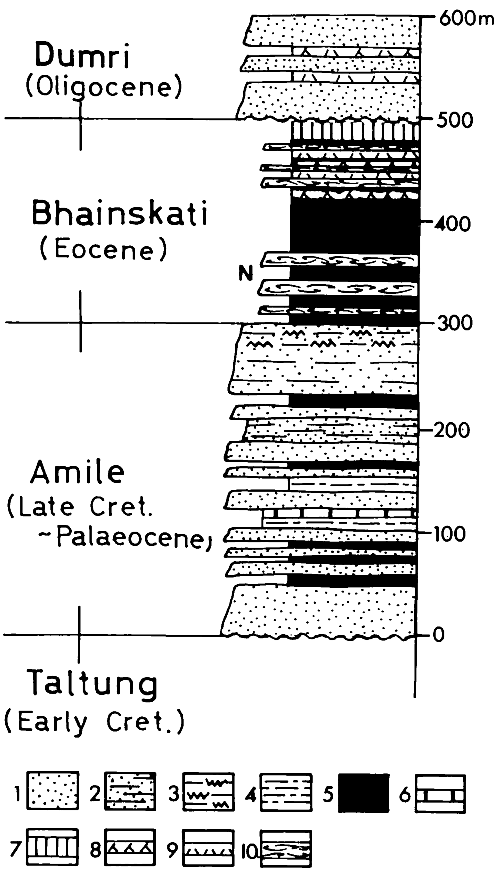


Figure 2. Map showing the stratigraphic succession of the Amile, Bhainskati and Dumri Formations, and nummulitic bed (N). 1, quartzose sandstone; 2, Sandstone with shale interbeds; 3, bioturbated mudstone; 4, siltstone; 5, black shale; 6, limestone; 7, variegated shale with oolitic hematite; 8, red shale; 9, green shale; 10, molluscan fossil beds.

In the Surkhet valley of western Nepal, 200 km further west of the Tansen area treated in this paper, Tewari and Gupta (1976) described a larger foraminiferal assemblage from a limestone of the Subathu Formation, including *Assilina* cf. *granulosa* (d'Archiac), *A. leymeriei* (d'Archiac and Haime), *A. granulosa* var. *chhumbiensis* Gill, *A. subdaviesi* Gill, *Nummulites* cf. *mamilla* (Fichtel and Moll), *N. atacicus* Leymerie and *N. djokjokartae* (Martin).

In this paper, the nummulitic limestone of the Subathu Formation, which is correlated with the Laki Formation of Pakistan (Nuttall, 1925), is interpreted to be indicative of shallow marine conditions where abundantly available carbonates led to the formation of nummulitic and other larger foraminiferal limestones. Although the Bhainskati Formation cannot directly be correlated with the Subathu Formation on the basis of the larger foraminiferal fauna. Nummulitic beds of both formations are similar in lithologic character and the paleoecological condition is referred to be shallow marine for both of them.

Description of species

Family Nummulitidae de Blainville, 1825
Genus *Nummulites* Lamarck, 1801
Nummulites beaumonti d'Archiac and Haime

Figures 5-1—14

1853 *Nummulites beaumonti* d'Archiac and Haime, p. 133, pl. 8, figs. 1a-e, 2-3.
1926 *Nummulites beaumonti*, Nuttall, p. 130-131, pl. 1, figs. 4-5.
1940 *Nummulites beaumonti*, Davies, p. 206-209, pl. 9, figs. 1-9.
1959 *Nummulites beaumonti*, Nagappa, p. 180, pl. 8, figs. 15-17; pl. 9, figs. 1-2.
1965 *Nummulites beaumonti*, Sen Gupta, p. 91-93, pl. 15, figs. 1-2, 5; pl. 16, figs. 3, 7, 9-10; pl. 17, figs. 1, 5-7, 12.
1972 *Nummulites beaumonti*, Blondeau, p. 149, pl. 24, figs. 11-14.
1981 *Nummulites beaumonti*, Schaub, p. 135-136, pl. 53, figs. 17-19, 22-25, tab. 14-p.

Description: —The test is small, thickly lenticular to biconvex, regularly sloping and sometimes depressive in the umbo. The sutures are visible as faint lines of radiating septal filaments near the surface. The spherical to subspherical protoconch is followed by a reniform deuteroconch of second chamber, and both chambers are followed by closely coiled whorls. The septa are straight, or slightly curved, usually near the distal end. The spiral wall is thick. The axial plugs are composed of radiating columns of shell materials. The measurements are given as follows:

Stratigraphic horizon: —A 5 to 10 cm thick shaly limestone bed bearing *Nummulites beaumonti* and *Assilina papillata*, lying about 50 m above the base of the Bhainskati Formation (Kirthar Series), Tansen Group.

Geological age: —Middle Kirthar, Middle Eocene (Lutetian).

Remarks: —As seen in the equatorial and axial sections of this form from the Tansen area, its small protoconch, a tight coiling of spiral wall, rhombic style of chamber form, and regularly straight and radial septa are the same as those in *Nummulites beaumonti* d' Archiac and Haime from Egypt, Lybia, and the type area of the Lower Tertiary rocks of the Pakistan-Indian region (d'Archiac and Haime, 1853; Nuttall, 1926; Davies, 1940; Nagappa, 1959; Sen Gupta, 1965 and others). Although isolating the Tansen specimens from the matrix for the examination of their surface markings was difficult, oblique and tangential sections of this form show radiating and regularly curved septal filaments, and nonpapilate surface. These features have already been observed in figures of *Nummulites beaumonti* d'Archiac and Haime by some of the authors stated above.

Diameter (mm), 2.3-3.3; thickness (mm), 1.6-2.2; form ratio, 1 : 1.4-1 : 2.0								
Protoconch (inner diameter, μ), 90-136; protoconch (outer diameter, μ), 126-167								
Number of whorls, 7 1/2-8								
Number of chambers in whorls (one specimen shown on Figure 5-13)								
Whorls	1	2	3	4	5	6	7	7 1/2
Chambers	13	25	34	38	41	44	42	36
Rate of growth of whorls (4 specimens measures, μ)								
Whorls	1	2	3	4	5	6	7	8
Height range	197—286	340—391	442—525	609—656	782 816	952—966	1150—1187	1360
mean	247.5	365.5	494.3	630.8	797.3	960	1149.3	—
Thickness of spiral lamellae (4 specimens measured, μ)								
Whorls	1	2	3	4	5	6	7	8
range	26-34	24-40	34-48	36-54	36-54	36-60	40-54	44
mean	29.5	33.5	41.5	43.5	46.7	45.3	48	—

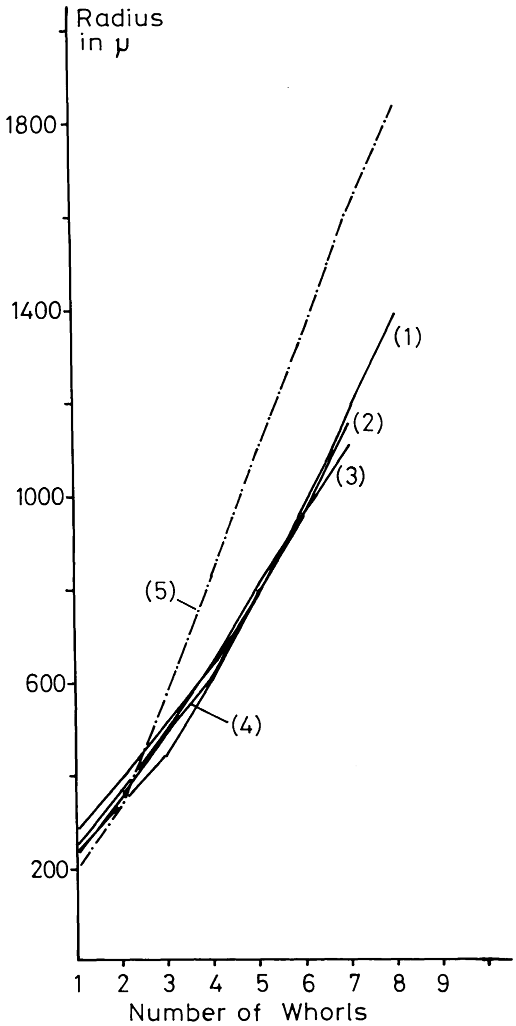


Figure 3. Spira-diagram of *Nummulites beaumonti* d'Archiac and Haime from (1) slide 18, (2) slide 14, (3) slide 2 (including a specimen of Figure 5-13), (4) slide 2 of the *Nummulites* bed of the Bhainskati Formation, Nepal and (5) one based on the average of 5 specimens from the Lutetian of Kutch, India (Sen Gupta, 1965, fig. 1), respectively.

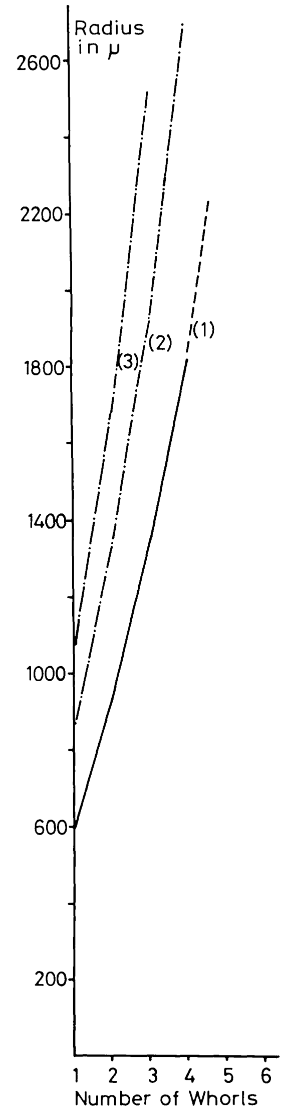
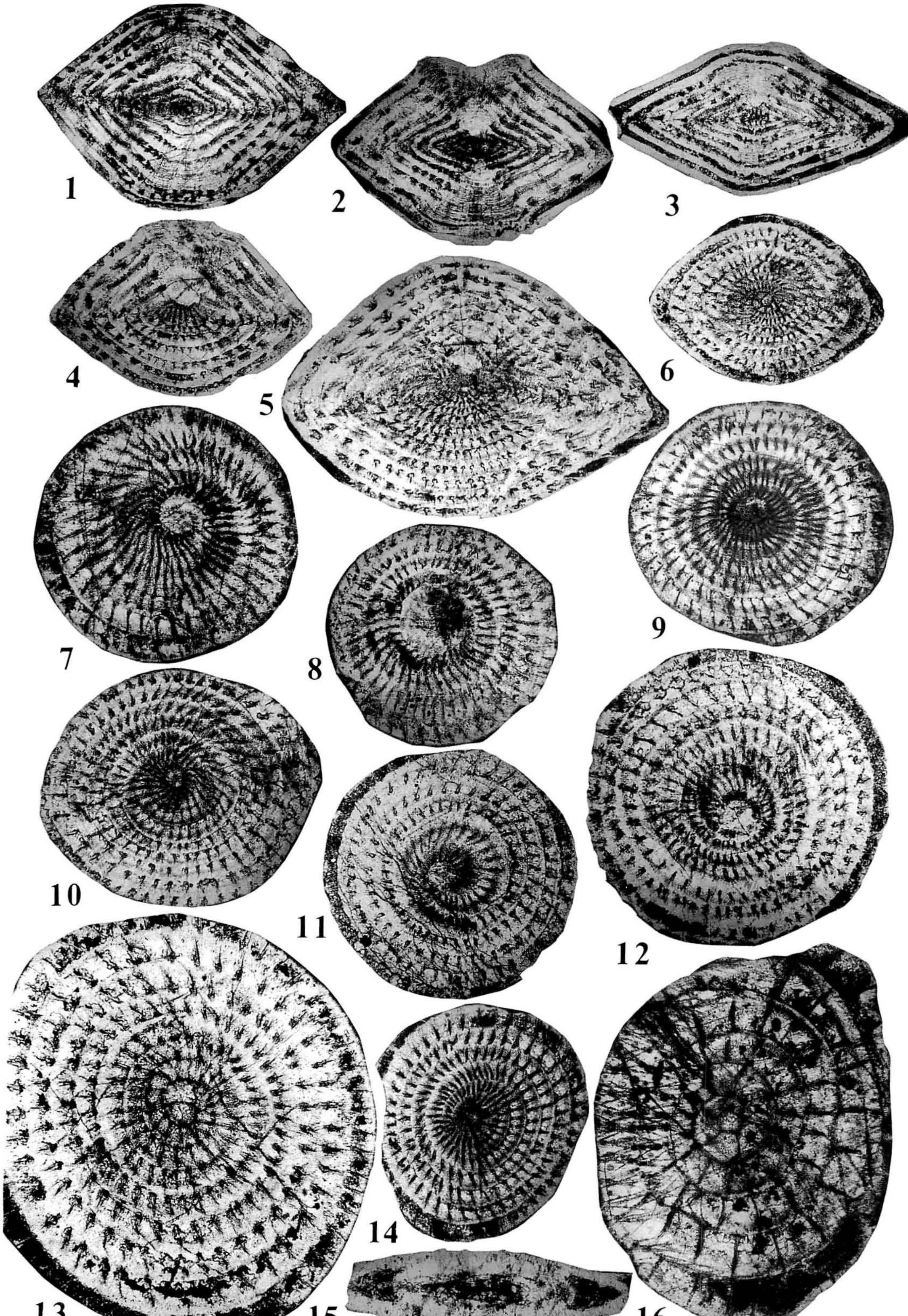


Figure 4. Spira-diagram of *Assilina papillata* Nuttall from (1) slide 6 of the *Nummulites* bed of the Bhainskati Formation, Nepal and (2) slide C31455/3 and (3) slide C31455/2, both from the Middle Kirthar (Lutetian) of Karachi District, Pakistan (Schaub, 1981, pl. 97, figs. 3-4), respectively.

→ **Figures 5.1—14.** *Nummulites beaumonti* d'Archiac and Haime, **1-3.** Axial sections. The axial plug is very conspicuous in a specimen of **2**; **4-7.** Oblique sectitons. The radial septal filaments are shown in the central part near the surface of test of **7**; **8-12, 14.** Tangential sections. **13.** Equatorial section. **15—16.** *Assilina papillata* Nuttall, **15.** Axial section. The whorls are not embracing to the umbonal region of test.; **16.** Equatorial section. All figures ×16, except ×30 of **13.**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As shown in Figure 3, the spira-diagram of *Nummulites beaumonti* from the *Nummulites* bed of the Tansen area shows that ontogenetic growth curves of coiled whorls of specimens are more tightly than those of *Nummulites beaumonti* d'Archiac and Haime from the Middle Eocene (Lutetian) of Kutch, western India (Sen Gupta, 1965). Sen Gupta (op. cit., p. 92) has once considered that *Nummulites beaumonti* d'Archiac and Haime may be a species showing much variation not only in external shape and size, but also in internal structure. Thus, difference between ontogenetic growth curves from Tansen specimens and Kutch ones shown in Figure 3 can be considered as a species variation of *Nummulites beaumonti*.

De la Harpe (1883, p. 166) once indicated that there is a shade of difference among the three species, *Nummulites beaumonti* d'Archiac and Haime, *N. discorbinus* (Schlotheim) and *N. striatus* Bruguière, on the view point of a tight coiling of spiral wall, chamber form and septa. This problem will be discussed near future.

Sen Gupta (1965) considered *Nummulites pengaronensis* Verbeek, *N. stamineus* Nuttall and *N. kelatensis* (Carter) to be a synonym of *N. beaumonti* d'Archiac and Haime. After all, Sen Gupta identified *Nummulites stamineus* Nuttall as a synonym of *N. beaumonti* d'Archiac and Haime, because he considered that the figures of *N. beaumonti* published by Davies (1940, pl. 9) are closely related to those of *N. stamineus*. Meanwhile, Smout (1954) considered *Nummulites stamineus* from Qatar as a synonym of *N. discorbinus* (Schlotheim), and he retained *N. beaumonti* as a valid species. Sen Gupta (1965) considered that although there is some confusion about the identity of *Nummulites kelatensis* of Carter (1861), *N. kelatensis* is closely connected with *N. beaumonti*. The present authors consider that the forms from Timor described as *Nummulites kelatensis* Carter by Henrichi (1934, p. 30–32) are definitely *N. beaumonti*, based on the increasing whorl, regular spacing of the septa and polar plug.

Sen Gupta (1965, p. 93) described that another synonym of *Nummulites beaumonti* d'Archiac and Haime is *N. pengaronensis* Verbeek. He mentioned as the typical features of *Nummulites beaumonti* are a tight coiling of spiral wall, which is almost uniformly thick, and small embryonic chambers. He also noted that these features are clearly recognized in the figures of *N. pengaronensis* by Cole (1957).

Doornink (1932) reported in detail the original descriptions of *Nummulites pengaronensis* from Borneo by Verbeek (1871) and *N. nanggoelani* from Java by Verbeek (1891), in addition to Vlerk's description and illustration of *N. pengaronensis* (1929, p. 20–21, figs. 12, 35a–b). He concluded that *Nummulites pengaronensis* is the megalospheric form and *N. nanggoelani* is the microspheric of the former. Doornink has the same opinion as Douville (1912) on this matter. Cole (1957) identified both megalospheric and microspheric specimens from the Eniwetok Atoll under the name *Camerina pengaronensis* (Verbeek), and Hashimoto *et al.* (1979) and Hashimoto and Matsumaru (1981) reported *Nummulites* cf. *pengaronensis* from Philippines, respectively. However, nobody except Sen Gupta identified *Nummulites pengaronensis* as a synonym of *N. beaumonti*.

Genus *Assilina* d'Orbigny, 1839

Recently, Hottinger (1977) included the genus *Assilina* in the *Operculina* d'Orbigny, 1826, based on the similarity of structures of stolons and canal systems in the wall of test. Schaub (1981) regarded the *Assilina* to be the subgenus of *Operculina*, being accepted with Hottinger's opinion. The authors do not have any data about the wall structures of *Assilina* specimens from Nepal, but regard as the *Assilina* having the peculiar characters of evolute form and straight septa, following a classification of Blondeau (1972).

Assilina papillata Nuttal

Figures 5-15—16

1926 *Assilina papillata* Nuttall, p. 144, pl. 6, figs. 5-7b.
1926 *Assilina subpapillata* Nuttall, p. 145, pl. 6, figs. 2-3a.
1940 *Assilina papillata*, Davies, p. 214, pl. 11, figs. 1, 3, 6, 8, 10-12b.
1959 *Assilina papillata*, Nagappa, p. 178, pl. 5, fig. 2.
1981 *Assilina papillata*, Schaub, p. 205-206, pl. 96, figs. 26-39; pl. 97, figs. 1-6, 8-12.

Description: —The diameter of the specimens would be more than 5 mm from the incomplete portions of the available sections in measurement. The thickness of the specimens through the centre of test is from 0.9 to 1.1 mm. The opening of the spire shows evolute form. The test is composed of approximately 5 volutions, with 7 chambers in the first whorl and 22 chambers in the 4th whorl. The chambers are higher than broad. The chamber walls are evenly and regularly straight, and are radial with a sharp curvature at distal ends. Transverse sections show the marginal cord with well developed pillar structures at the whorl junction. The chambers in transverse sections much higher than broad and typically tapering in shape.

Stratigraphic horizon: —The same bed as *Nummulites beaumonti* d'Archiac and Haime.

Geological age: —Middle Kirthar, Middle Eocene (Lutetian)

Remarks: —Although uncertainty of specific identification may exist in dealing with material of this type, these specimens are referred to *Assilina papillata* Nuttall on the basis of descriptions and illustrations given by other workers stated above. There are agreements in the peculiar curve of the spiradiagrams between only one investigated specimen from Nepal and those of *Assilina papillata* from the Middle Kirthar in Gandbo Hill, northwest Karachi, Pakistan (Schaub, 1981), as shown in Figure 3. Therefore, the present form is identified with *Assilina papillata* Nuttall.

Acknowledgments

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ネパール小ヒマラヤ山脈パルパ地方タンセン地域産 *Nummulites* および *Assilina*：上記地域のキルタール統バインスカチ累層から酒井は *Nummulites* 属および *Assilina* 属を採集し，松丸は両者についてそれぞれ *beaumonti* 種，*papillata* 種を同定し，それらを酒井に報告していた（酒井，1982，1983)。今回，両名は両種について記載を行い，他種間との同物異名についても議論した。これはネパールに認められる両種についての最初の記載論文である。両種産出層の古環境も簡単に触れた。

松丸国照・酒井治孝

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877. ON THE GENUS *PLICATOUNIO* (CRETACEOUS NON-MARINE BIVALVIA) FROM KOREA*

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Abstract. Fossils of *Plicatounio* were collected from ten localities including the type-locality of the type-species, *Plicatounio* (*Plicatounio*) *naktongensis*, all of which lie in the Hasandong Formation, Gyeongsang Group in Korea, and in addition, from two localities in the Wakino Subgroup and the Mifune Group in Japan.

This paper reviews the type species with special stress on the hinge structure. The crenulation on the postero-lateral hinge teeth is an original character and the presence or absence of it depends on the state of fossil preservation. Two new species, *P.* (*P.*) *okjuni* and *P.* (*P.*) *yooni*, are proposed.

Key words. Cretaceous, *Plicatounio*, non-marine, bivalve, Gyeongsang Group

Introduction

Since the genus *Plicatounio* was erected by Kobayashi and Suzuki (1936) based on *P. naktongensis* from the lower Gyeongsang Group, Korea, many species have been reported from the Cretaceous non-marine deposits in the Asian Continent (Hoffet, 1937; Yabe and Hayashi, 1938; Ota, 1959; Hase, 1960; Maeda, 1962; Kobayashi, 1963; Martinson, 1965; Kobayashi, 1968; Gu and Ma, 1976; Guo, 1981 and 1986; Tamura, 1982; Kobayashi, 1984) and even northern Africa (Mongin, 1963). The present genus, thus has been considered to be one of the most important non-marine bivalve genera in the late Mesozoic together with the genus *Trigonioides*.

However, the internal structure of the type-species, *Plicatounio* (*P.*) *naktongensis*, was not sufficiently known, and the original specimens are now missing except for several paratypes and a gypsum mould of the holotype deposited in the University of Tokyo. I have recently found several localities of the genus including the type-locality of the type-species and made a fairly large collection. And I have had opportunities to visit the fossil locality at Rikimaru, Fukuoka Pref. northern Kyushu, and the locality at Kosa Town, Kumamoto Pref., central Kyushu, Japan and collect fairly good specimens and observed also the collections deposited at Fukuoka University of Education and at Kumamoto University during my stay in Japan (1973-1975).

In this paper, I report the result of my study on *Plicatounio naktongensis* with special stress on the hinge structure and discuss the classification of the genus by comparison with other relevant species, proposing two new species from the lower Gyeongsang Group, Korea.

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Brief review of previous works on *Plicatounio*

1) Kobayashi and Suzuki (1936) reported *Plicatounio naktongensis* as a new genus and a new species based on several specimens from Yangpori, southern Korea. Its diagnostic characters were considered to be asymmetrical elongate outline, 4 or 5 plicae on the posterior part, and a hinge plate with crenulated pseudocardinal teeth and lamellar postero-lateral ones. They also reported *P. triangularis* as another new species from Rikimaru, northern Kyushu, Japan. After that, however, Kobayashi (1956) excluded it from *Plicatounio*.

2) *P. suzukii* and *P. maximus* were reported by Hoffet (1937) from a middle Cretaceous formation at Muong-Phalane, Laos.

3) Yabe and Hayashi (1938) reported *P. naktongensis manchuricus* from about 70 km northeast of Hoten (=Shen-yang), northeastern China.

4) Suzuki (1943) reported *P. naktongensis multiplicatus* from near Jinju, southern Korea, pointing out as its subspecific character the fine radial ribs on the anterior and middle parts besides 4 or 5 posterior plicae.

5) Ota (1959) first described the hinge structure of the genus in detail and reported *P. kwanmonensis* as a new species. He pointed out the hinge structure of *P. naktongensis* with three crenulated pseudocardinals on the right valve, two on the left valve; and with two lamellar postero-lateral ones on the right valve and one or two on the left valve. That of *P. kwanmonensis* is distinguished by crenulated postero-lateral ones. Subsequently, Ota (1963) proposed the subgenus *Kwanmonia* for *P. kwanmonensis* and redescribed the hinge structure of *Plicatounio* to possess five hinge teeth on both valves, showing the difference between *Plicatounio* (*P.*) and *Kwanmonia*. The former has lamellar while the latter has crenulated postero-lateral teeth.

6) Maeda (1962) reported *P. kobayashii* and *P. tetoriensis* from the upper formation of the Tetori Group, northwestern part of central Japan.

7) Ku (1962) reported *Plicatounio* ex. gr. *suzukii* and *Plicatounio* sp. from the late Cretaceous non-marine formation, Yunnan, China.

8) Mongin (1963) described *P. flattersensis* from a Cretaceous formation, Sahara, northern Africa.

9) Martinson (1965) reported *P. naktongensis* and *P. klaudziensis* from Cretaceous non-marine deposits, Fergana, U.S.S.R.

10) Kobayashi (1968) proposed a new family Plicatounionidae based on *Plicatounio* and described *P. namphungensis* from Nam Phung dam site, Thailand.

11) Gu and Ma (1976) .reported many species from Cretaceous non-marine deposits of China as follows: *P. naktongensis, P. multiplicatus, P. tetoriensis, P. manchuricus, P.* sp. aff. *P. suzukii, P. equiplicatus, P. zhejiangensis, P. fujianensis, P. latiplicatus, P. subrhombicus, P.* (*Kwanmonia*) *heilongjiangensis*.

12) Guo (1981) described *P.* (*P.*) *rostratus* from Cretaceous deposits, Yunnan, southern China.

13) Tamura (1981) considered that Ota's *P. "naktongensis"* from the Wakino Subgroup, Japan should be excluded from *P. naktongensis* from southern Korea on account of the difference in the postero-lateral

teeth, *i.e.*, with or without crenulations.

14) Guo (1986) described *Plicatounio* (*Enotrigonioides*) *alatus* from the upper member of the lower Cretaceous Jingxing Formation, west Yunnan, China.

As briefly reviewed above, the genus *Plicatounio* has been reported from worldwide localities with many species and some of the authors (Kobayashi, 1968, 1984; Guo, 1981, 1986) have evaluated as representing a distinctive family, but the hinge structure of the type-species of the genus *Plicatounio*, *Plicatounio* (s.s.) *naktongensis* has not been fully described yet.

Material and localities

The fossils at hand were collected from the following ten localities, all of which fall under the Hasandong Formation, the 2nd formation in ascending order, of the Gyeongsang Group.

Loc. 1 : Yangpori, Jingyo-myeon, Hadong-gun, Gyeongsangnam-do (type-locality of *Plicatounio naktongensis*) (Figure 1-B). This locality is in the upper part of the Middle Hasandong Formation which is composed of an alternation of dark grey limy siltstones and fine-grained sandstones intruded by andesitic dykes (Figure 1-B). Here, *Brotiopsis* spp. (Cretaceous non-marine gastropods) occur gregariously forming layers at 7 horizons, of which the 2nd and 4th contain occasionally *Plicatounio naktongensis* and *Trigonioides* (*T.*) *kodairai*.

Loc. 2 : At an island about 200 m southeast of Loc. 1 (Yangpori) (Figure 1-B). The *Brotiopsis* beds are more than 12 in number and lithology is similar to that of Loc. 1. Loc. 2 also falls within the upper part of the Middle Hasandong Formation. Among the 12 fossiliferous horizons, *Plicatounio naktongensis* has been collected from the 3rd and 5th beds.

Locs. 3 and 4 : At a beach near Impo, Hwanggeumri, Golyak-myeon, Jeolanam-do (Figure 1-D). The outcrop of these localities consists of grey fine-grained sandstone or siltstone alternated with medium-grained sandstone, which lies within the middle part of the Middle Hasandong Formation (Figure 2). The fossiliferous bed is about 10 cm in thickness. It contains *Wakinoa* sp., *Pseudohyria* sp. and *Brotiopsis* sp. as well as *Plicatounio* (*P.*) *yooni*, n. sp. (described below).

Loc. 5 : At a beach near Sumoondong, Keumnam-myeon, Hadong-gun, Gyeongsangnam-do (Figure 1-C) (type-locality of *Trigonioides kodairai*). The rock exposed at this locality consists of greenish grey fine-grained sandstone and siltstone alternated with medium- to coarse-grained sandstones, which fall under the upper part of the Middle Hasandong Formation (Figure 2). From here, *Plicatounio yooni* (described below) and *Trigonioides kodairai* have been collected.

Loc. 6 : At a beach about 200 m south to Hanchi, Sumoondong, Keumnam-myeon, Hadong-gun, Gyeongsangnam-do (Figure 1-C). This locality is represented by an alternation of light greenish grey siltstone and fine- to medium-grained sandstone, within the middle part of the Middle Hasandong Formation (Figure 2). Here also, *Plicatounio naktongensis* is associated with the crowded *Brotiopsis* sp. There are at least 8 *Brotiopsis* beds among which the 4th and 7th beds contain *P. naktongensis*.

