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

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Three Ordovician cephalopods from the Jigunsan Formation of Korea

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Abstract. Cephalopod species previously described from the Middle Ordovician Jigunsan Formation of Duwibong type Joseon Supergroup of Baegunsan Syncline, Kangweondo in Korea were re-examined taxonomically based on the type and figured specimens and newly collected ones. Three species, *Holmiceras coreanicum* (Kobayashi, 1927), *Sactorthoceras makkolense* (Kobayashi, 1927), and *Kotoceras grabaui* (Kobayashi, 1927) are described. Each species was restudied and compared with closely related species described by Kobayashi (1927, 1934) ; respective lectotypes are also designated herein. In this study, *Sigmorthoceras coreanicum*, based on its sigmoidally curved conch, was identified as belonging to *Holmiceras* which is characterized by the early loosely gyroceraconic shell portion. *Sinuitopsis kochiriensis*, previously identified as an Ordovician gastropod, is a juvenile shell of *H. coreanicum*, judging by the number of the volutions and prominent shell surface. Three species belonging to *Sactorthoceras* and also *Cycloceras taihakuense* were regarded, based on the existence or nonexistence of the preserved shell and the imploded internal structure, as junior synonyms of *Sactorthoceras makkolense* in a broad sense. *Kotoceras frechi* was rejected as an invalid taxon, since its septal angulation, broader siphuncle and rapid expansion of the conch are characteristics caused by secondary deformation.

Key words : cephalopods, gyroceraconic, lectotype, Middle Ordovician, secondary deformation, synonym

Introduction

Paleontological study of the invertebrate fauna from the Cambro-Ordovician formations in Kangweondo, Korea was initiated by Kobayashi (1927). At that time, he identified three units (fossil beds 13, 14, and 15) as the "Chikunsan fossil beds". From these beds, he described 16 nautiloid species belonging to 8 genera from the Maggol, Hwarari and Hwangjiri areas. He mentioned that the cephalopods from the "Jigunsan fossil beds" show an affinity with the Chazyan of North America, while the trilobites and brachiopods show European affinity. Kobayashi (1934) subsequently described a great number of cephalopod fossils which belong to 58 species of 29 genera, revising 11 hitherto described species, and stated that the Jigunsan cephalopod fauna is diagnosed by the age of orthoceroidal divergence in cephalopod macroevolutionary history. Later, Kobayashi (1966) made a comprehensive compilation of the Cambro-Ordovician formations and faunas of South Korea and divided the Middle Ordovician sequence of the Duwibong type Joseon Supergroup into five cephalopod assemblage zones i.e., *Manchuroceras, Polydesmia, Sigmorthoceras*, orthoceroid, and actinoceroid Zones in ascending order.

The Korean Ordovician cephalopods have been studied both taxonomically and biostratigraphically by Kobayashi (1927, 1934, 1966, 1969, 1977a, 1977b, 1978) and have not been revised by any subsequent researcher. The series of Kobayashi's works provides important phylogenetic clues and insight into the Asiatic and worldwide Ordovician paleogeography of fossil cephalopods. However, some Korean cephalopod specimens described by Kobayashi require additional restudy in view of the current knowledge of cephalopod taxonomy.

This paper aims to re-examine the systematics and taxonomy of three Ordovician cephalopod species from Korea on the basis of Kobayashi's (1927, 1934) type specimens and newly collected specimens from the type localities and other new localities.

Geological setting

The Cambro-Ordovician deposits are widely distributed in Kangweon-do, Korea. They have been divided into five types, based on the lithology and fauna ; viz., Duwibong, Yeongweol, Jeongseon, Pyeongchang, and Mungyeong types (Kobayashi *et al*., 1942). The cephalopod specimens

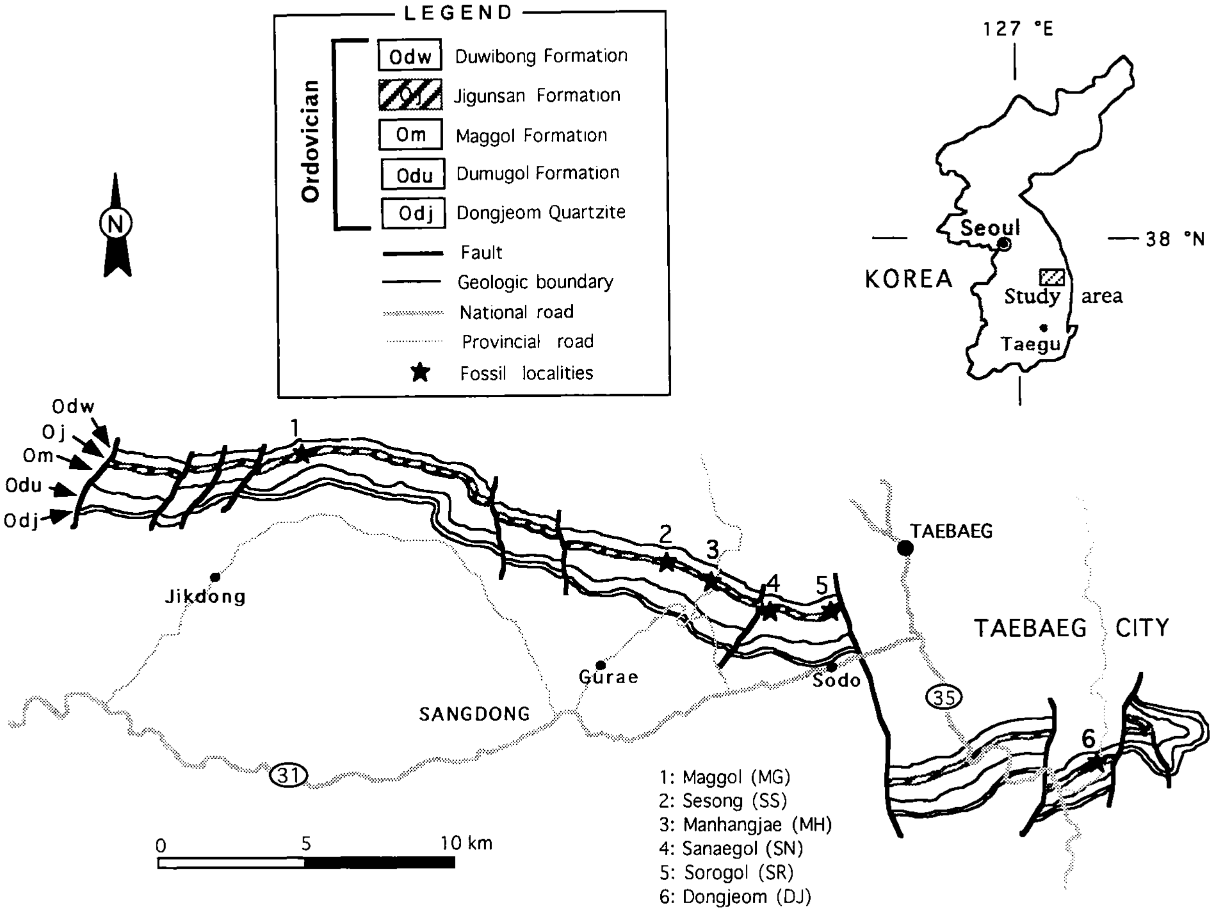


Figure 1. Geologic map of the study area, showing the cephalopod localities.

used in this study were collected from the Jigunsan Formation, Upper Joseon Supergroup which extends from east to west in the southern limb region of the Duwibong type Joseon Supergroup of the Baegunsan Syncline (Figure 1).

The Jigunsan Formation originally named as the "Chikunsan Shale" by Yamanari (1926), is about 50 m thick, conformably covers the Maggol Formation and grades into the overlying Duwibong Formation (Figure 2). This formation can be traced from east and west in the Taebaeg region. The Jigunsan Formation is lithostratigrahically divided into the lower, middle, and upper members. The lower member is essentially non-fossiliferous and consists mainly of black shale containing a little calcareous material; the middle member is composed of "worm-eaten" bioturbated limestone and vermicular shale intercalated by three or four limestone beds, each about 50 cm thick, and has yielded a large number of trilobites; the upper member consists of limestone and bioclastic grainstone with intercalating calcareous shale. The amount of carbonate gradually increases toward the top of the sequence and ultimately grades into the limestone of the Duwibong Formation; this member has yielded a rich cephalopod fauna.

The Jigunsan Formation is especially well exposed in the Sanaegol section (Figures 1, 2). It consists mainly of black shales and thin beds of calcareous nodules, in which orthocerid and lituitid nautiloids occur. The lower member is almost barren of fossils; the middle member is characterized by the abundant occurrence of *Holmiceras*; the upper member is represented by bioclastic grainstone with intercalating calcareous shale and contains abundant ormoceroid cephalopods.

According to Kobayashi (1934, 1966), the Jigunsan Formation is correlated with the Llandeilo in the European succession and the Chazy in the American sequence. Shimizu and Obata (1935b) described three graptolite species from the formation and correlated it with the Lower Llandeilian *Diplograptus teretiusculus* and *Nemagraptus gracilis* Zones in the Glenklin Shale, England and Pingliang Shale of Gansu Province in North China. Shikama and Ozaki (1969) distinguished three assemblage zones in the Jigunsan Formation in the Dongjeom area, namely, the *Orthis nipponica*, *Basilicus deltacaudus*, and *Basilicus yokusensis* Zones in ascending order, based on the macrofossils collected by a member of the Yokohama Geologists Club in 1967 (Ozaki and Ogino, 1968).

The Jigunsan trilobite fauna has been studied in detail by Lee *et al.* (1980), who described 15 species belonging to 5 genera and correlated the formation with the Llandeilo to

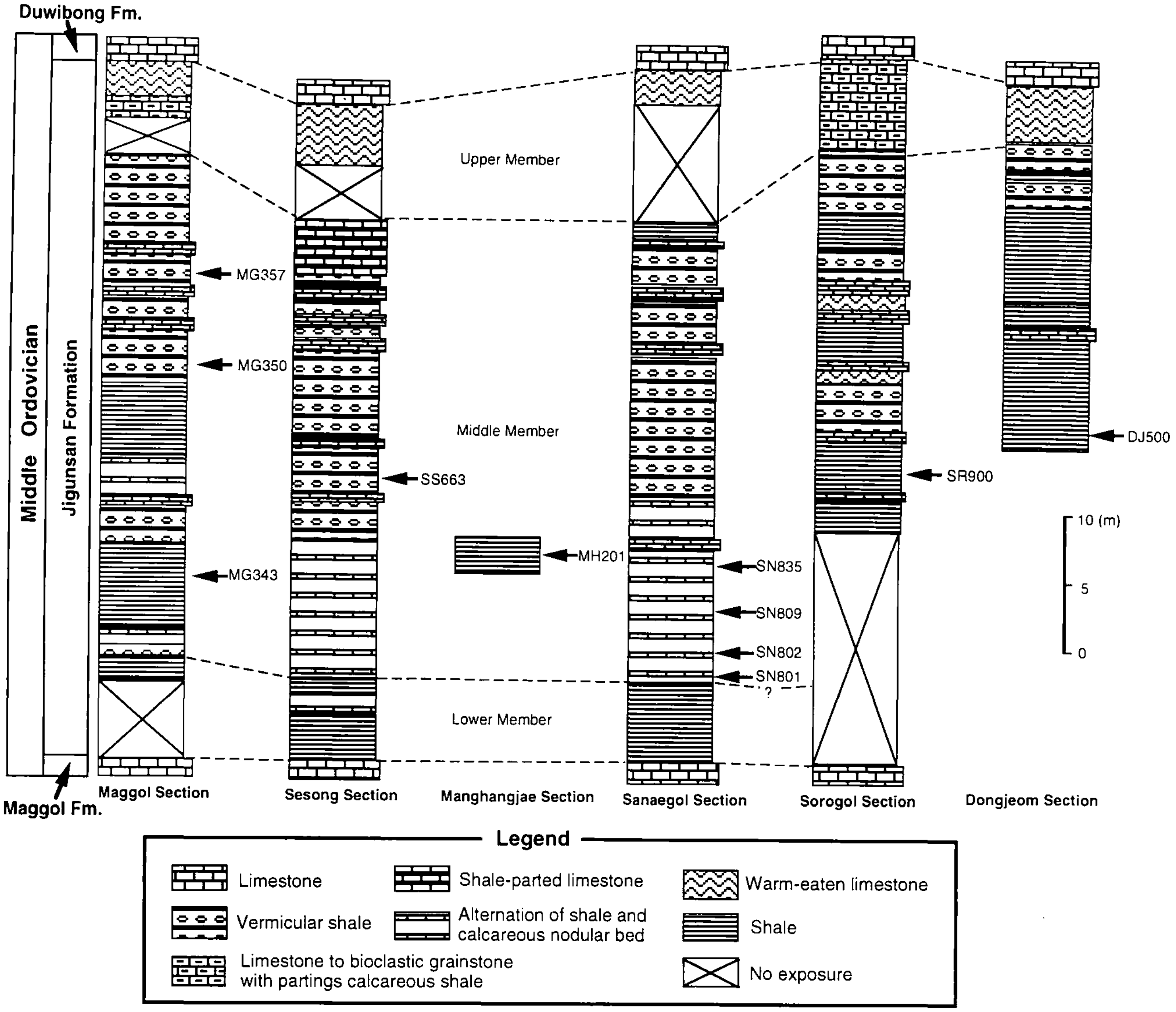


Figure 2. Geological columns of the Jigunsan Formation in the study area, showing the horizons of the cephalopod localities.

lower Caradoc interval in Europe.

Lee and Lee (1986) established a conodont biozone in the middle and upper parts of the Jigunsan Formation, namely, the *Eoplacognathus suecicus-Eoplacognathus jigunsanensis* Assemblage Zone. These authors correlated the conodont fauna with the *Eoplacognathus suecicus-Acontiodus ? linxiensis* Zone of the lower Upper Majiagou Formation in North China and with the Lower to Middle Llanvirn in the European type section. They also suggested that the Jigunsan Formation was deposited in a deep shelf environment, based on the conodont fauna.

Materials

Most cephalopod specimens described by Kobayashi were collected from Maggol in Korea, where strata indicative of the western part of the Duwibong type Joseon Supergroup are exposed (Loc. 1 in Figure 1). The list of type specimens re-examined in this study is shown in Table 1. The cephalopod type specimens in Table 1 are housed in the University Museum, University of Tokyo (UMUT).

Fifty-seven specimens listed in Table 2 were used for comparison with Kobayashi's type specimens. These new and unstudied specimens were collected by the present author and K. Tanabe on three occasions during May to August, 1997. All of them were discovered from the Middle Ordovician Jigunsan Formation in Kangweondo, Korea. They are deposited in the Department of Earth Science, Teacher's College, Kyungpook National University (KPE prefix), Taegu, Korea.

Table 1. List of cephalopod type specimens which were described by Kobayashi (1927, 1934) from the Jigunsan Formation and are re-examined in this study.

Registered no.	Scientific name	Locality	Type
UMUT PM 8	*Sigmorthoceras coreanicum*	Maggol	Syntype
UMUT PM 9	*Sigmorthoceras coreanicum*	Maggol	Syntype
UMUT PM 651	*Sigmorthoceras coreanicum*	Maggol	Syntype
UMUT PM 6	*Sactorthoceras makkolense*	Maggol	Syntype
UMUT PM 7	*Sactorthoceras makkolense*	Maggol	Syntype
UMUT PM 660	*Cycloceras* sp.	Hwangji	Syntype
UMUT PM 570	*Sinuitopsis kochiriensis*	Hwangji	Syntype
UMUT PM 571	*Sinuitopsis kochiriensis*	Hwangji	Syntype
UMUT PM 634	*Kawasakiceras densistriatum*	Maggol	Holotype
UMUT PM 652	*Sigmorthoceras sigmoidale*	Maggol	Holotype
UMUT PM 657	*Cycloceras taihakuense*	Maggol	Paratype
UMUT PM 658	*Cycloceras taihakuense*	Maggol	Paratype
UMUT PM 659	*Cycloceras taihakuense*	Maggol	Holotype
UMUT PM 650	*Sactorthoceras gonioseptum*	Maggol	Holotype
UMUT PM 643	*Sactorthoceras shimamurai*	Maggol	Holotype

Table 2. List of cephalopod specimens from the Middle Ordovician Jigunsan Formation, Kangweondo, Korea.

Species	Locality	No. of specimens
Holmiceras coreanicum	SN801, SN802, SN809, SN835, DJ500, MH201	32
Sactorthoceras makkolense	SN802, SN809, SN835, DJ500	15
Kotoceras grabaui	SR900, SS663, MG343, MG350, MG357	10

Systematic paleontology

Subclass Nautiloidea
Order Tarphycerida
Family Lituitidae
Genus ***Holmiceras*** Hyatt, 1894

Type species.—*Lituites praecurrens* Holm, 1891 from the Lower Ordovician (Kundan Stage) of Öland, Sweden.

Generic diagnosis.—Lituiticonic with adapically one-voluted gyroceraconic and adorally sigmoidal curved shell portion; septal necks orthochoanitic; surface ornamented with growth lines and annulations, forming ventral sinus and lateral salient in the earlier coiled stage and transverse or slightly undulating ones in the later stage.

Remarks.—Hyatt (1894) recognized that this genus is characterized by having distinct ventral and dorsal lobes in the ephebic stage, with low, broad, almost staight, lateral saddles.

Ancistroceras is most closely allied to *Holmiceras*, but differs from the latter in having small, tightly coiled whorls and a much more rapidly expanding conch. Sweet (1958) emphasized the sigmoid profile of the shell which is missing in *Ancistroceras*.

Holmiceras has long been an all-but-forgotten genus. However, Flower (1975) added *Holmiceras benetti* from the Middle Ordovician Table Head Formation in Newfoundland to the two previously known *Holmiceras* species. Presently, only four species in the world can be referred to *Holmiceras*; *Holmiceras praecurrens* (Holm, 1891), *Holmiceras kjerulfi* (Brögger, 1882), *Holmiceras benetti* Flower, 1975 and *Holmiceras coreanicum* (Kobayashi, 1927) which is described below. *Holmiceras coreanicum* from the Jigunsan Formation is a first reliable record of this genus from Asia.

Holmiceras coreanicum (Kobayashi, 1927)

Figures 3-1a, b, 2a, b; 4-1—10.

Orthoceras coreanicum Kobayashi, 1927, p. 181, pl. 18, fig. 6; pl. 19, figs. 3a-c.
Orthoceras makkolense Kobayashi, 1927, p. 181, pl. 19, figs. 2a-c.
Sigmorthoceras coreanicum (Kobayashi). Kobayashi, 1934, p. 413, pl. 22, fig. 7.
Sactorthoceras makkolense (Kobayashi). Kobayashi, 1934, p. 408, pl. 15, fig. 9.
Cycloceras sp. Kobayashi, 1934, p. 421, pl. 29, figs. 12, 13.
Sinuitopsis kochiriensis Kobayashi, 1934, p. 360, pl. 5, figs. 1-4.
aff. *Trilacinoceras* sp. Ozaki and Ogino, 1968, pl. 3, fig. 3.
Holmiceras coreanicum (Kobayashi). Yun, 1998, p. 78, figs. 1c-h.

Types.—A sigmoidally curved phragmocone figured by Kobayashi (1927, p. 181, pl. 19, figs. 2a-c) from the Jigunsan Formation of Maggol, Kangweondo, Korea, UMUT PM9, is here designated as the lectotype (see also Figures 3-1a, b). A slightly curved phragmocone specimen from the same locality, UMUT PM8 is also designated as the lectoparatype.

Material.—In addition to the above two type specimens, newly collected specimens from the Jigunsan Formation including 9 figured (KPE20001, KPE20002, KPE20003, KPE20004, KPE20005, KPE20006, KPE20007, KPE20020, KPE20026-1, KPE20302) and 23 other specimens were examined.

Specific diagnosis.—Sigmoidally curved conch with early loosely coiled portion ; body chamber long ; circular in cross section ; siphuncular segments somewhat expanded within camera ; septal necks orthochoanitic ; no cameral deposits detected ; surface ornamented with prominent annulations and very fine growth lines.

Description.—Conch large-sized lituiticone, composed of two different continuous shell portions, namely, early loosely coiled juvenile shell portion (Figures 4-1a-c—4) and later sigmoidally curved adult shell portion (Figures 4-6a, 7, 8).

The best preserved specimen, KPE20001 (Figures 4-1a—c), is broken into two portions, but when put together is about 63 mm long ; the early juvenile shell portion is loosely coiled, its umbilical opening being 3.2 mm across, first camera pointed anterolaterally, constricted to 1 mm at a height of 1.5 mm from the adapical apex, forming a subquadrate outline ; internal structure unknown owing to recrystallization ; septa moderately concave and closely spaced with septal spacing 0.7 mm on the dorsum and 1 mm on the venter, gradually increasing adorally ; slightly curved later shell portion, 58 mm long, circular in cross section, its diameter expanding from 7 mm at the adapical end to 15.7 mm at the broken upper end ; siphuncle central, narrow, its width one-eighth of the conch diameter ; siphuncular segments tubular to slightly inflated within camerae ; transverse septal suture and surface annulations crossing each other ; septal depth smaller than one cameral height on the concave side and larger than that on the convex side ; cameral height gradually increasing towards the top from 1.3 mm to 2.9 mm, five camerae equal in length to the conch diameter of 15.9 mm measured at the uppermost camera ; septal necks orthochoanitic, attaining 0.5 mm at the 3rd septum from the adoral end, occupying about one-third of the cameral height, distinguishable from the connecting ring by means of their thickness, septal suture transverse, but intersecting with annulations ; camera filled with crystalline calcite, no organic deposits detected ; siphuncle lined by endosiphuncular nonsegmental material along the inner siphuncular wall and leaving central narrow siphotube ; surface ornamented with low, narrow annulations separated by much broader intergrooves, both of which are covered with very fine transverse growth lines, showing different features during ontogeny, ventral sinus and lateral salients in juvenile coiled stage and then adorally run parallel to transverse axis, 7 annulations in a length equal to the conch diameter at the preserved adoral end, annulation density slightly larger than that of septal one, i.e., 8 growth lines occurring between two annulations.

KPE20002 (Figure 4-4) represents a young, possibly embryonic or early postembryonic shell with 10 camerae consisting of endogastrically curved gyroconic phragmocone and subsequent straight body chamber, small, 15.5 mm long, conch diameter rapidly enlarging from 2.2 mm near the adapical end to 4.9 mm at the base of the living chamber ; siphuncle central, its segments expanded within camerae, constricted at the septal necks ; septal depth corresponding to one cameral height ; siphuncle filled with imported matrix, camera filled with crystalline calcite ; surface annulated in longitudinal section, being arranged at intervals of 0.8 mm.

KPE20003 (Figure 4-2) judging from the silicone rubber cast, is the external mould of an early coiled shell portion, 17.5 mm long, composed of a loosely coiled embryonic shell portion, its umbilical opening about 3 mm across, conch expanding at a rate of 1 mm per 4 mm ; surface ornamented with prominent annulations and transverse fine growth lines, forming ventral and dorsal sinuses, and ventrolateral salients.

KPE 20004 (Figure 4-7), a sigmoidally curved phragmocone, 85.2 mm in length, conch diameter expanding moderately rapidly in the earlier stage from 3.8 mm to 10 mm at a distance of 21 mm and more slowly afterwards, conch circular in cross section ; siphuncle narrow, central ; septal necks orthochoanitic ; cameral height ranging from 1.7 mm to 3 mm ; septal depth slightly larger than one cameral height ; surface ornamented with primary annulations and very fine growth lines.

KPE20005 (Figure 4-5) is a sigmoidally cuved fragmentary phragmocone, 76 mm in length, conch diameter gently expanding from 10.2 mm at the adapical end to 22.9 mm at the adoral end ; siphuncle subcentral, narrow, occupying one-seventh of the conch diameter ; siphuncular segments slightly inflated within camera, dimensions 2.6 mm in length and 3 mm in maximum diameter at the midportion of the segment in the adoral end, constricted to 2.2 mm at the septal foramina ; septal necks suborthochoanitic, septa relatively deep, exhibiting one and a half of the cameral height ; septal distance varying from 1.9 mm to 2.8 mm ; nonsegmental endosiphonal linings along the siphuncular wall, leaving a central tube ; surface ornamented with distinct annulations and growth lines.

KPE20006 (Figure 4-10) is an external mould retaining well preserved surface ornamentation, consisting of annulations very closely spaced at intervals of approximately 1 mm, with ventral sinus formed by each annulus about 2.6 mm in width and about 1.3 mm in length in earlier shell portion, and of much more widely spaced, more prominent transverse annulations in later shell and further annulations again becoming narrower in gerontic shell, annulations and intergrooves both covered with very fine growth lines.

KPE20007 (Figures 4-6a, b) represented by a moderately curved, large-sized adult shell lacking an early coiled portion, is 162 mm long of which the body chamber is 57 mm long, adoral portion of phragmocone and body chamber secondarily depressed during fossilization, conch circular in cross section ; its diameter gently enlarging from 19.7 mm at the adapical end to 33.3 mm at a point 74 mm farther up ; siphuncle central, narrow, a little more than one-seventh of the conch diameter ; siphuncular segment as long as broad ; surface ornamentation on body chamber partly preserved, comprising annulations and growth lines.

KPE20302 (Figure 4-8), 53.5 mm in length, consists of a loosely coiled early shell portion and succeeding sigmoidally curved conch, but an initial chamber is not preserved ; umbilical opening about 2.8 mm across ; moderately expanding at a rate of 1 mm per 5 mm.

Remarks.—Sigmorthoceras coreanicum from the Jigunsan Formation of Maggol (Kobayashi, 1927, pl. 18, fig. 6 ; pl. 19, figs. 3a-c ; 1934, p. 413, pl. 22, fig. 7) is the type species of *Sigmorthoceras* which has been regarded as a doubtful taxon for a long time. Externally, the slightly curved conch was regarded as the diagnostic character by Kobayashi (1934). However, Shimizu and Obata (1935a) regarded the sigmoidal conch shape of specimens of *Sigmorthoceras* described by Kobayashi as a secondarily deformed *Sactorthoceras makkolense*. Such secondary deformation is common in other nautiloid fossils from this region. Flower (1946) stated that *Sigmorthoceras* is an erratic form deviation, perhaps not worthy of generic status.

However, the internal morphology of the sigmoidally curved conch of the present species is identical with that of the type specimens of *Sigmorthoceras coreanicum*. Based on the identical curvature of all the specimens, the secondary deformation conjecture by Shimizu and Obata (1935a) can be rejected. Thus, *Holmiceras coreanicum* is revealed to possess a loosely coiled early shell portion and slightly sigmoidal more mature conch.

It is well known that secondary deformation and dissolution of shelly matter during fossilization sometimes cause misidentification of fossil taxa. Kobayashi (1934) described *Cycloceras* sp. from the Jigunsan Formation of Homyeong (p. 421, pl. 29, figs. 12, 13), based on the annulated ornamentation. The annulations observed on the ventral portion near the adapical end of the specimen are more broadly spaced than those on the dorsal one. Accordingly, the specimen represents a portion of the shell shifting from the early coiled stage to the sigmoidally curved phragmocone in *Holmiceras coreanicum*. Furthermore, all the features observed in the longitudinal section agree well with those of *Holmiceras coreanicum*, although the state of preservation of the internal structure is rather poor.

Meanwhile, Kobayashi (1934) described a sinuitid gastropod, *Sinuitopsis kochiriensis* from the Jigunsan Formation of Homyeong, based on two incomplete external moulds (Kobayashi, 1934, p. 360, pl. 5, figs. 1-4). In general, the genus *Sinuitopsis* consists of a tightly coiled shell with 3 to 4 volutions (Knight *et al*., 1960, pl. 176, fig. 93-7a, b) and its surface is sculptured by fine growth lines without more raised primary annulations. However, the specimens described by Kobayashi (1934) as "*Sinuitopsis*" have loosely coiled shells having one volution and lacking the characteristic surface sculpture of true *Sinuitopsis*. In addition, its surface ornamentation consisting of ventral sinus and lateral salients is strong evidence to support the contention that the two external moulds belong to *Holmiceras*.

Sactorthoceras makkolense (Kobayashi, 1927) was proposed based on two individuals. One of them (UMUT PM7; Figures 3-2a, b), illustrated in Kobayashi (1927, pl. 19, figs. 2a-c) differs from the other specimen (UMUT PM6; Kobayashi, 1927, pl. 18, fig. 5; see also Figures 3-4a, b) in having more crowded septa and a narrower siphuncle. Accordingly, the former specimen (UMUT PM7) is dissimilar to the lectotype but has a cameral height of no more than two-thirds the diameter of the siphuncle. Moreover, the conch of the specimen has a slightly curved form, although its siphuncular position is more or less eccentric due to secondary deformation. In these respects, this specimen must also be assigned to *Holmiceras coreanicum*.

Ozaki and Ogino (1968, pl. 3, fig. 3) figured a single nautiloid, aff. *Trilacinoceras* sp. from the Jigunsan Formation of Dongjeom. It is represented by an early coiled phragmocone. However, its generic identification may be incorrect because of the less loosely coiled portion of the conch than those in the species of the genus *Trilacinoceras*. Based on the mode of coiling in the early portion of the conch and the surface ornamentation, this nautiloid is assigned with reservation to *Holmiceras coreanicum*.

Comparison.—In view of the external morphology, this species is closely allied to *Holmiceras kjerulfi* (Brögger) from the *Orthoceras* Limestone of the Oslo region, Norway (Brgger, 1882, p. 54, pl. 12, fig. 16), but differs from the latter species by its loosely gyroceraconic volution, somewhat curved cyrtoconic or sigmoidal adoral portion, circular section of the conch and slightly more crowded septa. This species is distinguished from *Holmiceras benetti* Flower from the Middle Ordovician Lower Table Head Limestone, Newfoundland (Flower, 1975, p. 151, pl. 4, figs. 1-6), which has a more rapidly expanding conch and lacks a sigmoidal adoral shell portion.

This species is similar to the Middle Ordovician species *Ancistroceras undulatum* Boll, 1857 recovered from erratic boulders in northern Germany (Foerste, 1929, p. 272, pl. 41, figs. 3, 4) and the Ampyx Limestone in Oslo-Asker district, Norway (Sweet, 1958, p. 129, pl. 13, figs. 2, 3, 5) in that the early coiled portion and the mode of surface ornamentation are similar to *H. coreanicum*, but this taxon is quite distinct from the latter in its more slowly expanding conch. Likewise, *Ancistroceras subcurvatum* Qi, 1980 from the upper Taiwan Formation, Lower Ordovician, Wuwei, Anhui, China (Qi, 1980, p. 256, pl. 1, figs. 1, 2) is similar to this species in general features but also differs from it by its own somewhat more rapidly expanding conch.

Occurrence.—This species is known to occur from various localities (SN801, SN802, SN809, SN835, DJ500 and MH201) in the Middle Ordovician Jigunsan Formation.

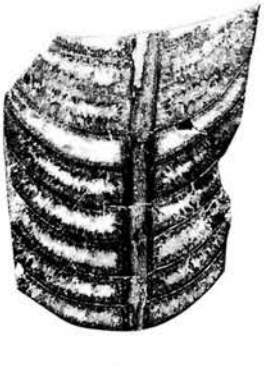
Order Orthocerida
Family Sactorthoceratidae
Genus **Sactorthoceras** Kobayashi, 1934

Type species.—*Sactorthoceras gonioseptum* Kobayashi, 1934 from the Jigunsan Formation of Maggol, Kangweondo, Korea.

→ **Figure 3. 1a, b, 2a, b.** *Holmiceras coreanicum* (Kobayashi, 1927). **1a, b.** A sigmoidally curved phragmocone, lectotype (UMUT PM9), ×1, 1a: lateral view, 1b: longitudinal section. **2a, b.** "*Sactorthoceras makkolense* (Kobayashi)", UMUT PM7, which is here assigned to *Holmiceras coreanicum* (Kobayashi), ×1, 2a: lateral view, 2b: longitudinal section. **3a, b.** *Kotoceras grabaui* (Kobayashi, 1927). The best preserved partial phragmocone, lectotype (UMUT PM631), ×1, 3a: ventral view, 3b. adoral view of the septa and siphuncle, venter down. **4a, b.** *Sactorthoceras makkolense* (Kobayashi, 1927). An adoral phragmocone, lectotype (UMUT PM6), 4a: longitudinal section, ×1, 4b: enlargement of the same section, ×2.


1a


1b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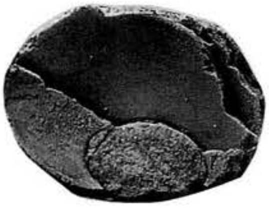
2a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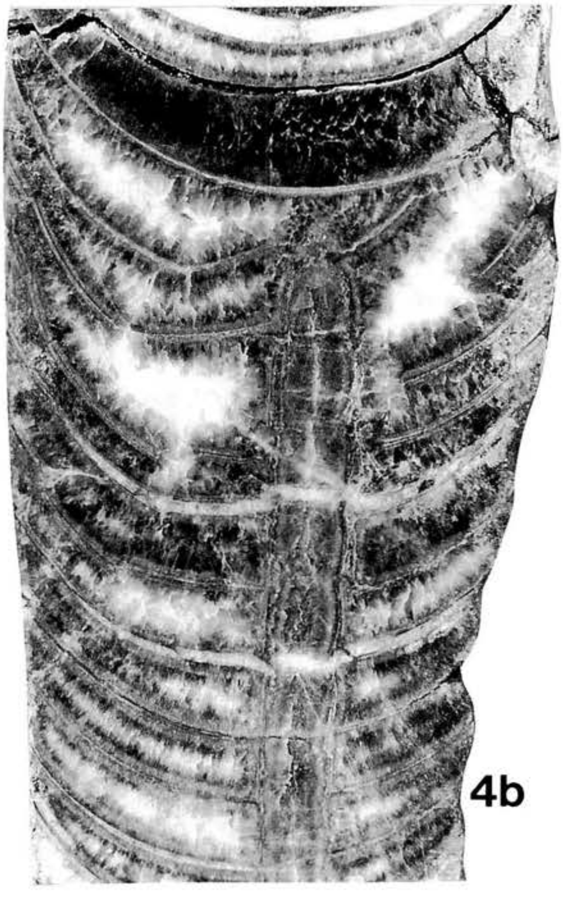
3a


4a


4b

Generic diagnosis.—Straight or slightly curved longiconic orthoceracone with subcentral siphuncle; siphuncular segments tubular or slightly expanded within camerae; cameral height nearly equal to or a little more than siphuncular diameter; no discernible cameral and endosiphuncular deposits; surface smooth or ornamented with closely spaced annulations and very fine transverse growth lines.

Remarks.—The genus *Sactorthoceras* is known from the Middle Ordovician formations in East Asia, Norway and northeastern America. Flower (1941) considered *Sactorthoceras* as the ancestor of the ascocerid nautiloids that make up a specialized group having siphuncular segments from orthochoanitic to cyrtochoanitic.

Indeed, *Sactorthoceras* may be not distinguished from *Holmiceras* when any specimen is found as an adoral broken phragmocone without an early coiled shell portion. However, the longitudinal section through the center of the siphuncle reveals that the siphuncle of *Sactorthoceras* is always broader and its septal distance is higher than in *Holmiceras*.

The generic assignment of *Cycloceras* M'Coy is based mainly on the surface ornamentation and not on internal structure. The Group 1 of *Cycloceras* which was divided artificially by Kobayashi (1934) is regarded as belonging to either *Sactorthoceras* or *Holmiceras*, because its internal structure and surface ornamentation agree well with the latter genera. Moreover, Sweet (1964) mentioned that "no species other than the type species should be referred to *Cycloceras* until its type is better known". Based on present knowledge, the genus *Cycloceras* may be superseded by *Wennanoceras*, which was proposed by Chen (1976) for shells having a strongly annulated surface and a central siphuncle.

Sactorthoceras makkolense (Kobayashi, 1927)

Figures 3-4a, b; 5-1—6; 6-1—4

Orthoceras makkolense Kobayashi, 1927, p. 181, pl. 18, fig. 5; not pl. 19, figs. 2a-c.

Sigmothoceras sigmoidale Kobayashi, 1934, p. 414, pl. 21, figs. 1-3.

Sactorthoceras gonioseptum Kobayashi, 1934, p. 412, pl. 16, fig. 6; pl. 18, figs. 1-3; pl. 20, fig. 9.

Sactorthoceras shimamurai Kobayashi, 1934, p. 408, pl. 19, figs. 1-3.

Kawasakiceras densistriatum Kobayashi, 1934, p. 397, pl. 14, figs. 6, 7.

Cycloceras taihakuense Kobayashi, 1934, p. 420, pl. 22, figs. 1, 2; pl. 23, figs. 1-5; pl. 24, figs. 4-6.

Sactorthoceras makkolense (Kobayashi). Kim *et al.*, 1986, p. 26, pl. 6, figs. 1, 2.

Type.—The type specimen, UMUT PM6, from the Jigunsan Formation of Maggol, Kangweondo, Korea is here designated as the lectotype (Figures 3-4a, b).

Material.—15 specimens including seven figured ones (KPE20030, KPE20031, KPE20032, KPE20033, KPE20036, KPE20037, UMUT PM634).

Specific diagnosis.—Longiconic orthoceracone; siphuncular segments tubular; septal necks orthochoanitic to suborthochoanitic; cameral height nearly equal to siphuncular diameter; surface ornamented with low annulations and very fine transverse growth lines.

Description.—Conch large-sized longiconic orthoceracone, enlarging at a rate of 1 mm per 8 to 10 mm in conch length; cross sections of conch and siphuncle subcircular; ratio of the siphuncular diameter versus conch diameter being 1 : 9 in KPE20030 (Figure 5-3); siphuncle subcentral, tubular; septa moderately concave forwards, septal depth nearly two to three times the cameral height, septal distance ranging from 3.3 mm to 5.4 mm, in other words, a little more than or equal to the siphuncular diameter, septal necks orthochoanitic, relatively long, approximately 2 mm in KPE20037 (Figure 5-6), bending smoothly toward adapical end and then forming a right angle with septa, septal suture directly transverse; connecting ring thin, distinguishable from septal neck by its thickness; in KPE20037 camerae comparatively high, ranging from 3.5 mm to 4 mm, 7 to 8 camerae in a distance corresponding to the conch diameter; no cameral or siphuncular deposits detected; surface marked with low, narrow annulations, separated by broader interspaces, both covered with very fine numerous transverse growth lines, 7 to 8 per 1 mm length, annulations being arranged at intervals of about 2 mm, but fluctuating within a narrow range.