Loc. 7 : A channel outcrop at Yusuri, Nadong-myeon, Jinyang-gun, Gyeongsangnam-do (see Yang, 1983 text-fig. 5). The rock exposed at this locality consists of light greenish grey siltstone and fine- to medium-grained sandstone within the upper part of the Upper Hasandong Formation (Figure 2). Here *Plicatounio naktongensis* has been collected together with *Trigonioides* (*T.*) *jaehoi*.

Loc. 8 : On a mountain side about 700 m south of Bulnodong, Hyoryeong-myeon, Kunwi-gun, Gyeongsangbuk-do (Figure 1-A). Lithology at this locality is composed of siltstone and fine-grained sandstone within the upper part of the Middle Hasandong

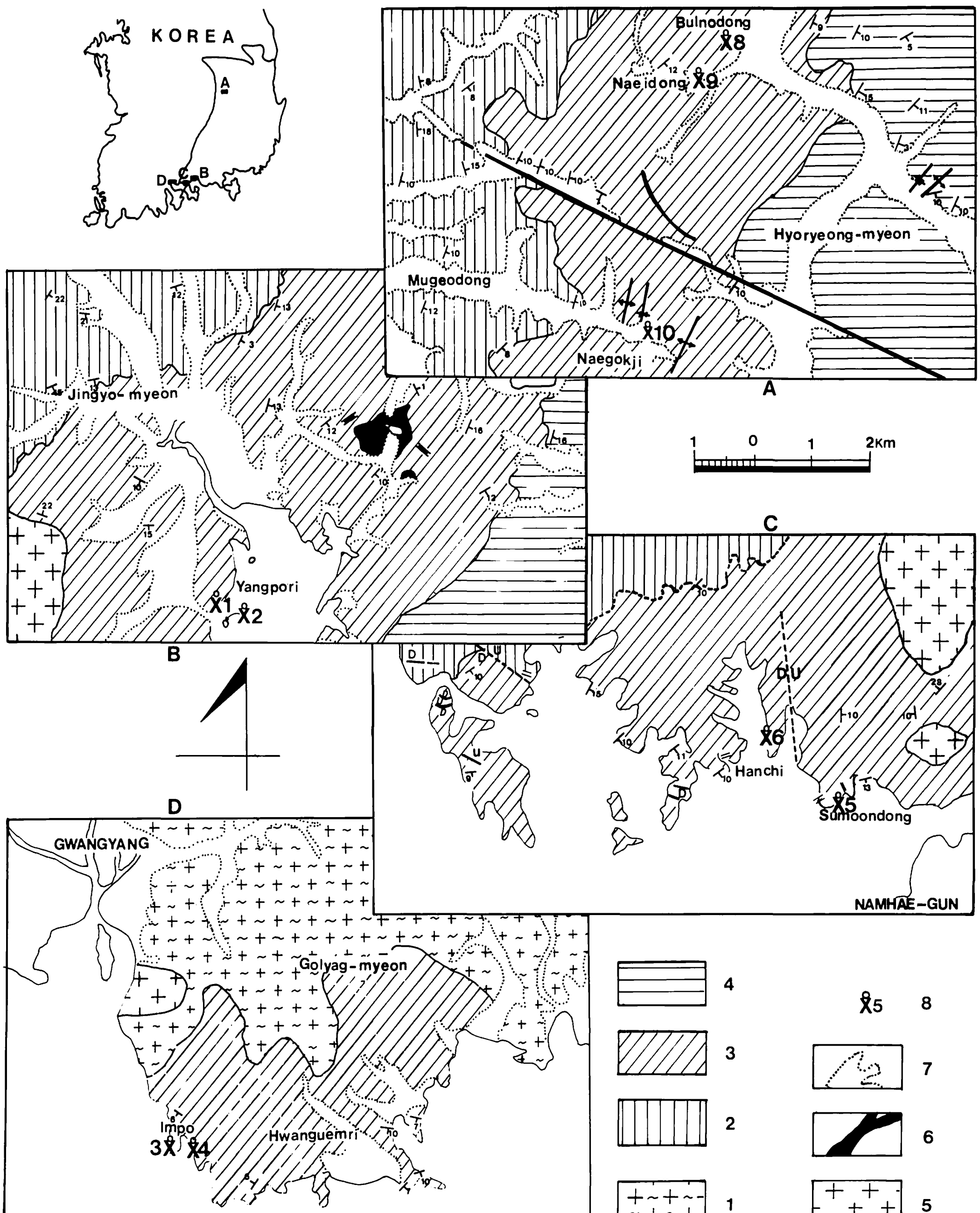


Figure 1. Geological maps around the fossil localities. 1. Metamorphic rocks (Precambrian), 2. Yeonhwadong Fm., 3. Hasandong Fm., 4. Dongmyeong Fm., 5. Bulguksa granodiorite, 6. intermediate to basic dykes, 7. Alluvium, 8. Fossil locality with locality number.

Formation. Here, *Plicatounio* (*P.*) *okjuni* (described below) and *P.* (*P.*) sp. cf. *P.* (*P.*) *yooni*, n. sp. (described below) have been collected together with *Wakinoa* sp. cf. *W. tamurai*, *Nagdongia soni* and *Viviparus* sp.

Loc. 9 : In the valley of Baetae, Naeidong,

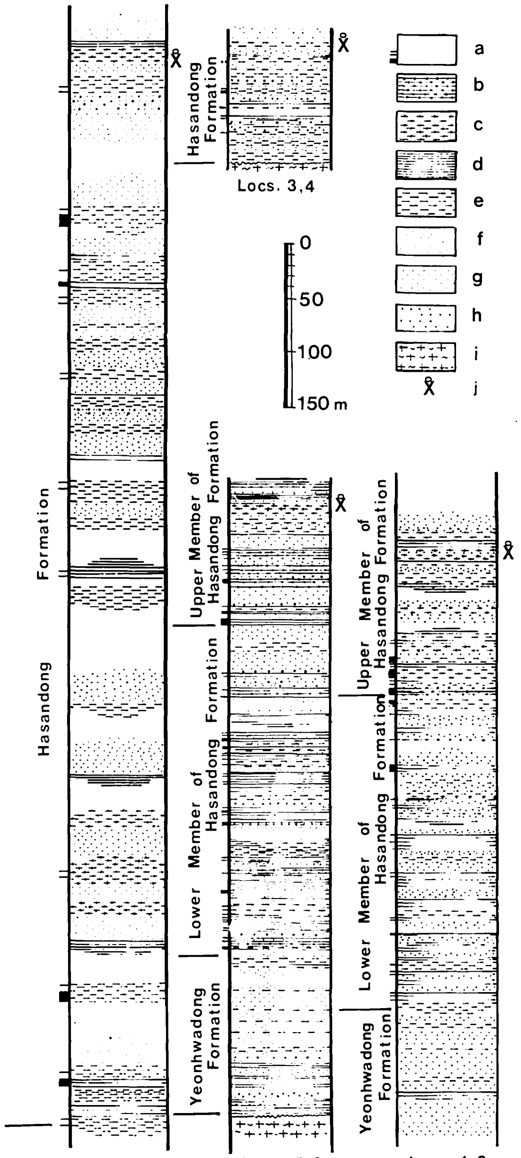


Figure 2. Stratigraphic columns. a. reddish bed, b. shale, calcareous nodule bearing, c. mud- or siltstone, calcareous nodule bearing, d. shale, e. silt- or mudstone, f. fine- to medium-grained sandstone, g. coarse-grained sandstone, h. pebbly sandstone or conglomerate, i. metamorphic rock, j. fossil horizon.

Hyoryeong-myeon, Kunwi-gun, Gyeongsangbuk-do (Figure 1-A). Lithology here is siltstone and fine- to medium-grained sandstone in the upper part of the Middle Hasandong Formation. *P. naktongensis* and *Trigonioides kodairai* are assembled here in a layer about 10 cm thick, associated with *Brotiopsis* sp.

Loc. 10: At a drainage side, Naegokji, Mukeodong, Jangcheon-myeon, Seonsan-gun, Gyeongsangbuk-do (Figure 1-A). Lithology is composed of light grey siltstone and limy mudstone in the middle part of the Middle Hasandong Formation. Here, *P. naktongensis, Nagdongia soni* and *Brotiopsis* sp. have been collected.

In addition to these, at the following two localities of Japan the fossils were collected: At Rikimaru, Miyata and Kurate of northern Kyushu (lower Wakino Formation, Kwanmon Group) and at a point 500 m southeast of Tashiro, Kosa Town of central Kyushu (Mifune Group).

Systematic description

Order Unionoida Stoliczka, 1871
Superfamily Unionacea Fleming, 1828
Family Unionidae Fleming, 1828
Subfamily Unioninae Fleming, 1828
Genus *Plicatounio* Kobayashi and Suzuki, 1936

Generic diagnosis.—Unioninae with surface ornamented with four or five posterior radial plicae and crenulated pseudocardinal hinge teeth.

Included subgenera.—Plicatounio Kobayashi and Suzuki, *Kwanmonia* Ota, and *Enotrigonioides* Guo.

Remarks.—Since Kobayashi (1968) proposed the family Plicatounionidae based on *Plicatounio* without any definition, Guo (1986) and Kobayashi (1984) have followed Kobayashi's opinion. But the taxonomic characters of *Plicatounio* do not seem to deserve familial distinction from the Unionidae.

Table 1. Measurements of *Plicatounio* (*P.*) *naktongensis* Kobayashi and Suzuki (linear dimension in mm).

Specimens	L	H	D	H/L	D/L
(Loc. 6)					
KPE 1093 (BV)*	58.7+	26.7	22.3+	.45	.38
KPE 1094 (LV)*	64.6	28.6	21.4	.44	.33
KPE 1095 (RV)*	64.0	30.7+	21.9	.48	.34
KPE 1096 (LV)	23.9	11.8	7.7	.49	.32
KPE 1097 (LV)	77.6	34.3+	20.5	.44	.26
KPE 2456 (BV)	77.6	39.6	25.4	.51	.33
KPE 2457 (BV)	90.8	46.6	30.1	.51	.33
KPE 2458 (BV)	98.5	42.3	38.8	.43	.39
KPE 2502 (BV)	75.9	35.4	24.6	.47	.32
KPE 2503 (BV)	102.2+	44.2	34.0	.43	.33
KPE 2504 (RV)	75.5	32.4	20.5	.43	.27
KPE 3042 (RV)	67.7	31.8	21.8	.47	.32
KPE 3043 (LV)	42.6	19.6	15.0	.46	.35
KPE 3045 (RV)	50.3	23.7	19.3	.47	.38
(Loc. 2)					
KPE 3001 (RV)	56.1+	33.6	21.3	.60	.38−
KPE 3002 (LV)	47.9	27.0	17.1	.56	.36
KPE 3003 (LV)	56.4+	29.4	20.7	.52	.37
KPE 3005 (RV)	60.8	32.1	20.8	.53	.34
KPE 3006 (BV)	52.4	27.7	18.8	.53	.36
KPE 3007 (LV)	60.9	31.7	20.0	.52	.33
KPE 3008 (LV)	25.8+	16.6	8.9+	.64	.34
KPE 3009 (LV)	59.5	27.5+	20.7	.46	.35
KPE 3012 (LV)	59.7	30.4	20.4+	.51	.34
KPE 3013 (LV)	67.9	33.6	22.7	.49	.33
KPE 3016 (LV)	56.8	30.1	19.8	.53	.35
KPE 3017 (LV)	64.2+	32.7	20.6+	.51	.32
KPE 3018 (LV)	65.8	33.4	18.3	.51	.28
KPE 3020 (RV)	55.7	32.6	20.8	.58	.37
KPE 3022 (LV)	56.9	30.5	19.0	.54	.33
KPE 2023 (LV)	60.3	32.7	21.8	.54	.36
KPE 3024 (RV)	65.1	35.2	20.8	.54	.32
KPE 3026 (RV)	63.4+	34.2	18.3	.54	.29
KPE 3028 (LV)	69.6	35.2	23.8	.51	.34
KPE 3033 (RV)	72.9	35.7	23.7	.49	.33
KPE 3034 (RV)	73.6	34.5	19.8+	.47	.27+
(Loc. 7)					
KPE 2111 (RV)	86.8	42.5	29.5	.49	.34
KPE 2112 (BV)	102.8	47.2	33.5	.46	.33
KPE 2114 (BV)	74.6	35.0	25.8	.47	.35
KPE 2115 (RV)	92.2	42.3	30.2	.46	.33
KPE 2116 (BV)	79.4	33.9+	32.3	.43	.41
KPE 2117 (BV)	74.5+	36.3	22.6	.49	.30
KPE 2146 (BV)	78.9+	35.5+	29.3	.45	.37
KPE 2147 (LV)	81.6	42.8	27.5	.52	.34
KPE 2148 (RV)	77.1+	37.8	24.6	.49	.32
KPE 2149 (BV)	86.9	41.2	24.5	.47	.28
KPE 2150 (RV)	82.2	40.5+	25.0	.49	.30
KPE 2501 (BV)	86.2	42.4	27.7	.49	.32
KPE 2359 (BV)	42.9	21.3	14.4	.50	.36
(Loc. 9)					
KPE 2380 (RV)	64.7	30.1	22.8	.47	.35
KPE 2381 (RV)	59.9	29.8	20.2	.50	.34
KPE 2382 (LV)	55.8+	24.9	18.5	.45	.33
KPE 2383 (RV)	70.6+	31.9	21.3	.45	.30
KPE 2389 (BV)	64.6	28.8	18.7	.45	.29
KPE 2390 (RV)	62.0	29.6	18.1	.48	.29
KPE 2392 (LV)	59.7+	28.9+	17.9	.48	.30
(Wakino)					
KPE 1071 (LV)	68.9	37.0	16.5	.54	.24
(Mifune)					
KPE 1295 (RV)	42.1	24.7	12.6	.59	.30
KPE 1297 (LV)	23.5	13.7	7.5	.58	.32

(BV)* : conjoined valve, (LV)* : left valve, (RV)* : right valve

Subgenus *Plicatounio* Kobayashi and Suzuki, 1936

Type-species.—*Plicatounio naktongensis* Kobayashi and Suzuki, 1936.

Subgeneric diagnosis.—*Plicatounio* with elongated elliptical shell and surface ornamented occasionally with fine radial ribs on the whole disc besides the four or five posterior plicae.

Included species.—*Plicatounio naktongensis* Kobayashi and Suzuki, *P. suzukii* Hoffet, *P. maximus* Hoffet, *P. manchuricus* Yabe and Hayashi, *P. kobayashii* Maeda, *P. tetoriensis* Maeda, *P. flattersensis* Mongin, *P. klaudziensis* Martinson, *P. namphungensis* Kobayashi, *P. equiplicatus* Gu and Yu, *P. zhejiangensis* Gu and Ma, *P. fujianensis* Gu and Ma, *P. latiplicatus* Gu and Yu, *P. subrhombicus* Gu and Yu, and the following two new species described below.

Plicatounio (*Plicatounio*) *naktongensis* Kobayashi and Suzuki, 1936

Figures 3-1A—16; 4-1A—7

1936. *Plicatounio naktongensis* Kobayashi and Suzuki, p. 252, pl. 28, figs. 1-4, 6-8.
1943. *Plicatounio naktongensis* Kobayashi and Suzuki; Suzuki, p. 210-211, pl. 16, figs. 14-15.
1956. *Plicatounio naktongensis* Kobayashi and Suzuki; Kobayashi, p. 80, pl. 5, fig. 3.
1959. *Plicatounio naktongensis* Kobayashi and Suzuki; Ota, p. 15, pl. 3, figs. 4-8.
1960. *Plicatounio* aff. *naktongensis naktongensis* Kobayashi and Suzuki; Hase, p. 313, pl. 39, fig. 1.
1963. *Plicatounio* (s.s.) *naktongensis* Kobayashi and Suzuki; Ota, p. 507, text-fig. 1.

Material.—The specimens at hand were collected from the following six localities; Loc. 1 (KPE 1191-4, 1726-7); Loc. 2 (KPE 3001-37); Loc. 6 (KPE 1093-1100, 3041-6); Loc. 7 (KPE 2111-50, 2456-65, 2501-11, 2527); Loc. 9 (KPE 2379-87, 2389-92, 2559); Loc. 10 (KPE 2446) (see the explanation of localities in the above 'Material and Local-

Table 2. Arithmetic means of the simple ratios H/L and D/L.

Loc.	ratio	N	$\bar{x} \pm t0.05\sigma\bar{x}$	s	V	$\sigma\bar{x}$	r	O.R.
2	H/L	21	.530±.019	.041	7.736	.009	.921	.46-.64
2	D/L	21	.336±.013	.029	8.631	.006	.835	.27-.38
6	H/L	14	.463±.015	.028	6.048	.007	.973	.51-.43
6	D/L	14	.332±.022	.037	11.145	.010	.904	.26-.39
7	H/L	13	.478±.015	.024	5.026	.007	.951	.43-.52
7	D/L	13	.335±.020	.034	10.149	.009	.857	.28-.41
9	H/L	7	.469±.019	.020	4.264	.008	.839	.45-.50
9	D/L	7	.314±.022	.025	7.962	.009	.574	.29-.35

N ; number of measurements, $\bar{x} \pm t0.05\sigma\bar{x}$; arithmetic mean with 95% confidence level, s ; standard deviation of the mean, V ; Pearson's coefficient of variation, $\sigma\bar{x}$; standard error of the mean, r ; correlation coefficient, O.R. ; observed range.

ities"). The above six localities of Korea fall under the Hasandong Formation, Gyeongsang Group. In Japan, the specimens referred to the present species were collected from the locality at Rikimaru, Fukuoka Prefecture (KPE 1069-74, 1080-9, 2569-2571) (lower Wakino Formation, Kwanmon Group) and from the locality near Tashiro, Kumamoto Prefecture (KPE 1295-9) (Mifune Group).

Measurements (in mm).—In regard to shell dimensions, length (L) is the greatest linear dimension measured roughly parallel to ventral line, height (H) is the greatest dimension measured normally to L and umbonal distance (D) the linear dimension between anterior end and umbo. From these data, the simple ratios, H/L and D/L and their 95% ranges are calculated and shown in Table 2.

Description.—Shell medium in size (about 50-90 mm in length), occasionally larger than 90 mm in length, equivalve and elongated elliptical, about twice as long as high (H/L ; 0.50), inequilateral ; umbo blunt, slightly prosogyrous, situated at about one third from the anterior end (D/L ; 0.33) ; anterior margin well rounded ; postero-dorsal margin long, gently curved ; posterior margin somewhat produced postero-ventrally ; ventral margin broadly arcuate. Escutcheon and lunule narrow and elongated ; ligament external and transversely and finely crenulated (Figures 3-4—5, 7).

Surface ornamented with four or five strong plicae running obliquely on the posterior part and on the main part of the disc in front of these plicae, with fine radial ribs counted more than 20, which become gradually finer and indistinct toward the anterior margin. The whole surface covered also with fine numerous growth-lines of irregular interval and prominence.

Hinge plate moderate in breadth, provided with pseudocardinal and postero-lateral teeth ; the pseudocardinal two on each valve, the postero-lateral ones one or two on the right valve, two on the left valve, forming the following dental formula :

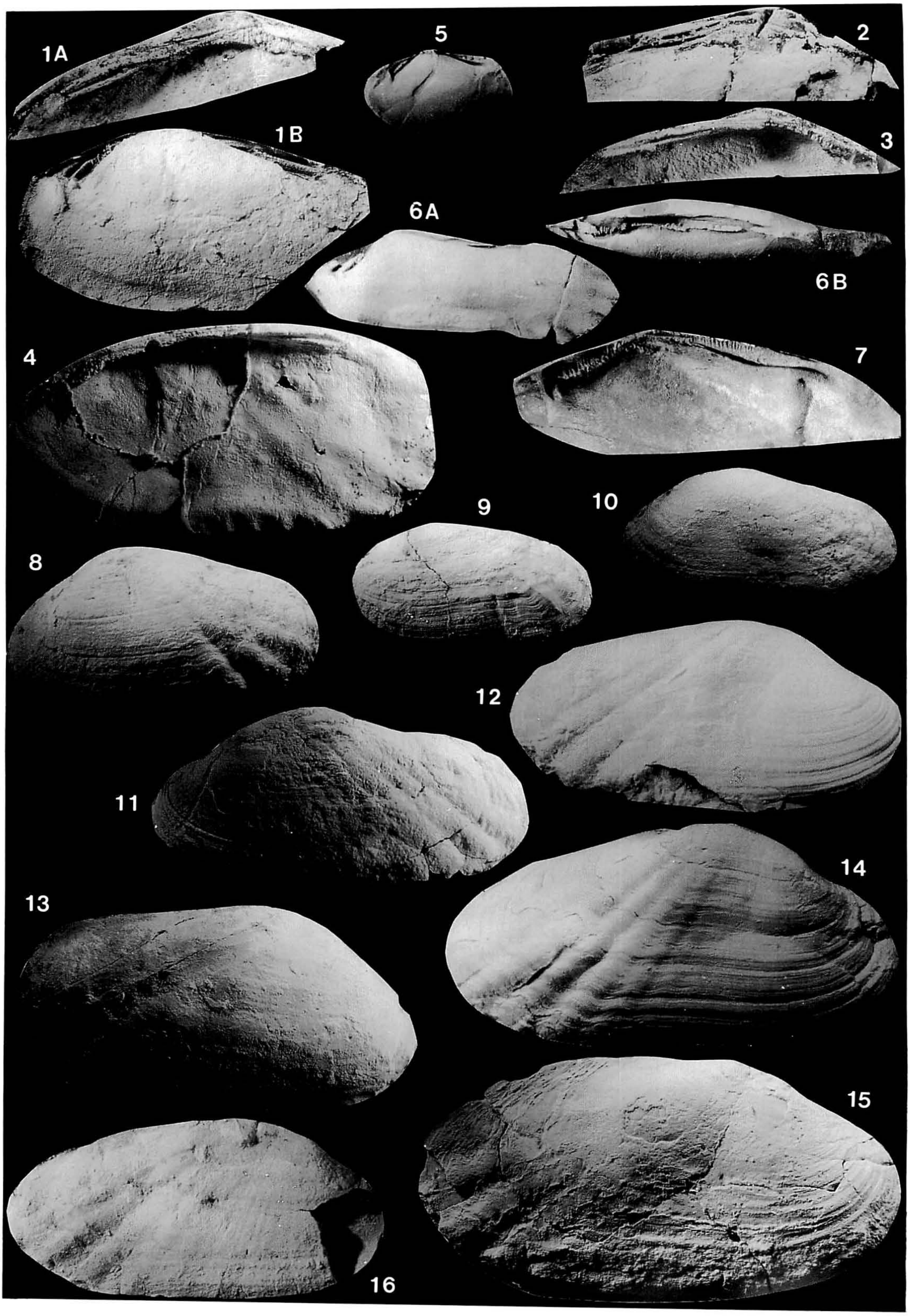
$$\frac{5 \quad 3 \qquad (PI) \qquad\qquad PIII \qquad\qquad}{\quad 4 \quad 2 \qquad\qquad PII \qquad\qquad PIV}$$

where 5 : narrow and low, with very fine transverse crenulations on the ventral (lower) side only,

3 : rather heavy and prominent, with very fine transverse crenulations on both sides, subparallel to antero-dorsal margin,

PI : low and elongated, appearing only on posterior half under PIII, occasionally indistinct,

PIII : elongated and prominent, with very


1A
5
2
1B
3
6A
6B
4
7
9
10
8
12
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fine striations on the crest, parallel to the postero-dorsal margin,

4: prominent and rather heavy, with very fine transverse crenulations on both sides, parallel to the antero-dorsal margin,

2: low and narrow, with very fine transverse crenulations on the dorsal (upper) side only, subparallel to the antero-dorsal margin,

PII and PIV: elongated and prominent, rather lamellar but sometimes faintly crenulated in the crest, parallel to the postero-dorsal margin.

Two adductor scars subequal in size, anterior one semicircular and strongly impressed, accompanied with a minute pedal scar, posterior one trigonally ovate and larger, but not so distinct. Inner ventral crenulations dense on the anterior margin, but gradually broader in proceeding backward. Umbonal cavity moderate in depth; test moderate in thickness and inflation rather weak.

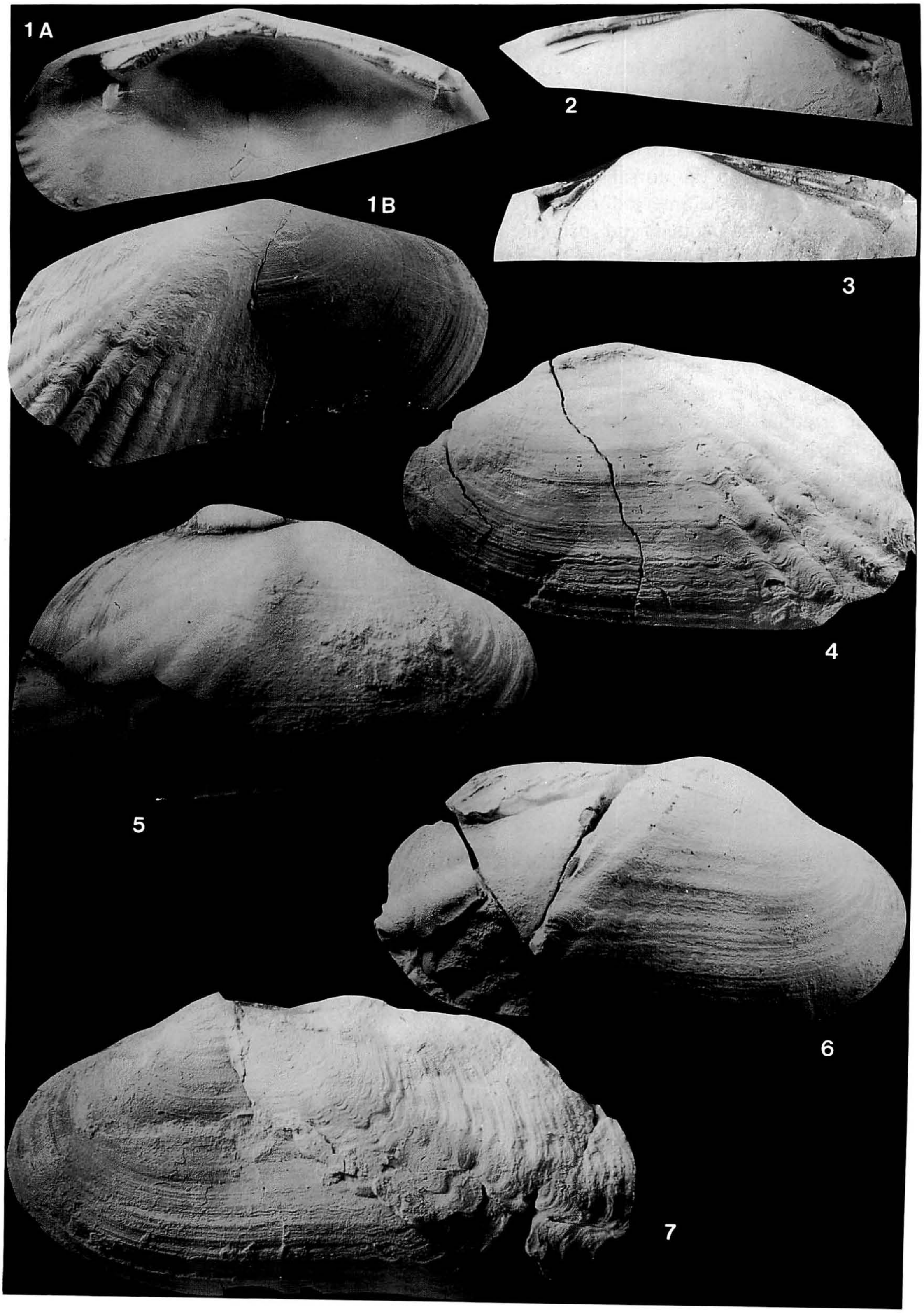
Observation.—Most of the specimens are so well preserved that the internal structures are observed on the internal mould made artificially with dilute hydrochloric acid. The internal structures are fairly stable, but on one exceptional specimen (KPE 2382, Figure 3-1), radial striations are discernible immediately below the umbo. The other characters are identical with those of other specimens. Thus, it cannot be separated from other specimens. It is, however, open to question what this exceptional character means.

Occurrence.—The present species is associated with *Trigonioides* (*T.*) *kodairai* at the type-locality (Yangpori, Loc. 1) where *Brotiopsis* spp. occurs gregariously. But the present species and *Trigonioides* (*T.*) *kodairai* are relatively rare and mostly represented by conjoined specimens. This mode of occurrence may suggest their nearly original habitats. At an island near Yangpori (Loc. 2), it is also found in a few beds with *Brotiopsis* spp. At the locality near Hanchi (Loc. 6) the present species is also rare in several fossiliferous beds containing abundant *Brotiopsis* spp. At the locality near Yusuri (Loc. 7), it is preserved *in situ* associated with *T.* (*T.*) *jaehoi*, but without *Brotiopsis* spp. At the locality near Baetae (Loc. 9), it is associated also with *T.* (*T.*) *kodairai* and *Brotiopsis* spp. forming a fossiliferous bed, but the present species is a main component and *T.* (*T.*) *kodairai* also in common, but *Brotiopsis* spp. are very rare. At the locality 10, it is associated also with *Nagdongia soni* and *Brotiopsis* sp.