Remarks.—Kobayashi (1927) described the present species as follows: "In the middle part of the polished specimen (pl. XVIII, fig. 5) the segmentation is quite abnormal, the double

→ **Figure 4.** *Holmiceras coreanicum* (Kobayashi, 1927). **1a-c.** Partial phragmocone steinkern (KPE20001) from SN801, 1a: ventrolateral view, showing the septal suture crossing annulations, ×1, 1b: dorsoventral section of coiled embryonic conch, ×1.3, 1c: longitudinal section of partial phragmocone made by an acetate peel, showing the details of siphuncle and septa, ×1.5. **2.** Silicon rubber cast of external mould (KPE20003) from DJ500, showing loosely coiled embryonic shell portion with annulated surface ornamentation, ×3. **3.** Juvenile shell (KPE20026-1) from MG343, dorsoventral section of the early coiled septated shell portion, ×3. **4.** Possibly embryonic conch (KPE20002) from SN801, dorsoventral section, showing the phragmocone and subsequent body chamber, ×3. **5.** Partial phragmocone (KPE20005) from DJ500, longitudinal section, showing details of siphuncule and septa, ×1. **6a, b.** Moderately curved conch (KPE20007) from SN801, ×1. 6a: lateral view. Surface ornamentation is partly preserved on body chamber. 6b: apical view, showing the position of the siphuncle. **7.** Longitudinal section of partial phragmocone (KPE20004) from SN801 made by an acetate peel, showing the sigmoidally cuved conch and details of siphuncle and septa, ×2. **8.** Early coiled and later sigmoidally curved conch (KPE20302) from SN802, ×1.5. **9a, b.** Partial phragmocone (KPE20020) from SN801, ×1, 9a: lateral view, 9b: apical view of septum and siphuncle, showing the position of siphuncle. **10.** Partial phragmocone (KPE20006) from DJ500, ventral view, silicon rubber cast of external mould, showing the well developed surface ornamentation, especially ventral sinus of annulations on earlier portion, ×2.5.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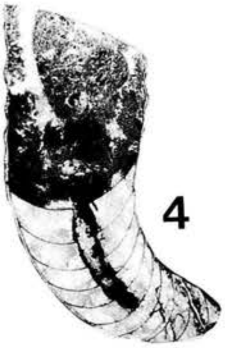
2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6a


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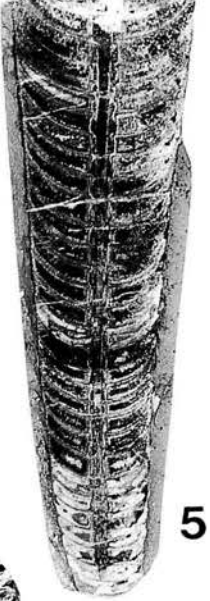
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7


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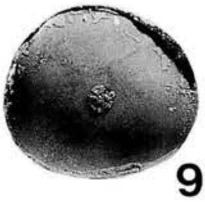
9a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10


6b

camerae on one side of the siphuncle corresponding to a single camera on the other....... It may be possibly be due to a pathological state". However, in the type specimens of this species (Figures 3-4a, b), the septa in the adoral portion of the phragmocone are distributed disorderedly here and there. This peculiar shell feature is considered to be an artifact created by recrystallization. As the result of restoration, the septa on each side in the each longitudinal section of the lectotype (UMUT PM6) correspond well one to one. This phenomenon is easily found in many cephalopods. For example, *Actinoceras bellefontense* Foerste and Teichert, 1930 shows a disagreement between septa on both sides owing to the diagenesis of internal components (Foerste and Teichert, 1930, p. 227, pl. 38, fig. 2B). Stridsberg (1990) suggested that internal destruction of septa may be caused by implosion due to increasing water pressure during postmortem sinking. Accordingly, the abnormal camerae observed in the lectotype of *Sactorthoceras makkolense* may not represent a pathological state during life, but were formed secondarily by taphonomic processes.

Taphonomic damage gave rise to other taxonomic problems too. Kobayashi (1934, p. 408, pl. 19, figs. 1-3) proposed *Sactorthoceras shimamurai* for a specimen with very rapid expansion of the conch, namely, at the rate of 1 mm per conch length of 4 mm. However, this specimen (UMUT PM643), which is represented by a fragmentary phragmocone with the last six camerae being closely spaced and a strongly compressed, large-sized body chamber, does not reflect the real expansion rate of the shell owing to secondary deformation of the body chamber and erosion of one side. Furthermore, since the last six camerae indicate the gerontic stage, more widely spaced camerae would be present in the adolescent stage. Consequently, *Sactorthoceras shimamurai* is regarded as a junior synonym of *Sactorthoceras makkolense*.

Sactorthoceras gonioseptum from the Jigunsan Formation of Maggol was described by Kobayashi (1934) as having a narrower siphuncle and more crowded septa than *Sactorthoceras makkolense*. He also emphasized the angulation of the septa shown in the holotype (UMUT PM650) as a diagnostic character of this species. However, this feature can not be observed in the specimen because of the crushed and distorted condition of the septa along the outer part of the cameral portion. Shell breakage during fossilization resulted in a pinched septal foramen with curiously angulated septal necks. Apart from the aberrant feature of septal angulation, *Sactorthoceras gonioseptum* can be regarded as a junior synonym of *Sactorthoceras makkolense*.

Kobayashi (1934) established *Sigmorthoceras sigmoidale* on the basis of a single sigmoidally curved specimen (UMUT PM652). He stated that this species is characterized by more broadly spaced septa and a broader siphuncle than in *Sigmorthoceras coreanicum*. Kobayashi (1934) described the shell surface of this specimen as smooth, but reanalysis of the same specimen revealed that it is actually sculptured by weak annulations and very fine transverse growth lines. Kobayashi (1934) emphasized that this species is closely similar to *Sactorthoceras makkolense*, except for the sigmoidal curvature of the conch. However, as Shimizu and Obata (1935a) pointed out, the sigmoidal mode of nautiloids from the Jigunsan Formation including *Sigmocycloceras kogenense* (Kobayashi), presumably originated by secondary deformation rather than from biological causes. Re-analysis of this specimen in longitudinal section indicates that over half of the right cameral portion is abraded and worn away and subsequently the chambers were filled with sediment. Therefore, this specimen probably suffered some secondary deformation from one side. It seems likely that this force together with compactional load changed this specimen to a sigmoidal form. Thus, the original morphological features of the type specimen of Kobayashi's *Sigmorthoceras sigmoidale* are identified with those of *Sactorthoceras makkolense*, indicating that the former species is a junior synonym of the latter.

Meanwhile, Kobayashi (1934) established *Kawasakiceras densistriatum* on the basis of its characteristic annulated and striated ornamentation on the surface. In the holotype (UMUT PM634), the large-sized ventral endosiphuncle which is a primary morphologic feature for the endoceroid nautiloids such as *Kotoceras* can not be detected. Reexamination of the specimen strongly suggests that Kobayashi mistakenly interpreted the fracture line through the center as holochoanitic septal necks in his retouched figure in longitudinal section with a body chamber (Kobayashi, 1934, pl. 14, fig. 7; see also Figure 6). The right-half portion of the logitudinally sectioned type specimen may have been regarded as a ventral siphuncle. Also, the endocone which is the vacant space formed by the last endosheath is not observed in the portion that was considered by Kobayashi (1934) as the siphuncle. Therefore the septa are extended to the ventral margin and continue to the right-half portion. This fact is revealed not only by the preserved successive septa in longitudinal section but also by the camerae exposed on the lateral side of the specimen. In this way, this longitudinally sectioned specimen appears to represent a remaining part through which the siphuncle does not pass. Unfortunately, the other half is missing. It is evident that *Kawasakiceras densistriatum* does not possess a large ventral siphuncle as in the species of *Kotoceras*, but has a centrally located narrow siphuncle. In addition, the surface

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→ **Figure 5.** *Sactorthoceras makkolense* (Kobayashi, 1927). **1a, b.** Partial phragmocone (KPE20036) from SN835, 1a: lateral view, ×1, 1b: details of surface ornamentation, showing the annulations and fine growth lines, ×5. **2a, b.** Fragmentary phragmocone (KPE20032) from DJ500, 2a: longitudinal section, showing the siphuncle and septa, ×1, 2b: septal view, venter down, showing the position of the siphuncle, ×1. **3.** Naturally weathered phragmocone (KPE20030) from DJ500, longitudinally polished section, ×1. **4.** Incomplete large conch (KPE20033) from SN835, lateral view of partial conch, showing the phragmocone and subsequent body chamber, ×1. **5.** Partial phragmocone (KPE20031) from DJ500, longitudinal section, showing the slightly inflated siphuncular segments, ×1. **6.** Partial phragmocone (KPE20037) from SN809, longitudinal section, showing the internal cameral structure, ×1.


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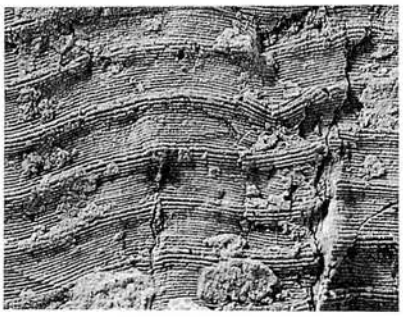
2a


2b


3


4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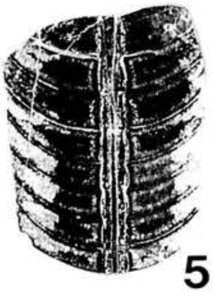
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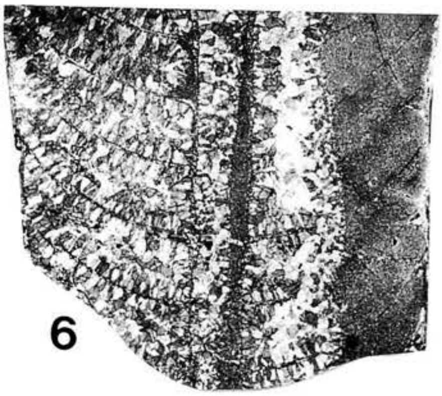
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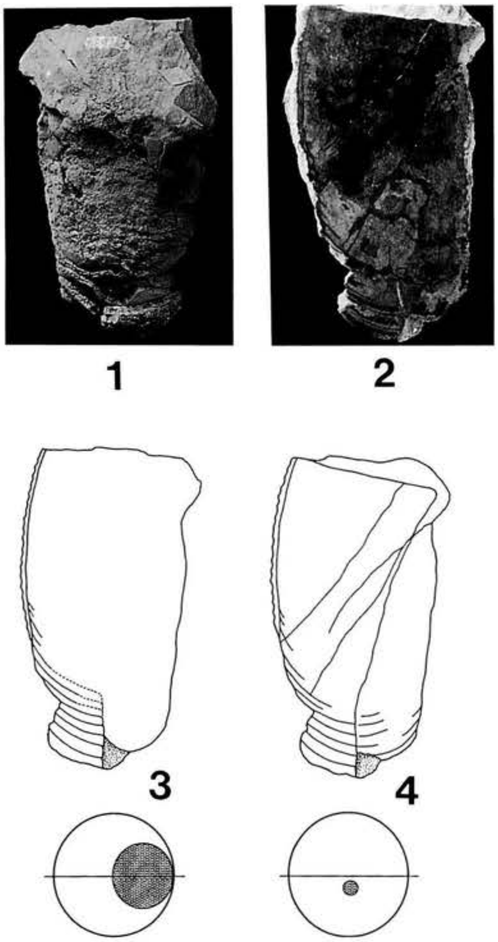

Figure 6. *"Kawasakiceras densistriatum Kobayashi"*, UMUT PM634, which is here assigned to *Sactorthoceras makkolense* (Kobayashi). **1.** Lateral view, ×0.5. **2.** Longitudinal section, ×0.5. **3.** Sketch based on Kobayashi's view, showing the broad ventral siphuncle. **4.** Sketch based on reexamination of the holotype, showing the septa instead of siphuncle. Longitudinal (upper) and cross (lower) sections are shown in **3** and **4**.

ornamentation agrees well with the pattern of the species of *Sactorthoceras*. Accordingly, this species is attributed to *Sactorthoceras makkolense* (Kobayashi, 1927), based on the moderately concave septa, probably central narrow siphuncle and annulated surface ornamentation with a fine transverse striation.

Comparison.—This species is similar to *Sactorthoceras wongiforme* Kobayashi from the Jigunsan Formation of Maggol and Hwangjiri (Kobayashi, 1934, p. 410, pl. 20, fig. 10; pl. 31, figs. 1, 2) in its tubular siphuncle and moderately concave septa, but differs from the latter in its broader siphuncle and higher camera.

Sactorthoceras tenuicurvatum Kobayashi from the Jigunsan Formation of Homyeong and Sanaegol (Kobayashi, 1934, p. 409, pl. 16, figs. 1, 2; pl. 17, figs. 9, 10) is readily distinguished from this species by its gentle curvature and elliptical section of the compressed conch.

This species resembles *Sactorthoceras* sp. from the Cephalopod Shale at Hovindsholm, Helgøya, Oslo region, Norway (Sweet, 1958, p. 60, pl. 3, fig. 12; pl. 4, figs. 1, 7), but its septal concavity is nearly three times of cameral height, while that of the latter species is less than half the length of a camera.

Occurrence.—Rarely occurs at the localities SN802, SN809, SN835, and DJ500 in the Middle Ordovician Jigunsan Formation.

Subclass Endoceratoidea
Order Endocerida
Family Endoceratidae
Genus ***Kotoceras*** Kobayashi, 1934

Type species.—*Kotoceras typicum* Kobayashi, 1934 from the Jigunsan Formation of Maggol.

Generic diagnosis.—Longiconic or somewhat curved orthoceracone, subcircular to ovate in cross section; siphuncle marginal, broad, nearly a half of the dosoventral conch diameter or less, in actual contact with slightly flattened ventral wall; endocones extending much farther forward ventrally than on dorsal side, apical end slightly closer to the dorsal side than the ventral one; septal necks holochoanitic; suture disconnected at ventral flattening; surface smooth.

Remarks.—*Kotoceras* is one of the Asiatic endemic genera from the Jigunsan Formation, Korea, and several species of the genus are known from China and Siberia. The diagnostic generic characters are the asymmetric endosiphocone and the disconnected septal suture on the ventral side. Kobayashi (1934) emphasized that *Kotoceras* is easily distinguished from other related genera, *Endoceras, Vaginoceras*, and *Cameroceras* in having the marginal siphuncle in actual contact with the shell wall on the broadly flattened venter. Flower (1958) recognized that his *Lamottoceras* is very similar to the Asiatic *Kotoceras*, in which holochoanitic septal necks are present. However, the genus *Lamottoceras* differs from *Kotoceras* in having aneuchoanitic septal necks and thick connecting rings.

Kotoceras grabaui (Kobayashi, 1927)

Figures 3-3a, b; 7-1—4; 8-1—4

Vaginoceras grabaui Kobayashi, 1927, p. 79, pl. 18, figs. 1a-c, 2.
Vaginoceras frechi Kobabyashi, 1927, p. 179, pl. 18, figs. 2a-c.
Kotoceras grabaui (Kobayashi). Kobayashi, 1934, p. 395, pl. 11, figs. 5-8; pl. 12, fig. 6; pl. 14, figs. 5-8.
Kotoceras frechi (Kobayashi). Kobayashi, 1934, p. 395 (not figured).

Type.—The best preserved and largest specimen (UMUT PM631) is designated here as the lectotype of *Kotoceras grabaui* (Kobayashi) (Figures 3-3a, b).

Material.—Eleven specimens including the five figured ones (KPE20042, KPE20043, KPE20044, KPE20045, UMUT PM3).

Specific diagnosis.—Subcircular to elliptical in cross sec-

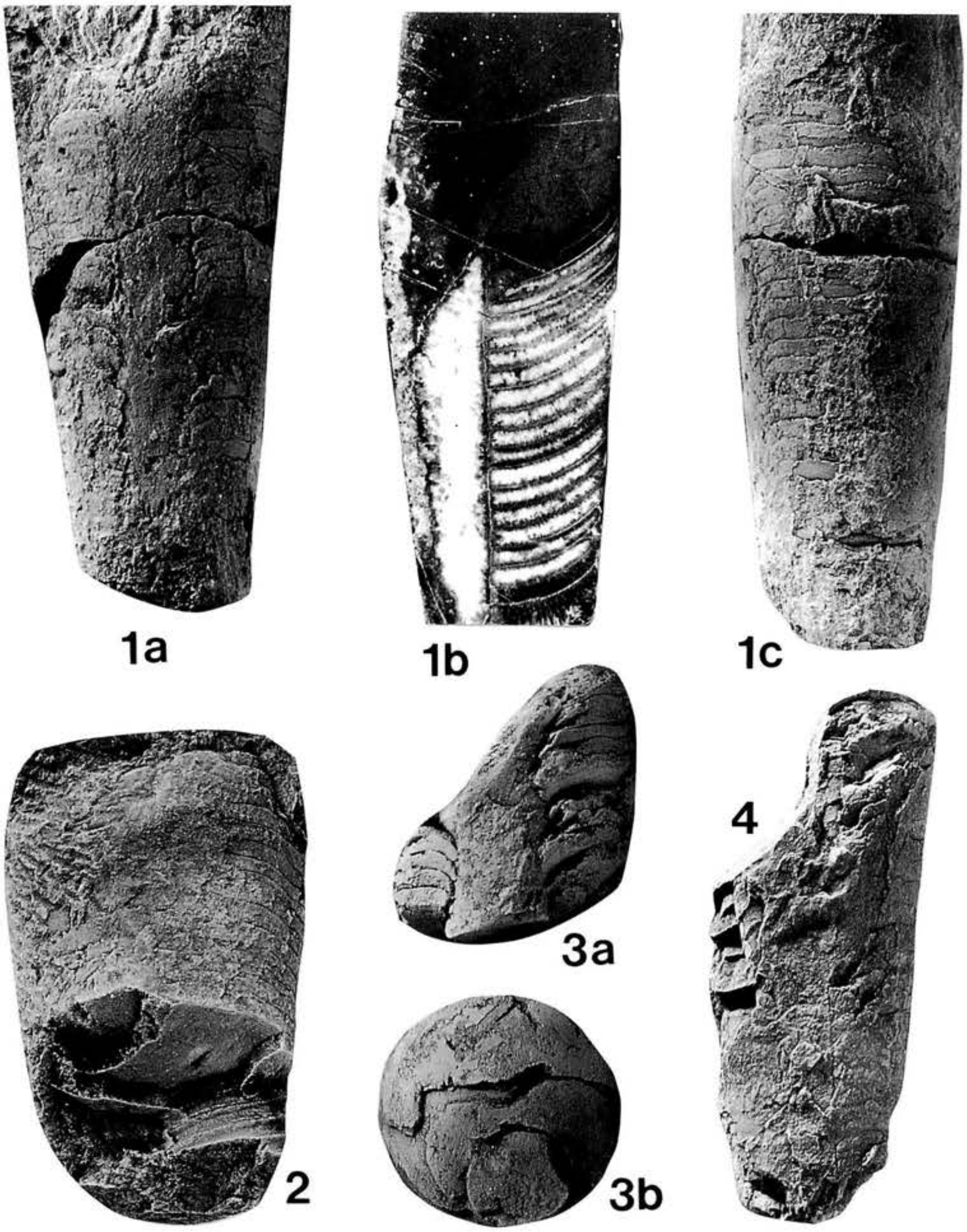

Figure 7. *Kotoceras grabaui* (Kobayashi, 1927). **1a-c.** Partial phragmocone (KPE20042) from SS663, ×1, 1a : ventral view, showing the disconnected septal suture, 1b : dorsoventral section, venter on left, showing the large siphuncle with endosiphuncular deposits and closely spaced septa, 1c : lateral view, venter on left side, showing the transverse septal suture. **2.** Strongly compressed phragmocone (KPE20043) from MG350, dorsolateral view, venter on right, showing the septal neck impressions on ventral side of the siphuncle, ×1. **3a, b.** Partial phragmocone (KPE20044) from MG357, ×1, 3a : ventral view, showing the siphuncle-septal neck portion, 3b : apical view of septum and siphuncle, showing the nearly circular conch cross section and slightly depressed siphuncle. **4.** Partial phragmocone (KPE20045) from MG357, ventral view, showing the somewhat flattened ventral side, ×1.

tion ; septal suture transverse, but gradually bends adapically and then turns into longitudinal section ; septal impressions sloping from venter to dorsal ; siphuncle large, nearly half or a little less than half the dorsoventral conch diameter ; camerae crowded.

Description.—Conch medium-sized longiconic orthoceracone, represented by several fragmentary phragmocones, its diameter gently enlarging at a rate of 1 mm per conch length of 9 mm in KPE20045 (Figure 7-4) ; conch elliptically ovate to subcircular in cross section, slightly dorsoventrally

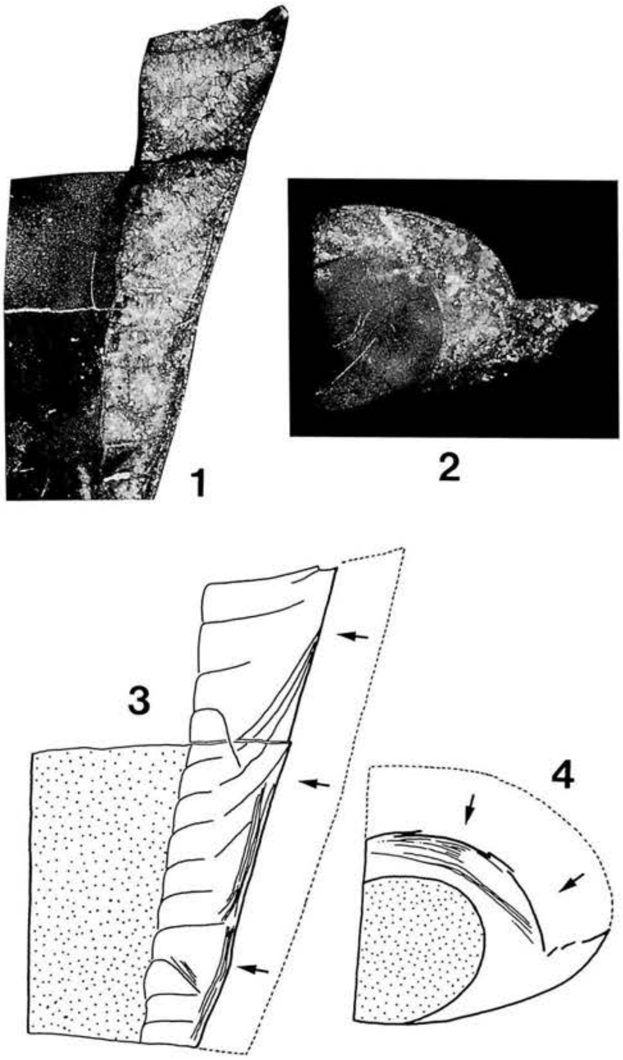

Figure 8. "*Kotoceras frechi* (Kobayashi)", UMUT PM3, which is here assigned to *Kotoceras grabaui* (Kobayashi). **1.** Longitudinal section shown by an acetate peel, ×2. **2.** Cross section by the same method, ×2. **3, 4.** Sketches of longitudinal section and cross section, respectively, showing the strongly depressed cameral portion and broken septa. Arrows indicate the direction of compaction.

depressed, ratio of the dorsoventral to lateral diameter of the conch near the adoral portion being 7 : 8 in KPE20042 (Figure 7-1) ; siphuncle marginal, in actual contact with the ventral wall, its cross section elliptical to subcircular, ventrally more flattened, expansion rate of the siphuncle commensurate with that of the conch ; septal impression on the siphuncle running obliquely down from ventral to dorsal, its distance being about 2 mm or more in KPE20043 (Figure 7-2) ; camerae crowded, averaging 11 in the distance of the dorsoventral diameter of the conch, tending to broaden adorally in the middle part of the phragmocone, but finally attaining a height of 1.5 mm in KPE20042 (Figure 7-1) ; septal necks holochoanitic ; septa moderately concave adorally, their depth corresponding to one and a half times the cameral height, increasing adorally where attaining a little more than twice the cameral height ; septal ridge on the siphuncle running obliquely from ventral to dorsal ; septal suture laterally transverse, but dorsally abruptly inclined backward, gradually bending posteriorly on the ventral side, and then becoming parallel to vertical axis ; no endocone observed ; camera filled with clastic sediments ; surface apparently smooth.

Remarks.—Kobayashi (1927) proposed *Vaginoceras frechi* from the Jigunsan Formation of Maggol, based on a single specimen (p. 179, pl. 18, figs. 2a-c ; UMUT PM3 ; Figure 8). Kobayashi (1934) subsequently reassigned this species to *Kotoceras*. According to his description, the characteristics of this species are summarized as follows : "The septum is gently inclined near the siphuncle but very steeply near the shell wall and is subangulated at a point where the septum bends from a gentle to a sharp angle". Kobayashi (1934) mentioned that this species is distinguished from *Kotoceras typicum* by having a more rapidly expanded conch, broader siphuncle and more concave septa.

However, the monotype of this species, UMUT PM3, is secondarily deformed along the dorsal margin, so that the above features may not fairly represent the specific diagnosis (Figure 8). Firstly, in the longitudinal section, septa of the dorsal portion are crushed by depression and then three or four septa are duplicated so as to be obliquely parallel with the shell wall. Most of the septa on the dorsal margin are irregularly arranged and broken. Because the clusters of broken septa are piled up longitudinally along the dorsal wall, the degree of convexity of each septum appears to change abruptly at a point midway on the septa. Secondly, the siphuncle has an unusually large diameter as compared with the conch diameter. In every species of *Kotoceras*, the siphuncle generally takes up one-third to a half of the conch diameter. The cameral portion in *Kotoceras frechi* is only one-third. The appearance must have been deformed by the effect suffered from sediments outside the dorsal portion. Thus, the diagnostic features of the specimen described as *Kotoceras frechi* by Kobayashi (1927, 1934) may be the result of diagenetic deformation, and therefore this taxon can be reassigned as a junior synonym of *Kotoceras grabaui* (Kobayashi, 1927).

In the meantime, Chen and Zou (1984, p. 80, pl. 16, fig. 6) identified a longitudinally sectioned specimen from the Lower Ordovician Yaoxian Formation of Shaanxi, North China as *Kotoceras frechi*. However, this specimen is assignable to *Kotoceras multiseptum* Kobayashi from the Jigunsan Formation of Maggol in having crowded and deeply concaved septa and a broad siphuncle.

Comparison.—This species is comparable to *Kotoceras stolbovense* Balashov from the Middle Ordovician Krivolutsky Formation of the Siberian Platform (Balashov, 1962, p. 32, pl. 26, figs. 1a-d) ; however, the present species has a much shallower septal concavity and slightly larger siphuncle.

Kotoceras typicum Kobayashi from the Jigunsan Formation of Maggol (Kobayashi, 1934, p. 392, pl. 11, figs. 1-4) is distinguished from *K. grabaui* by its more broadly spaced septa, nearly circular cross section of the conch in juvenile shell, and shell surface with fine growth lines.

In the septal distance and the shape of the cross section, *Kotoceras multiseptum* Kobayashi from the Jigunsan Formation of Maggol (Kobayashi, 1934, p. 394, pl. 12, figs. 1, 2; pl. 13, figs. 1-3) is closely allied to *K. grabaui*, but its conch expansion rate is much more rapid than that of the latter. *Kotoceras cylindricum* Kobayashi from the Jigunsan Formations of Maggol and Homyeong (Kobayashi, 1934, p. 393, pl. 12, figs. 7-9; pl. 13, figs. 8, 9) is easily distinguished from *K. grabaui* by its circular cross section with a depressed siphuncle and more crowded septa.

Occurrence.—Middle Ordovician Jigunsan Formation, localities; SR900, SS663, MG343, MG350 and MG357.

Acknowledgments

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Esgueiria futabensis sp. nov., a new angiosperm flower from the Upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan

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Abstract. Bulk sieving of samples from the Ashizawa Formation, Futaba Group (lower Coniacian) of northeastern Honshu, Japan, has yielded a well-preserved plant mesofossil assemblage comparable to those recently described from eastern North America, Europe and central Asia. The most distinctive component of the assemblage is a new species of the genus *Esgueiria* (*Esgueiria futabensis* sp. nov.), a fossil flower known previously only from the Upper Cretaceous (Campanian-Maastrichtian) of Portugal. A possible additional species of the genus has also been recovered from a second mesofossil assemblage in the Tamayama Formation (lower Santonian). The occurrence of *Esgueiria* in Europe and eastern Asia during the Late Cretaceous indicates that despite the vegetational differences between these areas inferred from fossil pollen, some elements were widespread across middle paleolatitudes, presaging the strong floristic similarities among mid- and high latitude regions of the Northern Hemisphere during the early Tertiary.

Key words: Angiosperm flower, Ashizawa Formation, Coniacian, *Esgueiria futabensis* sp. nov., Santonian, Tamayama Formation

Introduction

Studies of the early fossil history of flowering plants (angiosperms) have been revolutionized over the last 15 years by the discovery of abundant, small, well-preserved and systematically informative fossil flowers in assemblages of Cretaceous plant mesofossils from Europe and eastern North America (e.g., Friis and Skarby, 1982 ; Friis, 1983 ; Knobloch and Mai, 1984 ; Friis *et al*., 1994 ; Crane *et al*., 1994). These specimens have yielded important information relating to the early diversification of many lineages of extant angiosperms and the evolution of their pollination and dispersal biology (e.g., Crane *et al*., 1995). Only recently have similar mesofossil assemblages been recognized in central Asia (Frumina *et al*., 1995, Frumin and Friis, 1996, 1999), and we now report that they also occur in eastern Asia. In this paper we describe the most characteristic of several fossil flowers in newly discovered plant mesofossil assemblages from the Futaba Group (lower Coniacian-lower Santonian) of Northeast Japan.

Materials and methods

Plant fossils were isolated from two sets of bulk samples collected at two different levels in the Futaba Group exposed in Fukushima Prefecture, northeastern Honshu, Japan. The fossils are small, three-dimensional and charcoalified or lignitized mesofossils. The Kamikitaba plant mesofossil asssemblage (sample F16) was isolated from a poorly sorted, carbonaceous, black, sandy siltstone collected along a tributary of the Kitaba River in Kamikitaba, Hirono-machi (Study Route B of Ando *et al*., 1995 ; 37°12′N, 140°57′E). These samples were from the Asamigawa Member of the Ashizawa Formation, which is interpreted as alluvial fan sediments (Ando, 1997). The Kohisa plant mesofossil assemblage (sample F11), comprised a poorly sorted, beige, sandy siltstone with scattered carbonaceous flecks. It was collected along the Kohisa River, Kohisa, Ouhisa-machi northeast of Iwaki City (Study Route N of Ando *et al*., 1995 ; 37°10′N, 140°57′E). These samples were from the middle part of the Tamayama Formation, which is interpreted as braided river flood plain sediments with lagoonal facies in the uppermost part (Ando, 1997).

The Futaba Group comprises fluvial to shallow marine sediments in the southern Abukuma Belt of Northeast Japan (Ando *et al.*, 1995). The Ashizawa Formation is the lowermost formation in the Futaba Group, and is overlain by the Kasamatsu Formation, which itself is overlain by the Tamayama Formation. Based on the occurrence of lower Coniacian ammonites and inoceramids in the middle of the Ashizama Formation, and a lower Santonian inoceramid (*Inoceramus amakusensis*) in the upper part of the Tamayama Formation, the Futaba Group is thought to range in age from early Coniacian to early Santonian. The age of the plant-bearing sediments in the Asamigawa Member is probably early Coniacian (ca. 89 million years before present; Gradstein *et al.*, 1995), whereas the age of the plant-bearing sediments in the Tamayama Formation is probably early Santonian (ca. 85 million years before present; Gradstein *et al.*, 1995).

Bulk samples of ca. 500 kg of carbonaceous, black, poorly sorted sandy siltstone were dried in the laboratory, disaggregated in water and sieved through a 0.3 mm mesh. Recovered carbonaceous debris was then cleaned in hydrofluoric and hydrochloric acids, thoroughly rinsed in water, and dried in air. Individual specimens selected for scanning electron micrsocopy were mounted on scanning electron microscope stubs, sputter coated with platinum-palladium and examined in a Hitachi S-800 field emission scanning electron microscope. All specimens are deposited in the paleobotanical collections of the Field Museum of Natural History, Chicago (PP).

Systematic description

Class Magnoliopsida (angiosperms)
Genus ***Esgueiria*** Friis, Pedersen and Crane, 1992

The genus was established by Friis, Pedersen and Crane (1992) based on material from two localities of Campanian-Maastrichtian age in the northern part of the Western Portuguese Basin, Beira Litoral, Portugal. Two species were distinguished: *Esgueiria adenocarpa* from the Esgueira locality (the type species), and *Esgueiria miraensis* from the Mira locality.

Esgueiria futabensis sp. nov.

Figures 1-1—1-8, 2-1, 2-2, 2-4, 2-5

Material.— PP45389 (holotype). Other specimens; PP 45390-PP45417.

Type Locality and Horizon.—Kamikitaba plant mesofossil assemblage (sample F16), along a tributary of the Kitaba River in Kamikitaba, Hirono-machi, (Study Route B of Ando *et al.* 1995; 37°12′N, 140°57′E).

Etymology.—Named after the Futaba Group, the geological unit from which the specimens were recovered.

Specific Diagnosis.—Ovary and fruit narrowly elongate, rounded at the base. Peltate (glandular) trichomes on the base of the styles, and also in rows, often of ten or more, on the hypanthium. Simple trichomes densely spaced on the surface of the ovary, calyx and styles. Prominent receptacular mounds present between the stamens and the perianth.

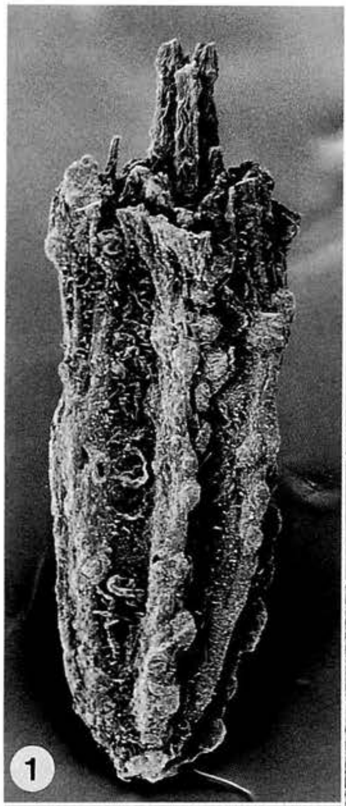
Dimensions.—All specimens lacking a well-preserved corolla: length of ovary: (1.85-) 2.76 (—3.3) mm; breadth of ovary: (0.7—) 1.12 (—1.5) mm; length of sepals: unknown; breadth of sepals: (0.3-) 3.62 (—0.4) mm: 25 specimens measured. Pollen not identified.

Description and Remarks.—The species is known from 29 complete or fragmentary flowers from the Kamikitaba assemblage preserved mainly as charcoalified specimens. Similar material from the Kohisa assemblage is not referred to *E. futabensis*, and probably represents a different species of *Esgueiria* (see below). Many of the specimens are broken or abraded fragments of the inferior ovary, but almost all show either the distinctive peltate glands, or the remains of the glands and their secretion in one or more longitudinal grooves in the ovary wall. None of the specimens is a bud and most of the material probably represents mature fruits with a partially persistent perianth and androecium. None of the specimens has yielded information on inflorescence structure, anthers, pollen or ovules.

Flower: Flowers are epigynous (Figure 1-1) and the calyx is visible in most specimens. Remains of filament and styles bases are also commonly preserved. Unequivocal remains of the petals are rarely present. None of the specimens have a pedicel or prophyll preserved.

Perianth: The calyx consists of five free sepals (Figure 1-2). In all specimens the calyx lobes are broken and their shape cannot be established reliably (Figures 1-2, 1-6, 2-5).