The beds containing the present species are generally light grey siltstone or dark grey or greenish grey shale. It is notable that the present species is found so far confined to the Hasandong Formation, Gyeongsang Group in Korea.

At Rikimaru, Kyushu, Japan, the present species is associated with *Wakinoa wakinoensis* Ohta, and at the locality near Tashiro, Kumamoto, Japan, it occurs with *Trigoni-*

← **Figures 3-1A—16.** *Plicatounio* (*Plicatounio*) *naktongensis* Kobayashi and Suzuki. 1. left valve (KPE 2382), **1A**; rubber cast, showing the postero-lateral hinge teeth striated finely, and radial striations immediately below the umbo, **1B**; internal mould, showing the internal structure (Loc. 9). **2.** internal mould of the right valve (KPE 1726), showing the weakly striated crest of the postero-lateral hinge teeth (Loc. 1). **3.** rubber cast of the left valve (KPE 2392), showing the lamellar postero-lateral hinge teeth (Loc. 9). **4.** rubber cast of the right valve (KPE 2383), showing the crenulated hinge teeth and the other internal structure (Loc. 9). **5.** internal mould of the left valve (KPE 1297), showing the crenulated postero-lateral hinge teeth (Loc.; type-locality of *Trigonioides* (*Kumamotoa*) *mifunensis*, see Tamura 1970). **6.** internal mould of the conjoined valve (KPE 1080), **6A**; dorsal view, showing the crenulated postero-lateral hinge teeth (Loc.; Rikimaru, Miyataku, Kyushu, Japan, see Ota, 1959), **6B**; side view. **7.** internal mould of the left valve (KPE 1071), showing the crenulated postero-lateral hinge teeth (Loc.; *ditto*). **8.** left valve (KPE 3002) (Loc. 2). **9.** left valve (KPE2285) (Loc. 9). **10.** left valve (KPE 3043) (Loc. 6). **11.** left valve (KPE 1094) (Loc. 6). **12.** right valve (KPE 2389) (Loc. 9). **13.** right valve (KPE 3026) (Loc. 2). **14.** right valve (KPE 3033) (Loc. 2). **15.** right valve (KPE 2148) (Loc. 7). **16.** right valve (KPE 2390) (Loc. 9). All figures are approximately of natural size.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oides (*Kumamotoa*) *mifunensis* Tamura.

Discussion.—Suzuki (1943) proposed *P. naktongensis multiplicatus* as a subspecies of the present species by the presence of the radial ribs in front of the strong posterior plicae. To my regret, I sought in vain any samples of this subspecies at the type-locality (Okbongdong, Jinjushi, Gyeongsangnam-do, Korea). However, the specimens similar to *P. n. multiplicatus* have frequently been found in association with the present species (Locs. 2, 6 and 7). Such a sympatric occurrence of two "subspecies" is unlikely; the difference is regarded as due to individual variation.

The postero-lateral hinge teeth have been described as lamellar by previous authors (Kobayashi and Suzuki, 1936; Ota, 1959 and 1963; Martinson, 1965; Gu and Ma, 1976). But Tamura (1982) observed crenulations on the postero-lateral teeth of a specimen collected at the type-locality (Yangpori) and insisted that Ohta's *P.* (*P.*) *naktongensis* from Rikimaru should be separated from the present species. However, in my collection from Rikimaru, I can also observe crenulations on the postero-lateral teeth (KPE 1080, 1071, Figures 3-6—7). Therefore, in my opinion, the different views are due to insufficient and poorly preserved material.

Without observation, I cannot give any comment on the specimens described under the name of *P. naktongensis* from China and U.S.S.R.

Plicatounio (*Plicatounio*) *okjuni*, sp. nov.

Figures 5-1A—2B

Etymology.—This species is dedicated to Emeritus Professer Okjun Kim of Yonsei University who has contributed much to tectonics of the Korean Peninsula.

Material.—Holotype (KPE 2261) and ten paratypes (KPE 2252, 2254, 2260, 2264, 2266, 2270, 2274, 2304, 2305, 2361,) collected from Loc. 8.

Measurements.—Carried out in the same way as in *P.* (*P.*) *naktongensis*.

Diagnosis.—Test thick for the genus and the posterior plicae low and wide, not so distinct.

Description.—Shell fairly large (about 80–90 mm in length), equivalve, inequilateral, generally elongated suboval or subquadrate in outline; the ratio of H/L about 0.52; anterior margin well rounded; postero-dorsal one long and rather straight; and posterior margin somewhat obtusely angulated at the postero-ventral corner; ventral margin broadly arcuate; umbo robust, fairly prominent, slightly prosogyrous, situated at about two fifths of shell length from the anterior extremity (D/L; 0.36). Test fairly thick. Surface covered with fine concentric growth-lines and ornamented with low but wide radial plicae on the posterior half, which become gradually indistinct towards the anterior part. The internal characters are unknown.

Observation.—The holotype (KPE 2261, Figure 5-1) is a conjoined specimen, 88.0 mm in length and 46.8 mm in height. The fossil

← **Figures 4-1A—7.** *Plicatounio* (*P.*) *naktongensis* Kobayashi and Suzuki **1.** right valve (KPE 2113): **1A.** internal view, showing the crenulated hinge teeth, **1B.** side view, showing the weak radial ribs on the antero-central part besides the strong posterior plicae (Loc. 7). **2.** internal mould of the right valve (KPE 2560), showing the crenulated postero-lateral hinge teeth (Loc. 7). **3.** internal mould of the left valve (KPE 2508), showing the crenulated postero-lateral hinge teeth (Loc. 7). **4.** left valve (KPE 2147), showing the weak wave-patterns of the growth lines on the antero-central part (Loc. 7). **5.** conjoided valve (KPE) right side view, showing the ligament on the postero-dorsal side (Loc. 7). **6.** right valve (KPE 2134), showing the weak radial ribs on the antero-central part (Loc. 7). **7.** conjoined valve (KPE 2112), left side view, showing the ligament on the postero-dorsal side and the weak wave-patterns of growth lines on the antero-central part (Loc. 7). All figures are approximately of natural size.

specimens now at my disposal are varied in outline, but this is evidently due to secondary deformation. One of the paratypes (KPE 2266) is fairly elongated, but this is due to vertical compression, as can be read from the extraordinarily large inflation. And another one (KPE 2264, Figure 5-2) is somewhat subquadrate in form, but this also is due to diagonal compression. The relatively well preserved specimens among the collection are conjoined and others are fragmentary, and so the internal structures can not be observed.

Occurrence.—The fossils are not gregarious, but are scattered. Many specimens are conjoined as pointed above. The occurrence seems to reflect preservation *in situ*. The present species is associated with *Wakinoa* cf. *tamurai, P.* (*P.*) sp. cf. *P.* (*P.*) *yooni* described below, very immature specimens of *Nagdongia soni* and *Viviparus* ? sp.

Comparison.—The present species is very similar to *P.* (*P.*) *naktongensis* in surface ornamentation. The former is ornamented with constantly low but wide plicae on the posterior half, within which the plicae do not show difference in strength and width, but the latter is ornamented with strong and wide plicae on the posterior portion and numerous finer radial ribs on the main part of the disc. In addition, the ratio of H/L is relatively larger in the present species that is larger than 0.55 in the present species, while less than 0.50 in *P. naktongensis*. The radial ribs of the present species are somewhat similar to those of *P.* (*P.*) *subrhombicus* Gu and Yu, but they are distinguished from each other in the thickness of the test. The test of the present species is distinctly thicker than that of any other described species of *Plicatounio*.

Plicatounio (*Plicatounio*) *yooni*, sp. nov.

Figures 6-1—7

Etymology.—This species is dedicated to Dr. Sun Yoon of Busan National University, who, one of my colleagues, specializes in Tertiary molluscs.

Material.—Holotype (KPE 2601) and fifty two paratypes (KPE 1053-9, 1090-2, 2540, 2561-5, 2602-37), collected from the following three localities; Loc. 3 (type-locality) (KPE 2601-20, 2622-37) and Loc. 4 (KPE 2621) and Loc. 5 (KPE 1053-9, 1090-2, 2540, 2561-5).

Measurements (in mm).—Carried out in the same way as above.

Diagnosis.—Surface ornamented with 4 or 5 strong posterior plicae and the distinct radial ribs counted more than 20 in front of the strong posterior plicae.

Description.—Shell fairly large in size

Table 3. Measurements of *Plicatounio* (*P.*) *okjuni*, n. sp. (linear dimension in mm).

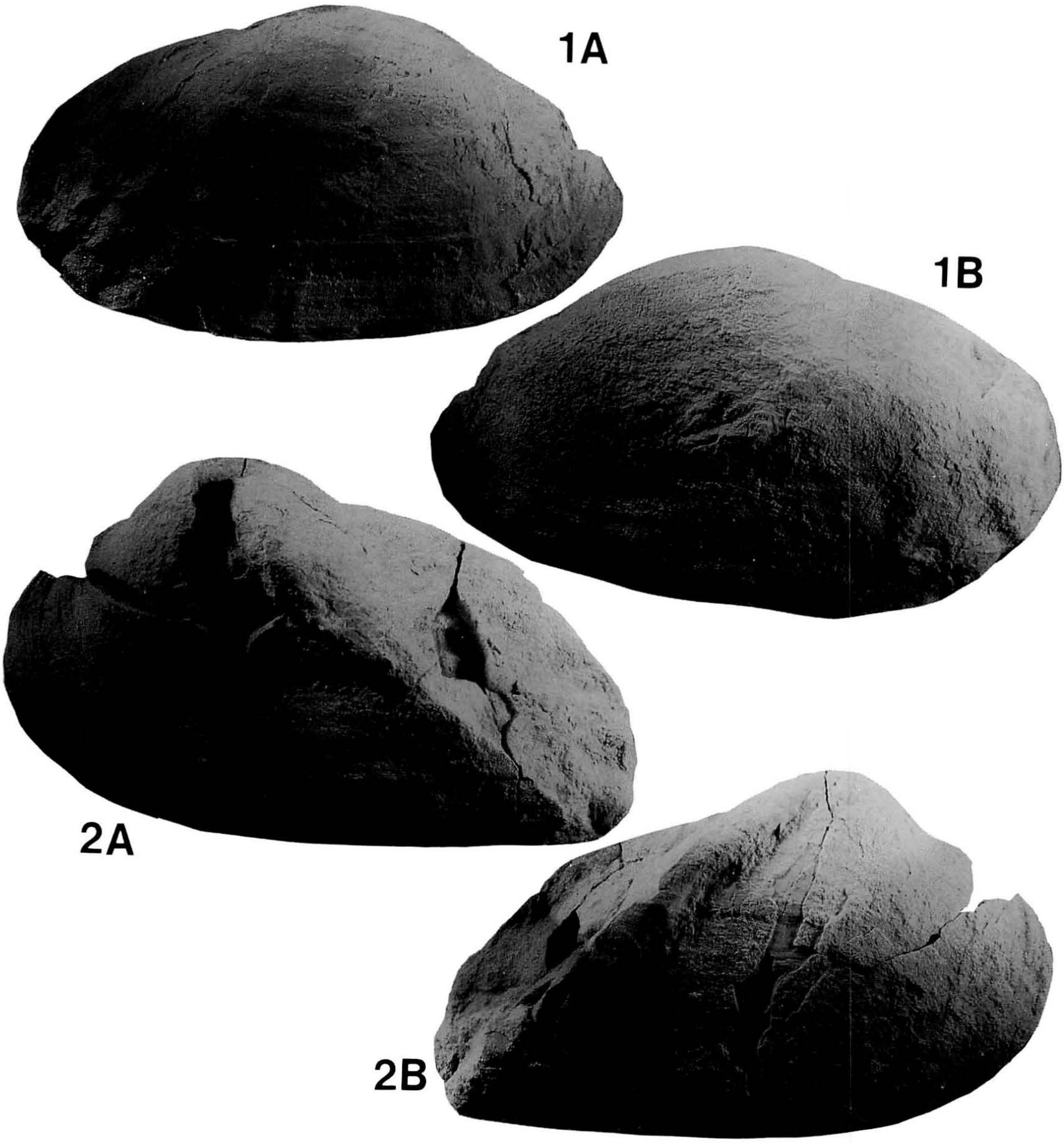
Specimes		L	H	D	H/L	D/L	Specimens		L	H	D	H/L	D/L
(Loc. 8)							KPE 2261*	(BV)	88.0	46.8	32.7	.53	.37
KPE 2252	(BV)	70.3+	36.0	31.7	.51	.45−	KPE 2264	(BV)	88.9	52.6	25.3	.59	.28
KPE 2254	(BV)	68.1+	37.6	25.9	.55	.38−	KPE 2266	(BV)	84.1+	37.2+	29.0	.44	.34

*KPE 2261 ; Holotype

Table 4. Arithmetic means of the simple ratios H/L and D/L.

Loc.	ratio	N	$\bar{x} \pm t0.05\sigma\bar{x}$	s	V	$\sigma\bar{x}$	r	O.R.
8	H/L	5	.524±.069	.056	10.687	.025	.769	.44-.59
8	D/L	5	.364±.078	.062	17.033	.028	.053	.28-.45

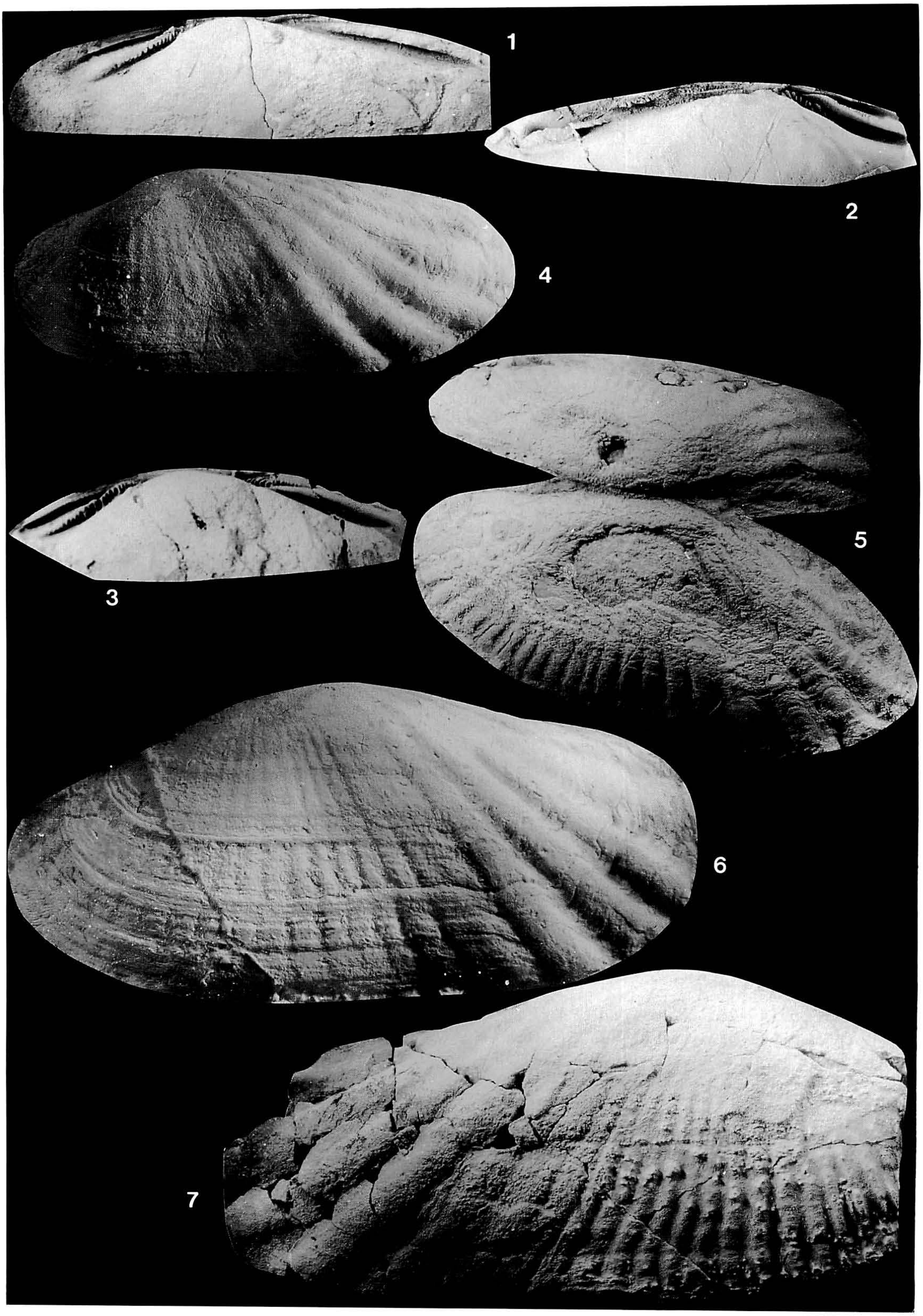
See page 83 (Table 2) for explanation of statistical parameters.



Figures 5-1A—2B. *Plicatounio* (*P.*) *okjuni*, n. sp. **1.** conjoined valve (KPE 2261), **1A ;** right side view, **1B ;** left side view (Loc. 8). **2.** conjoined valve (KPE 2264), **2A ;** left side view, showing the fairly thick test, **2B ;** right side view (Loc. 8). All figures are approximately of natural size.

(about 70-100 mm in length), equivalve, inequilateral, generally elongated suboval in outline, about twice as long as high (H/L 0.47) ; anterior margin somewhat projected and well rounded ; postero-dorsal one rather straight ; posterior margin obtusely angulate with postero-dorsal margin, sloping gently down to postero-ventral corner ; ventral margin broadly arcuate. Umbo blunt and fairly prominent, slightly prosogyrous, situated at about two-fifths of shell length from the anterior extremity (D/L ; 0.37). Test moderate in thickness ; umbonal cavity fairly deep.

Surface ornamented with four or five strong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plicae running from the umbo obliquely down to the posterior periphery and, on the main part of the flank in front of these plicae, with more or less narrow but distinct radial ribs. The fine radial ribs somewhat variable in width and the grooves between the ribs fairly narrow and counted slightly more than 20 in large specimens.

Table 5. Measurements of *Plicatounio* (*P.*) *yooni*, n. sp. (linear dimension in mm).

Specimens	L	H	D	H/L	D/L
(Loc. 3)					
KPE 2601* (BV)	84.8	34.7	28.5	.41	.34
KPE 2602 (LV)	112.3	49.8	43.2	.44	.38
KPE 2603 (LV)	80.0	32.1	23.4	.40	.29
KPE 2605 (LV)	95.9	39.0+	34.5	.41+	.36
KPE 2609 (RV)	98.9	38.9+	35.5+	.39+	.36
KPE 2611 (LV)	96.3	42.3	34.0	.44	.35
KPE 2615 (RV)	83.9	34.4	29.2	.41	.35
KPE 2618 (RV)	92.4	34.4	33.6	.37	.36
KPE 2620 (RV)	98.3+	44.1+	36.8	.45	.37
KPE 2625 (BV)	88.3+	41.9+	32.9	.47	.37
KPE 2628 (LV)	79.0	35.7	32.5	.45	.41
KPE 2629 (LV)	95.8	41.6	34.2	.43	.36
KPE 2631 (RV)	80.7	36.6	28.9	.45	.36
(Loc. 5)					
KPE 1053 (BV)	89.1+	46.6	38.5	.52	.43
KPE 1054 (RV)	83.7	38.6	32.9	.46	.39
KPE 1090 (LV)	59.4	30.4	25.2	.51	.42
KPE 1091 (RV)	53.4+	34.2	20.3	.64	.38

(KPE 2601)* ; Holotype

Hinge plate narrow in breadth, provided with the pseudocardinal and the postero-lateral teeth, the pseudocardinal ones two on each valve, the postero-lateral ones one on right valve, two on left valve, forming the following dental formula :

$$\frac{5 \quad 3 \qquad \mathrm{PIII} \qquad\quad}{\quad 4 \quad 2 \qquad \mathrm{PII} \qquad \mathrm{PIV}}$$

The hinge teeth, pseudocardinal and postero-lateral ones, finely crenulated or striated obliquely on one or both sides.

Anterior adductor scar strongly impressed, accompanied with a small but distinct pedal scar and posterior one somewhat larger but not so distinct. The ventral crenulation along the inner margin, fairly distinct on the main part, but weakened and becomes finer towards the anterior margin. Pallial line simple but hardly perceptible on the posterior portion.

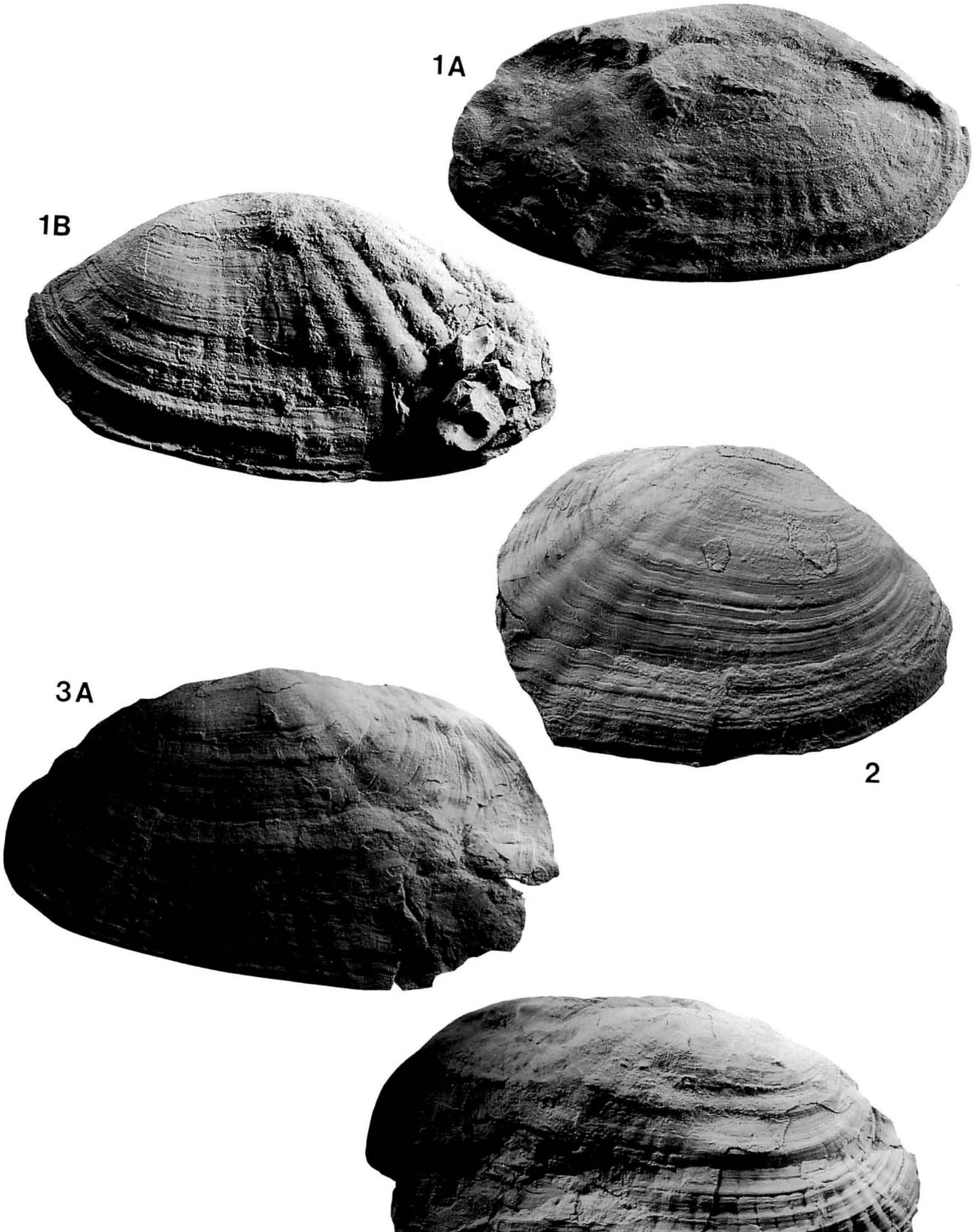
Observation.—The holotype (KPE 2601, Figure 6-5) has conjoined valves, 84.8 mm in length, 34.7 mm in height. The internal structures can be observed on the artificial mould made with dilute hydrochloric acid. The number of radial ribs is constant and different from that of other species. The outline seemingly varies in the specimens at

Table 6. Arithmetic means of the simple ratios H/L and D/L.

Loc.	ratio	N	$\bar{x} \pm t0.05\sigma\bar{x}$	s	V	$\sigma\bar{x}$	r	O.R.
3	H/L	13	.425+.017	.029	6.824	.008	.843	.37-.47
3	D/L	13	.358+.015	.027	7.542	.007	.895	.29-.41
5	H/L	4	.533+.121	.076	14.259	.038	.867	.46-.64
5	D/L	4	.405+.038	.024	5.926	.012	.980	.38-.43

See page 83 (Table 2) for explanation of statistical parameters.

← **Figures 6-1—7.** *Plicatounio* (*P.*) *yooni*, n. sp. **1.** internal mould of the left valve (KPE 2605), showing the crenulated pseudocardinal and the postero-lateral hinge teeth (Loc. 3). **2.** internal mould of the right valve (KPE 2604), showing the crenulated pseudocardinal and the postero-lateral hinge teeth (Loc. 3). **3.** internal mould of the left valve (KPE 2633). showing the crenulated hinge teeth (Loc. 3). **4.** rubber cast of the left valve (KPE 2603) (Loc. 3). **5.** rubber cast of the left valve (KPE 2601) (Loc. 3). **6.** rubber cast of the left valve (KPE 2602) (Loc. 3). **7.** right valve (KPE 2621) (Loc. 4). All figures are approximately of natural size.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hand, but this may be partly due to secondary deformation.

Occurrence.—The specimens at hand were collected at three localities. At the locality near Impo (Loc. 3), the present species occurs on the same bedding plane with *Wakinoa* sp., *Pseudohyria* sp., and *Brotiopsis* sp. At the locality 4 only one specimen (KPE 2621) was collected. The fossils of the present species are frequently conjoined at. Loc. 3. At the locality near Sumoondong (Loc. 5), it is associated with *Trigonioides* (*T.*) *kodairai*, and *Nagdongia soni*. The fossils occur not gregariously but scattered, and do not show any severe damage. This suggests that the fossils have been preserved *in situ* or at least near the original habitat.

Comparison.—The radial ribs of this species so closely resemble those of *P.* (*P.*) *naktongensis multiplicatus* that I (Yang, 1974, 1975) reported tentatively this species as *P.* (*P.*) *multiplicatus* (?). The fine radial ribs in front of the several strong plicae, however, are more distinct, the umbo is blunter and the anterior margin is more projected in the present species than in *P.* (*P.*) *multiplicatus*.

The present species is also closely allied to *P.* (*P.*) *kobayashii* and *P.* (*P.*) *tetoriensis* from Japan, but according to Maeda's description (1962), the latter two species have the umbo placed more anteriorly, at about one-fourth of the shell length from the anterior extremity, while the present species has the umbo situated at about two-fifths.

The present species is similar to *P. maximus* Hoffet, 1937 and *P. suzukii* Hoffet, 1937 in the radial ribs and outline, but the former differs from the latter two species in the number of ribs, that is, Hoffet's species are ornamented with denser radial ribs in front of the strong posterior plicae, more than 28 in number, while in the present species there are about 20 radial ribs.

Plicatounio (*P.*) sp. cf. *P.* (*P.*) *yooni*, n. sp.

Figures 7-1A—3B

Material.—Seventy one specimens collected from Loc. 8 (KPE 2253, 2255-8, 2260, 2262, 2265, 2267-9, 2271-3, 2275, 2277-2303, 2305-10, 2357-60, 2362-3, 2412-28).

Measurements (in mm).—Carried out in the same way as above.

Descriptive remarks.—The shell is generally the same as *P.* (*P.*) *naktongensis* in shape and size. The radial ribs in front of the posterior plicae are somewhat more distinct than those of the type-species but less than those of *P.* (*P.*) *yooni*, frequently becoming indistinct and effaced. If comapred with *P.* (*P.*) *okjuni* from the same locality, this species is characterized by the thinner test and different surface ornamentation.

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← **Figures 7-1A—3B.** *Plicatounio* (*P.*) sp. cf. *P.* (*P.*) *yooni*, n. sp. **1.** conjoined valve (KPE 2299), **1A**; right side view, **1B**; left side view (Loc. 8). **2.** right valve (KPE 2263), postero-ventral part broken out (Loc. 8). **3.** conjoined valve (KPE 2255), **1A**; left side view, **3B**; right side wiew (Loc. 8). All figures are approximately of natural size.

Table 7. Meaurements of *Plicatounio* (*P*). sp. cf. *P.* (*P.*) *yooni*, n. sp. (linear dimension in mm).

Specimens		L	H	D	H/L	D/L	Specimens		L	H	D	H/L	D/L
(Loc. 8)													
KPE 2251	(BV)	69.7	42.5	22.1	.61	.32	KPE 2302	(BV)	85.5+	49.3	29.6	.58	.35
KPE 2253	(RV)	71.6+	32.5+	29.3	.45	.41	KPE 2310	(BV)	67.5	37.4	24.4	.55	.36
KPE 2260	(BV)	87.4+	39.0	25.9	.45	.30	KPE 2357	(BV)	71.1	34.5	25.3	.49	.36
KPE 2265	(BV)	80.3	42.9	27.7	.53	.34	KPE 2360	(LV)	74.8	38.3	25.6	.51	.34
KPE 2267	(RV)	76.1+	44.7	25.3	.59	.33	KPE 2412	(RV)	79.5+	44.3	30.5	.56	.38
KPE 2281	(RV)	77.1+	40.7	24.1	.53	.31	KPE 2420	(LV)	35.3	20.1	10.0	.57	.28
KPE 2286	(RV)	73.9+	39.7	24.0	.54	.32	KPE 2427	(LV)	40.6	19.7	13.0	.49	.32

Table 8. Arithmetic means of the simple ratios H/L and D/L.

Loc.	ratio	N	$\bar{x} \pm t0.05\sigma\bar{x}$	s	V	$\sigma\bar{x}$	r	O.H.
8	H/L	14	.532±.028	.049	9.211	.013	.905	.45-.61
8	D/L	14	.337±.022	.036	10.682	.010	.922	.28-.41

See page 83 (Table 2) for explanation of statistical parameters.

n. 1, p. 35-43, pl. 3.

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Bulguksa 佛国寺, Bulnodong 不老洞, Dongmyeong 東明, Fukuoka 福岡, Golyak-myeon 骨若面, Gyeongsangbuk-do 慶尚北道, Gyeogsangnam-do 慶尚南道, Hadong-gun 河東郡, Hasandong 霞山洞, Hwanggeumri 黄金里, Hyoryeong-myeon 孝令面, Impo 林浦, Jangcheon-myeon 長川面, Jeolanam-do 全羅南道, Jingyo-myeon 辰橋面, Jinju (shi) 晋州(市), Jinyang-gun 晋陽郡, Keumnam-myeon 金南面, Kumamoto 熊本, Kunwi-gun 軍威郡, Kwangyang-gun 光陽郡, Mifune 御船, Mukeodong 黙語洞, Nadong-myeon 奈洞面, Naegokdong 内谷洞, Naegokji 内谷池, Naeidong 内梨洞, Okbongdong 玉峰洞, Seonsan-gun 善山郡, Sumoondong 水門洞, Wakino 脇野, Yangpori 良浦里, Yeonhwadong 蓮花洞, Yusuri 柳樹里

韓国白亜系産の非海生二枚貝 *Plicatounio* 属について：*Plicatounio* の模式種である *Plicatounio* (*Plicatounio*) *naktongensis* を模式地を含む 10 地点から採集した。これらはすべて韓国の Gyeongsang Group の Hasondong Formation に含まれる。さらに日本の御船層群ならびに脇野層群の 2 地点から本種を採集した。本論文では鉸歯構造 (hinge structure) に注目して模式種を検討した。後側歯 (postero-lateral hinge teeth) にみられる鋸歯状彫刻 (crenuation) は初生的な構造で，その有無は化石の保存状態に関係するものである。本研究で 2 新種 *P*. (*P*.) *okujuni* と *P*. (*P*.) *yooni* を提唱した。 梁 承栄

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878. UPPER CRETACEOUS ELASMOSAURID (REPTILIA, PLESIOSAURIA) FROM HOBETSU, HOKKAIDO, NORTHERN JAPAN*

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Abstract. An elasmosaurian fossil is described from the Upper Yezo Group exposed along the Sanushube River, Hobetsu-cho, Hokkaido, northern Japan. Other fossils associated with the elasmosaurian specimen indicate an early Campanian age (Late Cretaceous). The specimen is represented by a partial skeleton of the trunk and parts of limb bones. The specimen exhibits a characteristic morphology of the family Elasmosauridae (Reptilia, Plesiosauria, Plesiosauroidea), but its generic and specific positions are indeterminable. The distribution pattern of the known Jurassic and Cretaceous plesiosaurians suggests that the Cretaceous Plesiosauria of northeastern Asia is a migrant from North America through the North Pacific region.

Key words. Reptilia, Plesiosauria, Elasmosauridae, Cretaceous, Hokkaido, Northern Japan

Introduction

The Plesiosauria represents one of the most famous fossil reptiles in the Japanese Islands. The first plesiosaurian material is the one reported as *Plesiosaurus* sp. from the Futaba Group (Upper Cretaceous), Fukushima Prefecture, Honshu, Japan (Tokunaga and Shimizu, 1926). Many plesiosaurian fossils have been discovered from the Japanese Islands during these sixty years (Obata *et al*., 1970, 1972; Suzuki, 1984), but nearly all of these specimens have not yet been described. This paper presents a result of study of a plesiosaurian fossil from Hobetsu, Hokkaio, Northern Japan.

In June 1975, Shintaro Araki of Hobetsu Town found a block of mudstone containing digit bones in the riverbed of a tributary of the Sanushube River (42°55′N, 142°8′E; Figure 1). The importance of the discovery was well understood, because these bones are referable to plesiosaurians. The Hobetsu Research Group of Plesiosaurian Excavation

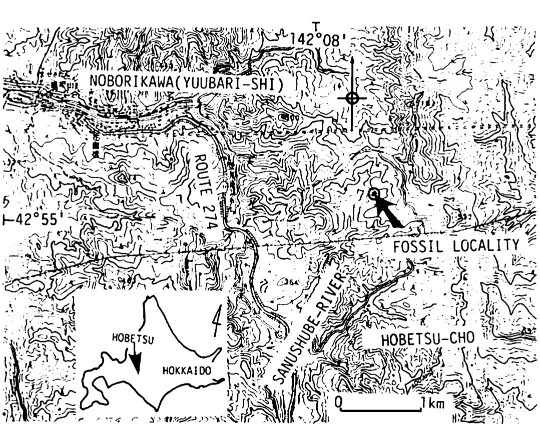

Figure 1. Locality map. Arrow shows the locality of the plesiosaurian fossil (HMG 1). (Base map after a 15-minute quadrangle topographic map "Momiziyama" of Geographical Survey Institute).

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(HRGPE) was soon organized by the joint participation of Hobetsu Town Board of Education, Mountain Club of Hobetsu, Conservation Club of Hobetsu, Historical Museum of Hokkaido, Geological Survey of Hokkaido and Hokkaido University. Nearly all of the specimens recovered were excavated by HRGPE from 4th to 8th of July, 1977 and contained of about ninety calcareous mudstone blocks (Nakaya, 1982). The plesiosaurian specimen, now being stored in Hobetsu Museum with the registration number HMG 1, was prepared by Tetsu Miyakoda of Hobetsucho Kyodo-Shiryou-Kan (later named Hobetsu Museum) from May 1978 to December 1981.

This plesiosaurian fossil was reconstructed by the present author in December, 1982 (Nakaya, 1984) (Figure 14-3). A part of this study was presented at the 88th and 89th Annual Meetings of Geological Society of Japan.

Geologic setting and occurrence

The Upper Yezo Group is exposed in the Hobetsu area (Otatsume, 1941 ; Matsumoto *et al*., 1979, Takahashi and Wada, 1985). A one meter thick layer of weathered mudstone of the Upper Yezo Group has yielded many calcareous nodules including various kinds of fossils. The calcareous nodules are distributed sporadically for a distance of about 20 meters along the Sanushube River. The plesiosaurian fossil was found both in mudstone and calcareous nodules.

The mode of occurrence of the plesiosaurian remains is briefly described as follows: Some articulated digits lie on top of rib bones. Some bones of the pelvic girdle were found lying on the top of the vertebral column and rib bones. Articulated cervical vertebral column turn round on the sagittal axis of rotation. Gastroliths are also found in these nodules.

It is inferred that the plesiosaurian body was not buried as a whole at the time of death, because the skull, neck part and tail were separated from the trunk and they are missing. Various body parts had been moved around from their original position, so that some parts of this specimen became piled up with each other. The specimen was later buried in sediments (Nakaya, 1985).

The following fossils occur in association with the plesiosaurian remains.

Elasmobranchii (Kuga, 1984) *Notorynchus* ? sp. ; Cephalopoda (Takahashi and Wada, 1985, Kito *et al*., 1986) *Neophylloceras subramosum* Spath, *Damesites* sp., *Gaudryceras tenuiliratum* Yabe, *Tetragonites* sp., *Eupachydiscus* sp. and *Polyptychoceras* sp. ; Radiolaria (Kito *et al*., 1986) *Acanthocircus parvulus* var. *latelarispinosus* (Campbell and Clark), *Patellula verteroensis* (Pessagno), *Kuppelella* sp., *Septinastrum* ? sp. and so on ; Planktonic foraminifera (Kito *et al*., 1986) *Silicosigmoilina futabaensis* Asano.

Inoceramus naumanni Yokoyama, which indicates a late Coniasian to early Campanian age, has been reported from a site near the plesiosaurian locality. Furthermore, radiolarians and planktonic foraminifers from the nodules which contained the plesiosaurian remains indicate a Campanian. Planktonic foraminifers *Globotruncana arca* (Cushman) and others which indicate an early Campanian to early Maastrichtian age, have been reported from an outcrop near the plesiosaurian locality. Therefore, the age of the plesiosaurian fossil seems to be an early Campanian from these macrofossil and microfossil evidence (Kito *et al*., 1986).

Preservation of materials

The vertebral column, consisting of posterior cervicals, pectorals, dorsals and sacrals, is found disjointedly. The dorsal ribs, ventral ribs (gastralia), parts of pectoral and pelvic girdles, forelimbs and hindlimbs are also present.

The vertebral centrum is very well preserved, but spinous processes and transverse processes are sometimes lacking due to a poor state of preservation. Almost all the costal fossa are evident, so the vertebrae can be identified by their positions. Some posterior cervical ribs and pectoral ribs are complete but almost all the dorsal ribs are incomplete. The gastralia (ventral ribs) are fragmented. The scapula, coracoid, clavicle and interclavicle are incomplete or fragmentary. The acetabular part of ischium and pubis is preserved. The ilium is fragmented.

In the forelimb, both humeri are damaged ; radius, ulna and carpal bones are preserved, but some carpal elements are lost. In the hindlimb, the shape of femur is similar to humerus, the tibia, fibula and tarsal bones are complete, the metatarsal bones are complete except for the first metatarsal. One fourth of the whole phalanges is preserved. Ten gastroliths (stomach stones) are found.

Systematic description

Class Reptilia
Subclass Synaptosauria Baur, 1887
Order Sauropterygia Owen, 1859
Suborder Plesiosauria de Blainville, 1835
Superfamily Plesiosauroidea Welles, 1943
Family Elasmosauridae Cope, 1869

Elasmosauridae gen. et sp. indet.

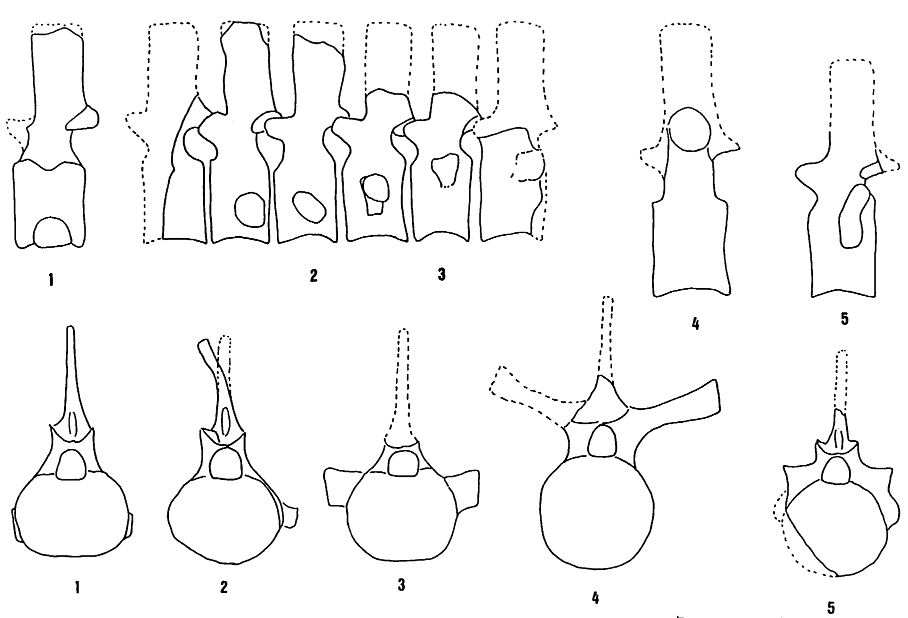
Figures 2—4, 10—14

Elasmosauridae gen. et sp. indet., Nakaya, 1985, 43-50, figs. 5-7, pl. 1.

The material list and measurements of the materials are shown in appendix.

Vertebra ; (Figures 2, 10-1—9)

The vertebrae are large, long, and amphicoelous, their articular faces being only slightly concave. The surface of the centrum is smooth in well-preserved specimens. The ventral surface has a pair of sagittal foramina



Figures 2. 1—5. Left lateral view of vertebrae (above) and anterior view of vertebrae (below) ; **1,** posterior cervical vertebra, HMG 1-3 ; **2,** the last cervical vertebra, HMG 1-8 ; **3,** pectoral vertebra, HMG 1-10 ; **4,** dorsal vertebra, HMG 1-14 ; **5,** sacral vertebra, HMG 1-45. scale = 10 centimeters, (after Nakaya, 1985)

and a weak sagittal keel. These vertebrae have a single costal fossa on each side. The spinous processes of the vertebrae are arranged vertically, and do not incline posteriorly.

Cervical Vertebra

The cervical vertebrae are more elongated antero-posteriorly than other vertebrae. The anterior and posterior faces are elliptical dorso-ventrally. The costal fossa is developed on the ventral edge of the centrum and gradually moves dorsally near the pectoral vertebra. The arch does not fuse with the centrum, and is sometimes completely separated.

Pectoral Vertebra

The costal fossa of the pectoral vertebra is developed partly on the centrum and partly on the arch. The anterior and posterior faces are higher than those of the cervicals.

Dorsal Vertebra

The centrum of the dorsal vertebra is higher and larger than that of other vertebrae and their ends are circular in cross section. The transverse processes are extended dorso-laterally and are cylindrical in outline. The costal fossa is present near the turminus of the transverse process.

Sacral Vertebra

The articular faces of the vertebra are elliptic in outline, flattened dorsally and swollen ventrally. The transverse processes are short but laterally high. The costal fossa is developed between the centrum and the arch of the vertebra. The fossa is a chevron-shaped depression.

Ribs ; (Figures 11-1—5)

The body of the rib is columnar. The rib has a single caput on the end of the body in well preserved material.

Cervical Rib

The body of the cervical rib is short and columnar. The cross section of the caput of the rib is circular and becomes elliptic dorso-ventrally in the posterior part. Some cervical ribs are fused with the vertebrae.

Pectoral Rib

The body of the pectoral rib is short and takes the form of triangular column with a crest. The caput of the rib is circular in cross section or becomes elliptic dorso-ventrally.

Dorsal Rib

The body of the dorsal rib is long, straight, thick and columnar. The cross section of the caput of the rib is elliptical dorso-ventrally. Almost all the dorsal ribs do not fuse with the vertebrae.

Sacral Rib

The body of the sacral rib is short, columnar and slightly bending ventrally. The caput of the rib is chevron shaped and is rectangular in cross section.

Gastralia (Ventral rib) ; (Figures 11-6—8)

Apart from these general features, the gastralia (ventral ribs) are morphologically divided into two types.

One is the normal type (Figure 11-6) which takes a normal shape as gastralia. Almost all the gastralia belong to this type. These gastralia are long with a dorsal groove but bear no caput (Figure 11-6).

Another is the atypical type (Figures 11-7, 8) which is characterized by a bifurcated body. Two gastralia belong to this type and they are somewhat different from each other. Namely, one is flattened (Figure 11-7) whereas the other is columnar (Figure 11-8). Also, these gastralia have no caput.

Pectoral girdle ; (Figures 12-1—3, 6)

Coracoid and Scapula

The medial part of the scapula and the antero-medial part of the coracoid form the "midline bar". The midline bar of the coracoid distinctively extends anteriorly. The lateral part of the scapula extends posteriorly. The scapula contacts with the coracoid, but they do not fuse with each other. The grenoid cavity is an elliptical opening antero-posteriorly. The posterior part of the coracoid is long, thin, and flat. The posterior edge of the coracoid seems to be curved posteriorly. The lateral edge of the coracoid is missing.

Clavicle and Interclavicle

The clavicle and interclavicle do not fuse with each other, and these bones are separated from the scapula and coracoid. The body of the clavicle is thick, platy and triangular in shape. The mesial edge of the body has a crest. The interclavicle is made of one element. The body is crescent shaped with round ends and bends ventrally. The anterior end of the interclavicle is thick and concave posteriorly.

Pelvic girdle ; (Figures 12-4, 5)

Ischium and Pubis

In comparison with the grenoid cavity of the pectoral girdle, the acetabulum of the ischium and pubis is turned caudo-laterally. The external line of the obturator foramen curves gently. The ischium and pubis are more robust than the pectoral girdle.

Ilium

The ilium is separated from the ischium and pubis. The body of ilium is platy and its platy end fans out dorsally. The dorsal part of the ilium is preserved.

Forelimb ; (Figures 3, 13-3—7, 14-1)

Humerus

The humerus is short and robust. The process of the humerus curves anteriorly. The shaft is thick and columnar. The distal part of the humerus is not well preserved, and its surface is suffered some damage. However, its tuberosity runs parallel to the head. The length and breadth of the ulnal articular surface of the humerus are slightly larger than those of the radial surface. The proximal and distal parts of the humerus are rugose. The rugosities of these parts extend to the end of the humerus.

Ulna and Radius

The ulna and radius seem to have no appendicular bone. The internal faces of the ulna and radius are concave. These bones are short and thick. In the medial view, these bones are flat pentagon in shape. The rugosity is developed on the proximal and distal parts of these bones.

Carpal and Metacarpal

The carpal bones are not complete, but the proximal and distal rows of the carpal possibly comprise three bones each in the row. The radiale is parallelogram-shaped with rounded corners. The intermedium is flat and hexagonal in shape. The metacarpal is shaped very similarly to the phalanx. Size alone distinguishes the metacarpal from the phalanx. The metacarpal is larger than the phalanx.

Phalanx

The number of phalanges in each digit seems to exceed more than ten. The phalanx of the forelimb is difficult to discriminate from that of the hindlimb. The body of the phalanx takes a spool-like shape. The proximal and distal articular surfaces of the phalanges are convex. Bodies of the first and fifth phalanx become thin laterally. The sagittal section of the whole forelimb shows a stream-lined shape.

Hindlimb ; (Figures 4, 13-1—2, 14-2)

Femur

The femur is slightly thinner, shorter and slender than the humerus. Its trochanter runs parallel to the head. The tibial

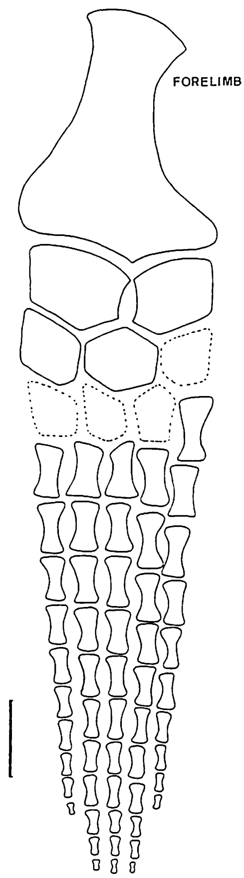


Figure 3. Reconstruction of forelimb. scale = 10 centimeters. (after Nakaya, 1985)

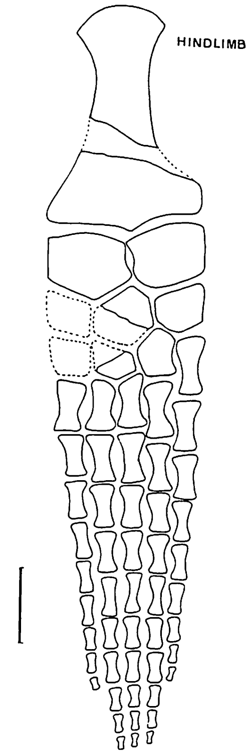


Figure 4. Reconstruction of hindlimb. scale = 10 centimeters. (after Nakaya, 1985)

articular surface of the femur is similar in size to its fibulal articular surface. Both the proximal and distal parts of the femur are covered by rugosities likely manner as those of the humerus.

Tibia and Fibula

The shape and rugosity of the tibia and fibula are similar to those of the radius and ulna, but these bones are slightly smaller than the radius and ulna. The tibia and fibula have no appendicular bones.

Tarsal and Metatarsal

The size of the tarsal bones is smaller than that of the carpal bones. The shape of these bones is similar to that of the carpal. The proximal and distal rows comprise three bones each in the row. The position of the fifth metatarsal moves proximally to that of the distal tarsal row. The metatarsal is very similar to the phalanx in shape.

Phalanx

The phalanx of the hindlimb resembles that of the forelimb. The hyperphalangy seems over ten phalanges. The sagittal section of the hindlimb is shaped in the same streamlined shape, as the forelimb.

Gastrolith

Subangular to round and pebble to cobble-sized stones with glossy surface are found in the trunk part of the plesiosaurian skeleton. These stones are mudstone, fine-grained sandstone, black shale, chert and green rock. They differ from rocks that include the fossil specimens. These stones are regarded as gastroliths (stomach stones).

Discussion

Comparison

A great deal has been written about the classification of Plesiosauria (*e.g.* Andrews, 1910, 1913; Williston, 1925; Nopcsa, 1928; Kuhn, 1934, 1964; Welles, 1943, 1952, 1962; Saint-Seine, 1955; Romer, 1956; Talro, 1960; Persson, 1963; Novozhilov, 1964; Müler, 1968; Brown, 1981). Many genera and species have been proposed, although some new species were based on only one vertebral body or one digit. According to Brown (1981), a large number of existing taxa are considered being invalid. It is now generally accepted that the suborder Plesiosauria can be divided into two superfamilies

Table 1. Comparison of characters of the limb bones of the Hobetsu specimen (HMG 1) and the Cretaceous Plesiosaurian superfamily, family and subfamily from Romer (1956) and Welles (1962). (characher present: 1, character absent: 0, in cervical rib, double headed: 2, single headed: 1)

Romer(1956)

Superfamily		PLESIOSAUROIDEA			PLIOSAUROIDEA			HMG 1
cervical centrum	short	1			0			1
	with lateral keel	1			0			1
Family		Plesio-sauridae	Thaumato sauridae	Elasmo-sauridae	Pliosa-uridae	Polyco-tylidae	Lepto-cleidae	HMG 1
head of cervical rib		2	2	1	2	1	1	1
epipodial	short	0		1	0	1	0	1
	with accessory bones	0		0	1	1		0

Welles(1962)

Superfamily	PLESIOSAUROIDEA			PLIOSAUROIDEA		HMG 1
cerv. centrum long	1			0		1
propodial long	0			1		0
fibual faset>tibial	0			1		0
Family	Plesiosauridae	Elasmosauridae		Pliosauridae	Dolicolincopidae	HMG 1
head of cervical rib	2	1		2	1	1
epipodial short	0	1		0	1	1
Subfamily		Elasmo-saurinae	Alzada-saurinae			HMG 1
midline bar	1	1	0			1

Plesiosauroidea and Pliosauroidea, but some taxa are referred two differing superfamilies by different authors. For example, *Thaumatosaurus* is classified as Pliosauroidea by Saint-Seine (1955), as Plesiosauroidea by Romer (1956) and as Plesiosauria incertae sedis by Novozhilov (1964). Therefore, the classification scheme of Plesiosauria is not yet settled.

In the Hobetsu specimen (HMG 1), the cervical vertebra is not long, the humerus is larger than the femur, and the tibial articular surface of the femur is similar in size to the fibulal articular surface. These characters indicate that the Hobetsu specimen belongs to the superfamily Plesiosauroidea (Romer, 1956; Welles, 1943, 1952, 1962). Furthermore, the ulna, radius, tibia and fibula are not slender and the caput of cervical rib is single headed. Such characters suggest that the specimen is assignable to the family Elasmosauridae (Romer, 1956; Welles, 1943, 1952, 1962; Novozhilov, 1964). Judging from Welles' description, the midline bar (pectoral bar) of the pectoral girdle of the present specimen shows those characters of the subfamily Elasmosaurinae (*Elasmosaurus* and *Brancasaurus*; Table 1). However, Brown (1981) claimed that this character is exclusively observed only in an adult (Table 1). Such elasmosaurids as, *Alzadasaurus*, *Hydrotherosaurus* and *Elasmosaurus* have no appendicular bone of the epipodial of both limbs, but such a bone is present in the forelimb of *Morenosaurus*, *Aphrosaurus* and *Thalassonomosaurus*.

The presence of appendicular bone of the epipodial is the important character for the particular group of the family Elasmosauridae. The Hobetsu specimen has no appendicular bone of the epipodial of the hindlimb. However, it can not be determined, whether or not the appendicular bone of the forelimb is present or not because of the state of preservation. In this respect, the Hobetsu specimen is referable to the family Elasmosauridae, but its generic and specific positions are indeterminate.

Analyzing morphological characters of the Upper Jurassic Plesiosauria, Brown (1981) divided them into four categories, *i.e.* "ontogenetic growth," "specific and generic diagnoses," "primitive and advanced grades" and "divergent evolutionary trends." He used not only the characters of limbs and girdles but also those of skull. Because skull characters play the essential role in the classification of Reptile, his classification is most useful. However, he did not deal with the Cretaceous Plesiosauria.

Nevertheless, the Hobetsu specimen (HMG 1) lacks the skull and a large part of girdles. Therefore, the Hobetsu specimen cannot be satisfactorily analyzed to ascertain the existence in it of those characters representing the four categories recognized by Brown (1981).

The Cretaceous strata of the Japanese Islands have yielded some plesiosaurian remains. Among them, only one small centrum from the Futaba Group (Late Cretaceous) was described by Tokunaga and Shimizu (1926), but other materials were reported only preliminarily.

Tokunaga and Shimizu (1926) assigned their specimen to the anterior cervical vertebrae of *Plesiosaurus* sp., but measurements of the specimen do not agree with the cervical vertebrae of the Plesiosauroidea. These authors measured its length, breadth and height as 22, 49 and 21 mm, respectively. Judging from their photograph (pl. 23, figs. 1a, b, c), the specimen seems too short anteroposteriorly being assigned to the cervical vertebrae of the Plesiosauria (original specimen was lost by air raid during the Second World War). It has two articular surfaces for cervical rib, being elongated laterally, and lacks lateral keel. Therefore, this material is identifiable with the cervical vertebrae of the Pliosauroidea.

The second plesiosaurian from the Futaba Group is well preserved (Obata *et al.*, 1970). This specimen consists of a skull, vertebra, ribs, pectoral and pelvic girdles and hindlimbs. Obata *et al.* (1970) mentioned that it resembles somewhat *Alzadasaurus*, *Hydrotherosaurus* or *Morenosaurus*, but it is distinct from any known species of Plesiosauria. Unfortunately, no systematic description of this material has been published, and the Hobetsu specimen cannot be compared in detail with this material.

Distribution

Around the Japanese Islands, specimens of the Plesiosauria have been recovered from the Late Cretaceous strata of the Iwaki region in Hoshu, Urakawa, Hobetsu, Mikasa, Obira, and Nakagawa areas in Hokkaido, and Sakhalin Island (Riabinin, 1915; Tokunaga and Shimizu, 1926; Obata *et al.*, 1970, 1972; Suzuki, 1984) (Figure 5). These plesiosaurians range in age from the Cenomanian to Maastrichtian. Most of them are fossils of the superfamily Plesiosauroidea, but a few belong to the superfamily Pliosauroidea. The materials reported by Tokunaga and Shimizu (1926) belong to the latter taxon, not to the Plesiosauroidea as originally given.