→ **Figure 1.** *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian), Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. **1.** Holotype, lateral view of well-preserved epigynous flower showing peltate and simple trichomes on the ovary wall, note remains of sepals and three styles at flower apex, as well as the protruding hemispherical glands in the outer tissues of the ovary wall, PP45389, ×35. **2.** Holotype, apex of flower showing sepals, possible remains of corolla, receptacular mounds, stamen filaments and three styles, PP45389, ×73. **3.** Holotype, detail of small, peltate, trichome from base of style, note also thick wall of broken trichome, PP45389, ×930. **4.** Lateral view of abraded specimen showing ovary with longitudinal ribs denuded of trichomes, note remains of sepals and stout style base at the apex of the flower, PP45403, ×35. **5.** Holotype, detail of peltate and simple trichomes from ovary wall, note also the opening of a hemispherical gland in the ovary wall, PP45389, ×100. **6.** Detail of apical portion of specimen in Figure 1-4 showing sepals, receptacular mounds, filament bases and stout base of style, PP45403, ×72. **7.** Holotype, detail of simple trichome from ovary wall, note verrucate surface, PP45389, ×920. **8.** Detail of apex of flower in Figure 1-4 showing remains of sepals, ten prominent receptacular mounds, eight (possibly nine) filament bases and stout base of style, PP45403, ×72.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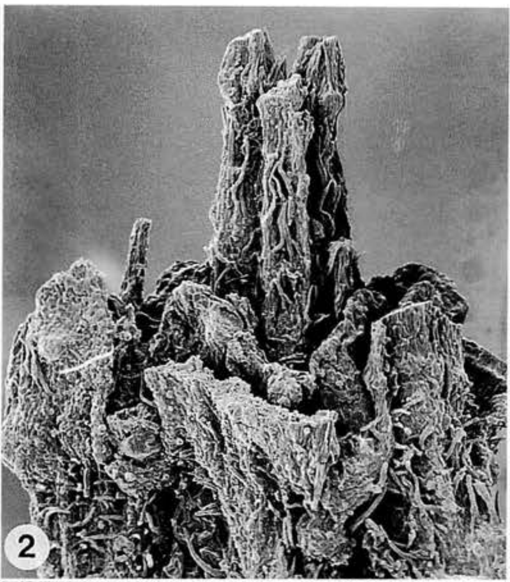
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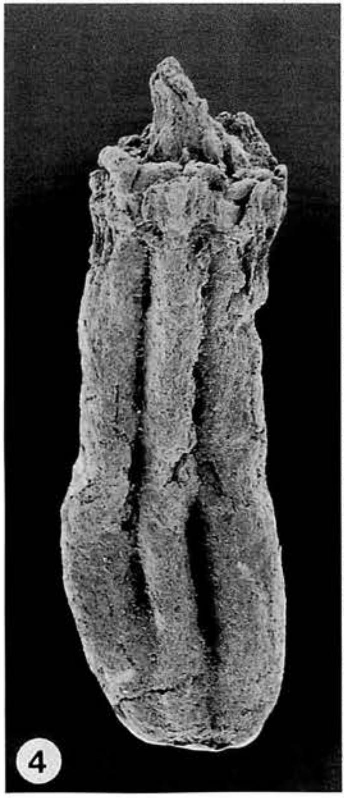
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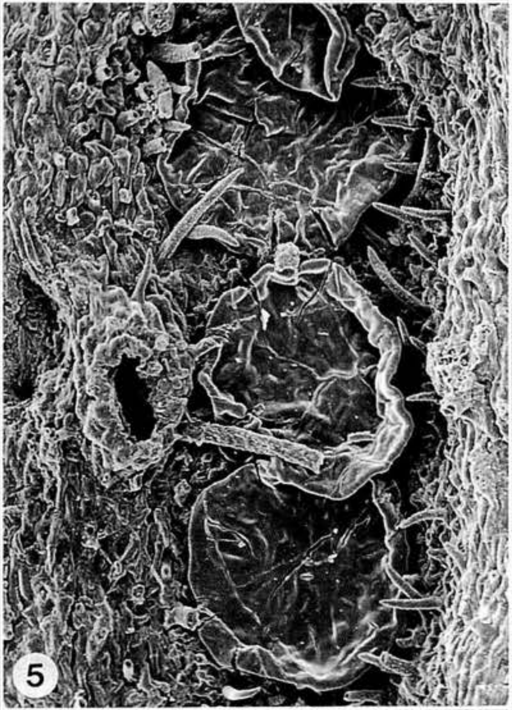
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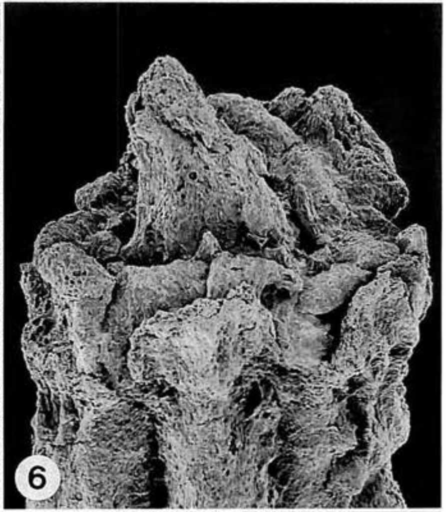
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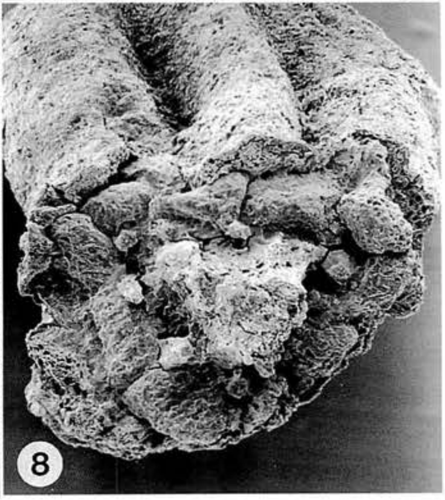
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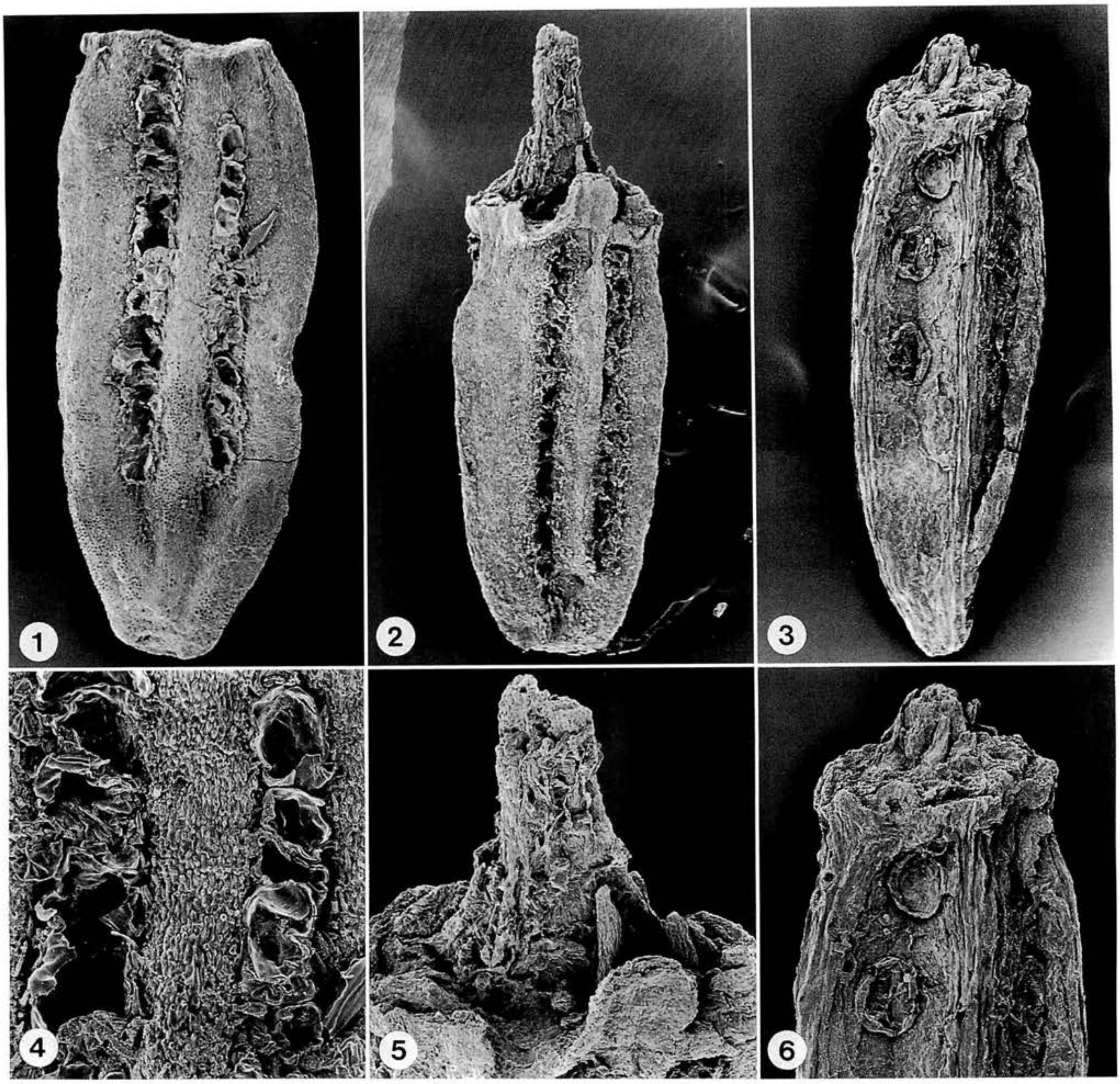

Figure 2. *Esgueiria futabenis* sp. nov. and *Esgueiria* sp., Futaba Group, Fukushima Prefecture, northeastern Honshu, Japan. 1, 2, 4, 5, *Esgueiria futabensis* sp. nov., Kamikitaba assemblage, Asamigawa Member, Ashizawa Formation (lower Coniacian). 3, 6, *Esgueiria* sp., Kohisa assemblage, middle part of the Tamayama Formation (lower Santonian). **1.** Lateral view of abraded specimen showing numerous peltate trichomes in two grooves in the ovary wall, PP45391, ×32. **2.** Lateral view of abraded specimen showing remains of peltate trichomes in two grooves in the ovary wall, note remains of sepals and stout base of style at the floral apex, PP45393, ×30. **3.** Lateral view of compressed specimen showing three prominent peltate trichomes on the ovary wall, note that the peltate trichomes are larger and fewer than in *E. futabensis*, PP45419, ×17. **4.** Detail of specimen in Figure 2-1 showing remains of peltate trichomes and unabraded portion of ovary wall, PP45391, ×90. **5.** Apex of specimen in Figure 2-2 showing sepals, bases of two filaments and stout base of style, PP45393, ×67. **6.** Apex of specimen in Figure 2-3 showing stamen filament surrounding stout base of style, note remains of receptacular mounds between the sepals and stamen bases, PP45419, ×27.

However, there are sufficient specimens in which parts of the calyx are preserved to infer that it was persistent through fruit development. The corolla is not clearly visible in any of the specimens, although a few show fragments of tissue that may represent the bases of petals. The rare presence of the corolla in more than 1,000 specimens of *E. adenocarpa* led to the conclusion that the corolla was probably caducous (Friis *et al.*, 1992), and this may also have been the case in *E. futabensis*.

Receptacular mounds: Most specimens show prominent, more or less ellipsoidal mounds of tissue, ca. 0.2 mm broad and ca. 0.1 mm deep, on the receptacle between the filament bases and the calyx (Figures 1-6, 1-8). In one specimen there are ten mounds that alternate with the stamen bases (Figure 1-8). The nature of these mounds is uncertain, but judging from their position and swollen structure (Figures 1-2, 1-6) it is possible that they are nectary lobes. A possible nectary was observed in *E. adenocarpa*, but in the more usual postion for a disc nectary, between the stamens and the style bases (Friis *et al.*, 1992). In *E. futabensis* it is clear that the receptacular mounds are outside the androecium between the sepals and the stamens (Figure 1-8).

Androecium: None of the specimens has a complete stamen preserved and we have been unable to detect pollen on any of the flowers. However, the position of the stamen filaments indicates stamens were both opposite to, and alternate with, the sepals (Figure 1-8). Based on this pattern an androecium of ten stamens would be inferred. However, the best preserved androecium (Figure 1-8) shows the remains of only eight (or possibly nine) filaments. It is uncertain whether this indicates incomplete preservation, or whether less than ten stamens developed as in *E. adenocarpa* (Friis *et al.*, 1992). There is no clear indication that stamens were arranged in more than one whorl (Figure 1-8).

Gynoecium: The ovary is inferior and unilocular. The holotype clearly shows that there were three free styles, at least distally (Figure 1-2). Proximally, however the styles appear to have been fused into a single, stout, style base (Figures 1-6, 2-5). The ovary is narrowly elongated, more or less parallel-sided and with a rounded base (Figures 1-1, 1-4, 2-1, 2-2). The ovary wall is pleated into five longitudinal grooves that alternate with sepals, and five longitudinal ridges that are on the same radius as the sepals. The ovary wall is about 0.05 mm thick. In several specimens there are protruding hemispherical glands, ca. 0.1 mm in diameter, in the outer tissues of the ovary wall. In abraded specimens that lack the epidermis the inner layers of the ovary wall are seen to be composed of small equiaxial sclerenchyma cells ca. 0.01 mm in diameter. Lining the locule there is a inner epidermis of larger cuboidal cells.

Trichomes: Two different types of trichomes have been observed on the specimens. They are best developed and most easily observed on the surface of the ovary but also occur on the stout style base.

Simple trichomes: Simple hairs are scattered all over the ovary and other floral organs. The hairs may be up to ca. 0.2 mm long, are more or less parallel-sided for much of their length, and appear to be unicellular (Figure 1-7). At the apex they have an acute point. Broken specimens show that the trichomes are thick-walled (Figure 1-3). The trichome wall close to the point of attachment seems to be thinner and somewhat collapsed (Figure 1-7). In well-preserved specimens the trichome wall is ornamented with distinctive elongated verrucae (Figures 1-3, 1-7).

Peltate trichomes: Peltate trichomes (inferred to have been glandular) are arranged in a single row in the grooves in the ovary wall (Figures 1-5, 2-4). The peltate trichomes never occur side-by-side. Smaller peltate trichomes also occur on the style bases (Figure 1-3). On the ovary wall the peltate trichomes are typically more or less circular, 0.12-0.18 mm in diameter, and appear to consist of a central stalk and a shieldlike head. A clear radiating structure among the cells comprising the head has not been seen. The number of peltate trichomes in a single row varies, but it is often between 10 and 20 (Figure 1-1, 2-1). Frequently, under the light microscope, the peltate trichomes appear to be embedded in a black shiny substance, which is often present even when the trichomes themselves are not clearly visible (Figure 2-2). We infer that this represents the remains of a secretion associated with the glandular trichomes. Peltate trichomes also occur on the style-bases of well-preserved specimens scattered among the simple hairs. These trichomes are generally smaller (ca. 0.06 mm in diameter) and less prominent than those on the ovary wall but are similar in structure (Figure 1-3).

Comparison

Esgueiria futabensis clearly shows the diagnostic features of the genus (Friis *et al.*, 1992). The flowers are small, epigynous and bisexual with the perianth and androecium organized on a basically pentamerous plan. There is a calyx of five free sepals and an androecium with more than five stamens. The ovary is unilocular with three styles. The indumentum consists of simple stiff hairs and the characteristic multicellular, peltate trichomes.

Esgueiria futabensis is clearly distinguished from the two other species of the genus. It differs from the type species, *E. adenocarpa*, in being generally larger: (1.85-) 2.76 (-3.3) mm rather than (1.5-) 1.88 (2.2) mm long. The shape of the ovary is also more or less parallel-sided, rather than obovate, and the base of the ovary is rounded rather than pointed (compare Figures 1-1, 1-4, 2-1, 2-2 with Friis, Pedersen and Crane, 1992, Plate 1). The peltate trichomes are smaller (0.12-0.18 mm in diameter) in *E. futabensis* than in *E. adenocarpa* (0.2-0.3 mm in diameter). Also significant is the number of peltate glands in a single groove on the ovary wall, which is often 10-20 in *E. futabensis*, compared with a maximum of five or six in *E. adenocarpa*.

The occurrence of peltate glands on the style bases (Figure 1-3) is a further difference between *E. futabensis* and *E. adenocarpa*, but a similarity with *E. miraensis*. However, compared to *E. miraensis, E. futabensis* is larger: length of ovary (1.85-) 2.76 (-3.3) mm compared to 0.8-0.95 mm. The ovary of *E. futabensis* is also long and narrow, rather than campanulate as in *E. miraensis*.

Other *Esguieria* flowers are known from the Kohisa plant mesofossil assemblage, which is younger (early Santonian) than the Kamikitaba assemblage that yielded *E. futabensis*. However, the Kohisa specimens are larger than those from Kamikitaba (length of ovary [2.75-] 3.5 [−4] mm), are more obovate in shape with a more pointed base, and also have significantly larger peltate trichomes (Figures 2-3, 2-6). These specimens may represent a fourth species of *Esgueiria*, but because only eight specimens are known (PP45418-PP45425), they are here left unassigned as *Esgueiria* sp.

Discussion

In terms of systematic affinities, *E. futabensis* does not add to previous discussions of a relationship between *Esgueiria* and the extant angiosperm family Combretaceae.., However, this new species is important in several respects. It documents the occurrence of mesofossil assemblages with well-preserved angiosperm flowers in the Upper Cretaceous of Japan that are comparable in their quality of preservation to those recently described from eastern North America, Europe and central Asia. It adds a new species to the very small number of fossil angiosperm reproductive structures so far described from the Upper Cretaceous of Japan (Stopes and Fujii, 1910; Ohana and Kimura, 1987; Nishida, 1985, 1991, 1994; Nishida and Nishida 1988; Nishida *et al.*, 1996). It also provides the first evidence of botanically informative plant fossil assemblages (other than palynofloras; Miki, 1977; Takahashi, 1988) in the Futaba Group.

The discovery of *Esgueiria futabensis* also has interesting biogeographic implications and extends substantially the range of a genus previously known only from the Campanian-Maastrichtian of Portugal. Based on pollen and spore assemblages Portugal was part of the Normapolles Province during the Late Cretaceous. Japan is generally included in the *Aquilapollenites* Province (Herngreen *et al.*, 1996) based on the first appearance of triprojectate grains in Late Cretaceous sediments younger than those of the Futaba Group (Miki, 1977). The occurrence of *Esgueiria* in both eastern Asia and southern Europe documents that some Late Cretaceous floristic elements had very broad geographic distributions, presaging the strong floristic similarities evident at middle and high latitudes of the Northern Hemisphere during the early Tertiary.

Acknowledgments

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Boreal-type brachiopod *Yakovlevia* from the Middle Permian of Japan

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Abstract. The following three species of the Boreal-type brachiopod genus *Yakovlevia* are described from the Middle Permian (Kungurian to Ufimian) of the Hida Gaien (=Hida Marginal) and South Kitakami Belts, Japan: *Y. kaluzinensis* Fredericks, *Y. mammata* (Keyserling) and *Y. mammatiformis* (Fredericks). The occurrence of *Yakovlevia* together with various Boreal- and Tethyan-type brachiopods in the Middle Permian of the two belts suggests that these regions were probably a continental shelf at the eastern margin of the Sino-Korean block in Middle Permian time.

Key words: **Boreal-type brachiopod, Hida Gaien Belt, Middle Permian, Sino-Korean block, South Kitakami Belt, *Yakovlevia***

Introduction

Brachiopods are important and useful for Permian global palaeobiogeography as the predominant element in the benthic fauna at that time (Stehli, 1973; Waterhouse and Bonham-Carter, 1975; Grunt, 1995; Shi *et al*., 1995; Jin and Shang, 1997). *Yakovlevia* is a typical Boreal-type, Middle Carboniferous to Middle Permian productoid genus belonging to the family Yakovleviidae Waterhouse, 1975. This genus was established by Fredericks in 1925, with *Chonetes* (*Yakovlevia*) *kaluzinensis* Fredericks, 1925 from the Middle Permian Chandalaz Formation of Cape Kalouzin in the Vladivostok area, South Primorye as the type species. The morphology and classification of *Yakovlevia* and related genera have been fully discussed by Licharew (1947), Muir-Wood and Cooper (1960), Kotljar (1961), Muir-Wood (1965), Cooper and Grant (1975), Waterhouse (1975), and Shi (1995). Concerning the relationship of *Yakovlevia* with *Muirwoodia* Licharew, 1947, I follow Kotljar (1961), Cooper and Grant (1975), and Shi (1995), all of whom considered *Muirwoodia* as a junior synonym of *Yakovlevia*.

The purpose of this paper is to describe three *Yakovlevia* species, *Y. kaluzinensis* Fredericks, 1925, *Y. mammata* (Keyserling, 1846), and *Y. mammatiformis* (Fredericks, 1926), from the Middle Permian (Kungurian to Ufimian) of the Hida Gaien and South Kitakami Belts, Japan, discussing their palaeobiogeographical significance. The material utilized is: eight specimens of *Y. kaluzinensis* from the lower part of the Moribu Formation in the Moribu area, Hida Mountains (Hida Gaien Belt), central Japan; two specimens of *Y. mammata* from the lower Kanokura Formation in the Kesennuma area, southern Kitakami Mountains (South Kitakami Belt), northeast Japan; and the single specimen of *Y. mammatiformis* from the upper Iriishikura Formation in the Takakurayama area, Abukuma Mountains (South Kitakami Belt), northeast Japan (Figure 1). These specimens are housed in the Department of Geology, Faculty of Science, Niigata University, Niigata (NU-B) and the Institute of Geology and Palaeontology, Tohoku University, Sendai (IGPS).

Palaeobiogeographical significance of *Yakovlevia*

Recently Shi (1995) summarized the stratigraphical and geographical distribution of *Yakovlevia* using 45 species of this genus. According to him, the genus is distributed from the Middle Carboniferous to Middle Permian of the Boreal Realm and the transitional zone between the Boreal and Tethyan Realms, namely, the Northern Transitional Zone (Sino-Mongolian Province) and the Cordilleran Province (see Shi, 1995, figs. 2, 3, table 1). The former transitional zone is almost equal to the Inner Mongolian-Japanese Transition Zone of Tazawa (1991).

As shown in Figure 2, the three *Yakovlevia* species described below clearly indicate a Boreal distribution. *Y. kaluzinensis* has been known from the Middle Permian (Kungurian to Ufimian) of South Primorye, eastern Russia, and the Hida Mountains, central Japan (Fredericks, 1925; Muir-Wood and Cooper, 1960; Kotljar, 1961; Licharew and Kotljar, 1978; Horikoshi *et al*., 1987; Tazawa, 1987). *Y. mammata* has been known from the Lower Permian (Artinskian) to Middle Permian (Guadalupian) of Spitsbergen; Timan and Pechora, northern Russia; Upper Yukon River, Yukon Territory; Grinnell Peninsula, Devon Island, Arctic Canada; Tien Shan, West China; Ekenalsileng, Jisu (Zhesi), Dong Ujimqin, Xi Ujimqin and Horqin Youyi Qianqi, Inner Mongolia, North China; South Primorye, eastern Russia;

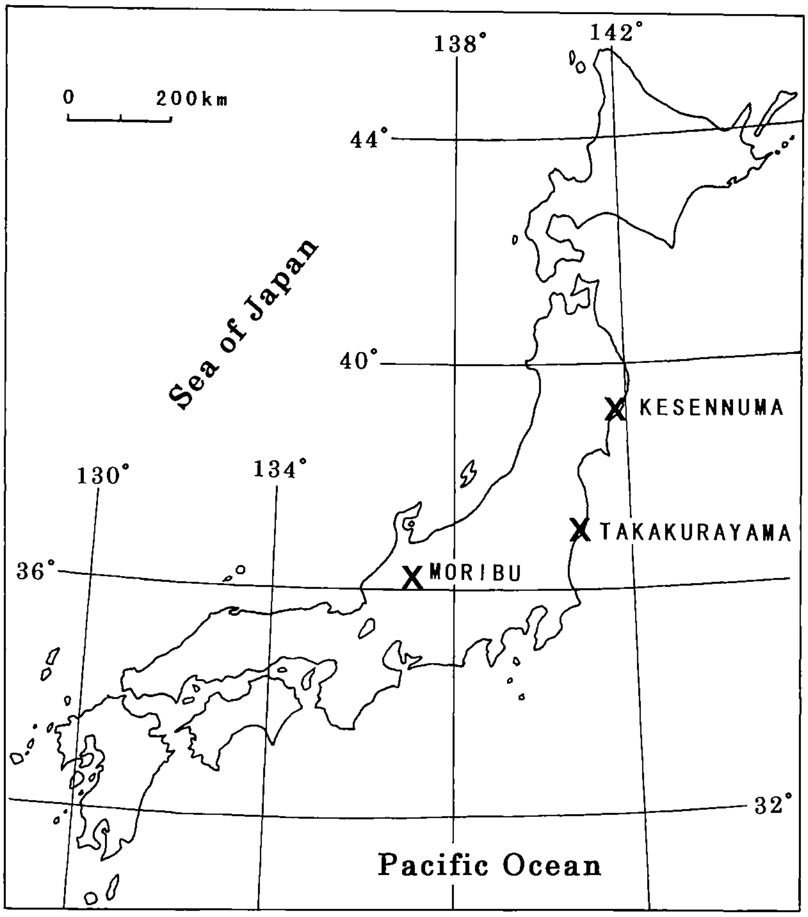

Figure 1. Map showing the fossil localities.

southern Kitakami Mountains, northeast Japan (Keyserling, 1846 ; Koninck, 1847 ; Tschernyschew, 1902 ; Keidel, 1906 ; Chao, 1927 ; Grabau, 1931 ; Stepanov, 1937 ; Muir-Wood and Cooper, 1960 ; Harker in Harker and Thorsteinsson, 1960 ; Kotljar, 1961 ; Gobbett, 1963 ; Brabb and Grant, 1971 ; Ifanova, 1972 ; Lee and Gu, 1976 ; Licharew and Kotljar, 1978 ; Lee and Gu in Lee *et al.*, 1980 ; Liu and Waterhouse, 1985 ; Tazawa, 1987 ; Malkowski, 1988 ; Zhang, 1990 ; Nakamura *et al.*, 1992 ; Kalashnikov, 1993). *Y. mammatiformis* is distributed in the Lower Permian (Sakmarian) to Middle Permian (Kungurian) of the northern Urals, Timan, Pechora Basin and Novaya Zemlya, northern Russia ; Omolon Massif, northeastern Russia ; South Primorye, eastern Russia ; Abukuma Mountains, northeast Japan (Fredericks, 1926 ; Kotljar, 1961 ; Mironova, 1964 ; Yanagisawa, 1967 ; Zavodowsky and Stepanov in Zavodowsky *et al.*, 1970 ; Ifanova, 1972 ; Kulikov, 1974 ; Kalashnikov, 1983, 1993).

The Middle Permian brachiopod faunas of the Hida Gaien and South Kitakami Belts are characterized by a mixture of Boreal and Tethyan elements, e.g., *Yakovlevia, Cancrinella, Waagenoconcha, Megousia, Stenoscisma*, and *Spiriferella* as the Boreal-type genera, and *Leptodus, Enteletes, Transennatia, Permundaria*, and *Urushtenoidea* as Tethyan-type genera (Tazawa, 1987, 1991, 1992 ; Nakamura and Tazawa, 1990), and closely resemble those of South Primorye, Northeast China and Inner Mongolia (Tazawa, 1987, 1991, 1992). The occurrence of *Yakovlevia* together with various Boreal- and Tethyan-type brachiopods in the Middle Permian of the Hida Gaien and South Kitakami Belts supports the opinion of Tazawa (1991, 1992), who considered that 1) the above regions belonged to the Southern Subzone of the Inner Mongolian-Japanese Transition Zone, and that 2) this subzone was being probably a piece of continental shelf bordering the eastern margin of the Sino-Korean block, which was situated at a middle northern palaeolatitude in Middle Permian time (Figure 2).

Systematic descriptions

Order Productida Waagen, 1883
Suborder Productidina Waagen, 1883
Superfamily Linoproductoidea Stehli, 1954
Family Yakovleviidae Waterhouse, 1975
Genus **Yakovlevia** Fredericks, 1925

Type species.—*Chonetes* (*Yakovlevia*) *kaluzinensis* Fredericks, 1925.

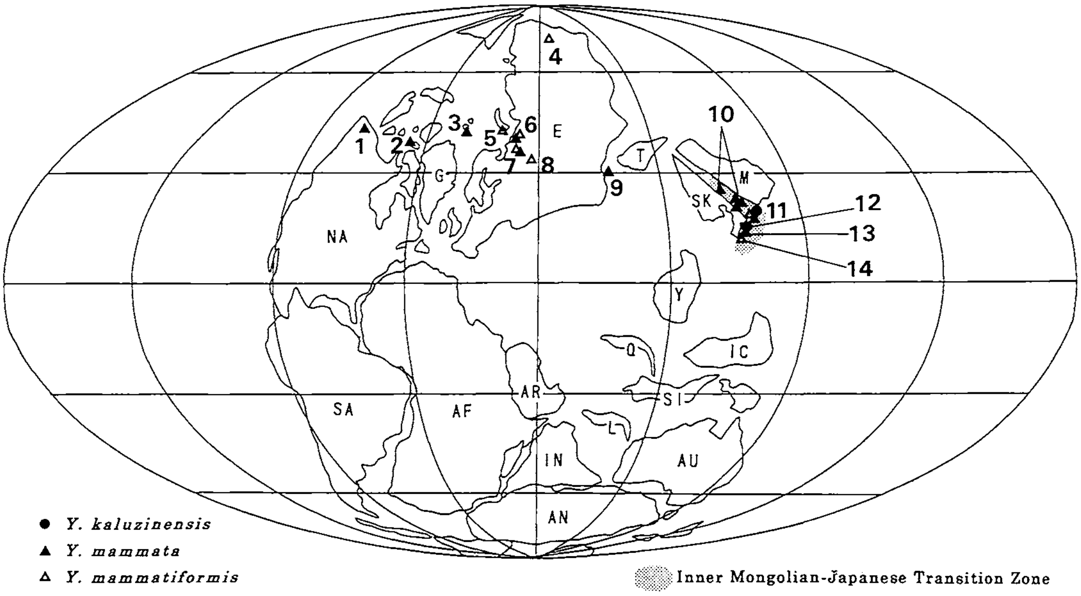

Figure 2. Geographical distribution of *Yakovlevia kaluzinensis* Fredericks, *Yakovlevia mammata* (Keyserling) and *Yakovlevia mammatiformis* (Fredericks) in Middle Permian. (Palaeogeographic map after Ziegler *et al*., 1996). **1.** Yukon Territory, **2.** Devon Island, **3.** Spitsbergen, **4.** Omolon Massif, **5.** Novaya Zemlya, **6.** Pechora Basin, **7.** Timan, **8.** northern Urals, **9.** Tien Shan, **10.** Inner Mongolia, **11.** South Primorye, **12.** Moribu, Hida Mountains, **13.** Kesennuma, southern Kitakami Mountains, **14.** Takakurayama, Abukuma Mountains. AF : Africa, AN : Antarctica, AR : Arabia, AU : Australia, E : Eurasia, G : Greenland, IC : Indochina, IN : India, L : Lhasa, M : Mongolia, NA : North America, Q : Qangtang, SA : South America, SI : Sibumasu, SK : Sino-Korea, T : Tarim, Y : Yangtze.

Yakovlevia kaluzinensis Fredericks, 1925

Figures 3-7—15

Chonetes (*Yakovlevia*) *kaluzinensis* Fredericks, 1925, p. 7, pl. 2, figs. 64-66.

Yakovlevia kaluzinensis Fredericks. Muir-Wood and Cooper, 1960, pl. 133, figs. 5, 6 ; Kotljar, 1961, text-figs. 1-3 ; Licharew and Kotljar, 1978, pl. 14, figs. 1, 2.

Yakovlevia sp. Horikoshi *et al*., 1987, text-figs. 3A, B ; Tazawa, 1987, text-fig. 1.7.

Material.—Eight specimens, from the lower Moribu Formation in the Moribu area, Hida Mountains (Hida Gaien Belt), central Japan : (1) external and internal moulds of a pedicle valve, NU-B157 ; (2) internal moulds of three pedicle valves, NU-B158-160 ; (3) external and internal moulds of two brachial valves, NU-B161, 162 ; (4) external moulds of two brachial valves, NU-B163, 164.

Description.—Shell large for genus, transversely subrectangular in outline, with greatest width at hinge line ; length about 37 mm, width about 44 mm in the smaller pedicle valve specimen (NU-B157) ; length 38 mm, width about 60 mm in the largest and best preserved brachial valve specimen (NU-B163).

Pedicle valve gently convex on venter, strongly geniculated, and followed by a long trail. Umbo small. Ears large, prominent, but not clearly differentiated from visceral part. Sulcus narrow and shallow, originating near umbo, and extending to anterior margin. External ornament of pedicle valve invisible except for a row of oblique spines just anterior to the posterior margin. Brachial valve nearly flat on visceral disc, strongly geniculated, and followed by a short trail. Fold narrow and low on anterior half of valve. External surface of brachial valve ornamented by numerous fine costellae and several weak, irregular concentric rugae on visceral disc, costellae only on trail ; costellae often bifurcating and intercalating, numbering 11-13 costellae in 5 mm at midvalve.

Pedicle valve interior with a pair of small, elongate subtrigonal adductor scars and two large diductor scars. Diductor scars striated anteriorly and encircled by a strong ridge posterolaterally., Internal structure of brachial valve obscure in the present material.

Comparison.—The Moribu specimens are referred to *Yakovlevia kaluzinensis* Fredericks, 1925, originally described by Fredericks (1925) from the Middle Permian in size and shape of the shells, especially in the transversely subrectangular outline.

Yakovlevia impressa (Toula, 1875, p. 236, pl. 5, figs. 1a-c) from the Middle Permian of Spitsbergen differs from *Y. kaluzinensis* in having larger and more prominent ears.

Yakovlevia mammata (Keyserling, 1846)

Figures 3-1—5

Productus mammatus Keyserling, 1846, p. 206, pl. 4, figs. 5-5b ; Koninck, 1847, p. 49, pl. 7, figs. 4a-e ; Tschernyschew, 1902, p. 295, pl. 35, figs. 4-6 ; Keidel, 1906, p. 367, pl. 12, figs. 5a,

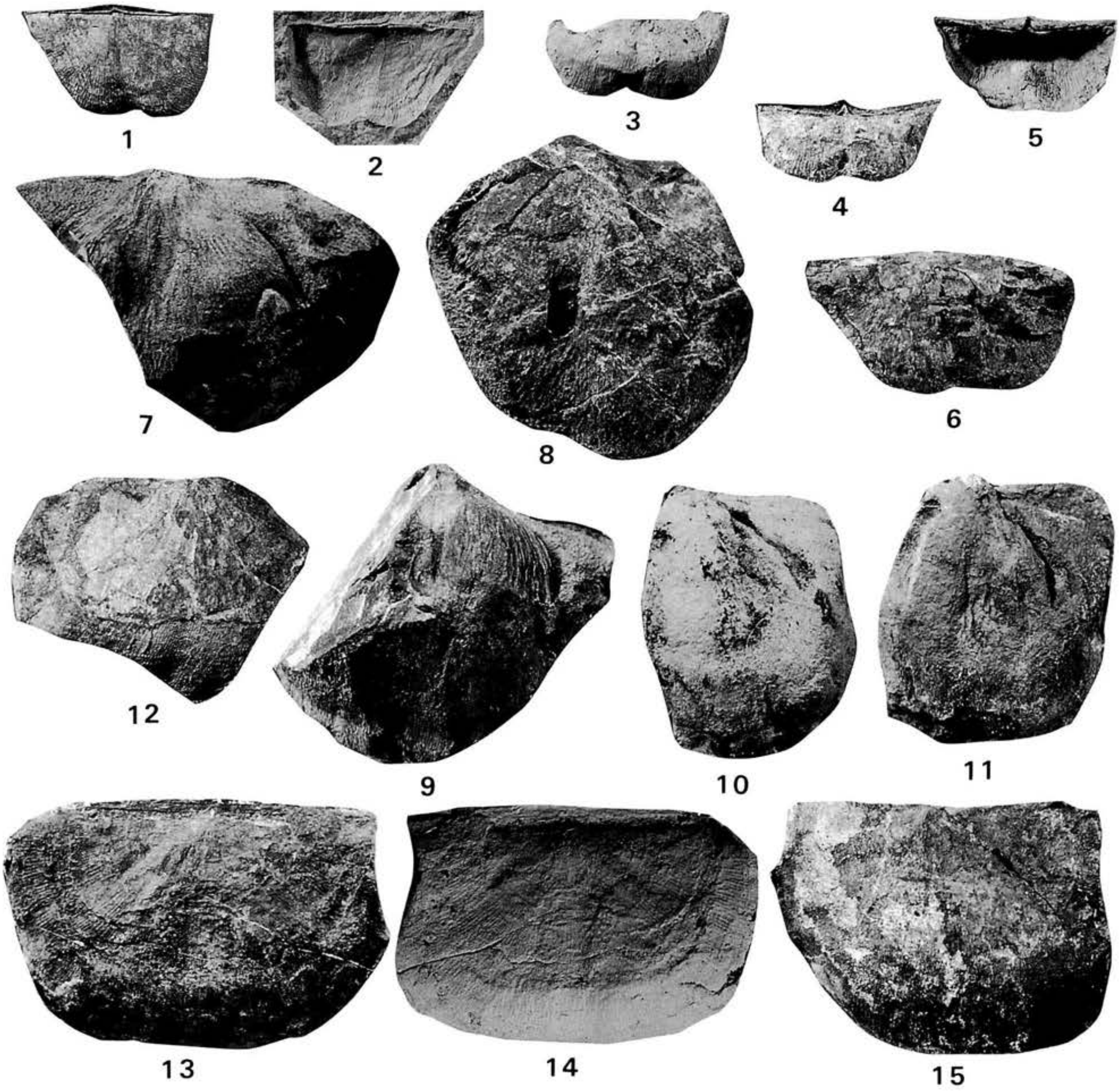

Figure 3. **1—5.** *Yakovlevia mammata* (Keyserling). **1, 2.** External mould of a brachial valve and the latex cast, NU-B166. **3—5.** latex cast of a pedicle valve exterior, external mould of a brachial valve and the latex cast, NU-B165. **6.** *Yakovlevia mammatiformis* (Fredericks), external mould of a brachial valve, IGPS coll. cat. no. 86649. **7—15.** *Yakovlevia kaluzinensis* Fredericks. **7—9.** internal moulds of pedicle valve specimens, **7.** NU-B158, **8.** NU-B160, **9.** NU-B159. **10, 11.** external mould of a pedicle valve and the latex cast, NU-B157 ; **12.** external mould of a brachial valve, NU-B162 ; **13, 14.** external mould of a brachial valve and the latex cast, NU-B163. **15.** external mould of a brachial valve, NU-B161. (All figures in natural size)

b.

Linoproductus ? *mammatus* (Keyserling). Chao, 1927, p. 146, pl. 15, figs. 10-14.

Productus (Linoproductus ?) *mammatus* Keyserling. Grabau, 1931, p. 288, pl. 29, figs. 10-14.

Productus (Thomasina) mammatus Keyserling. Stepanov, 1937, p. 127, 177, pl. 2, figs. 5-7.

Muirwoodia mammata (Keyserling). Muir-Wood and Cooper, 1960, pl. 120, figs. 9-11 ; Harker in Harker and Thorsteinsson, 1960, p. 58, pl. 16, figs. 1-5 ; Gobbett, 1963, p. 112, pl. 13, figs. 23-28 ; Lee and Gu, 1976, p. 263, pl. 159, figs. 7-9 ; pl. 163, figs. 2a, b ; pl. 164, figs. 3-4 ; pl. 170, figs. 6, 7 ; Licharew and Kotljar, 1978, pl. 14, figs. 3-5 ; Liu and Waterhouse, 1985, p. 17, pl. 4, figs. 4-6 ; Nakamura *et al*., 1992, pl. 1, figs. 4a, b ;

Kalashnikov, 1993, p. 63, pl. 19, figs. 1-3.
Yakovlevia mammatus Keyserling. Kotljar, 1961, text-figs. 4-6.
Yakovlevia mammata (Keyserling). Brabb and Grant, 1971, p. 16, pl. 1, figs. 9-12, 33-36; Ifanova, 1972, p. 121, pl. 7, figs. 4-5; Malkowski, 1988, p. 40, pl. 5, fig. 6; Zhang, 1990, pl. 2, figs. 4, 7, 9.
Yakovlevia paragreenlandica Lee and Gu in Lee *et al.*, 1980, p. 382, pl. 171, figs. 5-7.
Muirwoodia sp. Tazawa, 1987, text-fig. 1.6.

Material.—Two specimens, from the lower Kanokura Formation of Kamiyasse and Omotematsukawa in the Kesennuma area, southern Kitakami Mountains (South Kitakami Belt), northeast Japan: (1) external and internal moulds of a pedicle valve, NU-B165; (2) an external mould of a brachial valve, NU-B166.

Description.—Shell small for genus, transversely subtrapezoidal in outline, with greatest width at hinge line; length 13 mm+, width 28 mm in the pedicle valve specimen (NU-B165); length 16 mm, width 29 mm in the brachial valve specimen (NU-B166).

Pedicle valve moderately and unevenly convex in lateral profile, slightly convex on venter, strongly geniculated, and followed by a short trail. Cardinal extremities acute. Ears large, not clearly demarcated from visceral part. Sulcus narrow and shallow on venter, becoming wide and deep on trail. Brachial valve nearly flat on visceral disc, strongly geniculated, and followed by a short trail. Fold originating at about midvalve, narrow and low on visceral disc, but wide and distinct on trail. External surfaces of both valves ornamented by numerous fine capillae and several weak, irregular, concentric rugae on visceral disc, capillae only on trail; capillae often bifurcated and intercalated, numbering 14-15 capillae in 5 mm at midvalve.

Pedicle valve interior with large, flabellate diductor scars, occupying posterior half of valve, deeply depressed and bounded by marginal ridges posterolaterally. Other internal structures not observed.

Comparison.—The specimen numbered NU-B166, from the lower Kanokura Formation of the southern Kitakami Mountains, was first figured by Tazawa (1987, text-fig. 1.6) as *Muirwoodia* sp., but is now referred to *Yakovlevia mammata* (Keyserling, 1846), originally described by Keyserling in 1846 from the Lower Permian (possibly Sakmarian) of the Pechora Land, northern Russia, on the basis of similarities in size, outline and external ornament.

Yakovlevia paragreenlandica Lee and Gu (in Lee *et al.*, 1980), from the Middle Permian Dashizhai Formation of Horqin Youyi Qianqi, eastern Inner Mongolia may be conspecific with the present species.

The shells described and figured by Grabau (1936, p. 107, pl. 6, figs. 5-6; pl. 11, figs. 4-6) as *Productus mammatus* Keyserling from the Maping Limestone in the Guangxi and Guizhou Provinces, South China differ from *Y. mammata* in having smaller ears and coarser costellae.

Both species, *Yakovlevia artiensis* (Tschernyschew, 1889, p. 279, pl. 7, figs. 29-31) from the Artinskian of the Central Urals and *Yakovlevia greenlandica* (Dunbar, 1955, p. 103, pl. 16, figs. 1-17) from the Middle Permian (Guadalupian) of Central East Greenland are distinguished from the present species by their fewer and coarser costellae.

Yakovlevia mammatiformis (Fredericks, 1926)

Figure 3-6

Productus mammatiformis Fredericks, 1926, p. 87, pl. 3, figs. 4-6.
Yakovlevia mammatiformis Fredericks. Kotljar, 1961, text-figs. 7, 8.
Yakovlevia mammatiformis (Fredericks). Mironova, 1964, p. 97, pl., figs. 14a-v; Zavodowsky and Stepanov in Zavodowsky *et al.*, 1970, p. 114, pl. 35, figs. 8-10; Ifanova, 1972, p. 119, pl. 6, figs. 15-16; pl. 7, figs. 1-2; Kalashnikov, 1983, p. 210, pl. 49, figs. 5, 6, 9; Kalashnikov, 1993, p. 61, pl. 16, figs. 1-4.
Linoproductus cf. *mammatus* (Keyserling). Yanagisawa, 1967, p. 88, pl. 2, fig. 7.
Muirwoodia mammatiformis (Fredericks). Kulikov, 1974, p. 89, pl. 3, figs. 6a-v.

Material.—One specimen, an external mould of a brachial valve, IGPS coll. cat. no. 86649, from the upper Iriishikura Formation in the Takakurayama area, Abukuma Mountains (South Kitakami Belt), northeast Japan.

Description.—Shell medium for genus, transverse, subtrapezoidal in outline, with greatest width at hinge line; length 22 mm, width 42 mm in the brachial valve specimen.

Brachial valve gently concave on visceral disc, strongly geniculated at anterior margin of visceral disc, and followed by a short trail. Ears large, flat and prominent, obscurely demarcated from visceral disc. Fold moderately high, originating at about midvalve, and rapidly widening anteriorly. External surface of brachial valve ornamented by numerous fine costellae; costellae rounded, with narrow interspaces, numbering 10-11 costellae in 5 mm at midvalve. No spines or spine bases observed.

Comparison.—The single specimen from the Abukuma Mountains was first described by Yanagisawa (1967, p. 88) as *Linoproductus* cf. *mammatus* (Keyserling), but this specimen is referred to *Yakovlevia mammatiformis* (Fredericks, 1926) on the basis of its size, shape and surface ornament of the brachial valve.

Yakovlevia mammata (Keyserling, 1846) differs from *Y. mammatiformis* in its smaller and less transverse shell, ornamented by more numerous, fine capillae.

Yakovlevia transversa (Cooper, 1957, p. 39, pl. 5, figs. 1-13) from the Middle Permian of Oregon resembles *Y. mammatiformis* in general appearance, but the former is distinguished from the latter by its smaller dimensions, more developed fold commencing a little below the umbo, and fewer and coarser costellae on the brachial valve.

The shells described as *Y. mammatiformis* from the Middle Permian of Gansu, Northwest China (Ding and Qi in Zhang *et al.*, 1983, p. 292, pl. 99, figs. 9a, b), Inner Mongolia, North China (Lee and Gu, 1976, p. 264, pl. 164, figs. 6, 8; pl. 165, figs. 1, 5) and Heilongjiang, Northeast China (Lee *et al.*, 1980, p. 383, pl. 165, figs. 25a, b; pl. 172, fig. 3) are distinguished from the present species by their much larger size.

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Taxonomy and distribution of *Macoma* (*Rexithaerus*) (Bivalvia : Tellinidae) in the northwestern Pacific

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Abstract. Fossil and Recent *Macoma* (*Rexithaerus*) of the northwestern Pacific consist of the following three species : *Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov., *M.* (*R.*) *sectior* Oyama and *M.* (*R.*) *shiratoriensis* (Matsubara). Among them, the first species, which is new, is characterized by an elongate shell shape and a low pallial sinus, and is now living in the sea around Hokkaido, Kunashiri Island, Aniva Bay of Sakhalin, Peter the Great Bay and Ussuri Bay of Primorye. The oldest species, *M.* (*R.*) *shiratoriensis* appeared in subtropical waters in the late early Miocene. The Recent and allied species, *M.* (*R.*) *sectior* and *M.* (*R.*) cf. *hokkaidoensis* first occurred in middle Miocene deposits. From the middle Miocene to early Pleistocene, the subgenus was confined to the mild- to cool-temperate realm. In the Holocene, *M.* (*R.*) *sectior* has extended its range to subtropical waters, while *M.* (*R.*) *hokkaidoensis* now inhabits the cool-temperate to subarctic waters.

Key words : Distribution, *Macoma*, *Rexithaerus*, *Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov., taxonomy

Introduction

Rexithaerus Tryon, 1869 is a subgenus of *Macoma* Leach, 1819 and is characterized by a ridge running from beak to posteroventral corner, a bluntly truncated posterior end, a short, rather strong ligamental ridge, and upwardly elevated posterodorsal margin behind ligament.

Two Recent species of the subgenus, *Macoma* (*Rexithaerus*) *secta* (Conrad) and *M.* (*R.*) *indentata* Carpenter, are known from the northeastern Pacific (Coan, 1971). *Macoma expansa* Carpenter was also included in the subgenus *Rexithaerus* by Coan (1971). However, *M. expansa* Carpenter and a related species, *M. dexioptera* Baxter, 1977 do not belong to the subgenus *Rexithaerus* because they do not have the posterodorsal margin set off as a flange.

On the other hand, only one Recent form in this subgenus, "*M.* (*R.*) *sectior*" Oyama, has been recorded from around the Japanese Islands, Korea and Far East Russia in the northwestern Pacific (Habe, 1977 ; Kwon *et al.*, 1993 ; Kafanov and Lutaenko, 1996).

As a result of our review of the both living and fossil specimens from Japan and adjacent areas, we found a new living species of *Macoma* (*Rexithaerus*) from southern Hokkaido, Aniva Bay of Sakhalin and Primorye in Far East Russia, and Kunashiri Island.

Macoma (*Rexithaerus*) originated in northwestern North America in late Oligocene time and migrated westward into Far East Asia during the late early Miocene (Matsubara, 1994). Recently it has been revealed that many molluscan groups show such a pattern of migration (Amano *et al.*, 1993 ; Amano and Vermeij, 1998). However, little is known of the details of the process of climatological adaptation in these groups because most of the westward-spreading species have scattered fossil records owing to their rocky shore habitat. As the subgenus *Rexithaerus* lives in muddy bottoms, it is well suited for examining the above biogeographic invasion.

In this paper, we discuss the taxonomy of *Macoma* (*Rexithaerus*) in the northwestern Pacific in addition to the description of the new species. Based on the temporal and spatial distributions of *Macoma* (*Rexithaerus*), we will review the climatological adaptation of this genus after its migration to the Northwest Pacific.

Materials and methods

We have examined specimens of fossil and Recent species stored at Joetsu University of Education (JUE), Museum of Natural History, Tohoku University (IGPS), Sendai, Museum of Nature and Human Activities, Hyogo (MNHAH), Museum of Institute of Marine Biology (MIMB), and Zoological Museum, Far East State University (ZMFU), Vladivostok.

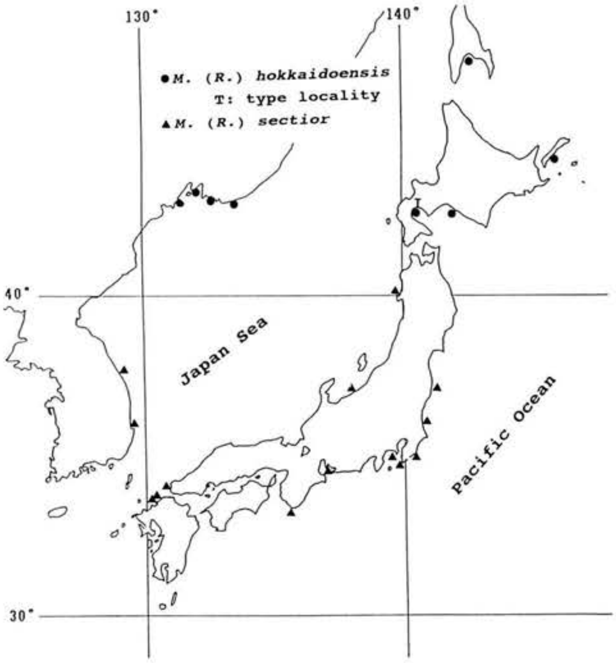

Figure 1. Locality map of the treated or illustrated Recent specimens of *Macoma* (*Rexithaerus*).

Concerning the new species, we have examined twenty-one right valves and seventeen left valves from the beach of Oshamanbe and Yufutsu along Funka Bay, Hokkaido, one specimen from the Pleistocene Narita Formation in Chiba Prefecture, and two fossil specimens from the upper middle Miocene Shibiutan Formation of Hokkaido (Figure 1). These specimens are all stored in JUE other than one Narita specimen, which is stored in IGPS. In addition, we also have examined seven right valves and eight left valves of the new form collected from the beach of Peter the Great Bay in Primorye (Figure 1). These are housed in ZMFU. Unfortunately, all materials were empty shells; we could not examine the soft parts.

For comparison with the above specimens, many Recent specimens of *Macoma* (*Rexithaerus*) *sectior* Oyama were examined from the following localities at hand and stored in IGPS and MNHAH: Katsuori (Ibaraki Pref.); Kagamigaura and Kazusa-Onjuku (Chiba Pref.); Kamakura and Zushi (Kanagawa Pref.); Mikawa-Isshiki (Aichi Pref.); Ise (Mie Pref.); Kushimoto and Shionomisaki (Wakayama Pref.); Ashiya (Fukuoka Pref.); Oga (Akita Pref.); Kakizaki (Niigata Pref.); and Pohang City and Kallam Village (South Korea).

We measured the following characters: shell length, shell height, shell depth, length of pallial sinus (PL) and height of pallial sinus (PH) (*see* Figure 2).

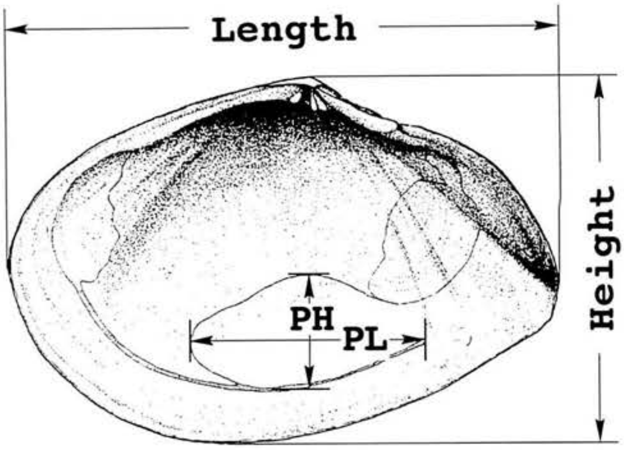

Figure 2. Measurement position.

Description of Northwestern Pacific species

Family Tellinidae de Blainville
Subfamily Macominae Olsson
Genus ***Macoma*** Leach, 1819

Type species.—*Macoma tenera* Leach, 1819 by monotypy (=*Tellina calcarea* Gmelin, 1791).

Subgenus ***Rexithaerus*** Tryon, 1869

Type species.—*Tellina secta* Conrad, 1837, by subsequent designation of Dall, 1900.

Macoma (Rexithaerus) hokkaidoensis Amano and Lutaenko sp. nov.
[Japanese name: Yezo-sagigai]

Figures 3—1-3, 5-6, 8; 4—6

Macoma sectior Oyama. Evseev, 1981, pl. 8, figs. 10, 12. [*non* Oyama, 1950]

Macoma (*Rexithaerus*) *sectior* Oyama. Kafanov and Lutaenko, 1996, p. 16-18, figs. 2a, c, 5, 6. [*non* Oyama, 1950]

Type specimens.—JUE no. 15652 (Holotype); JUE no. 15653, 15654 (Paratypes).

Type locality.—Oshamanbe, Hokkaido, Recent.

Description.—Shell of medium size (attaining 63.1 mm in shell length), rather thick, elongate-ovate, inflated, inequilateral, inequivalve; beak situated slightly posteriorly; orthogyrate or weakly opisthocline; posterior commissure line strongly flexed toward right valve; posterior part moderately gaping; periostracum thin, brownish gray in

→ **Figure 3. 1-3, 5, 6, 8:** *Macoma* (*Rexithaerus*) *hokkaidoensis* Amano and Lutaenko, sp. nov. 1, 5a-b, 6a-b; JUE no. 15652 (Holotype), Oshamanbe (Recent). 2a-b; IGPS no. 13981, Yamada, Chiba Pref., Narita Formation. 3a-b; ZMFU no. 9324/Bv-220, Gornostay Inlet of Ussuri Bay (Peter the Great Bay; Recent). 8a-b; ZMFU no. 10003/Bv-474, Kievka Bay (60 km east of Nakhodka; Recent). **4, 7:** *Macoma* (*Rexithaerus*) *sectior* Oyama. 4; MIMB no. 2404, Kallam Village near Samchok City, South Korea (Recent). 7a-b; JUE no. 15660, Hossaku, Chiba Prefecture, Narita Formation. All figures natural in size.


1


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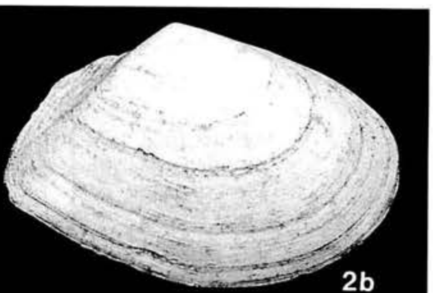
2a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3a


3b


2
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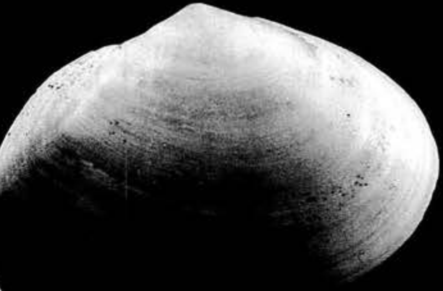
5a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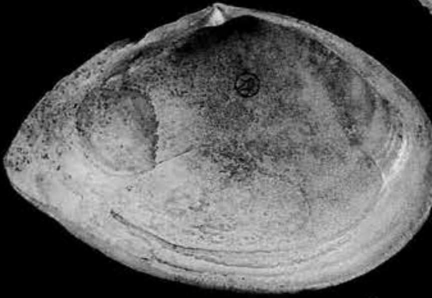
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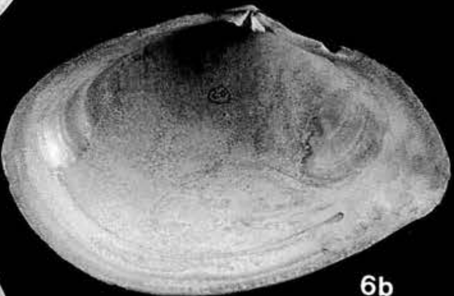
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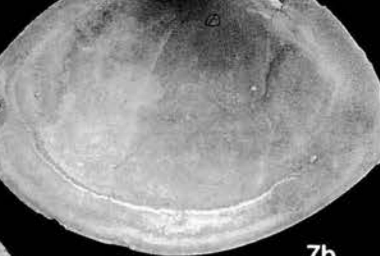
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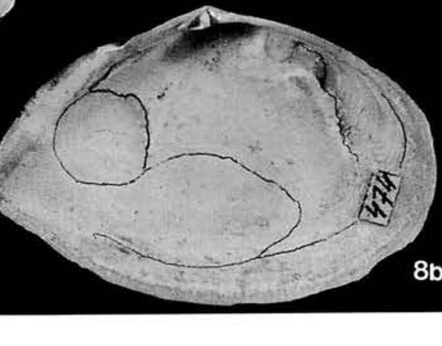
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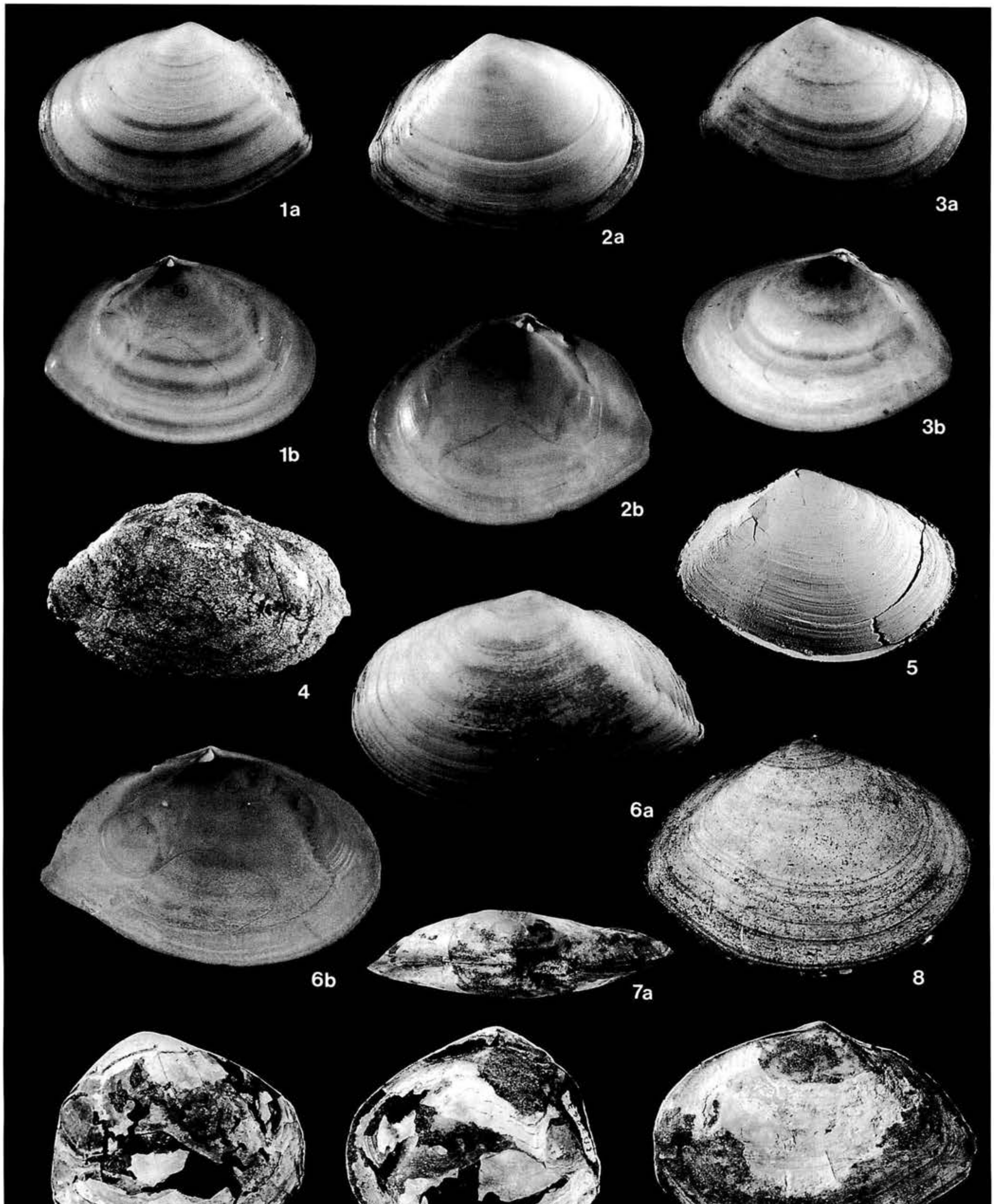
8b

Table 1. Measurements (in mm) of *Macoma* (*Rexithaerus*) *hokkaidoensis* Amano and Lutaenko, sp. nov.

Specimens	Length	Height	PL*	PH*	Valve
JUE no. 15652 (Holotype)	57.4	38.0	24.5	13.0	Right
〃	56.6	37.5	26.0	14.8	Left
JUE no. 15653 (Paratype)	51.7	34.8	22.9	13.4	Right
JUE no. 15654 (Paratype)	61.6	38.6	26.5	15.8	Left
JUE no. 15655-1	54.4	36.4	25.1	13.3	Right
JUE no. 15655-2	50.7	32.9	23.0	12.1	Right
JUE no. 15655-3	49.7	34.1	22.1	12.2	Right
JUE no. 15655-4	53.5	35.2	25.1	13.5	Right
JUE no. 15655-5	53.5	34.7	22.0	12.8	Right
JUE no. 15655-6	59.1	38.9	25.0	14.2	Right
JUE no. 15655-8	54.9	36.8	24.5	13.7	Right
JUE no. 15655-9	63.1	40.9	29.2	15.5	Right
JUE no. 15655-10	61.1	39.7	28.2	14.0	Right
JUE no. 15655-11	57.5	37.0	25.0	14.1	Right
JUE no. 15655-12	51.8	35.3	24.4	14.3	Right
JUE no. 15655-13	59.9	40.0	27.4	16.4	Right
JUE no. 15655-14	53.4	36.2	24.2	13.9	Right
JUE no. 15655-15	48.0	32.2	23.0	13.9	Right
JUE no. 15655-16	48.0	32.3	21.3	12.3	Right
JUE no. 15655-17	47.8	31.1	21.1	11.8	Right
JUE no. 15655-18	42.9	28.5	19.8	11.7	Right
JUE no. 15655-19	43.3	26.7	19.3	11.1	Right
JUE no. 15655-22	57.5	38.1	25.0	14.0	Left
JUE no. 15655-23	57.6	36.8	25.7	15.1	Left
JUE no. 15655-24	56.0	36.4	24.7	15.0	Left
JUE no. 15655-25	53.9	34.5	25.9	13.9	Left
JUE no. 15655-26	50.6	33.4	24.2	14.4	Left
JUE no. 15655-27	52.6	35.1	25.6	15.8	Left
JUE no. 15655-28	49.4	31.9	24.0	13.6	Left
JUE no. 15655-29	46.2	29.9	22.1	11.1	Left
JUE no. 15655-30	49.7	32.4	23.9	13.0	Left
JUE no. 15655-31	47.2	31.6	23.2	14.3	Left
JUE no. 15655-32	47.4	30.4	24.3	14.2	Left
JUE no. 15655-33	46.9	30.2	23.0	12.2	Left
JUE no. 15655-34	41.7	27.4	20.2	11.6	Left
JUE no. 15656-1	36.6	24.6	16.1	9.2	Right
〃	36.7	23.9	18.2	10.1	Left
JUE no. 15656-2	56.0	37.2	27.1	14.8	Left
ZMFU no. 220	56.1	38.8	26.9	15.3	Right
ZMFU no. 1621	44.1	30.2	21.8	12.3	Right
ZMFU no. 1553	42.3	29.1	21.3	10.3	Right
ZMFU no. 23407	60.4	40.0	28.5	16.6	Left
ZMFU no. 474	56.9	39.2	26.2	15.5	Right
〃	56.1	39.1	26.7	15.9	Left
ZMFU no. 1215	42.1	28.3	20.9	11.5	Left

* PL=length of pallial sinus; PH=height of pallial sinus. See Fig. 2.

→ **Figure 4. 1, 3, 5 :** *Macoma* (*Rexithaerus*) *sectior* Oyama. 1a-b, 3a-b; JUE no. 15657, Zushi, Kanagawa Prefecture (Recent). 5; JUE no. 15661, Kakuma, Ishikawa Prefecture, Omma Formation. **2a-b :** *Macoma* (*Rexithaerus*) *secta* (Conrad); JUE no. 15662, Monterey Bay, California (Recent). **4 :** *Macoma* (*Rexithaerus*) cf. *hokkaidoensis* Amano and Lutaenko, sp. nov.; JUE no. 15659, Kami-tokushibetsu, Hokkaido, Shibiutan Formation. **7-9 :** *Macoma* (*Rexithaerus*) *shiratoriensis* (Matsubara). 7a-b, 9a-b; IGPS no. 102563 (Paratypes), Shiratori, Iwate Prefecture, Kadonosawa Formation. 8; IGPS no. 102562 (Holotype), Shiratori, Iwate Prefecture, Kadonosawa Formation. All figures natural size.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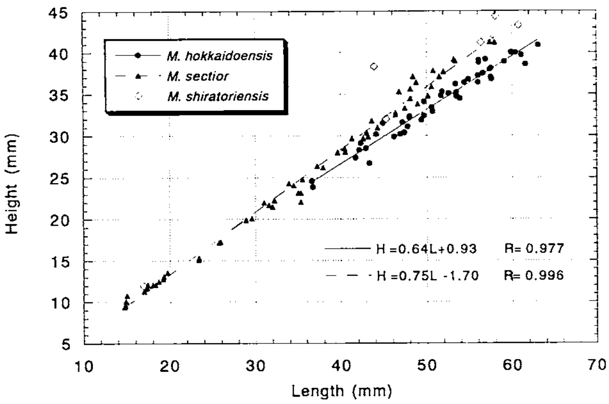

Figure 5. Relation between shell length and shell height.

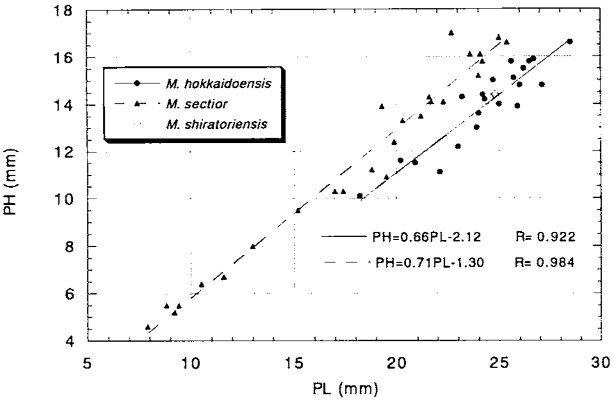

Figure 6. Relation between length of pallial sinus (PL) and height of pallial sinus (PH) of left valve.

color; nymph short, produced.

Right valve moderately inflated; a strong ridge running from beak to posterior corner; area in front of ridge distinctly concave, especially near ventral margin; anterodorsal margin broadly arcuate; posterodorsal margin behind ligament upwardly elevated forming dorsal flange; posterior margin obliquely truncated; anterior muscle scar elongated oblong and its inner margin undulated; posterior muscle scar subovate; pallial sinus deep, low ovate in shape, and slightly concave between highest and deepest end of pallial sinus; hinge plate rather wide; anterior cardinal tooth thin and smooth; posterior cardinal tooth large and subdivided by a distinct groove.

Left valve less inflated; a very weak ridge running from beak to posteroventral corner; a shallow groove running along just posterior part of ridge; anterodorsal margin broadly arcuate; posterodorsal margin behind ligament slightly upwardly elevated forming dorsal flange; posterior margin obliquely subtruncated; ventral margin broadly arcuate and excavated just before posteroventral corner; posteroventral corner bluntly pointed; anterior muscle scar deeply impressed, elongated oblong and its inner margin undulated; posterior muscle scar subcircular; pallial sinus deep, but low ovate in shape; anterior cardinal tooth elevated and subdivided by deep groove; posterior cardinal tooth very thin, inclined posteriorly and smooth.

Remarks.—The present species had already been illustrated as *Macoma sectior* Oyama from the Primorye region (Holocene and Recent), Russia (Evseev, 1981; Kafanov and Lutaenko, 1996). The previously figured specimens have a transversely elongate shell, obliquely truncated posterodorsal margin, less prominent dorsal flange, and low pallial sinus shape. Based on these characteristics, they are referred to the present new species.

Rexithaerus cf. *sectior* (Oyama) was recorded from the Middle Miocene Shibiutan Formation of northeastern Hokkaido by Fujimoto *et al.* (1998). Some specimens at hand (*e.g.* JUE no. 15659, see Figure 4—4) from this formation have an elongated shell with obliquely truncated posterior margin, a strong posterior ridge and low ovate pallial sinus, which are in common with the new species. However, it is difficult for them to be exactly identified with *Macoma* (*Rexithaerus*) *hokkaidoensis* because the shell material had eroded out. Thus, we compare the specimens from the Shibiutan Formation with the present new species.

Comparison.—The living species, *Macoma* (*Rexithaerus*) *sectior* Oyama, 1950, differs from *M.* (*R.*) *hokkaidoensis* by having a less elongated shell (Table 1; Figure 5), higher pallial sinus of both right and left valves (Figure 6), vertically truncated posterior margin, no concave area in front of the posterior ridge, a narrower hinge plate and a prominent dorsal flange. It is especially easy to distinguish the left valves of the two species by the shapes of the posterior part and pallial sinus.

Macoma (*Rexithaerus*) *shiratoriensis* was described from the uppermost lower to lower middle Miocene Kadonosawa Formation in Iwate Prefecture by one of the authors (Matsubara, 1994). This species closely resembles the present new one in its low pallial sinus (Figure 6), less prominent flange and obliquely truncated posterior margin. However, the straight line between the deepest and highest points of the pallial sinus, the higher shell and the concave area in front of the posterior ridge distinguish *M.* (*R.*) *shiratoriensis* from the present new species.

Macoma (*Rexithaerus*) *indentata* Carpenter, 1864, a Recent species of Northwest America, is similar to the present new species in its protruded posterior part and its elongated shell form. However, it is easy to distinguish the two species by comparing the pallial sinus shape. *M.* (*R.*) *indentata* has a much higher pallial sinus than *M.* (*R.*) *hokkaidoensis*. Moreover, *M.* (*R.*) *indentata* has a more elongate shell with a distinct depressed area in the posteroventral part of the shell, and a bill-like posterior end. Right valve of *M.* (*R.*) *indentata* has a pronounced flexure of gully-like type on the surface much deeper than in *M.* (*R.*) *hokkaidoensis*.

Macoma (*Rexithaerus*) *indentata flagleri* Etherington, 1931, described from the lower middle Miocene Astoria Formation of Washington, is an allied subspecies in its shell outline. However, *M.* (*R.*) *i. flagleri* lacks the pointed posteroventral corner. Unfortunately, we could not compare the internal shell characters of this subspecies because no description of the interior of the shell has been published.

Measurements (*in mm*).—See Table 1.

Distribution.—Late middle Miocene: Shibiutan Formation of Hokkaido (cf.). Pleistocene: Narita Formation in Chiba Prefecture. Recent: Oshamanbe and Yufutsu in Hokkaido, Aniva Bay in Sakhalin, Kunashiri Is., Peter the Great Bay and Ussuri Bay in Primorye, Russia.

Macoma **(*Rexithaerus*)** ***sectior*** Oyama, 1950
[Japanese name: Sagigai]

Figures 3—4, 7; 4—1, 3, 5

Macoma secta (Conrad). Yokoyama, 1922, p. 143-144, pl. 11, fig. 1; Nomura, 1938, p. 263-264, pl. 36, figs. 5, 6. [*non* Conrad, 1837]

Macoma (*Rexithaerus*) *sectior* Oyama, 1950, p. 3; Kira, 1954, p. 160, pl. 60, fig. 26; Yamamoto and Habe, 1959, p. 106, pl. 9, figs. 1, 2 ; Kaseno and Matsuura, 1965, pl. 17, figs. 10, 11; Habe and Kosuge, 1967, p. 163, pl. 61, fig. 24; Ohara, 1971, pl. Q-10, figs. 5a-b; Habe, 1977, p. 210, pl. 42, figs. 11, 12; Matsuura, 1985, pl. 42, fig. 15; Fujii and Shimizu, 1991, pl. 1, fig. 20 ; Fukuda *et al.*, 1992, p. 91, pl. 34, fig. 538; Izawa and Matsuoka, 1996, p. 8, pl. 6, fig. 9.

Macoma hokiensis Akutsu, 1964, p. 287-288, pl. 60, fig. 8.

Rexithaerus sectior Oyama. Chiba-ken Chigaku Kyoiku Kenkyu-kai, 1968, pl. 12, figs. 10a-b; Kuroda *et al.*, 1971, p. 697 (in Japanese), p. 458-459 (in English), pl. 100, fig. 5; Oyama, 1973, p. 113, pl. 52, figs. 14a-b; Ogasawara, 1977, p. 122-123, pl. 14, figs. 5a-b, 7; Koyama *et al.* eds., 1981, p. 134 ; Ogasawara *et al.*, 1986, pl. 74, figs. 9a-b; Ishii, 1987, p. 14, pl. 12, figs. 12a-b; Baba, 1990, p. 289; Baba, 1992, p. 540, pl. 69, fig. 11; Matsubara, 1994, pl. 2, figs. 6a-b, 7a-b.

Macoma sectior Oyama. Okutani and Habe, 1983, p. 139, 215; Nemoto and Akimoto, 1990, p. 42, pl. 11, fig. 7; Kondo, 1991, fig. 3-4.

Macoma (*Rexithaerus*) *sectior* (Oyama). Kwon *et al.*, 1993, p. 379, figs. 91-6-1, and 91-6-2.

Macoma "*hokiensis*" Akutsu. Matsubara, 1994, pl. 2, fig. 5.

non Macoma sectior Oyama. Evseev, 1981, pl. 8, figs. 10, 12. [=*Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov.]

non Rexithaerus sectior Oyama. Ogasawara, 1981, pl. 1, fig. 9. [=*Macoma* (*Macoma*) *tokyoensis* Makiyama, 1927]

non Rexithaerus sectior (Oyama). Ogasawara and Naito, 1983, pl. 7, fig. 3. [?=*Macoma* (*Macoma*) *tokyoensis* Makiyama, 1927]

non Macoma (*Rexithaerus*) *sectior* Oyama. Kafanov and Lutaenko, 1996, p. 16-18, figs. 2a, c, 5, 6. [=*Macoma* (*Rexithaerus*) *hokkaidoensis* sp. nov.]

Type specimen.—UMUT CM21317 (Lectotype, designated herein).

Type locality and Formation.—Otake, Narita City, Chiba Prefecture, Narita Formation, Pleistocene.

Original description.—"*Macoma secta*" in North America has a large, very high, rather thick shell, which is similar to *Nuttallia* in shape. On the other hand, the shell of the present new species [*M.* (*R.*) *sectior*] is normal in shape, low, thin, fragile, and does not attain a large size. Posterior ridge of American species is highly elevated while that of the present new species is rather weak. Inner side of posterior end of ligament becomes strongly thickened in American species, whereas that of the present new species does not. Posterior adductor muscle scar is situated rather near beak, and a contacting point between pallial line and sinus is separated from anterior adductor muscle scar. The type specimen was collected from Sagami Bay (Enoshima)." (translated from the Japanese original description)

Remarks.—Although Oyama (1950) designated the type locality of the present species as Enoshima in Kanagawa Prefecture, he neither designated nor illustrated the type specimen. In addition, the depository still remains unknown. However, Oyama (1950) did list *Macoma secta* of Yokoyama (1922) as a synonym. Consequently, we designate herein the specimen illustrated as *Macoma secta* by Yokoyama (1922) as the lectotype. This specimen is registered in the University Museum of the University of Tokyo as CM21317 (Oyama, 1973).