The migration route of the Plesiosauria is an important problem. According to the fossil record of the Plesiosauria, they distributed mainly in western Europe throughout the Early Jurassic Period (Figure 6). During Late Jurassic times, it invaded the region of Urals and China through the Tethys Sea and the mid-western region of North America (Figure 7). Furthermore, it spread to the Pacific coast of Central America and Australia during the Early Cretaceous

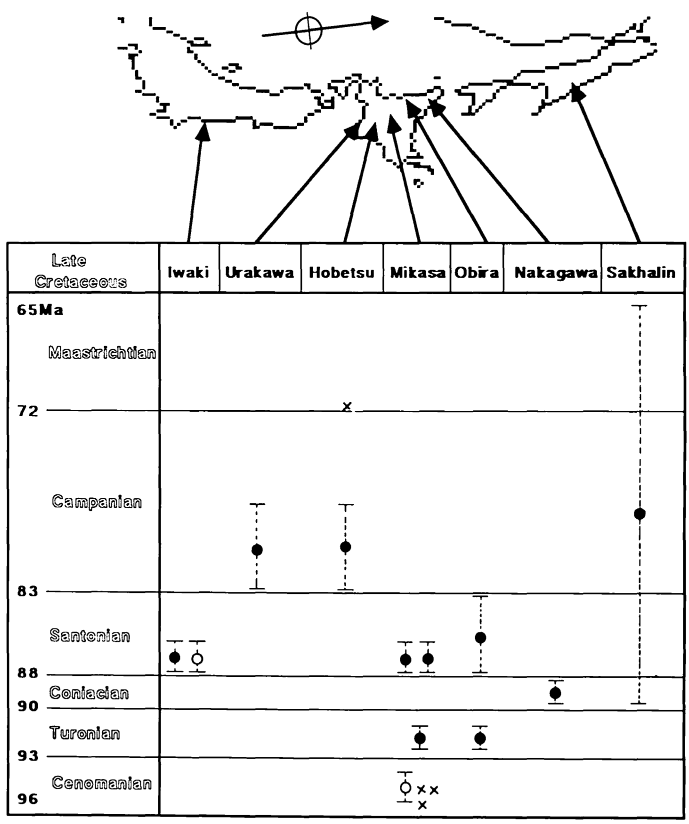


Figure 5. Temporal and spacial distribution of the Late Cretaceous Plesiosauria in northeastern Asia. (Revised from Riabinin, 1915; Obata *et al.*, 1970, 1972). Plesiosauroidea: ●, Pliosauroidea: ○, Plesiosauria indet.: ×.

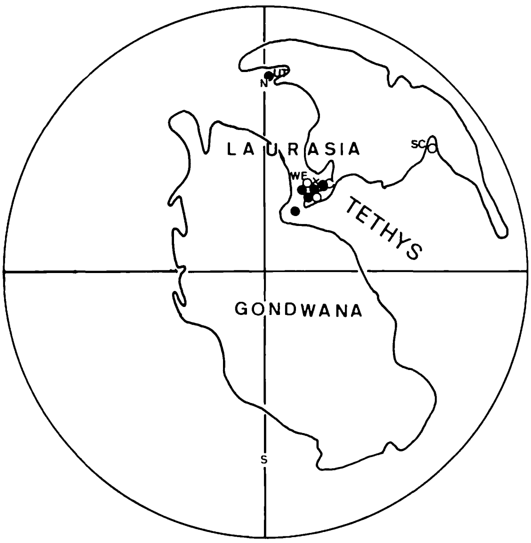


Figure 6. Distribution of the Plesiosauria in the Early Jurassic. (Paleocontinental arrangement is after Smith and Briden, 1977 with some revision; Paleogeographic distribution of the Plesiosauria is compiled from Persson, 1963; Obata *et al.*, 1970, 1972; Welles and Gregg, 1971; Dong, 1980; Suzuki, 1984; Zhang, 1985)
Plesiosauroidea: ●, Pliosauroidea: ○, Plesiosauria indet.: ×. N; North pole, S; South pole, AF; Africa, AN; Antarctica, AS; Asia, AU; Australia, EU; Europe, GN; Greenland, NA; North America, PA; Pacific Ocean, SA; South America, SC; Sichuan (South China), TE; Tethys Sea, UT; Urung-Tumus (North Siberia), WAF; West Africa, WE; West Europe.

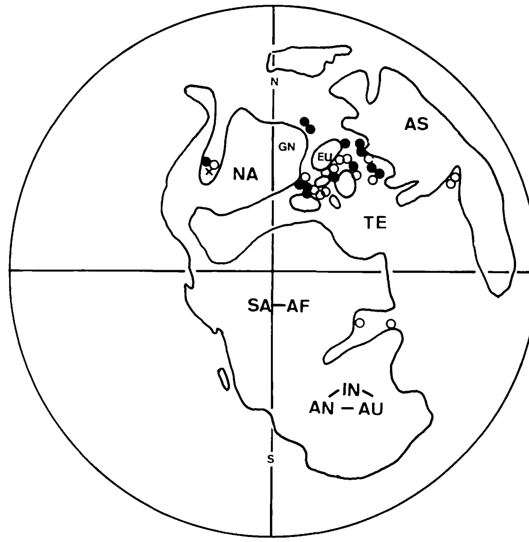


Figure 7. Distribution of the Plesiosauria in the Late Jurassic.

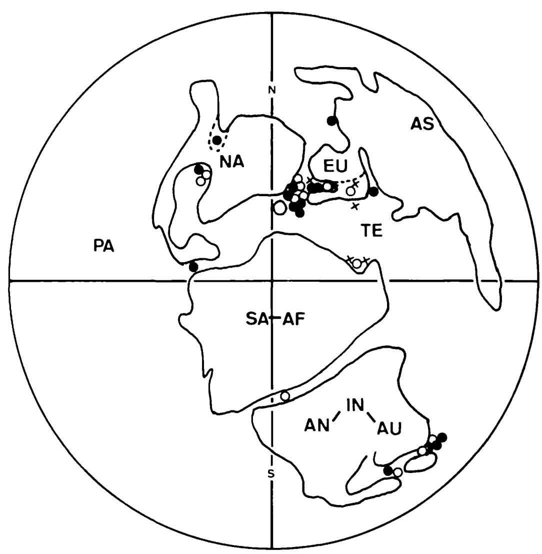


Figure 8. Distribution of the Plesiosauria in the Early Cretaceous.

Period (Figure 8). In the Late Cretaceous, the range of Plesiosauria expanded to the Pacific coast of South America, New Zealand and the Japanese Islands and attained the widest distribution (Figure 9).

According to the distribution of the Plesiosauria around the Japanese Islands, in Middle to Late Jurassic times, *Sinopliosaurus* (Young, 1944), *Bishanopliosaurus* (Dong, 1980) and *Yuzhoupliosaurus* (Zhang, 1985) seem to have migrated into the southern region of China through the Tethys Sea. However, the Late Cretaceous Plesiosauria occurred around the Japanese Islands probably migrated from North America and or North Europe into Japan through the North Pacific region. Especially, the present author considers the Plesiosauroidea of Japan is to be a possible boreal element, not of a Tethyan element, because at present there is no evidence of migration from the Tethys. This idea is also corroborated by the evidence based on the upper Cretaceous bivalves

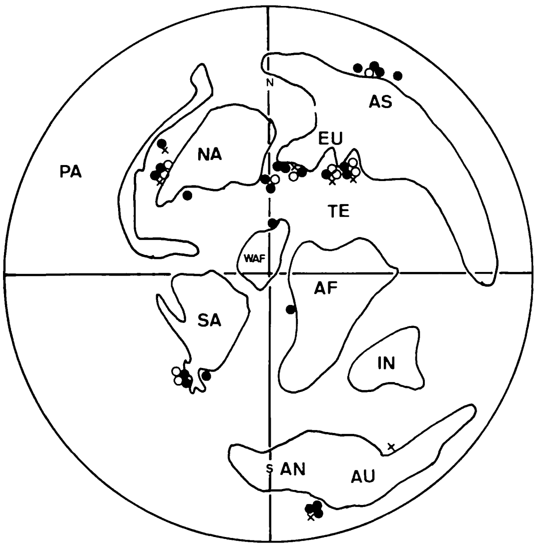


Figure 9. Distribution of the Plesiosauria in the Late Cretaceous.

(Tashiro, 1985).

Conclusions

The plesiosaurian specimen from Hobetsu, Hokkaido, northern Japan comprises the body part exception of skull, and such body parts as mandible, anterior cervical, and caudal vertebrae. The morphological characters of this specimen exhibit those referable to the family Elasmosauridae, although its generic and specific positions cannot be determined because of its poor state of preservation. This specimen was obtained from early Campanian rocks of the Upper Yezo Group as its age indicated by associated invertebrate fossils. The elasmosaurid of the Japanese Islands is interpreted to have migrated during the Late Cretaceous via North Pacific region in the likely manner as the marine bivalve faunas.

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*: in Japanese, **: in Japanese with English abstract, ***: in Chinese with English abstract, #: in Russian.

Appendix

Material list of HMG 1

cervical vertebra (HMG 1-)1—9, 12; pectoral vertebra 10, 11; dorsal vertebra 13—44; sacral vertebra 45, 46; cervical rib 9; pectoral rib 47-54; dorsal rib 55—115; sacral rib 116—119; rib or chevron 120, 251; gastralia (ventral rib) 121—136; bifurcated gastralia 137, 138; scapula 139; coracoid 140, 141, 145, 149; clavicle 142; interclavicle 143 ilium 144; pubis 150; ischium 151; humerus 153, 154; radius 158, 159; ulna 160; radiale 165, 172; carpal intermedium 166; distal carpal II 173: distal carpal III+IV 174; metapodial 195, 197-201; phalanx 179—194, 196, 202—217, 220—239, 241—246, 248—250; femur 155, 156, 157; tibia 161, 162; fibula 163, 164; tibiale 167, 168; fibulare 170; tarsal intermedium 169, 171; distal tarsal I 177; distal tarsal II 175; distal tarsal III+IV 176; carpal or tarsal 178, 252—255, 258, 259; bone fragments 175—177, 218, 219, 240, 247, 256, 257, 260, 261; gastrolith 262—271.

Table 2. Measurements of the vertebrae. (mm)

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*19′*	*20*	*20′*
(HMG 1-)																						
1		77	78		108	105	111		65				33	39	28	29		27				
2		76	75		111	115			63													
3	225	79	83	148	112	106	124	64	64	75	42	38	35	37	36	39	30	26				
4					111					53		38		38		32						
6			82				108					38					35	20				
7	229	79	81	149	115	114	126		61	94	45	43	25	27	28	26	31	25				
8		83	83	120	115	117	119		59	95	45	37	29	30	34	25	33	34				
9		82	79		116	112	117		61	94	42	33	35	34	43	30	27	30				
10		81	89		111	112	121		57		37	28	35	34	34	44	22	33				
11		101	91		114	118	120		64													
12		76	70		105	94			62	53							32	21				
13		88	88		102	107			65													
14	195	100	101	95	106	105		235+	75	47		45					30	33	45		35	
15		88			115																	
16		88	94			78		190+	64									51	37			
18				110				156+			46	45					29	32				
19					110				71													
20		100	107					150+														
21		106	108						73													
22		99	97		103	95			71													
23	194	102	104	94	82			80+	71	77	46						34	29				
24		95			107				57													
25		97	96			85+			72									32				
26			82						57								32	34				
27	145	84	82		99	78			65													
28				85				132		87	52	39							26	36	21	28
29								110+			52	41						22	49		35	
30					118			220+											49			35
34		99																				
37		90							73													
41											56	46						25	46		41	
43																			44			34
45	163	85	83	79	93	94	115	111	59	81	43	32	36	28	56	59	26·	30				

Explanation for the measuring points.

1 greatest height
2 height of the cranial face of the body
3 height of the caudal face of the body
4 height of the spinous process
5 breadth of the cranial face of the body
6 breadth of the caudal face of the body
7 breadth of the costal fovea part of the body
8 breadth of the transverse process
9 cranio-caudal length of the body
10 cranio-caudal length of the spinous process
11 breadth of the cranial articular process
12 breadth of the caudal articular process
13 cranio-caudal length of the costal fovea (left)
14 *ibid*. (right)
15 height of the costal fovea (left)
16 *ibid*. (right)
17 height of the vertebral foramen
18 breadth of the vertebral foramen
19 longer diameter of the end of the transverse process
19′ *ibid*. (opposite side)
20 shorter diameter of the end of the transverse process
20′ *ibid*. (opposite side)

Table 3. Measurements of the ribs (dorsal ribs). (mm)

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
(HMG 1-)								
52	45	21	29	15	15	9	264	18
55	42	22	27	15	23	14	146	17
57	24	18	21	14	16	9	104	
59	44	14	25	13	26	16	141	
60	48	29	24	12	21	13	109	
61	35	20	27	13	24	15	110	11
64	21	16	20	14	19	11	144	
66	26	12	19	15	20	8	257	22
67	24	13	19	13	11	20	242	16
68	20	15	20	14	29	5	264	25
69	27	21	25	19	27	19	223	18
70		18	29	18	26	18	172	19
71	35	26	23	11	10	10	203	9
72	43	25	27	19	25	21	203	30
73	22	14	16	15	16	16	167	
74	26	13	25	13	24	14	110	4
75	22	17	21	16	23	12	209	6
76	39	21	22	17				
77	27	19	16	16	10	15		
79	23	17	20	18	17	21	103	
80	25	13	25	13	26	13	125	
82							150	
83	38	14	29	15	28	17	116	7
84	22	21	22	18	20	14	173	
85	29	16	25	21	22	20	130	10
86	28	21	27	18	23	17	106	
87	44	29	23	16	24	19	165	24
88	51	30	33	20	25	19	144	15
89	43	35	27	13	21	14	157	16
90	21	16	25		25	10	164	
92	22	12	20	12	20	17	179	9
93	24	14	18	12	20	17	160	
94	25	19	24	17	23	19	212	9
95	26	17	24	18			197	
96	26	20	26	23	23	19	197	
97	41	15	26	18	25	22	207	
98	24	18	24	19	22	21	189	
100	33	14	23	26	16	24	210	23
101	36	24	19	20	23	17	189	19
102	24	22	25	23	23	20	147	
103	26	21	25	21	24	20	192	
104	22	15	24	17	24	23	191	
105	24	19	25	18	23	21	190	
106	32	17	27	17	23	21	208	
107	37	11	25	13	29	11	146	14
108	23	20	24	20	24	20	150	
109	24	19	23	19	21	19	145	
110	19	16	23	14	22	13	145	3
111	23	20	25	16	26	16	149	
112	25	16	22	18	24	19	145	
113	27	21	23	18	22	18	183	11
114	29	20	24	17	24	17	132	
115	30	21	23	15	22	17	187	
116	55	24	20	22	23	19	103	19
117	49	25	24	24	22	20	90	9
118	50	29						
119	59	25	24	25	44	23	104	22

Explanation for the measuring points.

1 longer diameter of the proximal end
2 shorter diameter of the proximal end
3 longer diameter of the middle of the body
4 shorter diameter of the middle of the body
5 longer diameter of the distal end
6 shorter diameter of the distal end
7 total length (remain part)
8 bending index

Table 4. Measurements of the metapodials and the phalanxs. (mm)

	1	*2*	*3*	*4*	*5*	*6*	*7*
(HMG 1-)							
179	34	22	17	15			
180	33	26	18	15			
181					40	29	
182	29	19	15	17	29	23	56
183	29	22	14	15	32	24	57
184	27	20	12	14			
186	38	27	19	17	42	27	77
187			24	20	43	30	
188	43	30	19	23	43	33	72
189	44	27	25	23	45	34	63
190	37	28	19	21	40	30	61
191	25	23	10	14	25		56
192	43	35	29	22	36	31	73
194	26	22	15	15	26	23	48
195	38	34	24	23	37	33	77
196	43	29	20	23	33	31	72
197	42		20		40	42	75
198	41	42					
199	44		30		46	45	69
200	45	43	24	32		37	73
201	35	44	26	22	47	40	68
202	41	39	23	27	44	36	65
203	39	39					
205	38	34	22	22	30	29	57
206	28	26	19	15	23		53
208	10	10	8	7	13	11	27
209			12	9	22	19	40+
210	11+	11+	9	7	15+	14+	36
216	18	11	10	8	18	15	31
217	22	17	14	13	25	20	43
218					37	28	
219			7+	6+	16	11	34+
220	27	17	14	11	22	15	41
221	25	16	11	10	21	16	43
222			12	12	32	24	
223	43	38	31	18	40	32	74
224	49	40	27	22			
225	46	46					
226	28	25	16	19	37	26	66
227	33	29	17	20	41	30	71
228	36	29	21	21	32	27	77
229	33	32					
230	40	31	20	22	42	35	69
231	42	35	20	24	41	36	76
232	41	37	24	28			
233	35	33	23	16	30	21	58
234	20		15		18		43
235	25	20	17	12	26	29	49
236	40	33	17	25	40	37	64
237	42	40	31	22	40	36	70
238	36	24	23	20	37	31	56
239	18	15	11	10			46+
240	37	32	17	17	31	27	60
241	44						
242					39+		
243	46	34	29	24	43	41	82
244	37		22				65+
245	49	41	29	30	46	45	74
246	51		34				65
248	40	24	19	13			
249	45	23	19	18	29	29	80
250	35	33	20				75

Measuring points are the same as for Table 5.

Table 5. Measurements of the limb bones (propodials, epipodials, metapodials). (mm)

	part	1	2	3	4	5	6	7
(HMG 1-)								
152	humerus			110	89	273	72	230+
153	humerus	222+	69	172+	66			
154	humerus	133	132	107	80			
155	femur	213	65	164	62			
156	femur					115	65	
157	femur	123	125	86	72			
158	radius	98	66	125	50	119	58	110
159	radius	120	55	116	40			
160	ulna	104+	56+	99+	30+			82+
161	tibia	110	50	112	42	117	45	84
162	tibia	79+	54	71+	42	84+	44	91+
163	fibula	107	57	101	49	102	52	81
164	fibula	64+	58	70+	49	87+	50	80
165	radiale	75	54	72	44	71	35	72
166	c-intermedium	96	56	90	41	83	50	69
167	tibiale				32	52	38	
168	tibiale	61	38	103	42			
169	t-intermedium	64	46		41		48	
170	fibulare	73	50	70	42	68	43	58
171	tibiale	70	44	95	46	67	37	75
172	radiale		41		34	54	48	50
173	carpal II	57	37	48	24	44	40	78
174	carpal III+IV	78	38	68	28	76	37	85
175	tarsal III+IV	48	37	42	30	42		72
176	tarsal II				38	66	46	
177		50	43	36	31	37	39	53
178			45		41		35	65

Explanation for the measuring points.
1 breadth of the proximal end
2 thickness of the proximal end
3 breadth of the middle of the body
4 thickness of the middle of the body
5 breadth of the distal end
6 thickness of the distal end
7 medio-distal length

Table 6. Measurements of th gastralia (ventral ribs). (mm)

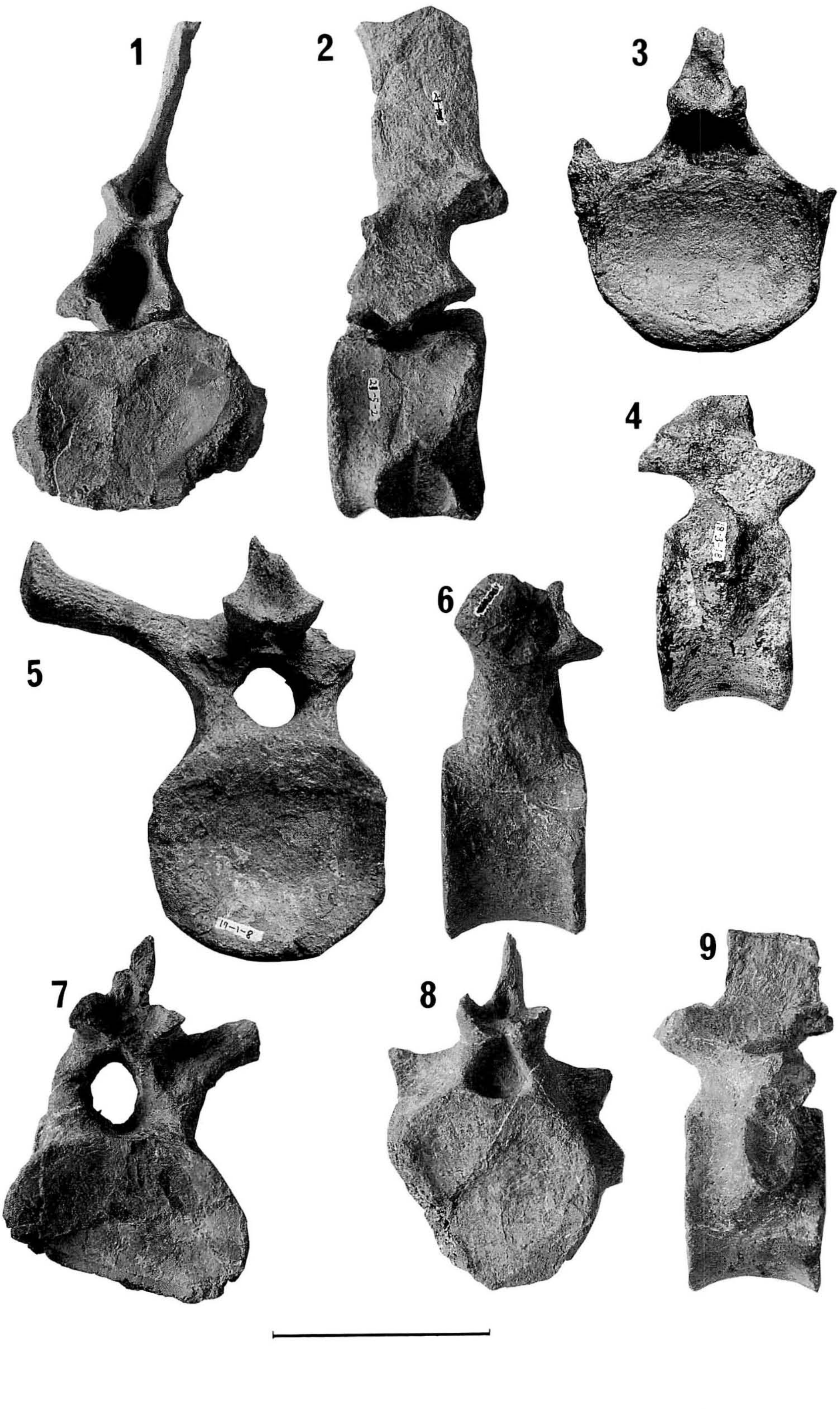
	1	2	3	4	5	6	7	8
(HMG 1-)								
121	18	11	21	14	16	14	171	12
122	25	17	21	16	20	12	150	5
123	20	14	18	11			143	
124	23	13	22	11	20	9	156	12
125	22	18	24	17	25	16	150	4
126	22	11	21	12	16	9	201	7
127	21	12	24	11	23	26	130	
128	17	12	15	11	11	7	102	
129	23	15	19	14	20	8	223	
132	23	15	23	9	12	6	217	7
134	18	7	21	12	14	13	313	31
137							315	
138							165	

Measuring points are the same as for Table 3.

Table 7. Measurements of the gastroliths. (mm)

	rock name	roundness	longer diameter	shorter diameter
(HMG 1-)				
262	mudstone	subround	29	17
263	mudstone	subround	30	21
264	fine sandstone	round	40	23
265	fine sandstone	round	42	21
266	black shale	round	41	25
267	black scale	round	102	60
268	chert	round	83	51
269	black shale	round	50	39
270	green rock	subangular	67	26
271	chert	subround	27	21

→ **Figures 10. 1,** posterior view of cervical vertebra, HMG 1-3, ×1/3; **2,** left lateral view of cervical vertebra, HMG 1-3, ×1/3; **3,** anterior view of first pectoral vertebra HMG 1-10, ×1/3; **4,** right lateral view of first pectoral vertebra, HMG 1-10, ×1/3; **5,** posterior view of dorsal vertebra, HMG 1-14, ×1/3; **6, 7,** anterior view of dorsal vertebra, HMG 1-17, ×1/3; **8,** anterior view of sacral vertebra, HMG 1-45, ×1/3; **9,** left lateral view of sacral vertebra, HMG 1-45 ×1/3. Scale=10 centimeters.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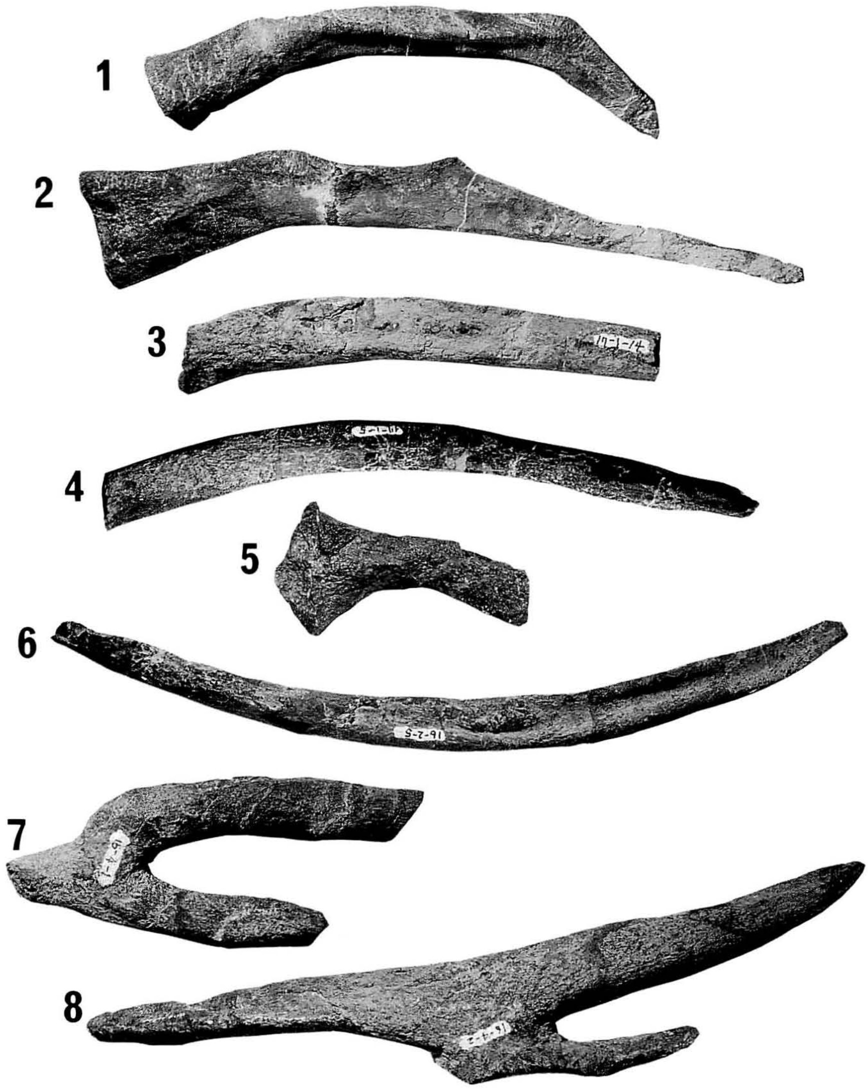
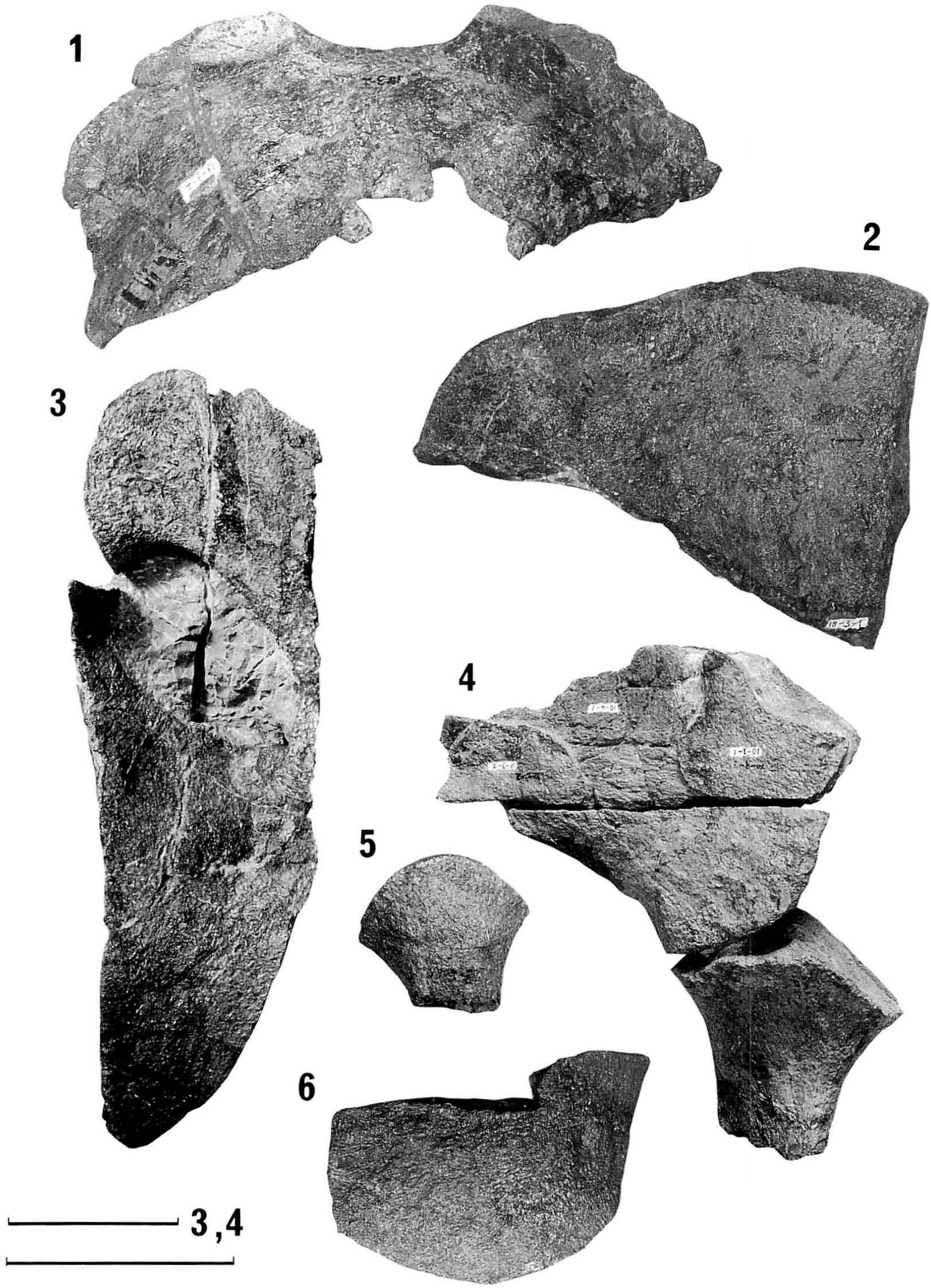
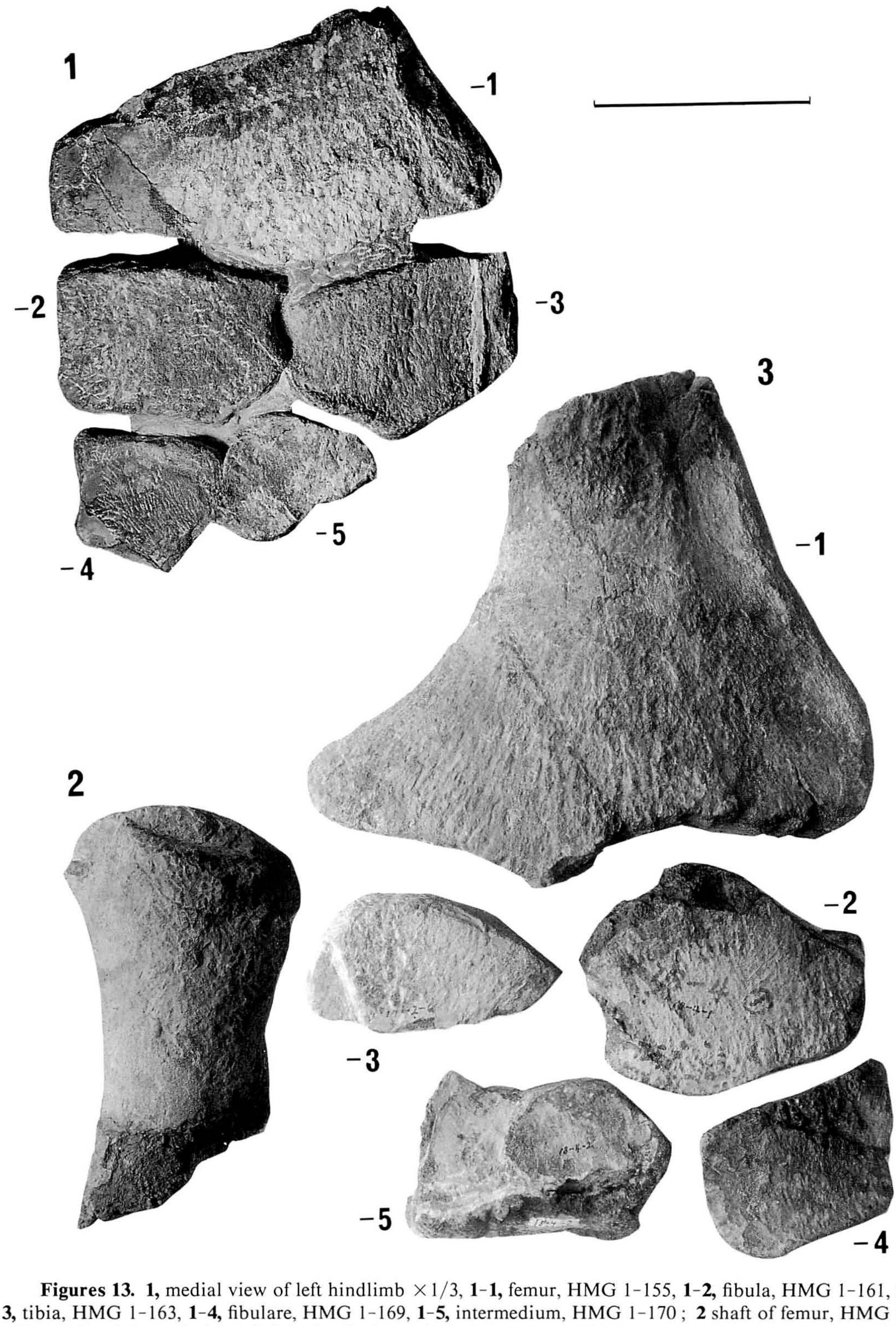