Macoma hokiensis Akutsu, 1964, described from the Kanomatazawa Formation in Tochigi Prefecture, is regarded as synonymous with the present species on the basis of its rather high shell and pallial sinus shape (see pl. 2, fig. 5 of Matsubara, 1994).

Macoma secta (Conrad) by Otuka (1940), from the lower middle Miocene Wakkauenbetsu Formation of Hokkaido, was recently considered as synonymous with *M.* (*R.*) *sectior* Oyama by Kafanov and Lutaenko (1996). However, at least the specimen shown in pl. 11, fig. 1 of Otuka (1940) is not referable to the subgenus *Rexithaerus* because of its rounded posterior margin and the absence of a posterior ridge.

Macoma izurensis illustrated by Masuda and Takegawa (1965), from the Fukuda Formation in Miyagi Prefecture, much resembles the present species in the pallial sinus shape rather than either *M.* (*R.*) *hokkaidoensis* or *M.* (*R.*) *shiratoriensis*. However, it differs in having a more obliquely truncated posterodorsal margin. Thus, we treat the specimens of Masuda and Takegawa (1965) as *M.* (*R.*) aff. *sectior* Oyama, although they were questionably referred to *M.* (*R.*) *shiratoriensis* by Matsubara (1994).

Comparison.—The present species closely resembles *Macoma* (*Rexithaerus*) *secta* (Conrad, 1837) (Fig. 4—2) known from the western coast of North America. However, *M.* (*R.*) *sectior* is distinguished from *M.* (*R.*) *secta* by having a smaller, lower, less inflated shell.

Distribution.—Late middle or early late Miocene: Kanomatazawa Formation in Tochigi Prefecture (Akutsu, 1964). Pliocene: Tatsunokuchi Formation in Miyagi Prefecture (Nomura, 1938); Mita Formation in Toyama Prefecture (Matsuura, 1985; Fujii and Shimizu, 1991). Early Pleistocene: Omma Formation in Ishikawa Prefecture (Kaseno and Matsuura, 1965; Ogasawara, 1977; Matsuura, 1985); Haizume Formation in Niigata Prefecture (this study); Nakatsu Group in Kanagawa Prefecture (Baba, 1992). Middle to late Pleistocene: Nagahama Formation in Chiba Prefecture (Baba, 1990); Narita Formation in Chiba Prefecture (Yokoyama, 1922; Chiba-ken Chigaku Kyoiku Kenkyu-kai, 1968; Oyama, 1973; Baba, 1990); Kioroshi Formation (?) in Chiba Prefecture (Kondo, 1991); Semata Formation in Chiba Prefecture (Ohara, 1968); Uji Shell Bed in Ishikawa Prefecture (Matsuura, 1985); Anden Formation in Akita Prefecture (Ogasawara *et al.*, 1986). Holocene: Yokohama in Kanagawa Prefecture (Matsushima, 1969); Osaka in Osaka Prefecture

(Ishii, 1987); Anan in Tokushima Prefecture (Nakao, 1995). Recent: Honshu, Shikoku, Kyushu and South Korea (Higo and Goto, 1993); ? Formosa (Taiwan) (Kuroda, 1941; Wu, 1980).

Macoma* (*Rexithaerus*) *shiratoriensis (Matsubara, 1994), combin. nov.

[Japanese name: Shiratori-sagigai]

Figures 4—7-9

Macoma cf. *tokyoensis* Makiyama. Ogasawara, 1973, pl. 13, fig. 4. [*non* Makiyama, 1927]

Macoma aomoriensis Nomura. Ogasawara, 1973, pl. 13, fig. 9. [*non* Nomura, 1935]

Macoma izurensis (Yokoyama). Ogasawara *et al.*, 1986, pl. 1, figs. 12, 13. [*non* Yokoyama, 1925]

Macoma sp. B. Ogasawara and Morita, 1986, pl. 2, figs. 25, 28.

Rexithaerus shiratoriensis Matsubara, 1994, p. 24-27, tab. 1, pl. 1, figs. 1, 2, 3a-c, 4a-c, 5a-b, pl. 2, figs. 1a-c, 2, 3, 4.

Type specimen.—IGPS no. 102562 (Holotype), 102563-1 to -10 (Paratypes).

Type locality.—A small tributary of the Shiratorigawa River, south of Shiratori, Ninohe City, Iwate Prefecture.

Remarks.—The present species is characterized by its moderate-sized (maximum length 61.4 mm), transversely elongate-ovate shell (height/length 0.71 to 0.79) with a rather weakly developed posterior ridge, less elevated dorsal flange, obliquely subtruncated posterodorsal margin and low pallial sinus.

All species questionably listed by Matsubara (1994), *Macoma* cf. *tokyoensis* and *Macoma aomoriensis* of Ogasawara (1973), and *Macoma izurensis* of Ogasawara *et al.* (1986), from the same locality belonging to the Nishikurosawa Formation in Akita Prefecture, are considered to be synonymous with the present species. On the other hand, *Macoma izurensis* of Kamada (1962), from the Honya and Nakayama Formations in Fukushima Prefecture, is not referred to the present species. As a result of the reexamination of the hypotypes, it becomes clear that the flange-like posterodorsal margin in the figures of Kamada (1962) is not original, but is due to matrix covering shell material. Thus, these specimens are referred to *Macoma* (*Macoma*) *izurensis* (Yokoyama, 1925) as Kamada (1962) thought.

Macoma sp. B of Ogasawara and Morita (1986) from the middle Miocene Yanagawa Formation in Fukushima Prefecture is considered to be *M.* (*R.*) *shiratoriensis* based on its transversely elongate ovate shell with obliquely truncated posterodorsal margin.

Comparison.—*M.* (*R.*) *shiratoriensis* closely resembles *M.* (*R.*) *indentata flagleri* Etherington, 1931. However, the former species can be distinguished from the latter subspecies by having a larger shell with less distinct growth lines and less developed posterior ridge. As already mentioned, the internal characteristics of *M.* (*R.*) *indentata flagleri* are unavailable and thus an exact comparison is difficult.

The present species is easily distinguished from *M.* (*R.*) *indentata indentata* Carpenter, a Recent northeastern Pacific species, by having a weaker ridge, less protruding posterior margin, less compressed posteroventral margin in front of a ridge, and lower pallial sinus.

Distribution.—Latest early Miocene: Kadonosawa Formation in Iwate Prefecture (Matsubara, 1994). Latest early-early middle Miocene Nishikurosawa Formation in Akita Prefecture (Ogasawara, 1973; Ogasawara *et al.*, 1986). Early middle Miocene: Yanagawa Formation in Fukushima Prefecture (Ogasawara and Morita, 1986).

Temporal and spatial distributions of *Macoma* (*Rexithaerus*) in Northwest Pacific

The subgenus *Rexithaerus* was considered to be one of those elements which originated in northwestern North America in late Oligocene and migrated into the Northwest Pacific by the late early Miocene (Matsubara, 1994). The earliest *Rexithaerus* species in the Northwest Pacific region, *M.* (*R.*) *shiratoriensis* (Matsubara), occurs from the upper lower to lower middle Miocene in formations in northeastern Honshu (Figure 7). According to the climato-paleogeographic map of Ogasawara (1994), this species lived in the subtropical realm, but could not invade the tropical one.

The next fossil occurrence is *M.* (*R.*) cf. *hokkaidoensis* from the upper middle Miocene Shibiutan Formation of Hokkaido, described above. According to Fujimoto *et al.* (1998), the molluscan assemblage including *M.* (*R.*) cf. *hokkaidoensis* is correlated with the upper sublittoral "*Pitar*"-*Anadara* Assemblage of the Lower Togeshita fauna (Amano, 1983, 1986). This fauna occupied the mild- or cool-temperate realm in the middle Miocene of Hokkaido (Ogasawara *et al.*, 1993; Ogasawara, 1994).

On the other hand, the earliest fossil record of *Macoma* (*Rexithaerus*) *sectior* Oyama is known from the Kanomata-

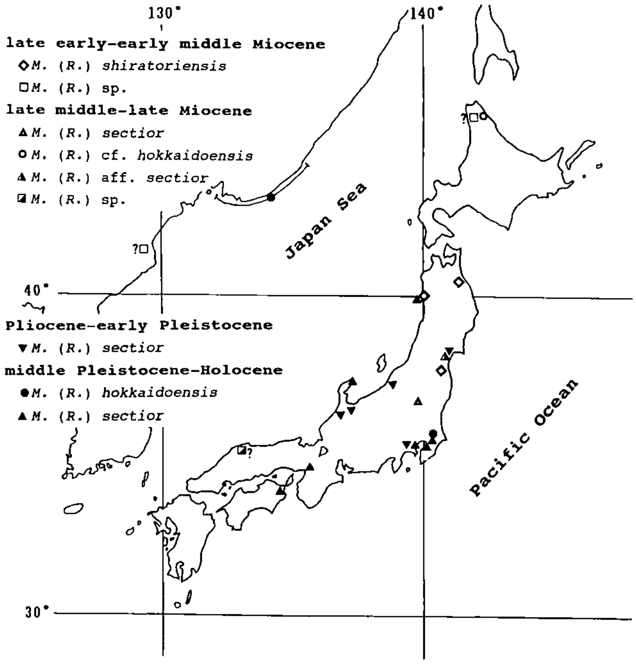

Figure 7. Distribution of the fossil *Macoma* (*Rexithaerus*).

zawa Formation in Tochigi Prefecture (Akutsu, 1964, as *Macoma hokiensis*). The age of the horizon bearing this species is somewhere between the N. 14 and N. 16 zones of the late middle to early late Miocene based on the planktonic foraminiferal data (Saito, 1963; Otsuki and Kitamura, 1986). According to Ogasawara (1994), the Kanomatazawa Formation was deposited in the warm-temperate realm. *Macoma secta* (Conrad) was recorded from the lower middle Miocene Ilyinskaya and the upper Miocene Ermanovskaya Formations in Kamchatka by Sinelnikova (1976) and Gladenkov *et al.* (1984). However, these are referred to *Macoma* s.s. because the specimens lack the posterior ridge.

Pliocene *M.* (*R.*) *sectior* is recorded in the cool- to mild-temperate realm. This species was described from the Tatsunokuchi Formation in Miyagi Prefecture (Nomura, 1938), whose age is the latest Miocene to early Pliocene (Yanagisawa, 1990, 1998). On the other hand, *M.* (*R.*) *sectior* was also illustrated by Fujii and Shimizu (1991) from the Mita Formation in Toyama Prefecture.

Early Pleistocene records of *M.* (*R.*) *sectior* Oyama exist from the Omma-Manganji fauna recognized in the Japan Sea borderland in central and northern Japan. The distribution of this species is restricted to the Omma-Manganji (proper) and Kanto-type subprovinces of Ogasawara (1986), both of which correspond to the mild-temperate marine climate (Ogasawara, 1994). Thus, *M.* (*R.*) *sectior* in the early Pleistocene was confined to the mild-temperate water.

In the Recent, *M.* (*R.*) *hokkaidoensis* lives in the cool-temperate and subarctic shallow waters in Hokkaido, south Sakhalin, south Kurile Islands and Primorye while *M.* (*R.*) *sectior* Oyama lives in the upper sublittoral (10-30 m in depth) of the mild-temperate to subtropical waters around Honshu, Kyushu, Shikoku, and South Korea (Higo and Goto, 1993).

After the subgenus *Rexithaerus* arrived in the northwestern Pacific, it lived in the subtropical realm during the late early to early middle Miocene, or the so-called "Climatic Optimum" age. By the late middle Miocene, the subgenus had adapted to the temperate zone as climates cooled after the "Climatic Optimum". From the late middle Miocene to the Plio-Pleistocene, the subgenus *Rexithaerus* lived in the mild- or cool-temperate realm. In the Holocene, *M.* (*R.*) *sectior* extended its range to subtropical waters. Kuroda (1941) and Wu (1980) only listed *M.* (*R.*) *sectior* from Formosa (Taiwan). If this is true, *M.* (*R.*) *sectior* may live in the tropical water. However, there is no illustration of the Formosa specimen.

The muricid gastropod genus *Ceratosoma*, a member of the westward-spreading group, shows a history of expansion similar to that of *Rexithaerus*. Both *Macoma* (*Rexithaerus*) and *Ceratostoma* invaded the subtropical waters around Japan by the early middle Miocene and adapted to the cool- to mild-temperate zone by the early Pleistocene. After or during the middle to late Pleistocene, their distribution extended southward to subtropical waters (Amano and Vermeij, 1998). On the other hand, one of the same westward-spreading muricids, *Nucella*, only lives in mild-temperate to arctic waters (Higo and Goto, 1993). One plausible reason why *Nucella* did not invade warmer waters may be related to its original adaptation not to the subtropical water as *Macoma* (*Rexitherus*) or *Ceratostoma*, but to the cool-temperate water around Japan in the early middle Miocene (Amano *et al.*, 1993).

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The turrilitid ammonoid *Mariella* from Hokkaido — Part 1

(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXV)

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Abstract. Three species of the genus *Mariella* (Turrilitidae) from the Lower Cenomanian (Cretaceous) of Hokkaido are described. They include the two widespread species, *M.* (*M.*) *dorsetensis* (Spath, 1926) and *M.* (*M.*) *oehlerti* (Pervinquière, 1910). The third species, *M.* (*M.*) *pacifica* sp. nov., is somewhat similar to but distinguished from *M.* (*M.*) *oehlerti*. It is also compared with some other species. The problem of dimorphism in the turrilitid ammonoids is discussed.

Key words : Cenomanian, dimorphism, Hokkaido, *Mariella*, Turrilitidae

Introduction

Ammonoids of the family Turrilitidae have been recorded from various regions of the world. They occur in the mid-Cretaceous (Albian and Cenomanian) and include a number of widespread species which are useful for biostratigraphic zonation and correlation. Some of them are, however, apparently endemic. Turrilitids would be also useful to investigate some aspects of palaeogeography and palaeoenviroments during mid-Cretaceous times.

Aside from several stratigraphic papers in which some turrilitid species are listed or briefly mentioned, very few species have been hitherto described from Japan, although such a magnificent example as *Turrilites komotai* Yabe, 1904 (p. 7, pls. 1, 2) [now referred to *Hypoturrilites*] was once reported. In our present knowledge ammonoids of the Turrilitidae occur fairly commonly in the mid-Cretaceous sediments of certain biofacies in Hokkaido. A rare but important occurrence of *Mesoturrilites* from Hokkaido has been recently reported (Matsumoto and Inoma, 1999). More species of the family are to be described successively. In this paper three species of the genus *Mariella* are described, of which two are well known and widespread. The third species is regarded as new and has not been known elsewhere.

Incidentally, T. M. had opportunities to examine some specimens at the Natural History Museum, London, and several other overseas institutions. Moreover, W. J. Kennedy kindly sent several specimens to Kyushu University as reference material.

Geographic and stratigraphic setting

The specimens dealt with in this paper were obtained mainly from the Soeushinai area [Shumarinai-Soeushinai area by some authors] of the Teshio Mountains, northwestern Hokkaido. The Cretaceous strata are exposed in the Shumarinai Valley, the Sounnai Valley and the smaller rivulets, such as the Kyoei-Sakin-zawa and the Sanjussen-zawa, which are all tributaries of the River Uryu, and also in the upper reaches of the River Kotanbetsu. This area was geologically mapped by Hashimoto *et al.* (1965) and has been recently reinvestigated by Nishida *et al.* (1992, 1993, 1996, 1997, 1998a, 1998b). The localities where megafossils and microfossils were collected are pinpointed in the papers by Matsumoto and Inoma (1975) and Inoma (1980) and, furthermore, in a number of route maps of the stratigraphic papers by Nishida *et al.* (1992, 1993, 1996-1998a, b). Moreover, a locality guide is to be given as an Appendix to this paper.

As has been clarified by the above authors, a thick series of strata comprehensively called the Middle Yezo Subgroup of late Albian through Turonian age is extensively distributed in this area. The conformably underlying Lower Yezo Subgroup and the transitionally overlying Upper Yezo Subgroup are partly observable in the area. In a revised scheme of Nishida *et al.* (1996, fig. 10) the Middle Yezo Subgroup in this area is lithostratigraphically subdivided into the Members My1 to My8 in ascending order. The Members My1 and My2, together with the uppermost portion of the Lower Yezo Subgroup, are Upper Albian, the Member My3 is Lower Cenomanian, and the Members My4 and My5 represent the rest of the Cenomanian. The age correlation is based on the assemblage of ammonoid and inoceramid species and also on that of some microfossils (Nishida *et al.*, 1992, 1993, 1996-1998a, b). As there is a lateral change in the lithofacies and thickness of the members from place to place, boundary planes of the successive members may be somewhat diachronous in some cases.

The turrilitid ammonoids have been obtained from the Members My2, My3 (most commonly) and My5 and also the upper part of the Lower Yezo Subgroup. These members consist primarily of mudstones, which are sometimes sandy or have intercalated sandy layers and laminae.

Conventions

Repository.—The illustrated and/or measured specimens are registered in the following institutions which are indicated by the abbreviated symbols as follows :

GK	: Type Room, Department of Earth and Planetary Sciences, Kyushu University, Hakozaki, Fukuoka
GS	: Geological Collections, Faculty of Culture and Education, Saga University, Saga
MCM	: Mikasa City Museum, Mikasa, Hokkaido
TKD	: Institute of Geosciences, Tsukuba University, Tsukuba [reconstitution of the Tokyo Kyoiku Daigaku]
UMUT	: University Museum, University of Tokyo, Hongo, Tokyo

Morphological terms.—For the morphological terms to describe the turrilitid ammonoids, we follow those used by Wright and Kennedy (1996). Setting the apex of the turrical shell at the top, the terms upper and lower or adapical and adoral [=abapical] are defined and the rows of tubercles or ribs on the face of each whorl are described in descending order as the first, the second and so on. The term flank (see Förster, 1975) may be used for the exposed whorl face of Wright and Kennedy (1996).

Palaeontological descriptions

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina, Wiedmann, 1966
Family Turrilitidae Gill, 1871
Genus ***Mariella*** Nowak, 1916

Type species.—*Turrilites bergeri* Brongniart, 1822 (p. 395, pl. 7, fig. 3) by original designation (Nowak, 1916, p. 10).

Remarks.—Wright and Kennedy (1996, p. 330) have given an ample generic diagnosis and discussed problems of nomenclature. The genus includes the two subgenera, *Mariella* (*Mariella*) Nowak, 1916 and *Mariella* (*Wintonia*) Adkins, 1920, the latter of which is a senior synonym of *Mariella* (*Plesioturrilites*) Breistroffer, 1953 (see Wright and Kennedy, 1996, p. 331). An undoubted example of *M.* (*Wintonia*) has not been so far found from Japan, whereas there are a number of specimens from Hokkaido which are referable to at least eight species of *M.* (*Mariella*).

Mariella* (*Mariella*) *dorsetensis (Spath, 1926)

Figure 1

Turrilites bergeri Brongniart. Sharpe, 1857, p. 65, pl. 26, fig. 11 only.
Turrilites dorsetensis Spath, 1926, p. 429.
Mariella dorsetensis (Spath). Spath, 1937, p. 513 ; Marcinowski, 1970, p. 431, pl. 3, fig. 1 ; Seyed-Emami and Aryai, 1981, p. 26, pl. 6, figs. 5, 6.
Paraturrilites lewesiensis (Spath). Benavides-Cáceres, 1956, p. 436 (pars.), pl. 40, figs. 8, 9 (?).

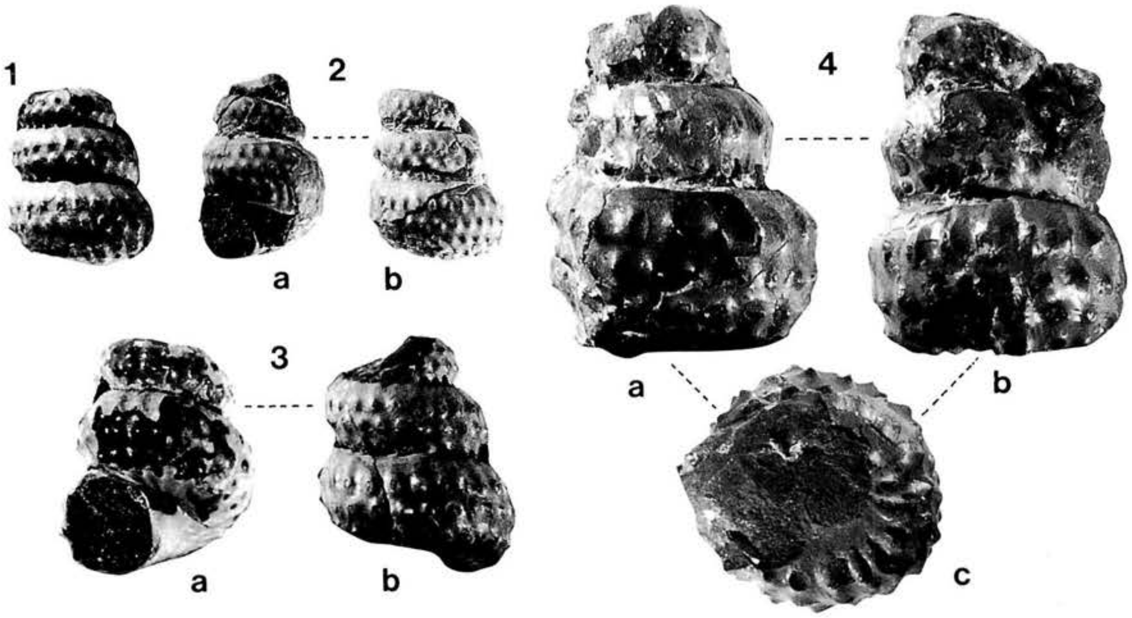

Figure 1. *Mariella* (*Mariella*) *dorsetensis* (Spath). **1.** GS. 180, ×1. **2a, b.** GK. H8504, two lateral views, ×2. **3a, b.** GS. G180, two lateral views (different sides from 1), ×2. **4a-c.** GS. G182, two lateral and basal views, ×1.5.

Mariella (*Mariella*) *dorsetensis* (Spath). Atabekian, 1985, p. 35, pl. 6, figs. 6, 9 ; Wright and Kennedy, 1996, p. 344, pl. 100, figs. 5, 11, 17, 19, 22, 25 ; pl. 102, fig. 7 ; text-figs. 136B, E (with full synonymy).

Holotype.—BMNH. C3834, figured by Sharpe, 1857, pl. 26, fig. 11 and named as *Turrilites dorsetensis* Spath, 1926, p. 429 (by monotypy).

Material.—GS. G180 (Figure 1-1, 3) and GS. G181, both from loc. R905 [=YKC080621b], Hotei-zawa ; GK. H8504 (Figure 1-2) from loc. R518p5, East Suribachi-zawa ; GK. H8505 from loc. R438p, GK. H8506 from loc. R433p, and TKD 30081A, B from loc. 81007, in the upper reaches of the Suribachi-zawa ; TKD 30080A-D from loc. 71204 in the middle course of the River Shumarinai ; GS. G182 (Figure 1-4), from loc. YKC060824, Sanjussen-zawa. These are all from the Lower Cenomanian Member My3 of the Soeushinai area.

Description.—The available specimens are all small and incomplete, as seen in the illustration (Figure 1). In general, the apical angle is acute (20-25° in our estimation). The whorl is rounded in section, showing a moderately or broadly convex outer face ; the whorl junction is well defined and crenulated.

The tubercles in four rows are of moderate density and number 20 to 25 per whorl in each row. The tubercles on the outer whorl face are disposed slightly obliquely in three rows at subequal intervals and of nearly equal moderate intensity. The tubercle of the first row is elongated upward to a distinct rib on the upper face of the whorl. In some specimens the fourth tubercle is slightly smaller than the others and close to the third one, although it is beyond the lower whorl seam. On the lower whorl face ribs run from the third row tubercles to the narrow umbilicus by way of the fourth row tubercles, showing a gentle curvature.

Septal sutures are partly exposed (GK. H8505).

Comparison.—The above-described specimens from Hokkaido are well comparable with the holotype and other examples of *M.* (*M.*) *dorsetensis* from England (Wright and Kennedy, 1996, pl. 100, figs. 5, 11, 17, 19, 22, 25) and also previously illustrated specimens from several regions of the world (see synonymy list). Affinities with other allied species are discussed below, together with some remarks on questionable points.

Occurrence.—As for material. This species has been reported from the Lower Cenomanian of southern England, northern France, Poland, Turkmenistan, Iran, Madagascar and Peru (see synonymy list).

Discussion.—*M.* (*M.*) *dorsetensis* is similar to and could be interpreted as a descendant from *M.* (*M.*) *bergeri* of the uppermost Albian. The apical angle of the former is smaller than that of the latter. In fact the apical angle of *M.* (*M.*) *bergeri* is recorded as 33-38° by Spath (1937, p. 511) and an example of Pictet and Campiche (1862, pl. 58, fig. 2) reillustrated by Renz (1968, pl. 18, fig. 4) gives 34°, as compared to the 20-25° of *M.* (*M.*) *dorsetensis*. On the average the tubercles are somewhat more crowded and more distinctly connected by longitudinal ribs in *M.* (*M.*) *bergeri*.

The relationship between *M.* (*M.*) *dorsetensis* and *M.* (*M.*) *lewesiensis* (Spath, 1926) is a moot problem, as has been discussed by Kennedy (1971, p. 28) and Klinger and Kennedy (1978, p. 31). The difficulty can be guessed from the confused state in the lists of synonymy between authors (even between the same palaeontologist writing on different dates) (see Wright and Kennedy, 1996, p. 339-340 and p. 344). Collignon (1964, pl. 331, fig. 1482) has shown an *example* of *M.* (*M.*) *dorsetensis* with a rostrate last whorl. This suggests the small size of this species. We notice, however, that an example of the same species illustrated by Atabekian (1985, pl. 6, fig. 6, 6b) is nearly as large as the holotype of *M.* (*M.*) *lewesiensis* (see Sharpe, 1857, pl. 20, fig. 10 or Wright and Kennedy, 1996, p. 101, fig. 3). There is no difference in the estimated apical angle between the two species. There may be differences in the ornament. The relative smoothness of the upper face of the whorl was regarded as a criterion by which to distinguish *M.* (*M.*) *lewesiensis* from *M.* (*M.*) *dorsetensis*, but some of the coarse tubercles of the first row in the former show faint elongations on a part of the upper whorl face, depending probably on the mode of lighting (see Kennedy, 1971, pl. 8, figs. 1, 4, 5, 8). Wright and Kennedy (1996, p. 340) have recently given their opinion that rounded subequal tubercles in the upper two rows plus feeble spiral (i.e. clavate) elongation of the tubercles in the lower two rows characterize *M.* (*M.*) *lewesiensis*. Indeed, the tubercles on the outer whorl face are coarse and globular in *M.* (*M.*) *lewesiensis* and rather granular but transversely elongated in *M.* (*M.*) *dorsetensis*, although there is no marked difference in the number of tubercles to a whorl. For us it is difficult to understand the significance of the "feeble spiral elongation of the lower tubercles". The tubercles of the lower two rows are clavate in the holotype, but the feature is not well shown in the illustration of some other specimens (e.g., Wright and Kennedy, 1996, pl. 100, figs. 23, 27).

According to Klinger and Kennedy (1978, p. 31, pl. 7, fig. F), in *M.* (*M.*) *lewesiensis* [=*M.* (*M.*) *dorsetensis* in their paper] ribs are absent or only a few traces are discernible on the lower whorl face, although they did not give a photograph of the basal view.

On the lower whorl face of the holotype ribs are extended very faintly from the tubercles of the fourth row (T.M.'s observation at the Natural History Museum, London). This character is also shown on some examples of *M.* (*M.*) *lewesiensis* by Atabekian (1985, p. 37, pl. 7, fig. 1, 1b ; pl. 8, fig. 1, 1a), whereas ribs are distinctly developed on the lower whorl face of *M.* (*M.*) *dorsetensis* from the Kopet Dag (see Atabekian, 1985, p. 35, pl. 6, fig. 6, 6b) as well as in our specimens (e.g., Figure 1-4 of this paper). If this difference is confirmed in a sufficient number of specimens, it would become one of the reliable criteria to distinguish the two species.

So far, an undoubted example of *M.* (*M.*) *lewesiensis* is not found in the material of the Soeushinai area. The specimens which were tentatively identified with *M. lewesiensis* by A.I. (as written on the labels) are actually *M.* (*M.*) *oehlerti* (Pervinquière).

Mariella* (*Mariella*) *oehlerti (Pervinquière, 1910)

Figures 2-4

Turrilites gresslyi Boule, Lemoine and Thévenin, 1907 (*non* Pictet and Campiche, 1861), p. 57, pl. 13, fig. 2, 2a.

Turrilites oehlerti Pervinquière, 1910, p. 53, pl. 5, figs. 14-17; Collignon, 1929, p. 65, pl. 6, figs. 16, 17; Matsumoto, 1938, p. 23, pl. 2, fig. 7; Collignon, 1964, p. 15, pl. 320, figs. 1398, 1399.

Mariella (*Mariella*) *oehlerti* (Pervinquière, 1910); Förster, 1975, p. 190, pl. 7, figs. 7, 8; text-fig. 52; Atabekian, 1985, p. 30, pl. 6, figs. 4, 5; Wright and Kennedy, 1996, text-fig. 138 J,O,V.

Mariella (*Mariella*) *oehlerti oehlerti* (Pervinquière, 1910). Klinger and Kennedy, 1978, p. 31, pl. 3E; pl. 4E; pl. 6H-N; pl. 7G; pl. 8G-H; text-figs. 1A, B; 7B, D; 8G.

Mariella (*Mariella*) *oehlerti sulcata* Klinger and Kennedy, 1978, p. 33, pl. 8, fig. D; text-figs. 3E, 8H (? non pl. 3D; text-fig. 3D).

Holotype.—The specimen figured by Pervinquière (1910, pl. 5, fig. 16) from the Cenomanian of Aumale, Algeria (by original designation). Klinger and Kennedy's (1978, p. 31) designation of a lectotype (Pervinquière, 1910, pl. 5, fig. 15) was misleading, and Atabekian (1985, p. 30) erroneously followed them.

Material.—A large number of specimens from the Member My3 of the Soeushinai area are referable to this species. The representative ones among them are as follows: GK. H8500 (Figure 2-1) and GK. H8501 obtained by T.M. at loc. R518p5 and GS. 166 (Figure 2-7) collected by Y.K. at loc. R518pl from the East Suribachi-zawa; TKD 30086A (Figure 3-2), TDK 30086B (Figure 3-3) and TKD 30086C (Figure 2-6) obtained by A.I. from a nodule at loc. 81001 in the Suribachi-zawa; TKD 30546B (Figure 2-2) and A collected by W. Hashimoto from a nodule at loc. P2 in the River Shumarinai and provided to A.I. for study; GS. G163 (Figure 2-3) and GS. G164 (Figure 2-4) collected by Y.K. at loc. YKC060824 in the Sanjussen-zawa; GS. G165 (Figure 2-5) collected by Y.K. at loc. YKC050610 in the Bishamon-zawa; GS. G167 (Figure 3-1) collected by Y.K. at loc. YKC591014 and also GS. G168 (Figure 4-1) and GS. G169 (Figure 4-2) collected by Y.K. at loc. YKC020619 in the Kyoei-Sakin-zawa.

Description.—Although completely preserved specimens are hard to come by larger examples are approximately estimated at 250 mm in total whorl height and 70 mm in diameter of the last whorl. Several specimens which preserve the rostrum suggest a size dimorphism. The above larger ones, as represented by GS. G168 (Figure 4-1), may represent a macroconch, whereas GS. G167 (Figure 3-1) and TKD 30086A, B (Figure 3-2, 3) may be microconchs, for they are half of the macroconch in size. The rostrate peristome of a larger form, exemplified by GS. G169 (Figure 4-2), is twice as large as that of a smaller form, e.g., TKD 30086C (Figure 2-6).

The apical angle is low but seems to be somewhat variable between individuals and probably also with growth. On account of incomplete preservation, the actual angle is hard to measure with precision. It is roughly estimated at 25° (±5°) on the average.

The whorl is asymmetrically subquadrate to broadly rhomboidal in section. Its upper flank [i.e. upper part of the exposed whorl face] slopes down, forming an obtusely angular (costal) or a subrounded (intercostal) shoulder at the first row of tubercles; its middle flank [i.e., main part of the exposed whorl face] is nearly vertical and forms an obtuse shoulder at the second row of tubercles with the narrow, lower flank which inclines steeply inward; the whorl junction is thus fairly deep and crenulated. The aperture is suboval and provided with a rostrum that extends at first downward and then recurves obliquely upward (see Figures 3-3; 2-6; 4-1, 2).

The tubercles are moderate in strength and coarseness; those of the first row are more prominent than others and extend upward to the ribs on the upper flank. Those of the three rows on the exposed whorl face are nearly equidistant, arranged more or less obliquely and sometimes connected by blunt riblets; those of the third row may be granular or sometimes rather clavate (i.e. extended spirally); the interspace between the second and third rows of tubercles is sometimes narrower than that between the first and second rows and, furthermore, it may be grooved to various depths (see Figure 2-5). The tubercles of the fourth row are close to those of the third row in some specimens but they are disposed along the outer margin of the basal part of the whorl. The tubercles of each row in our sample normally number from 20 to 28 to a whorl. TKD 30546B (Figure 2-2) may exemplify an extreme case (30 to a whorl), but it is referred to this species in consideration of other characters.

Aside from the bullate extension to the ribs, the tubercles of the upper two rows are conical with a rounded base. In some cases they may preserve a sharply pointed summit, but so far a highly extended spine has not been observed in our material.

Near the apertural margin the tubercles are obliquely bullate and extended to gently flexuous narrow ribs. The last rib goes on to form a blunt ridge on the rostrum, whereas the other side of the rostrum is ornamented by very fine and delicate riblets and dots (see Figures 2-6a, b, 4).

The septal suture is not well traced in our material, because the internal mould is not well exposed. It was illustrated by Förster (1975, fig. 52) on a young example from Mozambique and partly by Klinger and Kennedy (1978, fig. 1A, B) on middle-aged specimens from South Africa.

Comparison and discussion.—As the types originally described by Pervinquière (1910) and also the specimens dealt with by subsequent authors up to 1975 are so small it was difficult for us to understand the diagnosis of this species.

Based on a great number of specimens from the Lower Cenomanian of South Africa, Klinger and Kennedy (1978) have clarified the diagnosis of this species and also its relations with or distinctions from other species. Wright and Kennedy (1996, text-fig. 138 J,O,V) have finely reillustrated Pervinquière's holotype and paratypes. These two works have enlightened us in getting a proper conception of *M.* (*M.*) *oehlerti*.

In our material there are specimens which closely conform with the holotype. GK. H8500 (Figure 2-1) is such an example. They are, however, immature. The full-grown adult shell has a rostrate aperture. The three specimens illustrated in Figure 3 exemplify the abult shells of moderate size,

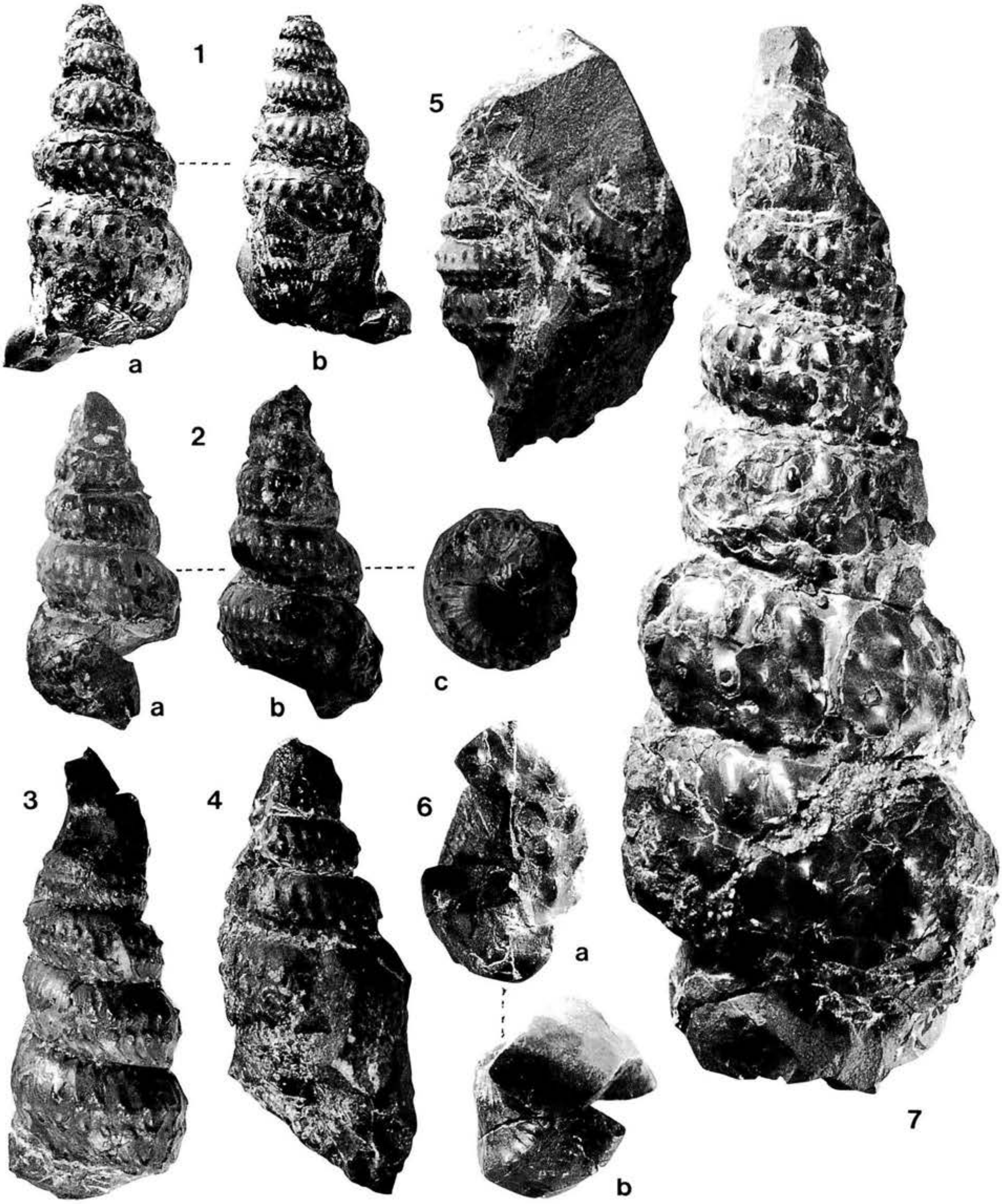

Figure 2. *Mariella* (*Mariella*) *oehlerti* (Pervinquière). **1a, b.** GK. H8500, two lateral views, ×1.2 (The terminal protuberance is not a rostrum but an attached juvenile of *Anagaudryceras* sp.). **2a–c.** TKD 30546B, two lateral and basal views, ×1.5. **3.** GS. G163, ×1.5. **4.** GS. G164, ×4/3. **5.** GS. G165, ×4/3. **6a, b.** TKD 30086c, detached rostrum, external and the other sides, ×1. **7.** GS. G166, a large but incomplete example, ×1.