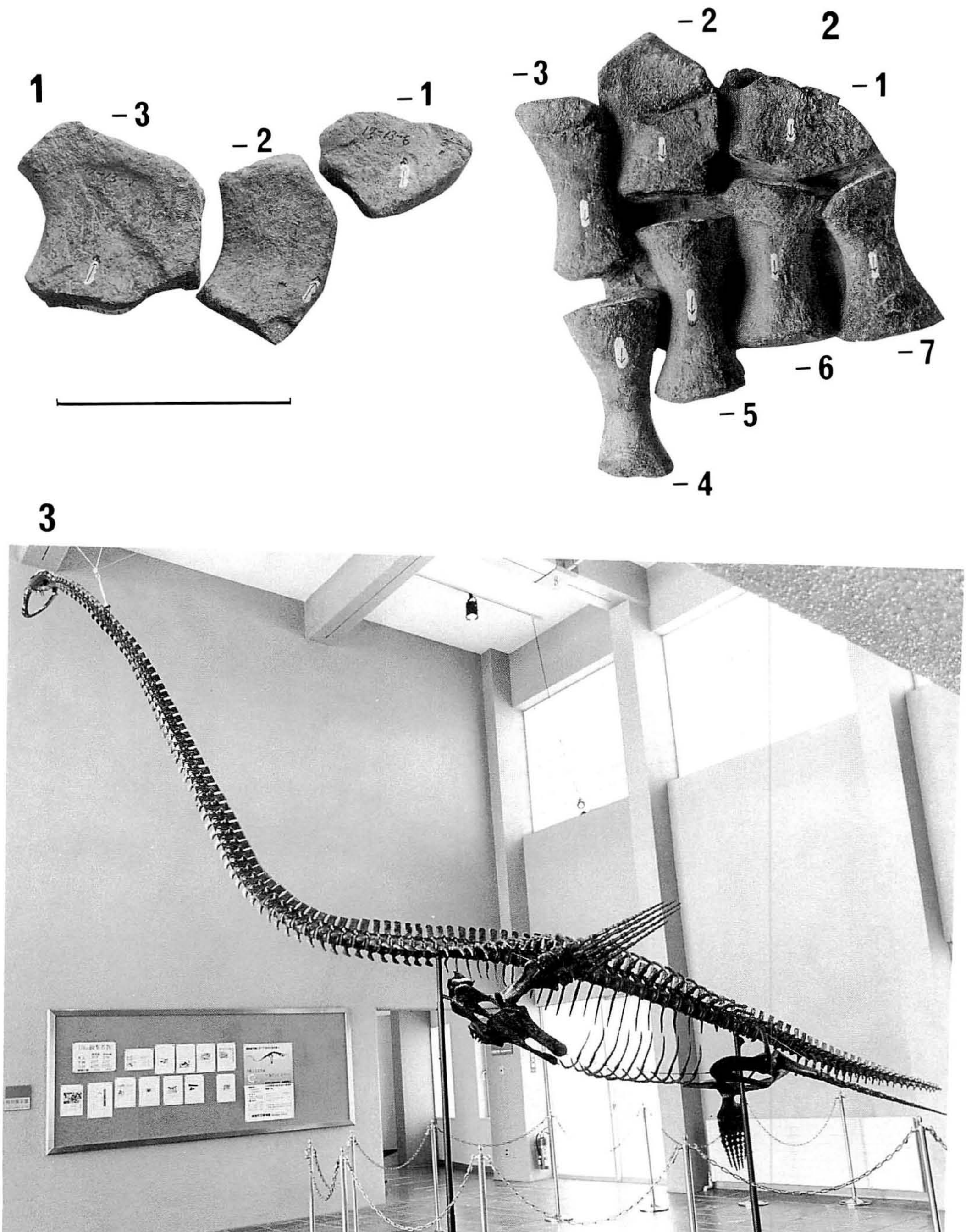
Figures 11. **1,** anterior cervical rib, HMG 1-48, ×1/3 ; **2,** posterior cervical rib, HMG 1-52, ×1/3 ; **3.** medial part of dorsal rib, HMG 1-105, ×1/3 ; **4,** lateral part of dorsal rib, HMG 1-66, ×1/3 ; **5,** medial part of sacral rib, HMG 1-116, ×1/3 ; **6,** grooved ventral rib, HMG 1-134, ×1/3 ; **7,** branched ventral rib, HMG 1-138, ×1/3 ; **8,** branched ventral rib, HMG 1-137, ×1/3. Scale = 10 centimeters.



Figures 12. 1, ventral view of interclavicle, HMG 1-143, $\times 1/3$; **2,** ventral view of clavicle, HMG 1-142, $\times 1/3$; **3,** ventral view of "Midline bar" part of scapula, HMG 1-139, and coracoid, HMG 1-140, $\times 1/4$; **4,** dorsal view of acetabulum part of ischium, HMG 1-151, and pubis, HMG 1-150, $\times 1/4$; **5,** dorsal part of ilium, HMG 1-144, $\times 1/3$; **6,** posterior part of coracoid, HMG 1-149, $\times 1/3$. Scale = 10 centimeters.



Figures 13. 1, medial view of left hindlimb ×1/3, **1-1,** femur, HMG 1-155, **1-2,** fibula, HMG 1-161, **1-3,** tibia, HMG 1-163, **1-4,** fibulare, HMG 1-169, **1-5,** intermedium, HMG 1-170 ; **2** shaft of femur, HMG 1-157, ×1/3 ; **3,** lateral view of right forelimb ×1/3, **3-1,** humerus, HMG 1-157, **3-2,** radius, HMG 1- 158, **3- 3,** ulna, HMG 1- 160, **3-4,** radiale, HMG 1-165, **3-5** intermedium, HMG 1-166. Scale=10 centimeters.



Figures 14. **1,** carpal bone ×1/3, **1-1,** radiale, HMG 1-172, **1-2,** distal carpal II, HMG 1-173, **1-3,** distal carpal III+IV, HMG 1-174 ; **2** tarsal bones, metatarsals and phalanx ×1/3, **2-1,** distal tarsal II, HMG 1-176, **2-2,** distal tarsal III+IV, HMG 1-175, **2-3,** fifth metatarsal, HMG 1-195, **2-4,** proximal phalanx, HMG-1-196, **2-5—7,** metatarsals, HMG 1-196—201 ; Scale = 10 centimeters. **3,** restoration of the elasmosaurid skeleton from Hobetsu, Hokkaido, HMG 1. (after Nakaya, 1984.)

Hobetsu 穂別, Hokkaido 北海道, Futaba 双葉, Fukushima 福島, Honshu 本州, Sanushube サヌシュベ, Yezo エゾ(蝦夷), Iwaki いわき, Urakawa 浦河, Mikasa 三笠, Obira 小平, Nakagawa 中川.

北海道, 穂別町の上部白亜系より産出したエラスモサウルス科（爬虫類, 鰭竜目, 長頸竜亜目）化石：北海道勇払郡穂別町のサヌシュベ川より発見された長頸竜（爬虫類, 鰭竜目, 長頸竜亜目）化石を記載した. 本標本にともなう軟体動物化石および微化石から化石の年代は後期白亜紀のサントニアンからカンパニアンと考えられる. 本標本は体幹と四肢の部分が保存されており, 死後, 頸部や尾部の先端が脱落した後に埋積されたと考えられる. またその形態的特徴は長頸竜の中でもプレシオサウルス上科のエラスモサウルス科に属することを示している. しかし属以下の分類群については不明である. 日本列島周辺の後期白亜紀の長頸竜はジュラ紀以降の長頸竜の分布を検討してみると, ユーラシアの北部または北アメリカから北太平洋を経由して移動してきたと考えられる. このことは同時代の海生二枚貝のデータとも調和的である. 仲谷英夫

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879. COMPARATIVE MORPHOLOGY OF *NIPPONITES* AND *EUBOSTRYCHOCERAS* (CRETACEOUS NOSTOCERATIDS)*

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Abstract. *Nipponites* and *Eubostrychoceras*, Late Cretaceous nostoceratid ammonites, seem to be closely related to each other as recognized from the similar shell surface sculpture and early shell morphology. As the result of detailed comparison of their shell morphology and stratigraphic occurrence, six discrete morphotypes were recognized by the shell surface ornamentation and mode of coiling as well as their ontogenetic change. Both of *Nipponites* and *Eubostrychoceras* slightly and stepwise changed their form with the time. Morphotype A, the most primitive form of *Nipponites*, shares many diagnostic characters with the coexistent Morphotype F of *Eubostrychoceras*, although there is a clear difference in the coiling pattern after their early growth stage. A saltatory evolution from *Eubostrychoceras* to *Nipponites* (meandrous form) is strongly suggested not only by theoretical aspect but also by empirical evidence.

Key words. *Nipponites, Eubostrychoceras,* Cretaceous, Hokkaido

Introduction

Nipponites is one of the most curious and conspicuous heteromorph ammonite genera from Japan. It was first described by Yabe (1904) as *Nipponites mirabilis* together with many Cretaceous ammonites from Hokkaido. First, some foreign investigators regarded it as a pathologic individual of some "*Bostrychoceras*-like" species, because it revealed too extraordinary meandrous shell unlike other heteromorph ammonites and because it was represented by only one specimen at that time. Subsequently, however, Shimizu (1926) reported the second specimen with similarly coiled shell, and taxonomic distinctness of *Nipponites* was generally confirmed.

Yabe (1904), also in the same paper, described another heteromorph species as "*Helicoceras* (?) *japonicum*" (treated here as *Eubostrychoceras japonicum* (Yabe) which has quite similar ornamentation to *N. mirabilis* on the helicoid whorls. He already recognized the affinity of *Nipponites* to such contemporary helicoid heteromorphs, and discussed the possibility of pathology. Berry (1928) speculated the origin of the meandrous whorls; it was produced by the extreme development of the retroversal hook of some heteromorphs (*e.g. Heteroceras* and *Nostoceras*). He also expected a "trochoid coiled" species as the ancestor of *Nipponites*. Matsumoto (1977) noticed the similarity of early stage coiling and surface sculpture between *N. mirabilis* and *E. japonicum*, and suggested that the former was derived from the latter. However, nobody yet acquired any transitional specimen between *Nipponites* and helicoid species.

Recently, I discussed this problem from a theoretical viewpoint and concluded that, even if the same computer program is applied, continuous change of hypothetical date results in a drastic change of three-dimen-

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sional shell architecture (Okamoto, 1988c). In this paper actual morphologic and stratigraphic data of *Nipponites* and *Eubostrychoceras* are summarized, and the phylogenetic relation between the two genera is empirically examined.

Material and methods

More than one hundred heteromorph specimens including four valid holotypes were examined. All of them (except one of the holotypes from Sakhalin) were collected from the Middle and Upper Yezo Groups in Hokkaido, and accompanying fossils indicate a Turonian or Coniacian age. They share simple transverse ribs which occur at regular intervals and lack any tubercles and spines. The shell outline of the middle growth stage can be classified into two discrete forms: dextral or sinistral torticone type and meandering type, which correspond to *Eubostrychoceras* and *Nipponites*, respectively. I provisionally use these two generic names in this paper to express the major features of shell coiling.

Information of early shell morphology and developmental process of suture line is generally important to reconstruct the phylogenetic relationship of ammonites. However, the ammonitella stage of heteromorph ammonite is rarely preserved, and even if they are observable, it might be difficult to distinguish the early shell morphology between such phylogenetically close groups. Furthermore, all the specimens of the two genera share the same sutural elements and their developmental characteristics. Yet, several morphotypes can be discriminated by the difference in the rib pattern and its ontogenetic change both in *Eubostrychoceras* and *Nipponites*. Phylogenetic relationships between these morphotypes can be estimated by comparing the rib patterns and stratigraphic occurrences.

The depository of specimens is as follows: UMUT, University Museum, University of Tokyo; GK, Department of Geology, Kyushu University; WEA, Institute of Earth Science, Waseda University; and KPMG, Kanagawa Prefectural Museum. Consecutive specimen numbers are also given for all of the specimens examined, and their collation with register numbers is shown in Appendix Table.

General morphology and remarks

Nipponites: 53 specimens of *Nipponites* were analyzed. Three growth stages (early, middle and late) are recognized in their ontogeny. The shell form in the early stage is usually open planispiral, but slight torsion and rather irregular coiling occasionally occur. The early whorls are followed by meandrous whorls in the middle stage. A "symmetric plane" and a "coiling axis" are recognized in the meandrous shell; meandering occurs equally on both side of the "symmetric plane", and the centers of whorl sections along the "symmetric plane" are located well on an equiangular spiral. The meandrous shell of *Nipponites* consists of three fundamental modes of coiling: crioceratoid, dextral and sinistral helicoids, and is produced as a result of regular switching of coiling mode (Okamoto, 1988c). The meandrous whorls become more or less loose and irregular in the late stage. A hook-like whorl is observed near the end of this stage in some specimens.

Six types of ribs are distinguishable in the surface ornamentation of *Nipponites* shell and are itemized as follows (see also Figure 1). 1. Normal ribs: these occur sequentially at regular intervals, and each of them is symmetrical in the growth directional cross section. 2. Serrated ribs: these also occur sequentially at regular intervals. The cross section is asymmetrical and less steep toward the growth direction. 3. Periodic ribs: solitary and strong (highly elevated) ribs which occur sparsely and periodically between normal ribs. 4. Periodic double ribs: pairs of

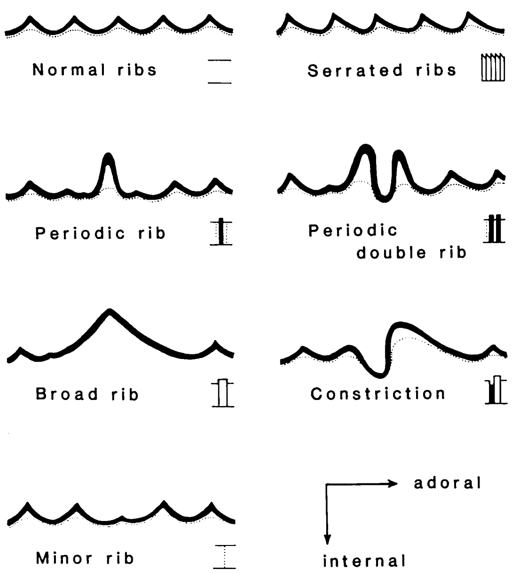


Figure 1. Index figure showing schematic cross sections of the transverse ribs and corresponding symbols for the description of the ontogenetic rib pattern. Dashed line indicates the exterior trace of inner mould.

strong (highly elevated) ribs which occur periodically at the end of the crioceratoid coiling. 5. Broad ribs: strong and broad ribs which are approximately symmetrical in the cross section. 6. Minor ribs: faint costa or secondarily inserted weak ribs.

Relative growth pattern between the whorl length and whorl height was analyzed in a well preserved specimen (Figure 2-A). The whorl height means the diameter of tube cross section along the ventral and dorsal margins, and the whorl length is defined as the length of tube center line. Because this diagram is shown in normal scale, constant relative growth is plotted on a straight line, and its inclination is related to whorl enlarging rate. Two constant growth phases are recognized in *Nipponites*; the first phase has a high whorl enlarging rate and the second has a relatively low enlarging rate. They correspond to early and middle-late stages of coiling, respectively.

The angle between a rib and a normal plane to the growth direction was measured

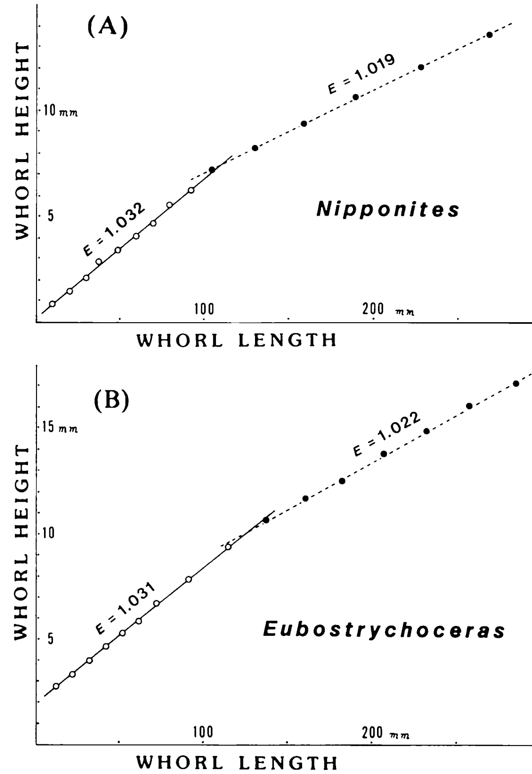


Figure 2. Relative growth pattern between whorl height and whorl length plotted on the normal scale. A, Morphotype A, specimen No. 71, B, Morphotype F, specimen No. 12. Two isometric phases are similarly recognized in Morphotypes A and F. *E* indicates the whorl enlarging rate in each phase.

as the rib obliquity. When ribs are rectiradiate, the value is about zero. The plus and minus signs of this value indicate rursiradiate and prorsiradiate ribs, respectively. Rib obliquity remarkably and regularly changes during the ontogeny of *Nipponites*. An example of rib obliquity change is shown in Figure 3-A. In the early crioceratoid stage, the obliquity is constantly small (nearly rectiradiate). Then the value gradually increases toward the transitional interval between early and middle stages. In the middle stage, rib obliquity frequently oscillates between rectiradiate to prorsiradiate corresponding to the switching of coiling mode; rib obliquity reaches maximum and

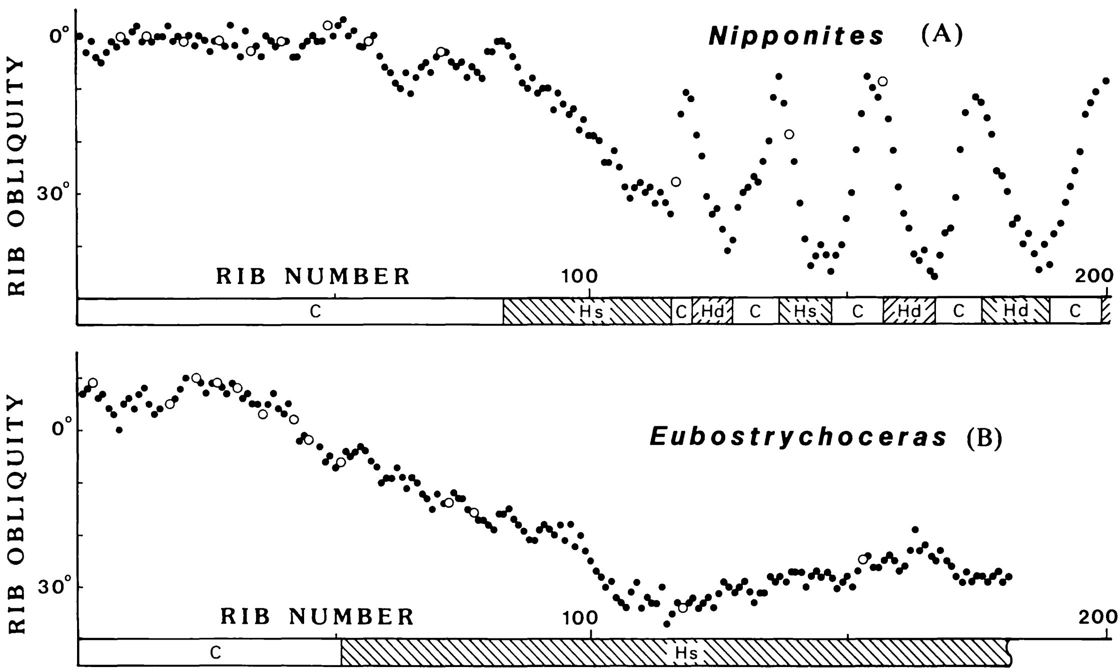


Figure 3. Ontogenetic change of the rib obliquity in *Nipponites* and *Eubostrychoceras*. A, Morphotype A, specimen No. 72, B, Morphotype F, specimen No. 12. Solid and open circles mean normal rib and periodic rib, respectively. The modes of coiling are also expressed with the rib number (C ; crioceratoid, Hd ; dextral helicoid, Hs : sinistral helicoid). After the consistent rectiradiate ribs in the early stages, the rib obliquity regularly oscillates in *Nipponites* corresponding to the switch of coiling mode, while in *Eubostrychoceras* the value increases and then maintains an almost constant prorsiradiate value.

minimum at the ends of helicoid and crioceratoid coiling modes, respectively. In some specimens the change of rib obliquity becomes a little obscure in the late stage.

The distribution of *Nipponites* is probably confined to the Middle Turonian to the Coniacian of the northern Pacific region : Hokkaido (Yabe, 1904 ; Shimizu, 1926, 1933 ; Matsumoto and Muramoto, 1967, and Matsumoto, 1977), Sakhalin and Kamchatka (Kawada, 1929 ; Druczic and Pergament, 1963 ; Verechagin *et al.* 1965 ; Mihajlova, 1983) and Oregon (Ward and Westermann, 1977).

Eubostrychoceras : Judging from the early shell morphology, the genus "*Eubostrychoceras*" contains two discrete groups ; one is characterized by a straight shaft around which later helicoid whorls are formed (*i.e. E. muramotoi* Matsumoto, 1967 and *E. matsumotoi* Cobban, 1988), and the other shows open planispiral whorls in the early stage (*i.e. E. japonicum* (Yabe, 1904). In this paper, I use this generic name restrictedly to the latter group, though the early morphology of the type species : *E. indopacificum* Matsumoto, 1967, is unknown. About 70 specimens of *Eubostrychoceras* were examined.

The post-ammonitella stage (early stage) of *Eubostrychoceras* in very similar to that of *Nipponites* and represented by open planispiral whorls. Unlike *Nipponites*, however, dextral or sinistral helicoid coiling mode is maintained throughout the middle stage. Therefore, a highly torticone shell is formed. The axis of helicoid coiling in the middle stage does not coincide with the axis of earlier planispiral coiling. A hook is occasionally observed in the adult stage. Some rib types are shared with *Nipponites* ; normal, periodic strong and broad ribs are also observed, but serrated and periodic double ribs never occur in *Eubostrychoceras*. Constriction is characteristic in one morphotype of this genus (Figure 1).

An example of relative growth pattern between whorl length and whorl height is shown in Figure 2-B. The pattern is very similar to that of *Nipponites* ; the whorl enlarging rate in the first phase is larger than that in the second phase, and the two phases correspond well to the early and middle stages defined by coiling pattern.

The ontogenetic change of rib obliquity was analyzed also in *Eubostrychoceras* (Figure 3-B). Nearly rectiradiate ribs occur in the early stage. After gradually increased during the transitional stage (about one whorl), the rib obliquity becomes about 30 degrees. The value is almost invariable throughout the middle stage.

The distribution of *Eubostrychoceras* is probably restricted to the Lower to Middle Turonian of the northwest Pacific region: Hokkaido (Yabe, 1904; and Matsumoto, 1977), Sakhalin and Kamchatka (Verechagin *et al.*, 1965; Mjhajlova, 1983), though a doubtful specimen was illustrated as "*Bostrychoceras otsukai*" from the Santonian of California (Matsumoto, 1959).

Morphotypes of *Nipponites*

Three morphotypes (A, B and C) of *Nipponites* are recognized by the difference of rib pattern (Figure 4). Each morphotype is defined also by the coiling pattern as follows.

Morphotype A is characterized by the appearance of periodical broad ribs during the late growth stage. Periodic ribs also frequently occur in the early stage of this morphotype at regular intervals of several normal ribs, but they are less frequent in the middle–late stage. The coiling pattern in the early stage is almost simple crioceratoid, though the ammonitella is not yet known. The shell of this stage is thus almost planispiral and represented by more than one and a half whorls. The whorl diameter of this stage is about 2–2.5 cm at most. Because of the regular switching of coiling pattern, a tightly meandrous shell is produced in the middle stage. The switching becomes blurred in the late stage, and the meandrous shell becomes somewhat loose in comparison with the middle stage.

Morphotype B can be distinguished by the serrated ribs developing in the middle-late growth stage. In the early stage this morphotype shares the combination of normal ribs and periodic ribs with Morphotype A. The asymmetricity in the cross section of serrated ribs is most distinct in the later part of the middle stage, and again becomes less typical in the late stage. The coiling pattern of this morphotype is similar to Morphotype A, though the coiling is looser in general. The early planispiral shell is about 3 cm in diameter. Gently meandering shell is produced in the middle stage, and is followed by an irregularly coiled whorl, which occasionally forms a retroversal hook in the late stage.

Morphotype C is characterized by the development of periodic double ribs which correspond to the switching point from crioceratoid to dextral or sinistral helicoid. Though the periodic double ribs do not always appear at the turning point, this feature serves a diagnostic character to distinguish clearly from the other morphotypes. Ribs occur at regular intervals relative to the whorl height. The rib pattern in the early stage is similar to Morphotypes A and B; some periodic ribs are observed among normal ribs. Serrated ribs, which are gradually changed from the normal ribs, are seen in the middle stage as in Morphotype B. The coiling pattern is sometimes irregular in the early stage. It becomes loose and slightly irregular

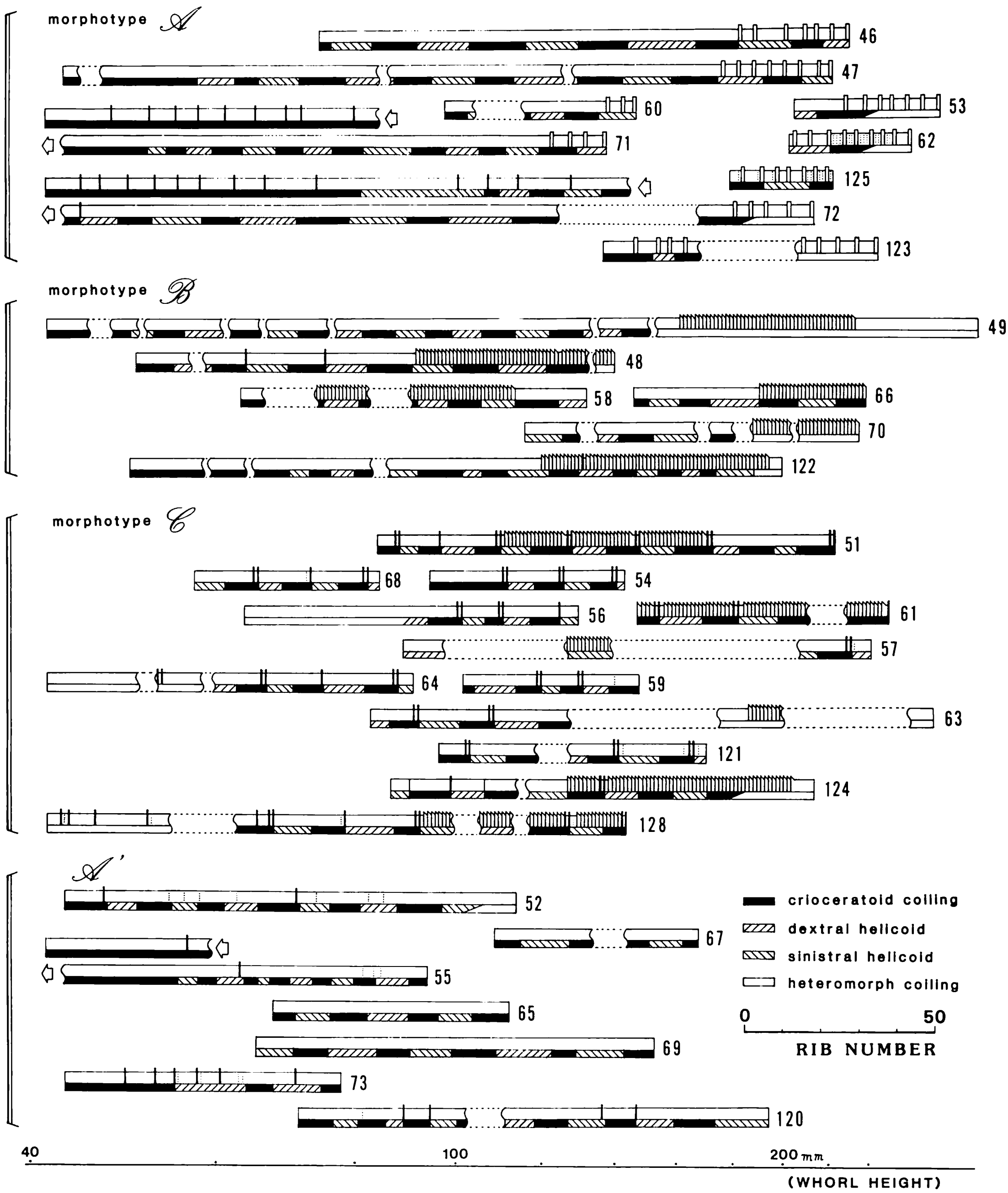


Figure 4. The onotogenetically analyzed rib pattern and modes of coiling of *Nipponites*. See Figure 1 for the rib form symbols. The rib number is taken in the abscissa and approximate scale of whorl height is also shown to express the specimen size. Three morphotypes can be recognized.

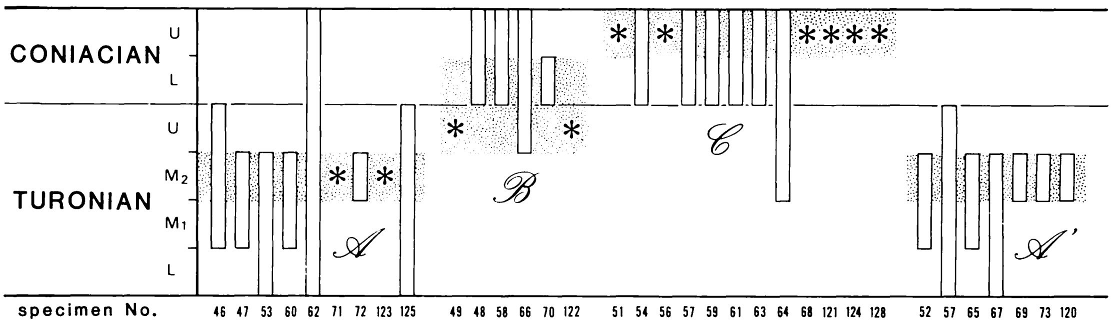


Figure 5. The stratigraphic occurrence of the specimens of *Nipponites* examined in Figure 4. An asterisk indicates *in situ* occurrence from outcrop. White rectangle indicates the possible stratigraphic horizon which is indirectly restricted from the locality and associated index fossils. Dotted area is the expected range of each morphotype. Three morphotypes can be distinguished also by the stratigraphic occurrence.

also in the late stage, but retroversal hook has not yet been confirmed in this morphotype.

Occurrence: The stratigraphic occurrence of each examined specimen is shown in Figure 5. Biostratigraphic age of the Middle and Upper Yezo Groups have been determined by leading fossils (*e.g. Inoceramus* and short-ranged ammonites, Matsumoto 1977, 1984). Morphotypes A, B and C are distinguished also by the different stratigraphic distribution ; they occur from the Middle Turonian, Upper Turonian, and Upper Coniacian, respectively (indicated as asterisk in Figure 5). On the other hand, specimens found in the derived nodules are stratigraphically less reliable, but their possible time span estimated by the biochronological data of assosiated fossils is consistent with the stratigraphic distribution of the three morphotypes (see white rectangles in Figure 5). Based on these direct and indirect stratigraphic data, the presumable shortest range of each morphotype is shown as a dotted area in Figure 5.

The stratigraphic range of Morphotype B may extend to the Lower Coniacian. Because the three morphotypes are distinguished by their stratigraphic occurrences, and because any two morphotypes never coexist in the same nodule, the rib pattern and its ontogenetic change are regarded as a good criterion for natural grouping of *Nipponites*.

There are several immature or fragmentary specimens (shown as A′ in Figures 4 and 5) in which all the characters aforementioned could not be observed. These specimens possess, however, some diagnostic characters of Morphotype A.

Furtermore, Morphotypes A and A′ share the same stratigraphic range, and they sometimes occur from the same nodule. Therefore, these specimens can be included in Morphotype A, though the ontogenetic change of rib pattern is by no means observable.

Relation to previously described species:

The following four species-group names have been proposed for *Nipponites* :

Nipponites mirabilis Yabe, 1904

N. mirabilis var. *sachalinensis* Kawada, 1929

N. bacchus Matsumoto and Muramoto, 1967

N. occidentalis Ward and Westermann, 1977

The holotypes of *N. mirabilis* [No. 46], *N. mirabilis* var. *sachalinensis* [No. 48] and *N. bacchus* [No. 49] were also examined. Morphotype A contains the holotype of *N. mirabilis* (Figures 4 and 14), and evidently it corresponds to this species. Morphotype B contains holotypes of *N. mirabilis* var. *sa-*

chalinensis (Figures 4 and 15) and *N. bacchus* (Figures 4 and 15). Though the two taxa cannot be distinguished by the surface ornamentation as examined in this study, they were defined by some other diagnostic characters; *N. m.* var. *sachalinensis* has small tube diameter relative to the tube length (Kawada, 1929), and *N. bacchus* is characterized by the presence of a retroversal hook at the end of growth (Matsumoto and Muramoto, 1967). The tube diameter is, however, quite variable in actual coexistent specimens of *Nipponites,* and the holotype of *N. m.* var. *sachalinensis* can be regarded as an end member of Morphotype B. The retroversal hook cannot be observed in this holotype because of its incomplete preservation or its immaturity. There is a slight difference in stratigraphic position between the two type specimens: [No. 49] was obtained from the uppermost Turonian, while [No. 48] is probably from the Coniacian. On the other hand, there is no described specimen corresponding to the Morphotype C. If the three morphotypes can be regarded as constituting distinct species, the Morphotype B should be called *N. sachalinensis*. I have not yet examined the detailed rib pattern about *N. occidentalis* from Oregon, U.S.A. So far as I examined the illustration by Ward and Westermann (1977), *N. occidentalis* may be another morphotype of *Nipponites*; the Oregonian specimens have serrated ribs, as in the Morphotypes B and C, and also some strong ribs occurring at the changing point of coiling mode, as double ribs in Morphotype C.

Whorl enlarging rate: The whorl enlarging rate (E) was defined in my previous article (Okamoto, 1988a) by the following equation:

$$\ln E = d/ds\ (\ln r)$$

where s and r indicate the growth stage and tube radius, respectively. This value can also be estimated from the relative growth diagram shown in Figure 2 and from the following equation:

$$E = 1 + dl/2dh$$

where dl/dh indicates the slope in the relative growth diagram.

The whorl enlarging rate in the later phase is measured in each specimen (Figure 8).

The histogram mode of this value is about 1.020 in Morphotype A, and slightly higher values are suggested in Morphotypes B and C, though the differences are statistically insignificant.

Rib density and obliquity: The rib density is defined as the number of ribs in a unit distance along the ventral margin. The unit distance is equal to the tube radius at any growth stage. The rib density, which is almost invariable throughout growth, was measured mainly in the middle growth stage (Figure 8). Morphotype A shows fairly variable rib density which ranges from 2.0 to 4.0. Unlike Morphotype A, the values in Morphotypes B and C lie around 2.0 with smaller deviations.

The rib obliquity in the middle stage of *Nipponites* regularly oscillates between two constant values (Figure 3-A). The oscillation range of rib obliquity is shown in Figure 9. The maximum value of rib obliquity is quite variable even within each morphotype, while the minimum value is almost constant in every specimen. Morphotype A reveals generally a wider obliquity range than Morphotypes B and C. Sometimes Morphotype C shows a very narrow range.

Meandering amplitude and frequency: There are peculiar measurements for the description of meandrous shell like *Nipponites*. The meandering amplitude is α/λ as shown in Figure 9, where α and λ means a half of wave height and a half of wave length measured along the tube center line. The meandering is generally strong in the Morphotype A and very weak in some specimens of Morphotype C. This measurement, however, does not serve a good criterion to distinguish these morphotypes because of the wide range of variation in each morphotype.

The meandering frequency is defined as the number of meandering cycles within one revolution in the "symmetric plane". Because the actual values of this character were obtained only from nine specimens in total, it is difficult to discuss the difference between these morphotypes. The meandering frequency in *Nipponites* is fairly constant, lying within the range from 2.5 to 3.0 (Figure 10).

Morphotypes of *Eubostrychoceras*

Three morphotypes are recognized by the difference of rib pattern in *Eubostrychoceras* (Figure 6). Each morphotype has two discrete forms: dextral and sinistral helicoids after the initial planispiral coiling. The ratio between dextral and sinistral individuals is almost even in each morphotype. The

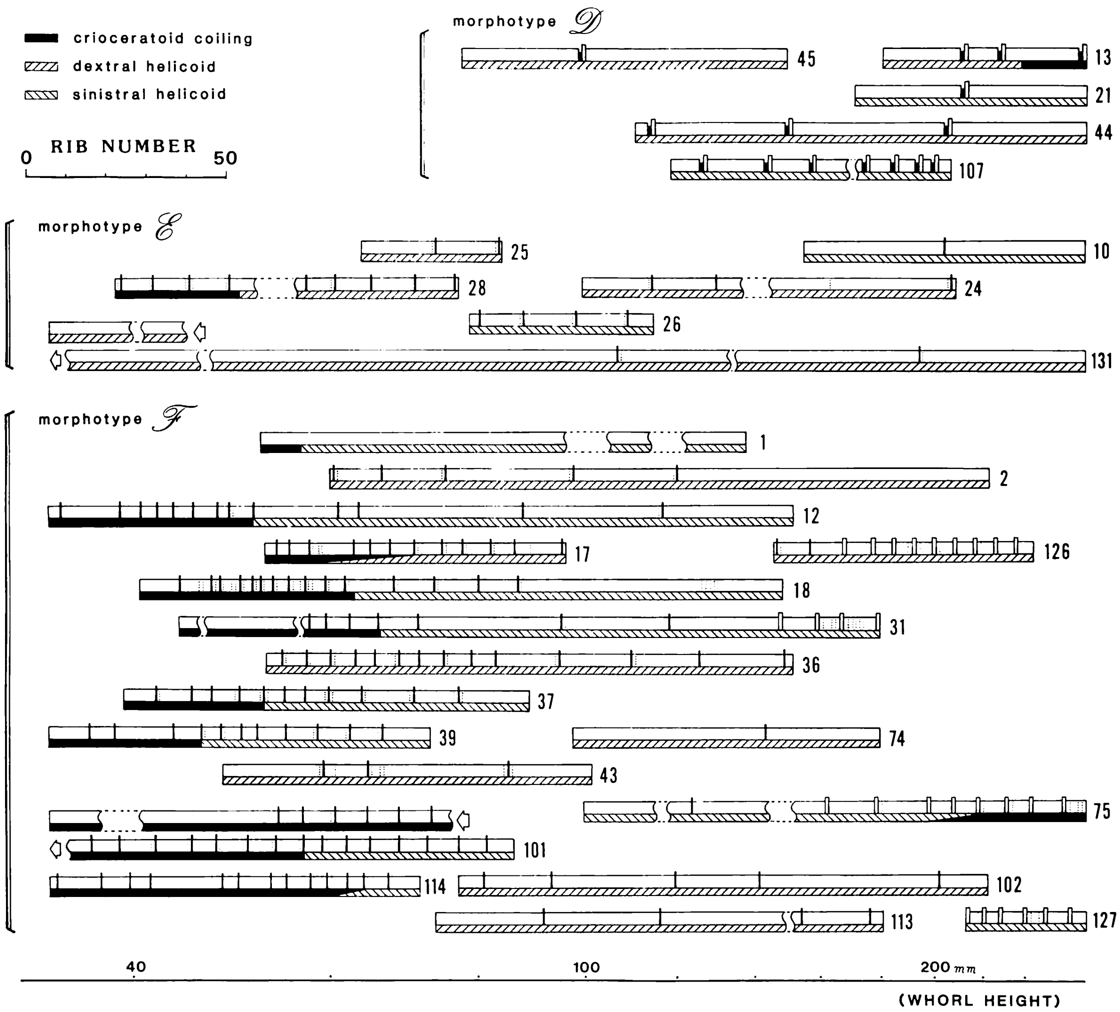


Figure 6. The ontogenetically analyzed rib pattern and mode of coiling of *Eubostrychoceras*. The rib form symbols are the same as Figure 4. Morphotype D can be distinguished by the existence of constriction. Morphotypes E and F, which show clear difference in rib density (Figure 8), cannot be distinguished only by this diagram.

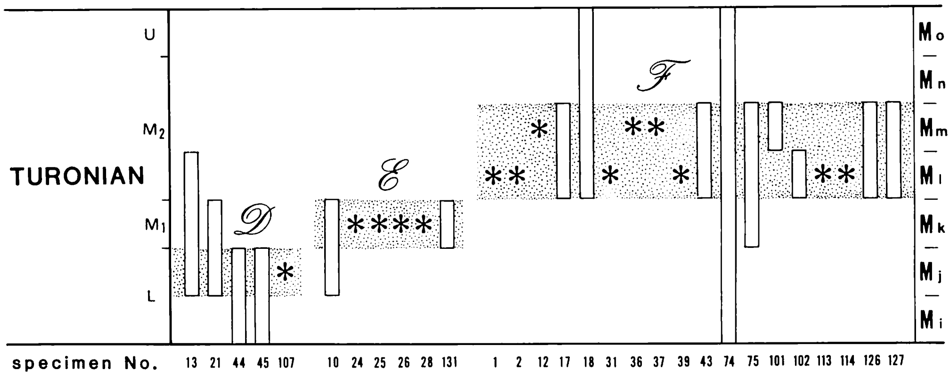


Figure 7. The stratigraphic occurrence of *Eubostrychoceras* examined in Figure 6. The format and symbols are the same as Figure 5. Three morphotypes are clearly distinguished in stratigraphic ranges. Because almost all the specimens are obtained from the Tappu area in Hokkaido, the stratigraphic subdivision by Tanaka (1963) is also shown on the right.

three morphotypes are defined as follows.

Morphotype D is characterized by the presence of constrictions. The constrictions correspond to the periodic strong ribs which occur two or three times per a whorl. Several fragmentary specimens are assigned to this morphotype. The ammonitella and early stage cannot be observed in these specimens. Transverse ribs appear at regular intervals during the middle stage. A hook, which is represented by an almost planispiral semiwhorl, is developed in the adult stage. The dextral and sinistral coilings can be regarded as intrapopulational variation in the middle stage of this morphotype.

Morphotype E has thick whorls with fine and dense ribs occurring at regular intervals. The ammonitella and the shell of the latest stage are unknown, and early planispiral stage is only partly observable in the specimen [No. 28]. Strong ribs occur periodically in the early stage and becomes less frequent with growth. Dextral and sinistral individuals often occur in the same nodule.

Morphotype F shows relatively loose and variable shell morphology in comparison with Morphotype E. The ammonitella of this morphotype, which was described as *Eubostrychoceras japonicum* by Tanabe *et al.* (1981), is very large and about 2 mm in diameter. A few planispiral whorls are formed in the early stage, and are followed by several helicoid whorls of middle growth stage. A hook observed in the late stage is represented by a rather simple and criocer-atoid semiwhorl without torsion. Ribs on whorls occur at regular intervals. Periodic strong ribs are frequent in the early stage, and become less frequent with growth. Periodic broad ribs can be observed on the later whorls of some mature specimens. Though the surface ornamentation during the growth is very similar to that of Morphotype E, the two morphotypes can be clearly distinguished by the density of ribs.

Occurrence : The stratigraphic occurrence of each examined specimen is shown in Figure 7. Many specimens of *Eubostrychoceras* were obtained from the Tappu area. Both Morphotypes E and F occur in the Middle Turonian, and their ranges are slightly but clearly different. So far as I am aware, Morphotype D never occurs with Morphotypes E or F in the same nodule. Though the stratigraphic data of Morphotype D is still deficient, its occurrence may be restricted to the Lower Turonian. The three morphotypes defined by shell ornamentation, therefore, probably represent the natural groups of *Eubostrychoceras*.

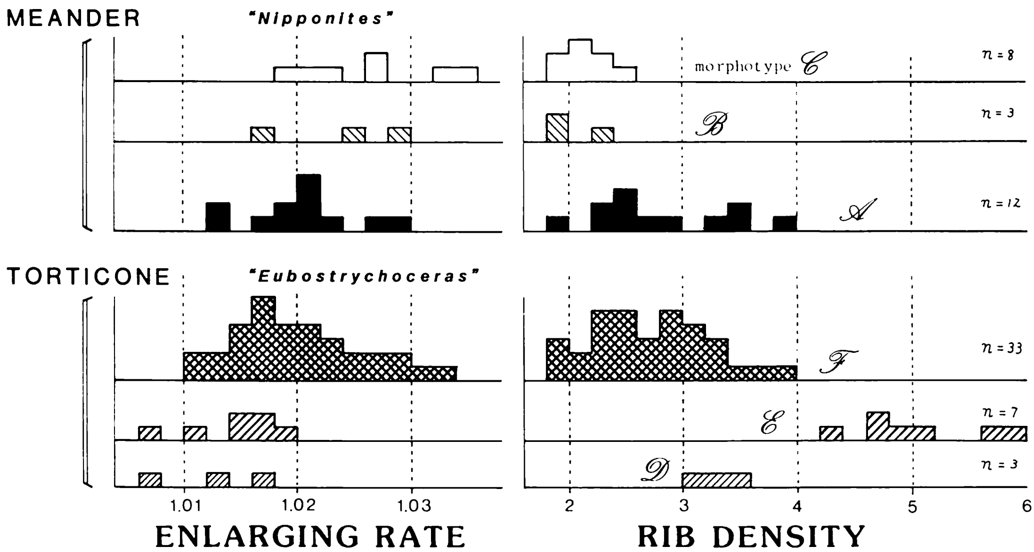


Figure 8. Histograms showing frequency distributions of whorl enlarging rate and rib density of six morphotypes measured in their middle growth stage. Morphotypes E and F can be discretely distinguished by the rib density. Morphotypes A and F show similar distributions both in the enlarging rate and rib density.

Relation to previously described species : Only one species name *Eubostrychoceras japonicum* (Yabe, 1904) has been used for these three morphotypes. The type specimen of *E. japonicum* (Figures 6 and 14), which is treated here as [No. 74] belongs to Morphotype F.

Whorl enlarging rate : The whorl enlarging rate in the middle stage was measured also in *Eubostrychoceras* (Figure 8). Morphotypes D and E have a relatively low enlarging rate which is usually smaller than 1.02. Morphotype F shows wide variation in this character ranging from 1.01 to more than 1.03. Though the range of variation in Morphotype F partly overlaps with those of Morphtotypes D and E, its mean value is significantly different.

Rib density : The rib density is variable in *Eubostrychoceras* but shows different frequency distributions among the three morphotypes (Figure 8). This character is useful to distinguish Morphotype E from F ; Morphotype E has very high rib density, which is usually more than 4.0, and is distinct from the Morphotype F having smaller value ranging from 1.8 to 4.0. Morphotype D has moderate rib density ranging from 3.0 to 3.6, though the sample size is small.

Comparative morphology of *Nipponites* and *Eubostrychoceras*

Six morphotypes are recognized in *Nipponites* and *Eubostrychoceras* by several distinct characteristics. The morphotypes in each genus are also distinguished by the difference of their stratigraphic distribution. Several characters examined in this study are summarized in Table 1. The surface ornamentation of *Nipponites* and *Eubostrychoceras* seems to have changed slightly but discontinuously with time : (Morphotype A → B → C in *Nipponites* and Morphotype D → E → F in *Eubostrychoceras*). The geographic distribution of both genera is almost identical and restricted to the north Pacific region.

Therefore, these morphotypes of *Nipponites* and *Eubostrychoceras* may represent monophyletic lineages.

Table 1. Itemized characteristics of six morphotypes. Shared characters with Morphotype A are shown by striped area, and Morphotype F is most similar to Morphotype A. The abbreviations are as follows: planispiral shell (plani.), meandrous shell (meand.), helicoid shell (helic.), heteromorph shell (hetero.), Turonian (Turon.) and Coniacian (Coniac.).

morphotypes	A	B	C	D	E	F
normal rib	X	X	X	X	X	X
serrated rib		X	X			
periodic rib	X			X	X	X
periodic double rib			X			
broad rib	X				X?	X
constriction				X		
rib density	2 - 4	2 ±	2 ±	3 - 4	4 - 6	2 - 4
crioceratoid	X	X	X	X	X	X
helicoid (dextral)	X	X	X	X	X	X
helicoid (sinistral)	X	X	X	X	X	X
enlarging rate	1.01-03	1.01-03	1.02-04	1.01-02	1.01-02	1.01-03
early stage	plani.	plani.	hetero.	?	plani.	plani.
middle stage	meand.	meand.	meand.	helic.	helic.	helic.
stratigraphic range	M.Turon.	U.Turon.	U.Coniac.	L.Turon.	L.Turon.	M.Turon.

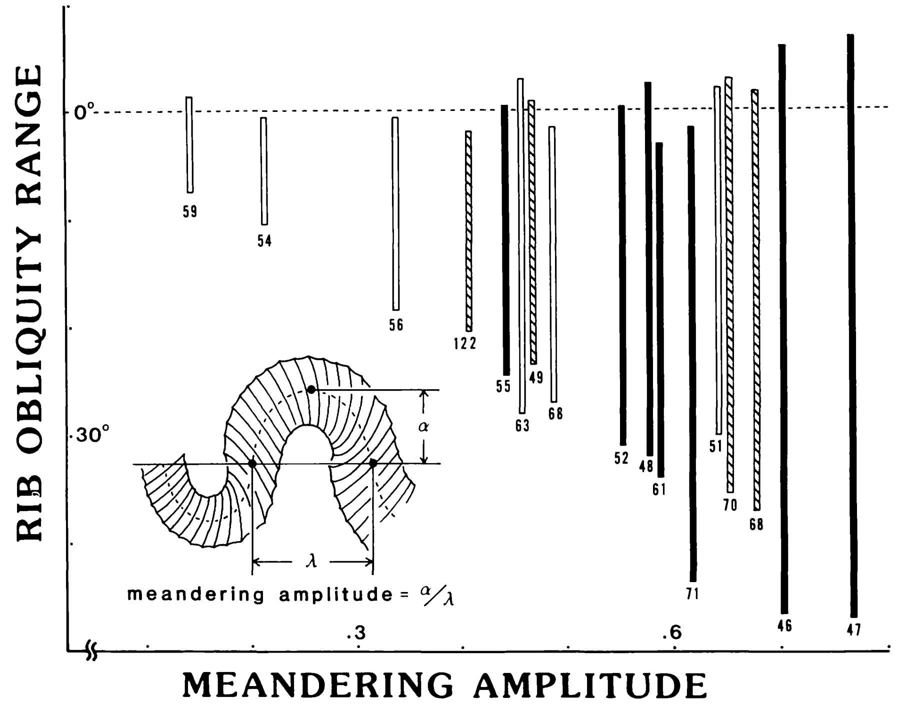


Figure 9. Relationship between the range of rib obliquity and meandering amplitude in *Nipponites*. Black, striped and white rectangles indicate Morphotypes A, B and C, respectively. Linear relationship can be generally recognized between the meandering amplitude and maximum value of rib obliquity. [Correction; The rectangle for the specimen 48 should be striped].

Morphotype B can be distinguished from Morphotype A by the development of serrated ribs in the middle stage and the absence of broad ribs in the late stage. Morphotype C is characterized by the addition of periodic double ribs which corresponds to the switching points of coiling from crioceratoid to helicoid. On the other hand, Morphotype D, the oldest form of *Eubostrychoceras,* is distinguished from Morphotypes E and F by the existence of constrictions accompanying periodic rib. Morphotype D is possibly the ancestral form of Morphotypes E and F, though its stratigraphic distribution is still obscure. Morphotype E changes to Morphotypes F with having coarser densed ribs and slightly loose helicoid whorls.

The most impressive similarity is recognized between Morphotype A of *Nipponites* and Morphotype F of *Eubostrychoceras*.

Morphotype A is the oldest and most primitive form of *Nipponites,* and Morphotype F is contemporary form of *Eubostrychoceras*. They can hardly distinguished by the surface ornamentation but for rib obliquity. They share not only similar early planispiral (crioceratoid) whorls, but also the basic modes of coiling throughout growth. The crioceratoid coiling, which is intermittently appears in the middle stage of Morphotype A, is occasionally observed in the late stage of Morphotype F. Both dextral and sinistral helicoid coilings are alternately appear in the middle stage of Morphotype A, while in Morphotype F dextral and sinistral helicoid coilings appear alternatively and consistently as dimorphism. The standardized torsion (see Okamoto, 1988a) of helicoid coiling in *Eubostrychoceras* is generally ranges from 0.02 to 0.04. These values seem to be almost equal to those of the helicoid parts of *Nipponites*, though it is very difficult to measure this value accurately in *Nipponites*. In spite of the similarity of the developmental patterns of surface ornamentation and basic modes of coiling, there is, needless to say, clear difference of shell outline between the two morphotypes in their three-dimensional architecture.

Another difference between Morphotypes A and F can be recognized in the rib obliquity of their middle stage (Figure 3).