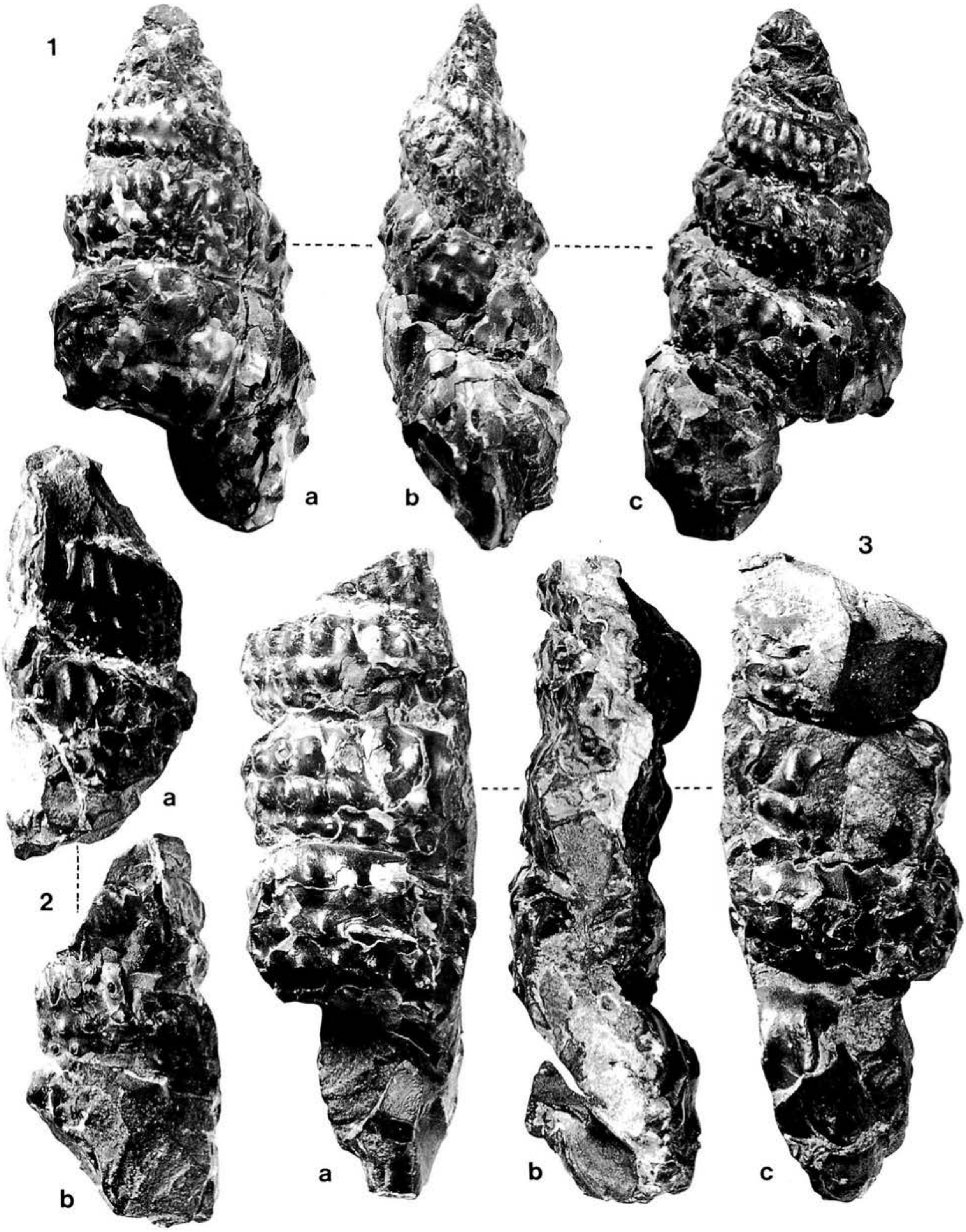

Figure 3. *Mariella* (*Mariella*) *oehlerti* (Pervinquière). More or less deformed examples of a smaller form with a rostrate peristome, all ×1. **1a-c.** GS. G167, three lateral views. **2a, b.** TKD 30086A, two lateral views. **3a-c.** TKD 30086B, three lateral views.

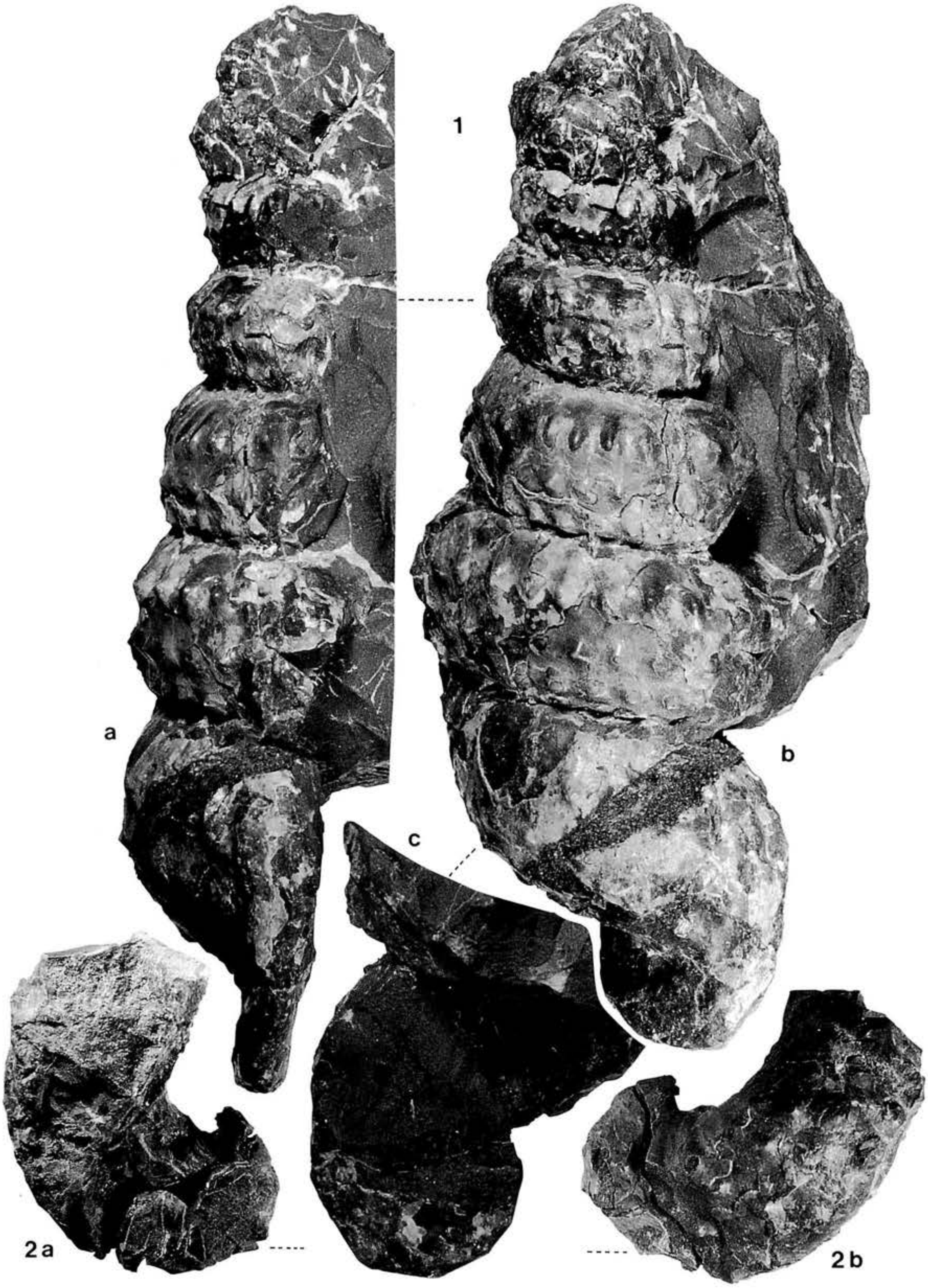

Figure 4. *Mariella* (*Mariella*) *oehlerti* (Pervinquière). Examples of a larger form, ×0.9. **1a–c.** GS. G168, two lateral views (a, b) and aperture (c). **2a, b.** GS. G169, two views of a detached rostrum.

although they are considerably affected by secondary deformation. Among a number of South African specimens, BMNH C79806 (Klinger and Kennedy, 1978, pl. 6, fig. K) is an illustrated example of the adult stage. It is similar in size to our examples mentioned above, but it preserves only two whorls of the late growth stage.

In our material from the Member My3 there are much larger adult specimens which preserve the rostrate oral part. GS. G168 (Figure 4-1) is an example of such a large form. It is nearly twice as large as the specimens mentioned above. GS. G166 (Figure 2-7) is referable to a similarly large form, although its later part is not preserved. GS. G169 (Figure 4-2) is a detached piece of a rostrate oral part. It is nearly twice as large as TKD30086C (Figure 2-6), which is a detached oral part of a smaller form.

The facts described above suggest the existence of a dimorphic pair in this species. To confirm the dimorphism, it is necessary to get further evidence from the materials of other regions. Although "several hundred specimens" of this species from South Africa have been treated by Klinger and Kennedy (1978, p. 32), they did not make mention of the size variation or dimorphism. The specimens figured by them are more or less incomplete, consisting of a few whorls. The largest example among them is BMNH C79860 (*op. cit*., pl. 8, fig. H). [Note that figure is actually ×5/4, although it was indicated as ×1.] It could be comparable with a part of the large specimen (GS. G168, Figure 4-1) from Hokkaido, but it lacks the oral end. On the other hand, a specimen from South Africa (*op. cit*., pl. 6, fig. K) which possesses an incomplete rostrum is comparable with the smaller form from Hokkaido.

Dimorphism in the Turrilitidae has been noted by Wright and Kennedy (1996, p. 349) for *Turrilites scheuchzerianus* Bosc and certain other species, but Lehmann (1998, p. 37) has given comments and suggested that the observed difference might simply be size variation. There could be, however, size variation in both microconch and macroconch. For a final conclusion one should examine a sufficient number of samples.

There is another problem to be discussed. Some specimens of *M.* (*M.*) *oehlerti* from the Member My3 of the Soeushinai area show a spiral sulcus between the second and third rows of tubercles. In such cases, the tubercles rest on low ridges and may be obliquely clavate. The groove is thus variable in its degree of distinctness among the specimens and the sulcate specimens often occur together with normal ones. This feature is similar to that already noticed in the material of South Africa. Klinger and Kennedy (1978, p. 33, pl. 3, fig. D; pl. 8, fig. D; text-figs. 3D, D; 8H) have established a subspecies *M.* (*M.*) *oehlerti sulcata*. One of us (T.M.) examined some of the specimens labelled as "*M.* (*M.*) *oehlerti sulcata*", such as BM. C79952 (*op. cit*., pl. 8, fig. D), C79951, C79950 and C79949. They seem to show a gradual change in morphology from "*M.* (*M.*) *oehlerti oehlerti*" to "*M.* (*M.*) *oehlerti sulcata*."

The holotype of the subspecies *M.* (*M.*) *oehlerti sulcata* Klinger and Kennedy, 1978 is SAS A2908. Although we have yet no opportunity to examine the actual specimen itself, its fine illustration (*op. cit*., pl. 3, fig. D) gives us a strong impression that it resembles a form of *Mesoturrilites aumalensis* (Coquand) such as was figured by Pervinquière (1910, pl. 14, fig. 22) (see Wright and Kennedy, 1996, text-fig. 138 S-T). Furthermore, we see that the specimen in question (SAS A2908) is similar to, if not identical with, *Mariella* (*Mariella*) *bicarinata* (Kner, 1852) (see Atabekian, 1985, p. 40, pl. 8, figs. 2-9; pl. 9, figs. 1, 2; Wright and Kennedy, 1996, p. 335, pl. 98, figs. 7, 12; pl. 102, fig. 11). We are thus, inclined to consider that it would be better to exclude the holotype of *M.* (*M.*) *oehlerti sulcata* from *M.* (*M.*) *oehlerti*. Incidentally, the above observation may be favourable to the suggestion of Wright and Kennedy (1996, p. 346) to seek the origin of *Mesoturrilites* in *M.* (*M.*) *bicarinata*.

Occurrence.—As for material. In addition, incompletely preserved specimens which can be called *M.* (*M.*) cf. *oehlerti* are found commonly in the Member My3 of the Soeushinai area. At least some of the specimens, including GK. H8500 and H8501, occur in the lower part of the Member My3 together with *Graysonites adkinsi* Young.

Records of this species from other areas in Hokkaido are so far poor, except for a fine specimen MCM A517 collected by Reishi Takashima and Koji Hasegawa from the Oyubari area. This is to be reported in detail on another occasion.

Outside of Hokkaido in Japan a few small specimens of this species were described by Matsumoto (1938, p. 23, pl. 2, fig. 7) from the Unit IIe of the mid-Cretaceous Goshonoura Group of Kyushu; *Graysonites* cf. *fountaini* Young occurs in the same unit (Matsumoto, 1960, p. 44, pl. 6, fig. 1; pl. 7, figs. 1-4; text-figs. 1-7, with Matsumoto *et al*., 1960, p. 51).

M. (*M.*) *oehlerti* has been reported from the Lower Cenomanian of Algeria, Madagascar, Mozambique, South Africa and Turkmenistan (Kopet Dag) (see references in the synonymy list). The record of its occurrence in the Gulf Coast (Texas and Mexico) (Young and Powell, 1978, pl. 8, figs. 4, 6) is not clear. As species of *Graysonites* occur there, undoubted example of *M.* (*M.*) *oehlerti* should be searched for.

Mariella* (*Mariella*) *pacifica sp. nov.

Figure 5

Material.—Holotype is GS. G170 (Figure 5-1) from a nodule contained in the siltsone of the middle part of the Member My3, collected by Y.K. and N. Egashira at loc. R905 of the Hotei-zawa, a branch stream of the River Shumarinai, Soeushinai area (see Figure 7 in the Appendix).

In the same nodule as that of the holotype there are ten specimens, of which registered paratypes are GS. G171 (Figure 5-2), GS. G172 (Figure 5-3), GS. G173 (Figure 5-4), GS. G174 (Figure 5-5), GS. G175 (without figure), GS. G176-G177 (Figure 5-6), GS. G178 (Figure 5-7) and GS. G179 (without figure). Unregistered specimens are recorded from R906, at a slightly higher horizon than R905.

TKD30558 (Figure 5-8) and TKD30559 (Figure 5-12) from a nodule at loc. P4 and TKD30561A, B (Figure 5-9, 10) from a nodule at loc. P2, all taken by W. Hashimoto and transferred to A.I. for study, are probably derived from the Member My3 exposed along the middle course of the River Shumarinai.

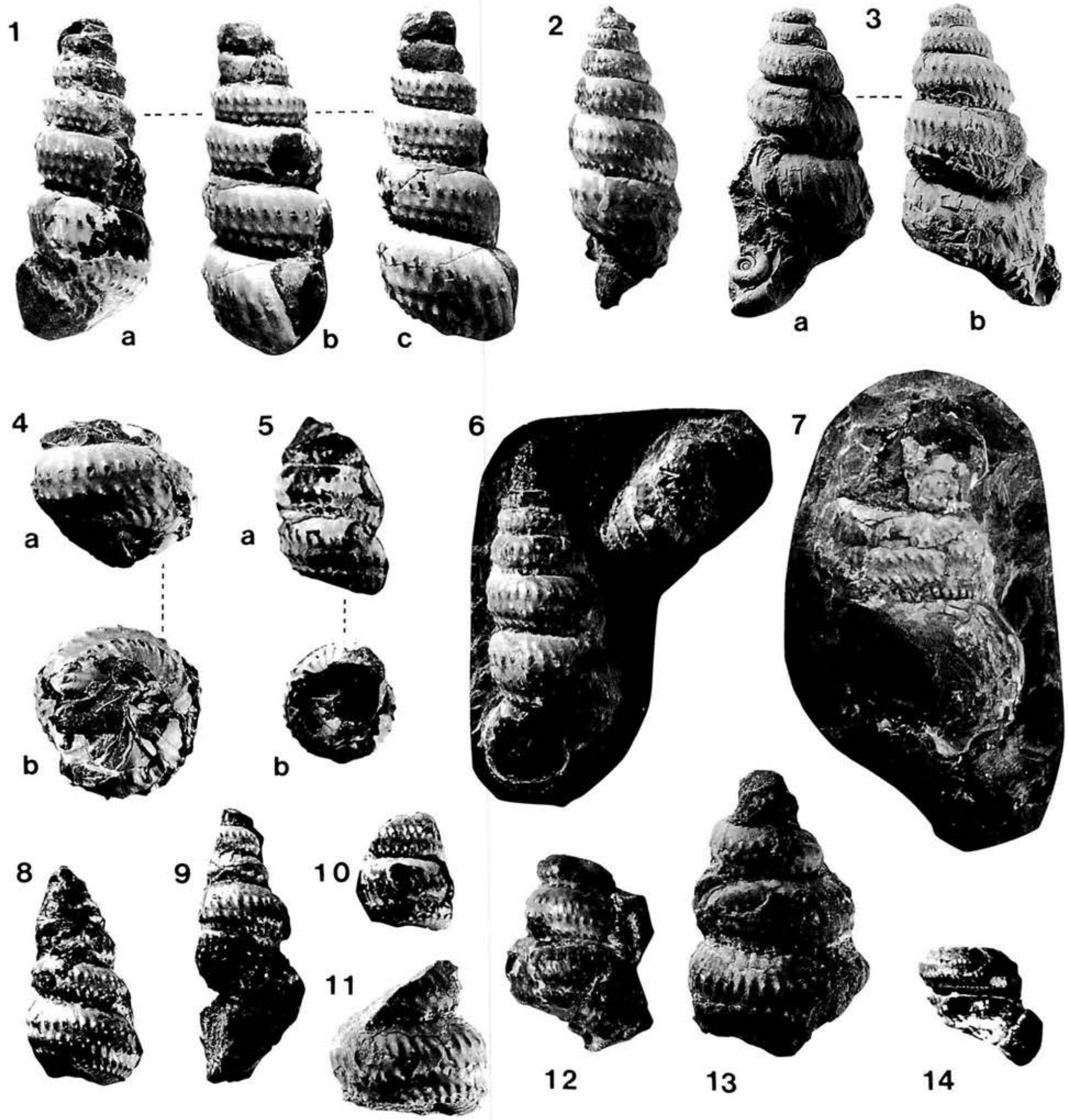

Figure 5. *Mariella* (*Mariella*) *pacifica* sp. nov. **1a-c.** Holotype, GS. G170, three lateral views, ×1.5. Note that the upper whorl of the holotype is encrusted with some other organism. **2.** GS. G171, with a rostrate oral part, ×4/3. **3a, b.** GS. G172, with a rostrate oral part where a juvenile *Anagaudryceras* sp. is attached, ×1.5. **4a, b.** GS. G173, lateral and basal views, ×2. **5a, b.** GS. G174, lateral and basal views, ×1.5. **6.** GS. G176 and G177 (obliquely embedded), ×1.5. **7.** GS. G178, deformed larger form with a rostrate oral part, ×4/3. **8.** TKD 30558, ×1.5. **9.** TKD 30561A, ×1.5. **10.** TKD 30561B, ×1.5. **11.** GK. H8503, ×2. **12.** TKD 30559, ×2. **13.** GK. H8502, ×2. **14.** TKD 30560, ×2. TKD 30560 is tentatively called *Mariella* (*Mariella*) aff. *pacifica.*

GK. H8502 (Figure 5-13) and GK. H8503 (Figure 5-11) obtained by T.M. at loc. R518 p5 of the lower part of the Member My3 in the East Suribachi-zawa, are probably referable to this species, although they are incompletely preserved.

Diagnosis.—Small, sinistrally coiled and slenderly shaped *M*. (*Mariella*), ornamented densely by numerous, small tubercles and delicate riblets in four rows at unequal intervals,

Table 1. Measurements of *Mariella* (*M.*) *pacifica*.

Specimen	GS. C170 (holotype)				G171		G172
Whorl	1°	2°	3°	4°	2°	3°	3°
Diameter	15.2	13.0	11.2	9.3	13.0	10.8	12.8
Height	9.6	7.5	5.7	4.3	7.0	4.6	6.2
H./D.	.63	.58	.51	.46	.54	.43	.48
Ribs	32	33	33	31	32	33	32

Height means the distance between the upper and lower seams at the adoral end of the measured whorl. Ribs mean the number of ribs or tubercles per whorl. 1°, 2°,⋯⋯ indicate the first, second, ⋯⋯ whorls in ascending order from the bottom. Note that an undeformed whorl is selected for the measurements. Linear dimensions are in mm.

with the interspace between the first and second rows at about the mid-flank. Ribs extend upward from the tubercles of the first row; often the tubercles of the second and third rows closely but obliquely disposed, forming weak spiral ridges with a narrow groove in between; the extended fine riblets recurved on the basal surface by way of the fourth tubercles.

Description.—The shell is small and slender; its apical angle is apparently low (less than 30°); junction of whorls rather shallow; whorl section suboval to subrhomboidal, with outward sloping and gently convex upper portion of flank, nearly flat or slightly convex main part of flank, and narrow and inward-sloping lower portion. Obtuse shoulders may thus be formed at the upper and lower edges of the main part of flank. Basal surface of the whorl is gently convex, sloping to a narrow umbilicus.

Ornament consists of numerous, densely set, fine tubercles and extended delicate riblets, numbering about 30 to 40 to a whorl in each row. The tubercles are normally in four rows at unequal intervals; the first row slightly above the mid-flank, the second somewhat below the mid-flank, the third close to the second and the fourth along the lower whorl seam on the outer margin of the basal surface, where riblets are recurved. The tubercles are of unequal intensity between the rows; those of the first row are slightly coarser than others and extend upward to short ribs; those of the second and third rows are finer, somewhat oblique and disposed en echelon; often they appear to form blunt spiral ridges with a sulcus in between. The tubercles of the fourth row are very fine and close to those of the third row; occasionally the fourth-row tubercles are scarcely discernible or undeveloped.

Near the apertural margin ribs become flexuous and continuous, connecting transversely elongates tubercles (see GS. G171, G172 and G178; Figure 5-2, 3, 7). Regrettably, the recurved part of the rostrum is not preserved. At any rate, the above three specimens represent the adult shell. The holotype (GS. G170) is also nearly adult. The three specimens, GS. G170, G171 and G172 (Figure 5-1—3) are equally small, with total whorl heights about 40 mm and diameters of last whorl 15 mm or so. On the other hand GS. G178 (Figure 5-7) is somewhat larger, although it is deformed and lacks earlier whorls. Again dimorphism can be considered, if not definitely concluded.

Measurements.—See Table 1.

Comparison.—In respect of a small and slender shell with numerous, fine and delicate tubercles and riblets, this species may be closely allied to *M.* (*M.*) *numida* (Pervinquière) (1910, p. 53, pl. 5, figs. 12, 13), from the Cenomanian of Algeria, but the holotype of that species (refigured by Wright and Kennedy, 1996, text-fig. 138L) is dextral and seems to possess a lower apical angle (about 18°) and four rows of tubercles wholly exposed on the outer face of a whorl. For the exact comparison more specimens including an adult example of *M.* (*M.*) *numida* are required.

In having numerous tubercles and obliquely extended riblets, *M.* (*M.*) *pacifica* is apparently similar to *M.* (*M.*) *torquatus* Wright and Kennedy, 1996 (p. 334, pl. 100, figs. 2, 20, 21), from the Lower Cenomanian of England. In the latter the rows of closely set tubercles form distinct spiral ridges. In the former the tubercles are normally not so much crowded and the ridges are weaker. TKD30560 (Figure 5-14) from loc. P1 is exceptional in that its tubercles and riblets are so crowded and numerous (about 50 to a whorl) that the rows of tubercles form fairly distinct spiral ridges. There is, however, some extent of variation in the distinctness of the ridges in *M.* (*M.*) *pacifica*. For instance, TKD30559 (Figure 5-12) and TKD30558 (Figure 5-8) appear to show intermediate features. There is, thus, a certain extent of variation in the fineness of tubercles and appearance of ridges in *M.* (*M.*) *pacifica* and also in *M.* (*M.*) *torquatus* (see the three figures cited above). The undoubted difference between the two species is in the disposition of the rows of tubercles. Namely, in *M.* (*M.*) *torquatus* the first row is higher in the upper part of the whorl face and the second row is at the middle of the whorl, whereas in *M.* (*M.*) *pacifica* the interspace between the first and second rows is at the mid-flank. This is maintained even in TKD30560. There is also a difference in whorl shape between the two species; rectangular versus suboval in whorl section.

In respect of the small and slender shell, *M.* (*M.*) *pacifica* is somewhat similar to *M.* (*M.*) *camachoensis* (Böse) (1923, p. 149, pl. 10, figs. 32-37) (see also Clark, 1965, p. 43, pl. 13, figs. 6, 8; pl. 18, fig. 8), from the Upper Albian (a unit correlatable with the Pawpaw Formation) of Mexico, but the tubercles of *M.* (*M.*) *pacifica* are more numerous and disposed in rows at unequal intervals; those of the first row are coarser and extended upward to ribs.

M. (*M.*) *pacifica* resembles *M.* (*M.*) *oehlerti* (Pervinquière) (*vide supra*) in general appearance and especially in the disposition of the rows of tubercles. The former is characterized by its slender shell shape, with a shallower interwhorl junction, suboval instead of subquadrate to rhomboideal whorl section and on the average finer, denser and more numerous tubercles and riblets in comparison with the latter. Should the suggested dimorphism be warranted in each of the two species, the size difference at the adult stage would be distinctive.

Klinger and Kennedy (1978) found in their South African material of *M.* (*M.*) *oehlerti* large variation in the number of tubercles. The number ranges from 15 to 28 per whorl with an exceptional 30; for the majority the range is from 18 to 24. This is conformable with our material of *M.* (*M.*) *oehlerti*. In the case of *M.* (*M.*) *pacifica* under investigation, the counted range is normally from 30 to 40 per whorl. The two species are thus separable on this point, although the range is fairly wide in each of them. However, TKD30560 mentioned above (with 50 tubercles per whorl) is rather extreme and it is better to call it tentatively *M.* (*M.*) aff. *pacifica*.

With respect to numerous, densely set tubercles, *M.* (*M.*) *miliaris* (Pictet and Campiche, 1861) (p. 136; 1862, pl. 58, fig. 5) (see Renz, 1968, p. 88, pl. 18, fig. 10 for the reillustration of holotype) is somewhat similar to *M.* (*M.*) *pacifica*, but the rows of tubercles are nearly equidistant and the apical angle has been described as larger in that species. It is closely related to *M.* (*M.*) *bergeri*, as Spath (1937, p. 515) has already mentioned. *M.* (*M.*) *miliaris* normally occurs in the Upper Albian but ranges up to the Lower Cenomanian in England (see Wright and Kennedy, 1996, p. 333).

Occurrence.—As for material. The type locality is in the middle part of the Member My3. This species occurs so far in the Lower Cenomanian of Hokkaido. Its true veritcal range and geographical distribution should be determined by further investigations.

Acknowledgments

For the material of this palaeontological study we are indebted to the cooperative field work conducted by W. Hashimoto and also by T. Nishida. We have been much enlightened by the results of previous palaeontological studies, especially those by Clark (1965), Klinger and Kennedy (1978), Atabekinan (1985) and Wright and Kennedy (1996), although our views may not be always agreeable with them. Naoko Egashira and Seiichi Toshimitsu helped us in photography and Kazuko Mori assisted us in preparing the manuscript.

Appendix

Locality guide for selected Cretaceous fossils of the Soeushinai area

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The localities of the Cretaceous fossils in the Soeushinai area and the lists of identified species (mainly Mollusca and Foraminifera) have been indicated in a number of route maps and tables in the papers by Nishida *et al.* (1992, 1993, 1996, 1997, 1998a, b). These papers are written in Japanese and the maps are too numerous. Hence, two comprehensive maps (Figures 6 and 7) are presented here. They are compiled from some of the previous maps with necessary modifications. The specimens of *Mariella* species with register numbers in the descriptions and a few unregistered ones are indicated in the maps. Moreover, the maps contain localities of selected mid-Cretaceous guide species which are particularly important for interregional correlation.

The geology is outlined in the maps. A thick broken line is a fault and a dotted line is a boundary of lithostratigraphic units. The Lower Yezo and Middle Yezo Subgroups are abbreviated to Ly and My. My1, My2, My3 and so on are successive members of My; T is the Tertiary (mainly Miocene); Q is a leucocratic intrusive body. A megafossil locality is indicated by a small solid circle (in situ) or by a cross mark (fallen or transported nodule).

Notes are briefly given below in accordance with the investigated routes, of which (1)-(3) are shown in Figure 6 and (4)-(10) in Figure 7.

(1) *Main course of the River Sounnai* (part) (upstream). —R887 (a nodule derived probably from the upper part of Ly): *Hysteroceras orbignyi* (Spath), *Pseudohelicoceras* sp. etc. R880 (nodules in mudstone in the upper part of My1): *Mortoniceras* (*Deiradoceras*) sp., etc. R34 (mudstone alternated with sandstone, lower part of My2): *M.* (*Durnovarites*) cf. *subquadratum* Spath etc. R803 (laminated mudstone and sandstone, upper part of My2): *Mariella bergeri* (Brongniart), *Mortoniceras* (*M.*) cf. *minor* Spath. R813 (ditto): *M. bergeri, Bhimaites kawai* Matsumoto and Egashira. The above faunules at four levels are correlated with successive zones of the Upper Albian.

(2) *East Suribachi-zawa* (E in Figure 6).—R525 (laminated mudstone in the upper part of Member My2): *Bhimaites* cf. *kawai* and *Inoceramus* n. sp. (small, nearly equivalve, finely ornamented species, probably identical with the late Albian species from Mont Risou illustrated in Gale *et al.*, 1996, figs. 21f, j; 31g). R520 (nodules derived from the basal part of My3): *Mariella* aff. *bergeri* (to be described in Part 2), *Graysonites adkinsi* Young, *Stoliczkaia* (*Lamnayella*) *sanctaecatherinae* Wright and Kennedy etc. R518 (nodules from the lower part of My3): *Mariella oehlerti, M. dorsetensis, M.* cf. *pacifica* etc. R515 (mudstone in the lower part of My3): *Graysonites* sp.

(3) *Suribachi-zawa* (S in Figure 6 and branch rivulets) (upstream).—R875 (a nodule derived from My3): *Mariella miliaris* (Pictet and Campiche) (to be described in Part 2). AI81001 (nodule from My3) and R543 (nodules in mudstone of My3): *M. oehlerti* etc. R575 (ditto): *M. dorsetensis, M. oehlerti, Graysonites* cf. adkinsis (nearby derived nodule). *Inoceramus* aff. *reachensis* Etheridge. R534 (nodules in laminated sandstone and mudstone of My2): *Inoceramus* n. sp. (same as sp. at R525), *Mortoniceras* cf. *minor* etc. R433 and IA81007 (nodules from My3): *M. dorsetensis, Stoliczkaia* (*Lamnayella*) cf. *sanctaecatherinae* etc. R438 (nodules from My3): *M. dorsetensis* etc. R471 (mudstone of My3): *Inoceramus* aff. *reachensis*. R449 (nodule from My3 ?): *M.* cf. *carrancoi* (Böse) (to be described in Part 2). R456 (nod-

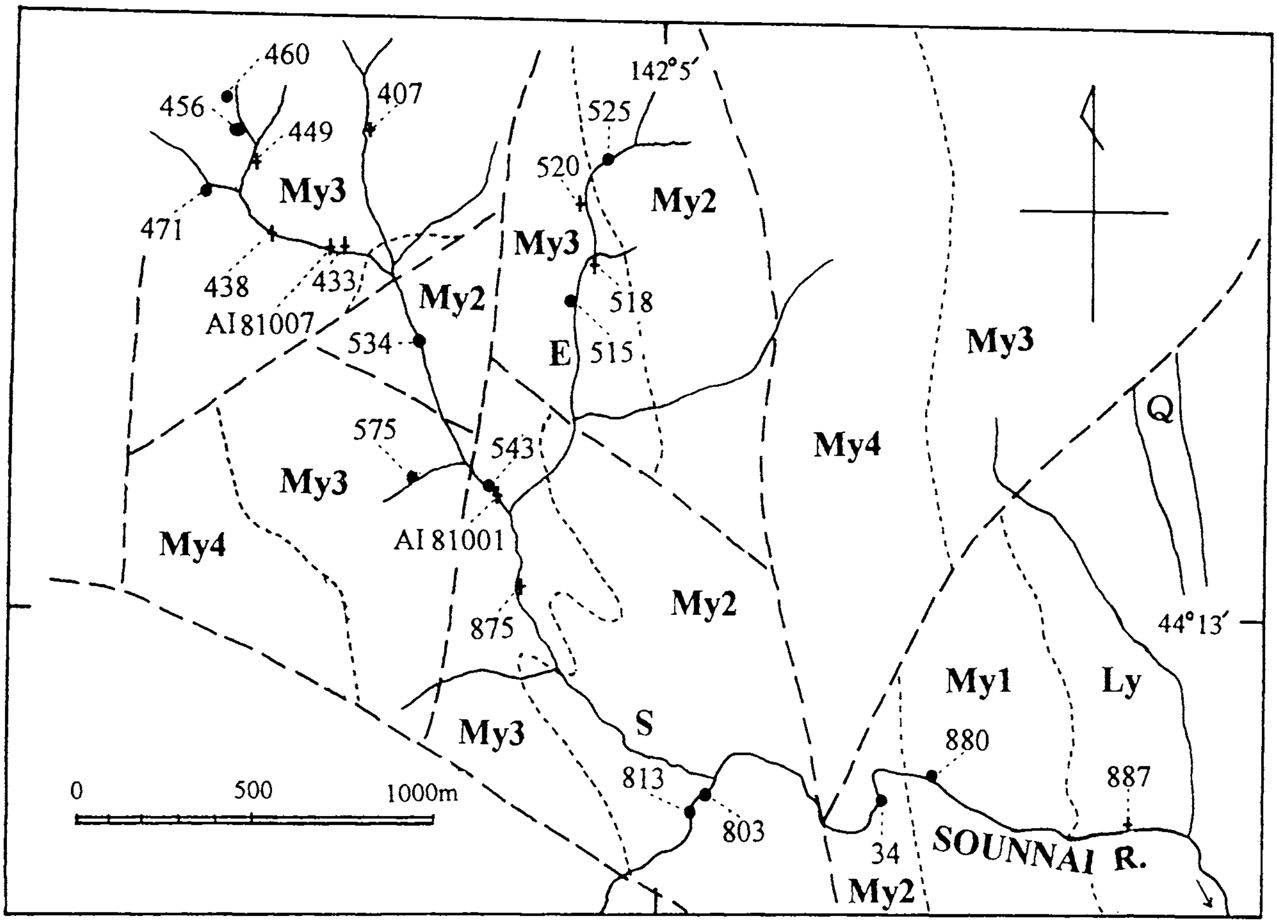

Figure 6. Route map of the Suribachi-zawa and part of the Sounnai River, showing localities of *Mariella* and selected guide species (compiled from Nishida *et al*., 1996, figs. 3-5 and 8 and also Nishida *et al*., 1997, figs. 1, 2). See text for the marks and abbreviations. Some of the numbered localities with prefix AI are referred to TKD specimens. Many others are concerned with the main material of this study. They should have the prefix R, which is omitted in this and the other map for brevity. Note that prefix AI is not used in the original label of TKD and in the main text of this paper.

ule in sandy sltstone of My3): *M. dorsetensis, Stoliczkaia* (*Lamnayella*) cf. *amanoi* Matsumoto and Inoma. R460 (nodule in mudstone of My3): *M. oehlerti, Graysonites* cf. *adkinsi*. R407 (nodule from My3): *M.* cf. *pacifica*.

(4) *NW branch rivulet of the Sanjussen-zawa*.—Loc. YKC060824 (nodule from My3): *M. dorsetensis, M. oehlerti* etc.

(5) *Upper reaches of the Kyoei-Sakin-zawa*.—At two localities YKC591014 and YKC020619 *Mariella oehlerti* was collected in nodules from My3. Not far from these localities *Graysonites wooldridgei* was obtained in situ at loc. YKC010618 and in a transported nodule at loc. YKC040808. Somewhat downstream from them at loc. KY768 *S.* (*L.*) *sanctaecatherinae* was obtained from a transported nodule. These localities are all in the area of My3. Still further downstream at locs. YKC060918 and KY356 *G. adkinsi* was collected from transported nodules. The two localities suggest a small outcrop of My3 within an otherwise Tertiary area.

(6) *Ebisu-zawa and Hotei-zawa* (EB, HT in Figure 7). —R557 and R560 (laminated mudstone and sandstone): *Inoceramus* n. sp. (same as the one from R525). R567 (nodule from My3): *M.* cf. *oehlerti*. R901 (nodule from My3): *Graysonites wooldridgei*. R905 (nodule in mudstone of My3): *M. pacifica, M. dorsetensis* etc. R906 (ditto): *M. pacifica, M. gallienii* (Boule, Lemoine and Thévenin), *S.* (*Lamnayella*) *sanctaecatherinae*.