The rib obliquity is, however, closely related to the life orientation in the sea water (Okamoto, 1988b, 1988c). The life orientation is determined by the positions of center of buoyancy and center of gravity, and can also be estimated by computer calculation and simulation. The life orientations of *Nipponites* and *Eubostrychoceras* in the middle stage, as theoretically inferred by computer simulation (Okamoto, 1988b for *Eubostrychoceras japonicum* and Okamoto, 1988c for *Nipponites mirabilis*), are completely different ; the elevation angle of growth direction in the middle stage of *Nipponites* regularly oscillates between the almost constant maximum and minimum values, while that of *Eubostrychoceras* is nearly constant throughout the middle stage. The rib obliquity well corresponds to the estimated change of

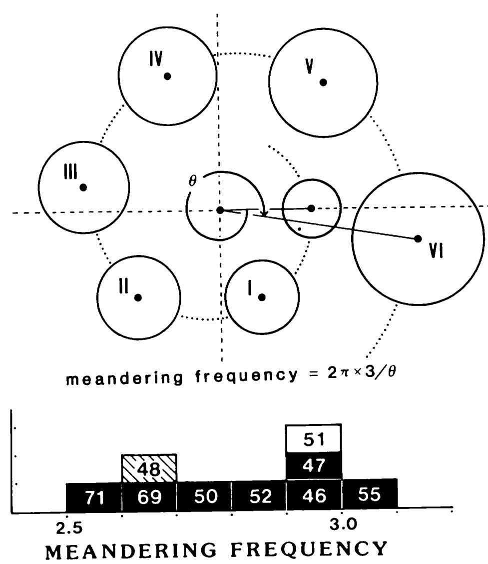


Figure 10. Histogram showing the variation of meandering frequency in *Nipponites*. Black, striped and white rectangles show Morphotypes A, B and C, respectively. Most specimens have the value between 2.5 to 3.0.

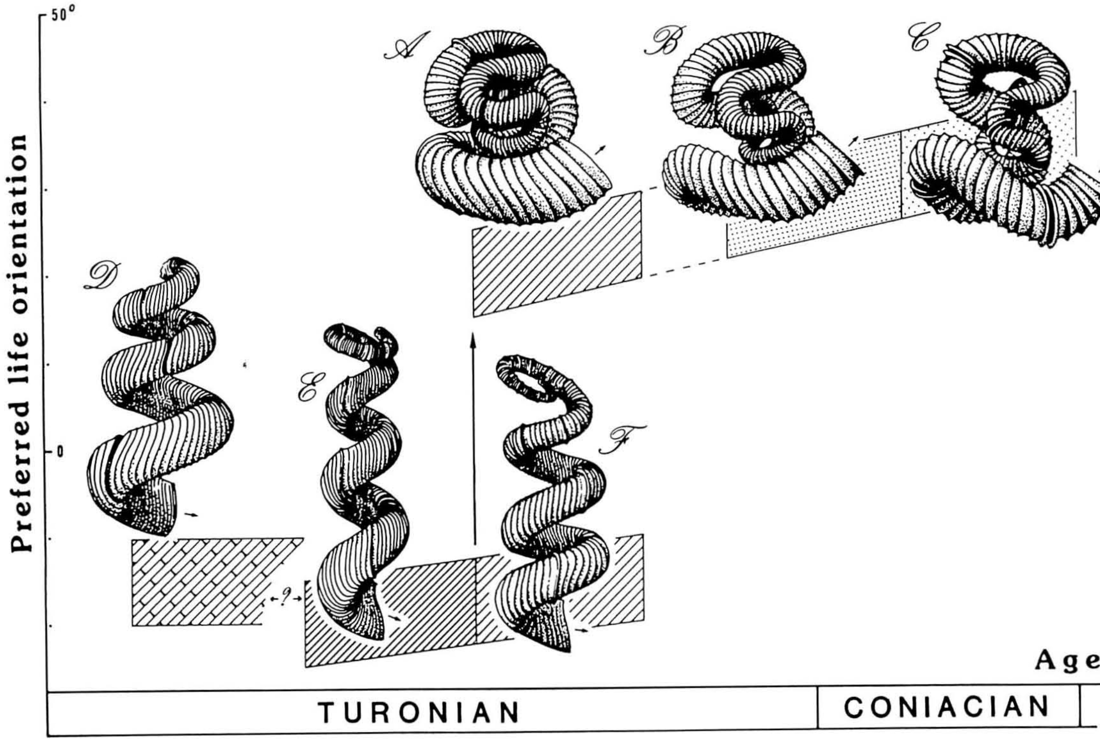


Figure 11. Concluding diagram showing the relationship of six morphotypes. The ordinate is time, and the abscissa indicates the preferred life orientation estimated by computer simulatiton and rib obliquity. Rib pattern changed slightly but stepwise during the time. The abrupt change of coiling from *Eubostrychoceras* to *Nipponites* strongly influences the preferred life orientation.

growth direction of *Nipponites* and *Eubostrychoceras*. Therefore, the difference of the rib obliquity between Morphotypes A and F is caused by the difference of growth direction during the middle stage, and it is also closely related to the different shell outline. The regulatory mechanism of rib obliquity can be regarded as identical between the two genera.

In spite of the impressive similarity between Morphotypes A and F, no intermediate form has been actually known. If *Nipponites* was phylogenetically derived from *Eubostrychoceras*, the morphological change must have been accomplished instantly.

Coiling regulatory hypothesis for the meandering shell

I previously suggested the morphological saltation between *Eubostrychoceras japonicum* and *Nipponites mirabilis* on the basis of a theoretical approach with computer simulations (Okamoto, 1988c). The "coiling regulatory model" applied in that study is briefly introduced below.

The three-dimensionally meandered shell in *Nipponites* is interpreted as an effect of homeostatic regulation of its life orientation. The meandered whorls are regularly disposed around a certain central point. This model hypothesized that the center of buoyancy is identical with the center of coiling, and the distance from the center of buoyancy to the aperture is assumed to increase isometrically with whorl height. The three modes of coiling, *i.e.* crioceratoid, dextral and sinistral helicoids, are introduced in this model. Crioceratoid is defined as a coiling mode in the vertical plane ; therefore, if the life orientation does not roll right or left during the growth of this coiling mode, planispiral whorls are produced. Crioceratoid coiling lifts the growth direction of apertural part or maintains a large elevation angle. On the other hand, helicoid (either dextral or sinistral) is defined as a spiral coiling mode with constant torsion (which is standardized by the tube radius and is assumed as 0.03 in this simulation, see Okamoto, 1988a). Therefore, helicoid coiling changes the growth direction downward or keeps a small elevation angle. The following three variables are also introduced in the computer simulation; P/T: ratio of phragmocone to total cone length, Up: the upper limit of growth direction, Lo: the lower limit of growth direction. These variables keep constant throughout one simulation. The life orientation is hydrostatically determined in every growth stage by assuming the neutral buoyancy and homogeneous materials for phragmocone and living chamber. If the elevation angle of growth direction exceeds upper limit by crioceratoid coiling, the mode of coiling switches to dextral or sinistral helicoid which is efficient to decrease the elevation angle. If the growth direction falls under the lower limit, the mode of coiling again becomes crioceratoid so as to elevate the growth direction. The computer simulation for the meandering growth of *Nipponites* was most successful with inputting the constant values of $P/T=0.55$, $Up=40°$ and $Lo=0°$.

Meandering variation is theoretically deduced with slight modification of initial conditions; the P/T ratio gives strong effect to the meandering frequency, and the range between the upper and lower limits is influential mainly to the meandering amplitude (Okamoto, 1988c). These expectations can be verified by the quantitative analysis of actual specimens.

According the computer simulation, the meandering frequency per one revolution (2π) increases approximately from 2 to 4 as the P/T ratio decreases from 0.7 to 0.4 (Okamoto, 1988c, figure 10A). On the contrary, the variation in meandering frequency of actual specimens is comparatively narrow. The meandering frequency in the almost all specimens is within the range of 2.5–3.0 (Figure 10). This meandering frequency is produced by the computer simulation with the P/T ratio of 0.6–0.5. Because considerable length of phragmocone is necessary to maintain the neutral buoyancy, the actual distribution of meandering frequency is quite reasonable. I did not measure the P/T ratio of actual specimens, but Ward and Westermann (1977) measured the values in two specimens of *N. occidentalis* as 0.55 and 0.57. From the result of calculation of total average density, they concluded that the species could maintain the neutral buoyancy in the sea water.

A strongly meandering shell was outputted when a wide growth direction range (Up–Lo) was inputted. A weakly meandrous shell was, in contrast, produced with a narrow direction range (Okamoto, 1988c, figure 10B). I assume that *Nipponites* kept a constant aperture angle relative to the horizontal plane during growth. Because the rib runs parallel to the aperture at every growth stage, if the above assumption is appropriate, the rib obliquity should be influenced by the meandering intensity. The linear relationship between the range of rib obliquity and meandering amplitude is also obvious in actual specimens (Figure 9). These lines of evidence indicate that the growth direction regulatory model is appropriate for the interpretation of meandrous coiling of *Nipponites*.

When an extremely small lower limit is inputted in the same computer program, a persistent torticone shell form is outputted, because the coiling feedback does not occur throughout the growth. This hypothetical coiling pattern is quite similar to that of *Eubostrychoceras japonicum*. As recognized by the simulation, the change from torticone shell to meandrous shell occurs abruptly without any intermediate form, even if the initial condition of growth direction range is


1
2
3
4
morphotype 𝒟
morphotype ℰ

continuously changed (Okamoto, 1988c, figure 11). The intermediate form between Morphotypes A and F does not appear not only empirically but also theoretically. A morphological saltation from torticone to meandrous shell is deduced also in the growth simulation based on the coiling regulatory model.

Origin of *Nipponites*

Both the result of computer simulations (Okamoto, 1988c) and the fossil records in Hokkaido strongly suggest that *Nipponites* was abruptly derived from *Eubostrychoceras* without any intermediate form. The stratigraphic ranges of the two genera partly overlap each other in the Middle Turonian (*Inoceramus hobetsensis* Zone); Morphotype A of *N. mirabilis* and Morphotype F of *E. japonicum* constitute a concurrent zone (Figure 11). Because gradual morphological change is theoretically impossible in this case, the origin of *Nipponites* may offer an interesting problem in evolutionary paleontology.

Several different interpretations may be possible about the biological relationship between Morphotypes A and F. In this case subspecific relation and ecophenotypic effect are rather unlikely, because the two morphotypes share the same stratigraphic range and often coexist in the same calcareous nodules. *Nipponites* is usually rarer in occurrence than *Eubostrychoceras*, but there is an exceptional nodule in which three individuals of Morphotype A are contained without any individual of Morphotype F. Pathologic anomaly is also unlikely for *Nipponites*, because Morphotypes B and C never coexist with any similarly ornamented *Eubostrychoceras* (Figure 11).

The origin of *Nipponites* should be sought in a (or a few) mutant individual with meandrous coiling which suddenly appeared in a population of *Eubostrychoceras*. If complete reproductive isolation is assumed simultaneously with the drastic mutation, the first appearance of *Nipponites* may represent instant speciation or "hopeful monster" of Goldschmidt's (1940) sense. The difficulty of such an instant speciation was discussed at length by Mayr (1963). Probably the "hopeful monster" could hardly find its suitable mate, unless an unusually high mutation rate were assumed.

On the other hand, if the morphological difference between the two morphotypes were only due to polymorphism in a randomly mating population, the evolution from *Eubostrychoceras* to *Nipponites* would be explained by phenotypic substitution (or transient polymorphism) like the famous industrial melanism of *Biston betularia*. Such a mode of evolution was well documented by Hayami (1973, 1984) in a Pliocene-Recent pectinid, *Cryptopecten vesiculosus*, and was also assumed by Hirano (1978) in the relation between two successive forms of *Gaudryceras*. The possibility of phenotypic substitution cannot be denied in this case. However, the morphological change from torticone shell to meandrous shell also yields drastic changes of life orientation and behavior. Even if there was no genetic difference, the decisive morphological and ecological gap may result in some difficulty of mating between the two morphotypes.

Though the data are too insufficient to solve the problem, I presume, as the third possibility, that some homogamy (preference of an individual to mate with similar phenotype) may have contributed to establish the new lineage of *Nipponites*. At least in the initial stage of speciation, incomplete repro-

← **Figure 12.** *Eubostrychoceras* from the Lower-Middle Turonian. **1,** UMUT MM18548 [=No. 44], Morphotype D, from Nakakinembetsu-gawa, Tappu, ×1. **2,** UMUT MM18530 [=No. 13], Morphotype D, from Hifumi-zawa, Tappu, ×0.9. **3,** WEA019Y [=No. 131], Morphotype E from Isojiro-zawa, Oyubari, ×1. **4,** UMUT MM18527 [=No.10], Morphotype E from Kamikinembetsu-gawa, Tappu, ×1.

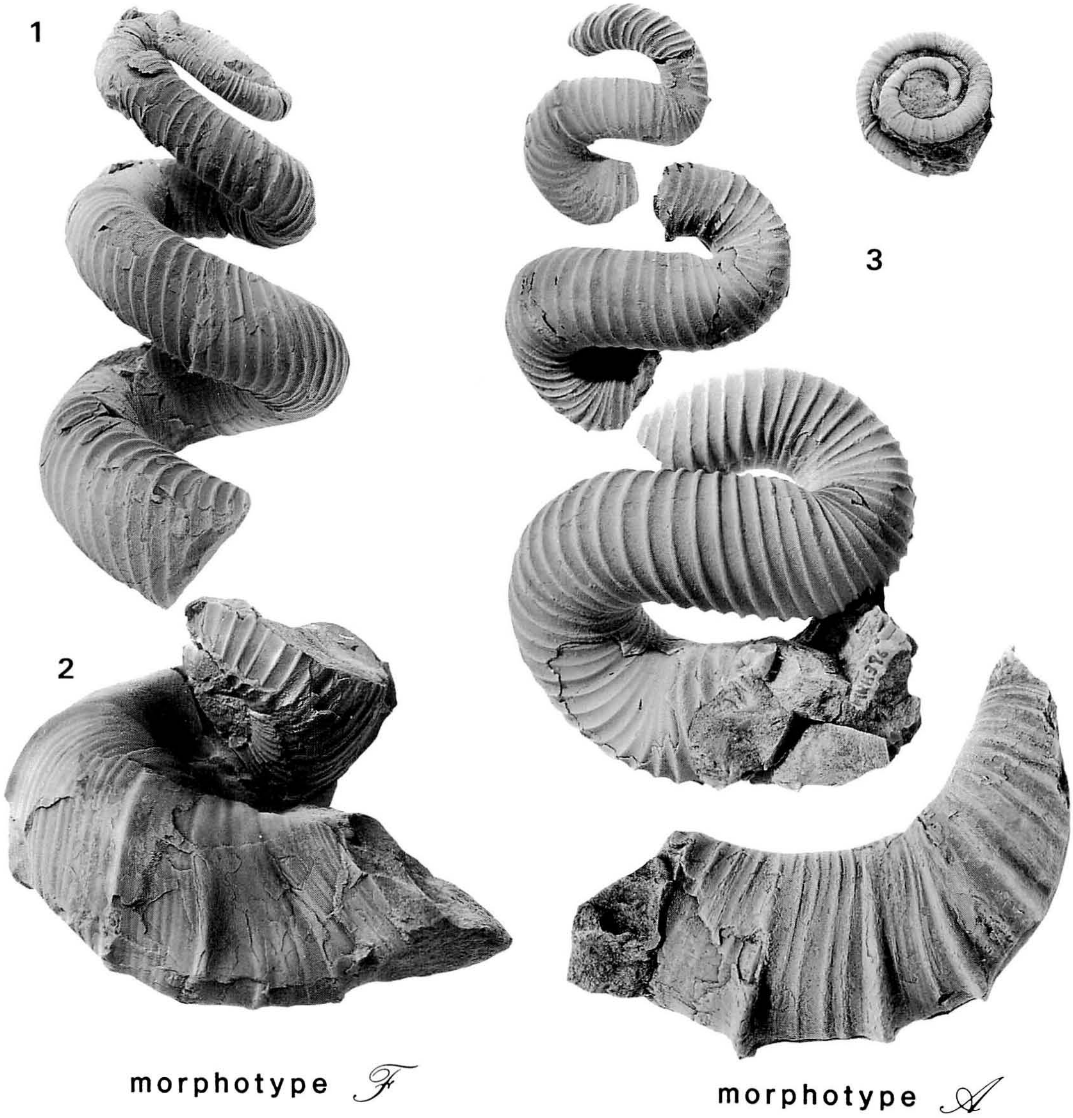
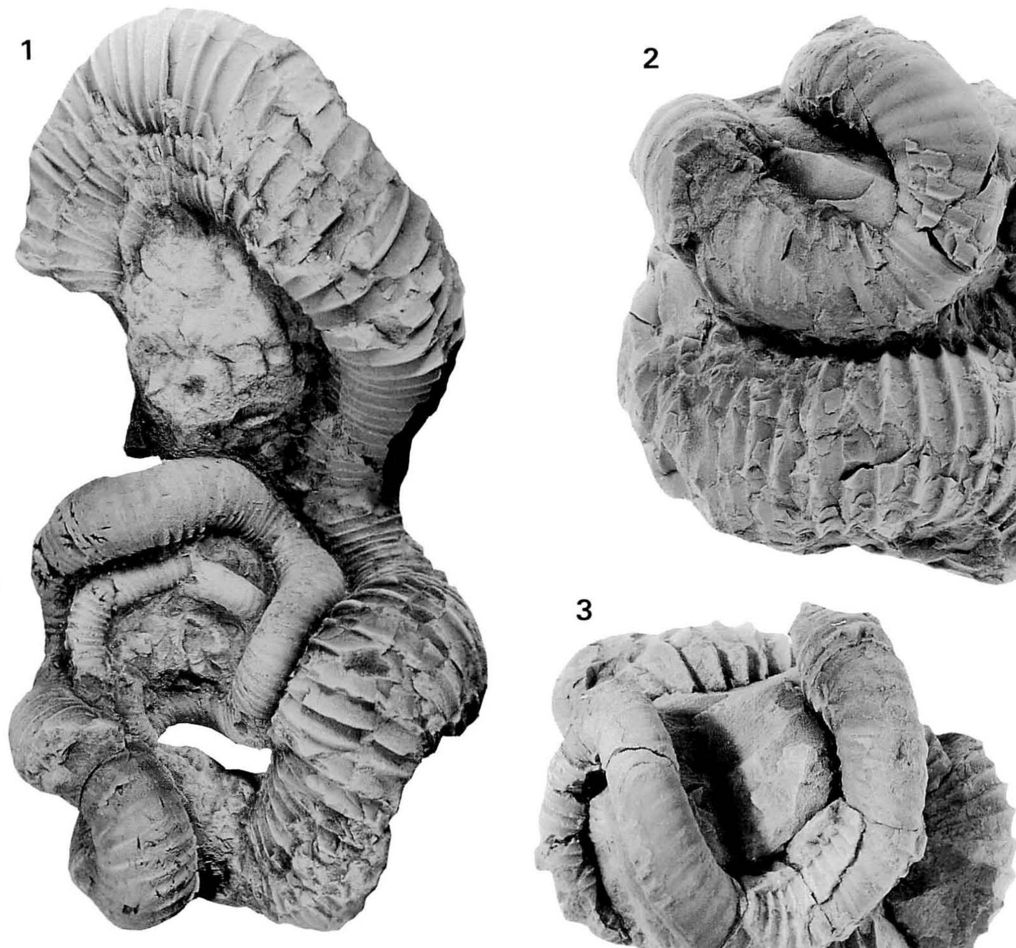


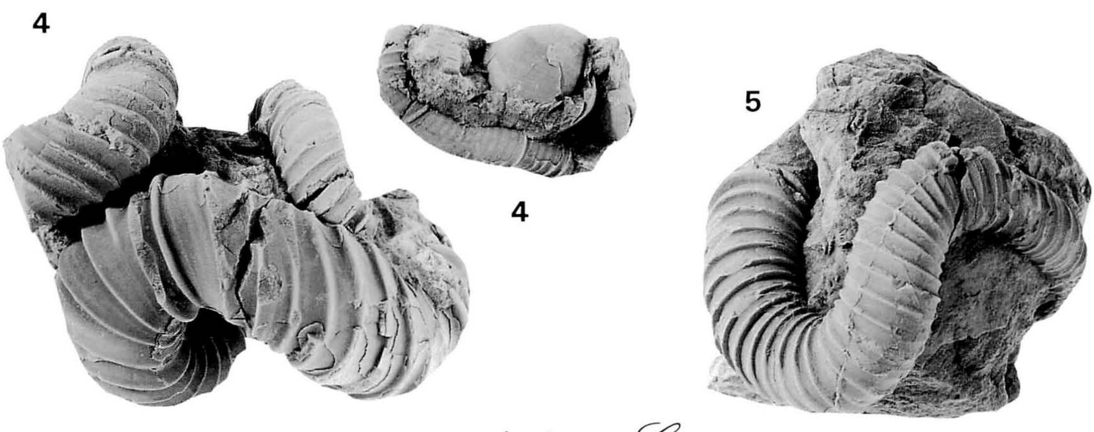
Figure 13. *Eubostrychoceras* and *Nipponites* from the Middle Turonian. **1,** UMUT MM18529 [=No. 12], Morphotype F, from Hifumi-zawa, Tappu, ×1. **2,** GK.H5796 [=No.130], Morphotype F, from Shirakin-zawa, Oyubari, ×1. **3,** UMUT MM18571a [=No. 72], Morphotype F, from Higashi-ura, Wakkanai, ×1.

→ **Figure 14.** *Eubostrychoceras* and *Nipponties* from the Middle Turonian. **1,** UMUT MM18524a [= No. 1], Morphotype F, from San-no-sawa, Tappu, ×1. **2,** UMUT MM18524b [=No. 2], Morphotype F, from the same nodule as above, ×1. **3,** UMUT MM18533 [=No. 17], Morphotype F, from Kamikinembetsu-gawa, Tappu, ×1. **4,** UMUT MM7559 [=No. 74], holotype of *Eubostrychoceras japonicum* (Yabe), Morphotype F, from Yubari-gawa, Yubari. **5,** UMUT MM7560 [=No. 46], holotype of *Nipponites mirabilis* Yabe, Morphotype A, from Obirashibe-gawa ?, Tappu, ×1. **6,** UMUT MM18254 [=No. 71], Morphotype A, from Kamikinembetsu-gawa, Tappu, ×1 **7,** UMUT MM18571a [=No. 72], Morphotype A, from Higashi-ura, Wakkanai, ×1.

morphotype $\mathscr{F}$ morphotype $\mathscr{A}$



morphotype $\mathscr{B}$



morphotype $\mathscr{C}$

ductive isolation may be required to increase the mutant individuals.

The coexistence of *N. mirabilis* and *E. japonicum* may be actually a result of allopatric speciation (and subsequent migration), but, if so, such a morphologic saltation must have occurred in the peripheral isolate. I emphasize here the possibility of sympatric speciation by drastic morphological (not necessarily genetic) saltation which prevents the mutant from random mating with the wild-type individuals. The causes of punctuated evolution in fossil organisms are of course multiple. The origin of *Nipponites* seems to suggest that a certain architectural factor (Seilacher, 1970) also is significantly related to the disjunct pattern of macroevolution.

Conclusion

Nipponites was probably derived from *Eubostrychoceras* in the Middle Turonian, judging from the similarities of surface ornamentation, basic mode of coiling and shell morphology in the early stage. The morphological difference between them can be recognized only in their three-dimensional shell architectures, though it is quite impressive. Unlike *Eubostrychoceras, Nipponites* developed the coiling regulatory mechanism so as to keep the slightly upward growth direction, and the meandrous shell was formed probably as a consequence of hydrostatic adjustment. Both fossil records and the computer simulation of coiling suggest that the morphological saltation occurred without any intermediate form. *Nipponites* took some minor stepwise changes during its lineage. The last morphotype of *Nipponites* having serrated ribs and periodic double ribs became considerably different from *Eubostrychoceras*. If the derived new form had prospered and diversified, it would have resulted in the origin of a new family. I emphasize here that such abrupt morphological saltation may cause the establishment of a higher taxonomic group. Unfortunately, the lineage of *Nipponites* became extinct probably at the end of Coniacian without leaving any descendant.

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← **Figure 15.** *Nipponites* from the Upper Turonian (**1, 2**) and Coniacian (**3-5**). **1,** GK.H5444 [=No. 49], holotype of *Nipponites bacchus* Matsumoto and Muramoto, Morphotype B, from Pombetsu-gawa, Ikushumbetsu, ×.6. **2,** UMUT MM18570 [=No. 70], Morphotype B, from Hidarimata-zawa, Ikushumbetsu, ×1. **3,** UMUT MM7666 [=No. 48], holotype of *Nipponites mirabilis* var. *sachalinensis* Kawada, Morphotype B, from Miho-gawa, south Sakhalin. **4,** WEA018T [=No. 128], Morphotype C, from Obirashibe-gawa, Tappu. **5,** UMUT MM18255 [=No. 68], Morphotype C, from Okufutamata-zawa, Tappu.

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北海道上部白亜系蝦夷層群より産する，ノストセラス科異常巻きアンモナイト：*Nipponites* および近縁種 *Eubostrychoceras japonicum* について，層序学的な形態変化をできる限り詳細に検討したところ，各々の系統では，時代と共に少しずつ，しかしながら段階的に殻表面の彫刻が変わっていくことが明らかになった。一方，*Nipponites* の系統で最も原始的な形態型の殻彫刻やその他の形質は，同時代の *Eubostrychoceras* のそれと，ほとんど区別できない。両者は，殻の三次元的構造が全く異なっており，これらの中間的形態も

知られていないが，前者は後者から派生したことが強く示唆される。本研究で示されたデータは，先に筆者によって理論形態学的に帰結された，“*Nipponites* は，*Eubostrychoceras* から全く突然に（中間型なしに）生じた” という仮説を，比較形態学的および層序学的側面から支持するものである。
岡本　隆

Appendix table. Collation of the consecutive specimen numbers and register numbers.

Specimen No.	Register No.
Nos. 1-4	UMUT MM18524a-d
Nos. 5-8	UMUT MM18525a-d
No. 9	UMUT MM18526
No. 10	UMUT MM18527
No. 11	UMUT MM18528
No. 12	UMUT MM18529
No. 13	UMUT MM18530
No. 14	UMUT MM18531
Nos. 15-16	UMUT MM18532a-b
No. 17	UMUT MM18533
No. 18	UMUT MM18534
Nos. 19-20	UMUT MM18535a-b
No. 21	UMUT MM18536
Nos. 22-23	UMUT MM18537a-b
Nos. 24-28	UMUT MM18538a-e
No. 29	UMUT MM18539
No. 30	UMUT MM18540
No. 31	UMUT MM18541
Nos. 32-34	UMUT MM18542a-c
Nos. 35-38	UMUT MM18543a-d
Nos. 39-40	UMUT MM18544a-b
No. 41	UMUT MM18545
No. 42	UMUT MM18546
No. 43	UMUT MM18547
No. 44	UMUT MM18548
No. 45	UMUT MM18549
No. 46	UMUT MM7560
No. 47	GK.H5846 (replica : UMUT MM18550)
No. 48	UMUT MM7666
No. 49	GK.H5444 (replica : UMUT MM18551)
No. 50	GK.H5853 (replica : UMUT MM18552)
No. 51	replica : UMUT MM18553
No. 52	replica : UMUT MM18554
No. 53	replica : UMUT MM18555
No. 54	replica : UMUT MM18556
No. 55	replica : UMUT MM18557
No. 56	replica : UMUT MM18558
No. 57	replica : UMUT MM18559
No. 58	replica : UMUT MM18560
No. 59	replica : UMUT MM18561
No. 60	replica : UMUT MM18562
No. 61	replica : UMUT MM18563
No. 62	replica : UMUT MM18564
No. 63	replica : UMUT MM18565
No. 64	replica : UMUT MM18566
No. 65	replica : UMUT MM18567
No. 66	replica : UMUT MM18568
No. 67	replica : UMUT MM18569
No. 68	UMUT MM18255
No. 69	UMUT MM17738
No. 70	UMUT MM18570
No. 71	UMUT MM18254
Nos. 72-73	UMUT MM18571a-b
No. 74	UMUT MM7559
No. 75	UMUT MM18572
No. 76	UMUT MM18573
No. 77	UMUT MM18574
No. 78	UMUT MM18575
No. 79	UMUT MM18576
No. 80	UMUT MM7667
No. 81	UMUT MM18577
No. 82	UMUT MM7668
No. 101	KPMG6373
No. 102	KPMG3258
No. 103	KPMG3215
Nos. 104-106	KPMG6372a-c
No. 107	WEA005T
No. 108	WEA006T
No. 109	WEA007T
No. 110	WEA008T
No. 111	WEA009T
No. 112	WEA010T
Nos. 113-115	WEA011T-1-3
No. 116	WEA012T
No. 117	WEA013T
No. 118	WEA014T
No. 119	WEA015T
No. 120	KPMG3215
No. 121	GK.H5988
No. 122	replica : UMUT MM18578
No. 123	WEA016T
No. 124	WEA017T
No. 125	replica : UMUT MM18579
No. 126	replica : UMUT MM18580
No. 127	replica : UMUT MM18581
No. 128	WEA018T
No. 129	GK.H5850
No. 130	GK.H5796
No. 131	WEA019T

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◎講演申込は共著を含めて一人2題までとし，講演時間は討論を含め15分です。一題目ずつ葉書で期日までに下記宛申し込んで下さい。

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