(7) *Middle course of the R. Shumarinai and a branch rivulet Fukuroku-zawa* (FR in Figure 7) (upstream).—R8003 (laminated mudstone and sandstone of My2): *Bhimaites kawai, Inoceramus* n. sp. (same at R525). AI71204 (nodule from My3): *M. dorsetensis*. KY350 [=R8054] (nodule in mudstone with sandy laminae of My3): *S.* (*L.*) *sanctaecatherinae*. AI P1. P2, P4 (nodules from My3): *M.* aff. *pacifica, M. oehlerti, M. pacifica*. R926 (large nodule derived from My3): *M. oehlerti* etc. R917 (nodule from My3): *M. oehlerti*. R919 (nodule in mudstone of My3): *M. oehlerti, Ostlingoceras* cf. *bechii* (Sharpe), *Inoceramus* aff. *reachensis* etc. R930 (nodule from My3): *M. oehlerti, I.* aff. *reachensis*. R931 (nodule from My3): *M.* cf. *oehlerti*.

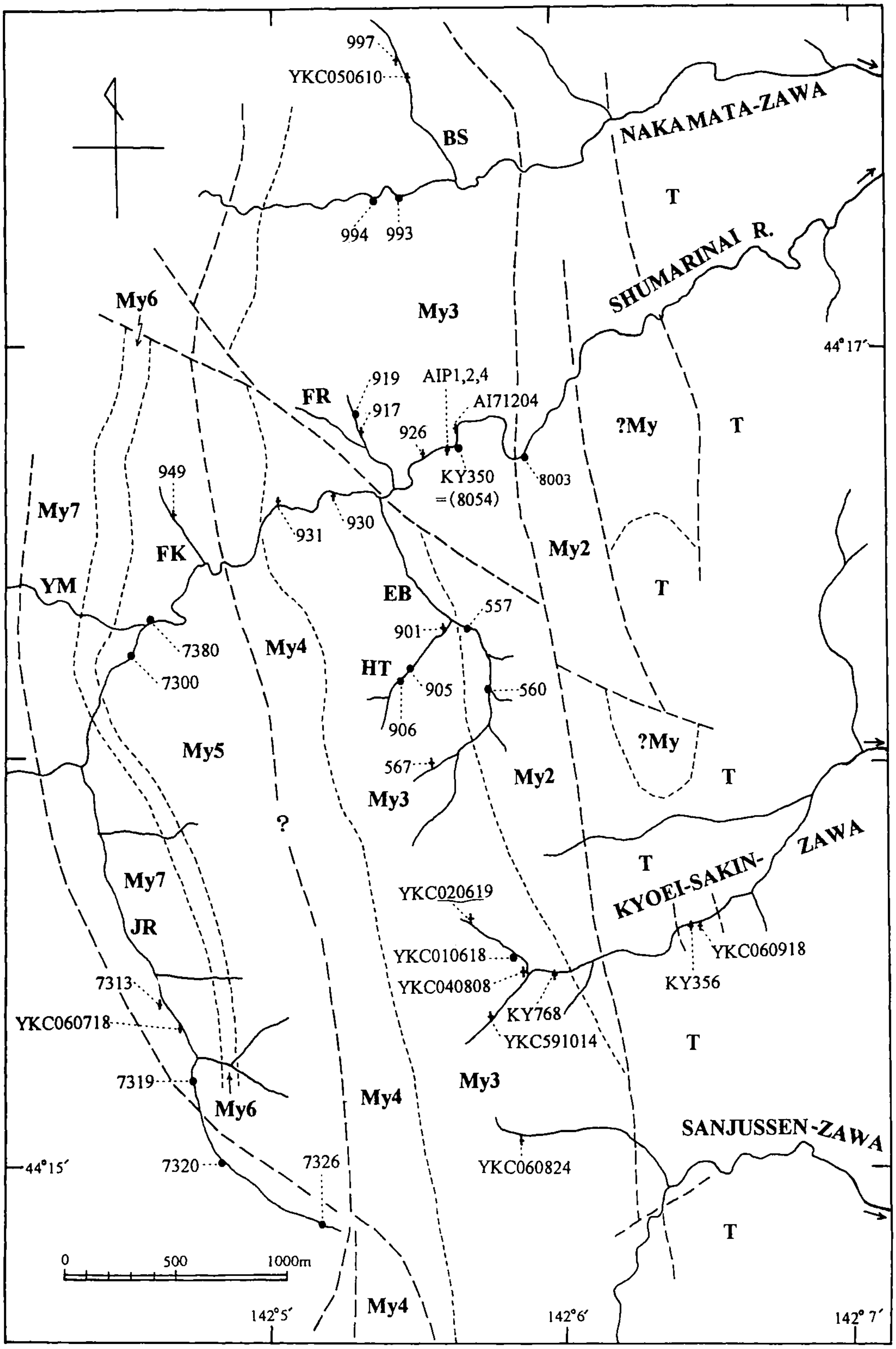

Figure 7. Route map of the area across the middle course of the Shumarinai River, showing localities of *Mariella* and selected guide species (compiled from Nishida *et al.*, 1996, fig. 7 ; Nishida *et al.*, 1997, figs. 7, 8 ; Nishida *et al.*, 1998b, figs. 2-4 and 7). See text for the marks and abbreviations. Prefix KY or YKC to a locality number refers to Katsujo Yokoi's or Y.K.'s collections by their independent field work. Other numbers are as for Figure 6.

(8) *Middle course of the Nakamata-zawa and its tributary Bishamon-zawa* (BS in Figure 7) (upstream).—YKC050610 (nodule derived from My3): *M. oehlerti*. R997 (nodule from My3): *S.* (*L.*) *sanctaecatherinae*. R993 (nodule in mudstone of My3): *M. oehlerti, M. pacifica, Graysonites* sp., *Zelandites* cf. *inflatus* Matsumoto. R994 (nodule in mudstone of My3): *Inoceramus* aff. *reachensis*.

(9) *Upper-middle course of the R. Shumarinai and a branch rivulet Fuku-no-sawa* (FK in Figure 7) (upstream). —R949 (nodule from lower part of My5): *Turrilites acutus* Passy, *Inoceramus pictus minus* Matsumoto. R7380 (mudstone in the middle part of My5): *Inoceramus ginterensis* Pergament. R7300 (sandy mudstone in the upper part of My5): *Wellmanites japonicus* Matsumoto, Takahashi and Sanada, *Inoceramus* cf. *pennatulus* Pergament etc.

(10) *Jyurou-zawa* (JR in Figure 7) (upstream).—R7313 (nodule from My7): *Vascoceras durandi* (Thomas and Peron). YKC060718 (nodule from My7): *Muramotoceras yezoense* Matsumoto, *Inoceramus kamuy* Matsumoto and Asai, *Mytiloides subhercynicus* (Seitz), etc. R7319 [=YKC010625] (huge nodules in mudstone of My7): *Pteropuzosia kawashitai* Matsumoto. Based on the above species My7 is referable to the lower part of the Turonian. No species of the Turrilitidae has been found from My7. Being separated by a fault, mudstones with some beds of sandstone are exposed in the uppermost course of the Jyurou-zawa where ammonoids and inoceramids of the upper to middle Cenomanian have been collected at locs. R7320-7326, while turrilitids have yet to be searched for.

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A new crayfish Family (Decapoda: Astacida) from the Upper Jurassic of China, with a reinterpretation of other Chinese crayfish taxa

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Abstract. The highly sporadic fossil record of freshwater crayfish is improved by the discovery of several new specimens from the Upper Jurassic Jehol Group of Liaoning Province, north-east China. As a result of work on this material, the Family Cricoidoscelosidae is erected to accommodate specimens possessing highly atypical features among the Infraorder Astacidea belonging to the new genus and species *Cricoidoscelosus aethus*. Furthermore, *Astacus spinirostrius* Imaizumi (1938) is synonymized with *A. lincenti* van Straelen (1928b) and is moved from the Family Astacidae to the family Cambaridae and to the new genus *Palaeocambarus*. Thus, a solution is suggested to the problematic biogeographic issue of the presence of the genus *Astacus* in a region presently occupied only by cambarid crayfish, a generic assignment that was made tentatively in the first place. In addition, new questions now arise with respect to the origins and early development of crayfish in the Asiatic region and perhaps even globally.

Key words: Astacida, China, crayfish, palaeobiogeography

Introduction

Members of the decapod Infraorder Astacidea, commonly referred to in English by the vernacular term 'crayfish', are also known by many other common names worldwide: crawfish, paper-shell crabs, ecrevisse, yabbies, mud-bugs, flusskrebs, rak, ditch bugs and koonac are just some of these names. With over 500 species currently known, which occur indigenously in tremendous numbers on all continents with the exception of Africa, this is perhaps not surprising (Adegboye, 1981; Hobbs, 1988; Pitre, 1993).

The evolutionary history of the Superfamily Astacoidea is currently the subject of some debate. The more traditional perspective, as suggested originally by Ortmann (1902, 1905), is that the crayfish as we know them today originated in a benthic marine environment similar to that occupied by the marine lobsters. From this ancestral stock emerged three major lines: the extinct Erymidae; the relatively conservative Nephropidae (ancestors of the modern true lobsters); and the highly varied and widely dispersed Astacoidea and Parastacoidea, the 'true crayfishes', which then moved into the freshwaters of Laurasia and Gondwana as the result of two separate invasions.

A more recent perspective, however, is that of Scholtz (1995) and Scholtz and Richter (1995), in which the freshwater crayfishes are more closely related to the Thalassinida and Meiura (Brachyura and Anomala) than to the Homarida (forming a monophyletic group they refer to as the Fractosternalia). They suggested that the worldwide distribution of freshwater crayfish is the result of a single invasion into freshwater during the Triassic onto the 'supercontinent' Pangaea, which then diversified into the groups Parastacoidea (in Gondwana) and Astacoidea (in Laurasia) with the Late Mesozoic break-up of Pangaea.

Despite their relatively long geologic history, the fossil record for the crayfish is not very well understood. Many of the recent references to fossil crayfish originate from the research group of Rodney Feldmann, including the description of new taxa and/or redescription of previously described taxa (Feldmann, 1994; Feldmann *et al.*, 1981) as well as such oddities as evidence of crayfish predation (Feldmann and May, 1991). Other sources of information on the palaeontological record for the Astacida include Rathbun (1926), van Straelen (1928a), Albrecht (1982, 1983) and Cope (1871). Much work has been done with respect to the global distribution patterns of the living Astacidea (e.g., Hobbs, 1988; Huxley, 1884; Ortmann, 1902), stemming largely from their wide use as an aquaculture crop; however, relatively little has been done with respect to a comprehensive analysis of the fossil members of this group beyond strict taxonomy.

Among the more intriguing of fossil astacidans has been material from the Late Mesozoic of China. We will here build on the original works of van Straelen (1928b) and Imaizumi (1938) and their respective description of two species of fossil freshwater crayfish, *Astacus licenti* and *A. spinirostrius*, from the Upper Jurassic (Jehol Group) of Liaoning Province, north-east China. This reassessment is prompted by the discovery of several new, well-preserved specimens from the region.

Collection localities

New material described in this paper was obtained from outcrops in Dawangzhangzi and Daxinfazi villages, Ling-yuan County, Liaoning Province, probably belonging to the Yixian Formation of the Upper Jurassic Jehol Group (Figure 1). While the general collection regions are known, their actual locations are vague because local farmers, who sell the specimens they collect to visiting academics, refuse to reveal their exact locations (one of which has actually been buried by the Chinese government to avoid poaching!). Enough is known of the geology of the region, however, to allow determination of the formations from which they have been collected.

Systematic Paleontology

Order Decapoda
Infraorder Astacida
Superfamily Astacoidea
Family Cambaridae
Subfamily Cambarinae
Genus ***Palaeocambarus*** gen. nov.

Type species.—Astacus licenti van Straelen, 1928b

Diagnosis.—Entire dorsal surface of cuticle covered with fine granulations. Rostrum with basal lateral spines. Elongate, bladelike scaphocerite. Chela of first pereiopod long and narrow with extensive pitting and spination. No hooks visible on ischia. Pleura large and rounded on abdominal segments 2-5, 2nd pleuron being largest. Pleopods elon-

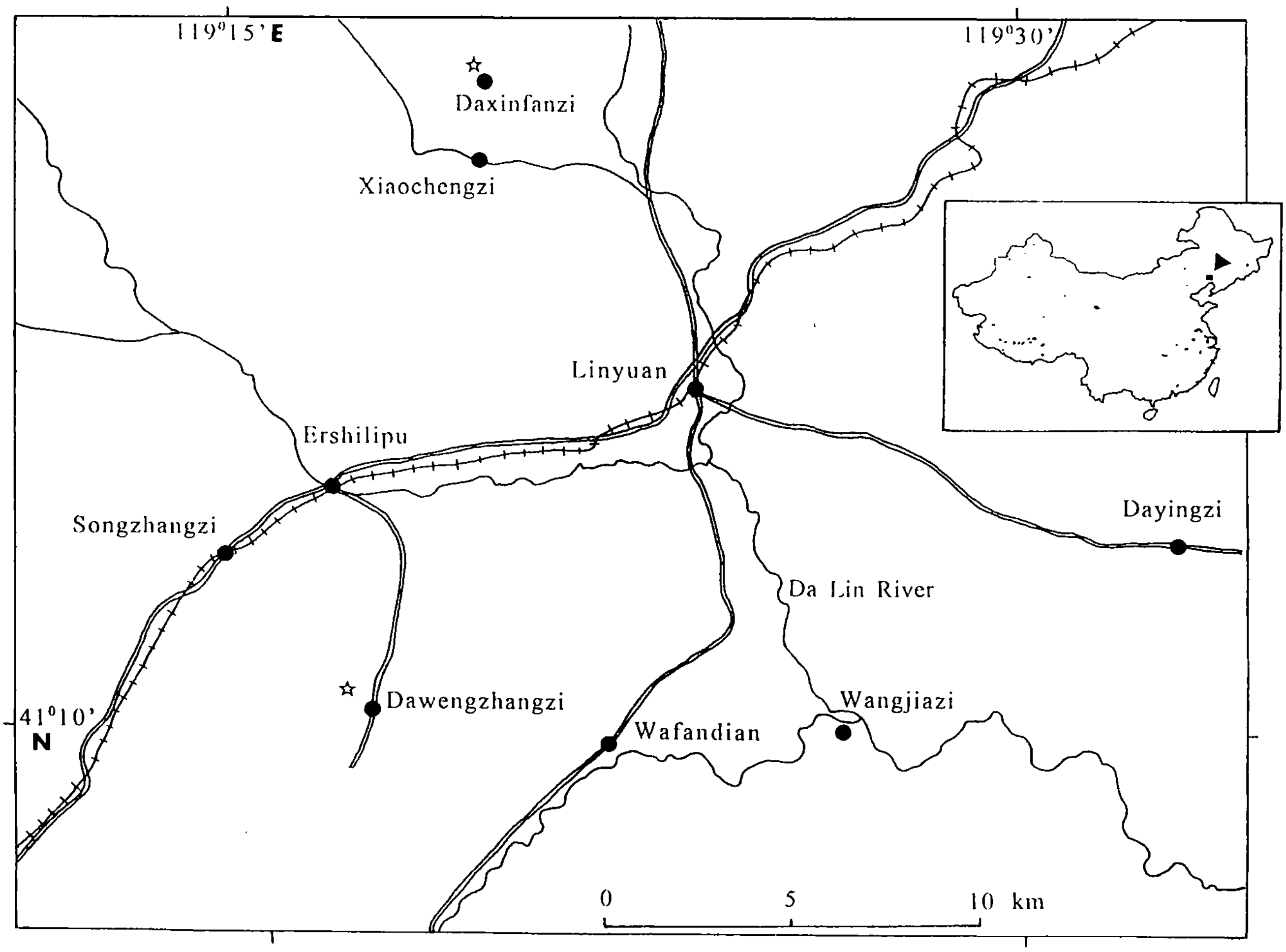

Figure 1. Locality map showing fossil crayfish collection localities near Daxinfanzi and Dawengzhangzi (stars).

gate and blade-like, with no specialization on first. Telson subrectangular with pair of large lateral spines and rounded distal margin.

Etymology.—The name of the genus is formed from 'palaeo', meaning 'ancient', in combination with '*Cambarus*', reflecting the new placement of its sole retained species in the Family Cambaridae.

Palaeocambarus licenti **(van Straelen), 1928b**

Figures 2, 4-6

Astacus licenti Van Straelen, 1928b, p. 133-135, figs. 1, 2; Imaizumi, 1938, p. 176, pl. 23, figs. 1, 2, 4, 5, 6, 11; Hamada and Itoigawa, 1983, p. 74, Pl. 3, fig. 6; Hobbs, 1988, p. 73.

Astacus spinirostrius Imaizumi, 1938, p. 176-177, pl. 23, figs. 9, 10, 12, 13, pl. 22, fig. 1; Hobbs, 1988, p. 73.

Diagnosis.—As for genus.

Emendation to Description.—Rostrum elongate and triangular with smooth margins. Approximately twice as long as wide at base (largest observed being 15 mm long and 7 mm wide at base). Length roughly one-third that of cephalothorax. A pair of anteriorly directed spines near base of rostrum that extend to approximately one-third rostrum's length (NIGP 126338). One specimen (NIGP 126342) shows two rows of small tubercles on ventral surface of rostrum. A single specimen (NIGP 126338) possesses small mid-dorsal spine at base of rostrum (Figures 4b, 4c).

Carapace developed, covers thorax completely. It extends partially over first pleomere mid-dorsally and completely so laterally due to slight postero-lateral enlargement (Figures 5a, 6a); simply decorated, possessing only a sinusoidal cervical groove (concave medially, curved convexly mid-laterally, concave again at lateral carapace margin) as well as a pair of short branchiocardic grooves that extend posteriorly from medial cervical groove (NIGP 126353, 126338: Figure 4c). A single specimen (NIGP 126338) possesses a pair of well-developed gastric spines (Figure 4c). A slight ridge along lateral and posterior edges, but not evident along anterior margin. Optic notch well developed; adjacent anterolateral margin gently rounded (Figure 6a). Entire carapace surface with granulated texture, several small spines/protrusions situated near cervical groove and around anterolateral region of carapace (NIGP 126338, 126353).

Antennules biflagellate, with medial flagellum larger than lateral flagellum. Peduncle not fully preserved on any specimens, although several specimens possess some peduncular segments. NIGP 126338 shows distal segment only, which is subrectangular in shape, slightly longer than wide, has rounded edges and is very small (less than 1 cm^2). NIGP 126346 with two distalmost segments, in shape with rounded edges and similar size dimensions. Middle segment noticeably more square than distalmost segment but equal in size. Distalmost segment similar in shape to others mentioned but with slight anterior projection on outer margin, possibly remains of small spine. Second segment approximately twice as wide as distal segment, suggesting it may be portion of basal segment, which is typically considerably larger than the other two antennular peduncle segments in recent crayfish. Antennular flagellae exceed 10 cm in length (Figures 4b, c, 5a, 6a).

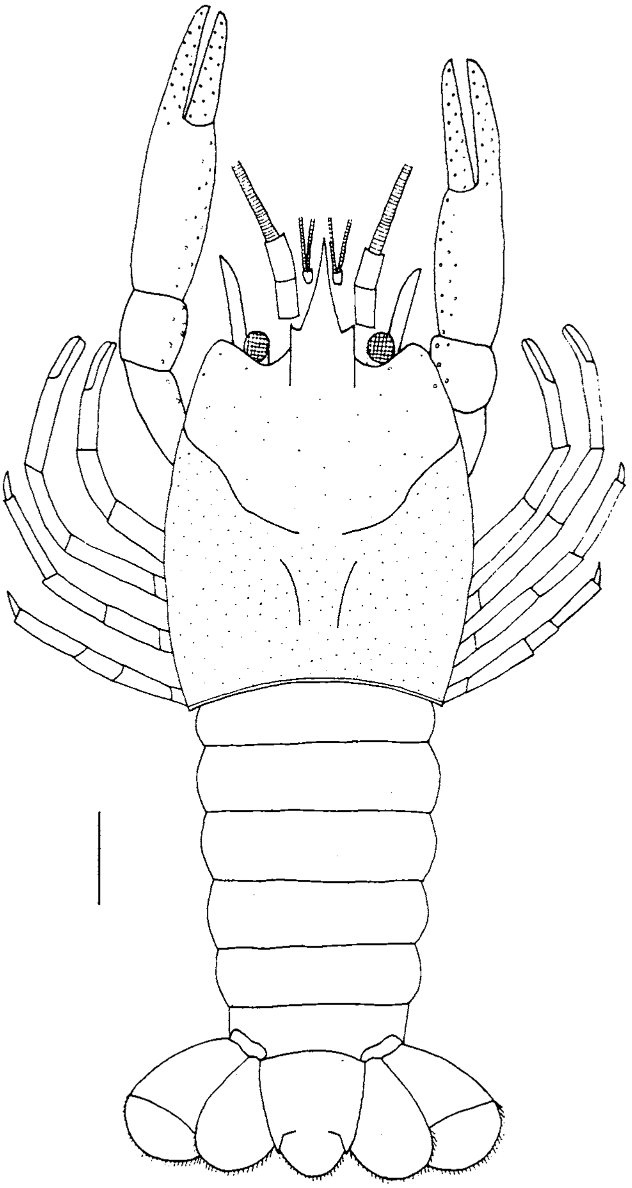

Figure 2. A reconstruction of *Palaeocambarus licenti* in dorsal view. Scale bar equals 1 cm.

Antennae each possess a single flagellum that is considerably longer than those of antennules (NIGP 126339 possesses a flagellum ~60 mm long, almost equal to total body length). Distal segments of peduncle relatively clear, but proximal peduncle arrangement difficult to interpret due to their frequently being overlapped by other structures such as antennal scales or rostrum. Distalmost segment rectangular in shape with concave proximal margin, long axis along length of antennae, and shows dimensions of approximately 3 mm width by 4 mm length. Adjacent segment similar in

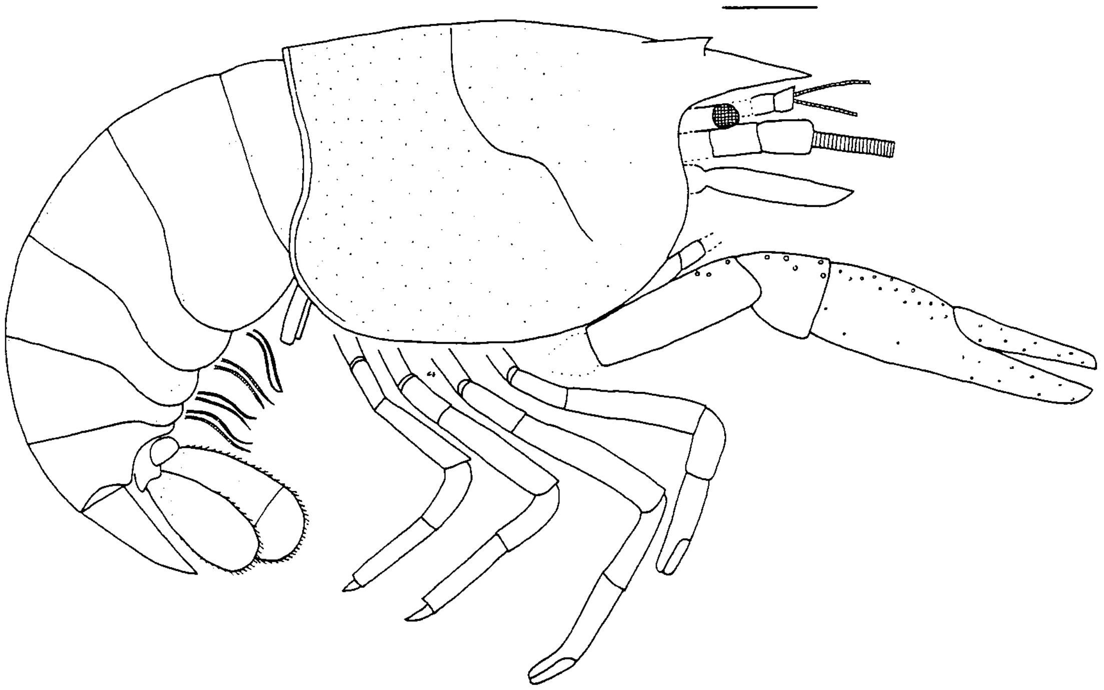

Figure 3. A reconstruction of *Cricoidoscelosus aethus* in lateral view. Scale bar equals 1 cm.

shape and size but lacks curved proximal edge. Middle segment rectangular in shape and similar in length to two distalmost segments, approximately 2/3 as wide as long; attached laterally to basis, which is short (approximately 2 mm) and wide (4 mm) and possesses an arcuate proximal margin. Coxa rectangular in shape with slightly convexly curved posterior margin, slightly less wide than basis and possesses medial anterior projection, which 'fills' the posterior groove in basis (NIGP 126338; Figures 4c, 6a).

Well-developed, blade-shaped scaphocerites extend from lateral half of each antennal basis. They reach maximum length of 15 mm, are setose along lateral margins (only setal bases, not setae themselves, preserved). One specimen (NIGP 126343) possesses small, medially directed process at anterior end of scaphocerite (Figures 4a, 4c, 5a, 6a).

Eyes located near base of scaphocerites, always somewhat deformed but were probably round or slightly ovoid and approximately 2 mm wide. They were probably closely associated with body, with short eyestalks of 1–2 mm, are always found superimposed over rostrum and/or antennal peduncle (i.e., NIGP 126342).

Prominent epistome, close to 10 mm in width, visible on ventrally preserved specimens suggesting it was heavily sclerotized in life (as seen with recent crayfish). It possesses an arched v-like shape and is directed anteriorly. Medial process present near the anterior end, with two small longitudinally arranged pits. Anteriormost end possesses forward-directed process, approximately one-quarter width of labrum and trapezoidal in shape, wider edge anteriormost (NIGP 126342: Figure 6c).

Some dorsoventrally oriented specimens show details of well-developed gastric mill, triangular in shape, directed posteriorly and found immediately behind labrum (NIGP 126342); made up of two sets of very small, serially arranged peg-like teeth in slightly inwardly curved rows, approximately 16 teeth per element. No median tooth present. Moulds of paired circular gastroliths, up to 7 mm in width, prominent in several specimens: in NIGP 126338 and 126353, one has rounded convex surface while other possesses an outer depressed ridge with raised circular region (Figures 4c, 5a, 6c).

Elements of first and second maxillipedes preserved on some specimens; however, they are impossible to interpret with any certainty due to being damaged and/or obscured by anterior structures such as carapace, 3rd maxillipede and 1st thoracomere. Third maxillipede possesses large ischium, up to 10 mm in length and 3 mm in width. Extensive crista dentata found along ischial inner margin. Merus is small, approximately 2 mm long and 4 mm wide and ovoid in shape. Carpus slightly less in width than merus and is rectangular in shape. Propodus rectangular in shape and approximately 2 mm by 4 mm. Dactyl slightly smaller than preceding segments, approximately 1.5 mm by 3 mm, and elongate with pointed distal end (NIGP 126338; Figures 4b, 6a).

Pereiopods 1 to 5 large and well developed. Pereiopod 1 considerably larger than others, propodus and dactylus modified to form large claw (heavily decorated with spines and pits, especially medially), may exceed 40 mm in total length. Carpus reaches maximum length of approximately 10 mm, is rectangular (almost square in some specimens) in shape and usually narrows slightly at proximal end. Merus

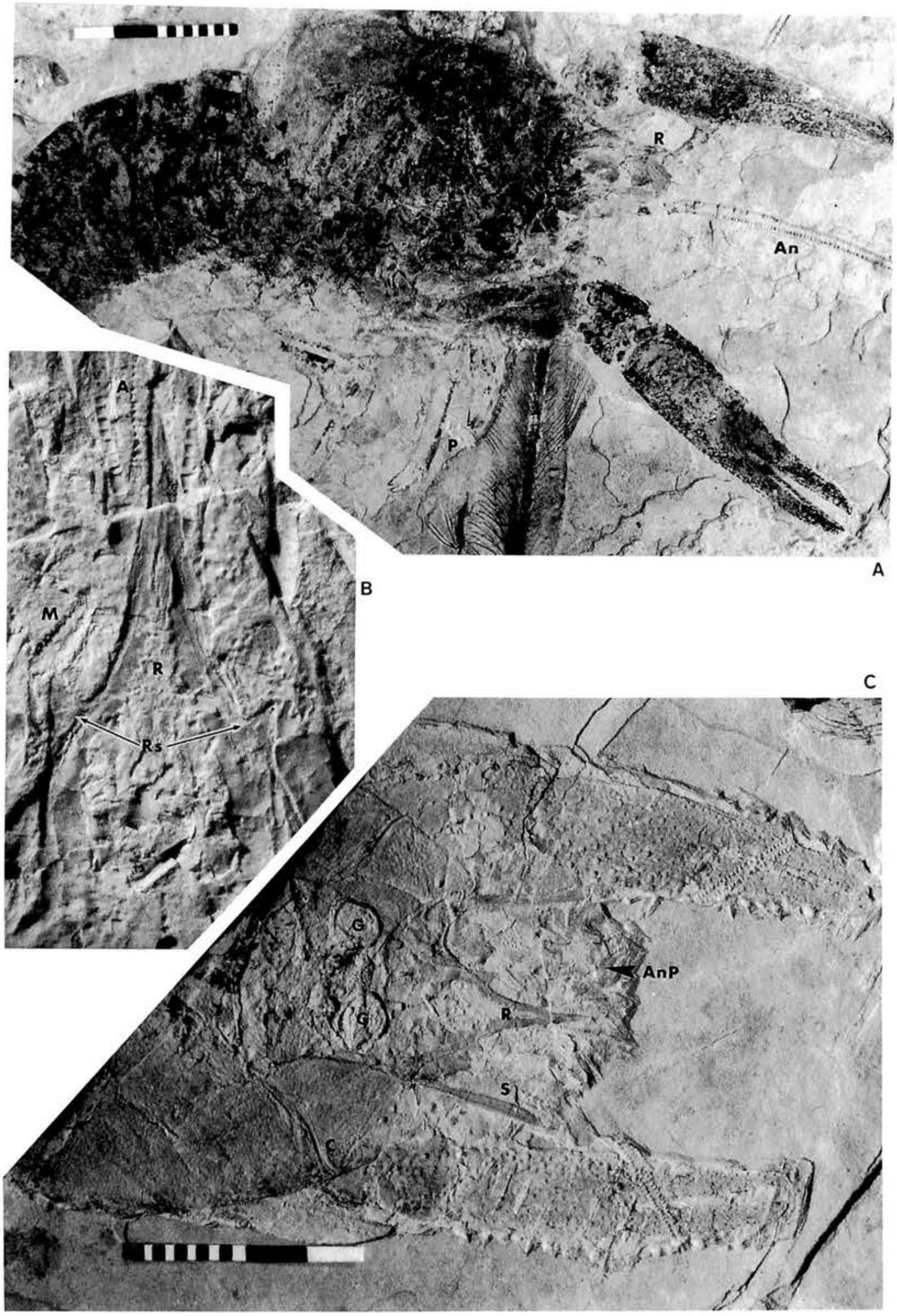

Figure 4. **A.** Lateral view of incomplete specimen (NIGP 126339) of *Palaeocambarus licenti* (with Lycopteran fish) (An = antenna, P = pereiopods, R = rostrum). Scale bar = 2 cm. **B.** Close-up of rostrum, distal end of 3rd maxillipede and antennules of specimen of *P. licenti* (NIGP 126338) (A = antennule, M = third maxillipede, R = rostrum, Rs = rostral spine) ×5.4. **C.** Anterior end of incomplete specimen of *P. licenti* (NIGP 126338) (AnP = antennal peduncle, C = cervical groove, G = gastrolith, R = rostrum, S = scaphocerite). Scale bar = 2 cm.

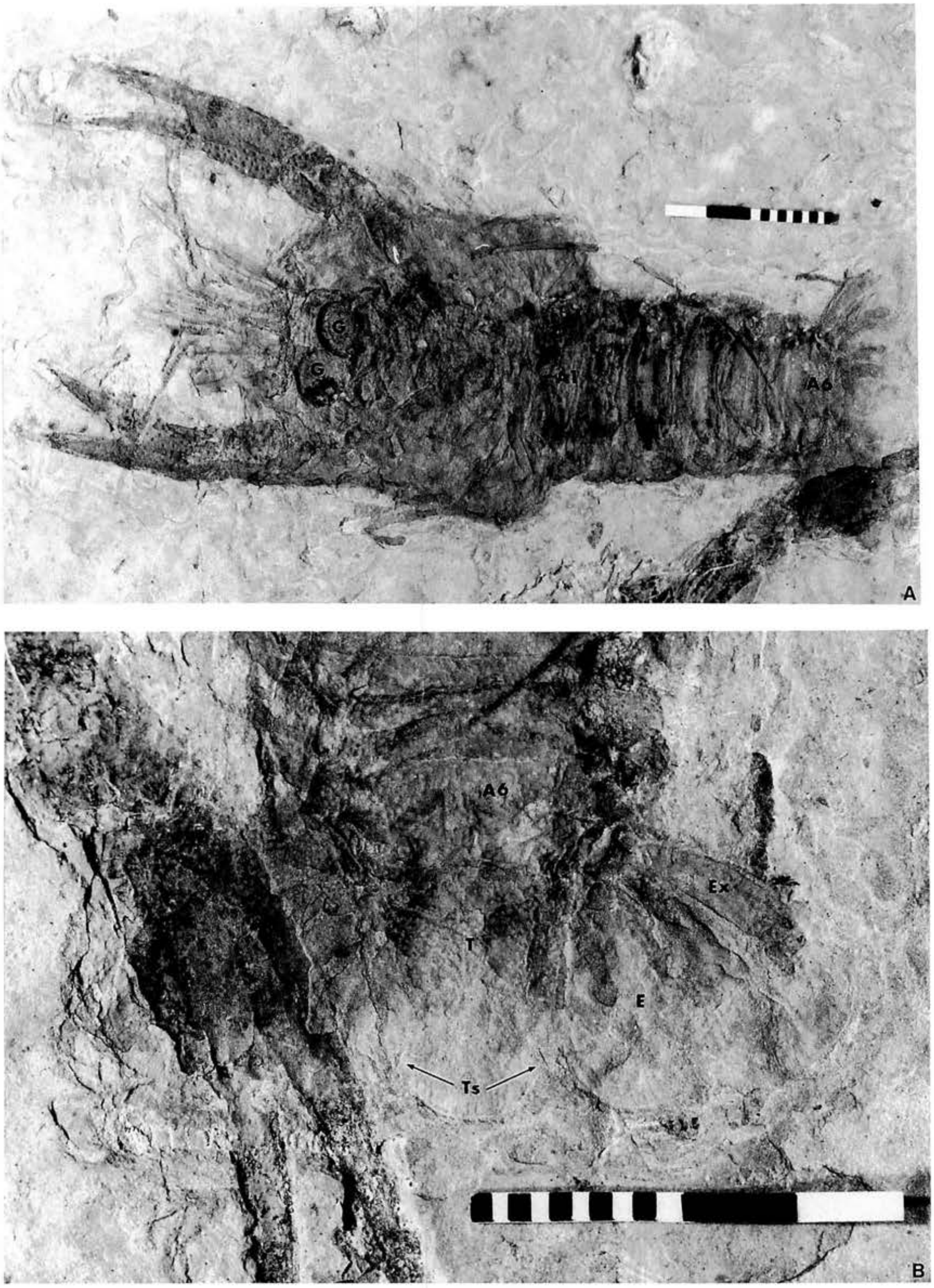

Figure 5. **A.** dorsal view of complete specimen (NIGP 126353) of *Palaeocambarus licenti* (with incomplete chelipede from another specimen) (A1 = first abdominal segment, A6 = sixth abdominal segment, G = gastrolith). Scale bar = 2 cm. **B.** close-up of tailfan of the same specimen (A6 = sixth abdominal segment, E = uropodal endopod, Ex = uropodal exopod, T = telson, Ts = telson spines). Scale bar = 2 cm.

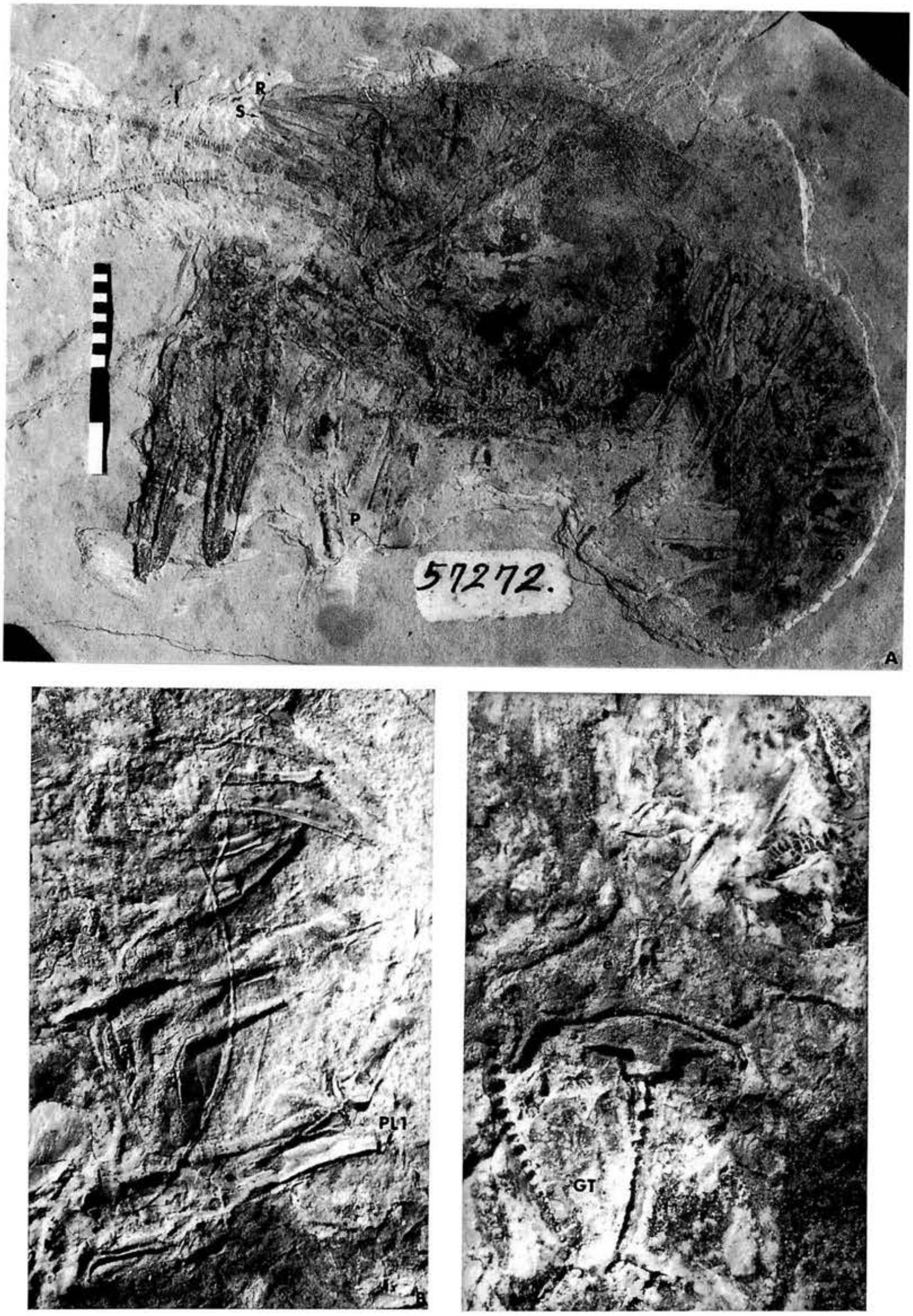

Figure 6. **A.** Specimen of *P. licenti* from Imaizumi's material (= "*Astacus spinirostrius*" : IGP 57272) (A1 = first abdominal segment, A6 = sixth abdominal segment, P = pereiopods, R = rostrum, S = scaphocerite). Scale bar = 2 cm. **B.** Close-up of pleopods of IGP 57272, anterior to bottom (A2 = second abdominal segment, PL1 = first pleopod). ×5.0. **C.** Ventral view of anterior end of specimen of *P. licenti* (NIGP 126342) (e = epistome, GT = gastric teeth). ×6.4.

is elongate and approximately one-half the length of propodus (up to 7-8 mm); is rectangular in lateral view but triangular in dorsal view, by far the most common style of preservation seen in this material. Dactylus, propodus, carpus and merus decorated with large spine-like processes, most commonly so on dactyl and propodus. Those on carpus and merus largest, reaching almost 1 mm in width at base (NIGP 126338). Ischium is small and roughly square in shape, showing no sign of hooks. Basis triangular in shape, with rounded proximal margin where it comes into contact with rectangular coxa (NIGP 126339; Figures 4a, 5a, 6a).

Pereiopods 2 to 5 considerably smaller than pereiopod 1, developed as walking legs (as opposed to the chela of pereiopod 1). Coxa possesses lateral distal groove to accommodate basis, is slightly longer than basis (NIGP 126339, 126346). Basis concave distally, forming a groove where it contacts ischium, but is rounded proximally and slightly wider at its distal than proximal end. Ischium short (approximately 0.4 cm) and tapered slightly where it connects with basis. Merus elongate (approx. 1.5-2.0 cm) while carpus considerably shorter (approx. 0.5 cm) and acts as 'knee joint' (NIGP 126339, 126354). In pereiopods 2 and 3, elongate (approx. 1.5 cm) propodus acts with dactylus to form small chelipede at distal end of pereiopod, much smaller than those of 1st pereiopods (NIGP 126339) (Figures 4a, 6a).

Abdomen elongate and rectangular in dorsal view, narrowing slightly distally. Segment length consistent over first 4 segments with largest specimen seen (NIGP 126353) showing lengths of 0.6 mm. Fifth and sixth segments somewhat shorter with lengths of 0.5 and 0.45 mm, respectively (Figure 5a). Pleura rounded and well-developed on tergites 2-5, 2nd expanded slightly posteriorly and thus larger than others. No pleurae seen on tergite 1, pleurae on tergite 6 greatly reduced to accommodate uropods. Sternites reduced in width distally, but sternite/tergite size ratio (sternites being approximately 70 percent as wide as tergites) remains fairly consistent along abdomen. Sternal bars 'bar-belled' in shape, narrow medially but several times wider distally; this results in ovoid gaps, pointed laterally, where arthrodial membranes would have been located in life (NIGP 126353, 126346; Figure 5a).

Circular/ovoid scars evident near antero-lateral regions of sternites. Pleopods elongate, blade-like in shape. There is no evidence of styliform first pleopod in material collected for this study (but see Discussion).

Tailfan very well developed (Figure 5b). Telson large and subrectangular with slightly convex anterior margin. Tapers distally, possesses straight lateral margins, with well-rounded setose distal margin, which is delineated by complete transverse suture. A pair of posteriorly directed spines located just posterior to transverse suture. Uropods are also large, with exopod slightly longer than endopod. Exopod possesses diaresis, is setose along its rounded distal end and along posteriormost portion of lateral margin. Endopod also setose along distal margin (NIGP 126346, 126353).

Etymology.—Van Straelen's specific epithet *licenti* is retained.

Measurements.—Measurements (in mm) are given in Table 1.

Types.—Van Straelen (1928b) indicated his 'nearly complete' specimen in Pl. 1, Figure 1 as the type specimen for *A. licenti*. His material was housed at Hoang Ho Pai Ho Museum, Tientsin, China. Imaizumi's (1938) material (Reg. Nos. 57254, 57267, 57271, 57272 and 57274) is stored in the Institute of Geology and Palaeontology (abbreviated here as IGP), Tohoku University, Sendai, Japan.

Material examined.—New material used in this study includes NIGP (Nanjing Institute of Geology and Palaeontology) 126338-126339, 126341-4 and 126346-126354. Several other uncatalogued specimens are currently in the NIGP collections, some of which were photographed for use in this study (owing to the difficulty in transporting the large slabs upon which these specimens are found or the inferior quality of preservation of several of these specimens). Specimens 57254, 57267 and 57272 from the Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan were also used in this study.

Occurrences.—The material used in the original description of *Astacus licenti* was collected from an unspecified locality, representing Upper Jurassic *Lycoptera*/*Ephemeropsis* shales, south-west of Shenyang City, Liaoning Province, China. *Astacus spinirostrius* was described from material collected from equivalent *Lycoptera* beds in Lingyuan County, Liaoning. The newest material was collected from beds believed to be of equivalent age in Daxinfanzi and Dawangzhangzi villages, Lingyuan County. This locality cannot be described with any greater detail, as these (as well as other) specimens were bought by the Nanjing Institute of Geology and Palaeontology from local farmers, who refused to divulge the exact locations.

Remarks.—The gastric teeth found in this taxon are atypical when compared to those of other crayfish and other decapods in general. Icely and Nott (1992) and Felgenhauer and Abele (1989) have described in considerable detail the foregut morphology as found in various decapod taxa. The physical make-up of the decapod foregut and the gastric mill in particular are particularly complex systems, made up of up to 60 ossicles of varying size and shape. While we are unable to determine the nature of these ossicles in our fossils, we are able to see evidence of the gastric mill elements. It would probably be best described as 'relatively primitive', based on the classification scheme provided by Felgenhauer and Abele (1989). In their 3-tiered system, the most primitive 'type I' foregut possesses heavily sclerotized lateral teeth that work in association with the median tooth to filter and/or masticate food. In their 'type II' foregut, the gastric mill is "completely absent": the median tooth is never present, while the lateral teeth may be replaced by setose lateral ridges. The gastric mill found in *P. licenti* appears to be an intermediate between these two forms: it possesses no medial tooth, but the paired lateral teeth are present and well developed.

However, the system suggested by Felgenhauer and Abele (1989) is derived from studies of the 'lower Decapoda' (including the suborders Dendrobranchiata and Pleocyemata). Recent crayfish are known to possess both a single medial and paired lateral gastric teeth (e.g., Holdich and Reeve, 1988). Thus, what we see with our material is a situation

Table 1. Morphological measurements (in mm) for *P. licenti* and *C. aethus.*

specimen[#]	cephalothorax length	rostrum length	rostrum width	abdomen length	abdomen width	left exopod length	left exopod width	right exopod length	right exopod width	left endopod length	left endopod width	right endopod length	right endopod width	telson length	telson width	left chelipede length	left chelipede width	right chelipede length	right chelipede width	left chelipede propodus length	right chelipede propodus length
P. licenti																					
126338		13	17													31.5	8.5	30	8	15	15
126339	38	13														35	9	35	9	18	18
126341																12	3	12	3		
126342	33	10	3.5													25	7.5	24	7		12
126343		15	7															45	11		23
126344	17	6.5						6	2.5	25		4.5	2.5	4.5			3.5		3.5		
126346	26	10	5	29.5		10	6	10	6		5		4.5	8	9	22	6.5	23	6.5	13	12
126353	31	11		35	23	13		12.5	8.5			10.5	7	12	10.5	27	6.5	28	7.5	13	14
57254	35	11	5	35	26	13	5	14	6	10	5	11	5	13	12	38	11	38	10	13	14
57267				24																	
57272	33	12	4.9													23	6	24	6	14	13
RT129	33	10		35.5	23			13	9			11	7.5	12	10	27	6.5		7	14	
RT130																28	7.5	29		15	14.5
RT131	44	10		33												35	10	37	10	15	18
RT132				16	11																
RT133	29	11.5		32												33	9			17	
RT134																		32	8.5		12
RT138	28	10														23	5.5	23	5	13	12
RT141								12.5	9.5			12.5	9		10.5	17	5			7.5	
RT143	30	10	6	31														23	6.5		12
RT146	21			24.5	16										7.5	16	4.5	17	5	7.5	8.5
RT150	17.5	4.5		23.5																	
C. aethus																					
126337	34	9	3										3.5	8	10	25	8	27.5	8	13	13
126340	22	7		30				7.5						5		13.5		14.5	4	8	7
126345				24				12	8.5			10	6.5	11.5	10						

possibly reflecting an intermediate state between the three-toothed array seen in recent crayfish and the reduced system seen in many of the 'lower' Decapoda.

Family Cricoidoscelosidae fam. nov.

Type Genus.—*Cricoidoscelosus* gen. nov.

Diagnosis.—Rostrum with rounded base and lateral spines. Bladelike scaphocerite. Well-developed first chelae. No ischial hooks on pereiopods. Rounded pleurae. First pleopod styliform in males, remainder annulate. Large telson with large lateral spines.

Etymology.—The name of this family is derived from the Greek words 'cricoides' (meaning 'annular') and 'scelos' (meaning 'leg').

Cricoidoscelosus gen. nov.

Type species.—*Cricoidoscelosus aethus* sp. nov.

Diagnosis.—Rostrum with rounded base and curved lateral spines. Scaphocerite long, bladelike. Chela of first pereiopod well developed, highly nodose. No ischial hooks evident. Rounded pleura on abdominal segments 2-5, the 2nd being the largest. Pleopods annulate, with the first specialized as styliform copulatory appendages in males. Female with paired circular 'pores' on 3rd abdominal sternite. Telson with large lateral spines and rounded distal margin.

Etymology.—Same as for the family.

Cricoidoscelosus aethus sp. nov.

Figures 3, 7-8

Diagnosis.—Same as for genus.

Description.—Rostrum elongate, approximately 9 mm in length, narrow and triangular along its anterior two-thirds; posterior third roughly circular in shape. Pair of short, curved spines projects anterolaterally from anterior end of basal portion of rostrum (NIGP 126337 : Figure 7a, b).

Carapace heavily sclerotized, covers thorax completely and partially covers first abdominal segment dorsally, almost completely covers first abdominal segment ventrolaterally due to enlargement (NIGP 126340). Sinusoidal cervical groove present, no other carapace grooves visible. Slight ridge visible along carapace dorsal and lateral margin. Optic notch well developed. Surface of carapace granulate with small spines near anteriormost end of carapace.

Antennules are biflagellate, medial flagellum slightly longer than outer flagellum. Peduncles not completely preserved on any specimens: two distalmost peduncular segments rectangular, approximately 1.5 mm by 1.5 mm. Other peduncular segments are unclear (NIGP 126337, 126340).

Antennae each with single elongate flagellum, longest seen 5.1 cm in length (NIGP 126337). No specimens with complete antennal peduncules, but some segments are preserved. Distalmost segment rectangular in shape, approximately 4 mm^2, with proximal margin concave. Adjacent segment similar in shape and size but with lateral side extended to approximately 5 mm long. Proximalmost segment rectangular and elongate, approximately 4 mm wide and 2 mm long. Coxa and basis unclear. Antennal gland present. Scaphocerites elongate, up to 10 mm in length: outer margin straight, inner margin slightly curved. Setal bases present along outer margin (NIGP 126337). Eyes present but not preserved intact: remains found lateral to base of scaphocerites. No peduncle preserved (NIGP 126337).

Epistome v-shaped and directed anteriorly, with anterior process as described for *P. licenti*. However, medial process possesses no pits and is anteriorly directed (NIGP 126337). Gastric structures not evident.

3rd maxillipede well developed, reaching anteriorly to antennal peduncles. Ischium large, 8 mm in length and 3 mm in width, with cristata dentata along inner margin. Merus ovoid, 2 mm wide and 4 mm long. Remaining elements unclear (NIGP 126337).

Pereiopod 1 with propodus and dactylus modified to form large claw (up to 25 mm long), decorated with spines and pits distally and medially. Carpus rectangular in shape, up to 7 mm wide and 5 mm long. Merus large and elongate, exceeding 10 mm. Ischium square, lacking hooks. Basis triangular, gently rounded at contact with rectangular coxa (NIGP 126337, 126355).

Pereiopods 2 to 5 reduced, developed as walking legs with small distal chelae on 2-3 formed from dactyl and propodus. Coxa slightly longer than basis, 2-3 mm in length. Basis with concave interface with ischium, which is approximately 5 mm long and slightly broader distally. Merus rectangular, may exceed 10 mm in length; carpus also elongate and rectangular, up to 10 mm in length (NIGP 126337, 126355).

Abdomen elongate and rectangular, slightly wider at its anterior. Segment length regular for first 4 segments, with last two slightly shorter in length. Abdominal pleura well developed, posterolaterally oriented. Pleurae absent on tergite 1, reduced on tergite 6 to accommodate uropods. Sternites developed across tergite ventral surface, pointed laterally (NIGP 126337, 126345, 126355).

Pleopod 1 visible in one laterally oriented specimen (NIGP 126355), developed as elongate, styliform appendage, probably utilized as a copulatory structure (as in Astacidae and Cambaridae). Distalmost portion only preserved: approximately 10 mm in length and 3 mm wide at base, tapering to slightly less than 2 mm wide distally. It is simple and undecorated (Figures 8a-b).

Telson large and subrectangular with convex anterior margin; tapers distally, has rounded setose distal margin with complete transverse suture. Pair of posteriorly directed spines adjacent to transverse suture, one on either side of telson. Uropods large, exopod slightly longer than endopod. Exopod and endopod with setose distal margins; exopod also with setose posterolateral margin and diaresis (NIGP 126337, 126345).

Etymology.—The species name is derived from the Greek word 'aethus' (meaning 'unusual').

Type.—Holotype NIGP 126337, paratype NIGP 126355; housed at the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, the People's

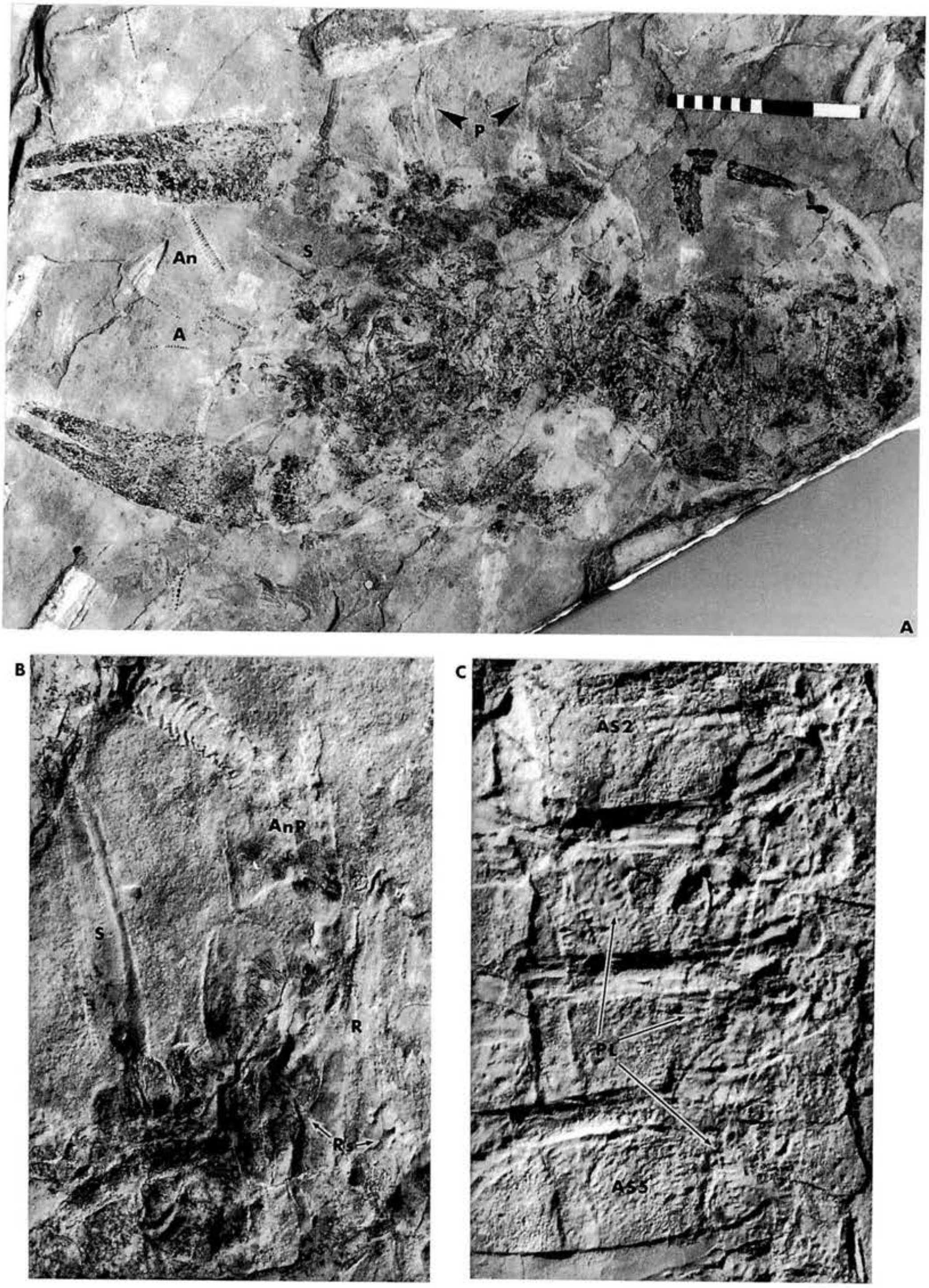

Figure 7. A. Ventral view of *Cricoidoscelosus aethus* holotype (NIGP 126337) (A = antennules, An = antenna, P = pereiopods, S = scaphocerite). Scale bar = 2 cm. **B.** Close-up of ventral view of *C. aethus* (NIGP 126337) (AnP = antennal peduncle, R = rostrum, Rs = rostral spines, S = scaphocerite). ×4.9. **C.** Close-up of ventral view of abdomen with pleopods of specimen of *C. aethus* (NIGP 126345) (AS2 = abdominal sternite 2, AS5 = abdominal sternite 5, PL = pleopods). ×5.4.

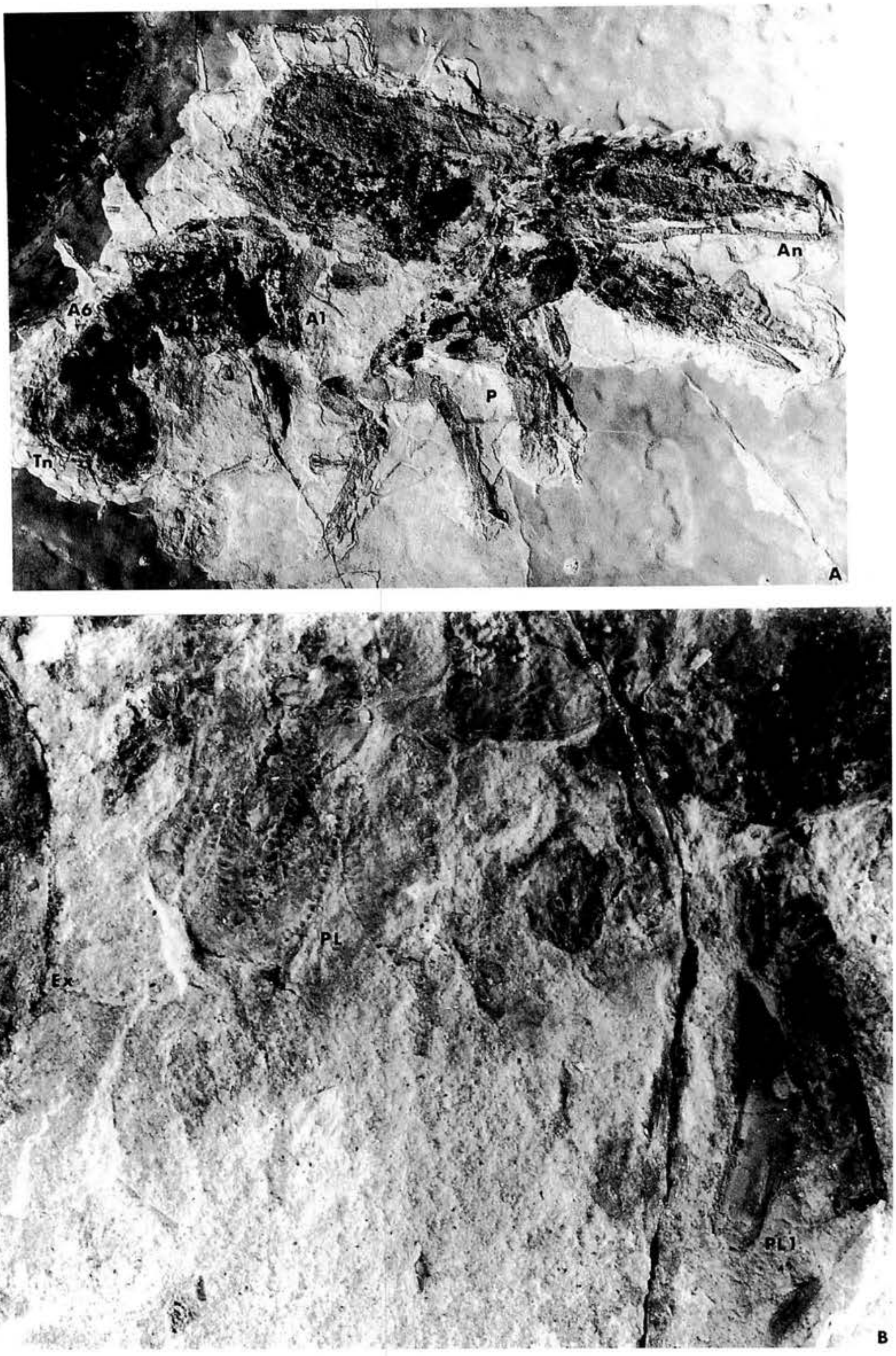

Figure 8. **A.** Lateral view of *Cricoidoscelosus aethus* paratype (NIGP 126355) (A1=first abdominal segment, A6=sixth abdominal segment, An=antenna, P=pereiopods, Tn=tailfan. ×0.64. **B.** Close-up of pleopods of the same specimen (PL=pleopods, PL1=first pleopod, Ex=uropodal exopod). ×4.1.

Republic of China.

Material examined.—NIGP 126337, 126340, 126345, 126355.

Remarks.—Few specimens exist that can definitively be placed in this taxon from the several specimens in our collections. There is no doubt as to its distinct nature, however, due to its highly characteristic and unique pleopods that are fortunately preserved in several orientations.

Discussion.—A reconstruction of *P. licenti* is provided in Figure 2 while *C. aethus* is shown reconstructed in Figure 3.

Astacus licenti was first described by van Straelen (1928b), based on 3 specimens collected from an unspecified "point south-west of Moukden, in Eastern Mongolia" (actually in north-east Liaoning Province, People's Republic of China). In this description, his assignment of this new species to the genus *Astacus* was "provisional... in the most extensive sense of the genus" (he felt, however, that it belonged "undoubtedly to the family of the Astacidae") (van Straelen, 1928b).

Imaizumi (1938) described a second species, *Astacus spinirostrius*, based on two new specimens collected from equivalent *Lycoptera davidii* beds from Niehhutzekow, near Lingyuan, China (three specimens of *A. licenti* were also collected at the same time from the region). In his paper, he discussed how both *A. licenti* and *A. spinirostrius* are in fact more similar ("particularly in the long slender chelipede and the rounded-off pleural plate") to the fossil form *Pseudoastacus* than to the recent *Cambaroides* [then *Astacus* (*Cambaroides*)] species in Asia (Imaizumi, 1938). Apparently there was, in the minds of both van Straelen and Imaizumi, considerable question as to the definitive generic assignments of these new fossil taxa.

Hobbs (1988) discussed how the chelipedes of *A. licenti* are in fact more similar to the eastern American cambarid genus *Procambarus* than to either *Astacus* or *Cambaroides*; he also suggested that the chelae and the abdominal pleurae of *A. licenti* more closely resemble those of the primitive cambarine genus *Procambarus* than either of the Eurasian genera. These issues, coupled with the discrepancies between the early descriptions and the nature of the fossils examined for this study, were keys that forced us to rethink the taxonomic affinities of this species.

Unfortunately, the key characters used to separate the Astacidae from the Cambaridae (Hobbs, 1974, 1989) are impossible to observe from our material. For example, cyclic dimorphism (present in the Cambaridae, absent in the Astacidae) is impossible to identify in these fossils; and the detailed nature of the 1st pleopod (subtubular distally and lacking ornamentation in the Astacidae, with shallow groove or deep sperm groove and with terminal ornamentation in the Cambaridae) is also not evident in the specimens described here. Our decision to move this taxon from the Family Astacidae to the Family Cambaridae is, then, based on less specific features, such as the absence of astacid crayfish from (and presence of cambarid genera in) the Asian region. The shape of the chelae is another feature mentioned by previous authors (Imaizumi, 1938; Faxon, 1885) as suggesting alternative relationships for *P. licenti*: it has been compared to the chelae of the extinct *Pseudastacus* and to the recent genus *Procambarus*, presumed to be the most 'primitive' of the cambarid genera (Hobbs, 1988). While we can give no definitive answer to the question of what *P. licenti* may be most closely related to, we feel that these points warrant the movement of this species from the Family Astacidae to the Family Cambaridae.

After examining the original plates of van Straelen (1928b) and Imaizumi (1938) and some of Imaizumi's original material (IGP specimens 57272, 57254 and 57267, Tohoku University, Japan), we determined that several of the features proposed by Imaizumi as distinguishing characters between *A. licenti* and *A. spinirostrius* are in fact artifacts of preservation. For example, his 'spines on the mid-dorsal line' of the rostrum appear to be the pair of lateral spines found near the base of the rostrum but viewed from a slightly skewed angle, giving them the appearance of projecting from the middle of the rostrum. These spines are clearly located on the posterolateral region of the rostrum when dorsally preserved specimens are examined, something Imaizumi lacked. The same is true for such features as the shape of the pleural plates and the relative lengths of the exo- and endopods of the uropods: these features appear to lose their usefulness in defining separate taxa when several specimens preserved in multiple orientations are examined.

Imaizumi (1938) also suggested the presence of gastric spines as being a characteristic of *A. licenti* not shared with *A. spinirostrius*. This question of the presence/absence of a pair of gastric spines is one that must be addressed here, for several reasons. First, no gastric spines were noted with re-examination of the material described by Imaizumi, removing this character as a potential feature in distinguishing between the previously established taxa from this region. Secondly, a single specimen of the new material examined does possess a set of well-developed, anteriorly directed gastric spines (closely associated with several smaller spines and processes). This specimen is, however, far from complete with only the 'head', anteriormost carapace and first pereiopods preserved; thus, it is impossible to compare it with the other specimens with respect to either abdominal or appendage characters. Gastric spines aside, this specimen is largely identical to the other specimens of *P. licenti* examined, suggesting that these gastric spines may not be a species-specific character. They may instead represent a sex-specific character, but this cannot be determined without a better understanding of other sex-specific differences within this species. Another possibility is that they may simply reflect a character that shows flexibility in expression and/or preservation and may vary from individual to individual within a species, as seen in the Palaeozoic pygocephalomorphs (Schram, 1979). Such features would seem to provide no taxonomic information for this material.

The question of sexual dimorphism is further complicated by the narrow range of morphological characters that exhibit a truly dimorphic state in the crayfish. Some dimorphic characters, such as the generally wider abdomen seen in females, are too general to be of any use in a study utilizing fossil specimens. Sexual dimorphism in the Cambaridae, for example, is characterized by several features: males exhibit cyclic dimorphism with the presence of a sperm groove (and sometimes ornaments such as spines) on the distal portion of the first pleopod, while females possess a seminal receptacle between the 4th and 5th pereiopods. In addition, males possess hooks on at least one set of ischia. Sexual dimorphism in the Astacidae is characterized by a lack of cyclic dimorphism and an unornamented subtubular first pleopod in the males, while the females lack a seminal receptacle (Hobbs, 1988). Such features are difficult if not impossible to determine with fossil material.

Such dimorphic features, in general, present a problem with respect to our material. None of our specimens of *P. licenti* possesses a styliform first pleopod: whether this is due to its complete absence in this species, to our having no males in our material, or to this feature simply not being preserved is impossible to evaluate. None of our specimens appears to possess hooks on the ischia; this may be due to our relative lack of males, as suggested earlier, or to the fact that few of our specimens possess well-preserved pereiopods. It is possible that perhaps those that we possess are female and thus would have not possessed these ischial hooks.

However, two (IGP 57272, 57254) of the specimens presented by Imaizumi (1938) do possess a pair of styliform first pleopods, whose distalmost segments are unfortunately the only parts preserved. Those of IGP 57272 are preserved laterally and are elongate, slightly curved anteriorly and tapered distally, being 5 mm in length and 1 mm wide at their widest point (Figures 6a, b). IGP Specimen 57254 shows only one of the pair of first pleopods, preserved in ventral view. It is 7 mm long and 1 mm wide, and is slightly laterally directed proximally. No other pleopods are visible on this specimen. These styliform pleopods suggest that this species belongs to either the Cambaridae or the Astacidae (both characterized by the presence of a styliform first pleopod in the males; it is absent in the Parastacidae). We consider these specimens to be males of the species *P. licenti*, supporting again a cambarid/astacid taxonomic position for this genus. Pleopods 2-6 of IGP 57272 are more 'typical' crayfish pleopods, being elongate and blade-like, than the annulate pleopods possessed by *C. aethus*.

The distinct annulate pleopods (2-6) of *C. aethus* are, we feel, sufficiently different from those seen in any other crayfish to warrant placing them in their own family. The presence of styliform first pleopods, however, is an indication that this taxon is related in some degree to at least one (if not both) of the northern hemisphere astacoidean families, Astacidae and Cambaridae.

One phenomenon that is shared by specimens of both *C. aethus* (NIGP 126340) and *P. licenti* (NIGP 126338, 126346, 126353, 126354) is the presence of gastroliths. Those in *P. licenti* are preserved here as moulds of their actual state in recent animals (e.g., Lowrey, 1988), in which the ridged face is the attachment surface to the wall of the cardiac region of the foregut. This is presumed to be the natural state in our animals as well. These gastroliths are present in freshly molted animals and act as calcium storage packages to be reused in the recalcification of the exoskeleton after ecdysis. It is evident that our sample possesses both recently molted and fully calcified animals. This also is reflected in the general preservation of these animals, as most of the specimens with gastroliths appear to have been less heavily sclerotized than those without gastroliths.

Ortmann [1902; 1905 (summarized in Hobbs, 1988)] made the first attempt to interpret the history of origin, diversification and dispersal for the crayfish, in a synthesis that has remained largely unchallenged until just recently. He suggested that the ancestors of the Potamobiidae (=Astacoidea) and Parastacidae lived in Sino-Australia (and possibly Antarctica) in the Lower Cretaceous, with *Astacoides* reaching Madagascar during the Middle Cretaceous via a Lemurian land-bridge. The Upper Cretaceous saw the splitting of eastern Asia and Australia, resulting in the differentiation of the Potamobiidae in eastern Asia (and then into western North America and Mexico) and the Parastacidae in Australia and Antarctica. In the Lower Tertiary, the genus *Cambarus* arose from *Potamobius* in Mexico, which then spread through eastern North America; while the Parastacidae extended its range through much of South America and Australia, splitting into several genera in the process. During and since the Upper Tertiary, the Potamobiidae moved into western Asia and Europe, with the Parastacidae remaining in South America, Australia and New Zealand. Following Ortmann's reasoning, the ancestor to the crayfish that we recognize today is believed to have originated in a benthic environment similar to that occupied by the modern marine lobsters. From this ancestral stock, three major lines emerged: the extinct Erymidae; the relatively conservative Nephropidae (ancestors of the modern true lobsters); and the highly varied and widely dispersed Astacoidea and Parastacoidea, the true crayfishes.

More recently, however, Scholtz (1995) and Scholtz and Richter (1995) have proposed a closer relationship between the Astacida and the Thalassinida and Meiura than between the Astacida and Homarida. This suggestion is based on phylogenetic systematic studies and a far better understanding of the fossil record for this group. Their research suggests that many of the morphological similarities once cited as uniting the Astacida and the Homarida are in fact plesiomorphic characters, with no true synapomorphies joining these two taxa. Instead, their phylogenetic analysis revealed two characters that support their taxon Fractosternalia (including the Astacida, Thalassinida, Anomala and Brachyura): a movable last thoracic sternite and a pattern of calcified pleural parts connecting thorax and pleon. Scholtz (1995) further goes on to suggest that the invasion into freshwater by the astacoidean ancestor occurred during the Triassic on the '"supercontinent" Pangaea. This ancestor then developed into the Parastacidae in the Southern Hemisphere and the Astacidae and Cambaridae in the Northern Hemisphere with the break-up of the Pangaea landmass into Amero-Eurasia and Gondwana.

Our fossil material, dating back to the Jurassic, confirms that crayfish did indeed move into freshwater considerably earlier than the time suggested by Ortmann. However, the features suggested by Scholtz and Richter (1995) as allying the Astacida with the Thalassinida instead of the Homarida are impossible to distinguish with the fossil material at hand.

It may perhaps be interesting to briefly comment on the rationales behind these two suggested evolutionary histories for the 'crayfish'. Ortmann's (1902, 1905) scheme was very much a product of his time, when distributions were believed by many [e.g., Darwin (1859, Chs. 12 and 13) and Wallace (1876 ; in Hallam, 1994)] to be strictly dispersalist in nature. By his reckoning, crayfish distributions enlarged slowly with the movement of these animals from one point to another and their subsequent establishment in these new territories. He explained problematic distributions, such as the appearance of crayfish on Madagascar, by the presumed presence of land bridges (in this case, a Lemurian land bridge). Scholtz's considerations, on the other hand, are a product of our modern understanding of how plate tectonics or continental drift (Wegener, 1924 ; in Hallam, 1994) and its association with vicariance biogeography (Croizat *et al.*, 1974) allow for the presence of closely related organisms in isolated localities via the movement of land masses towards and away from each other with time (Hallam, 1994).

Acknowledgments

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on January 23, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Kiyoharu Abe, Yoshimitsu Ishitobi, Hirotugu Kitahara,
Takahiro Sato, Tetsuo Hamada, Hikoichi Honda,
Yukio Miyake, Kouiti Yazima, Mitsuko Koike,
Tatsuhiko Yamaguchi, Hidesaku Ishiko, Akinori Takahashi.

Resigned members;

Kaoru Takenami, Yuji Yamaoka, Yuriko Matsumura,
Tomoyuki Kaneko.

During its meeting on February 27, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Kazuo Harada, Robert G. Jenkins, Miyuki Misezaki.

Resigned members;

Haruo Nakasuji, Shigeru Saito, Takashi Toyoda,
Hidetoki Noguchi, Yoshiyuki Hirohata, Sumie Takeda,
Tomoyoshi Ito, Seiichi Komura.

During its meeting on May 22, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Hideyuki Iwaki, Naokazu Yoshimoto, Saburo Sakai,
hirotsugu Tajima, Kazuhiro Sugawara, Nobutaka Hunayama,
Tomoyuki Tajima, Hideyuki Noguchi, Yoshitaka Matsuhashi,
Yasunori Kano.

Resigned members;

Satoshi Matsushita, Kazuyuki Nozu, Isao Konda,
Yen-Nien Cheng, Setsuji Nagai, Sueo Naneko.

行事予定

◎第2回日本古生物学会野外ワークショップは，「海産無脊椎動物の古生態学」をテーマとして，1999年9月23日～26日に高知大学を中心として行われます（世話人：近藤康生・金沢謙一）．参加申込・問い合わせ先：東京大学総合研究博物館　金沢謙一（電話：0888-56-0422；Fax：03-3815-7053；e-mail：kanazawa@um.u-tokyo.ac.jp）

◎2000年年会・総会は，2000年1月28日（金）～1月30日（日）に「早稲田大学」で開催されます．一般講演の申し込み締め切りは1999年12月3日です．

◎第149回例会（開催予定時期：2000年の6月末頃）には，「群馬県立自然史博物館」から開催申し込みがありました．

◎1999年総会で，2001年からの年会・総会と例会の開催時期の変更が決定されました．年会・総会は6月下旬から7月の初め頃（現在の例会の開催時期），例会は1月下旬から2月の初め頃（現在の年会・総会の開催時期）開催されます．開催を計画されている機関がありましたら，お申し込み下さい．

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